Journal of Range Management

TABLE OF CONTENTS: VOL. 53, NO. 3, May 2000

FEATURE ARTICLES

250 Viewpoint: Selecting the 5 most important papers in the first 50 years of the *Journal of Range Management* by Mitchel P. McClaran

255 Observations of predator activity at wildlife water developments in southern Arizona by Stephen DeStefano, Sarah L. Schmidt, and James C. Devos, Jr.

Animal Ecology

259 Livestock guard dogs reduce predation on domestic sheep in Colorado by William F. Andelt and Stuart N. Hopper

Economics

268 Economics of grazing weeping lovegrass with stockers in the Southern Great Plains by L. Allen Torell, Rex E. Kirksey, Gary B. Donart, and James D. Libbin

Grazing Management

277 Effect of grazing on the population biology of *Phalaris aquatic* by María José Leiva and Rocío Fernandez Alés

282 Forage removal and grazing time of cattle on small paddocks by Robert C. Broweleit, Walter H. Schacht, Bruce E. Anderson, and Alexander J. Smart

287 Elk presence inside various-sized cattle exclosures by Jeffrey A. Gross and James E. Knight

291 Livestock effects on reproduction of the Columbia spotted frog by Evelyn L. Bull and Marc P. Hayes

Hydrology

295 *Cryptosporidium parvum* transport from cattle fecal deposits on California rangelands by Kenneth W. Tate, Edward R. Atwill, Melvin R. George, Neil K. McDougald, and Royce E. Larsen

Improvements

300 Postburning legume seeding in the Flooding Pampas, Argentina by V.F. Juan, L. Monterroso, M.B. Sacido, M.A. Cauhépé

305 Biological control of leafy spurge with introduced flea beetles (*Aphthona* spp.) by Donald R. Kirby, Robert B. Carlson, Kelly D. Krabbenhoft, Donald Mundal, and Matt M. Kirby

309 Picloram, fertilizer, and defoliation interactions on spotted knapweed reinvasion by James S. Jacobs, Roger L. Sheley, and Joella R. Carter

The Trail Boss

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Measurement/Sampling

- 315 Quantifying spatial heterogeneity in herbage mass and consumption in pastures**
by Masahiko Hirata

Plant Animal

- 322 Herbivore dunging and endozoochorous seed deposition in a Mediterranean *dehesa*** by J.E. Malo, B. Jiménez, and F. Suarez
329 Late season toxic alkaloid concentrations in tall larkspur (*Delphinium* spp.) by Dale R. Gardner and James A. Pfister

Plant Ecology

- 335 Western ragweed effects on herbaceous standing crop in Great Plains grasslands** by Lance T. Vermeire and Robert L. Gillen
342 Age-stem diameter relationships of big sagebrush and theirmanagement implications by Barry L. Perryman and Richard A. Olson

Reclamation

- 347 Characterization of Siberian wheatgrass germplasm from Kazakhstan (Poaceae: Triticeae)** by Kevin B. Jensen, Kay H. Asay, Douglas A. Johnson, and Bao Jun Li

Soils

- 353 Soil properties and species diversity of grazed crested wheatgrass and native rangelands** by Maja Krzic, Klaas Broersma, Don J. Thompson, and Arthur A. Bomke

Book Review

- 359 Shinnners and Mahler's Flora of North Central Texas** by George M. Diggs, Jr., Barney L. Lipscomb, and Robert J. O'Kennon.

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Viewpoint: Selecting the 5 most important papers in the first 50 years of the *Journal of Range Management*

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Abstract

A graduate seminar to select the 5 most important papers published in the first 50 years of the *Journal of Range Management (JRM)*, 1948–1997, cultivated an appreciation for the development of the discipline of rangeland science and management, and provided some historical perspective to judge the *JRM*. A review of textbooks, and papers describing early milestones and the use of citation counting were helpful in developing criteria to discriminate the importance of papers. The greatest disagreement among the 9 participants focused on the use of citation counts as a criterion: 2 students used only counts and 3 students refused to use counts. Eighteen papers received at least 1 vote as a top 5 paper, and 2 plant succession-vegetation monitoring papers were clearly the most popular. The exercise revealed that discontent with the *JRM* is not new. Although the *JRM* now covers a wider variety of topics, including both reductionist and synthetic works, some students felt that it was less encompassing of multiple values of rangelands and the breadth of rangeland science than recent texts. The students found that the selection of important papers expanded their understanding of the discipline and their resolve to publish in the *JRM*. Ideally, others will be challenged to perform this review for the benefit of students, the discipline, and the *JRM*.

Key Words: education, disciplinary history, citation counting

The proximate goal of a graduate seminar at the University of Arizona in the spring semester of 1998 was to select the 5 most important papers published in the first 50 years (1948–1997) of the *Journal of Range Management (JRM)*. The ultimate goal was to cultivate an understanding and appreciation for the development of the discipline of rangeland science and management. The 50 continuous years of publication was a very efficient vehicle to move the students through the history of the discipline, while the selection of the 5 most important papers gave focus to the journey. This experience was especially valuable for the graduate students with degrees in other disciplines, and for all partici-

Resumen

Durante un seminario entre estudiantes de nivel de posgrado, donde se seleccionaron las 5 artículos más importantes publicados por la *Revista de Manejo de Pastizales* durante los últimos cincuenta años (1948–1997), se cultivó una apreciación sobre el desarrollo de la disciplina de manejo y ciencia de los pastizales, logrando también una perspectiva histórica para enjuiciar a la Revista. Una revisión de libros de texto y artículos que describen el inicio y el uso de conteo de citas fueron muy útiles en el desarrollo de criterios para discernir la importancia de los artículos. El desacuerdo más grande entre los nueve participantes se dio por el uso conteo de citas como criterio. Dos estudiantes utilizaron el conteo como único criterio y 3 estudiantes se negaron a utilizarlo. Dieciocho artículos recibieron cuando menos un voto como los mejores 5 y 2 artículos sobre el monitoreo de sucesión vegetal fueron los más populares. El ejercicio reveló que el descontento con la Revista no es nada nuevo. Aunque actualmente, la Revista de Manejo de Pastizales cubre una gran variedad de temas, incluyendo artículos reduccionistas y de síntesis, algunos estudiantes manifestaron que abarcaba menos de los múltiples valores existentes en los pastizales que algunos textos recientes. Los estudiantes encontraron que la selección de artículos importantes expandía el entendimiento de la disciplina y su decisión de publicar en la *Revista de Manejo de Pastizales*.

pants to reflect on current concerns about the purpose and vitality of the *JRM*.

This paper describes the course format and selected papers, briefly critiques the selections, summarizes students' evaluations, and provides commentary about the *JRM*. The purpose of the paper is to stimulate similar reviews and dialogue about the lessons available in the first 50 years of the *JRM*.

Course Form

Discussions about the criteria for selecting important papers took place in the first 3 class sessions. The 9 subsequent sessions were devoted to student presentations of selection criteria and selected papers to build a candidate list of papers for final consideration. The final class session was used to vote for and discuss the top 5 selections for the complete 50 years of the *JRM*¹ and to evaluate the course.

Acknowledgments: This paper is dedicated to the students who participated in this course: Carlos Alaca-Galvan, Deborah Angell, Sharon Biedenbender, Julie Conely, Paulette Ford, Barry Imler, Wilma Renken, Carolyn Watson, and Dave Womack. I thank S. Clark Martin for attending most of our class sessions, and helping us understand the context of developments and publications throughout the history of the *Journal of Range Management*. This manuscript was improved after receiving comments on an earlier version from David Briske, David Engle, Larry Howery, John Malechek, and 2 anonymous reviewers.

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¹Full-text copies of all articles in volumes 1–47 of the *JRM* are now available on the Internet at <http://jrm.library.arizona.edu>

Nine graduate students (5 Ph.D. and 4 M.S.) were enrolled in the seminar, and 1 to 3 faculty attended each weekly session. Two students had an undergraduate degree in rangeland science and management. Six of the students were enrolled in the rangeland science and management graduate program, and 1 student each in the wildlife and fisheries management, watershed management, and interdisciplinary renewable natural resources studies graduate programs. In general, student interests and previous course work were focused in vegetation ecology and management, wildlife ecology and management, and soil science. Expertise and interest in animal production and production economics was under-represented: only 7 of 9 students had at least 1 course in these subjects and no student had more than 2 courses in either subject.

Selection Criteria

Choosing selection criteria was the most difficult aspect of this exercise because there are no objective measures to identify a significant paper. The inherent subjectivity proved to be the basis for heated discussions that made a much greater impact in the students' appreciation for the development of the discipline than if they had followed a predetermined set of criteria.

Student-led discussions about selection criteria were aided by assigned readings of 10 textbooks (Heady 1975, Heady and Child 1994, Holechek et al. 1989, 1995, 1998, Sampson 1923, 1952, Stoddart and Smith 1943, 1955, Stoddart et al. 1975), a paper describing early milestones in the discipline (Chapline 1944), and a *JRM* paper illustrating the use of literature citation statistics to describe the evolution of scientific ideas (Joyce 1993). Textbooks were assigned because they reference the seminal works and synthesize the state-of-knowledge in a discipline. The textbooks were limited to those that had been revised at least once because revisions can reveal how new *JRM* papers influenced the authors to re-synthesize the discipline. For example, the Sampson (1923) and Stoddart and Smith (1943) texts provided pre-*JRM* baselines to judge the influence of early *JRM* articles in their respective textbook revisions (Sampson 1952, Stoddart and Smith 1955); whereas the later texts and their revisions provided benchmarks for the importance of later *JRM* papers. Chapline (1944) grounded the students in the state-of-knowledge prior to the publication of the *JRM*. Joyce (1993) illustrated the use of the Science Citation Index (Institute for Scientific

Information 1955–1997) to measure the popularity of *JRM* papers.

These references helped focus our discussions on the biases of citation counting versus its utility for estimating the importance of a paper. Students became aware of textbook and journal authors who frequently cited their own work, as well as the greater probability of paper citation in recent times because of the explosion of publishing scientists and periodicals. Furthermore, they discussed the problem of not knowing the context of the citation: was it used in a positive light or was it cited because it used flawed methods or made erroneous conclusions? In hindsight, the “invisible college” paper by Hart (1993) would have been an excellent addition to this list of readings because it exposed other sources of bias in the use of citation counting.

Each student developed their own selection criteria to rate the *JRM* papers. In general, they applied 3 classes of criteria: citation counts, contribution to disciplinary paradigms, and generality. Citation counting used the 43 printings of the *Science Citation Index* (Institute for Scientific Information 1955–1997), textbooks, and the *JRM*. The contribution to disciplinary paradigms addressed management principles and underlying models of rangeland science and management. The criterion for paradigms of management principles favored papers that described how the sustainable use of rangelands is related to the intensity, season, frequency and kind/class of use (where uses include herbivore grazing, recreation, and vegetation manipulations such as fire and fertilization). The criterion for underlying models favored papers that proposed new models and methods to apply these models. For example, Dyksterhuis (1949) proposed a method to operationalize the Clementsian-based model of plant succession. The generality criterion favored papers that focused on synthesis and universality over papers that were specific to a few locations or species. For both the paradigm and generality criteria, students favored papers that had longstanding significance or resolved some controversy. Citation counting was the sole criterion used by 2 students, 3 students rejected citation counting and used only paradigms and generality, and 4 students used all the criteria.

Selecting Top Papers

Five or 6 consecutive volumes of the *JRM* were assigned to each student to distribute a uniform time period and amount

of work. All students were required to review the papers in all of the *JRM* volumes to foster informed discussions. In each of 9 class sessions, a different student presented their criteria and the 5 most important papers in their 5 or 6 volumes. These presentations resulted in a list of 45 important papers published in the first 50 years of the *JRM*, and some intense discussions about the criteria used and the papers selected by students. Not all students were satisfied with their peers' selections, and therefore they added 5 “wildcard” papers to make a candidate list of 50 papers.

The most consistent debate concerned the reliance on citation counts as a surrogate for importance. Three students refused to use that criterion because counts reflected more on the popularity of a paper than its content or importance, but 2 students used counts as their only criterion. Debate about the importance of selections was common, for example Mueggler (1965) was challenged because it relied on the location of fecal material to infer animal distribution compared to direct measures of utilization used by Cook (1966). The third most common debate centered on the absence of papers from the lists, for example, economic analyses, grazing systems, and riparian management were among the under-represented topics.

Selecting the Top 5 Papers

Students took a week to apply their own criteria to select the 5 most important papers from the candidate list of 50 papers. These selections included a ranking of the papers and written statements justifying their selections. Each student's rankings was computed based on a score of 5 for their most important paper, and scores of 4, 3, 2, and 1 for their second, third, fourth and fifth most important papers, respectively. Individual scores were summed to create a class-wide score for each paper. With this method, the highest possible score would be 45 if all 9 students cast a top-paper vote for the same paper.

Eighteen papers received at least 1 vote, and papers by Dyksterhuis (1949), Westoby et al. (1989), Wilson and Tupper (1982), Bement (1969), and West (1993) were ranked as the 5 most important papers in the first 50 years of the *JRM* (Table 1). The students' ratings clearly elevated the papers by Dyksterhuis (1949) and Westoby et al. (1989) above the other 16 papers receiving votes, and there was little distinction among those 16 papers.

Table 1. Rank and score of students' votes for papers considered to be part of the 5 most important published in the *Journal of Range Management* volumes 1–50, 1948–1997.

Rank	Score	Citation in the <i>Journal of Range Management</i>
1	44	Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. 2:104–115.
2	35	Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. 42:266–274.
3	8	Wilson, A.D. and G.J. Tupper. 1982. Concepts and factors applicable to the measurement of range condition. 35:684–689.
4 tie	7	Bement, R.E. 1969. A stocking-rate guide for beef production on blue grama range. 22:83-86.
4 tie	7	West, N.E. 1993. Biodiversity of rangelands. 46:2-13.
6	6	Provenza, F.D. 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. 45:36-45.
7 tie	4	Mueggler, W.F. 1965. Cattle distribution on steep slopes. 18:255-257.
7 tie	4	Friedel, M.H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. 44:422-426.
9 tie	3	Heady, H.F. and D.T. Torrell. 1959. Forage preference exhibited by sheep with esophageal fistulas. 12:28-34.
9 tie	3	Reardon, P.O. and L.B. Merrill. 1976. Vegetation responses under various grazing management systems in the Edwards Plateau of Texas. 29:195–198
9 tie	3	Hanley, T.A. 1982. The nutritional basis for food selection by ungulates. 5:146-151.
9 tie	3	Task Group on Unity in Concepts and Terminology. 1995. New concepts for assessment of rangeland condition. 48:271-282.
13 tie	2	Campbell, R.S. 1948. Milestones in range management. 1:4-8.
13 tie	2	Lockwood, J.A. and D.R. Lockwood. 1993. Catastrophe theory: a unified paradigm for rangeland ecosystem dynamics. 46:282-287.
15 tie	1	Roach, M.E. 1950. Estimating perennial grass utilization on semidesert cattle ranges by percentage of ungrazed plants. 3:182-185.
15 tie	1	Cook, C.W. 1954. Common use of summer range by sheep and cattle. 7:10-13.
15 tie	1	Van Dyne, G.M. 1966. Application and interpretation of multiple linear regression and linear programming in renewable resources analysis. 19:356-362.
15 tie	1	Bailey, D.W., J.E. Gross, E.A. Laca, L.R. Rittenhouse, M.B. Coughenour, D.M. Smith and P.L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. 49:386-400.

[†]Score is the sum of 9 students ranking their top 5 papers from 5 = most important to 1 = fifth most important.

Critique of Top Papers

This critique is brief for 3 reasons. First, to maintain the focus on the selection process rather than the selections. Second, the small class size, narrow specialties, and southwestern United States orientation created important biases. Third, the method of selecting 5 candidate papers from 5 or 6 volumes assumed a regular distribution of important papers.

The top 2 papers, Dyksterhuis (1949) and Westoby et al. (1989) focused on important underlying models of rangeland plant succession and operational tools to implement the models for monitoring efforts. Two student comments illustrate justification for these rankings. About Dyksterhuis, one student wrote:

“...spelled out the principles of Clementsian succession and their application to rangeland condition assessment and grazing management. These principles endured for more than four decades and were widely used on rangelands across the world.”

About Westoby et al., one student wrote:

“Theories proposing multiple successional pathways and alternative stable states were not new... and the shortcomings of the traditional successional

model were well known, but the appearance of [this paper's] state-and-transition model heralded serious consideration [of these ideas] by the range profession. The state-and-transition model and its variations promise to have enduring and widespread impacts on the science of range management...”

The time from the proposal of a model to its application for management may be a measure of disciplinary progress. Dyksterhuis (1949) provided the operational tools to implement Clementsian ideas (Clements 1916) that were first articulated and modified for rangeland management 30 years earlier in Sampson (1919). Whereas, in only 8 years, the revision of the *National Range and Pasture Handbook* (Natural Resource Conservation Service 1997) began applying the concepts of Westoby et al. (1989) to organize empirical information about rangeland plant succession that built on multiple stable state theory (May 1977).

Student and Faculty Evaluations

Each student prepared a written evaluation of this exercise during the week that they were selecting their top 5 papers from

the list of 50 papers. The evaluations were largely positive, except for complaints about the large amount of reading. The students identified 3 types of benefits: acculturation with the rangeland science and management discipline, exposure to relevant information, and appreciation for the evolution of the discipline. About acculturation, 1 student wrote “I appreciated the small treasures of the time period such as photos of old faculty members, notorious quotes, and thought provoking book reviews”. The benefit of exposure to relevant information is apparent in this comment: “Each student was able to identify even the earliest papers published relevant to their research ...” Expressions of increased appreciation for the evolution of the discipline included statements like “This exercise provided exposure to the historical development of the most fundamental ideas”, “... presented me with tools and opportunities to develop my own philosophies of the range management profession”, and “I was surprised to discover that many if not most of today's issues already existed in 1948”.

One student's summary of this exercise was particularly gratifying because it suggests that the course achieved its goals of cultivating an appreciation of past accomplishments.

"The value of this exercise is not in the final list of articles; neither at the individual student level, nor at the class level. It is in the journey through the history of the science of range management, the understanding of that history, and increasing understanding of the driving forces and interests of other individuals, including your traveling partners."

This was one of the most rewarding teaching experiences of my career because the students learned a great deal about the *JRM* and the discipline, they expressed a sincere interest in doing the hard work to complete the assignment, and they took seriously their commitment to express opinions and respectfully engage in discussions that included important differences of opinion. Furthermore, it was a very efficient review of trends in the discipline. For example, they observed that early efforts at shrub management focused on elimination using herbicides (e.g. Hull and Vaughn 1951), later publications documented the shorter than expected lifespan of shrub control treatments (e.g. Johnson 1969), a later publication described seemingly antithetical efforts to establish shrubs (Giunta et al. 1975), and more recently a publication presented a more integrated approach to shrub management (Scifres 1987).

The entire experience resonates with Art Smith's (Smith 1952) sage commentary that the goal of teaching should be more about ideas and less about facts: "When a student has been stimulated to thinking about a particular field concerned, he can later acquire details, and moreover, he may uncover some new facts or provide some new tools in the process."

Future of the Journal

Completing this exercise gave all participants the license to contribute to the discussion about the status and relevance of the *JRM*. One student suggested that the *JRM*

"...has always been and remains a publication devoted to livestock production ... and it needs to take a broader view in order to become a more relevant force in the future [and] this transition seems to be underway in the modern textbooks which reflect the increasing importance of other uses of rangelands."

There is a long history of criticism about the *JRM* content in its first 50 years (e.g.

Schultz 1958). Recent, criticism includes devotion to trivia at the expense of larger socio-ecologic issues (Starrs 1998), a decline in scientific impact, credibility, and relevancy (Fuhlendorf et al. 1999), and a lack of broader syntheses relative to emphasis on narrower primary research (Schultz and Zamudio 1998).

I join those who want the *JRM* to be a more significant journal in its content and be recognized beyond the discipline. However, my assessment of the *JRM* is different from other commentators. First, the *JRM* is replete with detailed information found in many specific studies. Although this may appear to be trivial, detailed information definitely is required to build a disciplinary foundation for predictions about resource responses to management. Second, there has been an increasing number of *JRM* articles in the past 5–10 years that address the difficult social-ecological issues of rangeland policy (e.g. Loomis et al. 1989, Huntsinger and Fortmann 1990, Collins and Obermiller 1992, Rowan et al. 1994, Brunson and Steel 1996, Huntsinger and Hopkinson 1996, Mitchell et al. 1996, Moote and McClaran 1997, Raymond 1997) and I hope that trend will continue. Third, we should strive to attract a broader audience through the publication of both reductionist primary research as well as papers that synthesize and assess the merit, application and future challenges of a specific topic. Apparently, the students recognized that these are not mutually exclusive pursuits because 2 of the 9 invited papers in the current *JRM*-sponsored synthesis series (started in 1987) were included in their top 18 papers (i.e., West 1993, Bailey et al. 1996; Table 1). Finally, we must recognize that the future of the *JRM* rests primarily with those who publish research results about rangeland resources and their use. Therefore, it is incumbent upon us to submit our best work to the *JRM* because it can only be as important, credible, and broadly read as the quality of the manuscripts we submit for publication.

Benefits and Challenges

The lasting value of this review was in the students' development of a more complete understanding of the discipline of rangeland science and management. As a result, their work is more likely to build on the merits of past work, avoid repeating past mistakes, and be submitted for publication in the *JRM*. The students' list of

important papers will certainly be criticized for missing important works and over-valuing others because the student group was small and narrow in expertise. Ideally, by sharing the students' experience, others will be challenged to complete a similar review of the first 50 years of the *JRM* to recognize seminal works, cultivate a deeper understanding of the discipline, and stimulate submission of outstanding work for publication in the *JRM*.

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Observations of predator activity at wildlife water developments in southern Arizona

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Abstract

Wildlife water developments have been constructed and maintained throughout the arid western United States to benefit big game and upland gamebird populations. There is debate, however, over possible detriments to wildlife from artificial water sources in deserts and other arid environments. One concern is that water developments attract predators, which then impact the prey populations that these developments are intended to benefit. To examine the extent of predator activity around water developments, we examined 15 paired water and non-water (random) sites for sign (scats, tracks, visual observations, animal parts such as feathers and bones, and carcasses) of predators and prey. Predator sign was 7x greater around water sites than non-water sites ($P = 0.002$). Coyote (*Canis latrans* Say) sign accounted for 79% of all predator sign and was 7x greater near water than away from water ($P = 0.006$). Amount of sign for all prey species combined was not different between paired sites ($P = 0.6$), but results for individual species and groups of species was variable; passerine and gallinaceous bird sign was greater around water sites ($P = 0.008$), ungulate sign was not different between water and non-water sites ($P \geq 0.20$), and lagomorph sign was almost 2x greater away from water than near water ($P = 0.05$). Predators were probably attracted to wildlife water developments to drink rather than hunt; without water developments, predators may be even more concentrated around the fewer natural water sites.

Key Words: carnivores, desert ecology, raptors, predator-prey relationships, ungulates, wildlife management

Since the early 1900s, almost 6,000 wildlife water sites have been developed throughout the arid western United States in an effort to increase, stabilize, or otherwise benefit wildlife populations (Rosenstock et al. 1999). The Arizona Game and Fish Department spends up to \$500,000–1,000,000 annually to develop and maintain water sites (deVos et al. 1997b), and 9 other western states currently have active water development programs with annual costs >\$1,000,000 (Rosenstock et al. 1999).

In Arizona, the first wildlife water developments were built in 1941 (Broyles 1995), and since then >800 have been constructed

Resumen

A lo largo del árido oeste de Estados Unidos se han construido y mantenido aguajes para fauna silvestre para beneficiar las poblaciones de fauna silvestre mayor y las de aves para cacería de las mesetas. Sin embargo, hay un debate sobre los posibles detrimientos para la fauna silvestre en las fuentes artificiales de agua construidas en los desiertos y otros ambientes áridos. Una preocupación es que los aguajes artificiales atraen predadores, los cuales impactan en las poblaciones de presas que con estos aguajes se intentan beneficiar. Para determinar la magnitud de la actividad de predadores alrededor de los aguajes, examinamos 15 sitios apareados con aguaje y sin aguaje y elegidos al azar, en los sitios se examinaron señales de predadores y presas (huellas, observaciones visuales, partes de animal tales como plumas y huesos y cadáveres). La señal de predadores fue 7 veces mayor alrededor de los sitios con aguajes que en los sitios sin ellos ($P = 0.002$). Las señales de coyote (*Canis latrans* Say) contribuyeron con el 79% del total de las señales de predadores y fue 7 veces mayor cerca del agua que lejos de ella ($P = 0.006$). La cantidad de señales combinando todas las especies de presas no fue diferente entre los sitios apareados ($P = 0.6$), pero los resultados por especie individual y grupos de especies fue variable, las señales de aves gallinaceas fue mayor alrededor de los aguajes ($P = 0.008$), las señales de ungulados no fueron diferentes entre sitios con y sin agua ($P \geq 0.20$) y las señales de lagomorfos fue casi 2 veces mayor lejos del agua que cerca de ella ($P = 0.05$). Los aguajes para fauna silvestre probablemente atraerón a los predadores para tomar agua mas que para cazar, sin aguajes, los predadores pueden estar aun mas concentrados alrededor de los pocos sitios con aguajes naturales.

(deVos et al. 1997b). Several designs have been used, including drinkers (cement, metal, or fiberglass troughs supplied by asphalt, metal, or fiberglass collection surfaces [aprons] capable of filling the drinker from 1 storm), tinajas (rain- or well-fed rock basins and potholes in impervious granite and basalt), and tanks (large depressions in soil or rock that collect and hold precipitation and runoff) (Broyles 1997, deVos et al. 1997b). Above or below ground water holding tanks, which increase storage capacity and reduce the need for hauling water, have been added at many sites.

Water developments are thought to be important mitigation against extensive loss and degradation of natural waters, including springs and perennially and intermittently flowing streams, caused by agricultural and urban development (Campbell and Remington 1981, deVos et al. 1983, Tellman et al. 1997), and for management and recovery of the endangered Sonoran pronghorn

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(*Antilocapra americana sonoriensis* Ord) (Hervet et al. 1997).

There has been debate over the benefit of water developments for wildlife (Burkett and Thompson 1994, Broyles 1995, Brown 1997, deVos et al. 1997b). Some researchers question whether artificially provided water benefits native wildlife that are adapted to desert or arid rangeland conditions, while others feel that water developments may actually be harmful, either by spreading disease, encouraging exotic species, or increasing predation (Broyles 1995, Brown 1997, Krausman and Czech 1997).

Avian and mammalian predators are attracted to water (Cutler 1996). Important questions are whether this attraction increases predation rates directly by increasing opportunities for predators, or indirectly by improving fitness (i.e., improved survival or reproduction) and thus abundance of predators. These population-level questions are difficult to address and require long-term study over broad geographic areas to answer (deVos et al. 1997a). Before that expense and effort are expended, however, wildlife managers need to know the extent or magnitude to which local populations of predators are attracted to water developments and whether there is evidence that predation occurs around water sites. Our objectives were to compare predator and prey abundance around water sites versus non-water sites to determine which species were attracted to water, to determine the magnitude of that attraction, and to investigate whether attraction to water sites increased mortality of prey due to predation.

Study Site

Surveys took place on the Barry M. Goldwater Air Force Range and the Cabeza Prieta National Wildlife Refuge in southern Arizona (Fig. 1); combined area size was about 11,000 km². Topography was primarily basin and range. The major plant community was Sonoran desert upland; dominant vegetation consisted of paloverde (*Cercidium* [Torr.] Rose and I. M. Johnston spp.), mesquite (*Prosopis* L. spp.), and ironwood (*Olyneya tesota* Gray) trees, ocotillo (*Fouquieria splendens* Engelm.), saguaro (*Carnegiea gigantea* [Engelm.] Britton and Rose), prickly pear and cholla (*Opuntia* Mill. spp.) cacti, creosote bush (*Larrea tridentata* [DC.] Cov.) and bursage (*Ambrosia* [Cav.] Payne spp.).

Annual rainfall was about 15 cm, falling in a bimodal pattern of scattered winter

Fig. 1. The Barry M. Goldwater Air Force Range and the Cabeza Prieta National Wildlife Refuge in southern Arizona, where water developments have been constructed and maintained for wildlife populations.

rains (50%) and intense late summer thunder storms (50%). High temperatures commonly exceeded 38°C in summer and 20°C in winter. The landscape was dominated by riparian areas and washes, but water flow in these streams was intermittent and unpredictable. For most of the year, washes were dry and, aside from artificial water developments, there was very little perennial water available in the area (Broyles 1997). There were about 65 water developments on the eastern half of the Goldwater Range and the Refuge where we conducted our surveys (T. L. Cutler, personal communication).

Methods

We surveyed 15 paired water and non-water sites during January–March of 1995–97. Water sites were selected based on accessibility in the eastern half of the Goldwater Range and Cabeza Prieta Refuge. For each water site, we selected a non-water site that was in a random direction and distance (but within 0.4–0.8 km) from the water development. Each random site had similar topographic and vegetative conditions as its paired water site. We blocked by location (Kuehl 1994) to control for some of the variation in predator activity that may occur among different portions of the study area. We searched for predator and prey activity at all sites by recording visual observations and looking for sign (scats, tracks, trails, feathers) and evidence of kills (carcasses, feather piles). We identified bones when found, but did not necessarily attribute these to

predator kills, especially when bones appeared old and bleached from the sun. We refer to all feces as scats, including pellet groups from ungulates and lagomorphs. We attempted to identify sign to species; when we could not, we identified the sign to a higher classification (e.g., canid, carnivore, ungulate, lagomorph). Carnivore species on the study site included coyotes (*Canis latrans* Say), foxes (gray [*Urocyon cinereoargenteus* Schreber] and kit [*Vulpes velox* Say]), mountain lions (*Puma concolor* L.), bobcats (*Felis rufus* Schreber), and avian predators and scavengers (turkey vultures [*Cathartes aura* L.], common ravens [*Corvus corax* L.], loggerhead shrikes [*Lanius ludovicianus* L.], owls, hawks). The only ungulate sign that we consistently identified to species was from collared peccary (*Pecari tajacu* L.). We lumped sign from mule deer (*Odocoileus hemionus* Rafinesque), bighorn sheep (*Ovis canadensis* Shaw), and pronghorn as ungulates. Lagomorphs included black-tailed and antelope jackrabbits (*Lepus californicus* Gray, *L. alleni* Mearns) and desert cottontails (*Sylvilagus audubonii* Baird). Common avian prey included house finches (*Carpodacus mexicanus* Müller), gila woodpeckers (*Melanerpes uropygialis* Baird), and a variety of passerine and gallinaceous birds.

As we approached the water or the random non-water point we noted any animals that flushed from that spot. We then searched a 10-m² central plot around the water or random point, and continued this search along eight, 50-m transect lines radiating from the water or random point,

looking for sign within about 5 m on either side of the transect. We tallied all sign and observations by species or species group for the center plot and the 8 transects, and summed that for each site. Groups of sign (pellet groups, a line of tracks, scattered but likely related bones, piles of feathers) were counted as 1 observation, but when we encountered similar sign (e.g., coyote tracks) at different points along a transect or on different transects, each track or line of tracks was counted as a separate observation. Because we could not determine if sign was from 1 or several individuals, we tallied total amount of sign, rather than trying to determine number of individuals that may have visited a site.

We used paired *t*-tests to compare differences in amount of predator and prey sign between paired water and non-water sites. We report mean differences ($\bar{x}_D$) and 95% confidence intervals (CI) $\bar{x}_D$ for our 15 paired sites; 95% CIs that do not contain 0 indicate a significant difference between water and non-water sites.

Results

Of 15 water sites examined, 73% (11) were drinkers; the remaining 4 were improved tinajas or rock potholes. For all water and non-water sites combined, the majority of sign was scats or pellets (65%), followed by tracks (including ungulate trails) (12%) and visual observations (7%). We also found bones (*n* = 23), feathers (*n* = 10), and carcasses (*n* = 4). Scats made up the majority of sign for both types of site.

We recorded 20 observations of birds as we approached water sites (where a flock counted as 1 observation). Of these, house finches (40%) and gila woodpeckers (20%) were most common. Other bird species observed at water sites included black-throated sparrows (*Amphispiza bilineata* Cassin), mourning and white-winged doves (*Zenaida macroura* L., *Z. asiatica* L.), and Gambel's quail (*Callipepla gambelii* Gambel). No other wildlife was seen at water sites except for 1 black-tailed jackrabbit.

The most common predator sign at water sites was from coyotes (79%), followed by foxes (7.5%), avian predators and scavengers (mostly turkey vultures) (7.5%), mountain lions (4%), and bobcats (2%). The most common prey sign at water sites was from ungulates (deer, sheep, pronghorn) (40%), followed by lagomorphs (36%), passerine and gallinaceous birds (19%), and peccaries (5%).

Comparison of paired water and non-water sites indicated that the amount of sign for all predator species was greater at water than non-water sites (*P* = 0.002). This was also the case for each species or group of predators, including coyotes, foxes, felids, and avian predators and scavengers (*P* = 0.08; Table 1). Prey sign was not consistently more abundant at water sites than non-water sites (*P* = 0.57). Of the species or groups of prey that we examined (Table 1), sign was more abundant at water sites for only passerine and gallinaceous birds (*P* = 0.008). Sign for peccaries and all other ungulates was not different between water and non-water (*P* = 0.76 and 0.20, respectively). Sign for lagomorphs, although common at all water and non-water sites, was 1.7x greater at non-water sites than water sites (*P* = 0.05).

Discussion

Smith and Henry (1985) did not find a difference in predator sign on plots between 6 water and 5 non-water sites in Arizona. We, however, documented up to 7x more predator sign at water sites than non-water sites, indicating that predator use of water developments was high on our study area. This was especially true for coyotes, sign from which made up almost 80% of all predator sign that we observed. Cutler (1996) also reported high visitation rates by predators at water sites in the same area, where she used remote cameras at 2 water sites to document use by wildlife. About 55% of all photographs were of coyotes. Golightly and Ohmart (1984) reported that water needs for coyotes in deserts were greater during summer than winter (this was not true for kit foxes), and so the preponderance of coyote sign at our water sites could be even greater during summer.

Despite the abundance of predator sign at water sites, we found very little evidence of kills. This may be because not many kills were made at these sites, or the evidence of kills disappeared quickly. Of the 4 carcasses that we found, 2 were gila woodpeckers, 1 was a peccary, and 1 was a turkey vulture. The woodpeckers were obviously predated by a raptor, probably a Cooper hawk (*Accipiter cooperii* Bonaparte), as evidenced by what appeared to be a sudden loss of large amounts of feathers due to impact. For passerine and gallinaceous birds, we believe that water sites may function in a similar fashion to backyard bird feeders; birds are attracted to the site, congregate and linger there, and a few individuals are subsequently killed by raptors. Some raptors may even include water sites in their foraging territories, but we do not believe that this contributes in any significant way to avian mortality. We could not determine the cause of death of the peccary or the turkey vulture because of the ages of the carcasses, but both were relatively intact and did not appear to be predated or even scavenged very much.

It is more difficult to speculate on the influence of water developments on interactions between large mammalian predators and ungulates. Carnivore territories are large and distribution of kills widespread. Based on our findings, we can only say that predators were attracted to water sites; we cannot say that water increased predation rates, improved predator fitness, or that ungulates avoided water sites because of the periodic presence of predators. Although peccaries have been documented drinking at some of these water sites (Cutler 1996), in at least some instances they do not need free-standing water because of their diet of succulent plants (Zervanos and Day 1977). Thus, we were not surprised to find no difference in

Table 1. Mean differences ($\bar{x}_D$) and 95% confidence interval (CI) of the difference for amount of predator and prey sign between 15 paired water development and non-water (random) sites in the Sonoran desert, Arizona.

Species	$\bar{x}_D$	95% CI	<i>t</i> _{Paired}	P
Coyote	6.7	2, 11	3.24	0.006
Fox	0.7	0.5, 1.3	2.32	0.04
Felid	0.5	0, 1	1.97	0.07
Avian predators ¹	0.7	-0.1, 1.4	0.67	0.08
Avian prey ²	2.3	1, 4	3.12	0.008
Ungulate ³	3.5	-2, 9	1.33	0.20
Peccaries	0.1	-1, 1	0.31	0.76
Lagomorph	-3.8	-8, 0	-2.17	0.048

¹Includes predators and scavengers (turkey vulture, common raven, loggerhead shrike, hawks, owls).

²Includes passerine and gallinaceous species.

³Includes mule deer, bighorn sheep, and pronghorn.

peccary sign between water and non-water sites. The need for free-standing water by other ungulates is less clear; some authors report that ungulates do not seem to respond to water developments (Krausman and Leopold 1986, Krausman and Etchberger 1995), while others report that water developments are used by ungulates and may be beneficial (Leslie and Douglas 1979, Hervert and Krausman 1986, Ockenfels et al. 1991), depending on the species and season involved (deVos et al. 1997b). We did not document a difference in ungulate sign between water and non-water sites, but because we lumped all ungulate sign (except peccary) together, we cannot say how ungulate sign may have differed between water and non-water sites for individual species on our study area during winter. Lagomorph was the only taxon for which we found more sign away from water sites than around water sites. Although lagomorphs in desert environments will drink from water developments (Cutler 1996), they may not need free-standing water (Schmidt-Nielsen 1964, Nagy et al. 1976) and may not be compelled to visit water sites. In years of high numbers, rabbits and hares are probably important prey, especially for coyotes, and may act to disperse predation away from water sites.

Several researchers reported that free water is unnecessary for a variety of carnivores (Chevalier 1984, Golightly and Ohmart 1984, Green et al. 1984). Schmidt-Nielsen (1964) believed that the diet of most carnivores provides them with the water they need for most physiological functions, except perhaps heat regulation. Virtually all predators in the Sonoran desert will use free-standing water if it is available, and we suspect that predators come to these sites primarily to drink rather than to hunt. Kills at water sites do occur (Monson 1964, Cunningham and deVos 1992, Krausman and Etchberger 1993), but we speculate that kills at water sites in southern Arizona, when they do happen, are on an opportunistic basis and are trivial to prey population dynamics. We do not know whether providing water to predators increases their survival or reproduction.

Research and Management Recommendations

It has been established through this and other studies that predators frequent water developments. The next step is to determine what this means, if anything, to popu-

lation dynamics. The Arizona Game and Fish Department identified key research needs for the study of water developments and their potential effects on wildlife populations (deVos et al. 1997a, 1997b). Of these, the effects of water developments on population performance (distribution, abundance, survival, reproduction) and predation rates of mammalian predators were considered important. Long-term experiments with marked animals are needed to determine the influence of water developments on predation rates and predator demography, including experimental approaches where water sites are closed (or new ones opened) while monitoring the demographics of predator populations.

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Livestock guard dogs reduce predation on domestic sheep in Colorado

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Abstract

We surveyed the effectiveness of livestock guard dogs for reducing predation on domestic sheep in Colorado during 1993. The number of producers using dogs increased from about 25 in 1986 to >159 in 1993. The proportion of sheep with dogs increased from about 7% in 1986 to about 68% in 1993. Producers with dogs, compared to producers without dogs, lost smaller proportions of their lambs to predators, especially coyotes (*Canis latrans* Say), and smaller proportions of ewes and lambs to black bears (*Ursus americanus* Pallas) and mountain lions (*Felis concolor* L.). Overall, producers who did not have guard dogs lost 5.9 and 2.1 times greater proportions of lambs to predators than producers who had dogs in 1986 and 1993, respectively. Proportions of sheep killed by predators decreased with the number of years that producers used guard dogs. Mortalities of ewes to predators regardless of type of operation and lamb mortality on open range decreased more from 1986 to 1993 for producers who obtained dogs between these years compared to producers who did not have dogs. Of 160 producers using dogs, 84% rated their dogs overall predator control performance as excellent or good, 13% as fair, and 3% as poor. More producers (n = 105) indicated effectiveness of their dogs did not change with time, compared to producers (n = 54) indicating effectiveness changed. More producers (n = 35) also indicated their dogs became more effective over time compared to producers (n = 19) indicating their dogs became less effective. Estimates provided by 125 producers indicate that their 392 dogs saved \$891,440 of sheep from predation during 1993. A total of 154 of 161 (96%) producers recommend use of guard dogs to other producers.

Key Words: Akbash, black bear, *Canis latrans*, coyote, dog, *Felis concolor*, Great Pyrenees, Komondor, mountain lion, sheep, *Ursus americanus*

Predators kill substantial numbers of domestic sheep in the 17 western states (Pearson 1986, National Agricultural Statistics Service 1995). Several methods have been used to reduce these mortalities (Andelt 1996) including livestock guard dogs (Linhart et al. 1979, McGrew and Blakesley 1982, Coppinger et al. 1983, 1988, Green and Woodruff 1983b 1988 1990, Green et al. 1984, Andelt 1992). Andelt (1992) reported that producers with guard

Resumen

Durante 1993 realizamos un reconocimiento para determinar la efectividad de los perros guardianes de ganado bovino para reducir la predación de ovinos domésticos en Colorado. El número de productores que utilizan perros aumentó de aproximadamente 25 en 1986 a más de 159 en 1993. La proporción de ovinos con perros se incrementó de aproximadamente 7% en 1986 a aproximadamente 68% en 1993. Los productores con perros, comparados con los productores sin perros, perdieron menores proporciones de corderos debido a predadores, especialmente coyotes, (*Canis latrans* Say) y menores proporciones de borregos debido a osos (*Ursus americanus* Pallas) y leones de la montaña (*Felis concolor* L.). En general, las proporciones de pérdida de corderos debido a predadores registradas en 1986 y 1993 fueron 5.9 y 2.1 veces mayores que las de los productores que tenían perros. Las proporciones de ovinos asesinados por predadores disminuyeron con el número de años que los productores han utilizado perros guardianes. La mortalidad de borregos por predadores, independientemente del tipo de operación, y la mortalidad de corderos en pastizales abiertos disminuyeron más de 1986 a 1993 para los productores que obtuvieron perros en esos años comparado con los productores que no tenían perros. De 160 productores que utilizan perros, el 84% calificó el control de predadores de sus perros como excelente o bueno, el 13% como regular y el 3% como pobre. Más productores (n = 105) indicaron que la efectividad de sus perros no cambió con el tiempo, comparado con (n = 54) productores que indicaron que la efectividad sí cambió. Más productores (n = 35) también señalaron que con el tiempo sus perros llegan a ser más efectivos, comparado con los productores (n = 19) que indicaron que con el tiempo sus perros fueron menos efectivos. Las estimaciones proporcionadas por 125 productores indican que durante 1993 sus 392 perros evitaron pérdidas de ovinos por predadores por un valor de \$ 891,440 dólares. De 161 productores un total de 154 (96%) recomendaron a otros productores el uso de perros guardianes.

dogs sustained lower sheep losses to coyotes than producers without dogs. However, no data were available to compare changes in sheep mortalities for producers after they obtained dogs.

Green and Woodruff (1989) and Green et al. (1993) reported that guard dogs repelled black and grizzly bears (*Ursus arctos* L.) during most encounters. However, no studies have evaluated the effectiveness of dogs against black bear or mountain lion predation, nor have any authors reported on the relative effectiveness of guard dogs for deterring predation by different predators.

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Additional data are also needed to ascertain relationships between herd size, number of dogs/herd, and number of sheep/dog versus predation rates.

In this paper, we compare sheep mortalities to predators for producers in Colorado who had and did not have guard dogs. We present the effects of herd size, sheep/dog, dogs/herd, and number of years dogs were used on predation rates. We report changes in proportions of sheep mortalities from 1986 to 1993 for producers with and without dogs in both years, and producers who obtained dogs between those years.

Materials and Methods

We determined the effectiveness of guard dogs for protecting domestic sheep from predators by telephone surveys of 182 livestock producers with dogs and 60 producers without dogs during 1993. We believe that our survey included practically all producers who used guard dogs in Colorado. The 60 producers were a random sample of 143 producers who did not have guard dogs and responded to a 1986 survey (Andelt 1992).

We requested information on type of operation, number of ewes and lambs in the operation, ewe and lamb mortalities from all causes (weather, disease, predation, etc.), all predators, and specifically from coyotes, black bears, mountain lions and domestic dogs, ratings of effectiveness, and value of sheep saved based upon mortality rates before and after obtaining dogs, during 1993 or the last year that they used dogs. We compared these data to similar data obtained in 1986 (Andelt 1992).

We classified producer operations with sheep in fenced pastures, open range, fenced pastures plus open range, fenced pastures plus open range and feedlots, and fenced pastures and feedlots as all operations combined. We censored producers with sheep solely in feedlots because these operations usually included large numbers of sheep and low mortalities to predators. We classified operations with sheep in fenced pastures or in a combination of fenced pastures and feedlots as fenced pastures. We conducted separate analyses on fenced pasture versus open range operations because sheep were maintained under different conditions, and we anticipated that sizes of herds and predation rates were different. We defined all predators as the sum of all predators that killed sheep.

We compared the total number of ewes and lambs owned by producers with and

without guard dogs. We used total numbers of ewes and lambs owned to calculate mortalities to all causes, but we used the numbers of ewes and lambs that were guarded by dogs, or were not guarded by dogs, when calculating proportions of ewes or lambs killed by predators. For the 1993 survey, we compared mortalities to various predators only among producers who indicated the specific predator was found in their area. Numbers of ewes and lambs killed by predators for producers with guard dogs were reported only for periods when dogs were with sheep. When dogs were not with sheep for the entire year, we extrapolated the mortalities by dividing by the percentage of the annual period that dogs were with sheep to standardize the data for comparisons to producers without dogs.

We compared the numbers of ewes and lambs owned among producers with and without guard dogs using analysis of variance (ANOVA, GLM Procedure, SAS Inst. Inc. 1988) after transforming herd sizes to natural logarithms to equalize variances. We compared the numbers of ewe and lamb mortalities to all causes and to predators among respondents with and without dogs by testing the slopes of regression lines obtained by regressing the number of mortalities against the number of ewes or lambs owned or maintained with dogs. We conducted the analyses with the GLM procedure after weighting the number of mortalities by 1 divided by the number of ewes or lambs owned or by the number of ewes or lambs with dogs. When the overall F-test indicated significant treatment effects, we used 1-sided z-tests with a mean of 0 and a standard deviation of 1 to determine if mortalities for producers with guard dogs were lower than for producers without dogs, whereas 2-sided chi-square tests with 1 degree of freedom were used to determine if mortalities for producers with guard dogs and if mortalities for producers without dogs differed between years. We considered a $P < 0.0083$ as significant in these 6-treatment comparisons to maintain an experiment-wise error rate of 0.05.

We used linear regression weighted by the number of ewes or lambs with guard dogs (GLM Procedure) to determine the effect of number of ewes or lambs with dogs, number of ewes or lambs/dog, number of dogs/herd, and number of years that dogs were maintained with sheep on the proportion of ewes or lambs killed by predators in individual sheep operations. We determined changes in ewe and lamb mortalities from 1986 to 1993 for produc-

ers with and without guard dogs during both years, and for producers who did not have dogs in 1986 but used dogs by 1993. We assumed that coyotes, black bears, mountain lions, and domestic dogs were found in a producers area during 1986, if they were reported there in 1993, and thus made comparisons between our 1993 and 1986 data for these predators. We determined changes by subtracting proportions of ewe or lamb mortalities in 1986 from those in 1993 for individual producers. We compared these differences among treatments with ANOVA after weighting the differences for each producer by the mean number of ewes or lambs with dogs in 1986 and 1993 in guarded herds.

We assigned rankings to producer ratings (excellent = 4, good = 3, fair = 2, poor = 1, unacceptable = 0) as to effectiveness of dogs for deterring predation by various predators, effectiveness in fenced pastures compared to open range, effectiveness during 1986 compared to 1993, and compared these rankings with ANOVA using the GLM procedure. We used a binomial probability distribution to determine if the number of producers indicating effectiveness (effectiveness when surveyed compared to effectiveness when the dogs first established normal guarding behaviors) changed, or did not change with time, and if the number of reported positive or negative changes varied from equality. We used Spearman rank correlation to determine if ratings of effectiveness were associated with proportions of ewes or lambs killed by predators. We estimated the value of sheep saved by each guard dog by multiplying the average number of ewes and lambs/producer by differences in predation rates for producers with and without dogs, multiplying by the average value of sheep (\$77; Colorado Agricultural Statistics Service 1994), and dividing by the average number of dogs/producer. We used ANOVA to compare producer estimates of the value of sheep saved/dog between 1986 and 1993, and between fenced pastures versus open range operators after weighting the average saving/dog by number of dogs owned by each producer. We used the "protected" least significant difference test (Milliken and Johnson 1984:31–33) to determine which treatment pairs were different for the average number of ewes and lambs owned, percent changes in ewe and lamb herd sizes, changes in mortalities from 1986 to 1993 and producer ratings of effectiveness of dogs when the overall F-test indicated significant ($P < 0.05$) treatment effects.

Results

Survey response

We acquired complete or nearly complete surveys from 182 producers who used guard dogs between 1987 and 1993, 54 producers without dogs during 1993, and 6 producers without dogs who last maintained sheep in 1991 and 1992. We discarded 6 surveys for producers who used guard dogs but maintained sheep only in feedlots. Of 161 producers who used dogs for 1 year, 144 reported data for 1993 and 17 reported data for the last year that they used dogs (1987 to 1992).

Sheep and dog demographics

The number of producers using guard dogs who provided complete or nearly complete surveys increased from 25 in 1986 to 159 in 1993. The number of sheep with dogs in fenced pastures and on open range increased about 900% from 1986 to 1993, from 6% of 340,000 ewes and 8% of the annual lamb crop of 350,000 in 1986 to 59% of 325,000 ewes and 76% of 320,000 lambs in 1993 (Andelt 1992, Colorado Agricultural Statistics Service 1993, 1994, 1995a). An additional 19 producers (17 producers used dogs for 1 year and 2 used dogs for <1 year) used dogs with 13,650 ewes and 22,500 lambs between 1987 and 1992. Seventeen of 24 producers who used dogs in 1986 (Andelt 1992, and additional data) continued to raise sheep in 1993 and all 17 continued to use dogs. Of the 176 producers with dogs, 83 used Great Pyrenees, 34 used Akbash dogs, 15 used Komondors, 3 used Anatolians, and 41 used combinations of Akbash, Great Pyrenees, Komondors, Maremmas, Shar Planinets, hybrids, or unknown breeds.

Fig. 1. Percent mortalities of ewes and lambs to predators for producers with animals in fenced pastures (ewes: $P = 0.042$; lambs: $P = 0.0003$), on open range (ewes: $P = 0.089$; lambs: $P = <0.0001$), and in all operations combined (ewes: $P = 0.009$; lambs: $P = <0.0001$) in Colorado. Bars, within a group, with the same letters are not significantly different. Sample sizes are above each bar.

Herd sizes

Regardless of year surveyed, producers who had guard dogs tended to have more sheep than producers without dogs (Tables 1, 2). Furthermore, operations with dogs tended to increase in size from 1986 to 1993 whereas operations without dogs tended to decrease in size.

Modalities to all causes

Producers with guard dogs tended to lose smaller proportions of ewes and particularly lambs than producers without dogs regardless of operation or year of our survey (Tables 1, 2). Overall, mortalities tended to be higher during 1993 compared to 1986 but none of the differences were statistically significant.

Predation

Producers with guard dogs, compared to producers without dogs, generally lost smaller proportions of ewes and lambs to predators regardless of operation during both survey years (Fig. 1). These comparisons generally were statistically significant for lambs but not as dramatic for ewes. Producers who did not have guard dogs lost 5.9 and 2.1 times greater proportions of lambs to predators than producers who had dogs in 1986 and 1993, respectively. Non-predator mortalities (i.e. mortalities to all causes minus mortalities to all predators; Tables 1, 2; Fig. 1) were similar among producers regardless of whether they owned guard dogs.

Table 1. Mean number ewes/producer and percent mortality from all causes in relation to use of livestock guard dogs reported by sheep producers in Colorado during 1986 and 1993.

Characteristics of sheep operations	1986				1993				P ^a
	Dogs		No dogs		Dogs		No dogs		
	n	$\bar{x}$ or %	n	$\bar{x}$ or %	n	$\bar{x}$ or %	n	$\bar{x}$ or %	
Herd size ($\bar{x}$)									
All operations ^b	24	1,169B ^c	138	642A	161	1,265B	56	245A	<0.0001
Fenced pastures	11	105A	99	176AB	93	297B	49	120A	0.0008
Open range	11	2,336A	25	1,945A	47	2,982A	5	1,205A	0.089
All mortality (%)									
All operations	22	3.7A	138	5.6B	157	5.4AB	56	6.7B	0.036
Fenced pastures	11	3.3A	99	5.1A	93	4.5A	49	6.4A	0.119
Open range	9	3.7A	25	5.5A	45	5.6A	5	7.8A	0.306

^aProbability that the 4 means or regression slopes (% losses) in a row differ.

^bIncludes fenced pasture, open range, fenced pasture—open range, fenced pasture—open range—feedlot, and fenced pasture—feedlot operations.

^cMeans in a row followed by different letters are different ($P < 0.0083$ /comparison to obtain an experiment-wise $P = 0.05$).

Table 2. Mean number lambs/producer and percent mortality from all causes in relation to use of livestock guard dogs reported by sheep producers in Colorado during 1986 and 1993.

Characteristics of sheep operations	1986				1993				P ^a
	Dogs		No dogs		Dogs		No dogs		
	n	$\bar{x}$ or %	n	$\bar{x}$ or %	n	$\bar{x}$ or %	n	$\bar{x}$ or %	
Herd size ($\bar{x}$)									
All operations ^b	23	1,524B ^c	131	730A	157	1,451B	56	328A	<0.0001
Fenced pastures	10	193AB	92	184A	91	399B	49	175AB	0.0008
Open range	11	2,851A	25	2,144A	46	3,386A	5	1,491A	0.057
All mortality (%)									
All operations	20	6.1A	131	11.5B	149	8.3A	56	12.3B	<0.0001
Fenced pastures	9	4.5AB	92	10.2B	90	5.8A	49	9.5B	<0.0001
Open range	9	6.5A	25	12.2AB	41	8.9AB	5	17.9B	0.026

^aProbability that the 4 means or regression slopes (% losses) in a row differ.

^bIncludes fenced pasture, open range, fenced pasture—open range, fenced pasture—open range—feedlot, and fenced pasture—feedlot operations.

^cMeans in a row followed by different letters are different ($P < 0.0083$ /comparison to obtain an experiment-wise $P = 0.05$).

Regardless of guard dogs, producers lost similar proportions of ewes to coyotes, but producers with dogs generally lost smaller proportions of lambs (Fig. 2). Producers with guard dogs lost smaller proportions of ewes and lambs to black bears (Fig. 3) and mountain lions (Fig. 4) than producers without dogs in all operations combined and on open range. However, guard dogs did not appear to affect predation rates by black bears and mountain lions in fenced pastures where these rates were relatively low. Proportions of ewes and lambs killed by domestic dogs did not vary significantly regardless of the presence of guard dogs for any type of operation (Fig. 5). Coyotes, black bears, and mountain lions

generally killed similar proportions of ewes, but coyotes killed 5 to >10 times more lambs than either bears or lions.

Five producers with guard dogs and 4 producers without dogs reported that red foxes (*Vulpes vulpes* L.) killed 262 and 153 lambs, respectively. Four producers with dogs and 1 producer without dogs reported eagles (likely *Aquila chrysaetos* L.) killed 446 and 40 lambs. In addition, 1 producer with dogs reported American crows (*Corvus brachyrhynchos* Brehm) killed 2 lambs, and 1 producer indicated that a guard dog killed 2 lambs.

Open range versus fenced pastures

Mortalities of ewes to predators, and specifically to coyotes, black bears, moun-

tain lions, and domestic dogs did not vary significantly ($F = 0.00\text{--}2.50$; 1 15–132 df; $P = 0.117\text{--}0.970$, for the various comparisons) between fenced pasture and open range regardless of the presence of guard dogs during either year. However, ewe mortalities to all predators combined were greater ($F = 5.78$; 1,133 df; $P = 0.018$) on open range than in fenced pastures for producers with dogs in 1993. Lamb mortalities were greater ($F = 8.35\text{--}29.81$; 1,51–126 df; $P = < 0.0001\text{--}0.005$ for the various comparisons) on open range compared to fenced pastures to predators, and specifically to coyotes, for producers without dogs both years and for producers with dogs in 1993. Lamb mortalities to mountain lions also were higher ($F = 8.87$; 1,22 df; $P = 0.007$) on open range compared to fenced pastures for producers without dogs in 1993. In contrast, lamb mortalities to domestic dogs were higher ($F = 4.29$; 1,100 df; $P = 0.041$) in fenced pastures compared to open range for producers with dogs during 1993.

Relationships: Dog numbers/experience

Each producer used an average of 3.2 ($SE = 0.3$) dogs in all operations combined, 1.7 ($SE = 0.1$) dogs in fenced pastures, and 5.6 ($SE = 0.7$) dogs on open range. Each producer used an average of 1.8 ($SE = 0.1$) dogs/herd of sheep in all operations combined, 1.6 ($SE = 0.1$) dogs/herd of sheep in fenced pastures, and 2.2 ($SE = 0.2$) dogs/herd of sheep on open range. Each producer had an average of 716 ($SE = 67$) ewes and lambs/dog in all operations combined, 414 ($SE = 77$) ewes and lambs/dog in fenced pastures, and 1,245 ($SE = 115$) ewes and lambs/dog on open range.

Proportions of ewes killed by predators increased as the number of ewes maintained with guard dogs increased in all operations combined (intercept = 0.0057;

Fig. 2. Percent mortalities of ewes and lambs to coyotes for producers with animals in fenced pastures (ewes: $P = 0.803$; lambs: $P = 0.005$), on open range (ewes: $P = 0.324$; lambs: $P = < 0.0001$), and in all operations combined (ewes: $P = 0.022$; lambs: $P = 0.0001$) in Colorado. Bars, within a group, with the same letters are not significantly different. Sample sizes are above each bar.

Fig. 3. Percent mortalities of ewes and lambs to black bears for producers with animals in fenced pastures (ewes: $P = 0.186$; lambs: $P = 0.976$), on open range (ewes: $P = 0.033$; lambs: $P = 0.009$), and in all operations combined (ewes: $P = 0.002$; lambs: $P = 0.005$) in Colorado during 1993. Bars, within a group, with the same letters are not significantly different. Sample sizes are above each bar.

slope = 0.0000; $F = 63.06$; 1,153 df; $P < 0.0001$) and on open range (intercept = 0.0059; slope = 0.0000; $F = 28.28$; 1,41 df; $P < 0.0001$), whereas proportions of lambs killed by predators increased as the numbers of lambs with dogs increased only in all operations combined (intercept = 0.0256; slope = 0.0000; $F = 17.63$; 1,146 df; $P < 0.0001$). Proportions of sheep killed by predators did not vary ($P = 0.168$ – 0.823 for the various comparisons) by the numbers of ewes or lambs maintained/dog. Also, proportions of sheep killed by predators did not vary ($P = 0.173$ – 0.772) with the number of dogs maintained/herd of sheep regardless of the type of operation. Proportions of ewes and lambs killed by predators decreased with the number of years that individual producers used guard dogs for the analyses of all operations combined (ewes: [intercept = 0.0246; slope = -0.0020 ; $F = 31.99$; 1,153 df; $P < 0.0001$]; lambs: [intercept = 0.0526; slope = -0.0029 ; $F = 10.44$; 1,146 df; $P = 0.002$]) and for open range (ewes: [intercept = 0.0264; slope = -0.0022 ; $F = 20.41$; 1,41 df; $P < 0.0001$]; lambs: [intercept = 0.0582; slope = -0.0032 ; $F = 4.88$; 1,38 df; $P = 0.033$]).

Changes in mortality rates from 1986 to 1993

Although generally not statistically significant, predation for our entire sample of producers seemed to increase between

1986 and 1993. However, for the subset of producers who we surveyed during both 1986 and 1993, producers who obtained dogs after 1986 generally had decreases in predation, whereas predation generally increased for producers who did not obtain dogs and predation losses remained about

the same for producers who had dogs during both years (Tables 3, 4). Some of these predation rates were reduced significantly more for producers who obtained dogs relative to producers who did not have dogs. However, in fenced pastures, ewe and lamb mortalities to predators, specifically to coyotes, increased more in herds guarded by dogs both years compared to producers without dogs and producers who obtained dogs. These increases were attributed to 1 producer who reported coyotes killed 20 ewes and 55 lambs in 1993, whereas the other 8 producers with dogs did not lose any ewes or lambs to predators during either year.

Producer ratings of guard dogs' effectiveness

Of 160 producers using guard dogs for 1 year between 1987–93, 84% rated their dogs' overall predator control performance as excellent or good, 13% as fair, and 3% as poor. For sheep in all operations combined, producers rated guard dogs more effective against coyotes compared to black bears and mountain lions, and against domestic dogs compared to black bears ($F = 7.17$; 3,372 df; $P < 0.0001$; Table 5). For sheep within fenced pastures producers rated the effectiveness of guard dogs against coyotes, black bears, mountain lions and domestic dogs as similar ($F = 1.03$, 3, 194 df; $P = 0.379$). For sheep on

Fig. 4. Percent mortalities of ewes and lambs to mountain lions for producers with animals in fenced pastures (ewes: $P = 0.061$; lambs: $P = 0.283$), on open range (ewes: $P = 0.0007$; lambs: $P < 0.0001$), and in all operations combined (ewes: $P < 0.0001$; lambs: $P < 0.0001$) in Colorado during 1993. Bars, within a group, with the same letters are not significantly different. Sample sizes are above each bar.

Table 3. Mean differences in percent mortalities for ewes from 1986 to 1993 for producers who had guard dogs, did not have guard dogs, and those who obtained guard dogs after 1986 in Colorado. Positive values report increases in predation whereas negative values report decreases.

Source of predation loss	Dogs		No dogs		Obtained dogs		P ^a
	n	Difference	n	Difference	n	Difference	
All predators		(%)		(%)		(%)	
All operations ^b	19	-0.1AB ^c	55	0.9B	31	-0.9A	0.015
Fenced pastures	9	2.7B	48	0.4AB	13	-3.4A	0.019
Open range	6	-0.2A	3	3.3B	6	-1.4A	0.023
Coyotes							
All operations	19	-0.1A	54	0.1A	31	-0.4A	0.381
Fenced pastures	9	2.7B	48	0.1A	13	-0.3A	0.032
Open range	6	-0.3A	3	0.6A	6	-1.0A	0.348
Bears							
All operations	13	-0.0A	17	0.7A	22	0.1A	0.080
Fenced pastures	4	0.0A	12	0.2A	7	0.2A	0.840
Open range	6	0.1A	3	1.6A	6	0.2A	0.134
Lions							
All operations	10	0.0A	24	0.3A	20	-0.4A	0.214
Fenced pastures	3	0.0A	20	-0.3A	5	0.1A	0.955
Open range	3	0.0A	2	1.2A	5	-0.8A	0.400
Dogs							
All operations	18	0.0A	45	0.2A	21	-0.2A	0.739
Fenced pastures	9	0.0B	39	0.5B	10	-3.7A	0.024
Open range	5	0.0A	3	0.0A	4	0.2A	0.153

^aProbability that the 3 means or regression slopes (% losses) in a row differ; numerator df = 2, denominator df = sum of ns in a row minus 3.

^bIncludes fenced pasture, open range, fenced pasture—open range, fenced pasture—open range—feedlot, and fenced pasture—feedlot operations.

^cMeans in a row followed by different letters are different.

open range, producers rated guard dogs more effective against coyotes compared to black bears and mountain lions ($F = 3.76$, 3, 118 df; $P = 0.013$). Producers rated guard dogs more effective against black bears and mountain lions for sheep in fenced pastures compared to those on open range. Producer ratings of the effectiveness of guard dogs against all predators combined, coyotes, black bears, mountain lions, and domestic dogs were inversely associated ($n = 39$ –154; $r_s = -0.262$ – -0.557 ; $P = 0.043$ – <0.0001) with proportions of sheep killed by these predators. A total of 154 of 161 (96%) guard dog owners indicated they would recommend dogs to other livestock producers, whereas 3 owners indicated they would recommend dogs only under certain conditions, and 4 owners would not recommend dogs.

Changes in effectiveness

Producer ratings of the effectiveness of guard dogs for deterring predation by all predators combined were similar ($F = 0.06$; 1,180 df; $P = 0.807$) during 1986 ($n = 22$, $\bar{x} = 3.5$) and 1993 ($n = 160$, $\bar{x} = 3.5$). During 1993, more ($P < 0.0001$) producers ($n = 105$, including 64 producers in fenced pastures and 24 producers on open range) indicated effectiveness of their dogs did not change with time compared to those (n

= 54, including including 29 producers who used fenced pastures and 22 producers who used open range) who indicated effectiveness changed. More ($P = 0.010$)

producers ($n = 35$, including 19 producers who used fenced pastures and 14 producers who used open range) indicated their dogs were more effective compared to those ($n = 19$, including 10 producers who used fenced pastures and 8 producers who used open range) who indicated their dogs were less effective. Of the producers indicating their dogs were more effective, 29 attributed the better performance to maturity of the dogs, 3 indicated more effective dogs were used, and 2 indicated that their dogs learned to outsmart predators. Three producers indicated the federal animal damage control program was more effective than before, and 3 others indicated their own predator control efforts increased.

Of the producers indicating their dogs were less effective, 11 felt predators learned to outsmart the dogs, 4 indicated the dogs changed their behaviors, 3 indicated there were more predators, 3 indicated the dogs became too old, 2 indicated that predator control efforts decreased and 3 producers gave other reasons. Producer ratings of the effectiveness of guard dogs for deterring predation on sheep were not related (rating = 3.29 ± 0.03 years; $F = 3.39$; 1,158 df; $P = 0.068$) to the number of years that producers used dogs.

Fig. 5. Percent mortalities of ewes and lambs to domestic dogs for producers with animals in fenced pastures (ewes: $P = 0.201$; lambs: $P = 0.532$), on open range (ewes: $P = 0.443$; lambs: $P = 1.000$), and in all operations combined (ewes: $P = 0.442$; lambs: $P = 0.482$) in Colorado during 1993. Bars, within a group, with the same letters are not significantly different. Sample sizes are above each bar.

Table 4. Mean differences in percent mortalities for lambs from 1986 to 1993 for producers who had guard dogs, did not have guard dogs, and those who obtained guard dogs after 1986 in Colorado. Positive values report increases in predation whereas negative values report decreases.

Source of predation loss	Dog		No dogs		Obtained dogs		P ^a
	n	Difference	n	Difference	n	Difference	
All predators		(%)		(%)		(%)	
All operations ^b	17	0.7A ^c	55	3.0A	27	0.7A	0.162
Fenced pastures	7	5.3A	48	-0.7A	11	-1.8A	0.183
Open range	6	0.2A	3	9.2B	6	-0.3A	0.006
Coyotes							
All operations	17	0.8A	54	1.5A	27	0.5A	0.637
Fenced pastures	7	5.3A	48	0.0A	11	-1.0A	0.156
Open range	6	0.2A	3	6.2B	6	-0.5A	0.009
Bears							
All operations	12	-0.1A	18	0.1A	18	0.4A	0.054
Fenced pastures	3	0.0A	13	0.2A	5	0.7A	0.468
Open range	6	0.0A	3	0.3A	6	0.5A	0.353
Lions							
All operations	9	0.0A	25	0.3A	16	0.6A	0.467
Fenced pastures	2	0.0A	21	-1.4A	3	0.0A	0.690
Open range	3	0.0A	2	2.4B	5	1.0A	0.015
Dogs							
All operations	16	0.0A	45	0.1A	20	-0.1A	0.934
Fenced pastures	7	0.0A	39	0.2A	9	-0.9A	0.664
Open range	5	0.0A	3	0.0A	4	0.0A	1.000

^aProbability that the 3 means or regression slopes (% losses) in a row differ; numerator df = 2, denominator df = sum of ns in a row minus 3.

^bIncludes fenced pasture, open range, fenced pasture—open range, fenced pasture—open range—feedlot, and fenced pasture—feedlot operations.

^cMeans in a row followed by different letters are different.

Table 5. Producer ratings of the effectiveness of livestock guard dogs for deterring predators from preying on domestic sheep in Colorado during 1993.

Predator	All operations		Fenced pastures		Open range		P ^b
	n	$\bar{x}$	n	$\bar{x}$ ^a	n	$\bar{x}$	
All predators	160	3.46	92	3.57	47	3.33	0.088
Coyotes	160	3.49C ^c	92	3.58A	47	3.38B	0.160
Black bears	64	2.93A	16	3.38A	35	2.76A	0.038
Mountain lions	43	3.02AB	17	3.47A	19	2.61A	0.022
Domestic dogs	109	3.30BC	73	3.36A	21	3.05AB	0.193

^a4 = excellent, 3 = good, 2 = fair, 1 = poor, 0 = unacceptable.

^bProbability that the means for fenced pastures and open range do not differ.

^cMeans in a column followed by the same letter do not differ (P < 0.05).

Estimated savings/dog

Estimates, by producers who used guard dogs for 1 year, of the average value of sheep saved/dog from predators within all operations combined were similar (F = 0.97; 1,134 df; P = 0.327) during 1986 (n = 12 producers) and 1987–1993 (n = 124 producers; Table 6). Estimates of the average value of sheep saved/dog from predators within fenced pastures also were similar (F = 0.27; 1,72 df; P = 0.604) during 1986 (n = 5 producers) and 1987–1993 (n = 69 producers), and savings on open range were similar (F = 0.04; 1,41 df; P = 0.840) during 1986 (n = 6 producers) and 1987–1993 (n = 37 producers). Producers estimated that each dog saved a greater value of sheep on open range than within fenced pastures during both 1986 (F =

15.02; 1,9 df; P = 0.004) and 1987–1993 (F = 8.55; 1,104 df; P = 0.004). From our data on herd sizes, predation rates, value of sheep, and number of dogs/producer,

Table 6. Producer estimates and our estimate of the average value (dollars) of domestic sheep saved from predators by each guard dog in Colorado during 1986 and 1993.

Year	All operations		Fenced pastures		Open range	
	n ^a	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Producer						
1986	33	3,733	7	686	24	4,100
1993	396	2,506	116.5 ^c	1,149	202.5	3,610
Authors						
1993		1,685 ^d		683		4,832

^aRepresents number of dogs.

^bWeighted by number of dogs.

^cOne dog was used for half the year.

^dEstimated by multiplying the average number of ewes and lambs/producer by differences in predation rates for producers with and without dogs, multiplying by the average value of sheep, and dividing by the average number of dogs/producer.

we estimated that the average value of sheep saved/dog was somewhat lower than producer estimates in all operations combined and fenced pastures, but higher on open range (Table 6).

Estimated savings during 1993 by 114 producers ($\bar{x}$ = \$2,276) who used 374 dogs for 1 year and 11 producers ($\bar{x}$ = \$2,242) who used 18 dogs for <1 year totaled \$891,440. Estimates provided by 12 of 19 producers who used dogs between 1987 and 1992 but not during 1993 indicated that each of their 24 dogs saved an average of \$5,986 of sheep annually from predation.

The number of guard dogs used by individual producers increased with the number of sheep maintained with dogs in all operations combined (number dogs = 1.90 + 0.00050 x number sheep; F = 73.76; 1,122 df; P < 0.0001) and on open range (number dogs = 3.36 + 0.00038 x number sheep; F = 8.00; 1,35 df; P = 0.008), but not in fenced pastures (number dogs = 1.62 + 0.00009 x number sheep; F = 1.30; 1,67 df; P = 0.259). Producer estimates of the value of sheep saved from predators by each dog during 1987–1993 were directly related to the number of ewes and lambs that producers maintained with dogs in all operations combined (saved = 1,424 + 0.33 x number ewes and lambs; F = 17.38; 1,122 df; P < 0.0001) and in fenced pastures (saved = 558 + 0.85 x number ewes and lambs; F = 57.00; 1,67 df; P < 0.0001), but not on open range (saved = 3,212 + 0.22 x number ewes and lambs; F = 1.39; 1,35 df; P = 0.247).

Discussion

We found that 7 of 24 producers using guard dogs in 1986 stopped raising sheep by 1993. This rate of going out of business is similar to an overall rate of decline in the number of sheep producers from 2,200–2,600 in the 1980's to 1,800 in

1993 in Colorado (Colorado Agricultural Statistics Service 1994, 1997). We also found that the number of producers using guard dogs and the number of sheep with dogs increased significantly in Colorado between 1986 and 1993 even though the number of sheep producers declined. Colorado Agricultural Statistics Service (1995b, 1998) reported 30% of sheep producers in Colorado used guard dogs in 1994 and 44% used guard animals (perhaps mostly guard dogs) in 1997 suggesting a continued increase in use of dogs. Our data indicate that larger percentages of animals are being protected by dogs rather than proportions of producers who have dogs. Most producers without guard dogs on open range who we surveyed in 1986 obtained dogs by 1993. These data indicate that primarily the larger producers have incorporated dogs.

Although not statistically significant, predation tended to increase from 1986 to 1993 in herds guarded by dogs. We found that the proportion of ewes and lambs killed by predators increased with the size of operations using guard dogs in 1993. Thus, the increase in predation from 1986 to 1993 in guarded herds may be related to the larger size of operations in 1993 compared to 1986.

Green and Woodruff (1989) and Green et al. (1993) reported that guard dogs repelled black and grizzly bears during most encounters. We found that producers using guard dogs, compared to producers without dogs, sustained lower predation on ewes and lambs by black bears and mountain lions, and rated dogs as successful for deterring those losses. These observations indicate guard dogs can be successful against large carnivores.

Coppinger et al. (1988) and Green and Woodruff (1990) reported that effectiveness of guard dogs did not differ between fenced pasture and open range operations. We also found that producer ratings of guard dogs did not differ between fenced pasture and open range operators for deterring predation by predators, and specifically coyotes and domestic dogs, but guard dogs were rated as more effective in fenced pastures than on open range against black bears and mountain lions. Our data on sheep killed by black bears and mountain lions suggests the opposite with guard dogs being more effective on open range than in fenced pastures. Producers using guard dogs also sustained higher mortalities to predators, especially coyotes, on open range compared to fenced pastures, and reported that each dog saved a larger value of sheep on open

range than in fenced pastures which probably was due to having larger herds of sheep on open range.

Coppinger et al. (1983) reported that guard dog performance was similar between small and large flocks of sheep. Green and Woodruff (1983a) reported that 2 or more dogs, compared to 1 dog, provided better protection of sheep from predators, but no data were provided. We found that proportions of ewes reported killed by predators on open range were directly related to the size of the herd with dogs. However, our direct relationship between proportions of sheep killed by predators in all operations combined versus the number of sheep in an operation may not reflect greater mortalities with greater herd size, but may be related to greater mortalities on open range than in fenced pastures and the associated larger herds on open range.

Mortalities to predators in this study did not vary with the number of ewes or lambs/guard dog nor with the number of dogs/herd of sheep. This relationship does not necessarily mean that the number of ewes or lambs/dog or the number of dogs/herd does not affect predation rates. Rather, this relationship may reflect producers adjusting numbers of ewes or lambs/dog or numbers of dogs/herd for each operation until mortalities are reduced to a certain level.

We surveyed more producers with sheep in fenced pastures than on open range, however, our mortality rates for all operations combined generally emphasize rates on open range because we weighted our analyses by herd sizes which were much larger on open range. Mortality rates to coyotes likely are reflective of mortality rates across Colorado because coyotes were reported in the area of practically all fenced pasture and open range operations that we surveyed. However, mortality rates to black bears and mountain lions likely exaggerates mortality rates across Colorado, especially in fenced pastures, because our data represent mortalities where these predators were present, and only about one-third of the producers in fenced pastures indicated black bears and mountain lions were found in their areas.

Colorado Agricultural Statistics Service (1995b) estimated that predators killed \$2.20 million of sheep and lambs in Colorado during 1994. Estimated total numbers of mature sheep and lamb mortalities divided by the inventory of breeding sheep (320,000) and annual lamb crop (255,000; Colorado Agricultural Statistics Service 1995a) indicate that predators

killed 2.0% of ewes and 11.4% of lambs which was similar to our percentages for producers without guard dogs. Mortality rates to coyotes, black bears, mountain lions, and domestic dogs also were similar for the 2 surveys. Coyotes were the major predator of lambs in both surveys. In our study, producers estimated that their guard dogs saved \$891,440 of sheep from predation during 1993. This savings has an economic "multiplier effect" of about 2.7 (Hoag et al. 1995) which suggests the use of guard dogs added about \$2.4 million of value to Colorado's economy during 1993.

Producer estimates were higher than our estimates of the average value of sheep saved/guard dog in all operations combined and in fenced pastures. Producer estimates were based upon mortalities before compared to after obtaining dogs, whereas our estimates were based upon producers with and without dogs. These differences could be explained if producers that obtained dogs had higher mortalities before obtaining dogs than producers that did not obtain dogs. Our estimates were higher than producer estimates of the average value of sheep saved/dog on open range. These differences could be based upon our limited sample size for estimating predation rates for producers without dogs.

Producer estimates of the average value of sheep saved/dog/year from predators in fenced pastures (\$1,149) and on open range (\$3,610) in this study exceeds the purchase price of guard dog pups (\$240) and adults (\$690) plus \$26 in shipping fees (Andelt 1985) and annual maintenance (food, veterinary care, and miscellaneous costs) which averaged \$250 (Andelt 1985) and \$286 (Green et al. 1984)/year. The value of each guard dog increased with the number of sheep that producers maintained in fenced pastures but not on open range. This probably resulted because the number of guard dogs increased with the number of sheep owned by individual producers on open range, but not in fenced pastures.

We found that most producers indicated effectiveness of their dogs did not change with time and, of the producers indicating effectiveness changed, more producers felt their dogs became more effective. In addition, ewe and lamb mortalities to predators decreased with the number of years producers used dogs. Thus, our data concur with a subset of the data (Green et al. 1994) indicating performance of the majority of dogs remained the same or improved with time.

Conclusions and Management Recommendations

Guard dogs are an important tool for reducing sheep mortalities to predators. Producers with guard dogs, compared to producers without dogs, lost smaller proportions of their lambs to predators, specifically to coyotes, and also lost smaller proportions of their sheep to black bears and mountain lions. Ewe and lamb predation generally was lower for producers who obtained dogs relative to producers who had not obtained dogs. In addition, 84% of producers rated the effectiveness of their dogs as excellent or good, most producers indicated that their dogs did not decrease effectiveness with time, >96% of producers indicated that they would recommend dogs to other producers, all 17 producers that used dogs in 1986 and continued in the sheep business still used dogs in 1993 and 125 producers using guard dogs in 1993 indicated that their dogs saved over \$891,000 in sheep from predators; these estimates of savings were conservative because 32 producers did not provide estimates. Thus, use of guard dogs is a successful method for combating predation on domestic sheep.

In a recent synthesis of coyote and depredation control literature, Knowlton et al. (1999) suggest that there may be a difference in predation risk between pastured sheep and those on open range. We found lambs on open range are significantly more likely to be killed by predators than those in fenced pastures. Knowlton et al. (1999) also report that no techniques to control depredations are universally effective and that guard dogs are effective in some situations but not in others. Based on our data and the opinions of nearly all producers, dogs, when properly used, are effective in the majority of situations against a variety of predators. However, it is interesting to note that according to our data, guard dogs do not significantly change predation rates on ewes from coyotes or domestic dogs regardless of the operation, but do significantly protect lambs. Ewes might be more capable of defending themselves against canids, and the effects of guard dogs may be less apparent. On the other hand, lambs are more vulnerable to coyotes, and they often are maintained with ewes which likely reduces predation on ewes, and makes the effects of guard dogs less apparent. Guard dogs do not eliminate all depredation losses but significantly reduce them, and they are economically effective. On the basis of our data and opinions of producers, we

recommend guard dogs as essential components of sheep production in Colorado, especially to protect lambs against coyotes, to protect ewes and lambs against black bears, mountain lions, and domestic dogs, and especially for producers using open rangelands.

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Economics of grazing weeping lovegrass with stockers in the Southern Great Plains

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Abstract

Because of the relatively low cost of seed and ease of establishment, more than 0.4 million ha of weeping lovegrass (*Eragrostis curvula* (Shrad.) Nees.) were planted on Conservation Reserve Program (CRP) lands in the Southern High Plains. Dryland cropping alternatives including wheat and grain sorghum, give relatively low and variable economic returns. The objective of this study was to evaluate the economics of the lovegrass grazing alternative. Using a tract of weeping lovegrass in Curry County, N.M., animal performance and the economics of 5 grazing management treatments were evaluated, including 12-month and 6-month continuous grazing, seasonal grazing during only the spring and fall, and a 6-pasture rotation system. Fertilization of the pastures was also evaluated for the spring/fall grazing treatment. Average daily gain (ADG) for yearlings grazing weeping lovegrass pastures was found to decline rapidly as the grazing season progressed. The ADG was over 1.36 kg day⁻¹ in early May but gradually declined over the grazing season to less than 0.45 kg day⁻¹ by the end of August. To maximize profit, stocker cattle would be sold in early September. All of the grazing systems yielded similar net economic returns, but substantially higher economic returns could be made by adjusting stocking rates to market conditions. Returning CRP land to dryland cropping or grazing with stocker cattle was estimated to yield nearly identical economic returns. Neither growing traditional crops or grazing lovegrass pastures appear to be economically viable alternatives without government assistance programs in place.

Key Words: Conservation Reserve Program, *Eragrostis curvula* (Shrad.) Nees., forage quality, optimal stocking rates, dryland farming, grazing systems

One of the highest Conservation Reserve Program (CRP) participation rates in the nation was found in Eastern New Mexico and West Texas. Nearly one-fourth the cropland acreage in this region was planted to perennial grasses as a result of the CRP, a voluntary long-term cropland retirement program. Dryland farming in the area is risky with variable and limited profit potential. As reported by the New Mexico State University (NMSU) crop

Resumen

Debido a su habilidad de establecimiento y al bajo costo de la semilla, aproximadamente, 400,000 ha de Weeping Lovegrass (*Eragrostis curvula* (Shrad.) Nees.) fueron cultivadas en los terrenos del Conservation Reserve Program (CRP) en la planicie del Sur. En adición, cultivos como el Trigo y el Sorgo en zonas semidesérticas son asociados con pobres ganancias y tasas de retorno bajas. El objetivo fue evaluar la viabilidad económica del uso de Lovegrass en condiciones pastoreo con bovinos en Curry County, N.M. Los tratamientos fueron: 1) Pastoreo Continuo por 12 meses, 2) Pastoreo continuo por seis meses, 3) Pastoreo en Otoño, 4) Pastoreo en Primavera, y 5) Sistema rotacional de seis días. La ganancia de peso de los bovinos por día (GDP) pastoreando Weeping Lovegrass disminuyó rápidamente conforme avanzó la estación de pastoreo. La ganancia de peso fue 1.36 Kg/día a principios de Mayo y disminuyó gradualmente hasta .45 Kg/día a finales de Agosto. Para maximizar las ganancias los becerros destetados fueron vendidos a principios de Septiembre. Todos los sistemas de pastoreo produjeron retornos económicos similares. Sin embargo, la rentabilidad financiera pudiera incrementarse ajustando la carga animal a las condiciones del mercado. Retornos económicos similares fueron observados con cultivos de secano o pastoreo de bovinos en el CRP. El cultivo tradicional de granos y el pastoreo de Lovegrass con bovinos parecen ser sistemas de producción poco rentables sin el apoyo de programas de cooperación técnica del Estado.

cost and return series (Hawkes and Libbin 1997a, 1997b), return to land and risk was negative in 7 of the most recent 13 years in Quay County and 4 of 13 years in Curry County. With average New Mexico CRP program payments of \$94 ha⁻¹ (Osborn et al. 1995) many area farmers believed the CRP was a more profitable alternative and signed up for the program in the early years.

Because of its relatively low seeding cost and ease of establishment, weeping lovegrass (*Eragrostis curvula* (Shrad.) Nees.) was one of the most prevalent grass species planted on CRP land in the Southern Great Plains. It is a long-lived perennial bunchgrass that grows and produces well on a wide variety of soils. Lovegrass is an excellent soil stabilizer and is drought tolerant. But, weeping lovegrass is generally considered to be a poor forage for grazing livestock.

Under new guidelines and requirements for CRP participation (USDA-FSA 1997), many individuals who planted monocultures of weeping lovegrass, especially those with a tighter less erodible soil, were not renewed into the continuing CRP program (person-

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al communication Richard Shaw, USDA-NRCS, Clovis, N.M. Field Office, 18 August 1998). These producers must now decide the future use of their lands, and other CRP enrollees will eventually face similar decisions. A primary factor in this decision will be the relative productivity and profitability of using these lands for grazing versus converting back to crop production. The objective of this study was to evaluate the performance of stocker calves grazing weeping lovegrass under different management strategies. The economics of alternative grazing systems for lovegrass pastures are compared to traditional cropping alternatives.

Materials and Methods

Theoretical Grazing Concepts

As shown by Hildreth and Riewe (1963), Workman (1986) and Hart et al. (1988), determining the economically optimal (profit maximizing) grazing strategy means selecting the stocking rate and grazing system that maximizes net economic returns per ha for the defined price/cost situation. Defining this optimal grazing strategy requires definition of expected beef prices and costs over the planning period. It also requires definition of relevant biological input/output relationships using the production function. In defining the production function we use the standard definition of stocking rate to relate the total demand for forage to the area used to provide it. Stocking rate (SR) is defined to be the number of stocker cattle grazing per ha over a grazing period of length T (Vallentine 1990)¹.

In addition to the standard analysis of how SR affects animal performance and profit, an additional consideration is how declining forage quality affects livestock production and profitability. This would be especially important for a plant like weeping lovegrass where forage quality deteriorates quickly over the grazing season. Yet, few economic studies have considered forage quality when making man-

agement prescriptions. Huffaker and Wilen (1991) found that when nutrient deterioration of tall fescue pastures in Tennessee was high, an intensive early grazing strategy (IES) that doubled the conventional season-long stocking rate early and then rested the pasture with no stocking as forage nutrients began to play out would be economically optimal. If the grass cultivar exhibited low nutrient deterioration over the season then the conventional season-long grazing strategy outperformed the IES.

To consider both stocking rate and deterioration of forage quality over the grazing season, average daily gain (ADG) cannot be defined in the typical way, with an average rate of gain for the grazing season assumed, or with ADG considered to be a function of SR only (Workman 1986). Rather, diminished livestock gain must be explicitly recognized. There are at least 2 alternative ways to do this. First, the strategy used by Huffaker and Wilen (1991) can be employed with grazing animals allocated between pasture grazing and the next best feeding alternative. Depending on pasture production and forage quality, cattle are allocated between alternative feed sources so as to maximize profit. The second alternative, as used here, is to stock the pasture with animals at the start of the grazing season. All animals are then removed at some point once forage quality has deteriorated to an unacceptable level, or when a threshold amount of forage remains. Cattle could be sold at this point or they could be moved to alternative pastures or feedlots. Stocking rate of the pasture is a choice variable in the model and with adequate data to define input/output relationships the stocking rate used could be an economically optimal rate.

To develop the economic model, let average daily gain (ADG) be defined as a concave function of stocking rate (SR) and time of year (t), with deteriorating forage quality (Q) the factor reducing ADG over time.

$$ADG = f(SR, Q(t)), \quad (1)$$

with $f/ SR < 0$, $f/ Q > 0$ and $Q/ t < 0$ over the economically relevant range of production. Time (t) could also be used as a direct proxy for forage quality if recognition is given to the importance that forage quality has in determining livestock performance at different points in time. The time variable defines the day of the grazing season, either as the Julian date or as the elapsed number of days that stocker cattle have been in the pasture.

The total kg of beef sold per ha is defined by multiplying the number of ani-

mals grazing per ha times the average sale weight (W_s), less a market shrink:

$$b(SR, T) = SR \times W_s \times \left(1 - \frac{\% \text{ Shrink}}{100}\right) \quad (2)$$

The sale weight, given by $W_s = \left[W_p + \int_{t=1}^T f(SR, Q(t)) dt\right]$, is determined by the stocking rate decision. Increasing stocking rates will decrease ADG and sale weight, but except in the extreme, more beef will be produced per ha. Average sale weight will also depend on purchase weight (W_p) and the decision about when to market the cattle (i.e., the selection of sale period (T)). As the length of time cattle remain in the pasture is extended there will be a continued decrease in ADG because of declining forage quality.

Heavier feeder cattle generally sell for less per kg (Sartwelle et al. 1995). While sale price is determined by market forces outside the livestock producer's control, the producer determines which market price to accept by the size and type of cattle produced. Size of cattle depends on stocking rate and marketing decisions, such that in addition to market forces, sale price (P_s) is a function of SR, sale date and livestock characteristics;

$$P_s = g(W_s(SR, T), X) \quad (3)$$

where X is a vector of exogenous variables that identify relevant characteristics of the stockers at time of sale (e.g., breed, frame size, health, fill, sex, muscling).

The livestock producer selling in the competitive market is faced with the problem of choosing the stocking rate and sale date that maximizes profit, with profit defined to be the residual return to land and risk (\$/ha):

$$(SR, T) = g(W_s(SR, T), X) \times b(SR, T) - SR \left[P_p W_p + r \right] + \int_{t=1}^T C(t) dt - a \quad (4)$$

where P_p is stocker purchase price (\$/kg), $P_p W_p$ is per head animal purchase cost, and r is additional per head costs of receiving the cattle, including shipping, vaccinations, labor, and other miscellaneous charges. In addition to receiving costs (r) and fixed costs (a), there are additional daily costs [$C(t)$] to keep the stocker cattle in the pasture, like periodic checking of animals, supplemental feeds, salt, minerals, and a pasture charge (if the forage is leased on a per-head basis by the month). This daily cost may be different at different times of the year because of weather or pasture conditions. Further, pasture charges could be calculated on a cost per kg of gain. In this case, accumulated daily

¹The budget and design of the grazing trials conducted here did not allow us to compare net returns at alternative stocking rates (SR, i.e., animals ha⁻¹, animal days of grazing ha⁻¹) or grazing pressures (GP, i.e., animal or head days of grazing per unit of herbage produced). The economic model used to evaluate optimal grazing strategies is the same, however, with or without variation in stocking rate. In the more limited applications where SR is not a choice variable, grazing systems can only be compared at the rates used in the grazing trial.

costs would be defined as $\sum_{t=1}^T C(f(SR, Q(t)))$ and would add the complication that because average daily gain (ADG) declines with falling forage quality, grazing costs decrease as forage quality deteriorates over the grazing season.

Following the well known marginal principles of production economics, the profit maximizing stocking rate will occur when the last animal added to the pasture adds nothing to profit (Workman 1986). Similarly, the optimal time to sell the animals will occur when the value of the additional animal gain from keeping the animals another day is just equal to the marginal costs of keeping the animals that extra day. The economically optimal stocking rate and sale date will change as economic and pasture conditions change. See Torell et al. (1999) for a more detailed discussion of how economically optimal management strategies would be determined when declining forage quality is an important consideration.

Grazing Trials

A tract of weeping lovegrass in Curry County, N.M. that had been enrolled in the CRP was developed for a grazing trial in spring 1994. The tract site is approximately 24 km north of Clovis, N.M. on the Wayne Palla Farm. Soils are Pullman and Mansker loams. Mean annual precipitation in the area is 44 cm (NOAA Various issues).

From the time the weeping lovegrass cover was established in 1987, until spring 1994, the tract received no cultural management operations, except for a single mowing in 1988 to reduce competition from annual forbs. The entire tract was subjected to a controlled burn on 13 April 1994 to renovate the decadent grass stand. A 146 ha portion of the tract was selected for use as a grazing trial and was developed with a livestock watering system and cross-fenced with hi-tensile electric fencing.

The grazing area was divided into 10 pastures which consisted of 2 replications of 5 grazing management treatments: 1) 12-month continuous grazing (12-Mo), 2) 6-month continuous grazing (6-Mo), 3) grazing only during the spring and fall (S/F), 4) spring/fall grazing with fertilizer application (S/F w/F), and 5) a 6-pasture rotation scheme (Rot). The 12-Mo pastures were 24 ha in size, all others were 12 ha. Thus, for the continuous grazing treatments, grazing pressure was held constant by adjusting the acreage to accommodate the longer grazing season. The location of the individual grazing treatments did not change during the 3-year study period.

The 12-Mo treatment consisted of year-

round use of the available forage while the other treatments consisted of grazing during the spring, summer and fall months only. The planned objective of the continuous grazing treatments (12-Mo and 6-Mo) was to use a nearly constant stock density so as to fully utilize all available forage during the predetermined grazing period.

During the early part of the growing season (spring), stock density for the spring/fall grazing treatments (S/F and S/F w/F) was set at a high enough rate to utilize all available forage by mid- to late July. These pastures were then allowed to regrow for 3 to 4 weeks during the summer without grazing pressure. During this 3 to 4 week regrowth period, stocker cattle grazed an adjacent pasture of weeping lovegrass. For the S/F and S/F w/F treatments during the fall the stock density was set at one-half the rate used during the spring grazing period. The S/F w/F pastures received a broadcast application of urea fertilizer prior to the initiation of grazing each year. Application dates and rates were as follows: 3 June 1994, 38 kg ha⁻¹ N; 18 April 1995, 43 kg ha⁻¹ N; 9 July 1996, 50 kg ha⁻¹ N. As shown in Table 1, only minimal differences in stocking rates occurred between the fertilized and unfertilized S/F treatments, but there was unused forage at the end of the season on fertilized areas. Stocking rates could have been increased or the grazing season extended during the spring or fall period with fertilizer application.

The pastures utilized for the rotational grazing treatment were subdivided into 6 paddocks. In 1994, individual paddocks were grazed for a 21-day period. After all paddocks had been grazed once (by 19 October) the cattle were provided free access to the entire pasture. Individual paddocks were grazed for 3 to 7 days per rotation cycle in 1995. This shortened grazing cycle was used because the longer rotation did not result in adequate livestock performance and management adjustments were made during subsequent years. Due to the lack of available forage during the early part of 1996, the rotation grazing sequence was not initiated until 12 July. After that date, individual paddocks were grazed for 2 to 4 days each rotation cycle.

Pastures in the grazing study were burned in early April 1995 to even out differences in forage availability created by the 1994 grazing treatments. Many of the pastures did not burn completely, as there was insufficient fuel to carry the fire.

On 15 June 1994, 140 head of yearling crossbred heifers (average body weight 228 kg) were delivered to the grazing trial. The heifers which had been preconditioned in a lot at Dalhart, Tex., were sorted randomly into 10 uniform groups and placed on the individual grazing treatments. From 15 June to 9 November 1994 there was no supplemental feeding. From 9 November to 29 November cattle remaining for the continuous grazing treatment received a 37% protein block supplement (HI-PRO #1406, HI-PRO feeds, Friona, Tex.) at the rate of 0.5 kg head⁻¹

Table 1. Stocking rates of the CRP grazing trials, 1994-96.

Treatment	Treatment Description	Year	Dates Grazed	Stocking Rate (head/ha)
12-Mo	12 Month Continuous	1994	15 Jun. - 26 Jul.	0.412
		1995	9 May - 21 May	0.450
6-Mo	6 Month Continuous	1994	15 Jun. - 29 Nov.	0.823
		1995	9 May - 16 Nov.	0.914
		1996	4 Jun. - 14 Nov.	0.914
S/F	Spring/Fall	1994	15 Jun. - 27 Jul.	1.647
			7 Sep. - 29 Nov.	0.914
		1995	9 May - 26 Jul.	1.763
			23 Aug. - 16 Nov.	0.914
S/F w/F	Spring/Fall with Fertilizer		4 Jun. - 23 Jul.	1.763
			20 Aug. - 14 Nov.	0.951
		1994	15 Jun. - 27 Jul.	1.647
			7 Sep. - 29 Nov.	1.074
Rot	6-Pasture Rotation		9 May - 26 Jul.	1.763
			23 Aug. - 16 Nov.	0.914
		1996	4 Jun. - 23 Jul.	2.058
			20 Aug. - 14 Nov.	0.988
Rot	6-Pasture Rotation	1994	15 Jun. - 29 Nov.	0.823
		1995	9 May - 17 Oct.	1.299
		1996	4 Jun. - 14 Nov.	1.235

day⁻¹. From 29 November to 4 April 1995, heifers on the 12-Mo treatment received the equivalent of 0.86 kg of 37% protein block day⁻¹.

One-hundred eighty steers for the 1995 grazing trial were received from NMSU's Clayton Livestock Research Center (CLRC) on 9 May (average body weight 207 kg). One-half of the steers had been backgrounded on winter wheat; the other half had been backgrounded in a feedlot. Within each background group, steers were sorted randomly into 10 groups (grazing treatments). Supplemental feeding began on 5 December 1995. From that date until 22 January 1996, steers on the 12-Mo treatment received a 37% protein block supplement at a rate of 1 kg head⁻¹ day⁻¹. From 22 January until the steers were removed from the 12-Mo treatment on 1 May 1996, the rate of supplementation was 1.18 kg day⁻¹.

On 4 June 1996, 196 yearling steers of mixed breeding (average body weight 237 kg) were received at the grazing trial from the CLRC. As in 1995, one-half the steers came from a feedlot background; the other half came from winter wheat pasture. Steers from each background group were sorted randomly into the grazing treatments. The 12-Mo treatment was not included during 1996. Consequently, there was no supplemental feeding during the 1996 grazing season.

Animal body weights were recorded at 21-day intervals in 1994 and at 28-day intervals in 1995 and 1996, except during the winter months. Body weights for the heifers and steers on the 12-Mo treatment were not recorded at regular intervals once the cattle were removed from the other treatment groups. They were weighed again before sale in the spring.

At all times during the grazing trial, cattle were provided free access to white salt and 12:12 (Ca:P) mineral block (HI-PRO #1406, HI-PRO feeds, Friona, Tex.). The supplemental feeding of protein blocks was done 3 times per week.

In this analysis, an economic comparison is only made between grazing treatments at or near the level stocked in the grazing trials. Although the economic model has been developed to evaluate optimal stocking rates, SR is not a choice variable in this application. The stocking rates used for each treatment may or may not be an optimal rate for the defined price/cost situation. However, with the exception of the S/F w/F treatment, by the end of the grazing period, the weeping lovegrass pastures had little unused forage. A greatly increased stocking rate would not have been possible.

Grazing Data Statistical Analysis

Animal weights, recorded periodically throughout the grazing season, were used to evaluate animal performance under the various grazing treatments and at alternative times during the grazing season. Average daily gain was the key measure of production estimated by the grazing trial data. Other measures of animal performance including gain per ha, animal weights, and total beef production per ha were algebraically determined from the estimated average daily gain (ADG) function for the given stocking rate. The ADG at time *t* was computed for each animal by dividing the change in weight between weigh periods by the number of days between each weigh period. The mid-point between weigh dates was used to define the point in time of the calculation.

The computed ADG was used for regression analysis to estimate how ADG varied throughout the grazing season for the alternative grazing systems. Because stocking rate was not a variable considered in the grazing trials, SR was not included when estimating the ADG functions. Time was defined to be the number of days past 1 May (i.e. 15 May = 14, 31 July = 91). Dummy variables were also used to test for significant differences in ADG between years, between seasons, for the type of backgrounding used, and for fertilized versus unfertilized treatments. Only variables that were significant at the = 0.10 level were included in the final equations.

Economic Model Specification

Economic comparisons were made between stocker cattle grazing CRP land and representative dryland crops typically grown in Curry County and eastern Quay County, as reported in the NMSU crop cost and return estimate series. These comparisons were made for all years that the series had been published, 1984–96. Annual differences in beef price situations were used to compute a return to land and risk (RLR)² (\$ ha⁻¹) that could be compared to returns from traditional crop production alternatives.

Historically reported whole-farm RLR estimates were adjusted to constant 1996 real price levels using the unadjusted CPI for all urban consumers. Because variation

in prices and yields were explicitly considered in the annual crop cost and return series (Hawkes and Libbin 1997a, 1997b) both price and production risk were considered.

Crop subsidy payments are gradually being phased out (USDA-ERS 1996) and thus were not included in the net return comparison for future land use decisions. Government payments reported in the historical crop cost and return series were removed for this comparison.

In the beef production analysis, only the annual purchase price and sale price of beef were varied. Receiving costs, daily expenses, and overhead expenses, as further defined, remained unchanged at a level appropriate for the 1996–97 production years. The ADG and beef production per ha were defined by the estimated regression equations without a stochastic element. Thus, the stocker production analysis included only price risk. This is justified somewhat by the results of the 3-year grazing trial. For predicting ADG of all animals in the pasture, the 95% confidence interval for mean daily gain was relatively narrow (less than 0.05 kg day⁻¹ for all grazing treatments until late in the fall). Thus, the results of the grazing trials indicated that the mean ADG of grazing animals would be accurately estimated by the ADG function with a narrow confidence interval. The confidence interval for any one individual animal would of course be much wider.

The beef price models developed by Sartwelle et al. (1995, 1996a, 1996b) were used to relate purchase and selling price of calves and feeder steers to their weight (*w*). A reduced form of the Sartwelle et al. (1995) regression model that included only sale weight as the explanatory variable was used. By excluding other explanatory variables in the Sartwelle regression models, including lot size, health, breed, condition, and others, the assumption was made that the average effect of these other factors would be captured in the base price defined for the Clovis, N.M. market (Table 2). Purchase price (*P_p*) was based on 204 kg calves and sale price (*P_s*) on 295 kg feeder steers. A 3% sale shrink was assumed at the time of sale. The reduced beef price equations were defined as:

$$P_p = \text{Base}_c - 1.77 \times 10^{-3}(w - 204)^2 - 1.46 \times 10^{-6}(w^2 - 204^2) \quad (6a)$$

$$P_s = \text{Base}_f - 7.29 \times 10^{-5}(w - 295) - 7.29 \times 10^{-7}(w^2 - 295^2) \quad (6b)$$

Considering the 1995 average calf price (Base_c) at the Clovis, N.M. market of

²Return to land and risk is the residual return on the investment in the land, and for accepting the risk of the investment. All other production expenses and opportunity costs have been subtracted, including a return for management and operator labor, and for investments in cattle, crops, and machinery.

Table 2. Clovis, N.M. auction beef prices and weight adjusted purchase price (Pp), 1984-96.

Year	April Clovis Price (181-227 kg) ^a	P _p in equation 6a ^b	Aug. - Sept. Clovis Price (272-318 kg) ^c	Buy/Sell Price Differential ^d
	-----\$/kg-----			
1984	1.63	1.57	1.37	0.26
1985	1.76	1.70	1.28	0.48
1986	1.52	1.46	1.37	0.15
1987	1.94	1.87	1.70	0.24
1988	2.36	2.29	1.79	0.57
1989	2.27	2.20	1.90	0.37
1990	2.38	2.31	2.01	0.37
1991	2.60	2.54	1.83	0.77
1992	2.25	2.18	1.83	0.42
1993	2.29	2.23	1.94	0.35
1994	2.29	2.23	1.70	0.59
1995	1.92	1.86	1.39	0.53
1996	1.37	1.30	1.17	0.20

^aAverage monthly Clovis auction price reported for April and used to set base^c for stocker purchase prices in the Sartwell price model (Equation 6a).

^bPurchase price estimated for a 227 kg steer calf using the average April Clovis, N.M. price as the base.

^cAverage monthly Clovis, N.M. auction price reported for August and September. These prices were used to set base^f for stocker sale prices in the Sartwell price model (equation 6b). Estimated sale prices will be different for different grazing systems, sale weights and sale dates.

^dDifference between April 181-227 kg calf price and August/September 272-318 kg feeder steer price.

\$1.92 kg⁻¹ (Table 2), with a 227 kg animal purchased, the adjusted purchase price, using equation 6a, would be \$1.86 kg⁻¹. Using equation 6b, the computed sale price in the fall will be slightly less than the \$1.39 kg⁻¹ feeder cattle base price (Base_p) used in the analysis, depending on the sale date and sale weight.

Production expenses were estimated by considering the inputs necessary for the grazing trials, from published NMSU cost and return estimates for yearling producers in northeast New Mexico (Torell et al. 1998), and from dryland crop cost and return estimates prepared for Curry and Quay counties in eastern New Mexico (Hawkes and Libbin 1997b). It was estimated that in addition to the purchase of stocker calves (P_pW_p), a livestock producer could expect to spend about \$11 head⁻¹ for vaccinations, transportation and labor to receive the cattle (r). The daily expense [C(t)] of checking and caring for the cattle was estimated to be \$0.18 head⁻¹ day⁻¹ during the summer months, or about \$32 head⁻¹ for a 180-day grazing season. This would include labor, salt and minerals, and other miscellaneous expenses. During the winter months C(t) was estimated to more than double to \$0.47 head⁻¹ day⁻¹ because supplemental feeds must be fed [assumed 0.91 kg head⁻¹ day⁻¹ of cottonseed cake] and labor requirements are increased. An interest charge of approximately \$0.12 day⁻¹ was also added to C(t). This interest charge was calculated using a 9% annual interest rate (0.0247% daily rate) and was charged each day on the estimated market value of the animal at that point.

Hawkes and Libbin (1997b) estimate overhead expenses to be about \$34.50 per planted ha (excluding roads and homestead) for a typical 648 ha dryland farm in Curry County, N.M. and this same overhead expense was included for grazing options considered here. Overhead expenses include electricity, telephone, vehicle mileage, insurance, taxes, building repair and maintenance, and other miscellaneous expenses not associated with any specific crop or livestock enterprise. A management charge of 8.5% of gross livestock sales less purchased livestock and feed expenses was also included as a fixed expense item (Torell et al. 1998).

Weeping lovegrass pastures must be fenced and watered for grazing; a fixed charge for this was included as well. Fence costs were estimated with a 3-wire electric perimeter fence (\$884 km⁻¹) and 2-wire electric cross fencing (\$720 km⁻¹) for the 6-pasture rotation system, using USDA-NRCS statewide average costs (personal communication Joe Whitehead, USDA-NRCS, Clovis, N.M. Field Office, 18 August 1998). Assuming a square perimeter fence and a 10-year life, annual fence and water costs were estimated to be \$3.71 ha⁻¹ for the 6-pasture rotation system with cross fencing, and \$2.47 ha⁻¹ for other grazing systems that need only a perimeter fence.

Fertilizer application of about 45 kg ha⁻¹ N was applied to the S/F w/F at an approximate cost of \$20.50 ha⁻¹ with custom application. This amount was included as part of the fixed expense for the S/F w/F treatment.

It was assumed in the economic analysis that 227 kg steer calves would be purchased. Grazing dates used in the economic models were similar to those used in the grazing trials. They were different depending on the grazing system. For all grazing systems the assumed date when stockers entered the pasture was 1 May. The optimal sale date was calculated by the economic model for the continuous and 6-pasture rotation systems. For continuous grazing, stocking rate (SR) was set at 0.91 steers ha⁻¹ and all animals remained in the pasture until the economically optimal sale date. For rotational grazing the stocking rate was increased to 1.24 steers ha⁻¹.

Numerous marketing strategies are possible for the spring/fall (S/F) grazing treatment. First, following the strategy used in the grazing trials, stocker cattle could be grazed during both the spring and fall periods. This would require additional land for grazing when cattle are not on the treatment area or when SR is reduced on the pastures during the fall. In this case it was assumed that animals would graze the S/F treatment area from 1 May until 25 July at a stocking rate of 1.76 steers ha⁻¹. Over this period, animals are assumed to gain at the rates estimated by the S/F ADG function with the dummy variable DFALL= 0. Stockers are then moved to a different ungrazed weeping lovegrass pasture and stocked at the rate of the continuous grazing strategy. During this continuous grazing period, yearlings are assumed to gain at the rates defined by the continuous grazing average daily gain (ADG) function. Half of the stockers remain in the continuous grazing pasture and half of the animals are returned to the S/F treatment area on 27 August.

Different ADG functions are then used for the 2 groups of cattle and the fall dummy variable is set to one to reflect the fall season. Over the grazing season, a total of 0.81 ha would be needed to support the 1.76 steers ha⁻¹ initially stocked on the S/F treatment area. The stocking allowance for the total grazing season is then 1.14 ha steer⁻¹ (SR = 0.88 steers ha⁻¹).

As a second marketing strategy, the S/F grazing area could be stocked during the spring at the relatively heavy rate of 1.76 steers ha⁻¹ (as was done in the grazing trials). Animals could then be sold as they exited the S/F grazing area on 25 July. The important difference between S/F marketing alternatives is that additional land was allotted when the grazing season was extended to the fall period. Thus, production per ha is diminished as the grazing season is extended.

To evaluate the economic consequences of fertilizing the S/F treatment area, one scenario considered sale of stocker animals during the fall, similar to what was done in the grazing trials. Animals were assumed to be moved to an adjacent ungrazed weeping lovegrass pasture for a month during the summer. They were then reintroduced to the pasture on 27 August and grazed until the optimal sale date. This was the same rotation that was assumed with the S/F treatment with fall sale but included the additional ADG from the fertilization. Dummy variables for season of use and fertilization were appropriately adjusted for this analysis.

If stocker animals were not to be returned to the treatment area in the fall, extra forage would be available for grazing in the fertilized pastures during the spring and summer grazing periods. The stocking rate could be increased or the period of grazing extended. Thus, as a second marketing alternative for fertilized pastures, marketing in either late summer or fall (at the optimal date) without leaving the S/F w/F treatment area was also evaluated. That is to say, for the fertilized scenario the 25 July sale date restriction was removed and stocker animals were carried to the optimal sale date. The benefits of the fertilization in this case was the extra ADG and the extended grazing period.

The economic models developed for each grazing system are spreadsheet based. The spreadsheets incorporate the assumptions about prices, costs, and production strategies as described above. Sale weights, production per ha, and net returns per ha and per animal are computed for alternative sale dates and for the specified stocking rate. The affect of declining forage quality is directly incorporated into the economic models through the specification of the ADG function and other beef production functions.

Results

Livestock Response

Continuous grazing average daily gain (ADG) was estimated to decline as a quadratic function of time (Table 3). The estimated equation shows ADG would be negative after 11 November and reach a minimum of $-0.12 \text{ kg head}^{-1} \text{ day}^{-1}$ on 10 January. The 6-Mo and 12-Mo treatments were not statistically different. The year of treatment also did not have an effect.

The ADG function of the 6-pasture rotation treatment was similar to the continuous grazing function with ADG a quadrat-

Table 3. ADG functions estimated from grazing trials and used in economic stocking rate models.

Average Daily Gain (kg/head/day) ^a		
ADG = $f(t) = 1.8566 - 0.01547t + 0.000003t^2$	$R^2 = 0.59$	<u>Continuous Grazing</u>
(0.0496) ^b (0.00006) (0.00000173)	n = 742	
ADG = $f(t) = 1.4232 - 0.0101t + 1.0406\text{Dfall}$	$R^2 = 0.44$	<u>Spring/Fall Grazing</u>
(0.0919) (0.0015) (0.1853)	n = 602	
-0.0033tXDfall + 0.1267 Dfert		
(0.0018) (0.0372)		
ADG = $f(t) = 1.478 - 0.0117t + 0.0000267t^2$	$R^2 = 0.41$	<u>6-Pasture Rotation</u>
(0.1131) (0.0022) (0.00000978)	n = 345	
-0.3049D94		
(0.0537)		

^aThe equations for ADG were estimated from the grazing trial data using ordinary least squares regression. Sale weight, gain per ha, and beef production per ha were algebraically estimated from the ADG function, using the equations described above. The explanatory variables in the ADG equations are defined as follows:

t = time, number of days past 1 May.

Dfall = fall dummy variable, 1 if grazing period is fall and 0 if spring.

Dfert = fertilizer dummy variable, 1 if fertilized and 0 if not fertilized.

D94 = year dummy variable, 1 if year was 1994 and 0 otherwise.

^bThe standard error of the estimate is presented in parentheses.

ic function of time (Table 3). ADG was statistically less during 1994 as compared to 1995 and 1996 ($-0.30 \text{ kg head}^{-1} \text{ day}^{-1}$) as indicated by the statistical significance of the 1994 dummy variable (D94). The 21-day rotation used in 1994 was too long and negatively impacted livestock performance. All economic comparisons were made with D94 set at zero.

The ADG for the S/F treatment was found to be a linear function of time. The intercept was higher and the slope steeper during the fall grazing period. Fertilizer added $0.13 \text{ kg head}^{-1} \text{ day}^{-1}$ to ADG (Table 3). Beef production was 19 kg ha^{-1} more with the fertilizer application by the end of the spring grazing period on 25 July.

During the spring grazing period, the continuous grazing system was estimated to give the highest ADG, but this was at the lightest stocking rate of the 3 treatments. The ADG was $0.32 \text{ kg head}^{-1} \text{ day}^{-1}$ greater in early May for the continuous grazing system. There was no statistical difference between the gains obtained with 6-month versus 12-month continuous grazing.

With continuous grazing, beef production per ha reaches a maximum by early November when ADG reaches zero and then turns negative. The ADG did recover somewhat during the following spring, but beef production per ha remained below the November peak level. This means that to maximize profit, even if additional days of grazing were free, one would never carry stocker animals past early November, unless increasing beef prices were expected in the near future.

Because of the higher stocking rate and the improved ADG during the fall, beef production per ha would increase from a maximum of about 340 kg ha^{-1} with continuous grazing to about 450 kg ha^{-1} with

the 6-pasture rotation system. The doubling of stocking rate with the S/F treatment would increase maximum beef production to about 560 kg ha^{-1} if the animals were sold 25 July. If more land were allotted to carry the animals to the fall then beef production per ha would decline to below what could be produced with continuous grazing. This is because beef production is then spread over more acreage.

Economic Response

Grazing System Comparison

For the various price scenarios evaluated, the grazing system that maximized return to land and risk (RLR) varied between the continuous grazing system and the S/F w/F treatment with optimal sale³. In those years when feeder cattle prices were relatively high, and the spread between buy and sell prices was relatively narrow—years favorable for yearling stocker production—the S/F w/F with optimal sale yielded the highest RLR. During these years a relatively high return would be made of between \$35 and \$54 ha^{-1} (Table 4). In less favorable price years, the continuous system was economically best, but net returns would be negative in many of these unfavorable price years and the light stocking rate of the continuous system would minimize losses. In these years at least part of the fixed costs could be covered by using the continuous grazing system.

³While the designation of "optimal sale" has been used to differentiate this treatment from the treatment with a period of pasture rest during the summer, economically optimal sale dates are in early fall. The important distinction is that in this case animals would not be removed from the S/F pasture until sale at the optimal date.

Table 4. Economic results for alternative stocker grazing systems.

Year	Continuous	Rotation	S/F optimal sale	S/F with fall sale	S/F w/F optimal sale	S/F w/F fall sale	Optimal Grazing System ^a
RLR (\$ ha⁻¹)							
1984	1.93	-4.10	-9.14	-38.11	-4.12	-54.61	1.93
1985	-48.34	-70.49	-100.28	-60.98	-98.65	-77.88	-37.05
1986	23.04	24.40	31.54	-27.84	36.58	-44.36	36.58
1987	36.93	37.99	35.54	-24.95	53.82	-39.17	53.82
1988	-18.11	-37.57	-76.82	-52.64	-54.91	-66.29	-18.11
1989	30.28	26.21	8.65	-30.21	35.15	-43.18	35.15
1990	40.73	38.80	20.85	-26.23	51.94	-38.48	51.94
1991	-51.97	-83.86	-145.19	-69.53	-121.47	-82.94	-37.05
1992	15.59	7.31	-14.94	-36.68	8.79	-50.07	15.59
1993	38.68	36.95	21.66	-26.53	49.99	-39.25	49.99
1994	-30.63	-53.18	-94.70	-57.80	-76.42	-72.03	-30.63
1995	-46.71	-70.10	-104.41	-62.15	-98.50	-78.47	-37.05
1996	-3.41	-7.95	-6.67	-36.83	-9.06	-54.34	-3.41
Average	-0.92	-11.97	-33.38	-42.34	-17.45	-57.01	6.28
Optimal Sale Date							
1984	04-Sep	19-Sep	25-Jul	05-Aug	27-Aug	03-Aug	04-Sep
1985	01-Sep	13-Sep	25-Jul	16-Jul	24-Aug	29-Jul	None
1986	04-Sep	19-Sep	25-Jul	05-Aug	27-Aug	03-Aug	27-Aug
1987	14-Sep	07-Oct	25-Jul	18-Sep	02-Sep	24-Sep	02-Sep
1988	16-Sep	10-Oct	25-Jul	20-Sep	04-Sep	26-Sep	16-Sep
1989	18-Sep	15-Oct	25-Jul	22-Sep	05-Sep	29-Sep	05-Sep
1990	20-Sep	20-Oct	25-Jul	23-Sep	06-Sep	01-Oct	06-Sep
1991	18-Sep	12-Oct	25-Jul	21-Sep	04-Sep	27-Sep	None
1992	17-Sep	13-Oct	25-Jul	20-Sep	04-Sep	27-Sep	17-Sep
1993	19-Sep	17-Oct	25-Jul	22-Sep	05-Sep	29-Sep	05-Sep
1994	15-Sep	06-Oct	25-Jul	18-Sep	02-Sep	24-Sep	15-Sep
1995	05-Sep	20-Sep	25-Jul	06-Aug	28-Aug	15-Sep	None
1996	30-Aug	05-Sep	25-Jul	11-Jul	21-Aug	18-Jul	30-Aug
Optimal Sale Weight (kg head⁻¹)							
1984	357	343	311	318	338	328	357
1985	356	341	311	305	337	324	None
1986	357	343	311	318	338	328	338
1987	361	349	311	347	341	364	341
1988	362	350	311	348	341	366	362
1989	362	352	311	349	341	367	341
1990	362	352	311	349	342	368	342
1991	362	351	311	348	341	366	None
1992	362	351	311	348	341	366	362
1993	362	352	311	349	341	367	341
1994	361	349	311	347	341	364	361
1995	358	344	311	319	339	358	None
1996	355	338	311	302	336	317	355
Average	360	347	311	334	340	353	
Optimal Beef Production (kg ha⁻¹)							
1984	327	423	548	280	597	288	327
1985	326	421	548	269	595	286	None
1986	327	423	548	280	597	288	597
1987	330	431	548	301	600	315	600
1988	330	432	548	301	601	315	330
1989	332	433	548	302	601	316	601
1990	332	436	548	302	603	317	603
1991	332	432	548	302	601	315	None
1992	330	433	548	301	601	315	330
1993	332	435	548	302	601	316	601
1994	330	431	548	301	600	315	330
1995	327	424	548	280	598	310	None
1996	325	417	548	265	594	278	325
Average	329	429	548	291	599	306	

^aThe "Optimal Grazing System" column repeats production rates and returns for the grazing system that maximizes RLR for the specified price year (as shown by boxes). If economic losses exceed the assumed fixed costs (\$37.05 ha⁻¹) then not producing at all would minimize losses and this is the indicated optimal strategy for that year.

These 2 grazing strategies are very similar. By extending the grazing season to the optimal sale date, the S/F w/F grazing treatment is just like the continuous system, but at nearly twice the stocking rate. In fact, it is likely that the ADG differences are not the result of the grazing system but rather stocking rate differences. This is consistent with the findings of Hart et al. (1988). These authors found that 3 alternative grazing systems, including season-long continuous grazing, rotationally deferred grazing and short duration rotation, did not affect steer gains differentially when compared at the same stocking rates under proper management. It highlights that stocking rate (SR) needs to be a choice variable in the management decision.

There were 3 years (1985, 1991, and 1995) when beef prices were such that not producing at all and losing fixed costs (\$37 ha⁻¹) would have minimized losses (Table 4). Recognizing these years obviously take perfect foresight about future market conditions. Yet, even without this foresight, some generalizations and conclusions from the analysis are obvious. First, grazing weeping lovegrass pastures with yearlings is not an economically viable alternative, but if yearlings are grazed, the optimal grazing strategy for weeping lovegrass pastures is a continuous grazing scheme whereby stocker cattle enter the pasture and remain there until being sold in early September. This would be about a month earlier than when stockers are usually sold from native rangeland in New Mexico (Torell et al. 1998). Second, if yearlings are to be produced, annual planning and analysis will be required to evaluate economic feasibility, to determine whether to fertilize the pastures, and to set the annual stocking rate. Different production strategies and stocking rates should be used each year depending on market expectations. Forward contracting could potentially be very valuable in helping reduce price risk.

The net economic benefit of fertilizing the pastures was found to be variable. When market conditions were such that relatively heavy stocking rates were most profitable, fertilizing to facilitate stocking rate increases resulted in positive economic returns. As shown in Table 4, when the S/F w/F optimal sale was best (during the 1986, 1987, 1989, 1990, and 1993 price years) fertilization of the pasture resulted in an average RLR increase of \$11.56 ha⁻¹, relative to the lightly stocked continuous treatment without fertilizer. The annual

average percentage increase in RLR ranged from 29% to 45% during these years. However, during other years when the light stocking of the continuous treatment was economically optimal, fertilization of the pasture and management as S/F w/F optimal sale would result in an average loss of \$21.78 ha⁻¹, slightly more than the cost of the fertilizer and application.

In the grazing trials, cattle were removed from the S/F treatment area each year near the end of July. Yet, with fertilization it was felt that the grazing season could have been extended, and the economic analysis has considered that the season would be extended to the computed optimal sale date (Table 4). The relatively heavy stocking rate and extension of the sale date to late August or early September may not be possible during some years depending on rainfall and forage conditions, but this extended grazing season is important for realizing positive economic returns from the fertilizer treatment. For the S/F w/F treatment, if cattle were sold on 25 July instead of the optimal date, net returns would have been reduced by an average of \$16.25 ha⁻¹ over the 1984 to 1996 period.

Cropping Versus Grazing Comparison

Average New Mexico CRP program payments have been \$93.86 ha⁻¹ (Osborn et al. 1995), and the CRP clearly gave eastern New Mexico farmers a higher average rate of return than cropping alternatives. As a comparison, the CPI was used to adjust traditional dryland crop production returns, as reported in Hawkes and Libbin (1997a, 1997b) for the 1984–96 period, to constant 1996 levels. This analysis shows that with crop subsidy program payments in place, Eastern New Mexico dryland farmers had an average return of \$37 ha⁻¹ in Curry County and \$10 ha⁻¹ in Quay County (Fig. 1). If crop subsidy payments are removed, as they supposedly will be (USDA-ERS 1996), average returns over the 1984–96 period would have been -\$14.94 ha⁻¹ in Curry County and -\$25.30 ha⁻¹ in Quay County⁴. Positive returns would have been realized in only 4 of the 13 years in Curry County and 3 of the years in Quay County.

⁴This assumes no change in production practices and input use. It would be anticipated that without crop subsidies, crop supplies will decrease and prices will increase. For this to happen marginal producers must leave the business. This may well be dryland farms in the Southern Great Plains that are considered here.

Fig 1. Comparison of constant 1996 RLR (\$/ha) for traditional cropping alternatives, with and without price support payments, versus grazing weeping lovegrass pastures with yearling stockers.

Dryland farming in the Southern Great Plains has traditionally yielded relatively low rates of return and removal of crop subsidies would be expected to cause major changes in land use for these dryland farming areas.

Leaving weeping lovegrass pastures in place for yearling stocker production does not appear to provide a viable economic alternative either⁵. Average return to land and risk (RLR) from grazing yearlings with beef prices realized over the 1984–96 period was estimated to be \$6.28 ha⁻¹ if optimal production strategies were followed (Table 4). Net returns actually realized

will likely be less because the after-the-fact knowledge about fall sale prices, as used in the economic analysis, will not be available to farmers as they make annual production decisions. It is likely that realized net returns from grazing will be negative on average. This is similar to expectations for cropping alternatives without price supports. If the estimated average optimal RLR of \$6.28 ha⁻¹ were realized this would still be less than a 1% rate of return on an approximate \$494 ha⁻¹ average land investment value (personal communication, Trevor Ashby, Farm Credit Services, Clovis, N.M., 5 November 1998). Further, positive economic returns from yearling stocker production only occurred in 6 of the 13 years with optimal production (stocking rate) adjustments (Fig. 1). These stocking rate adjustments must be made to take advantage of favorable market conditions and to minimize losses during unfavorable conditions.

⁵This is not to say that grazing weeping lovegrass pastures with other animal classes would not be economically feasible. Using lovegrass in rotation with other native grass species or as a place to maintain brood animals may be feasible but these alternatives were not considered in this research.

tions if on average RLR is to remain positive. As shown in Table 4, no one grazing system (constant stocking rate) would have yielded an average positive RLR over the 1984-96 period.

Discussion

In hindsight, the decision to plant relatively low-cost weeping lovegrass when entering the CRP program was an economic mistake. New CRP enrollment guidelines (USDA-FSA 1997) have precluded many of these lovegrass pastures from continued enrollment in CRP because they do not provide the wildlife cover and habitat desired by the extended CRP program. Cropping alternatives look dismal without continued crop subsidies, and grazing the weeping lovegrass pastures with stocker cattle does not provide a viable economic alternative either.

Under provisions of the 1996 Federal Agriculture Improvement and Reform (FAIR) Act (P.L. 104-107) federal outlays to the farm sector will decline until 2002, after which they are scheduled to be eliminated. The FAIR Act removes the link between income support payments and farm prices by providing for 7 annual fixed but declining market transition payments (USDA-ERS 1996). Farmers in the Southern Great Plains, and other areas, will receive these payments regardless of whether they crop or graze the land, provided the acreage was included under previous farm programs.

With these market transition payments, or with continued CRP enrollment, farmers have government support until 2002. However, without CRP and without crop subsidies, dryland farmers in the Southern Great Plains face an increasingly uncertain future. Farmers have historically been willing to accept rates of return on investment that are unacceptable by standard investment criteria. As a group, farmers and ranchers are optimists who always believe the next season will be a good one. This analysis shows, however, that the free market commodity pricing proposed for the future will be especially hard on dryland farmers in the Southern Great Plains.

What is the future for these lands? Some have argued that great stretches of the arid, wind-swept Great Plains are not suited to conventional settlement, and never really were. They contend that only with ever expanding crop and water subsidy programs was cropping of these marginal lands possible, and that it is now time to

tear down the fences, replant native grasses and restock buffalo and other native species (Popper and Popper 1994, Matthews 1992). This research also finds that dryland farming in the Southern Great Plains is likely not economically sustainable without subsidy programs. It is widely believed that these government programs have been capitalized into land values as the continued perpetual existence of these programs came to be expected (Helmberger 1991). If elimination of these price support programs is in fact implemented, major market adjustments would be expected. Land values should fall and marginal farming areas should revert to rangeland and natural vegetation. Some believe that this transition would be desirable and that the Great Plains can provide sustainable income only by reverting to the natural rangeland vegetation and crops originally found on the prairies (Eisenberg 1989). The future use and management of these farming areas has major implications for rural communities and the people who live there.

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Effect of grazing on the population biology of *Phalaris aquatica*

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Abstract

To examine the effect of grazing and potential interactions among grazing and biological traits of plants, we studied patch dynamics, seed production, and seedling survival in a Mediterranean population of the perennial grass *Phalaris aquatica* L. in grazed and ungrazed plots in southern Spain. Grazing by cattle induced an important (70%) decrease in the abundance of plants over 4 growing seasons. In the ungrazed plots, abundance of plants remained stable. Within these plots there was some (30%) spatial replacement of plants. However, replacement was by tillering and not by genets, genetically different individuals produced from seeds. The lack of genet replacement within the ungrazed plots agrees with results on mortality of young plants that were obtained from an independent field experiment, in which 85–95% of plants in different cohorts died within 1 to 3 growing seasons. This mortality of seedlings and young plants was concentrated in summers, especially when drought was prolonged. In contrast, seed production was apparently not a limiting factor for plant recruitment in ungrazed plots as seed output of the perennial grass ($25,312 \pm 3,255$ seeds m^{-2}) was of the same magnitude as seed output in annual grasses that were abundant in the study site. Intensive grazing limited tiller production, patch size, and a summer drought limited recruitment of new adult individuals. These factors resulted in a low tolerance to episodes of high stocking rates from which the perennial grass was unable to recover.

Key Words: mediterranean grassland, overgrazing, perennial grasses, plant recruitment, seedlings survival, summer-drought

Mediterranean grasslands in Spain, California, Israel, and Australia are dominated by annuals (Rivas and Rivas 1963, Rossiter 1966, Gulmon 1977). In these grasslands perennial grasses are much less abundant. However, the latter species show potential for improving the value of grasslands for use by livestock because they have longer growing seasons than annuals (Joffe et al. 1987).

Much evidence supports the hypothesis that overgrazing and other human disturbances are major causes of scarcity of perennial grasses in these grasslands (Joffe et al 1987, Rossiter 1966, Stoddart et al. 1975). For instance, in Spain and elsewhere in the

Resumen

Para examinar el efecto del pastoreo y potenciales interacciones entre pastoreo y características biológicas de las plantas en una población del sur de España de la gramínea perenne *Phalaris aquatica* L., se ha estudiado la dinámica de manchas, la producción de semillas y la supervivencia de plántulas en parcelas pastadas y sin pastar. El pastoreo por ganado vacuno produjo importantes (70%) decrementos de abundancia a lo largo de 4 estaciones de crecimiento. En las parcelas no pastadas la abundancia de las plantas se mantuvo constante pero hubo algún (30%) recambio espacial de las plantas. Este recambio fue por ahijamiento y no por instalación de nuevos individuos. La falta de reemplazamiento de individuos genéticamente distintos en las parcelas no pastadas concuerda con los resultados sobre mortalidad de plantas jóvenes obtenidos en un experimento independiente. Entre el 85 y el 95% de las plantas jóvenes de distintas cohortes murieron durante 1 a 3 estaciones de crecimiento. Esta mortalidad se concentró durante el verano, especialmente cuando le sequía fue prolongada. Por el contrario la producción de semillas no fue, aparentemente, un factor limitante en las parcelas no pastadas ya que dicha producción (25.3 ± 3.255 semillas m^{-2}) fue de la misma magnitud que la producción de semillas de varias gramíneas anuales abundantes en el área de estudio. El efecto del intenso pastoreo limitando el ahijamiento y el tamaño de las manchas y el efecto de la sequía estival limitando el reclutamiento, resultaron en una baja tolerancia a episodios de altas presiones ganaderas de los que la gramínea perenne no pudo recuperarse.

Mediterranean basin, grazing has been continuously important for at least 7000 years (Naveh 1987). In California, overgrazing by livestock and an exceptional drought in the 1860s promoted expansion of annuals at the expense of perennial bunchgrasses (Huenneke 1989, Heady et al. 1991). In Israel, perennial grasses consistently decrease in grazed areas compared with adjacent ungrazed plots (Noy-Meir et al. 1989). However, little is known about the mechanisms implied in the decrease of perennial grasses. In this study we analyzed effects of grazing on vegetative growth and reproduction of a perennial grass, *Phalaris aquatica* L., which occurs in Mediterranean grasslands of southern Spain. We also studied the inherent rate of recruitment of new individuals in the population.

Materials and Methods

Farm description and management

The study was conducted on a representative farm in Sierra

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Morena, 30 km north of Seville, southern Spain (37°40'N, 5°59'W, 280 m above sea level), from 1988 through 1991. Climate was Mediterranean with 720 mm mean annual precipitation and 16°C mean annual temperature. Rainfall was concentrated from mid-September to mid-May and was usually negligible during the summer. However, the length of dry and wet periods varies greatly among years in this region (Ortega 1987). The vegetation was a holm oak savannah (40 trees ha⁻¹) with the understory dominated by annuals. The farm was dedicated to extensive beef cattle production with a total of 350 head of cattle on 1,200 ha of terrain. Cattle followed the breed composition of the major beef cattle of the region. Cows were of a local land race called Retinta and bulls were Retinta and Charolais. Cattle management followed the usual practices of the region. Animals were divided in lots with different composition (cows in pregnancy or lactation, dry cows, bulls, heifers) that moved rotationally among the 10 paddocks of different size (20–200 ha) in which the farm was divided. The number and kind of grazing animals in each paddock and the time they remained in them during each year did not depend on grassland offer but on other criteria such as facility for handling animals (Daza 1997). As a consequence, these parameters varied greatly among paddocks and from year to year. The paddocks that were closer to the headquarters often had high grazing intensity at peak intervals and were grazed by cows in late pregnancy and lactation because these paddocks were equipped with feedings troughs and animal health-care installations. Calves were born from September until January and the off-spring were usually sold at weaning.

Study site

The study was conducted in a paddock about 31 ha in size that was close to the headquarters. The terrain was flat and soils, derived from granite rock, were slightly acid. Grassland was composed of an annual sward dominated by the grasses *Bromus hordeaceus* L., *Agrostis pourretii* Willd., and *Vulpia geniculata* (L.) Link, the legume *Trifolium glomeratum* L., and the forbs *Chamaemelum mixtum* (L.) All. and *Leontodon longirostris* (Finch & P.D. Sell) Talavera. There were also interspersed patches of the perennial grass *Phalaris aquatica* L. This perennial grass was re-seeded in the paddock in 1968 with seeds collected from scattered individuals naturally occurring in the surrounding area (Joaquin Terceño personal

comm. 1987). There was also a 0.25 ha fenced plot, which excluded grazing, in the middle of the paddock. This plot was established 3 years before the beginning of our study. At this time, species composition inside and outside the fence was very similar (Joffre 1987).

Grazing treatment

The fenced plot continued ungrazed during the years of our study. For the rest of the paddock, information on the number and kind of animals, grazing season, supplementary feedings and animal care was obtained from the farmer (Miguel Huges personal comm. 1991 and 1999) and from personal observations during our visits to the field. From these data we calculated Cattle Units (C.U.) following recommendations of the French Institute of Agronomic Research (INRA), which are based on energy requirements of the animals (Jarrige 1990). A dry cow (500 kg) corresponded to 1 C.U., a cow in late pregnancy or lactation to 2 C.U., and a heifer (200 Kg) to 1.3 C.U. The stocking rate per month was calculated as the number of C.U. that grazed the paddock each month (during the grazing season) divided by the size (in ha) of the paddock. We also calculated the mean stocking rate per year as the stocking rate per month multiplied by the length (in months) of the grazing season and divided by 12 (number of months per year; Table 1).

Most animals that grazed our paddock were cows in late pregnancy and lactation, especially during the first 2 years of the study. This was due to the proximity to the headquarters and the facilities for supplementary feeding and vaccination of the offspring in the site. The herd size was similar in 1988 and 1989 but it was increased in 1990 and 1991 by adding 10 replacement heifers. Animals were usually

moved to the paddock in early-winter, except for the year 1990 when they were moved in mid-autumn. This year, cattle remained in the paddock for 8 months instead of the 3 or 4 months of the other years (1987, 1988, and 1991). As a result mean stocking rate per year was 3-fold higher in 1990 than in the other years. Animals were supplemented yearly with straw and dry fodder from November until February and were provided with salt.

Patch dynamics and seed production in *Phalaris aquatica*.

In December of 1987, 4 permanent transects, 0.6 m x 10 m, were established in the grasslands. Each transect was divided into 150, 20- x 20-cm cells. Transects were placed on a mixed sward with patches of *Phalaris* and some patches of annuals. Two transects were inside the fence and the others were outside it, about 30 m apart from the former transects. In winter of 1988, a presence-absence map of each transect was recorded by hand, based on visual observations. Cells in which 1 or more shoots of *Phalaris* occurred were considered as present, and cells with no shoots of the species as absent. Mapping was conducted twice a year (in winter and spring) until winter of 1991.

To study seed production, in summer of 1988 we chose at random 15 presence-cells within each transect. All the spikes of *Phalaris* produced inside each cell were marked and were measured for length. The number of seeds per spike was estimated using a regression equation of the number of seeds and the length of the spike (seeds/spike = 1.43 *length of the spike (in mm) + 26.23) ($r = 0.67$, $p < 0.01$). This equation was obtained on a set of 20 spikes that were collected close to the transects inside the fence. In the grazed transects, all spikes that were marked were

Table 1. Grazing treatment. The length of the grazing seasons, the number and kind of animals that grazed the paddock each year and the calculated stocking rates are indicated.

Year	Grazing season	Herd composition	Stocking rate per month ¹	Mean stocking rate per year ¹
------(C.U. ha ⁻¹)-----				
1988	Jan. - April	17 Lp. ² and lactation cows 10 dry cows	1.4	0.47
1989	Jan. - April	18 Lp. and lactation cows 8 dry cows	1.4	0.47
1990	Oct.- May	23 Lp. and lactation cows 4 dry cows 10 replacement heifers	2	1.35
1991	Jan.- March	21 Lp and lactation cows 5 dry cows 10 replacement heifers	1.9	0.47

¹Cattle Units, calculated by procedure of Jarrige (1990)

²Late pregnancy.

eaten by cattle before seed ripening. Thus, there was no seed input into the soil's seed bank in these transects, and the spikes produced within them were not considered in our study.

Plant recruitment

In November 1987, eight, 50 cm x 50 cm plots were established at regular intervals inside the fence. Plots were sown at 5,000 seeds m^{-2} with seeds of *Phalaris* that had been collected in spring at the site described above. Plots were free of patches of *Phalaris* or any other perennial before sowing and were about 30 m apart from the closest patches of the perennial grass. To avoid competition among young plants of *Phalaris* and annuals, we removed all seedlings of annuals by hand in early autumn, before sowing the perennial grass (treatment annuals-). In the other 4 plots, annual seedlings were not removed (treatment annuals+). At the end of the first growing season (May 1988), the number of individuals of *Phalaris* that were established in each plot was recorded (the 1988 cohort). The censuses were repeated at the beginning and at the end of the growing seasons of the next 3 years (1989–1991). Individuals of *Phalaris* occurring inside each plot were assumed to belong to the initial seedling cohort because the newly established plants did not produce seeds during our study, presumably because they were too young. Moreover, seed drop from nearby patches of *Phalaris* inside the plots was unlikely to occur because of the long distance. Inside the annuals- plots, competition among plants was assumed to be of low intensity because of the low density (100 seedlings m^{-2}) of the established individuals of *Phalaris* from the beginning of the study.

Most annuals + plots were destroyed by rodent mounds during the first winter and we had to discard these plots from the experiment. A new experiment was performed in autumn of 1990 using 8 new plots that were assigned to identical treatments as in the first experiment, and the individuals established from this sowing (the 1990 cohort) were similarly monitored.

Results

Annual rainfall and its distribution varied greatly among years (Fig. 1). Both 1988 and 1990 were wet years with 1454 and 1268 mm rainfall, respectively. However, in 1988, the dry season was very short (112 days), while in 1990 it was very long (169 days). The other 2 years,

Fig. 1. Frequency of *Phalaris* (presence cells/total number of cells) in grazed and ungrazed transects (each point represents the mean of 2 transects (SE bars). Bars indicate monthly rainfall.

1989 and 1991 were dry, with 553 and 585 mm of rainfall, respectively. The length of the dry season in 1989 was intermediate (130 days).

In the grazed transects, frequency of *Phalaris* (i.e., presence cells/total number of cells) decreased slowly from the beginning of the study until spring of 1990 (Fig. 1). However, frequency of the species decreased more rapidly (62% losses) in winter of 1991, after the intensification of grazing. In the ungrazed transects, frequency of *Phalaris* changed very little during the years of this study (Fig. 1). The majority (67%) of cells in which the species occurred in autumn of 1989 (class 1 cells) contained it also at the end of the study (Table 2). We called these cells "permanents." Losses of *Phalaris* from the rest of class 1 cells were compensated by colonization of new cells (class 2 to 7 cells). However, colonization was ephemeral and the species disappeared again from most of these cells. Similar patterns (i.e., ephemeral colonization of some cells) were found in the grazed transects. However, in the latter transects, colonization did not compensate losses of the species from class 1 cells and net changes in frequency were negative. Cell colonization took place in the border of permanent cells and was due to spread of vegetative

tillers. No seedlings of *Phalaris* were observed in the transects during our study.

Protected transects of *Phalaris* produced $25,312 \pm 3,255$ seeds m^{-2} (mean $\pm$ standard deviation) in 1988. Although seed output varied greatly among years and production in 1988 cannot be taken as an absolute value, we observed significant spike and seed production in *Phalaris* during the 4 years of this study.

Seedlings of *Phalaris* that were established in experimental plots in spring of 1988 (i.e., 1988 cohort) comprised 2% of the sown seeds. Seedlings that were established in spring of 1990 (i.e., 1990 cohort) comprised 1.5% and 0.9% of the seeds that were sown in the annuals - and annuals + plots. Seedling survival was very low in the 2 cohorts (Fig. 2). About 91% of the individuals of the 1988 cohort had died by the end of the experiment. The highest mortality (57%) was suffered during the first summer, when seedlings were very young. Mortality was lowest (7%) in the second summer when plants were older and drought length was intermediate. Mortality increased again (22%) the third summer when drought was the longest during the study period. During the last dry season, the majority of seedlings of the 1990 cohort died also. In this cohort mortality was moderately lower (83%)

Table 2. Number of cells in which *Phalaris* occurred at different times (presences). Class 1 are cells in which the species occurred at the beginning of the study. Class 2 are cells that were colonised by the species in spring of 1988 and so on. Values are total number of cells in fenced and grazed transects.

Cell class	1988		1989		1990		1991
	Winter	Spring	Winter	Spring	Winter	Spring	Winter
Fenced transects							
1	119	104	104	98	94	86	80
2	—	7	7	4	4	4	2
3	—	—	23	14	8	8	2
4	—	—	—	4	0	0	0
5	—	—	—	—	11	5	4
6	—	—	—	—	—	20	8
7	—	—	—	—	—	—	25
Grazed transects							
1	80	74	65	53	52	44	20
2	—	7	2	1	1	1	0
3	—	—	6	4	4	2	0
4	—	—	—	7	5	0	0
5	—	—	—	—	11	10	1
6	—	—	—	—	—	7	1
7	—	—	—	—	—	—	2

when annuals were removed from plots (annuals - plots) than when annuals were not removed (95% mortality in the annual + plots).

Discussion and Conclusions

The substantial decrease of *Phalaris* in grazed transects vs. the small changes that

occurred in transects protected from grazing (Fig. 1) are in agreement with patterns found in other Mediterranean grasslands where perennial grasses consistently decreased in areas grazed by cattle (Noy-Meir et al. 1989). Our results also agree with studies on the effect of general disturbances in grassland reducing locally the cover of perennial grasses (Gomez-García et al. 1995, McIntyre et al. 1995, Milton et

al. 1997). The delayed response to overgrazing in *Phalaris*, which decreased in abundance in the year after grazing intensification, has been also found in other perennial grasses in Mediterranean and semiarid grasslands. This delay is probably related to a decrease of energy reserves stored by plants which decrease regrowth of new tillers in autumn (Trlica and Cook 1972, Singh et al. 1980).

During the years of this study, there was some (30%) spatial replacement of plants of *Phalaris* within the transects, with ephemeral colonization of cells adjacent to permanent cells (i.e., cells in which the species occurred from the beginning of the study until the end). This replacement was among ramets, the vegetative tillers that were presumably produced from below-ground plant parts (rhizomes and crowns) rooted in permanent cells. However, there was no replacement associated with new genets, the genetically different individuals produced from seeds, because no seedlings of *Phalaris* were found in any transect.

In the grazed transects, lack of seedlings could be explained by almost complete consumption of *Phalaris* spikes by cattle before seed dispersal, effectively preventing seed input to the soil. However, seedlings were also absent in protected transects although *Phalaris* plants produced and dispersed abundant seeds each year. In 1988, seed output of *Phalaris* ($25,312 \pm 3,255$ seeds m^{-2}) was similar to seed output of representative annual grasses abundant in the study site. For instance, *Bromus hordeaceus*, an annual grass of similar seed size as *Phalaris*, produced $53,434 \pm 2,138$ seeds m^{-2} and *Vulpia geniculata* $30,308 \pm 2,150$ seeds m^{-2} (Leiva 1992). Lack of seedlings and young plants of *Phalaris* in protected transects disagree with results of our experiment on plant recruitment, in which we did find 1- to 3-year old plants of this species (Fig. 2). Thus, seedlings and young plants of *Phalaris* could have been underestimated in protected transects because of accumulated litter and green biomass, which made it difficult to find tiny plants. Potential underestimation of young plants, however, does not substantially change our conclusion on the scarcity of genet replacement even in protected transects, since the summer mortality (85-95%) of young plants of *Phalaris* observed in the plant recruitment experiment indicated a low probability for individuals to reach maturity (Fig. 2). The low tolerance to summer drought that we found in young *Phalaris* plants is in agreement with observed influence of summer

Fig. 2. Survival curves of cohorts of seedlings of *Phalaris* (each point represents the mean of 4 replicates (SE bars). Annuals - and annuals + indicate treatments for 1990-cohorts. Monthly rainfall as in Figure 1.

drought on seedling survival in many species in other Mediterranean ecosystems (Horton and Kraebel 1955, Keeley and Zedler 1978, Aschman 1984, Frazer and Davis 1988). Populations of herbaceous perennials have been considered to be at a regressive stage when they have lost their ability to produce seeds and replace genets (Harper 1977). This stage can also be reached if, as in our case, mortality of young plants is very high and there is a lack of recruitment of adult plants. Mediterranean populations of some endangered plants that fail in recruitment of new individuals also show high sensitivity to grazing (Aparicio and Guisande 1997).

We conclude that in the Mediterranean population of *Phalaris* studied, grazing decreased tiller production and patch size. Summer drought limited recruitment of new adult individuals, resulting in a low tolerance to episodes of heavy grazing from which the perennial grass was unable to recover. Recovery could have been higher under more favorable climatic and edaphic conditions. We propose that, in any given habitat, a grazing intensity should be considered as overgrazing if it promotes irreversible declines in populations. Thus, the threshold level of overgrazing is species and habitat dependent.

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Forage removal and grazing time of cattle on small paddocks

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Abstract

Animals used in grazing trials with small paddocks usually have not been exposed to the experimental site and related research procedures. Grazing trials conducted in May and August 1996 on smooth brome grass (*Bromus inermis* Leyss.) quantified forage removal and grazing time of heifers adapted or not adapted to small paddocks. Treatments consisted of adapting heifers for 4 days to small paddocks (0.054 ha) and a control treatment of heifers continuously stocked in larger paddocks (>16 ha). On day 5, each group of heifers was moved to similar small paddocks and forage utilization and cattle grazing times were measured after 4 and 24 hours of grazing. In May, when sward structure was comparable in the large and small paddocks, tiller height reduction, leaf length reduction, herbage biomass reduction, and grazing time were similar ($P > 0.10$) for experienced and inexperienced heifers after 4 and 24 hours of exposure to day-5 paddocks. In August, when sward structure differed between the large and small paddocks, leaf length reduction after 4 hours was greater ($P < 0.10$) by experienced cattle than inexperienced cattle. Herbage reduction in August by experienced cattle was 435 kg ha^{-1} greater ($P < 0.05$) than by inexperienced cattle after 24 hours. Cumulative grazing time was 76 minutes ($P < 0.10$) greater at 4 hours for the experienced cattle than the inexperienced cattle. Grazing animals appear to adapt immediately to small paddocks but other unfamiliar grazing conditions, e.g., sward structure, may require short adaptation periods for experimental animals.

Key Words: grazing trials, ingestive behavior, sward structure

Reliability of information from grazing management research depends in part on the ingestive behavior of the experimental animals. Grazing trials commonly are conducted in small paddocks (<0.5 ha) with high stock densities and short grazing periods (Binnie and Chestnutt 1991, Howard et al. 1992, Forbes and Coleman 1993). Small paddocks greatly reduce logistic and funding requirements and allow researchers to implement studies in which confounding variables can be controlled more effectively. Investigators generally assume that ingestive behavior of grazing animals is not affected by paddock size, periodic movement in and out of small paddocks, or experience with different sward

Resumen

Los animales utilizados en experimentos de apacentamiento con potreros pequeños usualmente no han sido expuestos al sitio experimental y los procedimientos de investigación relacionados. En ensayos de apacentamiento, conducidos en mayo y agosto de 1996 en praderas de "Smooth brome grass" (*Bromus inermis* Leyss.), se cuantificó la remoción de forraje y el tiempo de apacentamiento de vaquillas adaptadas y no adaptadas a potreros pequeños. Los tratamientos consistieron en adaptar las vaquillas a potreros pequeños (0.54 ha) durante un periodo de 4 días y un tratamiento control de vaquillas que habían apacentado continuamente en potreros grandes (> 16 ha). En el día 5, cada grupo de vaquillas se movió a potreros pequeños similares y después de 4 y 24 horas de apacentamiento se midió la utilización de forraje y los tiempos de apacentamiento. En Mayo, cuando la estructura de la pradera fue similar en los potreros grandes y pequeños, la reducción de altura de los hijuelos, la reducción de la longitud de las hojas, la reducción de biomasa del forraje y el tiempo de apacentamiento fueron similares ($P > 0.01$) tanto para las vacas experimentadas como las vacas inexpertas a las 4 y 24 horas de exposición en el día 5. En Agosto, cuando la estructura de la pradera difirió entre los potreros grandes y pequeños, la reducción de la longitud de la hoja a las 4 horas fue mayor ($P < 0.10$) con el ganado experimentado que con el ganado inexperto. Después de 24 horas, la reducción de forraje por el ganado experimentado fue 435 kg ha^{-1} mayor ($P < 0.01$) que la reducción ocasionada por el ganado sin experiencia. A las 4 horas, el tiempo acumulado de apacentamiento del ganado experimentado fue 76 minutos ($P < 0.01$) mayor que el tiempo del ganado inexperto. Los animales en apacentamiento parecen adaptarse inmediatamente a los potreros pequeños, pero ante otras condiciones de apacentamiento desconocidas, por ejemplo, la estructura de la pradera, los animales experimentales puede requerir de pequeños periodos de adaptación.

structures. As a consequence, animals used in trials with small paddocks often lack experience or adaptation to grazing conditions in small paddocks. Various researchers (Forbes and Hodgson 1985, Bailey et al. 1989, Dougherty et al. 1992, Krysl and Hess 1993) have questioned experimental procedures that do not allow for exposure of animals to conditions unique to the experimental design prior to initiation of a grazing trial.

Information is lacking on grazing animal response to small experimental paddocks that could influence results. The objective of this study was to quantify forage removal and grazing time of cattle that were either adapted or not adapted to small paddocks (0.054 ha).

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Study Site

Research was conducted at the University of Nebraska's Agricultural Research and Development Center, located 45 km northeast of Lincoln, Neb. (41°10'N, 96°25'W) at an elevation of 350 m. Soils are Sharpsburg silty clay loams (fine smectitic mesic Typic Argiudolls) derived from loess materials and with 0 to 2% slopes. The climate is continental. Long-term average annual precipitation at the research site is 68 cm with 50 cm as rain during the growing season from 1 April to 30 September. Annual precipitation in 1996 was 69 cm with 57 cm coming during the growing season.

The study was conducted in a 2-ha, rectangular pasture with a smooth brome grass (*Bromus inermis* Leyss.) monoculture and bordered by 4 rows of mature, eastern redcedar (*Juniperus virginiana* L.) trees on the north and south perimeters. The experimental site was cut for hay in 1995 and fertilized on 23 February 1996 with ammonium nitrate (34-0-0) at 18 kg N ha⁻¹. Pretreatment management resulted in a rapidly growing sward that was free of standing dead residue in spring 1996. Six small paddocks (0.054 ha) were fenced at each end of the 2-ha pasture. Hereafter, these paddocks are referred to as day-5 paddocks. Distance between these 2 sets of paddocks was a minimum of 300 m.

Methods

Two grazing trials, each lasting 18 days, were conducted from 7 to 24 May (Trial 1) and 31 July to 16 August 1996 (Trial 2). Each trial was a randomized complete block design with cattle allotted to 6 replications of 2 treatments consisting of animals experienced or inexperienced with daily rotation among small paddocks. Source of cattle was a herd of 48 yearling heifers of MARC III breeding (1/4 Hereford, 1/4 Angus, 1/4 Red Poll, and 1/4 Penzguar). The heifers were born in spring 1995 and had grazed the surrounding pastures of smooth brome grass, ranging from 16 to 25 ha in area, since birth.

On the first day of each 18-day trial, heifers were allocated randomly in groups of 8 to the 6 replications and kept in separate pastures of 16 ha or larger. Following the first day, a new replication of animals was selected randomly every other day to begin a 4-day adaptation period. Four of 8 heifers per replication were left in their assigned larger paddock until day 5. The other 4 heifers were moved to adaptation

paddocks and rotated daily through 1 of 6 sets of 4 ungrazed, contiguous 0.054-ha paddocks that were isolated from the day-5 paddocks. At 0700 hours on day 5, the 2 treatment groups were placed at opposite ends of the 2-ha pasture in the day-5 paddocks. Each group remained in its respective paddock until 0700 hours of day 6 when they were moved off the study site. All plant and animal data used to determine heifers response to adaptation were collected in the day-5 paddocks.

Starting date for each replication of heifers was staggered to maintain treatment independence and avoid social interaction among treatment groups while in the day-5 paddocks. The adaptation paddocks were out-of-sight of the day-5 paddocks either south of the redcedar rows or in the area between the day-5 paddocks. Overall, the experimental protocol assured minimal disturbance of the experimental animals caused by animal movement or proximity to other groups of grazing animals. Similar trials conducted in 1995 on warm-season, tallgrass pasture (Broweleit 1997) indicated that proximity of treatment groups to each other likely affects ingestive behavior.

At the initiation of Trial 1, swards in all paddocks were similar and in a vegetative stage of growth. Smooth brome grass grew rapidly during Trial 1 and swards progressed from an early elongation stage to a 3-node stage by the end of Trial 1. Average tiller height and leaf length at the beginning of Trial 1 (10 May) was 27 and 59 cm, respectively. By the end of Trial 1, mean tiller height and leaf length was 44 and 72 cm, respectively.

Trial 2 exposed cattle to a structurally-unique sward in small paddocks. The monoculture of smooth brome in the day-5 and adaptation paddocks was mowed to a height of approximately 20 cm in June 1996, and then allowed to regrow until August. The sward consisted of new tillers that initiated after mowing and a layer of stubble about 20 cm tall. The larger pastures grazed by the inexperienced animals until day 5 of a grazing period had not been mowed and lacked the stubble layer.

Live weight of cattle averaged 308 kg head⁻¹ (± 11.9 kg) and 343 kg head⁻¹ (± 9.3 kg) for Trials 1 and 2, respectively. Mean standing crop biomass, on a dry matter (DM) basis, at the beginning of Trial 1 was 3,690 kg ha⁻¹ (± 139 kg). Standing crop was estimated by clipping vegetation at ground level from 20 quadrats (0.56 m²) randomly located across the day-5 paddocks. Clipped samples were dried at 65°C to a constant weight in a forced-air

oven, and weighed. Herbage allowance was 74 kg DM per animal unit day (AUD⁻¹) and stocking density was 75 yearlings ha⁻¹. At the beginning of Trial 2, mean standing crop biomass was 4,180 kg ha⁻¹ (± 152 kg). Of the available standing crop in Trial 2, an estimated 30% was vegetative regrowth and 70% consisted of stubble that remained following mowing in June. Allowance of vegetative regrowth was about 22.55 kg DM AUD⁻¹. These sward composition estimates were determined at the beginning of Trial 2 by the same quadrat method as used in Trial 1. Tillers from the clip samples were hand separated into vegetative regrowth and stubble fractions before drying and weighing.

All heifers in Trial 1 were implanted with norgestomet (Merial Limited, Iselin, N.J.) at the initiation of the 4-day adaptation period of each replication to reduce reproductive function and estrous activity during the trial. Heifers used in Trial 2 were in their first trimester of pregnancy and did not exhibit estrous behavior. Heifers used on both grazing trials were accustomed to handling as would be typical on many experiment stations. Efforts were made during the months prior to the trials to minimize the number of times these animals were taken off pasture and placed in corrals. All supplemental feeding had ceased 21 days prior to initiation of Trial 1.

At the beginning of each 4-day adaptation period, 2 heifers were selected randomly from each treatment group, fitted with 8-day vibracorders (Stobbs 1970, Walker and Heitschmidt 1989), and allowed to adapt to the vibracorders until day 5 when grazing time was measured. Data from the recording disc in a vibracorder were interpreted as to the amount of total grazing time within each 30-minute period. Grazing time for contiguous sets of 2-hour intervals up to 24 hours were summed on day 5 to compute cumulative grazing time. Interval grazing time was based on amount of grazing time in each 2-hour period within the 24 hours on day 5 and was used to determine when grazing time responses occurred.

Tiller height reduction and leaf lamina length reduction of smooth brome grass on day 5 were estimated based on measuring 60 marked tillers in each paddock. On day 4 of each grazing period, 20 tillers were located along each of three, 20-m transects in each day-5 paddock. Tillers were marked with colored wire and tiller height and total length of leaf lamina were measured. Tiller height was measured from the base of the tiller at ground level to the

highest point on the tiller with leaves extended upward (Briske and Stuth 1982). Leaf lamina length was measured from the tip of the leaf blade to the collar of each leaf (Curl and Wilkins 1982). Measurements were taken again at 4 and 24 hours after movement into the day-5 paddocks. Marked tillers in Trial 2 were classified as either stubble or vegetative regrowth and were located alternately along 3 transects in each day-5 paddock.

Herbage removal by the grazing animals was estimated by clipping standing crop biomass in 8 large quadrats using a flail harvester before and after 24 hours of grazing in each of the day-5 paddocks (Matches 1966). Quadrat size was 0.9 m wide and quadrat length was variable but averaged 3.0 m. The length of each quadrat was measured immediately after clipping. Clipping height was about 10 cm. Subsamples were taken of the harvested material and dried at 65°C in a forced-air oven to a constant weight to estimate DM yields of the herbage.

Data were analyzed using the Statistical Analysis System (SAS Institute 1994) generalized linear models (GLM) procedures. The experimental unit was the day-5 paddock. Treatment means from each day-5 paddock for tiller height reduction, leaf lamina reduction, grazing time, and herbage biomass reduction were used as observations for the analysis, and were evaluated separately by analysis of variance using a randomized complete block design. A separate analysis of variance was conducted on data for each trial. When significant treatment differences ($P < 0.10$) were indicated by F-tests, treatment means were compared using least significant differences.

Results and Discussion

Trial 1

Tiller height reduction by experienced and inexperienced cattle in the day-5 paddocks did not differ in Trial 1 at 4 hours ($P = 0.46$) or at 24 hours ($P = 0.31$; Table 1). Leaf lamina length reduction also was not different between treatments at either 4 hours ($P = 0.64$) or 24 hours ($P = 0.42$). There was no treatment difference ($P = 0.26$) in reduction of standing herbage biomass over the 24-hour period. Grazing times did not differ between treatments for either cumulative grazing time ($P = 0.97$) or for any of the 2-hour intervals ($P > 0.10$; Fig. 1).

Cattle adapted readily to small paddocks when sward structure was homogeneous and similar to previous grazing conditions.

Fig. 1. Grazing time in 2-hour intervals for a 24-hour period beginning at 0700 hours on day 5 for heifers experienced or not experienced with small paddocks in May 1996. There were no differences ($P > 0.10$) between treatment means for any intervals during the 24-hour period.

Growing conditions during Trial 1 favored rapid vegetative growth of the bromegrass sward that was similar for both the day 1 through day 4 small paddocks grazed by the experienced heifers and the larger pastures where the inexperienced cattle grazed from day 1 through 4. Herbage allowance also was relatively high (72 kg DM AUD⁻¹) which provided an abundance of good quality forage.

Trial 2

In Trial 2, tiller height ($P = 0.11$) and leaf lamina length ($P = 0.07$) were reduced

more in the first 4 hours on the day-5 paddocks by experienced than by inexperienced heifers (Table 1). The 24-hour measurements of these variables, however, were not different ($P = 0.14$ and $P = 0.34$, respectively) between treatments (Table 2). Experienced heifers removed more ($P = 0.03$) standing herbage biomass after 24 hours of grazing than did inexperienced heifers.

Tiller height ($P = 0.027$) and leaf lamina length ($P = 0.006$) were reduced more on vegetative regrowth tillers than on stubble tillers after 24 hours of grazing (Table 2).

Table 1. Mean reduction ($\pm$ SE) in tiller height, leaf lamina length, and standing herbage biomass in a smooth bromegrass pasture grazed by heifers experienced or not experienced with the grazing environment in May 1996 (Trial 1) and August 1996 (Trial 2).

Treatment	Reduction				Biomass
	Tiller height		Leaf lamina length		
	4 h	24 h	4 h	24 h	
	----- (cm) -----				
Trial 1					--- (kg ha ⁻¹)---
Experienced	2.1 ^a ± 0.46	8.2 ^a ± 1.05	7.1 ^a ± 1.34	27.0 ^a ± 3.17	617 ^a ± 147
Not experienced	1.6 ^a ± 0.46	6.1 ^a ± 0.43	6.1 ^a ± 1.85	23.7 ^a ± 1.51	872 ^a ± 236
Trial 2					
Experienced	3.4 ^a ± 0.77	6.8 ^a ± 1.12	9.6 ^a ± 1.79	17.8 ^a ± 2.62	972 ^a ± 164
Not experienced	1.7 ^a ± 0.49	5.3 ^a ± 0.81	5.0 ^b ± 1.49	15.3 ^a ± 2.61	537 ^b ± 196

^{ab}Different letters in a column within a trial indicate means are different ($P < 0.10$).

Table 2. Mean ($\pm$ SE) tiller height and leaf length reduction for vegetative regrowth and stubble tillers in smooth brome grass paddocks grazed by heifers during August 1996 (Trial 2).

Tiller type	Beginning tiller height	Tiller height reduction		Beginning leaf length	Leaf length reduction	
		4 h	24 h		4 h	24 h
Vegetative regrowth	19.8	3.0a $\pm$ 0.33	7.1a $\pm$ 0.43	43.8	9.0a $\pm$ 0.96	21.0a $\pm$ 1.24
Stubble	25.2	2.2a $\pm$ 0.32	5.0b $\pm$ 0.43	27.2	5.6b $\pm$ 0.87	12.1b $\pm$ 1.14

^{ab} Different letters in a column indicate means are different ($P < 0.10$).

Differences between vegetative regrowth and stubble tillers after 4 hours of exposure to grazing were detected ($P = 0.068$) only for leaf length. Both experienced and inexperienced heifers preferred the vegetative regrowth over the stubble as the vegetative regrowth tillers were defoliated most frequently ($P < 0.001$). There was no interaction between treatment and tiller type as both experienced and inexperienced heifers defoliated marked tillers at similar frequencies ($P > 0.10$).

During the first 2 hours (0700–0900 hours) following rotation onto the day-5 paddocks, experienced heifers spent 64 minutes more ($P = 0.002$) time grazing than did inexperienced heifers (Fig. 2). For each remaining 2-hour interval of the

24 hours, grazing time for experienced and inexperienced heifers did not differ ($P > 0.10$). Although grazing time did not differ during any of the remaining 2-hour time intervals, cumulative grazing time over the first 8 hours was 50% greater ($P < 0.10$) for the experienced heifers than for the inexperienced heifers. A minimum difference of 64 minutes in grazing time was maintained between treatments throughout the 24 hours; however, cumulative grazing time did not differ ($P = 0.33$) from 8 hours into the trial until the end. Overall, the heifers adapted to novel conditions rapidly and 8 hours appeared to be adequate as an adaptation period for this unique sward; however, estimates of forage removal and grazing time were not collected beyond 24 hours.

Mean grazing time in Trial 2 was about 3 hours greater than in Trial 1. Increased grazing time in Trial 2 may have been related to the relatively low availability of palatable forage. Mean biomass of standing herbage before grazing on the day-5 paddocks was 490 kg ha⁻¹ greater for Trial 2 than for Trial 1; however, 70% of the total biomass in Trial 2 consisted of dry, mature brome grass stubble that was considerably less palatable than the green regrowth. Allowance of vegetative regrowth was relatively low (22.5 kg DM AUD⁻¹) in the small paddocks and may have resulted in a lower intake rate. Furthermore, the vibracorder method used to estimate grazing time did not discriminate between actual grazing time and search time (Stobbs 1970). We observed the heifers spending a high proportion of their time in Trial 2 with their heads down searching for palatable forage rather than continuously prehending forage. Jamieson and Hodgson (1979) and Hodgson (1981) also reported longer grazing times for cattle grazing stands of mature grass.

Differences in sward structure and forage allowance in Trial 2 were created by mowing spring growth in adaptation and day-5 paddocks after stem elongation was complete. The resulting layer of brome grass stubble probably restricted grazing of the highly palatable young tillers that regrew after mowing, similar to the pseudostem barrier described by Barthram and Grant (1984). Until day 5, inexperienced cattle grazed in larger pastures where the sward consisted of smooth brome grass that was allowed to regrow for 45 days following moderate spring defoliation through mid-June by mature cattle. The larger pastures were not altered by mowing prior to Trial 2. Treatment differences in the measured vegetation variables may have been due to the inability of inexperienced animals to adjust immediately to the unfamiliar sward structure and (or) low forage allowance within the small paddocks.

In summary, cattle readily adjusted to small paddocks in Trial 1 when forage resource characteristics were similar to those of the larger pastures and required

Fig. 2. Grazing time in 2-hour intervals for a 24-hour period beginning at 0700 hours on day 5 for heifers experienced or not experienced with small paddocks in August 1996. There was a difference ($P = 0.002$) between treatment means for the first 2-hour interval (0700 to 0900 hours) only; grazing time in all other intervals were not different. Cumulative grazing time during the first 8 hours was higher ($P < 0.10$) for experienced than inexperienced heifers.

only 8 hours in Trial 2 when sward structure in the small paddocks was unique and heterogeneous. Even though the cattle adapted readily to new grazing conditions, we concluded that an adaptation period should be used when research protocols involve novel grazing conditions and short grazing periods of 24 hours or less.

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Elk presence inside various-sized cattle exclosures

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Abstract

Accurate measures of the relative resource impacts from elk (*Cervus elaphus*) and cattle (*Bos taurus* and *B. indicus*) improve land management planning wherever these species cohabitate. Comparisons of utilization inside and outside cattle exclosures are often used for this purpose. The objectives of our study were to determine if (1) elk presence differed inside and adjacent to several different-sized cattle exclosures; (2) there was a relationship between cattle exclosure size and elk presence in exclosures; and (3) a minimum cattle exclosure size is appropriate for assessing elk impacts. Seven different-sized cattle exclosures (4.00, 2.00, 1.00, 0.50, 0.25, 0.10, and 0.05 ha) were compared in western Montana during the spring of 1996 and 1997. Trackplots (1-m² areas cleared of vegetation) were used to detect elk presence. Chi-square tests indicated elk presence inside all exclosures was less ($P < 0.10$) than elk presence adjacent to the exclosures. Regression analysis indicated exclosure size and elk presence were correlated ($P < 0.03$). Elk presence inside exclosures increased with increasing exclosure size. Our results did not support the minimum exclosure size (0.4 ha) recommended in the literature. Cattle exclosures larger than 4 ha appear needed to accurately measure relative resource impacts from elk and cattle; however, this does not ensure that an exclosure > 4.0 ha in size will solve all of the problems associated with this technique.

Key Words: *Cervus elaphus*, exclosure size, livestock/wildlife relations, wild ungulates

Cattle (*Bos taurus* and *B. indicus*) and elk (*Cervus elaphus*) cohabitate extensive areas of western North America. When the condition or trend of these rangelands is unacceptable, and changes are considered to existing resource management plans, it is important to distinguish the relative impacts of elk versus cattle (Smith and Doell 1968). Accurate measurements of these relative impacts should improve planning efforts. The most widely used technique to delineate cattle and elk impacts on rangeland is the use of exclosures (Cook and Stubbendieck 1986, Laycock 1994).

Two types of exclosures are generally used. The first is a cattle exclosure constructed of 3 to 4-strand barbed wire fence 0.8 to 1.0 m in height and the second is a big game exclosure constructed of 1.8 to 2.5 m tall woven wire fence (Young 1956, Austin et al. 1983, Austin and Urness 1986). By excluding cattle and/or elk from a given area, comparisons can be made between areas accessible to both cattle and elk (generally located adjacent to an exclosure), areas accessible to elk only (inside cattle exclosures),

Resumen

Las medidas precisas del impacto relativo del alce (*Cervus elaphus*) y el ganado (*Bos taurus* y *Bos indicus*) sobre los recursos ayudan a mejorar la planeación del manejo de los terrenos donde estas especies cohabitan. A menudo la comparación del grado de utilización dentro y fuera de exclosures de ganado se utiliza para este propósito. Los objetivos de nuestro estudio fueron determinar si (1) la presencia del alce difirió dentro y en áreas adyacentes a exclosures de ganado de diferente tamaño; (2) Si hubo una relación entre el tamaño de la exclusión para ganado y la presencia del alce en las exclosures y (3) determinar el tamaño mínimo de exclusión para ganado necesario para evaluar el impacto del alce. Se compraron exclosures para ganado de 7 tamaños diferentes (4, 2, 1, 0.5, 0.25, 0.1 y 0.05 ha), la comparación se realizó en el oeste de Montana durante la primavera de 1997 y 1998. Para detectar la presencia del alce se utilizaron parcelas de 1-m² en las cuales se limpió la vegetación. Las pruebas de Chi-cuadrada indicaron que la presencia del alce dentro de las exclosures fue menor ($P < 0.10$) que en las áreas adyacentes. Los análisis de regresión indicaron que el tamaño de la exclusión y la presencia del alce estuvieron correlacionadas ($P < 0.03$). La presencia del alce dentro de las exclosures se incrementó al aumentar el tamaño de la exclusión. Nuestros resultados no confirman el tamaño mínimo de las exclosures (0.4 ha) que es recomendado en la literatura. Las exclosures de ganado mayores de 4 ha aparentemente requieren de medir en forma precisa los impactos relativos del alce y el ganado en los recursos; sin embargo, esto no asegura que una exclusión mayor de 4 ha resolverá todos los problemas asociados con esta técnica.

and areas to which neither have access (inside big game exclosures).

This approach assumes that elk accessibility to the area inside the cattle exclosure is unimpeded by the fence. If elk are not freely entering the cattle exclosure, differences between the area inside and adjacent to the cattle exclosure may lead to overestimation of impacts due to cattle alone.

Young (1958) suggested that elk were less likely to enter small livestock exclosures. Several other sources also have addressed the effects of exclosure size on the likelihood that wild ungulates will enter an exclosure (Young 1956, Julander 1958, Tueller and Tower 1979, Yoakum et al. 1980, Cook and Stubbendieck 1986, Laycock 1994). These sources suggest livestock exclosures should be a minimum of 0.4 ha in size in areas populated by wild ungulates. Young (1956), Julander (1958), and Tueller and Tower (1979) are the only sources we were able to find that scientifically tested wild ungulate presence in livestock exclosures; however, none of these sources tested elk presence in exclosures.

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The purpose of our study was to determine if elk presence differed inside and adjacent to several different-sized cattle exclosures. We also wanted to determine if there was a relationship between elk presence inside the exclosures and exclosure size. Finally, we wanted to determine how large a cattle exclosure must be to facilitate equal elk presence inside and adjacent to the exclosure.

Materials and Methods

Study Area

In 1995, livestock exclosures were constructed in 2 pastures on the Blackfoot Clearwater Wildlife Management Area approximately 70 km northeast of Missoula, Mont. Pasture A was about 450 ha and pasture B was about 250 ha. Vegetation in Pasture A was dominated by timothy (*Phleum pratense* L.) and vegetation in Pasture B was dominated by rough fescue (*Festuca scabrella* Torr.). These pastures are part of an elk winter range, but due to snow pack from January through April the pastures are not used by elk until spring.

Study Design and Exclosure Layout

Square exclosures were constructed of 3 strands of barbed wire with the top and bottom strands 1.0 and 0.25 m above the ground. Metal t-posts, spaced 6.0 m apart, supported the wire between wood corner posts.

A randomized block design was used. In Pasture A, 2 sets of 7 different-sized exclosures were randomly located along a line with a minimum of 50.0 m between each exclosure (Fig. 1). Exclosures were 0.05, 0.10, 0.25, 0.50, 1.00, 2.00, and 4.00 ha in size. In Pasture B, 2 sets of 3 different-sized exclosures were randomly located along a line with a minimum of 50.0 m between each exclosure. Exclosures were 0.05, 0.50, and 2.00 ha in size.

Each transect in the 2 pastures represented a block for a total of 4 blocks. Each exclosure size represented 1 treatment for a total of 7 treatments. The experimental unit was defined as an individual cattle exclosure with 2 replicates of the 0.10, 0.25, 1.00 and 4.0-ha exclosure sizes, and 4 replicates of the 0.05, 0.50, and 2.00-ha exclosure sizes. Exclosure sizes tested were chosen to reflect sizes equal to, above, and below those recommended by Julander (1958), Tueller and Tower (1979), Yoakum et al. (1980), and Young (1956). Vegetative condition, species

Fig. 1. Example of exclosure and trackplot layout.

composition, exposure to grazing, slope and exposure were similar inside and adjacent to each exclosure.

Monitoring Elk Presence

Elk presence inside and adjacent to each exclosure was monitored with trackplots. Trackplots (1-m² areas cleared of vegetation to expose bare soil) were evenly spaced across the center of each exclosure parallel to the line the exclosures are located along (Fig. 1). Three track plots were located in the 0.05, 0.10, 0.25, 0.50, and 1.00-ha exclosures, 5 in the 2.00-ha exclosures, and 7 in the 4.00-ha exclosures. An equal number of trackplots were located 25 m outside each exclosure, spaced equally to those inside the exclosure. Trackplots were monitored every 2–4 days when the ground was free from snow and elk were present in the study area (mid-April to mid-June). Data was collected on 13 different days in 1996 and 20 different days in 1997.

When 1 or more elk hoof prints were found in a trackplot the trackplot was considered hit. Total number of hit trackplots inside and adjacent to each individual exclosure were recorded on each day data were collected. Elk hoof prints were cleared from trackplots each day data were collected. Total number of trackplots hit inside each individual exclosure and total number of trackplots hit adjacent to each individual exclosure were pooled at the end of each year. If there were no track-

plots hit during an observation, data from that observation was dropped from the final data set. Zero hits during an observation indicated there were inadequate numbers of elk in the vicinity of the exclosure to make a valid comparison of elk presence inside and adjacent to the exclosure. If these observations were included in our data set they would have indicated equal elk presence, which could have biased our results toward equal use. Mean number of trackplots hit inside and adjacent to each exclosure size tested were used to quantify elk presence.

Trackplots hit were converted to a proportion. Proportion of trackplots hit inside an exclosure equaled the number of trackplots hit inside an individual exclosure divided by the total number of trackplots hit inside and adjacent to the same individual exclosure. This eliminated bias associated with variability of the relative area sampled by trackplots in different sized exclosures. For example, a proportion allows analysis using a 2-ha exclosure with 5 trackplots and a 4-ha exclosure with 7 trackplots.

Statistical Analysis

Chi-square was used to compare elk presence inside and adjacent to each size of exclosure tested. Mean number of trackplots hit inside and adjacent to each exclosure size was used in this test. All values were tested at $P < 0.10$.

Fig. 2. Elk presence inside and adjacent to exclosures on the Blackfoot Clearwater Wildlife Management Area, Montana, April–June, 1996–97. Asterisk* indicates a significant chi-square value, $P \leq 0.10$.

Regression analysis was conducted, using the general linear model procedure of SAS (1985) to determine if there was a correlation between trackplots hit and exclosure size ($P < 0.10$).

Results and Discussion

Elk Presence Inside and Adjacent to Exclosures

Elk presence adjacent to exclosures was greater ($P < 0.10$) than elk presence inside exclosures (Table 1, Fig. 2). An explana-

Table 1. Chi-square values comparing elk presence inside and adjacent to exclosures.

Exclosure Size (ha)	χ^2	Degrees of Freedom	P-value
0.05	16.0	5 ¹	0.007
0.10	6.6	3 ²	0.085
0.25	2.7	1 ³	0.100
0.50	13.3	3	0.004
1	9.6	3	0.022
2	18.3	3	0.003
4	11.6	3	0.009

¹ $\chi^2_{0.1}$ with 5 d.f. = 9.2

² $\chi^2_{0.1}$ with 3 d.f. = 6.3

³ $\chi^2_{0.1}$ with 1 d.f. = 2.7

tion of why elk presence was less inside our exclosures may be that sometimes elk simply choose not to cross fences. We have observed elk approach a fence and instead of jumping over it, parallel the fence in an apparent attempt to find a way around. In addition, the 4 sides of an exclosure may present a greater visual

obstacle than a single stretch of fence (pasture perimeter fence). This increased visual obstacle may increase an elk's reluctance to cross an exclosure fence.

Elk Presence in Different-Sized Exclosures

Our regression analysis ($R^2 = 0.33$) indicated elk presence inside exclosures increased as exclosure size increased (Fig. 3). A possible explanation is that as exclosure size increases the elk is less likely to see all sides of the exclosure, which could decrease the visual obstacle presented by the exclosure and increase the likelihood that an elk will enter an exclosure.

The coefficient of determination for our regression was 0.33. The logistics of this experiment limited our sample size, which restricted the level of power. This may partially explain the low coefficient of determination. Our model indicates that an exclosure needs to be larger than 4 ha in size to facilitate equal elk presence inside and adjacent to the exclosure (Fig. 3). We are not suggesting that simply building an exclosure > 4.0 ha in size will solve all of the problems associated with this technique.

Young (1956) was the only study we found that examined the effect of more than one exclosure size on wild ungulate presence inside exclosures. Young (1956) compared livestock exclosures from < 0.2 to 1.7 ha in size and concluded that elk presence differed among exclosure sizes. Young's conclusion that elk presence inside exclosures increases with increasing exclosure size is supported by our results. However, Young's conclusion that a 0.4-ha exclosure had equal elk presence inside and adjacent to it was not supported by our results.

Conclusions and Management Implications

The results of this study have important management implications to federal, state, and private resource managers in areas with elk and cattle. Accurate measures of relative resource impacts from cattle and elk are needed to make proper management decisions (Wisdom and Thomas 1996). Previous management decisions

Fig. 3. Proportion of total trackplots hit inside exclosures, on the Blackfoot Clearwater Wildlife Management Area, Montana, April–June, 1996–97.

based on information from cattle exclosures may have been incorrect, especially if cattle exclosures were 4.0 ha in size.

Logistically, it may be impractical to build an exclosure large enough to minimize the effects of size on elk presence and there is no guarantee that an exclosure > 4.0 ha in size will eliminate all of the problems associated with this technique. The reluctance of elk to cross fences could still pose a problem no matter how large an exclosure is built. A solution to this may be to drop the fence of the exclosure when cattle are not present. This could be applicable to an elk wintering area that is being grazed by cattle only during the growing season. Elk are generally dispersed and in low numbers in these areas when cattle are present (during the growing season) and concentrated when cattle are absent (winter) (Lyon 1985). Another solution may be to erect an exclosure when elk are not present in high densities (growing season), collect vegetation data at the end of the growing season, and construct a new exclosure in a new location the following growing season. Although cattle exclosures may be used as an effective management tool to separate elk and cattle impacts, precautions should be implemented to minimize or account for

the potential biases resulting from the reluctance of elk to cross cattle fences.

Additional questions could be explored concerning this technique. How do elk use exclosure sizes above 4.0 ha? How is elk use effected by fence design (fence height, fence materials, exclosure shape and layout), and exclosure location in the landscape (vegetation condition, slope and exposure)?

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Livestock effects on reproduction of the Columbia spotted frog

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Abstract

We evaluated reproduction and recruitment of the Columbia spotted frog (*Rana luteiventris* Thompson) in 70 ponds used by beef cattle and in 57 ponds not used by beef cattle in northeastern Oregon. No significant differences were detected in the number of egg masses or recently metamorphosed frogs in grazed and ungrazed sites. No pond characteristic measured could predict egg mass numbers, but percent aquatic vegetation and dissolved oxygen had some ability to predict recently metamorphosed frog numbers. Both variables explained 65% of the variability in recently metamorphosed frog numbers in grazed ponds. At ungrazed ponds, 4 additional variables (presence of fish, elevation, percent of rock, and conductivity) were required to achieve the same level of variability in predicting recently transformed frog abundance. The egg mass volume was larger at grazed than at ungrazed ponds suggesting that grazed ponds may have a greater food abundance or larger (older) individuals.

Key Words: livestock grazing, northeastern Oregon, *Rana luteiventris* Thompson

Global amphibian declines have precipitated the need to determine the status of many amphibian populations and identify factors influencing those populations. The recently described Columbia spotted frog (*Rana luteiventris* Thompson) (Green et al. 1997) is known to reproduce in and occupy aquatic habitats associated with riparian zones (Turner 1960) and has experienced some declines within its range (Hovingh 1993, Munger et al. 1996). Grazing is a prominent feature in many of these aquatic ecosystems, including northeastern Oregon (Kauffman et al. 1983, Green and Kauffman 1995). The influence of livestock on the physical characteristics (Bohn and Buckhouse 1986), vegetation (Roath and Krueger 1982, Sedgewick and Knopf 1991, Allen and Marlow 1994), fishes (Platts 1981), and avifauna (Thomas et al. 1979, Mosconi and Hutto 1982) in riparian ecosystems is reasonably well studied and could influence spotted frog habitat. Beyond discussions of potential impacts (Horusp et al. 1993, Jennings and Hayes 1994, Hayes 1997), the influence of livestock

Resumen

Evaluamos la reproducción y la iniciación de la rana "Columbia spotted" (*Rana luteiventris* Thompson) en 70 estanques utilizados por ganado bovino para carne y en 57 estanques no utilizados por bovinos para carne localizados en el nordeste de Oregon. No se detectaron diferencias significativas en el número de masas de huevecillos o de ranas recientemente metamorfoseadas entre los sitios con y sin apacentamiento. Las características de los estanques que fueron medidas no pudieron predecir el número de masas de huevecillos, pero el porcentaje de vegetación acuática y el oxígeno disuelto tienen cierta capacidad para predecir los números de ranas recientemente metamorfoseadas. Ambas variables explicaron el 65% de la variabilidad de ranas recientemente metamorfoseadas en los estanques de sitios con apacentamiento. En estanques de sitios sin apacentamiento, 4 variables adicionales (presencia de peces, elevación, porcentaje de rocas y conductividad) se requirieron para lograr el mismo nivel de variabilidad para predecir la abundancia de ranas recientemente transformadas. El volumen de la masa de huevecillos fue mayor en los estanques de sitios con apacentamiento que en los de sitios sin apacentamiento, lo que sugiere que en los estanques de áreas con apacentamiento puede haber una mayor abundancia de alimento o individuos más viejos.

on amphibians has been only recently addressed. In southwestern Idaho, Munger et al. (1994) found that sites with adult Columbia spotted frogs had significantly less grazing pressure than sites without spotted frogs, but he found no differences in a subsequent year (Munger 1996).

This paper describes our preliminary assessment of the relationship between grazing and the Columbia spotted frog in northeastern Oregon. Using the number and volume of egg masses and number of recently metamorphosed juveniles to assess spotted frog reproduction and recruitment, respectively, we measured biotic and abiotic variables at 127 breeding sites of Columbia spotted frogs to determine differences between grazed and ungrazed sites.

Methods

Egg Masses (Reproduction)

We searched for Columbia spotted frog breeding sites in 5 major watersheds (Grande Ronde River, Eagle Creek, John Day River, Malheur River, and Wallowa River) in Union, Umatilla, Baker, Grant, and Wallowa counties. Spotted frogs were known

Thad W. Heater, Karen L. Gray, Janet E. Hohmann, Karen Kronner, Chris Pearl, and Jay F. Shepherd assisted with field work. The following private land owners allowed us to search for frogs on their property: Vic Coggans, Cunningham Sheep Co., Margarite Fahrenwald, Eastern Oregon Agricultural Research Center, La Grande Rifle and Pistol Club, Doug McDaniel, Nevada First Corp., Bob Schiller (deceased), Nyoda Scott, and Dick Snow.

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to occur in these watersheds based on historical records (Ferguson 1952, 1954; Ferguson et al. 1958; unpublished data on file at Pacific Northwest Research Station, La Grande, Ore.). We selected specific watersheds to search based on several criteria: presence of a perennial stream with quiet water in the form of ponds, marshes, and backwaters nearby; streams with a wide valley bottom (< 10% gradient) and open meadows adjacent to coniferous forests (forest types of ponderosa pine [*Pinus ponderosa* Dougl. ex Laws], lodgepole pine [*P. contorta* Dougl. ex Loud], or mixed conifer); within 2 km of a road; and on public land or on private land for which we had permission to search. Beef cattle grazing occurred in some of each watershed sometime between June and October, although significant portions of each watershed were currently ungrazed. Grazing systems had typically been in place within each watershed for at least 5 years.

We searched for egg masses between 22 March and 20 May 1997. The date a particular site was searched depended on water temperature. We conducted 1 search at each site when the water temperature exceeded 8°C, which was the water temperature above which successful embryonic development could occur (Johnson 1965). Each site with eggs was revisited weekly to count egg masses until no additional egg masses were recorded in 2 successive visits. Eggs hatched in 13–23 days, depending on the water temperature (Morris and Tanner 1969). The number of egg masses at each breeding site were counted if individual masses could be distinguished. The length, width, and depth of individual masses were measured to estimate their volume. Egg masses that occurred in the same stream but were in separate bodies of water (where larvae could not interact) were considered independent samples.

Only standing water or very slowly moving water was searched for egg masses and adults by walking along the edge of the stream and checking all oxbows, backwaters, pools, marshy areas, and adjacent ponds using a modified form of the basic visual-encounter survey (Scott and Woodward 1994, Thoms et al. 1997). Searches were focused in shallow water (< 30 cm) because Columbia spotted frog egg masses occur in these situations (Turner 1960, Morris and Turner 1969, Hovingh 1993, Munger et al. 1996).

We classified each site as a *pond excavated for livestock or wildlife*, *gravel pit*, *dredge tailings*, *marsh*, *oxbow*, *beaver pond*, or *other*. We recorded *elevation*,

surface area of breeding site (m²), *maximum water depth* (m), and *distance to a permanent stream*. Substrate of the pond was identified as *mud*, *cobble*, or *stone*. The percent of water surface area that contained *algae*, *suspended vegetation*, and *open water* were recorded at each site. Ground cover within 2 m of the pond edge was recorded as the percent of *grass*, *shrub*, or *rock*. The presence of *beavers* (*Castor canadensis* Linnaeus) was noted.

Recently Metamorphosed Individuals (Recruitment)

We selected 54 of the 127 breeding sites based on accessibility and grazing activity to assess frog recruitment; 29 were ungrazed, and 25 were grazed sites. We searched for recently metamorphosed individuals between July and September by walking the perimeter of each breeding site and counting juvenile frogs seen in water or on land. Searches continued at 1-week intervals until metamorphs were no longer metamorphosing. The maximum number of recently metamorphosed juveniles at each site was used for the analysis.

In August, we recorded the same habitat characteristics measured during the spring. Water quality variables (pH, conductivity, nitrates, and dissolved oxygen) were measured at each site. Duration and intensity of grazing varied considerably among sites, so evidence of livestock activity was recorded in 3 ways: degree of utilization, number of dung pats, and trampling (hoof-print density). All 3 characteristics were given a rating from 0 to 3 with 0 = none, 1 = slight evidence, 2 = moderate evidence, and 3 = extensive evidence.

To determine abundance of potential predators, we recorded the number of garter snakes observed at ponds on each visit but used the maximum number recorded on any visit as the independent variable. The presence and kind of fish were recorded. We sampled aquatic invertebrates by taking 8 sweeps with a dip net at each site and counting leeches (Hirudinea), giant water bugs (Homoptera: Belostomatidae), diving beetles (Coleoptera: Dytiscidae), and backswimmers (Homoptera: Notonectidae).

Analyses

Mann-Whitney tests (Conover 1980) were used to compare the number of egg masses, volume of egg masses, number of recently metamorphosed individuals, and ratio of recently metamorphosed individuals per egg mass in grazed and ungrazed

sites. Nonparametric Spearman's rank correlations (Conover 1980) were used to determine the relationship between number of egg masses and elevation for all sites and for grazed and ungrazed sites. Simple linear regressions were used to compare: (1) number of egg masses and elevation for grazed and ungrazed sites, (2) mean egg mass volume and elevation for grazed and ungrazed sites, and (3) mean egg mass volume and elevation for sites with 3 egg masses at grazed and ungrazed sites. Kruskal-Wallis nonparametric ANOVAs (Conover 1980) were used to compare number of egg masses, mean egg mass volume, number of recently metamorphosed juveniles, and the ratio of recently metamorphosed juveniles per egg mass among pond types. The habitat characteristics that best predicted number of egg masses and abundance of recently metamorphosed juveniles were identified using a stepwise logistic regression using all ponds combined, only grazed ponds, and only ungrazed ponds.

Results and Discussion

We located 127 Columbia spotted frog breeding sites across a 5-county area in eastern Oregon. Seventy (55%) ponds were grazed by cattle; the remaining 57 (45%) were ungrazed. Thirty-nine percent of the breeding sites were *dredge tailing ponds*, 24% were *oxbows*, 17% were *excavated for livestock or wildlife*, 14% were *marshes* near streams, 3% were created by *beaver dams*, 2% were in *gravel pit ponds*, and 1% was a natural spring-fed pond. Breeding sites were typically small; 92% had a surface area <2,500 m² and only 8% were 2,500–30,000 m². Thirty-four percent of the ponds were <1 m deep while the remainder were 1–5 m deep. All ponds had a fine benthic substrate (mostly mud).

Egg Masses

The number of egg masses at grazed sites was not statistically different from the number at ungrazed sites (Table 1). Breeding sites occurred between 922 and 1,860 m in elevation. The elevational distribution of grazed and ungrazed ponds differed primarily because all grazed sites were below 1,500 m. At grazed sites there was a weak, but significant inverse correlation ($p = 0.03$, adjusted $r^2 = 0.06$) between number of egg masses and elevation. At ungrazed sites, a weak but significant positive correlation ($p = 0.05$, $r^2 = 0.05$) existed between number of egg

Table 1. Mean values, standard errors, and ranges of independent and dependent variables measured at Columbia spotted frog breeding ponds in northeastern Oregon, 1997.

Variable	N	Ungrazed $\bar{x} \pm \text{SE}$	Range	N	Grazed $\bar{x} \pm \text{SE}$	Range
Dependent						
No. egg masses	58	6.9 $\pm$ 2.34	1–25	65	6.9 $\pm$ 2.52	1–30
Egg mass volume (cm ³)*	41	762 $\pm$ 18.44	340–1,872	55	888 $\pm$ 19.8	261–2,142
Egg mass volume at sites < 1,200 m (cm ³)*	9	688 $\pm$ 165.3	340–1,872	29	954 $\pm$ 77.7	261–2,172
No. transformed frogs	29	57 $\pm$ 20.62	0–563	25	39 $\pm$ 10.15	1–230
Independent						
Elevation (m)	58	1,317 $\pm$ 24.67	922–1,860	68	1,184 $\pm$ 16.78	940–1,470
Surface area (m ²)	55	1,434 $\pm$ 546.67	8–30,000	68	1,079 $\pm$ 323.42	12–19,872
Water depth (m)	54	1.5 $\pm$ 0.27	0.5–5	67	1.2 $\pm$ 0.11	0.2–5
Distance to stream (m)	58	80 $\pm$ 26.93	0–1,000	48	61 $\pm$ 15.01	0–600
Aquatic vegetation (%)	56	44 $\pm$ 4.07	0–100	68	47 $\pm$ 3.98	0–100
Algae (%)	56	11 $\pm$ 2.64	0–80	68	10 $\pm$ 2.24	0–80
Cattails (%)*	29	7 $\pm$ 2.09	0–40	25	4 $\pm$ 2.82	0–60
Utilization ¹ *	47	0 $\pm$ 0.02	0–1	66	1.3 $\pm$ 0.11	0–3
Trampling ¹ *	49	0.2 $\pm$ 0.08	0–1	67	0.9 $\pm$ 0.12	0–3
Dung pats ¹ *	49	0.1 $\pm$ 0.06	0–1	68	1.3 $\pm$ 0.09	0–3
pH	29	8.2 $\pm$ 0.16	6.0–10.6	23	8.1 $\pm$ 0.20	6.6–10.4
Conductivity ($\mu\text{S}/\text{cm}$)	29	151 $\pm$ 15.48	14–376	25	144 $\pm$ 16.28	59–473
Nitrates (ppm)	29	0.1 $\pm$ 0.1	0.1–0.1	25	0.1 $\pm$ 0.01	0–0.1
Dissolved oxygen (ppm)	29	7.7 $\pm$ 0.70	1.0–16.0	25	6.2 $\pm$ 0.79	1.0–16.2

* Significant at $p < 0.05$.

¹ These variables were coded from 0 to 3, indicating relative abundance of each variable.

masses and elevation. Number of egg masses did not differ among pond types. Egg mass volume differed significantly between grazed and ungrazed sites (Mann-Whitney U: $Z = -2.07$, $p = 0.04$) (Table 1). No relationship existed between mean egg mass volume and elevation for either grazed or ungrazed sites. Because of variability in egg mass volume and at many sites only one egg mass was available to measure, we compared the relationship between mean egg mass volume and elevation at sites where 3 or more egg masses were measured. A significant relationship was displayed between mean egg mass volume and elevation for both grazed ($p = 0.02$, adjusted $r^2 = 0.15$) and ungrazed sites ($p < 0.01$, adjusted $r^2 = 0.24$) with volume increasing with elevation. Because egg mass size increased with elevation and more grazed sites were present at lower elevations, we compared egg mass size at all sites and at sites with 3 or more egg masses at or below 1,200 m and above 1,200 m. The only significant comparison was between grazed and ungrazed sites at or below 1,200 m (Mann-Whitney U: $U = 69$, $U' = 192$, $p = 0.03$).

The larger egg mass volume at grazed sites suggests that grazing did not have a negative effect, in addition to our observation that 6 of the 8 most productive sites (> 20 egg masses) were grazed. Because grazed sites were below 1,500 m, we considered the possibility that variation in egg mass volume might be influenced by elevation. The possibility of such a confound-

ing factor was rejected because the data showed that egg mass volume increased with elevation. Larger egg masses may reflect larger females (Corn and Fogelman 1984), which could be a result of a more abundant food supply or an older population structure (Turner 1960).

No pond characteristics measured satisfactorily predicted the number of egg masses. The stepwise logistic regression selected elevation, percent aquatic vegetation, and percent open water as able to achieve a maximal predictive value of only 7% of the total variability.

Recently Metamorphosed Frogs

Neither the number of recently metamorphosed frogs nor the ratio of recently metamorphosed frogs to number of egg masses was significantly different between the 25 grazed and 29 ungrazed sites (Table 1). There were also no significant differences between grazed and ungrazed sites in water characteristics (dissolved oxygen, nitrates, pH, and conductivity). However, correlation analysis revealed that numbers of recently metamorphosed frogs were inversely correlated with the presence of fishes (Spearman's Rank, $\rho = -0.41$, $p = 0.0028$) for all sites. Longnose dace (*Rhinichthys cataractae dulcis* Valenciennes) and rainbow trout (*Oncorhynchus mykiss* Walbaum) were identified at the breeding sites with fish. Inverse correlations between frog larvae and fish have been demonstrated often (Hayes and Jennings 1988, Bradford 1989,

Bradford et al. 1993) and may be reflected by the inverse correlation between recently metamorphosed frogs and fish in this study.

Numbers of recently metamorphosed frogs were positively correlated with garter snakes (Spearman's Rank, $\rho = 0.52$, $p < 0.01$) for all sites. The common garter snake (*Thamnophis sirtalis* Linnaeus) and the wandering garter snake (*T. elegans vagrans* Baird and Girard) were present in about equal proportions at the ponds. Garter snakes were observed preying on recently metamorphosed frogs at several sites. Most of the predation by garter snakes occurred after or during metamorphosis, and after we had obtained our highest counts of frogs. It is likely that ponds with high numbers of metamorphosing frogs attracted more snakes than ponds with low numbers of frogs.

In comparisons of habitat variables between grazed and ungrazed sites, only percent cattails (Mann-Whitney U: $Z = -2.37$, $p = 0.02$), utilization ($Z = -4.55$, $p < 0.01$), trampling ($Z = -4.97$, $p < 0.01$), and dung pat density ($Z = -5.01$, $p < 0.01$) were significantly different (Table 1). A correlation analysis revealed that percent of cattails was positively correlated with pond size (Spearman's Rank, $\rho = 0.37$, $p < 0.01$).

Selected habitat characteristics were successful predictors of the abundance of recently metamorphosed frogs. For all 54 ponds, 5 variables were retained in the analysis with percent aquatic vegetation explaining 25% of the variability; the remaining 4 variables (dissolved oxygen,

elevation, utilization, and pond depth) explained another 16% of the variability. In ungrazed ponds, 6 variables (fish, percent aquatic vegetation, elevation, percent of rock on shore, dissolved oxygen, and conductivity) explained 65% of the variability. In grazed ponds, percent aquatic vegetation explained 35%, and dissolved oxygen explained 30% of the variability. Percent aquatic vegetation and dissolved oxygen were the only variables that were retained in all models (combined, grazed, and ungrazed).

Percent aquatic vegetation, dissolved oxygen, and presence of fish all contributed significantly to predict the abundance of recently metamorphosed frogs, which may reflect a fundamental aquatic vegetation effect. Aquatic vegetation is known to provide shelter for frog larvae and metamorphs from fish and other predators (Licht 1969). Levels of dissolved oxygen are directly linked to coverage of aquatic vegetation (Carpenter and Lodge 1986).

Conclusions

These data failed to reveal that grazing had a negative effect on reproduction and recruitment of the Columbia spotted frog in northeastern Oregon. The high variability in the results of this study may be linked to the breadth of the grazing variable encompassing a broad range of conditions in landform features, water quality, vegetation, predators, and invertebrates. Future studies need to pay particular attention to measuring grazing intensity and timing to detect potential effects on Columbia spotted frogs.

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Cryptosporidium parvum transport from cattle fecal deposits on California rangelands

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Abstract

Cryptosporidium parvum is a fecal borne protozoan parasite that can be carried by and cause gastrointestinal illness in humans, cattle, and wildlife. The illness, cryptosporidiosis, can be fatal to persons with compromised immune systems. At question is the potential for *C. parvum* in cattle fecal deposits on rangeland watersheds to contaminate surface water. First, *C. parvum* oocysts must be released from fecal deposits during rainfall, becoming available for transport. In 1996, we examined the transport of *C. parvum* oocysts in overland flow from fecal deposits under natural rainfall and rangeland conditions at the San Joaquin Experimental Range in Madera County, Calif. Our null hypothesis was that *C. parvum* oocysts are not released from fecal pats and transported 1 m downslope as overland flow with rainfall. Paired plots were located on 10, 20, and 30% slope sites. Each plot was loaded with four, 200 g fecal pats dosed with 10^5 oocysts g^{-1} . Pats were placed 1.0 m above the base of each plot. Composite runoff samples from each plot were analyzed for oocyst concentration following each of 4 storm events. Oocysts were transported during each storm. Slope was a significant factor in oocyst transport, with oocyst transport increasing with slope. Although not significant, there was an apparent flushing effect of oocysts across storms, with the majority transported in the first 2 storms. A pilot rainfall simulation experiment also revealed a flushing phenomenon from pats during individual rainfall events. *C. parvum* oocysts in fecal pats on rangeland can be transported from fecal deposits during rainfall events, becoming available for transport to water-bodies. Future studies need to examine surface and subsurface transport of oocysts on rangeland hillslopes for distances greater than 1 m.

Key Words: pathogens, water quality, fate and transport, buffer strip

Cryptosporidium parvum (Tyzzer 1912), a fecal-oral protozoan parasite, is an important etiologic agent of enterocolitis in mammals. *C. parvum* appears to be infectious for and is shed by humans, domestic animals, and wildlife species (Casemore et al. 1997). Waterborne transmission to humans has emerged as a leading public health problem here and abroad (MacKenzie et al.

Resumen

Cryptosporidium parvum es un protozooario parásito que se transporta en las heces fecales y que puede ser acarreado por humanos, bovinos y fauna silvestre a los que puede causar enfermedades gastrointestinales. La enfermedad cryptosporidiosis puede ser fatal para personas con un sistema inmunológico débil. Se cuestiona el potencial del *C. parvum* contenido en las heces fecales de bovinos depositadas en las cuencas hidrológicas de pastizal para contaminar las aguas superficiales. Primero, los oocistos del *C. parvum* deben ser liberados de las heces fecales durante la ocurrencia de lluvias para estar disponibles para ser transportados. En 1996, en la Estación Experimental de Pastizales de San Joaquín en el condado de Madera, Calif., examinamos el transporte de oocistos de *C. parvum* en el flujo superficial proveniente de áreas con depósitos fecales bajo lluvia natural y en condiciones de pastizal. Nuestra hipótesis nula fue que los oocistos de *C. parvum* no son liberados de los depósitos fecales y transportados 1 m cuesta abajo como en el flujo superficial de la lluvia. Se localizaron parcelas apareadas en sitios con 10, 20 y 30% de pendiente. En cada parcela se colocaron 4 depósitos fecales de 200 g de dosificados con 105 oocistos g^{-1} , las heces fecales se colocaron 1 m arriba de la base de cada parcela. Se analizaron muestras compuestas del escurrimiento de cada parcela para determinar la concentración de oocistos después de cada uno de 4 eventos de lluvia. Los oocistos fueron transportados durante cada tormenta. La pendiente fue un factor significativo en el transporte de oocistos, incrementándose el transporte al aumentar la pendiente. Aunque no significativo, hubo un efecto aparente de lavado de los oocistos a través de las tormentas, en donde la mayoría de ellos se transportaron en las primeras 2 tormentas. Un experimento piloto con simulador de lluvia también reveló este fenómeno de lavado durante eventos individuales de lluvia. Los oocistos de *C. parvum* de heces fecales localizadas en pastizales pueden ser transportadas durante los eventos de lluvia, llegando a ser disponibles para su transporte a cuerpos de agua. Se necesitan estudios futuros para examinar el transporte superficial y subterráneo de oocistos en las montañas de pastizal a distancias mayores de 1 m.

1994, LeChevallier and Norton 1995). Public health officials have considered cattle as possible sources of this parasite because of *C. parvum* infection within cattle populations (MacKenzie et al. 1994). In 1997, the City of San Francisco, Calif. proposed to terminate long-standing grazing leases and ban cattle from 12,000

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ha of rangeland it owns due to concerns about *C. parvum* from cattle grazing in watersheds providing drinking water (Stephens 1997). This proposal was dropped following development of a comprehensive water quality control plan for the watershed in question (Barry et al. 1998), but public and regulatory agency concerns about the link between grazing, water quality, and human health are still quite high. Normal drinking water treatment does not remove oocysts from source water, and alternative treatment methods are expensive.

For bovine-derived *C. parvum* to be a waterborne health risk, the infectious stage of the parasite (oocysts) must reach source water via direct deposition in water or via hydrologic transport from upland and riparian areas. Direct contamination of source water occurs when fecal material is deposited within a stream or its flood plain. Larsen et al. (1988) report that free ranging cattle in Oregon deposited 3.4% and 1.7% of their feces in a stream in August and November, respectively. In a system where the stream provided the only cattle drinking water, Gary et al. (1983) found that 6.7% to 10.5% of defecations by beef cattle were deposited directly into streams.

For cattle feces deposited in upland watershed areas to contaminate source water, oocysts must be transported from fecal pats during hydrological events such as rainfall or snowmelt. Under simulated irrigation, Mawdsley et al. (1996) observed overland and subsurface leaching transport of *C. parvum* oocysts from liquid manure slurries applied to tilted (7.5%) soil boxes (80 cm long x 56 cm wide x 25 cm deep). The boxes were filled with poor draining silty clay loam soil and planted with perennial ryegrass. Transport of indicator bacteria from cattle fecal deposits under artificial rainfall and plot scenarios has been documented (Buckhouse and Gifford 1976, Thelin and Gifford 1983, Kress and Gifford 1984, and Larsen et al. 1994). Studying fecal coliform transport from cattle fecal pats, Larsen et al. (1994) report that on average 17% of fecal coliforms in the pats were transported from the pats during 0.5 hour simulated rainfall events. The authors report an average reduction of 83 and 95% of fecal coliforms in overland flow passing through grass turf at 1.37 and 2.13 m below the fecal pats, respectively. Kress and Gifford (1984) found that age of fecal deposit and recurrent rainfall both reduced fecal coliform release below that of new and once rained on deposits. Buckhouse and Gifford (1976) examined

fecal and total coliform transport from 1 month old fecal deposits on rangeland in Utah under simulated rainfall. They report fecal coliform concentrations in overland flow of 75,000 bacteria 100 ml^{-1} at 0 m from the pat, and 23 bacteria 100 ml^{-1} at 1 m from the pat.

The objective of this study was to document the transport of *C. parvum* oocysts from cattle fecal deposits on California rangelands under natural rainfall and hill-slope conditions. Establishing this fact is the logical precursor to detailed experiments examining oocyst transport processes on rangeland hillslopes. Our null hypothesis was that *C. parvum* oocysts are not released from the fecal deposits and transported 1 m as overland flow during natural rainfall events. We selected this distance based upon the work of Larsen et al. (1994) and Buckhouse and Gifford (1976) which shows significant reduction in coliform transport as overland flow beyond 1 m. Because land slope is an important factor controlling overland flow generation (Haan et al. 1994) and in determining the spatial distribution of cattle fecal deposition (Larsen 1989, Tate et al. 1998), we also examined the effect that percent slope had on the concentration of *C. parvum* oocysts in overland flow collected 1 m from fecal deposits.

Methods

Study Site

The study was conducted on the 1,772 ha San Joaquin Experimental Range (SJER) located in Madera County, Calif. The SJER is representative of grazed hardwood rangeland in central and southern Sierra Nevada west slope foothills, and is grazed year-long by a 210 cow, commercial type cow-calf herd. Elevation at SJER ranges from 213 to 518 m. Climate is Mediterranean with an average annual precipitation of 485 mm falling almost entirely as rainfall November through May. Upland watershed areas are dominated by the coarse textured Ahwahnee soil series, a *Mollic Haplustalf*. Upland soil depth ranges from 0.2 to 0.6 m, lain over weathered granitic parent material. Vegetation at SJER is oak woodland/savanna with annual grassland understory. Blue oak (*Quercus douglasii* Hook & Arn.) and interior live oak (*Quercus wislizenii* A.DC.) dominate the overstory while wild oats (*Avena fatua* L.), rip-gut brome (*Bromus diandrus* Roth), soft chess (*Bromus rubens* L.), redstem filaree (*Erodium cicutarium* (L.) L'Her), and oth-

ers dominate the annual grassland understory.

In 1994, three sets of paired overland flow plots (total 6 plots) were constructed on the upland Ahwahnee soil type. All plots were located within a 138 ha, grazed experimental watershed. Precipitation and streamflow are automatically monitored on a 0.25 hour time step at the outlet of this watershed. Paired plots (2 replicates) were located on 10%, 20%, and 30% slopes. A 1.0 m buffer was maintained between the 2 plots at each site. Each plot was 2 m wide (parallel to slope) by 22.1 m long (uphill-downhill). The upper and side boundaries of each plot were bordered with metal flashing inserted 15 cm into the soil to insure overland flow from adjacent areas did not flow into the plots. A collection system was installed at the bottom of each plot to allow for composite sampling of overland flow. The design did not allow for accurate measurement of total runoff volume from each plot. Plots were protected from grazing and cattle fecal deposition for a year prior to this study. All existing fecal deposits were removed from the plots 1 year prior to the experiment. Average soil characteristics for the 6 plots were; bulk density = 1.5 g cm^{-3} , porosity = 44.1%, pH = 6.5, EC = $0.58\text{ mmhos cm}^{-1}$, organic matter content = 1.11%, total carbon = 1.15%, cation exchange capacity = $6.67\text{ meq }100\text{ gm}^{-1}$, and percent sand/silt/clay 78%/18%/4%. There were no trees on the plots, nor within 30 m of the plots. Herbaceous dry matter on the plots averaged $1,669\text{ kg ha}^{-1}$ at 2 Feb. 1996.

Treatments

Two experiments were conducted in this study. For the first experiment, each of the 6 overland flow plots was loaded with four, 200 g fecal pats dosed with 1×10^5 *C. parvum* oocysts g^{-1} . We used a concentration of 1×10^5 *C. parvum* oocysts g^{-1} because this level represented a moderately high shedding intensity for calves. Concentrations of oocysts often exceed 1×10^5 oocysts g^{-1} for both naturally and experimentally infected calves (Xiao and Herd 1994, Fayer et al. 1998). Pat size is representative of pats from calves less than 4 months old, the primary bovine source of *C. parvum* oocysts on California's rangelands (Atwill et al. 1999). The total amount of fecal material is representative of loading around feeding stations, water troughs, and other cattle concentration areas on rangeland (Hafez 1969, Larsen 1989 and Tate et al. 1998). Experimentally constructed fecal pats

allow us to control the load of *C. parvum* oocysts on each plot. Source of fecal material for experimentally constructed fecal pats was fresh fecal material collected from cattle at the SJER and which tested negative for *C. parvum* based on immunofluorescent microscopy (MERIFLUOR *Cryptosporidium/Giardia* direct immunofluorescent detection kit, Meridian Diagnostics, Inc. Cincinnati, Ohio). Source of *C. parvum* oocysts for experimentally constructed fecal pats were from feces from naturally-infected dairy calves and were purified using a previously described technique (Arrowood and Sterling 1987). The concentration of purified oocysts was determined with a hemacytometer. Naturally-infected calves were from several commercial dairies located in Kings and Tulare counties, Calif.

On 2 February 1996, the 4 fecal pats were placed 1.0 m above the bottom of each plot. A composite overland flow sample was collected from each plot following 4 subsequent storm events during the remainder of the 1 October 1995 to 30 September 1996 water year. Runoff volume from each plot was not measured. Concentrations of oocysts were measured for each sample by adding 2.5 ml of 10% Tween 80, 1Q% SDS solution to 250 ml aliquot of each sample, mixing 30 seconds, then filtering through mesh size 40, 100, and 200 sieves. The suspension was centrifuged, supernatant removed, and the pellet resuspended in 0.25 to 4 ml of 0.2% Tween 20 in distilled water. Ten μ l of suspension was dried onto a commercially prepared glass slide and the direct immunofluorescent assay performed according to the manufacturer's instructions (MERIFLUOR *Cryptosporidium/Giardia* direct immunofluorescent detection kit, Meridian Diagnostics, Inc. Cincinnati, Ohio). The total number of oocysts was enumerated for each sample and the concentration of oocysts for each water sample determined by adjusting for the estimated percent recovery of the immunofluorescent assay. An ANOVA with repeated measures (Dixon 1992) was used to determine significance, with slope (3 levels) as the fixed factor and sample date (4 storm events) as the repeated measure whereby the runoff from 6 plots (3 slopes x 2 replicates/slope) was sampled across 4 storms.

In the second experiment, we conducted a single artificial rainfall experiment to provide preliminary information for development of a future laboratory-based study of the transport of oocysts throughout a rainfall event. Due to natural plot variabil-

Fig. 1. Rainfall (mm) and storm flow (liter sec⁻¹) from the San Joaquin Experimental Range watershed during the study period.

ity, uncertain weather and flow, as well as logistics it is difficult to obtain this type of detailed time-dependent information in-the-field under natural rainfall scenarios. For this trial, a sprinkler type rainfall simulator (Wilcox et al. 1986) was used to apply rainfall at a rate of 7.62 cm hour⁻¹ to a 0.5 m², 10% slope, ungrazed plot located adjacent to the 10% slope overland flow plot site. This rainfall intensity exceeds the estimated 100 year return period 30 minute duration rainfall event for the site. Rainfall was applied to the plot until equilibrium overland flow had been achieved. At that point four, 200 g fecal pats dosed with 1 X 10⁵ *C. parvum* oocysts g⁻¹ of feces were added to the plot. All overland flow from the plot was captured for 90 minutes starting immediately prior to and at 10 minute increments following fecal pat deposition. Concentrations of oocysts in the samples were measured for each sample by the same method described above.

Results and Discussion

Precipitation and stream flow from the 138 ha experimental watershed containing the plots was recorded on a 0.25 hour time

step (Fig. 1). These data are presented to illustrate the timing and magnitude of the storms experienced during this experiment. Overland flow generated by 4 discrete storm events commencing on 3 February 1996, 4 February 1996, 18 February 1996, and 11 March 1996 was composite sampled during the study. The storm commencing 3 March 1996 generated no overland flow from the plots. Composite overland flow samples from the plots were collected at approximately 1500 hours on 4 February 1996, 8 February 1996, 22 February 1996, and 12 March 1996. Total rainfall for the 4 February 1996, 8 February 1996, 22 February 1996, and 12 March 1996 sample periods was 46, 55, 64, and 32 mm respectively. Following 12 March 1996, no overland flow was realized from the plots for the remainder of the 1995 water year.

Figure 2 illustrates *C. parvum* concentration by slope and sample date. ANOVA with repeated measures (sample date) reveals that while the effect of slope was significant at the 0.05 confidence level, sample date (storm event) and the potential interaction between slope and sample date were not significant (Table 1). Tukey comparison of means reveals that *C. parvum* concentrations are significantly

Table 1. Analysis of variance with repeated measures of square root transformed *C. parvum* concentration (No. oocysts liter⁻¹), with slope as the fixed factor and sample date as the repeated measure.

Source	df	Sum of Squares	Mean Sum of Squares	F	P
Mean	1	28971	28971	28.06	0.01
Slope effect	2	21523	10762	10.42	0.04
Error	3	3097	1032		
SampleDate	3	11333	3778	2.15	0.16
Slope x Sample Date	6	16534	2756	1.57	0.26
Error	9	15842	1760		

Table 2. Mean and standard error for *C. parvum* concentration (No. oocysts liter⁻¹) in runoff, stratified by slope and pooled across sample date.

	Slope		
	10%	20%	30%
	(No. oocysts liter ⁻¹)		
Mean	112.5 ^a	2587.5 ^{ab}	9462.5 ^b
SE Mean	78.9	2432.5	3843.6
n	8	8	8

different at the 10% and 30% slopes, but that neither the 10% and 20% slopes or the 20% and 30% slopes are statistically different (Table 2).

Greater concentrations of *C. parvum* were detected in the runoff with increasing slope. Given the low bulk density, high porosity, and high sand content of the soil type, we would expect high infiltration rates and substantial subsurface flow. For a given soil, the amount of infiltration, and thus overland flow, on a plot is in part a function of slope. Velocity of overland flow increases as slope increases, thus flow has less time and opportunity to infiltrate over a 1.0 m distance as slope increases. We speculate that the increase in *C. parvum* concentration in runoff as slope increases can be explained by an increase in overland flow volume and a decrease in the filtration efficiency of the buffer strip as slope and runoff volume increases. Under the assumption that a greater volume of water per storm moved across the 1 meter buffer with increasing slope, we hypothesize that the depth of overland flow is nec-

essarily increased, thereby decreasing the filtration efficiency of the buffer strip for removing oocysts suspended in overland flow. In their study of oocyst transport from liquid manure slurry, Mawdsley et al. (1996) observed the greatest overland oocyst transport from soil boxes with the greatest overland flow volume.

Although sample date was not significant, there is a tendency for oocyst concentrations to decline over time (Fig. 2). Concentrations for the 22 February 1996 sample period were much lower than the 4 February 1996 and 8 February 1996 sample period, despite the greater rainfall and total runoff during the 22 February 1996 sample period. This suggests that the

majority of oocysts available for overland transport were "flushed" from the fecal pats and the 1.0 m buffer by the initial storms following fecal deposition on 2 February 1996. Kress and Gifford (1984) observed this same flushing phenomena for fecal coliforms as a function of age of fecal pat and recurrent simulated rainfall. Over their 70 day trial, Mawdsley et al. (1996) reported a steady decline in oocysts in overland flow until day 21. Oocysts in leachate also steadily declined until day 70.

There was an evident "flushing" of oocysts from the 4 fecal pats and the 0.5 m² plot during the 90 minute rainfall simulation period (Fig. 3). The majority of the oocysts available for overland transport left the plot early in the simulation, with a tailing effect after 60 minutes. Given that equilibrium overland flow (12 ml min⁻¹) was occurring throughout the experiment, the "flushing" effect is a function of oocyst supply for transport rather than the transport potential, which was constant. This trial also provides insight into the ratio of runoff to subsurface flow on these hillslopes. At a rainfall intensity of 7.62 cm hour⁻¹, a 90 minute simulation, and a plot area of 0.5 m², 28.57 liters of water were applied to the plot but only 1.08 liters of overland flow left the plot. Assuming no loss to interception or evaporation, 27.49 liters (96%) of applied rainfall left the plot as subsurface flow. This indicates that leaching of oocysts via subsurface flow is likely the major transport path on these rangelands, and is the next logical hillslope transport process to examine.

Fig. 2. *C. parvum* concentrations in overland flow sampled 1.0 m from fecal pats by slope and storm event from the San Joaquin Experimental Range watershed.

Fig. 3. *C. parvum* concentration in overland flow sampled 1.0 m from fecal pats at 10 minute increments during a simulated rainfall trial.

Conclusions

The hypothesis that *C. parvum* oocysts are not transported at least 1.0 m as overland flow from fecal deposits with natural rainfall can be rejected. Transport of *C. parvum* oocysts increases as slope increases, which we hypothesize to be the result of reduced filtration efficiency of the buffer strip subsequent to the larger volume and depth of water moving across the buffer. There is an apparent "flushing" of oocysts by the initial storms following fecal deposition. The rainfall simulation experiment also indicates a "flushing" of oocysts during the first 20 minutes of a storm event. Under the realistic scenario examined in this study, it is clear that *C. parvum* oocysts in fresh fecal pats on rangeland can be released with rainfall and become available for transport to waterbodies. Overland, as well as vertical and lateral subsurface, transport of oocysts on rangeland hillslopes needs further examination at distances greater than 1 m and on a variety of soil types. This information will be important in assessing the potential for buffer strips to prevent surface water contamination with this parasite from bovine and other fecal sources.

It is also important to note that in order for these bovine-derived oocysts to become a public health threat, oocysts have to be transported out of fecal pats, and they need to remain infective while being transported to a susceptible host. Environmental conditions on rangeland, such as heating, freezing, or drying, can rapidly inactivate large numbers of oocysts (Walker et al. 1998), but only a few oocysts would need to remain infective in order to pose a risk to humans. The illness can be fatal to persons with compromised immune systems. Experimental studies in healthy humans determined that as few as 30 bovine-derived oocysts were capable of initiating cryptosporidiosis in humans (DuPont et al. 1995). Addressing the potential for *C. parvum* in cattle fecal deposits on rangeland watersheds to threaten human health will require site-specific examination of the sources in the watershed (Atwill et al. 1999), viability of oocysts under harsh rangeland conditions (Walker et al. 1998), hydrologic transport of oocysts within the watershed, and the spatial and temporal distribution of fecal material in relation to surface water bodies (Tate et al. 1998).

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Postburning legume seeding in the Flooding Pampas, Argentina

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Abstract

In Argentina, *Paspalum quadrifarium* Lam. (paja colorada) forms tall dense grassland communities in the flooding pampas. Referred to locally as “pajonales”, these grasslands generally have very low nutritional value for cattle, except at the post-burn regrowth stage. To improve forage quality and consumption by breeding cattle, *Lotus tenuis* Walst et Kit. is over seeded immediately after burning of paja colorada pajonales. The objectives of this experiment were to follow the after seeding cover of lotus, evaluate weed control, and assess disease incidence and severity. The experiment was carried out in Azul, Buenos Aires province of Argentina, between September 1993 to September 1996. The postburn seedbed was very favorable for lotus germination and establishment. The most effective chemical weed control was obtained with 2,4-DB used alone or in combination with dicamba. *Lotus* increased markedly the quality of the pasture forage due to its high crude protein content. Four fungus diseases were found: *Botrytis cinerea* Pers., *Stemphylium* sp. Wallroth, *Uromyces loti* Blytt. and *Fusarium* spp. Link ex Fr. However, these caused only light foliar damage and did not impair lotus germination or establishment. The overseeding of lotus after burning of *P. quadrifarium* pajonales, is a very effective technique to improve carrying capacity and animal performance.

Key Words: *Paspalum quadrifarium*, *Lotus tenuis*, fire, weed control, diseases, species diversity

Paspalum quadrifarium Lam. (paja colorada) forms dense tall (1-1.5 m) grassland communities referred to locally “pajonales”. Some researchers believe that it was the predominant vegetation of the Flooding Pampas at the end of the 19th Century (Vervoorst 1967). Because of the low carrying capacity of the “pajonales”, ranchers tend to replace them with seeded pastures. There is concern about the impact that this replacement process has on the biodiversity of the region by decreasing the native fauna that is strongly attached to the pajonales communities.

Paja colorada has very low nutritional value for cattle except at the postburn regrowth stage. *In vitro* digestibility varies around 50%, crude fiber exceeds 70% and crude protein rarely reaches 12% on a dry matter basis. Consequently, it does not provide suit-

Resumen

En las pampas inundables de la Argentina el *Paspalum quadrifarium* Lamb. (Paja colorada) forma densas matas de pastizal. Estas comunidades son conocidas localmente como “pajonales” y generalmente tienen muy bajo valor nutritivo para los bovinos domésticos, excepto en los rebrotes postquemados. Para mejorar la calidad de forraje y el consumo de los pajonales de paja colorada, se sobresembró *Lotus tenuis* al voleo postquemado de dichos pajonales. Los objetivos de este experimento fueron monitorear las variaciones en la cobertura de *Lotus* y los demás componentes del pastizal luego de la siembra, evaluar el control de las malezas y la incidencia y severidad de enfermedades en *Lotus*. El experimento se condujo entre setiembre de 1993 y setiembre de 1996, en Azul, Provincia de Buenos Aires, Argentina. La cama de siembra postquemada favoreció la germinación y establecimiento del *Lotus*. El control químico de malezas más efectivo se obtuvo con 2,4-DB utilizado solo o en combinación con dicamba. El *Lotus* incrementó marcadamente la calidad del forraje del lote debido a su alto contenido de proteína cruda. Fueron determinadas 4 enfermedades fúngicas en *Lotus*: *Botrytis cinerea* Pers., *Stemphylium* sp. Wallroth, *Uromyces loti* Blytt. y *Fusarium* spp. Link ex Fr. las que solo causaron un ligero daño foliar y no impidieron la germinación y establecimiento de esta especie. La siembra en cobertura de *Lotus* inmediatamente luego de la quema de los pajonales de *Paspalum quadrifarium* es una técnica muy efectiva para mejorar la capacidad de carga y la respuesta animal.

able forage for young cattle or breeding females with high levels of nutrient requirements. The over seeding of lotus (*Lotus tenuis* Walst et Kit. is a naturalized forage legume in the region) immediately after burning of paja colorada pajonales, appears to have potential to improve forage quality and consumption by breeding cattle. However, a range of diseases caused by pathogens in Argentina (Wolcan and Dall Bello 1988, Dall Bello and Wolcan 1992) could affect the lotus survival.

The adequacy of postburned “seedbed” (formed by ashes and bare ground) for lotus germination, the competition with perennial weeds and the effect of diseases, could affect the establishment of the lotus plants. The objective of this experiment were to follow the after seeding cover development of lotus, evaluate the efficiency by weed control and to describe the diseases affecting its aerial plant parts.

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Materials and Methods

The experiment was carried out in a "pajonal" situated 70 km north of Azul in the center of Buenos Aires province of Argentina, between September 1993 to September 1996. The climate is sub humid and temperate (Thornthwaite and Mather 1957) with an annual rainfall of 900 mm and mean temperatures of 16°C. The pajonal was covered with 70% paja colorada growing over hydromorphic soil with pH varying between 7.5 and 8.0 and 4% organic matter. The soil belongs to the edaphic dominion 23 group (INTA-CIRN 1989).

Four randomized 20 x 34 m blocks with a factorial arrangement were divided into 2 equal sized plots, 1 of which was seeded and the other remained as a control. Burning was done in early spring (12 September 1993) with prescript fire. Immediately after burning, 2 kg/ha of scarified, inoculated and pelleted *Lotus tenuis* seed was hand broadcast.

Two month after sowing plots were divided into 6 subplots: control, dicamba (3,6-dichloro-2-methoxybenzoic acid) 57.5 g ai ha⁻¹, 2,4 DB (4-(2,4-dichlorophenoxy) butanoic acid) 800 g ae ha⁻¹, MCPA (4-chloro-2-methylphenoxyacetic acid) 280 g ae ha⁻¹, 2,4DB 800 g ae ha⁻¹ + dicamba 57.5 g ai ha⁻¹, MCPA 280 g ae ha⁻¹ + dicamba 57.5 g ai ha⁻¹. All treatments included a 0.2% rate of non-ionic detergent in the aspersion volume that was equivalent to 170 liter/ha. Overall, the main treatments were: seeded or control and sub-factors were 5 herbicide treatments and control. The effects were evaluated with ANOVA and means tested with the SNK test at P = 0.05.

The Braun-Blanquet (1979) method was used to determine the establishment and growing of lotus, weeds, paja colorada and bare ground 2, 8, 12, 14, and 29 months after sowing. Biomass was harvested in the 12, 20, and 29 month after sowing and dry matter and crude protein determined on subsamples by standard procedures. Seedling emergence of lotus was measured by presence and abundance parameters. The effectiveness of herbicide treatments was evaluated using a visual percent scale method in which zero represents the control treatment and 100%, the treatment with a total control of weeds.

Plant pathogens were studied in lotus plants. Ten, 0.5 m² quadrats were sampled in each of the sites for 2 situations: lotus plants in associate growth with paja colorada and lotus growing in the area between paja colorada plants. The inci-

*, Paja Colorada □ Weed = Lotus tenuis . Bare Ground - Other Grasses

Fig. 1. Cover changes occurred throughout the experimental time.

dence and severity of plant pathogens were appraised from emergence until the 24th month by estimating the percentage of leaf and shoot area affected by disease on a visual 0–6 scale (modified from James 1971), where 0 = no disease and 6 = leaf/shoot very severely affected.

Results and Discussion

Vegetation cover changes after burning and lotus seeding

Figure 1 shows the changes in ground cover observed throughout the experiment. Prior to burning in September 1993, cover was made up of 70% dead paja colorada, 10% broad-leaved weeds (*Plantago lanceolata* L., *Rumex crispus* L., *Hydrocotyle bonariensis* Lam., *Mentha pulegium* L., *Eryngium echinatum* Urban.) and 20% bare ground. A number of other weeds

(*Anagallis arvensis* L., *Carduus acanthoides* L., *Stellaria media* (L.) Vill., *Leontodon taraxacoides* (Vill.) Merat, *Sonchus oleraceus* L.) germinated after the burning treatment.

After 45 days from sowing, lotus accounted for 33% of ground cover. Weeds cover increased to 23% and paja colorada and bare ground diminished to 40% and 4%, respectively. After 8 months (Fig. 1), the cover of paja colorada and bare ground were unchanged, but lotus increased to 43% and weeds decreased to 8%. A new component, other grasses, emerged with values close to 5%. The decreased weed cover is associated with the chemical controls, although cover data is an average of a range of control effects given by the different herbicides used. The relationship between decreased weed cover and increased lotus cover, suggest the importance of weed suppression on lotus establishment. Once established,

Table 1. Weed cover 2 months after burning.

Species	Cover		Phenological Stages
	Without Lotus	With Lotus	
	(%)	(%)	
<i>Anagallis arvensis</i> L.	8.0	4.0	Seedlings
<i>Carduus acanthoides</i> L.	11.0	5.0	Seedlings
<i>Eryngium echinatum</i> Urban.	5.0	5.0	Adults
<i>Hydrocotyle bonariensis</i> Lam.	11.0	18.0	Adults
<i>Leontodon taraxacoides</i> (Vill.) Merat	3.0	3.0	Seedlings
<i>Mentha pulegium</i> L.	22.0	27.0	Adults
<i>Rumex crispus</i> L.	22.0	24.0	Adults
<i>Sonchus oleraceus</i> L.	8.0	5.0	Seedlings
<i>Stellaria media</i> (L.) Vill.	8.0	5.0	Seedlings

Table 2. Efficacy of chemical control.

Treatment	Efficacy
	(%)
Dicamba	21 d
2,4-DB	69 ab
MCPA	54 bc
2,4-DB + Dicamba	79 a
MCPA + Dicamba	47 c

lotus is highly competitive with weeds (Ortega and Laterra 1995).

After 12 months, the cover percentage of paja colorada and lotus stabilized at 37 and 40%, respectively. However, during the second year, a very severe winter drought occurred which killed plants thereby increasing the proportion of bare ground. After the spring rains, lotus cover recovered and in the 29th month occupied most of the vegetable cover. Paja colorada cover and bare ground decreased markedly. It was observed that cattle consumed a larger proportion of the paja colorada plants when lotus grew together with them. This probably explains the decrease in paja colorada cover when lotus is present.

Adults plants of *Eryngium*, *Rumex*, *Mentha* and *Hydrocotyle* spp. which were present prior to burning, sprouted after burning and did not suffered the effect of lotus presence. The annual weeds (*Anagallis arvensis*, *Carduus acanthoides*, *Sonchus oleraceus* and *Stellaria media*) germinated after burning and showed a significant lower plant cover on plots

Fig. 3. Pathogens on *Lotus tenuis* in a 24-month period.

where lotus were present, as compared to plots not sown with lotus (Table 1).

The chemical control of weeds (Table 2) was equally effective for 2,4-DB when used alone or when combined with dicamba with values close to 80%. The least effective treatment was with dicamba. Intermediate control was obtained with the MCPA's formulas. Due to the low presence of annual weeds, significant differences were not detected on the chemical control between lotus seeded or unseeded plots. Consequently, chemical control data was analyzed independently from the lotus seeding treatment.

Mixtures of 2,4-DB with dicamba, as well as dicamba used alone, were effective only with the postburn regrowth of adult plants of *Rumex crispus*. This species, as all the *poligonacea* are not satisfactorily controlled by the herbicides 2,4-D, 2,4-DB and MCPA.

Biomass accumulation

Lotus dry biomass accumulated 86 g/m² 12 months after burning and seeding which accounted for 16 % of total dry biomass. The lotus biomass contribution to total biomass increased to 18 % and 28 % after 20 and 29 months, respectively. There was no difference in total biomass between the unseeded and seeded treatments. This indicates that the lotus growth occurred at the expense of paja colorada growth. Also it seems to show that once established, lotus has the ability to maintain or even increase pasture biomass (Fig. 2).

The crude protein content of accumulated biomass increased from 7 % for paja colorada to 21% for lotus. The protein content in paja colorada is lower than the nutritional requirements for beef cattle. The lotus plots offered about 30g/m² of crude protein compared to only 10 g/m² in unseeded plots. In earlier studies, paja colorada postburn regrowth reached a crude protein content of 12% for the first regrowth after burning, but decreased thereafter (Sacido et al. 1995). An increase in available soil nitrogen availability from N fixed by legumes and liberation of N of microbial biomass facilitated by the early heating of soil have been suggested as possible explanations for this increase in

Fig. 2. Dry biomass (kg m⁻²) of treatments with or without lotus.

Fig. 4. Incidence and severity of *Uromyces loti* in leaflets of *Lotus tenuis* a) in associate growth with *P. quadrifarium* plants, b) growing in the area between *P. quadrifarium* plants.

the quality of paja colorada (Ojima et al. 1990, García 1992). The replacement of broad leaves weeds by forage legumes also improves the primary productivity and forage quality of native grasslands (Quinos, et al. 1994, De Battista and Miller 1995, Colabelli and Miñón 1993, Teglia et al. 1992, Montes and Cauhépe 1985).

Diseases in *Lotus tenuis*

Four fungal diseases were found on lotus plants throughout the experiment: leaf spot (*Botrytis cinerea* Pers.) in leaflets and stems, the disease did not injure more than 20% of plants and the severity never reached grades above 1 in leaflets and stems. Cold and moist weather was coincident with these symptoms (Fig 3). Rust

(*Uromyces loti* Blytt.) was found also on lotus leaflets and stems. Lotus plants growing in close proximity to paja colorada exhibited high rust incidence (100% with and severity grade 2) whereas for plants growing in the area between paja colorada the incidence was reduced (70% and severity grade 1). During February and May 1995, another rust attack was registered (Figs. 3 and 4).

Fusarium spp. Link ex Fr., (predominantly *F. oxysporum* Schlecht.), affected 20-30% of roots and stems during November 1995 (14 months after burning) with a grade 3 severity. In April 1996, the incidence was 90% and the severity was also grade 3. Although the incidence was high, the disease did not cause plant death.

The leaf spot caused by *Stemphylium* sp. Wallroth, affected 30% of leaflets with the more severe attacks in the summer months. The location of lotus plants affected the severity of attack with grades 2 to 3 found in lotus plants growing in associated growth with paja colorada, but only grade 1 in the lotus growing between paja colorada plants.

Conclusions

(1) The postburn seedbed was very favorable for lotus germination and establishment. After 29 months of treatments of burning and seeding, lotus reached a cover of 20%; paja colorada and bare ground cover decreased significantly during the same period.

(2) Lotus showed a high competitive ability with the annual broad-leaved weeds. The most effective chemical control was obtained with 2,4-DB formulated pure or mixed with dicamba.

(3) Lotus increased markedly the forage quality of the pasture due to its high crude protein content.

(4) Four fungus diseases were found: *Botrytis* and *Stemphylium* leaf spots, leaf and shoot rust and *Fusarium* wilt. However, they caused only light damage and did not impair lotus germination or establishment.

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Biological control of leafy spurge with introduced flea beetles (*Aphthona* spp.)

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Astract

Flea beetles (*Aphthona* spp.) were introduced into leafy spurge (*Euphorbia esula* L.)-infested rangeland in east-central North Dakota. The study objectives were to evaluate the effects of the introduced insects on leafy spurge cover, density, and yield, and grass and grass-like yield of associated plant communities. *Aphthona* spp. were released in 1988 and 1989 at 2 sites near Valley City, N.D. Aboveground vegetative sampling for leafy spurge cover, density and yield, and grass and grass-like yield was conducted between 1993 and 1995. Belowground sampling of root density, dry weight and root buds was conducted between the release date and 1995. *Aphthona* spp. reduced aboveground cover, density and yield of leafy spurge and increased yield of grass and grass-like species. Leafy spurge root density, weight, and number of root buds decreased on insect release sites between release dates and 1995. Reduced stem density of leafy spurge and increased grass and grass-like yield, should enhance cattle use and production from these sites.

Key Words: biological control, leafy spurge, insects, flea beetles, range improvement

Biological control of introduced noxious weeds using insects has received limited use on rangelands (Vallentine 1989). Successful biological control efforts using insects has been reported for St. John's-Wort (*Hypericum perforatum* L.) (Huffaker and Kennett 1959), pricklypear (*Opuntia* spp.) (Goeden et al. 1968), and tansy ragwort (*Senecio jacobaea* L.) (Hawkes 1968). Efforts to control leafy spurge (*Euphorbia esula* L.) with insects has been ongoing since the 1960s with significant expansion in the 1970s and 1980s (Harris 1984, Pemberton 1985).

Leafy spurge is an introduced plant from Eurasia that is extremely persistent and competitive in grazed rangelands (Dunn 1979). It is considered a prime candidate for biological control because of its propensity to invade a variety of habitats such as grasslands, woodlands, riparian areas and waterways where alternative control efforts may be limited and it is a perennial weed providing a continuous source of food to organisms capable of utilizing portions of the plant. Unfortunately, leafy spurge's defense mechanisms such as the milky latex make utilization of the plant difficult except for well adapted insects that have evolved means to overcome these defenses (Best et al. 1980).

Resumen

Se introdujeron "Flea beetles" (*Aphthona* spp.) en pastizales de la región centro-este de North Dakota los cuales estaban infestados con "leafy spurge" (*Euphorbia esula* L.). Los objetivos del estudio fueron evaluar los efectos de los insectos introducidos en la cobertura, densidad y rendimiento del "Leafy spurge" y en el rendimiento de zacates y planta similares a los zacates de las comunidades vegetales asociadas. Los *Aphthona* spp. Se liberaron en 1988 y 1989 en 2 sitios cerca de Valley City, N.D. El muestreo de las partes vegetativas aéreas para determinar cobertura, densidad y rendimiento del "Leafy spurge" y el rendimiento de los zacates y plantas similares a zacates se condujo entre 1993 y 1995. El muestreo de las partes subterráneas para determinar la densidad y peso seco de raíces y yemas radicales se condujo entre la fecha de liberación de los insectos y 1995. Las especies de *Aphthona* redujeron la cobertura, densidad y rendimiento de "leafy spurge" e incrementaron el rendimiento de las especies de zacates y plantas similares a ellos. La densidad de raíces de "Leafy spurge", el peso y numero de yemas radicales disminuyo entre la fecha de liberación y 1995 en los sitios en donde se liberaron los insectos. La reducción de tallos de "Leafy spurge" y el aumento del rendimiento de zacates y plantas similares a estos debe incrementar el uso de ganado bovino y la producción en estos sitios.

Eight insects have been released to control leafy spurge in North Dakota since the 1980s (Lym and Zollinger 1995). Of these, flea beetles (*Aphthona* spp.) have been the most successful for establishment, reproduction and redistribution. However, limited quantitative information is available regarding the impact of *Aphthona* spp. on leafy spurge and the associated plant community. The objectives of this study were to evaluate the effects of *Aphthona* spp. on leafy spurge cover, density and yield, and grass and grass-like yield of associated plant communities.

Material and Methods

Experiments to evaluate leafy spurge control with an introduced biological control agent *Aphthona* spp. were established at 2 sites in east-central North Dakota. A total of 80 flea beetles were released in 1988 at a site that was approximately 15 km northwest of Valley City (North) on the Katie Olson Wildlife Management Area (98°10'N 47°15'W). Biological control agents at this site were

2 flea beetle species, *A. czwalinae* and *A. lacertosa*. A second site was located approximately 15 km southeast of Valley City (South) on private land (97°50'N 46° 50'W). Approximately 1,000 *A. nigriscutis* were released at this site in 1989.

Both sites are located within the Sheyenne River drainage system, which is highly dissected and steeply sloping (>15%). Soils were a Kotten silty clay loam (fine, montmorillonitic Udertic Haploboroll) at the North site and a Nutley silty clay (loamy, mixed Lithic Haploboroll) at the South site. Both sites supported northern mixed grass prairie (Barker and Whitman 1989) with infestations of leafy spurge exceeding 200 stems/m². Annual average precipitation for east-central North Dakota is 45 cm with approximately 75% received during the growing season (April through September). Annual precipitation received between 1988 and 1995 was similar to the long-term average, 50 cm, with 80% occurring during the growing season.

Aboveground vegetative sampling was initially conducted at the North experiment in 1988. Sampling was abandoned after 1990 because the insect colony migrated to an adjacent area. Vegetative sampling resumed between 1993 and 1995 after the insect colony became permanently established. Vegetative sampling was initiated in 1993 at the South experiment to allow time for the insect colony to permanently establish. Three random transects each were located in insect colonized and insect free areas at both study sites. Leafy spurge cover and density were estimated from eight 0.1 m² quadrats positioned randomly along each transect. Leafy spurge, and grass and grass-like yields were determined by clipping and drying (60°C) the vegetation within four, 0.1 m² quadrats along each transect. Vegetative measurements were conducted at the peak standing crop in late July each year.

Soil samples for root characterization were initiated in 1988 at the North site and 1989 at the South site. At North and South sites, 4 and 3 random transects were placed at insect colonized and insect free areas, respectively. The insect free transect sampling was terminated at both study locations in 1991 due to movement of the insects into these areas. On each transect, 5 random soil cores 15-cm deep (12-cm diameter) were collected using a 12-cm diameter golf cup-cutter each October and stored in plastic bags at -4°C. The leafy spurge roots from each core were extracted from the soil and washed. The number of individual root segments and root buds for each segment were recorded. The root

Fig. 1. Leafy spurge cover (%) following *Aphthona* spp. colonization of leafy spurge-infested rangeland. Bars with different letters differ ($P < 0.05$).

segments were then dried at 60°C for dry weight determinations.

The effect of flea beetle control on leafy spurge was evaluated as a randomized complete block design at 2 locations with 3 blocks (transects) and 2 treatments (insect free and insect colonized). Blocks were found to be nonsignificant between locations so a completely randomized design was utilized. Vegetative and root data by treatment and year were analyzed using a one-way ANOVA (SPSS, Inc. 1994) and mean differences were considered significant at the 5% probability level using Tukey's h test.

Results and Discussion

Foliar cover of leafy spurge was reduced ($P < 0.05$) on *Aphthona* spp. colonized sites compared to insect free sites (Fig. 1). Pre-treatment estimates (1988) of leafy spurge cover were 45% (data not shown) which was similar to the control sites in 1994 and 1995. A 6- to 7-fold decrease in leafy spurge cover occurred on release sites over this same time period. Stromme et al. (1996) reported a similar reduction in leafy spurge foliar cover, 40% to 1.7%, five years after *A. nigriscutis* were released near Edmonton, Canada.

Leafy spurge stem densities were reduced on *Aphthona* spp. release sites

compared to pre-study estimates (218/m²) and control sites (Fig. 2). By 1994, *Aphthona* spp. had reduced leafy spurge stem densities nearly 40-fold to only 5/m². Stem density reductions have also been reported by Hansen (1993), Baker et al. (1996), Lym et al. (1996) and Stromme et al. (1996). However, only Stromme et al. (1996) reported reductions in leafy spurge stem densities of the magnitude evaluated in this study.

Stem densities of leafy spurge have been reported to influence cattle grazing behavior (Lym and Kirby 1987). Stem densities exceeding 100/m² decreased cattle use of leafy spurge-infested rangeland. Leafy spurge stem densities on insect release sites were reduced to a level that would allow cattle grazing.

Total herbaceous yields were greater on control sites compared to the insect release sites each year due to the biomass contribution from leafy spurge (Table 1). Leafy spurge biomass was reduced each year on the insect release sites compared to the controls, while graminoid yields were greater on *Aphthona* spp. release sites in 1994 and 1995 compared to the controls. Stromme et al. (1996) reported a decrease in leafy spurge biomass from 1,730 to 17 kg/ha and an increased grass biomass from 14 to 433 kg/ha which are comparable to those reported in this study.

Year	Grass and Grass-like	Leafy Spurge	Total Herbaceous
		----- (kg/ha) -----	
		INSECT FREE	
1993	919 ± 177a ¹	3381 ± 255a	4300 ± 229a
1994	1067 ± 107a	1140 ± 115b	2207 ± 144b
1995	998 ± 103a	1248 ± 95b	2246 ± 198b
		INSECT COLONIZED	
1993	1041 ± 100a	742 ± 57c	1783 ± 111c
1994	1612 ± 189b	105 ± 39d	1717 ± 188c
1995	1526 ± 147b	110 ± 30d	1636 ± 176c

Grass and grass-like yield increased approximately 50% on *Aphthona* spp. colonized sites compared to insect free sites. However, yields were lower than sites without leafy spurge infestation (Table 1). Silty and clayey range sites in this vegetation zone would be expected to produce 2,600 kg/ha under average environmental inputs (USDA, SCS 1984). However, leafy spurge stem densities on insect colonized sites were reduced below 100 stems/m²; therefore, normal cattle foraging activities would be expected to occur on these sites. Given average stocking rates for these range sites without leafy spurge infestation (2.2 AUM/ha) and the forage yields as reported in this study, stocking rates would be 1.3 AUM/ha of treated leafy spurge.

sites and competing for limited growth resources such as moisture and nutrients. This competition for resources may be playing a role in suppressing the establishment and survival of graminoid seedlings and vegetative recolonization of the study sites.

Leafy spurge root density, weight and number of root buds decreased on *Aphthona* spp. colonized sites between 1988 and 1995 (Fig. 3). Data for insect free sites is not available as the *Aphthona* spp. migrated through the root-harvest control transects. *Aphthona* larvae feed on the root system of leafy spurge when soil temperatures exceed 9°C and emerge as adults in early summer. Root biomass reduction is probably the main causative agent in the decrease in aboveground

cover and density of leafy spurge on the sites. Despite a significant reduction in root bud number over the 7 to 8 years of the study, 10 to 15 root buds per 10 cm² of topsoil remained. Given the number of root buds in the topsoil, leafy spurge could rapidly recolonize a site without the continued presence of the *Aphthona* spp.

The introduction of *Aphthona* spp. into leafy spurge-infested rangeland resulted in decreased cover, density and biomass of leafy spurge and increased yield of grass and grass-like species. Significant reductions in leafy spurge root biomass occurred within 2 to 3 years, yet beneficial aboveground changes occurred only after 5 years following insect colonization. Grass and grass-like yield had not recovered after 7 to 8 years following insect colonization.

The results of this study should not be interpreted too broadly. Only 3 of 8 *Aphthona* spp. were released with soils limited to silty/clayey on steep sideslopes in this study. Nowierski et al. (1996) characterized habitat associations for leafy spurge and flea beetles in Europe, yet little is known of the establishment and habitat

JOURNAL OF RANGE MANAGEMENT 53(3), May 2000

Fig. 3. Root density, dry weight and root buds ($\bar{x} \pm S.E.$) from soil cores at 2 locations following *Aphthona* spp. colonization of leafy spurge-infested rangeland. Means by location followed by a different letter differ ($P < 0.05$).

requirements of *Aphthona* spp. in North America. *Aphthona* spp. establishment in sandy soils, overflow or subirrigated range sites, and in shrubby or riparian areas have not been successful to date. Questions concerning successful establishment procedures and habitat barriers such as soil, slope, aspect, root demographics, leafy spurge density, surface litter, initial release sizes, over-winter survival, population size, persistence, rate of spread and more remain to be answered.

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Abstract

Picloram, fertilizer, and defoliation interactions on spotted knapweed reinvasion

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Abstract

Spotted knapweed (*Centaurea maculosa* Lam.) management may be enhanced by integrating strategies that stimulate and maintain competitive grasses. The objective of this study was to determine if picloram, fertilizer, and timing and frequency of grass defoliation could be integrated to minimize spotted knapweed reinvasion. Sixteen chemical treatments [4 picloram rates (0.00, 0.14, 0.28, and 0.42 kg a.i. ha⁻¹) and 4 fertilizer rates (source: 16-20-0, N-P-K; material: 0.0, 66, 132, 198 kg ha⁻¹)] were applied in the spring of 1994 to 4 by 4 m plots and factorially arranged in a randomized-complete-block design. Within each plot, 6 grass defoliation treatments were randomly applied to 1 by 1 m sub-plots. From 1994 through 1997, 60% of the above ground grass biomass was hand clipped and removed from the plots during the spring, summer, fall, alternating spring/fall, all 3 seasons. A control received no grass defoliation. The experiment was replicated 4 times at 2 sites dominated by spotted knapweed. At peak standing crop in 1997 spotted knapweed density, grass and spotted knapweed biomass; and percent cover of spotted knapweed, grass, litter, and bare ground were measured. Data were analyzed as a split-plot using analysis of variance. Four years after treatment all rates of picloram reduced spotted knapweed density, biomass, and cover, and increased grass yield. Nitrogen and P fertilizer tended to increase spotted knapweed density and biomass. Nitrogen and P fertilizer plus defoliation in all 3 seasons caused a greater increase in spotted knapweed reinvasion at the site with Kentucky bluegrass (*Poa pratensis* L.) than the site with timothy (*Phleum pratense* L.) and smooth brome (*Bromus inermis* Leys.). Fall-only defoliation and no defoliation appear to deter spotted knapweed reinvasion better than defoliation in all 3 seasons and alternately in the spring and fall.

Key Words: *Centaurea maculosa*, integrated weed management, grass defoliation, grazing management

Spotted knapweed (*Centaurea maculosa* Lam.), a short-lived perennial native to Eurasia, is rapidly invading rangeland throughout western North America. This aggressive weed has been spreading at about 27% per year and infests over 2.8 million hectares in Montana, and adjoining states and Canadian provinces (Chicoine et al. 1985, Lacey et al. 1989). Spotted knapweed can be found in 326 counties in the western United States (Sheley et al. 1998). Impacts associated with this species include reduced forage production (Watson and Renney 1974), plant species

Resumen

El manejo de "Spotted knapweed" (*Centaurea maculosa* Lam.) puede ser mejorado mediante la integración de estrategias que estimulan y mantienen los zacates competitivos. El objetivo de este estudio fue determinar si el picloram, la fertilización y la época y frecuencia de defoliación del zacate pudieran ser integrados para minimizar la reinvasión de "Spotted knapweed". En primavera de 1994 se aplicaron 16 tratamientos químicos [4 dosis de picloram (0.00, 0.14, 0.28 y 0.42 kg i.a ha⁻¹) y 4 dosis de fertilizante (0.0, 66, 132 y 198 kg ha⁻¹; fuente: 16-20-0, N-P-K)] en parcelas de 4 x 4 m bajo un diseño de bloques completos al azar en arreglo factorial. Dentro de cada parcela se aplicaron 6 tratamientos de defoliación, los cuales se asignaron aleatoriamente a subparcelas de 1 x 1 m. De 1994 a 1997, durante las épocas de primavera, verano, otoño, alternadamente en primavera/verano y en las tres estaciones del año, se cortó y removió manualmente el 60% de la biomasa aérea de las parcelas. Las parcelas control no recibieron defoliación del zacate. El experimento se repitió 4 veces en 2 sitios en los que predominaba el "Spotted knapweed". En 1997, cuando se alcanzó la máxima producción de biomasa en pie, se midió la densidad de "Spotted knapweed", la biomasa de los zacates y del "Spotted knapweed", y el porcentaje de cobertura de "Spotted knapweed", zacates, mantillo y suelo desnudo. Los datos se analizaron mediante análisis de varianza y bajo el diseño experimental de parcelas divididas. Cuatro años después de aplicar los tratamientos, todas las dosis de picloram redujeron la densidad, biomasa y cobertura de "Spotted knapweed" e incrementaron el rendimiento de forraje de los zacates. La fertilización nitrogenada y fosforada tendieron a incrementar la densidad y biomasa de "Spotted Knapweed". La fertilización nitrogenada y fosforada mas la defoliación en las tres estaciones causó una mayor reinvasión de "Spotted knapweed" en el sitio con "Kentucky bluegrass" (*Poa pratensis* L.) que en el sitio con "Timothy (*Phleum pratense* L.) y "Smooth brome" (*Bromus inermis* Leys.). Defoliar solo en otoño y el no defoliar parece detener la reinvasión de "Spotted knapweed" mejor que la defoliación en todas las tres estaciones y alternativamente en primavera y otoño.

diversity (Tyser and Key 1988), wildlife habitat (Bedunah and Carpenter 1989) and increased bare ground, surface water runoff and stream sedimentation (Lacey et al. 1989), and management costs (Griffith and Lacey 1989).

Most broadleaf herbicides are effective in reducing spotted knapweed populations. Picloram (4-amino-3,5,6-trichloropicolinic acid) applied at a rate of 0.28 kg active ingredient (a.i.) ha⁻¹ provides control for 2 to 5 years (Davis 1990). Although the per-

sistence of picloram in the soil affects weeds for 12 to 30 months (Hamaker et al. 1967), extended control is enhanced by competition from residual perennial grasses that are released by the herbicide application (Sheley et al. 1998). Combining herbicide and fertilizer applications has increased forage production on rangelands (Hart et al. 1995); however, little is known about combining them to control knapweed and enhance forage production.

Integrating picloram and fertilizers may have a synergistic effect on providing spotted knapweed control and enhanced grass production. In a pilot study, Sheley and Roché (1982) combined picloram (0.28 kg a.i. ha⁻¹) and fertilizer (N + P: 17.9 + 22.4 kg ha⁻¹) which increased grass yield from 275 (control) and 660 (picloram alone) to 2,200 (picloram plus fertilizer) kg ha⁻¹, 2 years after application. In that study, knapweed control was also greater where picloram was combined with fertilization than the control and picloram alone. More recently, Sheley and Jacobs (1997) found no picloram by N + P fertilizer interactions in Montana. Picloram treatments (0.14 to 0.42 kg a.i. ha⁻¹) reduced spotted knapweed to nearly zero, and fertilization at the highest rate (180 kg ha⁻¹; 16-20-0 NPK) increased grass yield on the site with a substantial grass understory.

Spotted knapweed seeds can remain dormant in the soil for up to 8 years and reinvasion on sites treated with picloram usually begins within 2–5 years after herbicide application (Davis et al. 1993). While many factors affect picloram persistence in the soil including photodegradation, precipitation, and soil texture (Davis 1990), and therefore longevity of spotted knapweed control, it is believed that the competitive ability of the residual grass on treated sites also affects spotted knapweed reinvasion (Sheley et al. 1998). The competitive interaction between weeds and perennial grasses is affected by frequency, timing and intensity of defoliation which in turn affects the ability of perennial grass communities to withstand weed invasion (Maschinski and Whithan 1989, Jacobs and Sheley 1997). Although studies suggest that moderate grazing does not accelerate invasion of knapweeds (*Centaurea* spp.) into rangeland (Sheley et al. 1997, Jacobs and Sheley 1997), we found no studies that attempt to quantify the effects of defoliation on their reinvasion after control.

An important concern of rangeland managers is how to prevent or reduce weed reinvasion on areas where weeds have been controlled. The overall objective of this study was to determine the effect of the

timing and frequency of grass defoliation on spotted knapweed reinvasion on areas treated with picloram and fertilizer combinations. Specific objectives were to 1) determine if picloram and fertilizer interact to increase long-term spotted knapweed control or grass yield, and 2) determine if timing and frequency of grass defoliation affected spotted knapweed reinvasion. We hypothesized that picloram and fertilizer would interact to increase spotted knapweed control and grass yield, which would limit reinvasion. In addition, we believe that spotted knapweed reestablishment would be greater in areas with more frequent grass defoliation and defoliation in the spring than summer and fall defoliations.

Materials and Methods

Study Sites

Field studies were conducted from 1994 through 1997 on 2 sites located 15 km west of Bozeman, Mont. (111°5'36"W, 45°35'26"N). Both sites were within a *Festuca idahoensis*/*Agropyron spicatum* habitat type (Mueggler and Stewart 1980), and dominated by spotted knapweed. Site 1 was an abandoned hayfield. Spotted knapweed densities were 470 ± 140 plants m⁻². Associated grass species were smooth brome (grass) (*Bromus inermis* Leys), timothy (*Phleum pratense* L.), and Kentucky bluegrass (*Poa pratensis* L.). Associated grass on site 2 was predominantly Kentucky bluegrass. Spotted knapweed density was 140 ± 107 plants m⁻². Soils at both sites consisted of 70% Beaverton cobbly loam (loamy-skeletal over sandy or sandy-skeletal mixed, Typic Argiborolls) and 30% Hyalite loam (fine-loamy, mixed, Typic Argiborolls). Sites were nearly level and at an elevation of 1,340 m. Annual precipitation ranges from 380 to 480 mm and the frost-free period ranges from 90 to 110 days at both sites.

Experimental Design

Sixteen chemical treatments (4 picloram rates, 4 fertilizer rates) were applied to 4 by 4 m plots and factorially arranged in a randomized-complete-block design. Within each plot, 6 different defoliation treatments were randomly applied to 1 x 1 m sub-plots. The experiment was replicated 4 times at both sites.

Picloram rates of 0.0, 0.14, 0.28, and 0.42 kg a.i. ha⁻¹ were applied using a 6 nozzle backpack sprayer delivering 130 liters ha⁻¹ spray solution. Granular fertilizer was broadcast at N + P rates of 0.0 + 0.0, 10.5 + 13.2, 21.1 + 26.4, and 31.7 + 39.6 kg ha⁻¹

(source: 16-20-0, N-P-K; material: 0.0, 66, 132, 198 kg ha⁻¹) using a hand-cyclone applicator. Both sites were treated on 2 May 1994 when spotted knapweed was in the rosette stage. Air temperature, soil temperature (surface), and relative humidity were 17.5°C, 21°C, and 90%, respectively, at the time of application. Winds ranged from 0 to 6 km hr⁻¹. Individual 4 x 4 m plots were spatially separated from each other by a 2.1 m buffer zone treated with 0.28 kg a.i. ha⁻¹ of picloram to prevent spotted knapweed seed contamination from neighboring plots.

From fall 1994 through fall 1997, six defoliation regimes differing in the frequency and timing of defoliation were applied as 1 x 1 m sub-plots. They were control (no defoliation), spring, mid-summer, fall, alternating spring/fall, and repeated defoliations in spring, summer, and fall. Defoliation treatments were applied by hand-clipping grasses to 60% of the above-ground biomass. Defoliation level was calibrated by clipping grass from ten, 0.2 x 0.5 m plots estimated at 60% and comparing their average weight with the average weight of grass clipped to the soil surface from ten, 0.2 x 0.5 m plots. All clippings were removed from the plots. Repeated defoliations removed 60% of the remaining foliage including all regrowth.

Sampling

At peak standing crop (August), above-ground biomass within 1 randomly located 0.5m² hoop was harvested from each sub-plot in 1997. Grass and spotted knapweed were separated and dried at 60°C until weights were constant (48 hrs minimum) and then weighed. Juvenile (plants without flower stems) and total spotted knapweed density (plants m⁻²) were counted within randomly located 0.2 x 0.5 m frames in each sub-plot prior to biomass harvest. Within the same frame visual estimations of percent cover were estimated for spotted knapweed, all grass species, litter, and bare ground.

Data Analysis

Sites were analyzed separately. Data were analyzed as a split-plot using analysis of variance (SAS Institute, Inc. 1990). Picloram and fertilizer were applied as whole-plots. Defoliation was applied as sub-plots. Picloram, fertilizer, and their interaction were tested using block*picloram*fertilizer as the error term. Defoliation, picloram*defoliation, fertilizer*defoliation, and the 3-way interaction were tested using the residual error. When significant (P <

0.05) F-test were calculated, differences among means were tested using protected least significant differences procedures (Peterson 1985).

Results

Density

Juvenile ($p < 0.001$) and total spotted knapweed ($p < 0.001$) density were affected by picloram 4 years after treatment at site 1. All picloram rates reduced juvenile and total spotted knapweed density below that of the control. Juvenile density was reduced from 144 plants m^{-2} (0.0 kg a.i. ha^{-1} picloram) to 33, 6, and 1 plants m^{-2} (0.14, 0.28, 0.42 kg a.i. ha^{-1} picloram, respectively, $LSD_{0.05} = 45.9$). Picloram applications of 0.14, 0.28, and 0.42 kg a.i. ha^{-1} reduced total spotted knapweed densities to 49, 10, and 2 plants m^{-2} from 192 plants m^{-2} in the control ($LSD_{0.05} = 53.9$).

The effect of fertilizer on total spotted knapweed density was dependent upon the rate of picloram at site 2 ($p < 0.03$). Without picloram, fertilizer applied at 132 kg a.i. ha^{-1} provided total spotted knapweed densities higher than the other fertilizer rates (Table 1). At all other picloram rates, spotted knapweed densities were similar.

At site 2, the effect of defoliation on total spotted knapweed density was dependent upon the rate of fertilizer applied ($p < 0.03$). Without fertilizer, all defoliation treatments yielded similar total spotted knapweed density (Table 2). At 66 kg ha^{-1} , defoliation in all 3 seasons had higher spotted knapweed density than plots defoliated in the spring, summer, or fall. Alternating spring/fall grass defoliation yielded higher spotted knapweed densities than spring defoliation. All other treatments had similar spotted knapweed density at that fertilizer level. However, at 132 kg ha^{-1} fertilizer, defoliating grass all 3 seasons had the highest total spotted knapweed density, but was similar to those plots defoliated each spring. Total spotted knapweed density was lowest in plots without defoliation, but was similar to plots defoliated alternating spring/fall at this fertilizer level. At 198 kg ha^{-1} fertilizer, all defoliation treatments yielded similar total spotted knapweed density. Furthermore, total spotted knapweed density at this fertilizer level was similar to where fertilizer was not applied.

The effect of grass defoliation on the density of juvenile spotted knapweed plants was dependent upon the rate of picloram applied at site 2 ($p < 0.05$). When no picloram was applied, spring

Table 1. Effect of picloram fertilizer combinations on total spotted knapweed density at site 1.

Picloram (kg a.i. ha^{-1})	Fertilizer (N + P kg ha^{-1})			
	0	66	132	198
0.0	40	64	102	40
0.14	3	21	10	8
0.28	10	18	28	5
0.42	8	7	5	10
LSD $=0.05 = 25$				

Table 2. Effect of fertilizer and defoliation combinations on total spotted knapweed density at site 2.

Fertilizer (N + P kg ha^{-1})	Defoliation					
	None	Spring	Summer	Fall	Alternate	Sp-Su-Fa
0	18	13	23	18	13	7
66	29	14	21	21	38	41
132	13	43	35	38	29	59
198	11	13	24	14	14	20
LSD $=0.05 = 19$						

defoliation resulted in the lowest juvenile spotted knapweed density, but was similar to alternating spring/fall defoliation (Table 3). Defoliation in the summer, fall, and all 3 seasons resulted in the highest densities of juvenile spotted knapweed plants. Picloram applied at 0.28 kg a.i. ha^{-1} , had higher juvenile spotted knapweed densities when the plots were defoliated alternating spring/fall than when they were not defoliated. There were no differences in defoliation treatments when picloram was applied at 0.14 kg a.i. ha^{-1} and at 0.42 kg a.i. ha^{-1} .

Four years after treatment, picloram also interacted with fertilizer to affect juvenile spotted knapweed density at site 2 ($p < 0.001$). In the picloram control, juvenile spotted knapweed density was higher in the 66 and 132 kg ha^{-1} fertilizer treatments than the 0 and 198 kg ha^{-1} treatments (Table 4). Juvenile spotted knapweed densities were higher in plots treated with 66 kg ha^{-1} fertilizer than the fertilizer control when 0.14 kg a.i. ha^{-1} of picloram was applied. At the 0.28 kg a.i. ha^{-1} rate of picloram, juvenile spotted knapweed densities were higher in plots treated with 132 kg ha^{-1} of fertilizer

compared to 0 and 198 kg ha^{-1} . Juvenile spotted knapweed density was similar among all fertilizer treatments when picloram was applied at 0.42 kg a.i. ha^{-1} .

Biomass

Biomass of spotted knapweed ($p < 0.001$) and grass ($p < 0.001$) were affected by picloram on site 1, four years after treatment. Spotted knapweed biomass was the highest (192 kg ha^{-1}) when no picloram was applied ($LSD_{0.05} = 54$). Spotted knapweed biomass was 49, 10, and 2 kg ha^{-1} at picloram rates of 0.14, 0.28, and 0.42 kg a.i. ha^{-1} , respectively. Grass biomass was lowest (2,250 kg ha^{-1}) when no picloram was applied ($LSD_{0.05} = 893$). Plots treated with 0.14 kg ha^{-1} of picloram had 5,060 kg ha^{-1} of grass which was less than those treated with 0.28 (5,960 kg ha^{-1}) and 0.42 kg a.i. ha^{-1} (5,830 kg ha^{-1}).

Biomass of grass was also affected by grass defoliation at site 1 ($p < 0.001$). Grass biomass was lower in plots defoliated in all 3 seasons, (3,940 kg ha^{-1}), than in all other defoliation treatments ($LSD_{0.05} = 561$). The control (no defoliation) had the highest grass biomass of 5,600 kg ha^{-1} ,

Table 3. Effect of picloram and defoliation combinations on juvenile spotted knapweed density at site 2.

Fertilizer (kg a.i. ha^{-1})	Defoliation					
	None	Spring	Summer	Fall	Alternate	Sp-Su-Fa
0.0	34	16	54	46	26	52
0.14	14	6	5	4	13	13
0.28	4	9	13	11	21	17
0.42	3	9	9	9	4	11
LSD $=0.05 = 15$						

Table 4. Effect of picloram fertilizer combinations on juvenile spotted knapweed density site 2.

Picloram (kg a.i. ha ⁻¹)	Fertilizer (N + P kg ha ⁻¹)			
	0	66	132	198
0.0	22	50	67	13
0.14	3	18	8	8
0.28	8	15	22	4
0.42	8	7	5	10
LSD =0.05 =14				

although it was similar to plots defoliated in the fall (5,090 kg ha⁻¹). There were 4,620, 4,630, and 4,530 kg ha⁻¹ of grass in the spring, summer, and alternating spring/fall defoliations, respectively.

The effect of defoliation on spotted knapweed biomass was dependent upon the fertilizer treatment at site 2 ($p < 0.05$). When fertilizer was not applied, all defoliation treatments were similar (Table 5). When fertilizer was applied at 66 kg ha⁻¹, defoliation in the spring resulted in the lowest spotted knapweed biomass, although it was similar to defoliation in the summer, fall, and the control. At 132 kg ha⁻¹ of fertilizer, defoliation in all 3 seasons resulted in spotted knapweed biomass higher than all other defoliation treatments. When fertilizer was applied at 180 kg ha⁻¹, all defoliation treatments yielded similar spotted knapweed biomass.

Table 5. Effect of fertilizer and defoliation combinations of total spotted knapweed biomass at site 2.

Fertilizer	Defoliation					
	None	Spring	Summer	Fall	Alternate	Sp-Su-Fa
0	18	13	23	18	13	7
66	29	14	21	21	38	41
132	13	43	35	38	29	59
198	11	13	24	14	14	20
LSD =0.05 =20						

The effect of defoliation on grass biomass was dependent upon the rate of picloram applied at site 2 ($p < 0.05$). When picloram was not applied, defoliation in all 3 seasons yielded the lowest grass biomass, although it was similar to the effect of defoliation in the summer, spring, and alternating spring/fall (Table 6). The control, which was not defoliated, yielded the highest grass biomass and was similar to fall defoliation. When picloram was applied at 0.14 kg a.i. ha⁻¹, alternating spring/fall defoliation resulted in the highest grass biomass. However it was similar to all treatments except summer defoliation and defoliation in all 3 seasons, which yielded lower biomass. At 0.28 kg a.i. ha⁻¹, picloram applications interacted with

alternating spring/fall grass defoliation to yield grass biomass lower than plots with no defoliation. When picloram was applied at 0.42 kg a.i. ha⁻¹, alternating spring/fall defoliation resulted in the highest grass biomass. This treatment was similar to summer defoliation and defoliation in the fall only. Grass defoliation in the spring resulted in the lowest grass biomass, and was similar to the control and to defoliation in all 3 seasons.

Cover

At site 1, there was a main effect of picloram on spotted knapweed cover 4 years after treatment ($p < 0.001$). Without picloram spotted knapweed cover was 26%, which was higher than all 3 picloram treatments (LSD =0.05 = 7.6). Picloram, applied at 0.14 kg a.i. ha⁻¹, had spotted knapweed cover of 9% which was similar

and 0.42 kg a.i. ha⁻¹) increased grass cover (24, 31, and 30%) similarly over the control which was 15% (LSD =0.05 = 9).

Picloram had the only effect on spotted knapweed cover at site 2 ($p < 0.001$). All picloram treatments (0.14, 0.28, and 0.42 kg a.i. ha⁻¹) provided lower spotted knapweed cover (4, 4, and 2%) than the control which had a spotted knapweed cover of 25% (LSD =0.05 = 11).

Grass cover was affected by the interaction of picloram and fertilizer at site 2 ($p < 0.04$). When picloram was applied at 0.28 kg a.i. ha⁻¹, a fertilizer rate of 66 kg ha⁻¹ produced the highest grass cover, however, it was similar to plots treated with picloram at 0.42 kg a.i. ha⁻¹ and fertilizer applied at 132 kg ha⁻¹ (Table 7).

Grass cover at site 2 was also affected by defoliation treatments ($p < 0.01$). Plots not defoliated produced the highest grass cover (52%), although they were similar to those defoliated in the summer, which had grass cover of 47% (LSD =0.05 = 8). Grass cover in plots defoliated in all 3 seasons (33%) was similar to grass cover in plots defoliated in alternate spring/fall (40%).

Percent cover of litter at site 1 was affected by fertilizer rate ($p < 0.002$). Fertilizer applied at the highest rate yielded a higher litter cover (43%) than applications of 66 and 132 kg ha⁻¹ (30 and 36%), however, it was similar to the cover (36%) in plots that received no fertilizer (LSD =0.05 = 7.26).

The effect of defoliation on litter cover was dependent upon the picloram rate at site 1 ($p < 0.04$). When picloram was not applied, plots that had not been defoliated had higher litter cover than those defoliated alternating spring/fall and all 3 seasons (Table 8). When picloram was applied at 0.14 kg a.i. ha⁻¹, grass defoliation in all 3 seasons had lower litter cover than all other defoliation treatments. Rates of 0.14, 0.28, and 0.42 kg a.i. ha⁻¹ that were not clipped provided higher litter cover than all other defoliation treatments. Also, when picloram was applied at 0.28 kg a.i. ha⁻¹, defoliation in all 3 seasons produced lower litter cover than all other treatments except fall-only defoliation.

Table 6. Effect of picloram and defoliation combinations on grass biomass at site 2.

Fertilizer (kg a.i. ha ⁻¹)	Defoliation					
	None	Spring	Summer	Fall	Alternate	Sp-Su-Fa
0.0	4995	2793	3200	4103	2850	1982
0.14	3165	2867	2531	4100	4161	2668
0.28	5205	4556	4261	4713	3553	3838
0.42	4315	3173	5710	5160	5990	3888
LSD =0.05 =1430						

Table 7. Effect of picloram and fertilizer (kg ha⁻¹) combinations on percent grass cover at site 2.

Picloram (kg a.i. ha ⁻¹)	Fertilizer			
	0	66	132	198
0.0	30	36	27	34
0.14	37	40	48	38
0.28	46	68	37	50
0.42	46	41	55	44
LSD =0.05 =15				

Table 8. Effect of picloram and defoliation combinations on percent litter cover at site 1.

Fertilizer (kg a.i. ha ⁻¹)	Defoliation					
	None	Spring	Summer	Fall	Alternate	Sp-Su-Fa
0.0	34	33	28	30	20	18
0.14	58	43	33	29	34	22
0.28	63	38	35	33	40	24
0.42	64	44	39	40	39	32
LSD =0.05 =9						

Percent cover of bare ground at site 1 was affected by defoliation treatments ($p < 0.001$). Plots that did not receive defoliation had lower bare-ground cover (12%) than spring (27%), summer (32%), fall (33%) and alternating spring/fall (28%), while plots that were defoliated all 3 seasons had the highest bare ground cover (41%, $LSD_{0.05} = 6$). Bare-ground cover was also affected by the rate of fertilizer applied at site 1 ($p < 0.006$). Bare-ground was higher when 66 kg ha⁻¹ of fertilizer was applied (37%) than 0 (28%), 132 (27%) or 198 (23%) kg ha⁻¹ fertilizer rates ($LSD_{0.05} = 9$).

Percent cover for both litter ($p < 0.05$) and bare-ground ($p < 0.01$) were affected only by defoliation at site 2. Grass defoliation in the spring had higher litter cover (46%) than none (40%), summer (39%), fall (40%), Alternating spring/fall (41%) and continuous (40%) ($LSD_{0.05} = 5.0$). Bare ground cover at site 2 was lower in plots that were not defoliated (5%) than spring (9%), summer (10%), fall (9%) and alternating spring/fall (10%) ($LSD_{0.05} = 4$). Defoliation in all 3 seasons resulted in the highest cover of bare-ground (16%).

Discussion

We found a consistent trend of increased spotted knapweed densities at fertilizer applications of 66 and 132 kg ha⁻¹ over those observed at 0 or 198 kg ha⁻¹. We believe that spotted knapweed's rapid growth rate allowed it to capture available resources before neighboring desirable species (Sheley et al. 1993). Addition of

66 and 132 kg ha⁻¹ of fertilizer may have provided spotted knapweed juvenile plants nutrients needed for success, while providing no benefit to the grasses. When 198 kg ha⁻¹ of fertilizer was applied, we speculate that the grasses were able to use the nutrients to their advantage.

Alternating spring/fall defoliation resulted in higher spotted knapweed density and biomass than annual spring or fall defoliation. Alternating spring/fall grazing is often recommended to improve range health because grasses are allowed to set seed and receive a rest period to allow seedling establishment (Rogler 1951, Johnson 1965, Frisna 1992). However, these recommendations do not take into account competition from a perennial weed. While alternating spring/fall defoliation provided the highest grass biomass at site 2, it also produced higher spotted knapweed density and biomass than annual spring or fall defoliations. We believe the grasses are placed at a competitive disadvantage when spring defoliation directly follows fall defoliation. Defoliation in the fall reduces the photosynthetic ability of the plant, which may result in the reduction of carbohydrate reserves (Deregibus et al. 1982). If the plants are defoliated the next spring, they may not have the carbohydrate reserve to recover. This potentially shifts the competitive balance to spotted knapweed, allowing it to establish new seedlings which may be able to out compete the suppressed grasses.

Fall defoliation alone appeared to be the most appropriate defoliation treatment for minimizing spotted knapweed reinvasion after weed control. It resulted in grass and

spotted knapweed biomass that were similar to the undefoliated control. This was expected since grasses generally tolerate fall defoliation well. Because growth rates have slowed, removal of photosynthetic material does not draw large amounts of nutrients from the plants reserve (McLeen and Wikeem 1985). While fall-only defoliation may minimize spotted knapweed reinvasion, it may only be practical for a few livestock operations. As forage matures their nutritional quality decreases (Greene et al. 1987). Therefore, fall grazing may provide poor quality forage with low protein and digestability (Huston and Pinchak 1991).

One of the most significant results from this study was the difference between sites. Site 1, with a residual understory of smooth brome grass and timothy, was much more responsive to the picloram treatments than site 2, which had a residual understory dominated by Kentucky bluegrass. The Kentucky bluegrass site was generally more affected by fertilizer and clipping treatments. Sheley and Jacobs (1997) reported that 2 years after application, picloram and fertilizer did not interact to affect grass yield or spotted knapweed density on either study site. In contrast, data from this study shows picloram and fertilizer interacted to decrease spotted knapweed density at site 2. We believe the main effect of picloram faded to allow the more subtle effects of the fertilizer to be evident. The smooth brome grass and timothy at site 1 were more responsive to applications of picloram and showed no effect from the fertilizer on spotted knapweed density, cover, or biomass even 4 years after application. We can conclude, therefore, that if a residual understory of strong, grazing tolerant grasses exists, reasonable grazing practices will not accelerate spotted knapweed reinvasion. However, if weaker grasses, such as Kentucky bluegrass, dominate the understory, avoiding improper grazing is critical to prevent reinvasion of spotted knapweed.

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Quantifying spatial heterogeneity in herbage mass and consumption in pastures

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Abstract

A sward-based technique for quantifying the spatial heterogeneity in herbage mass and consumption was developed and tested in a bahia grass (*Paspalum notatum* Flüggé) pasture grazed by cattle. For five, 2-day grazing periods from May to October, pre- and post-grazing herbage masses were nondestructively estimated with an electronic capacitance probe at 182, 50 x 50 cm locations along 2 permanent line transects. At the same time, undisturbed herbage accumulation during grazing was measured inside exclosures and the results used to estimate accumulation under grazing at each location. Estimation of herbage mass was relatively good; $R^2 = 0.88$ to 0.98 . Spatial heterogeneity in herbage mass and the stability of the spatial pattern were well quantified. The pattern of spatial heterogeneity observed early in the grazing season remained quite stable for 5 months until the late grazing season. Spatial heterogeneity in the rate of defoliation was also well quantified in spite of some negative values. The technique is of potential value for quantifying the spatial heterogeneity in herbage mass and consumption by animals in grazed pastures, though further studies are necessary for testing the applicability of the technique to pastures of other plant species or of multiple species.

Key Words: electronic capacitance probe, patch grazing, patch stability, rate of defoliation, spatial pattern, *Paspalum notatum*

Vegetation of grazing systems is spatially heterogeneous (Vallentine 1990). Even in virtually monospecific pastures, vegetation forms a mosaic in which short, heavily grazed patches having small herbage mass alternate with tall, ungrazed or lightly grazed patches having large herbage mass, with a transitional zone of intermediate height, utilization and mass (Illius et al. 1987, Liu and Hirata 1995, Hirata and Fukuyama 1997, Cid and Brizuela 1998, Hirata 1998).

It is well known that such heterogeneity is created and maintained by selective (spatially heterogeneous) grazing by animals: i.e., animals visit and graze heavily grazed patches more frequently than the surrounding patches (Illius et al. 1987), preferring the higher digestibility and nitrogen concentration in heavily grazed patches (Illius et al. 1987, Cid and Brizuela 1998).

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Resumen

Se desarrollo una técnica basada en la pradera para cuantificar la heterogeneidad espacial de la masa de forraje y el consumo, y se probó en una pradera de "Bahia grass" (*Paspalum notatum* Flüggé) apacentada por bovinos. En 5 periodos de apacentamiento de 2 días comprendidos entre mayo y octubre, se estimó la masa de forraje antes y después del apacentamiento mediante el método no destructivo de la sonda de capacitor electrónico, la estimación se realizó en 182 cuadrantes de 50 x 50 cm localizados en 2 transectos de línea permanentes. Al mismo tiempo se midió la acumulación de forraje sin disturbio ocurrida durante el apacentamiento, lo cual se hizo dentro de exclusiones y los resultados se utilizaron para estimar la acumulación de forraje bajo apacentamiento en cada localidad. La estimación de forraje fue relativamente buena; $R^2 = 0.88$ a 0.98 . La heterogeneidad espacial de la masa de forraje y la estabilidad del patrón espacial se cuantificaron bien. El patrón de la heterogeneidad espacial observado al inicio de la estación de apacentamiento permaneció muy estable durante 5 meses hasta finales de la estación de apacentamiento. La heterogeneidad espacial de la tasa de defoliación también fue bien cuantificada a pesar de algunos valores negativos. La técnica es de valor potencial para cuantificar la heterogeneidad espacial de la masa de forraje y consumo por animales en praderas apacentadas, aunque son necesarios mas estudios para probar la aplicabilidad de esta técnica en praderas de otra especies vegetales o praderas con mas de una especie.

However, few workers have measured the utilization of individual patches in terms of herbage consumption or intake. Frequent grazing of heavily grazed patches does not necessarily mean that herbage consumption in these patches is greater than that in other patches, because low herbage availability of heavily grazed patches may limit the intake rate of animals. Since herbage consumption, as well as herbage accumulation, is a factor determining the changes in herbage mass, information on the herbage consumption in individual patches in a pasture is important in understanding the mechanisms behind patch development and stability.

Hirata and Fukuyama (1997) developed a sward-based technique for estimating herbage consumption by grazing animals at a small patch scale and used the technique on a bahia grass (*Paspalum notatum* Flüggé) pasture grazed by cattle. An electronic capacitance probe was used to estimate herbage mass in a number of fixed locations (50 x 50 cm) along permanent transects before and after grazing, and herbage consumption in each location was estimated from the change in the herbage mass with grazing.

However, the results had limitations because the herbage consumption was estimated without taking the herbage accumulation during grazing into account. The aims of the present study were to overcome such limitations and examine the usefulness of the technique for quantifying the spatial heterogeneity in herbage mass and consumption in a grazed pasture.

Materials and Methods

Study site and grazing and pasture management

The same paddock as in the previous study (Hirata and Fukuyama 1997), i.e., a 1.1-ha paddock of a bahia grass pasture at the Sumiyoshi Livestock Farm (31°59'N, 131°28'E), Faculty of Agriculture, Miyazaki University, Japan, was used. The paddock was 1 of 5 paddocks rotationally grazed by Japanese Black Cows. The vegetation was highly dominated by bahia grass. According to the measurements in the previous year (1995), bahia grass accounted for 87% of herbage mass (above a 3 cm height; on a dry matter (DM) basis) in May, and 97 to 100% from June to October (Hirata and Fukuyama 1997).

During the grazing season (May–October) of 1996, the paddock was grazed by 28 to 32 animals with a 2 to 6-day duration at intervals of 11 to 37 days. The total duration of grazing periods was 23 days. The annual fertilization rates in the paddock were 77 kg N (split application in

March and August), 20 kg P (March) and 30 kg K (March) ha⁻¹. The meteorological conditions during the study are shown in Fig. 1.

Measurement periods

Five, 2-day periods at approximately monthly intervals were selected from the rotational grazing periods as Periods 1 to 5 (Table 1), representing the first 2 days of a grazing period. Pre- and post-grazing herbage mass, herbage accumulation and rate of defoliation were estimated for these 5 selected periods. The duration of 2 days was selected to ensure enough reduction in herbage mass by grazing for detection with a capacitance probe.

Electronic capacitance probe

An electronic capacitance probe (PastureProbe™, Mosaic Systems Ltd., New Zealand) was used to estimate herbage mass. PastureProbe™ is a single probe capacitance meter, which is light in weight and highly portable (Hirata et al. 1993). There have been many reports evaluating electronic capacitance probes, and results indicate that the single-probe capacitance meter is at least as good and more labor saving than any other alternatives for indirect herbage mass measurement (Frame 1993). The accuracy of PastureProbe™ in estimating herbage mass of bahia grass swards was tested by Hirata et al. (1993). Because the relationship between herbage mass and corrected meter reading of electronic capacitance probe

Table 1. Outlines of selected grazing periods for measurements.

Period	Date	Number of cows	Mean liveweight (kg cow ⁻¹)
1	25–26 May	28	462
2	29–30 Jun.	28	454
3	3–4 Aug.	28	446
4	14–15 Sep.	29	452
5	26–27 Oct.	32	468

(CMR) is known to vary with such factors as sward type, season of growth (developmental stage), herbage moisture content and ratio of green to dead material (Frame 1993, Hirata et al. 1993), and was anticipated to vary also with grazing, calibration equations were developed separately for individual measurement occasions as described later.

Pre- and post-grazing herbage mass

Horizontal distribution of herbage mass was measured both at the beginning and the end of the 5 selected periods, i.e., on 10 occasions. On each occasion, CMR was measured at 1-m intervals along 2 permanent line transects crossing the paddock. Each transect was 90 m long and, therefore, the CMR was determined at 182 locations (including both ends of the transect). For each location, the CMR was measured at 6 points within an area of 50 × 50 cm (4 at individual corners and 2 in the center), irrespective of the vegetation of the points (plant species and plant parts), and the mean value was recorded as the CMR of the location. The area of 50 × 50 cm was selected based on the feeding station (Coleman et al. 1989) of cattle used.

Immediately after the measurements of CMR along the transects, ten, 50 × 50 cm locations whose CMR values covered the CMR range of the transects were selected in the paddock, avoiding the proximity of the transects, and the herbage was cut to a 3-cm height. The samples were oven-dried at 85°C for 72 hours for dry matter determination. In Period 5, the number of samples was decreased to 5 to reduce labor requirement.

Calibration equations for estimating herbage mass (M, g DM (2500 cm²)⁻¹) from CMR were developed fitting the following model to data:

$$M = a_0 + a_1 \times \text{CMR} + a_2 \times \text{CMR}^2 \quad (1)$$

where a_0 , a_1 and a_2 are constants. The independent variables, CMR and CMR², were incorporated into the equation only when their partial regression coefficients (a_1 and a_2 , respectively) were significant (P

Fig. 1. Ten or 11 day average of maximum (---), mean (—), and minimum (.....) air temperatures, daily total shortwave solar radiation, and 10 or 11 day totals of rainfall during the study period.

<0.05). Using the equation developed for each measurement occasion, the CMR at each location along the transects was converted into herbage mass (DM in an area of 50x 50 cm and above a height of 3 cm).

Characteristics of the spatial distribution of herbage mass were expressed by the mean, minimum, maximum, SD and C.V. of data from the 182 locations along the transects. Similarity of the spatial patterns of herbage mass on 2 occasions was represented by a correlation coefficient (n=182).

Herbage accumulation

Undisturbed herbage accumulation during each selected period was measured at 6 different herbage masses using enclosure cages (1 x 1 m in area and 75 cm in height), to develop the relationship between the accumulation rate and herbage mass (described later as Equation 2, also see Fig. 6 and Equations 4 to 8). At the beginning of each selected period, six, 50 x 50 cm areas whose CMR values covered the CMR range of the transects at approximately equal intervals were selected in the paddock, avoiding the proximity of the transects, and the cages were placed on these areas. Then, the CMR of the areas was measured again 7 to 10 days after the end of the selected period. Initially, I intended to measure the final CMR at the end of the selected periods, but herbage accumulation during the 2 days was too small to detect with the capacitance probe. The initial and final CMR of each area was determined as the mean of 5 measurements (4 at individual corners and 1 in the center), and converted into herbage mass (DM in an area of 50 x 50 cm and above a height of 3 cm) as described above.

The rate of undisturbed herbage accumulation (G_{undist} , g DM (2500 cm²)⁻¹ d⁻¹) was related to the mean herbage mass during the accumulation period (M_{mean} , g DM (2500 cm²)⁻¹) assuming the following model:

$$G_{undist} = b_0 + b_1 \times M_{mean} + b_2 \times M_{mean}^2 \quad (2)$$

where b_0 , b_1 and b_2 are constants. The independent variables, M_{mean} and M_{mean}^2 , were selected in the same way as in Equation 1.

Rate of defoliation

Rate of defoliation or daily herbage consumption (D , g DM (2500 cm²)⁻¹ d⁻¹) at each location along the transects was calculated as:

$$D = (M_{pre} - M_{post})/t_g + G_{dist} \quad (3)$$

where M_{pre} and M_{post} are respectively the

Fig. 2. Relationships between herbage mass and corrected meter reading (CMR) by an electronic capacitance probe. Three asterisks indicate significance at $P < 0.001$.

pre- and post-grazing herbage masses at the location (g DM (2500 cm²)⁻¹), t_g is the duration of the selected grazing period (d), and G_{dist} is the rate of disturbed herbage accumulation at the location during grazing (g DM (2500 cm²)⁻¹ d⁻¹). The first term, $(M_{pre} - M_{post})/t_g$, corresponds to the rate of decrease in herbage mass during grazing (apparent consumption). In this study, $t_g = 2$ (Table 1). G_{dist} was estimated from the mean herbage mass during the selected grazing period ($M_{mean} = (M_{pre} +$

$M_{post})/2$) using Equation 2. Thus, the use of the model assumes that G_{dist} , the rate of herbage accumulation under grazing, equals the rate of undisturbed herbage accumulation when the herbage mass is the same.

Characteristics of the spatial distribution of the rate of defoliation were expressed by the mean, minimum, maximum, SD and C.V. of data from the 182 locations along the transects.

Fig. 3. Pre- and post-grazing distributions of herbage mass along the transects. The statistical parameters are minimum, maximum, mean, SD, and C.V.

Results and Discussion

Labor requirement

The present technique required a relatively small amount of labor. An operator of a capacitance probe and a recorder who also calculated the mean corrected meter reading (CMR) at each location were enough for the measurements. It took approximately 2.5 hours for 2 persons to measure CMR at the 182 locations and in the 6 exclosures and collect 10 vegetation samples for developing a calibration equation. Reducing the number of samples to 5 in Period 5 shortened the time by approximately half an hour.

Estimation of herbage mass

Herbage mass was linearly or quadrati-

cally related to CMR (Fig. 2). The linear and quadratic terms were not incorporated at the same time because their partial regression coefficients were not simultaneously significant ($P > 0.05$). All the calibration equations were highly significant ($R^2 = 0.88$ to 0.98 , $P < 0.001$) with SE of estimation of 4.4 to 16.8 g DM (2500 cm^2)⁻¹. The SE tended to be greater as the range of herbage mass broadened. Replacing the linear term by the quadratic term in Periods 1, 3, and 5 increased R^2 by 0.00 to 0.06 and decreased SE of estimation by 0.3 to 7.3 g DM (2500 cm^2)⁻¹. These results are similar to those from the previous study (Hirata et al. 1993). The slope of the line was always steeper, i.e., the regression coefficient was always greater, after grazing than before grazing. This may be mainly due to the decreased leaf to stem ratio of the sward with grazing.

Heterogeneity in herbage mass

Pre- and post-grazing herbage masses were spatially heterogeneous, as shown by the C.V. values of 0.304 to 0.857 (Fig. 3). With grazing, the mean and minimum herbage masses always decreased and, contrarily, C.V. always increased. Such an increase in C.V. with grazing accords with previous observations (Shiyomi et al. 1983, 1984, Hirata 1993a, 1993b, Liu and Hirata 1995, Hirata and Fukuyama 1997) and confirms that grazing by animals is a crucial factor in the development and maintenance of the heterogeneity (Bakker et al. 1983, Edwards et al. 1996).

There were always positive correlations between pre- and post-grazing herbage masses along the transects (Fig. 4). Furthermore, pre-grazing herbage mass in Periods 2 to 5 was always positively corre-

Fig. 4. Relationships between pre- and post-grazing herbage masses along the transects. Three asterisks indicate significance at $P < 0.001$.

Fig. 5. Relationships between pre-grazing herbage masses along the transects in Period 1 and subsequent periods. Three asterisks indicate significance at $P < 0.001$.

lated with that in Period 1 (Fig. 5). These results show that the spatial pattern of herbage mass was more or less stable at least for 5 months during the grazing season, which agrees with previous reports (Bakker et al. 1983, Willms et al. 1988, Cid and Brizuela 1998, Hirata 1998). The stability of the spatial pattern of herbage mass in the paddock during a 2 and a half-year period has been investigated and discussed in Hirata (1998).

Herbage accumulation during grazing

The rate of undisturbed herbage accumulation (G_{undist}) was linearly or quadratically related to the mean herbage mass

during the accumulation period (M_{mean}) (Fig. 6). The relationships in Periods 1, 2, 3, 4, and 5 were expressed by Equations 4, 5, 6, 7, and 8, respectively (SE given in brackets):

$$G_{undist} = 0.117 (0.055) + 0.0203 (0.0022) M_{mean} \quad (R^2 = 0.96, P < 0.001, SE \text{ of estimation} = 0.079) \quad (4)$$

$$G_{undist} = 0.575 (0.452) + 0.0299 (0.0092) M_{mean} \quad (R^2 = 0.73, P < 0.05, SE \text{ of estimation} = 0.493) \quad (5)$$

$$G_{undist} = -0.253 (0.450) + 0.0534 (0.0104) M_{mean} - 2.61 \times 10^{-4} (0.50 \times 10^{-4}) M_{mean}^2 \quad (R^2 = 0.90, P < 0.05, SE \text{ of estimation} = 0.272) \quad (6)$$

$$G_{undist} = 0.307 (0.150) + 0.0207 (0.0026) M_{mean} - 1.11 \times 10^{-4} (0.10 \times 10^{-4}) M_{mean}^2 \quad (R^2 = 0.99, P < 0.001, SE \text{ of estimation} = 0.041) \quad (7)$$

$$G_{undist} = 0.0029 (0.0036) + 0.00149 (0.00011) M_{mean} - 7.65 \times 10^{-6} (0.66 \times 10^{-6}) M_{mean}^2 \quad (R^2 = 0.99, P < 0.01, SE \text{ of estimation} = 0.003) \quad (8)$$

The relationship between G_{undist} and M_{mean} was mostly quadratic, with the maximal G_{undist} and the optimum M_{mean} for the maximal G_{undist} changing with season. This relationship was linear in

Fig. 6. Relationships between rate of undisturbed herbage accumulation and mean herbage mass in Periods 1 (○), 2 (Δ), 3 (▽), 4 (□), and 5 (◇). See text for equations.

Periods 1 and 2, apparently caused by the low, narrow ranges of M_{mean} . The quadratic relationship between growth rate and herbage mass which produces the logistic growth agrees with models developed by Noy-Meir (1978) and Hart (1989).

Heterogeneity in herbage consumption

The rate of defoliation was spatially heterogeneous, as shown by the C.V. values of 0.428 to 0.904 (Fig. 7). The heterogeneity (C.V.) tended to increase as the mean pre-grazing herbage mass increased (Fig. 3) ($r = 0.87$, $P = 0.05$). This phenomenon reflects the fact that animals are more selective and patch grazing is more prevalent under lower grazing pressure (Willms et al. 1988, Vallentine 1990, Cid and Brizuela 1998). In the present study, high-

Fig. 7. Distributions of rate of defoliation along the transects. The statistical parameters are minimum, maximum, mean, SD, and C.V.

er mean herbage mass coincided with lower grazing pressure because the paddock size was fixed and the number of animals and their mean liveweight were almost constant throughout (Table 1).

There were positive correlations between the rate of defoliation and pre-grazing herbage mass along the transects in Periods 1, 2 and 3, and no significant correlations in other periods (Fig. 8). This fact shows that animals did not consume more from the locations with lower herbage mass. Because the current study did not measure ingestive behavior of animals, it is unknown whether the animals visited the locations with lower herbage mass more

calculated by substituting $(M_{pre} + M_{post})/2$ for M_{mean} in the equations. Thus, the use of a capacitance probe may be taken as the first possible cause for the negative rates in terms of the errors of M_{pre} and M_{post} .

Secondly, the present technique estimated G_{dist} at each location along the transects from its mean herbage mass during grazing, with an assumption that G_{dist} equals G_{undist} as a function of herbage mass (Fig. 6, Equations 4 to 8). Therefore the technique has limitations in estimating disturbed or grazed herbage accumulation separately in different locations in a pasture, because the locations may differ not only in herbage

Fig. 8. Relationships between rate of defoliation and pre-grazing herbage mass along the transects. One, 2, and 3 asterisks indicate significance at $P<0.05$, $P<0.01$, and $P<0.001$, respectively.

frequently than the locations with higher herbage mass. Further studies are therefore necessary to relate herbage consumption at individual locations to ingestive behavior of animals such as the number of visits, residence time, biting rate and bite weight.

Calculation of the rate of defoliation (Equation 3) sometimes produced negative values (Figs. 7 and 8). From the components of Equation 3, the negative values of the rate of defoliation are first attributable to the errors of estimation of M_{pre} , M_{post} and/or G_{dist} . The errors in G_{dist} are further attributable to the errors of M_{pre} , M_{post} and/or Equations 4 to 8 (Fig. 6), because G_{dist} was

calculated by substituting $(M_{pre} + M_{post})/2$ for M_{mean} in the equations. Thus, the use of a capacitance probe may be taken as the first possible cause for the negative rates in terms of the errors of M_{pre} and M_{post} .

Secondly, the present technique estimated G_{dist} at each location along the transects from its mean herbage mass during grazing, with an assumption that G_{dist} equals G_{undist} as a function of herbage mass (Fig. 6, Equations 4 to 8). Therefore the technique has limitations in estimating disturbed or grazed herbage accumulation separately in different locations in a pasture, because the locations may differ not only in herbage

mass but also in other aspects such as leaf area, soil fertility and influences of treading and feces and urine deposition by animals. The errors in Equations 4 to 8 are taken to partly reflect these limitations. In addition, the periods during which the undisturbed herbage accumulation was measured were 7 to 10 days longer than the selected 2-day periods.

Despite these limitations, no better technique was available for estimating the pre- and post-grazing herbage masses and the rate of disturbed herbage accumulation at the 182 locations individually, non-destructively and rapidly. Furthermore, the negative values of herbage consumption (Figs. 7 and 8) were not replaced by zero, because the replacement would produce some bias in the data as a whole.

One may question the reliability of the present technique in estimating the location and intensity of grazing by the animals, on the grounds that I did not observe whether or not the locations were actually grazed. However, the way in which the rate of defoliation was calculated (Equation 3), i.e., as the sum of the rate of net defoliation $((M_{pre} - M_{post})/t_g)$ and the rate of disturbed herbage accumulation (G_{dist}), is normally used to estimate herbage consumption on a basis of a whole pasture (Meijs et al. 1982).

The present technique may also be supported by the mean rate of defoliation along the transects (Fig. 7). The daily herbage intake by the animals that was calculated from the mean rate of defoliation, the paddock area, and the number and mean liveweight of animals (Table 1) was 18.0, 20.4, 25.4, 22.0, and 14.9 g DM

(kg LW)⁻¹ d⁻¹ for Periods 1, 2, 3, 4, and 5, respectively. These values agree closely with the grazing intake of Japanese Black Cows (AFFRCS 1995) when the mean pre-grazing herbage mass (Fig. 3) and the digestibility of a bahia grass pasture (Higashiyama and Hirata 1995) are taken into account.

Furthermore, the present technique, owing to the large number of data sets from the pasture (n=182), is considered to give reliable trends of spatial distribution of herbage consumption. An example is the increase in the spatial heterogeneity in herbage consumption with the increased mean pre-grazing herbage mass (Figs. 3 and 7) as discussed above. We can understand which locations of the pasture were heavily defoliated or lightly defoliated. Because of the small labor requirement, it may be possible to establish more locations for measurements so that they can cover the whole area of a pasture.

Conclusions

Previous studies have mainly used 2 techniques for quantifying the spatial heterogeneity in vegetation in grazed pastures. One is a random sampling of sward height (Gibb and Ridout 1986, 1988) or herbage mass (Shiyomi et al. 1983, 1984, Hirata 1993a) from a pasture, and the other is a monitoring of degree of utilization (Bakker et al. 1983, Willms et al. 1988, Cid and Brizuela 1998) or sward height (Edwards et al. 1996) in some permanent areas in a pasture. The latter technique is advantageous over the former because it can follow the temporal dynamics in vegetation characteristics in the same locations in a pasture and therefore can estimate the patch stability. However, few workers have used the latter technique to monitor herbage mass, i.e., a most important vegetation characteristic, because estimation of herbage mass normally requires destructive sampling.

The present technique, by using an electronic capacitance probe, can follow the temporal dynamics in herbage mass in a number of fixed locations in a pasture with a relatively small amount of labor. Spatial heterogeneity in herbage mass and the stability of the spatial pattern of herbage mass were well quantified (Figs. 3 to 5). Spatial heterogeneity in the rate of defoliation was also well quantified in spite of some negative values (Fig. 7). The present technique is therefore considered to be of potential value for quantifying the spatial heterogeneity in herbage mass and con-

sumption by animals in grazed pastures, though further studies are necessary for testing the applicability of the technique to pastures of other plant species or of multiple species.

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Herbivore dunging and endozoochorous seed deposition in a Mediterranean *dehesa*

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Abstract

Spatial patterns of herbivore defecation within grazing systems are important as they directly affect pasture growth and composition. These effects are partially linked to seed dispersal in dung, a little studied process. This paper focuses on: (i) quantification of dung and seeds deposited by herbivores in a Mediterranean grazing system, and (ii) analysis of the spatial variability of dung and seeds deposited within and among plant communities. We carried out year-long monthly quantifications of the depositions of rabbit (*Oryctolagus cuniculus*), fallow deer (*Dama dama*), red deer (*Cervus elaphus*), and cow (*Bos taurus*) dung to 32 plots distributed in *Quercus rotundifolia* Lam. and *Fraxinus angustifolia* Vahl woodlands, mixed scrub, and *Cistus ladanifer* L. scrub. We also quantified the germinable seed content of dung. The results revealed differences ($p < 0.05$) in dung deposition, varying (i) among the 4 species, (ii) within species (except for the red deer) among plant communities, and (iii) within plant communities. An average of 735 seeds/m² were returned to the soil via dung, with the highest numbers in open woodlands (870–1,888 seeds/m²) and the lowest numbers in scrubs (83–315 seeds/m²). Cows dispersed the most seeds (68%), followed by red deer (20%), rabbits (7%), and fallow deer (5%). Spatial variability in deposition led to accumulations of up to several thousand seeds at points covered by the dung. The effect of seed input to the seed bank and on vegetation may be low at large and medium-sized spatial scales, but it can be very important at small scales and for colonization processes.

Key Words: spatial pattern, dispersal, dung, herbivores, endozoochory, Mediterranean pastures

Deposition and degradation of herbivore dung are key processes that alter soil characteristics, botanical composition, and productivity in grazing lands (McNaughton 1984, Georgiadis and McNaughton 1990, Malo and Suárez 1995a) but little information exists concerning spatial patterns of herbivore defecation (e.g. Putman et al. 1991). Seed dispersal via herbivore dung (endozoochory) is known to happen, but effects on vegetation dynamics are poorly defined (Janzen 1984) with the exception of dispersal

Resumen

Los patrones de defecación de los herbívoros en los sistemas pastorales son de gran importancia, dado que afectan a la composición y el crecimiento del pastizal, y sus efectos se encuentran parcialmente ligados a un proceso muy poco estudiado, la dispersión de semillas en los excrementos. El presente estudio se centra en: (i) la cuantificación de los excrementos y semillas defecados por los herbívoros en una dehesa de la Península Ibérica, y (ii) en el análisis de la variabilidad espacial de la deposición de excrementos y semillas entre formaciones vegetales y dentro de las mismas. A lo largo de un año cuantificamos mensualmente los excrementos de conejo (*Oryctolagus cuniculus*), gamo (*Dama dama*), ciervo (*Cervus elaphus*) y vaca (*Bos taurus*) depositados en 32 parcelas distribuidas en zonas adehesadas de *Quercus rotundifolia* Lam. y de *Fraxinus angustifolia* Vahl, en matorrales mixtos, y en jarales de *Cistus ladanifer* L. Paralelamente, cuantificamos el contenido de semillas germinables de los excrementos de los cuatro herbívoros. Los resultados mostraron diferencias significativas ($p < 0.05$) en la deposición de excremento (i) entre los 4 herbívoros, (ii) individualmente para cada animal (excepto el ciervo) entre las cuatro formaciones vegetales, y (iii) dentro de cada una de éstas. Estimamos una deposición media para toda la finca de 735 semillas/m², correspondiendo los valores más altos a los pastizales arbolados (870–1.880 semillas/m²) y los más bajos a los matorrales (83–315 semillas/m²). La variabilidad de la deposición es muy grande, por lo que en los lugares ocupados por los excrementos se producen acumulaciones de miles de semillas. Las vacas son los principales dispersantes (68% de las semillas), seguidos de los ciervos (20%), los conejos (7%) y los gamos (5%). El efecto de la defecación de semillas sobre el banco de semillas y la vegetación puede ser poco relevante a escalas espaciales grandes y medianas, pero a pequeña escala, y en los procesos de colonización vegetal, puede ser muy importante.

of woody legumes (Miller and Coe 1993) and attempts to use livestock to sow pasture species (Ocumpaugh et al. 1996). High seed densities were recorded in herbivore dung in the Mediterranean (Russi et al. 1992, Malo and Suárez 1995b) and Australia (Jones et al. 1991, Gardener et al. 1993) while much lower densities occurred in other areas (Collins and Uno 1985, Welch 1985). However, information is lacking on quantification of seeds dispersed endozoochorously by herbivores. Objectives of this research were (i) to quantify herbivore dung and seed input to soil in an extensive grazing system on the Iberian Peninsula, and (ii) to analyse the spatial patterns of dung and seed

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deposition at 3 spatial scales: among and within plant communities, and at the scale of individual depositions.

Material and Methods

Study Area

The field work was done on the Castillo de Viñuelas estate, a roughly 3,000 ha *dehesa* (open woodland) 20 km north of Madrid (Central Spain, 40°37' N, 3°38'W, 670 m above sea level). The *dehesa* ranching system is based on multiple uses (grazing, firewood extraction, hunting, and ploughing) of vegetation complexes formed by open woodlands, scrubland, and wooded pasture. Although human management has changed the former balance of woodland, scrubland, and pasture areas, the *dehesa* systems are considered to be similar to those that have existed in Western Iberia since prehistoric times (Aschmann 1973).

The property lies on Tertiary sands resulting from the erosion of the nearby Sierra de Guadarrama in an area with a dry mesomediterranean climate, an annual rainfall of around 550 mm and a dry summer from June to mid-September. The potential vegetation of the area is sclerophyllous forest dominated by Holm oak (*Quercus rotundifolia* Lam.) mixed with different scrub communities and replaced on valley floors by stands of ash (*Fraxinus angustifolia* Vahl). Due to the traditional use of the estate, 4 main plant communities can now be distinguished (J.M. de Miguel, unpubl. manuscript): (i) pastures with ash on the valley floors (ash woodlands hereafter, 16% of the estate area), (ii) pastures with large Holm oaks on the upper terraces and in other more or less flat areas (oak woodlands, 26%), (iii) mixed scrubland with *Santolina rosmarinifolia* L. and *Thymus zygis* L. along with small Holm oaks and a few Gum cistus (*Cistus ladanifer* L.) on the slopes, ploughed up occasionally to open up pastures (mixed scrub, 22%), and (iv) practically monospecific scrubland of Gum cistus with a few Holm oaks in the highest zones (*Cistus* scrub, 36%).

The estate now has a grazing-hunting usage similar to the traditional one, with a herd of 400 free ranging cattle throughout the estate. The main wild herbivores are fallow deer (*Dama dama*, approximately 0.28 individuals/ha), red deer (*Cervus elaphus*, 0.14 individuals/ha) and rabbit (*Oryctolagus cuniculus*, 6–18 individuals/ha, J.E. Malo unpubl. data).

Quantification of Endozoochory

To ascertain the number of seeds deposited, we (i) measured the input of cow, red and fallow deer, and rabbit dung in each of the 4 main plant communities of the estate, and (ii) quantified the seed content of the dung of each of the 4 herbivores.

To quantify dung deposition by the 4 herbivores over a year, we chose a roughly 0.8 km² section of the estate away from human influence where the 4 vegetation types were in close proximity. On 25 March 1991, we delineated 32 plots of 2 x 25 m (8 in each vegetation type) in the ash woodland, oak woodland, mixed scrubland, and *Cistus* scrub. Plots were marked by pegs along the maximum slope line, parallel to each other, and 15 m apart. At one corner of each plot we established a 1 x 1 m subplot defined by string pegged to the ground. After establishing the plots, we removed all dung of red deer, fallow deer, and cows. In addition, rabbit pellets were removed from each of the 1 x 1 m subplots.

At monthly intervals, coinciding with dung collections for seed content analysis (see dates in Fig. 1) we measured the dung deposited in the 32 plots. For this purpose we collected all the red and fallow deer dung in each 2 x 25m plot and counted the number of dung groups containing more than 5 pellets (Rowland et al. 1984). We also counted and measured the diameter and mean depth of each cow pat in the plots. These pats were then removed from the plots to prevent double counting on subsequent visits. We also collected and counted the rabbit pellets deposited in the 1 x 1 m subplots.

The rabbit, fallow deer, and red deer dung was dried and stored in paper bags at room temperature until it was weighed to a precision of ± 0.01 g in autumn 1992. The amount of cow dung was calculated from the diameter and average depth of the pats and the density of dry cow dung (0.37 g/cm³, Malo and Suárez 1995c).

Viable seed content of the dung was determined by greenhouse germination. Between April 1991 and April 1992, coinciding with dung collections from the sampling plots (see dates in Fig. 1), we carried out 11 samplings of dung deposited by the 4 herbivores. Each collection consisted of 8 independent samples of fresh dung from each herbivore species, which were dried and stored at ambient temperature. In autumn of the collection year, 3 g from each sample was crushed gently and prepared for greenhouse germination in a mixture with 20 g of sterile sand over a bed of moist vermiculite. The samples were kept moist during the 2 October–June periods following collection (1991–92 and 1992–93 for the first 7 collections, and 1992–93 and 1993–94 for the rest). Given that in the field in this location, seeds germinate almost exclusively in autumn, this procedure simulated natural conditions. The proportion of ungerminated viable seeds in the samples after the 2 germination cycles was minimal: after keeping the samples of the first 7 collections in the greenhouse for another year (1993–94), only 49 germinations were found in comparison with 5,715 germinations during the first 2 years (less than 0.9%). For the purpose of simplicity, “seeds” refers hereafter to “seeds germinable during 2 seasons”.

Fig. 1. Seed content (mean $\pm$ standard error) of 3-g dung samples from 4 herbivore species over 1 year in the *dehesa* de Viñuelas. The red deer datum for 25-VII-1991 (249 ± 124 , marked with a star) has been deleted to maintain the clarity of the representation.

In our interspecific comparisons of defecation, we used the data on dung weight per plot (in g/m²). The data on the number of seeds deposited (per m² or per defecation) were calculated from the average seed content in the dung on each collection date, and using individualized calculations of the defecations for each plot and date. In all calculations we assumed that the seed content in the herbivore dung was constant throughout plant communities. This assumption should be quite accurate for the 3 ungulates due to (i) the scope of their daily movements in the context of the size of the vegetation patches, permitting them to feed and defecate indiscriminately in all of them, and (ii) the length of time taken by the seeds to pass through the herbivores' digestive tracts, estimated to be between 2 and 6 days (Yamada and Kawaguchi 1972, Courtney 1973). On the other hand, the much smaller home range of rabbits might have resulted in overrating the dispersal role of rabbit dung in scrubs, although, as discussed below, this bias had no significant effect on the main conclusions.

The data were analysed using the SYSTAT programme using standard non-parametric procedures due to the lack of normality in the data sets. Due to the lack of precision of the non-parametric multifactorial analyses (Seaman et al. 1994), the comparisons between herbivores, plant communities, and plots in each community were done sequentially. The values obtained for p in each of the analyses are shown in tables 1–4, but to ensure that these probabilities satisfy the requirements for multiple inferences on data sets, the level of statistical significance taken as the base ($p < 0.05$) was corrected using the sequential procedure proposed by Rice (1989). Corrected values of the level of statistical significance are shown in each table.

Results

Dung Deposition

The total amount of dung deposited in the 32 sampling plots differed ($p < 0.05$) among the 4 herbivores (Table 1), ranging from a maximum for cows and rabbits (17–21 g dung/m²) to a minimum for the red deer and fallow deer (4–6 g dung/m²). There were also differences in amount of dung deposited among the plant communities by all herbivores except for red deer (Kruskal Wallis test; $p < 0.05$; Table 2). Cows and fallow deer had proportionally the lowest defecation rates in both scrub types (especially *Cistus* scrub). The

Table 1. Amount of dung (g dry weight/m²) deposited by 4 herbivore species in 32 permanent plots in a Mediterranean grazing system during one year^a.

	Herbivore species				Friedman test	
	Rabbit	Fallow deer	Red deer	Cattle	F	p
	(g/m ²)					
Dung	21.6	4.3	5.7	17.1	15.9	0.001
	25.6±3.3	8.5±1.8	7.8±1.2	45.2±14.3		

^aUpper row: median values and result of their comparison using Friedman test for associated samples. Lower row: mean ± s.e. for the data set. Level of statistical significance is $p < 0.05$.

amount of rabbit dung collected in the mixed scrub was intermediate between the level in the 2 wooded pastures and appreciable, although lower, in the *Cistus* scrub. Finally, the defecation pattern of red deer among vegetation types was more homogeneous, though the difference among plant communities was close to statistical significance. As a result of these defecation patterns, *Cistus* scrub received the least herbivore dung of the 4 plant communities (0–8 g/m² of each species), followed, with the exception of the rabbit (26 g/m²), by mixed scrub (2–11 g/m²). In contrast, wooded pastures received much higher amounts: 7–45 g/m² in the ash woodlands and 9–38 g/m² in the Holm oak woodlands.

There were large differences in amount of dung deposited by each herbivore species among the plots within each plant community (Table 3). In some cases these differences corresponded to defecation patterns that were maintained among sample collection dates. Thus, there were differences ($p < 0.05$) in amounts of rabbit dung collected in the sub-plots of the 4 plant communities (Friedman test for repeated samples, Table 3). For fallow deer, differences ($p < 0.05$) occurred among samples from plots in ash and oak woodlands and for red deer only among plots from the oak woodlands. Cow dung showed no significant trends in spatial variation maintained over the whole sampling period in any of the plant communities.

Dung Seed Content

A total of 527 seeds germinated from the 88 rabbit dung samples (equivalent to 2.0 seeds/g of dry dung), 1,320 from fallow deer dung (5.0 seeds/g), 3,265 from red deer dung (12.4 seeds/g), and 982 from cow dung (3.7 seeds/g). The germinable seed content showed large seasonal variation in all 4 herbivore species, and the dispersal pattern also differed among species (Fig. 1). Thus, the highest seed concentration in dung was at the end of spring for rabbits and cows (4.7 and 10.7 seeds/g respectively), in mid-summer for red deer (83.0 seeds/g), and at the start of autumn for fallow deer (11.5 seeds/g). However, a few germinable seeds were found in dung at almost any time of the year.

Seed Deposition

Dung deposition and seed content data were used to calculate the number of seeds defecated by each animal species in each plant community and, using the proportion of each community on the estate, the average number deposited on the entire property (Table 4). Across communities and herbivores, this revealed an input of some 735 seeds/m² via dung. Cows were responsible for almost 500, red deer approximately 140, rabbits 50, and fallow deer 40. There were also large differences among plant communities: nearly 1,900 seeds were deposited per m² of oak woodland, less than 900 in ash woodlands, a little over 300 in mixed scrub and less than 100 in *Cistus* scrub. Differences in amount of

Table 2. Mean dry dung weight (in g/m²) deposited during one year by 4 herbivore species in plots in 4 plant communities in the dehesa of Viñuelas, a Mediterranean grazing system^a.

	Deposited dung				Kruskal-Wallis	
	Ash woodland	Oak woodland	Mixed scrub	<i>Cistus</i> scrub	H	p
	(g/m ²)					
Rabbit	32.5	18.9	26.3	8.5	11.4	0.010^b
Fallow deer	7.1	18.4	2.3	0.9	24.0	<0.001^b
Red deer	7.0	9.5	5.6	2.9	9.3	0.025
Cattle	44.5	37.9	11.0	0.0	15.8	0.001^b

^aN=32 for each animal species.

^bProbabilities below the corrected level of statistical significance according to Rice (1989; $p < 0.025$).

Table 3. Range of variation in the amount of dung (in g/m²) deposited by 4 herbivore species in 8 sample plots located in 4 plant communities in a Mediterranean grazing system, and results of Friedman test on repeated samples for the amount of dung deposited in them in 11 time periods.

	Plant communities			
	Ash woodland	Oak woodland	Mixed scrub	<i>Cistus</i> scrub
Rabbit (g m ⁻²)	17-65 F = 31.2 p < 0.001^a	11-64 F = 33.8 p < 0.001^a	4-57 F = 39.2 p < 0.001^a	2-25 F = 42.5 p < 0.001^a
Fallow deer (g m ⁻²)	2-18 F = 28.7 p < 0.001^a	10-38 F = 21.5 p = 0.003^a	1-4 F = 8.6 p = 0.280	0-4 F = 12.1 p = 0.098
Red deer (g m ⁻²)	4-15 F = 8.1 p = 0.325	3-30 F = 21.6 p = 0.003^a	3-14 F = 5.8 p = 0.565	1-9 F = 7.9 p = 0.339
Cattle (g m ⁻²)	17-161 F = 4.3 p = 0.748	0-375 F = 6.1 p = 0.533	0-61 F = 1.5 p = 0.982	0 F = 0.0 p = 1.000

^aProbabilities reaching the corrected level of statistical significance, according to Rice (1989, sequence: p < 0.0167; p < 0.0125; p < 0.01; p < 0.0083).

dung defecated among plots within each plant community (Table 3) are reflected in the wide range of seed numbers deposited in them (Table 4). In most cases, these differences were of an order of magnitude, and sometimes considerably larger.

Using the weight and number of droppings collected, we calculated the effect of seed input by the 4 herbivores at the very small spatial scale. The seed concentration in rabbit pellets varied from 0.01 seeds per pellet in January and February to 0.45 seeds per pellet in June (Fig. 2).

With each deposition (group of pellets identified during sampling), fallow deer defecated between 5 and 184 seeds (in December and September, respectively), and red deer between 3 (January) and 1,750 (June, Fig. 3). Finally, for each cow pat (600 cm², Welch 1985) there was an input to the pasture ranging from 570 seeds in January to 9,900 in May (Fig. 4), the approximate equivalent of 1 to 16 seeds/cm² of area occupied by dung.

Discussion

Results show the high variability at different spatial scales in the defecation rates among the 4 herbivore species, and among and within different plant communities. To our knowledge, this is also the first presentation of data on endozoochorous seed deposition by all main herbivores sharing a pastoral system and in each of its plant communities.

Dung Spatial Patterns

Rabbits and cows deposited the largest amount of dung in the study area, between

4 and 5 times that of the red and fallow deer. The role of rabbits is especially noteworthy. Despite their small size, rabbits play a key role in this and many other aspects of the ecology of Mediterranean ecosystems within their natural range of distribution (Rogers et al. 1994) or where they have been introduced (Gibb and Williams 1994, Myers et al. 1994). This is also backed by the fact that red and fallow deer densities on the estate can be considered average-high (Braza et al. 1994), while the cattle density (0.13 cows/ha) is only about half that of the average in dehesa systems with a lower hunting use (approx. 0.25 cows/ha). The rabbit density on the estate during the study year may be regarded as normal in the context of Mediterranean ecosystems (Soriguer 1981).

The spatial patterns of herbivore defecation reveal interesting differences among and within plant communities. These differences are closely linked to land use at

small and medium scales (tens and hundreds of meters respectively) by different species, and the behavior of each one. While the spatial patterns of herbivore defecation do not exactly match their spatial use, they are generally considered to be a good approximation of land use (Neff 1968, Rowland et al. 1984, Wood 1988).

At the plant community scale, there were considerable differences in the amount of dung deposited in the 4 vegetation types by the herbivores, although the reason for this behavior was not common to all 4 animals. With the exception of the red deer, these differences were statistically significant in all herbivores, and even in the red deer they were close to the significance threshold.

Daily activity of the 3 ungulates involves ranging over considerable distances in relation to the size of the patches of the plant communities (a few hundred meters). Differences among them in the amount of dung collected may, therefore, be linked to their daily use patterns (Braza and Alvarez 1987, J.M. de Miguel, unpubl. manuscript). Thus, the different diets and daily land use of these 3 herbivores explains the differences found in the samples: cows and fallow deer are basically grazers, while red deer are mixed feeders with a more balanced diet between grazing and browsing on woody stems (Hofmann 1989). This stronger browsing tendency in red deer and its preference for sheltered areas with a dense shrub cover (Braza and Álvarez 1987) explains the smaller differences among plant communities in the amount of dung of this species found during sampling. Red deer use of wooded pastures was higher than that of the shrubby communities.

Cows and fallow deer lie at the opposite extreme with regard to vegetation preferences. Cows mainly use the open ash and

Table 4. Estimated number of seeds deposited per square meter of plant community in dung of 4 herbivore species during 1 year in a Mediterranean grazing system^a.

		Plant communities				Whole estate
		Ash woodland	Oak woodland	Mixed scrub	<i>Cistus</i> scrub	
		(no/m ²)				
Rabbit	mean	88	70	68	19	54
	range	33-209	24-174	6-131	3-62	
Fallow deer	mean	54	95	15	7	40
	range	10-115	36-200	5-31	0-26	
Red deer	mean	166	214	187	57	144
	range	33-398	22-587	84-539	19-157	
Cattle	mean	561	1,510	45	0	497
	range	298-1,374	0-5,732	0-137	-	
Total		870	1,888	315	83	735

^aMean (top row) and range of values (bottom row) of deposition in each plant community in the dehesa of Viñuelas, and weighted mean for whole estate taking into consideration the percentage of area occupied by each one.

Fig. 2. Seed content (mean $\pm$ standard error) of rabbit pellets along the year. Calculation based on seed content in dung, and weight and number of pellets collected in the 32 sub-plots on each sampling date.

oak woodlands, make some use of mixed scrub communities and do not feed in *Cistus* scrub, although they might enter them in winter in search of shelter from the cold. The fallow deer is the species most clearly associated with grasslands, although some of its dung was collected in the mixed and *cistus* scrub, where it also feeds (Venero 1984, Braza and Álvarez 1987).

In contrast to the ungulates, the territory of the rabbit barely reaches 1 ha (Soriguer 1981, Cowan 1991), and hence the differences in dung densities among areas can be linked to the distinct rabbit densities in the 4 environments. Thus, rabbit density appeared to be highest in the ash woodlands, followed by mixed scrub, oak woodlands and *Cistus* scrub. This result is linked to the abundance of food and shelter in each plant community (Venero 1984, Soriguer 1988). *Cistus* scrub provides good shelter but has little grass; mixed scrub also has a good woody cover but an intermediate amount of grass, and wooded pastures provide the highest amount of food and the least shelter.

At a smaller spatial scale, the herbivore defecation patterns in each plant community in the course of the year indicated the animals' spatial selection, which depended on their size. The smallest animals perceive and use different points of each plant community (like a coarse-grained landscape), while the larger herbivores use the land more homogeneously, like fine-grained landscapes. Thus, in the 4 plant communities, rabbits consistently defecate more in certain 1 x 1 m plots throughout the annual cycle, in correspondence with their smaller size and familiar habit of overwhelmingly defecating at certain points (Wood 1988, Gibb 1993).

In the 3 ungulates, differences among plots were maintained throughout the year in the ash and oak woodlands for the fallow deer, only in the oak woodlands for the red deer, and in none of the plant communities for the cows. These differences, which can be linked to body size (fallow deer: 35–70 kg; red deer: 45–120 kg; cow: 500–600 kg) match the priority use of certain areas of passage or rest by fallow deer in the pastures, the more mobile nature of red deer within and among adjacent plant

communities, and the widespread movements through the entire estate by cows through most of the year, though in summer they concentrate near the only permanent stream (see also Putman et al. 1991, Kie and Boroski 1996). All of these trends illustrate the huge spatial variation at different scales of the herbivore defecation patterns, which should be reflected in both the effect of dung deposition and in others associated with grazing (trampling, urination, etc.), leading to highly variable conditions in grazing systems.

Seed Defecation Patterns

The potential effects of endozoochory on the vegetation communities under analysis depend on both the above-mentioned defecation patterns and the seed content in their dung. Herbivore dung seed content had an annual cycle with a spring (cow and rabbit) and summer (red deer and fallow deer) peak, and a winter minimum. These maxima coincide, respectively, with the spring fruiting peak in herbaceous species and the summer peak in *Cistus ladanifer*, a species for which seed was abundant in red deer dung (Malo and Suárez 1998) and somewhat lower in the fallow deer dung. Species for which seed was abundant in fallow deer summer dung include *Biserrula pelecinus* L. a herbaceous legume whose seeds also appear in

Fig. 3. Number of seeds (mean $\pm$ standard error) deposited in each fallow and red deer defecation throughout the year. Calculation based on dung seed content, and weight and number of pellet groups collected in all 32 plots on each date. Note logarithmic scale of Y axis.

Fig. 4. Number of seeds (mean $\pm$ standard error) deposited within an average-sized (600 cm²) cow pat. Calculation based on (i) dung seed content, (ii) density of cow dung and (iii) mean depth of cow pats measured in all 32 plots on each date. As no cow pats were counted in the sampling plots on 23-VIII or 26-IX, data for these dates (marked with stars) were calculated using mean depth of all pats measured during the study.

its dung in winter and spring (Malo and Suárez 1994), and *Juncus bufonius* L. Cow and rabbit dung contain seeds from a large number of herbaceous species, particularly *Poa annua* L., *Cerastium glomeratum* Thuill. and *Biserrula pelecinus* in the cow, and *Sisymbrium runcinatum* Lag. ex DC. and *Sagina apetala* Ard. in the rabbit.

These temporal patterns and the plant species of which seed was disseminated were quite similar to those found in the same area in a 1990 spring–summer sampling campaign (Malo and Suárez 1995b), although inter-annual meteorological differences caused variations in the seed densities and composition. In 1990, a particularly rainy year, seed densities found in dung, with the exception of the red deer, were between 2 and 3 times higher than those of spring–summer 1991–92. This difference was due to the overall decline in the numbers of seed of herbaceous species in dung, countered only by a steep rise in *Cistus ladanifer* seeds in red deer dung and to a lesser extent in fallow deer dung. The dry 1990–91 and 1991–92 years (369 mm and 250 mm rainfall between September and May contrasted to 575 mm in 1989–90) restricted the growth and fruiting of grasses, which led to a higher consumption of the fruit (and possibly stems) of the predominant shrub species.

Using these data, we estimate an average annual deposition by herbivores of around 735 seeds/m² for the whole estate, a relatively low amount. The seed banks of Mediterranean grasslands contain 30,000–40,000 seeds per m² in normal years, and can surpass 100,000 seeds per m² in years of high production (Ortega et

al. 1997), while woody communities have 800–66,000 seeds/m² (Parker and Kelly 1989). Although some of these seeds are part of the permanent soil bank (Thomson and Grime 1979), the relative importance of endozoochory is still small in overall terms, even in years when there is a higher seed density in dung.

In the study area, most of the endozoochory was done by large animals. Cows were responsible for dispersing almost 68% of the seeds, followed by red deer (20%), rabbits (7%), and fallow deer (5%). Although these percentages may show interannual variations, cows are obviously the main dispersers in the area due to the large amount of dung they deposit and its high seed content. In contrast, rabbits disperse a relatively small number of seeds despite the fact that they deposit the largest amount of dung in the area, along with cows. The number of seeds disseminated by rabbits may actually be even lower than our findings: in the scrub zones, rabbit have a mixed diet which includes a certain amount of shrubs (Soriguer 1988), and, thus, the seed content in their dung may be slightly lower in such areas.

The predominantly herbaceous plant communities received the highest seed input via herbivore dung, although in no case was the level comparable to the amount in the soil seed banks. Parallel to the differences among plant communities in the volume of dung deposited, the number of seeds deposited varied by more than an order of magnitude. Thus, *Cistus* and mixed scrub only received 83 seeds/m²

and 315 seeds/m² respectively, in contrast to 870 seeds/m² in ash woodlands and 1,888 seeds/m² in the oak woodlands.

However, at small spatial scales, seed deposition along with herbivore dung can have important effects on seed banks and vegetation. Given that the sustainable stocking density in a grazing system such as the study area is relatively low, the dung density on the ground is somewhat limited and its direct effect on vegetation, therefore, moderate. However, the areas which are covered by herbivore dung receive a substantial density of seeds. Practically any defecation by a herbivore contains some seeds, the number deposited in a single spring–summer defecation potentially being hundreds in the case of fallow deer, more than 1,000 in red deer, and close to 10,000 in the case of cattle.

The effect of this seed input to the vegetation ranges from the localized introduction of species to the creation of gradients associated with grazing. On the one hand, the possibility that herbivores might cause the local introduction of species whose seeds are dispersed in dung has been proved (Malo and Suárez 1994, Ocumpaugh et al. 1996), and is also postulated as being the most important effect of herbivore endozoochory (Gardener 1993, Zedler and Black 1992, Sevilla et al. 1996). Species introduction may also occur with woody plants, leading to the invasion of pastures by scrub (Miller and Coe 1993, Peinetti et al. 1993, Malo and Suárez 1998).

On the other hand, herbivore endozoochory can also change the interspecific competitive balance among plants, favouring those which are disseminated via dung. In the grasslands similar to the study area, the vegetation growing in areas occupied by cow pats has been found to be determined by the dung seed content (Malo and Suárez 1995a). Cow pats act as local disturbances which eliminate the predominant perennial grass (*Poa bulbosa* L.) and introduce annual species, which grow in the gap caused by the cow pat. Given enough time, they are displaced by the *Poa bulbosa* recolonisation, which takes more than 4 years to regain its cover (Malo and Suárez 1996). A less dramatic but similar process probably takes place with dung pellets, where hundreds of seeds in deer pellets, and even the isolated seeds in rabbit dung, are able to find a place to germinate. However, the high germination rates in dung can also lead to high mortality rates due to competition (Sevilla et al. 1996).

Finally, the irregular spatial defecation patterns of herbivores complicates this panorama, and probably leads to vegetation mosaics associated with the different input of nutrients and seeds via dung. The different feeding and defecation habits of herbivores thus help to increase plant diversity at different scales in extensive grazing systems such as the Iberian *dehesas*.

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Late season toxic alkaloid concentrations in tall larkspur (*Delphinium* spp.)

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Abstract

Tall larkspurs [*Delphinium barbeyi* (L. Huth), *D. occidentale* (Wats.), *D. glaucescens* (Rydb.), *D. glaucum* (Wats.)] pose a serious poisoning threat to cattle on many summer ranges. Livestock producers often defer grazing until larkspur is mature, but specific information is lacking on toxic alkaloid concentrations in larkspur from pod stage to senescence. Tall larkspur leaves and seed pods were collected about every 2 weeks during the pod stage to senescence from marked plants in locations in Utah (Logan and Salina), Idaho (Ashton, Humphrey, and Oakley), Colorado (Yampa and Montrose), and California (Carson Pass) from 1995 to 1997. Toxic alkaloid concentrations in pods ($\bar{x}$ = 2.9 mg/g) exceeded leaf alkaloid concentrations ($\bar{x}$ = 1.5 mg/g in all species, but the magnitude of the difference varied among the 4 species. Leaves showed a more rapid decrease in toxic alkaloid concentration with plant maturity compared to pods. Seed pods did not begin to lose substantial amounts of toxic alkaloid until larkspur matured and pods began to desiccate. At seed shatter, *D. glaucescens* pods retained more toxic alkaloid than the other species, and alkaloid concentration was sufficiently high after pods had shattered (3.5 mg/g) to pose a moderate grazing risk. After seed shatter, the toxic alkaloid concentrations in leaves and pods of *D. barbeyi*, *D. occidentale*, and *D. glaucum* were generally less than 2 mg/g; thus, risk of losing cattle would be low for the remainder of the grazing season.

Key Words: diterpenoid alkaloids, poisonous plants, grazing management

Tall larkspurs (*Delphinium barbeyi* (L. Huth), *D. occidentale* (Wats.), *D. glaucescens* (Rydb.), *D. glaucum* (Wats.)) are toxic plants that are often fatally ingested by cattle on western rangelands. The presence of larkspur often dictates summer grazing management of mountain rangeland as producers attempt to reduce or avoid livestock losses (Pfister et al. 1997). A long-established management practice is to defer grazing until larkspur is mature, vaguely defined as the late flower or pod stage of growth (Marsh et al. 1916). Late-season grazing can provide 6 to 8 weeks of grazing depending on larkspur phenology, elevation, available forage, and weather (Pfister, personal observations).

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Resumen

Las especies de "Tall larkspur" [*Delphinium barbeyi* (L. Huth), *D. Occidentale* (Wats.), *D. glaucescens* (Rydb.), *D. glaucum* (Wats.)] son una seria amenaza de envenenamiento para el ganado que apacenta en pastizales de verano. Los ganaderos a menudo difieren el apacentamiento hasta que el "Larkspur" esta maduro, sin embargo, se carece de información específica respecto a las concentraciones de alcaloides tóxicos que contiene el "larkspur" desde la producción de vainas hasta la senescencia de la planta. De 1995 a 1997, durante la etapa de producción de vainas a senescencia, se colectaron hojas y vainas "Tall larkspur" aproximadamente cada 2 semanas, la colecta se realizó en plantas marcada en localidades de Utah (Logan y Salina), Idaho (Ashton, Humphrey y Oakley), Colorado (Yampa y Montrose) y California (Carson Pass). Las concentraciones de alcaloides tóxicos de las vainas de todas las especies fueron mayores ($\bar{x}$ = 2.9 mg/g) que las concentraciones de las hojas ($\bar{x}$ = 1.5 mg/g), pero la magnitud de la diferencia vario entre las 4 especies. Al madurar, la concentración de alcaloides tóxicos de las hojas descendió mas rápidamente que la concentración de las vainas. Las vainas no empezaron a perder cantidades substanciales de alcaloides tóxicos hasta que el "Larkspur" maduró y las vainas comenzaron a desecarse. En la etapa de caída de semilla, las vainas de *D. glaucescens* retuvieron mas alcaloides tóxicos que otras especies y la concentración de alcaloides en ellas después de haber liberados las semillas fue suficientemente alta (3.5 mg/g) para poseer un riesgo moderado durante el apacentamiento. Después de la caída de la semilla las concentraciones de alcaloides tóxicos en hojas y vainas de las especies *D. barbeyi*, *D. occidentale* y *D. glaucum* generalmente fueron menos de 2 mg/g; así, el riesgo de perder ganado sería bajo para el resto de la estación de apacentamiento.

Major deficiencies in this recommendation include: (1) the concentration of toxic alkaloids (i.e., toxicity) in tall larkspurs often decreases with maturation, but this decrease is not constant or consistent (Pfister et al. 1994, Ralphs et al. 1997); (2) grazing during the late-flower period may expose cattle to a high risk of poisoning (Pfister et al. 1997); and (3) information specific to late summer and fall alkaloid concentrations and plant toxicity is insufficient to make definitive grazing recommendations.

Previously we evaluated seasonal changes in tall larkspur toxicity, but usually stopped sampling during the early pod stage (Pfister et al. 1994, Ralphs et al. 1997). Seed pods may take longer than 6 weeks to mature and shatter; furthermore, green leaves may remain after pods have shattered (Pfister, personal observations). Information on late-season toxicity is necessary for livestock pro-

ducers to determine when the risk of poisoning is sufficiently low to allow grazing. In this study we provide information for toxic alkaloid concentrations in seed pods and leaves from the pod stage of growth to senescence.

Methods

Sample Collection

We collected tall larkspur leaves and seed pods about every 2 weeks from the early pod stage of growth to senescence from marked plants in each location ($n = 8$), with some exceptions (Table 1). Generally, sampling occurred from early August to late September or early October in each year, and where possible, was timed to represent 4 phenological stages: early pod, pod, late pod, and seed shatter. We marked 20 individual plants with a numbered fiberglass rod. Tall larkspurs generally have multiple stems, and sampling leaves and seed heads from a single stem provides a representative sample of the entire plant (Manners and Pfister 1996). Therefore, during each collection we selected an individual stem from each plant at random, and we harvested all the leaves and the seed head (i.e., entire seed pod including stem from upper 15 to 20 cm of the stem) from this stem. The harvested leaves and seed heads mimic the plant parts that cattle generally select (Pfister et al. 1988). All plant parts were maintained separately for alkaloid analysis. A sample size of 20 plants is usually sufficient to provide an alkaloid concentration within $\pm 10\%$ of the population mean with 95% confidence (Manners and Pfister 1996). We packed samples in ice

for transport to the laboratory, where they were frozen at -20°C , freeze-dried, then ground to pass through a 1 mm screen for later analysis. We did not mark individual plants at Humphrey, Ida. because *D. glaucescens* seldom has sufficient stems for repeated sampling of the same plant. Instead, during 1995 and 1997, we selected 20 plants at random during each collection period, and collected leaves and seed heads. In 1996 at Ashton, Ida, we collected leaf and pod samples from 20 different plants on each date. We also collected seeds during 1996 from plant populations at Logan, Yampa, and Montrose; during 1997 we collected seeds from Oakley, Yampa and Montrose.

Alkaloid analysis

The primary toxins in tall larkspurs are 2 norditerpenoid alkaloids: methyllycconitine (MLA) and 14-deacetylnudicauline (DAN). These alkaloids have nearly identical mammalian toxicity (mice LD_{50} 4.0 to 4.7 mg/kg; Manners et al. 1995). The combined concentration of these 2 toxic alkaloids (i.e., MLA + DAN = toxic alkaloid concentration) was determined by Fourier transform infrared spectroscopy (FTIR, Gardner et al. 1997).

This methodology also provides a measurement of the total alkaloid (i.e., toxic + less-toxic alkaloids) concentration. Less-toxic alkaloids are 2 to 4 orders of magnitude less toxic than MLA (Manners et al. 1995) because they lack the correct structural specificity to impart significant toxicity. The total alkaloid concentration has relevance when producers use sheep as a management tool to reduce cattle losses (Ralphs and Olsen 1992), as higher concentrations of total alkaloids reduce lark-

spur consumption by sheep (Pfister et al. 1996). Because total alkaloid concentrations are less important than toxic alkaloids, only a brief summary is presented.

Statistical Analysis

The data were analyzed using the GLM procedure of SAS (1988) with the following effects: years, species, locations nested within species, plant part, phenological stage, and individual plants (subsampling term), and resulting interactions. Years, species, and the year $\times$ species interaction were tested using the sum of the location within species term and the year $\times$ location within species term as the single error term. Plant parts, year $\times$ part, species $\times$ part, and year $\times$ species $\times$ part were tested using the sum of the part $\times$ location within species and the part $\times$ year $\times$ location within species terms as the single error term. Phenological stage, year $\times$ stage, species $\times$ stage, year $\times$ species $\times$ stage, part $\times$ stage, year $\times$ part $\times$ stage, species $\times$ part $\times$ stage, species $\times$ part $\times$ stage, and the 4-way interaction were tested using the sum of the part $\times$ location within species $\times$ stage term and the part $\times$ year $\times$ location within species $\times$ stage term as the single error term. When significant F-tests were found, the Duncan's multiple range test was used to compare means. Differences in locations within each species (where applicable) were examined with the GLM procedure of SAS (1988) using a model with location, year within location, part, part $\times$ location, part $\times$ year within location, stage, stage $\times$ location, stage $\times$ year within location, stage $\times$ part, stage $\times$ part $\times$ location and stage $\times$ part $\times$ year within location. The year within location term was used to test for differences in location; part and

Table 1. Location of each tall larkspur collection, years of collection, elevation, associated vegetation type, and sampling methods.

Delphinium spp.		Location	Years	Elevation (m)	Vegetation Type	Sampling Method ¹
<i>D. barbeyi</i>	Montrose, Colo.	38°18'N 108°12'W	1995-97	2871	Conifer/Aspen	Marked plants
	Yampa, Colo.	40°12'N 107°04'W	1995-97	2580	Conifer/Aspen	Marked plants
	Salina, Ut. ²	38°44'N 111°39'W	1995-97	2895	Aspen	Marked plants
<i>D. occidentale</i>	Logan, Ut.	41°54'N 111°34'W	1996-97	2400	Conifer/Aspen	Marked plants
	Ashton, Ida.	44°05'N 111°08'W	1995-96	1815	Aspen	Marked plants ³
	Oakley, Ida.	42°10'N 114°11'W	1995-97	2247	Aspen	Marked plants
<i>D. glaucescens</i>	Humphrey, Ida.	44°32'N 112°10'W	1995,97	2396	Grass meadow	No marked plants ⁴
<i>D. glaucum</i>	Carson Pass, Calif.	38°40'N 119°59'W	1996-97	2700	Wet meadow	Marked plants ⁵

¹Unless noted otherwise, 20 individual plants were marked, and all leaves and the seed head were collected from 1 stem during each sample period; sampling recurred at approximately 2 week intervals during the pod stage until senescence.

²This larkspur population includes some *D. occidentale*, but is primarily *D. barbeyi*.

³Twenty different unmarked plants were sampled during each collection in 1995; 20 plants were marked and sampled during 1996.

⁴Individual plants of *D. glaucescens* often do not have sufficient stems for multiple samples, therefore leaves and seed heads were collected from 20 different plants during each collection period during 1995 and 1997. Whole plants collected during 1996 were not included in the statistical analysis.

⁵A composite sample from at least 20 plants was collected during each period in 1996; 20 plants were marked and sampled during 1997.

Fig. 1. Toxic (A) and total (B) alkaloid concentration (mg/g + SE) in leaves and pods of 4 *Delphinium* species during the later portion of the growing season.

Fig. 2. Toxic alkaloid concentration (mg/g + SE) in *Delphinium* spp. pods and leaves in various growth stages during the later portion of the growing season.

the part x location interaction were tested using the part x year within location error term; stage and stage x location were tested using the stage x year within location term; stage x part and stage x part x location were tested using the stage x part x year within location error term. Correlation coefficients for alkaloid concentrations in plants were determined using mean concentrations for each plant for each location and year.

Results and Discussion

Years

Overall, the toxic alkaloid concentration averaged 2.1 mg/g (SE $\pm$ 0.05; range = 17.4). Years did not differ and year x species did not interact ($P > 0.1$). Ralphs et al. (1997) reported year differences in alkaloid concentrations for all species except *D. glaucescens*, but Pfister et al. (1994) found that concentrations in *D. barbeyi* in Colorado differed in only 1 of 3 years. We speculate that years did not differ in our study because sampling was confined to the late summer period when concentrations were relatively low, and therefore more stable, relative to vegetative and bud stages (Pfister et al. 1994, Ralphs et al. 1997). We caution that year-to-year variation in toxicity may be high, particularly at earlier stages of maturity.

Plant Parts

The plant part x species interaction was significant, as toxic alkaloid concentrations in pods exceeded leaf alkaloid concentrations in all species, but the magnitude of the difference varied among the 4 species (Fig. 1). We have noted in previous studies that pod toxicity generally exceeds that for leaves (Pfister et al. 1994, Ralphs et al. 1997). Seed pods apparently accumulate both toxic and less-toxic alkaloids early in the maturation process, although the degree of accumulation differs among species.

Phenological Stage and Species

Toxic alkaloid concentrations declined ($P < 0.05$) as tall larkspur matured. Leaves showed a more rapid decrease in toxic alkaloid concentration than pods (Fig. 2). Seed pods began to lose substantial amounts of toxic alkaloid beginning at the late pod stage (i.e., pods beginning to desiccate). In all species except for *D. barbeyi* at Salina, Utah, we found no indication of the late-season increase in leaf toxic alkaloids that we previously reported

Fig. 3. Toxic alkaloid concentration (mg/g + SE) for 4 *Delphinium* species at various growth stages during the later portion of the growing season.

during one season in Colorado (Pfister et al. 1994). Pods apparently lose some alkaloids because of alkaloid-containing seeds dropping from the pods. Some alkaloids must be retained in the shattered pods because, as noted below, residual pods from *D. glaucescens* remained toxic after seed shatter. Seeds collected from *D. barbeyi* in Colorado (Yampa and Montrose) averaged 5.4 mg/g of toxic alkaloid, whereas *D. occidentale* seeds from Oakley, Ida. and Logan, Utah contained 7.1 and 0.25 mg/g of toxic alkaloid, respectively. No seeds were found in *D. glaucescens* plants at Humphrey, Ida. We speculate that the toxic alkaloid concentration remained high in the residual pods of *D. glaucescens* because seed formation and subsequent loss were incomplete.

D. glaucescens and *glaucum* exhibited higher initial toxic alkaloid concentrations than *D. barbeyi* and *occidentale*. At seed shatter, most tall larkspur species contained about the same concentrations of toxic alkaloid, except *D. glaucescens* retained more toxic alkaloid than the other species (Fig. 3). Previous work in our laboratory (Ralphs et al. 1997) determined that *D. glaucum* contained the highest overall concentration of toxic alkaloid, but the present study showed that toxic alkaloid concentration in *D. glaucum* decreased greatly during pod formation.

Same Species at Different Locations

D. barbeyi was sampled at 3 locations (Montrose, Salina, and Yampa). There were no location effects nor interactions ($P > 0.1$). We found a significant stage $\times$ part interaction for toxic alkaloids in *D. barbeyi*. Toxic alkaloid concentrations decreased more with maturation in *D. barbeyi* leaves than in pods (Fig. 4).

For *D. occidentale* the location $\times$ plant part interaction was significant; stage of

growth was also a significant factor. The interaction with location occurred because the Logan tall larkspur population had much lower toxic alkaloid concentrations over the late summer compared to either Ashton or Oakley, and concentrations at Logan were largely unaffected by stage of growth (Fig. 5). Furthermore, leaves and pods at the Logan location had almost identical, but very low, concentrations of toxic alkaloids which changed little over time. Conversely, at both Ashton and Oakley, toxic alkaloid concentrations declined as plants matured and were lowest at seed shatter (Fig. 5).

We offer no explanation for the much lower concentration of toxic alkaloids in *D. occidentale* collected near Logan compared to collections from Oakley and Ashton. Ralphs et al. (1997) similarly reported that *D. occidentale* collected near Bozeman, Mont. and Jackson, Wyo. had much lower concentrations than the Oakley population. In the Ralphs et al. (1997) study, collections from Jackson and Bozeman were from a single year; nonetheless, concentrations were similar to our results from Logan. The Logan population was also unusual in that total alkaloid concentrations were high (pod $\bar{x}$ = 18.4 mg/g; leaf $\bar{x}$ = 5.6 mg/g).

Correlation coefficients relating toxic and total alkaloid concentrations in leaves and pods from individual plants were low ($r=0.2$ to 0.5), indicating that generally toxic and total alkaloid concentrations

Fig. 4. Toxic and total alkaloid concentrations (mg/g + SE) for *Delphinium barbeyi* leaves and pods at various growth stages during the later portion of the growing season.

vary independently in plant parts. Because it seems unlikely that environmental conditions are sufficiently different in these mountain habitats to produce such large differences in toxicity, we speculate that genetic differences in populations are responsible. Current work in our laboratory is exploring genetic differences in populations and related alkaloid concentrations (Li, Gardner, Wang, and Ralphs, unpublished data).

Total Alkaloid Concentrations

Overall, total alkaloid concentration averaged 7.0 mg/g (SE $\pm$ 0.12; range = 29.9). Total alkaloid concentrations in pods and leaves averaged 9.4 (SE $\pm$ 0.18) and 4.7 mg/g (SE $\pm$ 0.12), respectively. Pod concentrations of total alkaloids in *D. glaucescens* and *occidentale* were 2 to 3 times greater than found in leaves (Fig. 1), but smaller differences were found in *D. barbeyi* and *glaucum*. Total alkaloid concentrations averaged 10.3, 7.8, 5.0, and 4.4 mg/g for the early pod, pod, late pod, and shattered stages, respectively. Pod and leaf concentrations at various phenological stages are shown in Fig. 4. In general, the leaves and pods of most tall larkspur species contained insufficient total alkaloids to be potentially deterrent to sheep grazing. We found earlier that total alkaloid concentrations above 12 mg/g deter consumption by sheep (Pfister et al. 1996); most concentrations in this study were below this threshold except for pods from *D. occidentale*.

Management Implications

Risk, the potential to poison livestock from larkspurs, is a continuum from low to high, and degree of risk depends largely on the amount that cattle eat and the concentration of toxic alkaloids in the ingested larkspur (Pfister et al. 1997). Previous studies have determined that at toxic alkaloid concentrations below 3 mg/g, toxicity and the resultant likelihood of poisoning is low, at 3 to 6 mg/g toxicity is moderate, and above 6 mg/g toxicity is high (Pfister et al. 1997). In assessing risk to cattle from eating seed pods, we assumed that all of the alkaloids in the seed pods are extracted in the gut and that bioavailability is complete (i.e., worst case scenario), but we have not tested this assumption.

D. glaucescens

The average toxic alkaloid concentration for *D. glaucescens* was sufficiently high

(4.4 mg/g) that grazing risk would be moderate on rangelands with abundant populations of this species, even after seed shatter. More than 70% of the *D. glaucescens* pod samples that we collected had toxic alkaloid concentrations above 3 mg/g ($\bar{x}$ = 6.1 mg/g), whereas about 4% of the leaf samples contained more than 3 mg/g. *D. glaucescens* leaves showed a large decrease in toxic alkaloids from 2.5 to 0.6 mg/g from the pod to seed-shatter stage. Thus, cattle eating only leaves would not be at risk during the later part of the grazing season. Pods averaged almost 9 mg/g of toxic alkaloid in the early pod stage, and only declined to 3.5 mg/g when shattered. Thus, cattle eating pods before seed shatter would be at high risk. Even after seed shatter, cattle could potentially become intoxicated because of the residual toxic alkaloids remaining in the plant. Ranchers with cattle grazing on range-

lands with populations of *D. glaucescens* must exercise caution throughout the entire grazing season. Unlike *D. occidentale* and *barbeyi*, we have not determined when cattle eat *D. glaucescens* in relation to plant phenology, although Ralphs and Olsen (1992) observed that cattle readily ate flowering *D. glaucescens*. On ranges with dense patches of *D. glaucescens*, grazing sheep ahead of cattle may be the only viable grazing management option to reduce risk to cattle (Ralphs and Olsen 1992).

D. occidentale

In some locations (e.g., near Logan, Ut.), *D. occidentale* would not be a threat to poison livestock because of low toxicity in both pods and leaves. At other locations (e.g., Ashton, Ida. and Oakley, Ida.) pods were sufficiently toxic (near 4 mg/g)

Fig. 5. Toxic alkaloid concentrations (mg/g + SE) for *Delphinium occidentale* leaves (A) and pods (B) at 3 locations (Ashton and Oakley, Ida.; Logan, Ut.) at various growth stages during the later portion of the growing season.

before maturation to pose significant risk to grazing cattle. Moderate risk persisted until seed shatter and toxicity declined to 1 to 2 mg/g. Generally, *D. occidentale* leaves were less toxic than pods and therefore pose less of a risk to cattle. Previous grazing studies have determined that cattle eat substantial amounts of *D. occidentale* pods during the late summer (Pfister and Manners 1991). At toxic alkaloid concentrations near 4 mg/g, cattle could be poisoned by eating 30% of their daily diet as pods (Pfister et al. 1997). Once *D. occidentale* pods have shattered, cattle would have to eat >60% of their diets as pods in order to be poisoned. This level of consumption only rarely occurs (Pfister et al. 1988).

D. barbeyi

Leaves and pods of *D. barbeyi* during the pod stage at the various locations contained 2 to 3 mg/g, indicating that poisoning risk is generally low once pods have lost their green color. At Salina, Utah, the average toxic alkaloid concentration in leaves actually increased from 1.3 mg/g at the pod stage to 2.5 mg/g at seed shatter. This increase in late-season leaf toxicity has been noted at other times (Pfister et al. 1994). We speculate that this increase occurred because of late-season environmental conditions allowing leaves to translocate or synthesize toxic alkaloids. Even with this increase, leaves were not highly toxic at Salina at the end of the season, and cattle would need to eat >50% of their diets as tall larkspur leaves to be poisoned. In the other locations where *D. barbeyi* was sampled, leaf toxicity decreased to very low levels (0.4 to 0.9 mg/g) when pods shattered, and risk would have been correspondingly low if cattle ate only leaves. Toxic alkaloid concentrations in pods at all 3 locations were < 2 mg/g when pods shattered, thus risk of losing cattle would be low for the remainder of the grazing season.

D. glaucum

Although *D. glaucum* is the most toxic tall larkspur early in the growing season (Ralphs et al. 1997), toxicity declined rapidly once pods began to develop. Toxic alkaloid concentrations in leaves decreased from 3.4 mg/g in the early pod stage to 1.3 mg/g in the pod stage and below 0.5 mg/g thereafter until seed shatter. Developing pods had toxic alkaloid concentrations of 5.4 mg/g, and fully ripe pods also contained 4.9 mg/g of toxic alkaloids. Thus, if cattle eat substantial amounts of pods (> 30 % of their daily diet), risk of poisoning is moderate until

seed shatter. After shattering, toxic alkaloid concentration decreased to 1.2 mg/g in seed heads, and risk to cattle would be very low.

In summary, livestock producers with tall larkspur on their summer ranges need to determine which species of tall larkspur is present. Once tall larkspur is identified, these results can guide grazing management decisions from the pod stage until pods shatter. Current research in our laboratory is partially focused on development of methods suitable for field estimation of toxic alkaloid concentrations by extension personnel or livestock producers (Pfister et al. 1999). In the meantime, for specific determination of toxic alkaloid concentrations on a site-by-site basis, livestock producers may contact the authors regarding sampling and analysis of tall larkspur.

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Western ragweed effects on herbaceous standing crop in Great Plains grasslands

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Abstract

Western ragweed [*Ambrosia psilostachya* DC.], a major forb species in mixed and tallgrass prairies, is considered to have little value for cattle grazing but is an important food item for bobwhite quail [*Colinus virginianus*]. While often thought to be a strong increaser with grazing pressure, information on the actual relationship between western ragweed and grasses is contradictory. Our objectives were to 1) determine the effect of western ragweed on grass standing crop, and 2) determine the effect of vegetation type and grazing on survival and shoot morphology of western ragweed. Western ragweed did not appear to reduce grass standing crop. Instead, standing crop (40 to 620 kg ha⁻¹) and density (6 to 41 shoots m⁻²) of western ragweed were positively related to grass and grass-forb standing crop in mixed prairie. Standing crop of western ragweed was not related to grass standing crop in tallgrass prairie. Competitive thresholds for western ragweed in mixed and tallgrass prairies appear to be above the levels observed in this study. Density of western ragweed shoots decreased over the growing season under both grazed and ungrazed treatments. Survival of western ragweed shoots from June to September was greater in mixed prairie (81%) than in tallgrass prairie (63%) and was greater in ungrazed (76%) than grazed plots (68%). Western ragweed shoots weighed less per unit of height in tallgrass prairie. Western ragweed shoots in ungrazed plots were taller than shoots in grazed plots but weighed less per unit of height. These differences in shoot morphology are consistent with increased competition for light in tallgrass prairie and in ungrazed sites. Western ragweed may not directly reduce grass standing crop but, rather, increase only when grasses are reduced by other stresses such as improper grazing.

Key Words: *Ambrosia psilostachya*, plant competition, grazing effects

Western ragweed [*Ambrosia psilostachya* DC.] is often the most abundant forb in Great Plains grasslands. Western ragweed is considered a detriment to livestock production because of competition with forage grasses (Elder 1951). On the other hand, seeds of western ragweed are the most important single food item for bobwhite quail [*Colinus virginianus*] in Oklahoma (Baumgartner et al. 1952). The response of western ragweed to grazing is variable. Western ragweed increases with increasing stocking rates in tallgrass prairie (Elder 1951, Sims and Dwyer 1965). In mixed prairie, western ragweed decreases with increasing stocking rates (Launchbaugh 1967, Heitschmidt et al. 1989). Brummer et al. (1994) and Reece et al. (1994) observed greater

Resumen

"Western ragweed" (*Ambrosia psilostachya* D.C.), una de las principales especies herbáceas de los pastizales mixtos y altos, se considera de poco valor para el ganado bovino, pero es un importante componente de la dieta del "Bobwhite quail" (*Colinus virginianus*). Mientras que a menudo se considera que con presión de apacentamiento esta es un especie increosora, la información acerca de la relación actual entre el "Western ragweed" y los zacates es contradictoria. Nuestros objetivos fueron 1) determinar el efecto del "Western ragweed" en la biomasa en pie de los zacates y 2) determinar el efecto del tipo de vegetación en la sobrevivencia y morfología de las ramas del "Western ragweed". El "Western ragweed" parece no reducir la biomasa en pie de los zacates. En cambio la biomasa en pie (40 a 620 kg ha⁻¹) y la densidad (6 a 41 ramas m⁻²) del "Western ragweed" se correlacionaron positivamente con la biomasa en pie de los zacates y la biomasa en pie del conjunto zacates-hierbas de las praderas mixtas. La biomasa en pie del "Western ragweed" no se relaciona con la biomasa en pie de los zacates de las praderas altas. Los umbrales competitivos del "Western ragweed" en las praderas mixtas y altas parece ser mayor de los niveles observados en este estudio. La densidad de ramas de "Western ragweed" disminuyó a través de la estación de crecimiento tanto en los tratamientos con y sin apacentamiento. La sobrevivencia de ramas de "Western ragweed" en el periodo de Junio a Septiembre fue mayor (81%) en las praderas mixtas que en las praderas altas (63%), y fue mayor en las parcelas sin apacentamiento (76%) que en las que recibieron apacentamiento (68%). En las praderas altas las ramas de "Western ragweed" pesaron menos por unidad de altura. Las plantas de "Western ragweed" de los potreros sin apacentamiento fueron mas altas que las de los potreros con apacentamiento, pero pesaron menos por unidad de altura. Estas diferencias en la morfología de la planta son consistentes con el aumento de competencia por luz en los potreros sin apacentar de las praderas altas. El "Western ragweed" puede no reducir directamente la biomasa en pies de los zacates, mas bien se incrementa cuando los zacates se reducen por otras causas estresantes como el manejo inadecuado del apacentamiento.

western ragweed production when grazing was initiated early in the growing season, but intensive-early stocking significantly reduced western ragweed by mid July (Smith and Owensby 1978, McCollum et al. 1990). The impact of western ragweed on other plants is also variable. Western ragweed reduced grass standing crop in tallgrass prairie (Dwyer 1958). In mixed prairie, a posi-

tive relationship existed between western ragweed and grass standing crops as long as standing crop of western ragweed did not exceed 1,230 kg ha⁻¹ (Launchbaugh 1967). It is difficult to determine the effect of western ragweed on grass growth from herbicide studies because of the presence of other forbs affected by the treatment (Dahl et al. 1989, Powell et al. 1982, Rice and Stritzke 1989). Given the conflicting information on the ecology of western ragweed, it is difficult to prescribe management recommendations, especially the need for and timing of control measures. The objectives of this study were to determine: 1) the effect of western ragweed on grass production, and 2) some basic growth characteristics of western ragweed in tallgrass and mixed prairies.

Materials and Methods

Study Area

The first study area, supporting high-seral tallgrass prairie was located in north-central Oklahoma on the Oklahoma State University Research Range, about 21 km southwest of Stillwater (36°04'N, 97°13'W, elev. 280 m). The climate is continental with average annual precipitation of 831 mm, 65% of which falls as rain from May to October (Myers 1982). The 204-day frost-free growing period occurs from April to October. In January, daily minimum and maximum temperatures average -4°C and 9°C. Daily minimum and maximum temperatures in July average 21°C and 34°C. The study was conducted on shallow prairie ecological sites with slopes of 2 to 3%. The soil was a Grainola clay loam (fine, mixed, thermic Vertic Haplustalf), with a clay loam surface, a clay subsoil, and a solum depth of 50 to 80 cm. Dominant plant species included big bluestem [*Andropogon gerardii* Vitman], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], indiangrass [*Sorghastrum nutans* (L.) Nash], and tall dropseed [*Sporobolus asper* (Michx.) Kunth]. The second study area, supporting high seral mixed prairie, was in southwest Oklahoma on the Marvin Klemme Range Research Station near Clinton (35°22'N, 99°04'W, elev. 490 m). The climate at this site is also continental. The average annual precipitation is 766 mm with 69 percent falling as rain from April to September. The frost-free growing period is 205 days from April to October. Daily minimum and maximum temperatures in January average -4°C and 10°C. In July, daily minimum and maximum temperatures average 21°C and 36°C.

C. The study was conducted on red shale ecological sites with slopes of 2 to 3%. The soil was a Cordell silty clay loam (loamy, mixed, thermic Lithic Ustochrept). Cordell soils are shallow with a depth of 25 to 36 cm over hard siltstone (Moffatt and Conradi 1979). Dominant plant species included sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], and blue grama [*Bouteloua gracilis* (H. B. K.) Lag. ex Steud.].

Methods

Four similar sites were selected for study within each vegetation type. Sites were 0.8 to 8 km apart and located in different pastures. Pastures were 20 to 49 ha in size. Two plots, each measuring 3 x 7m, were established at each site. One plot was open to grazing by yearling cattle from late April to September and one plot was fenced to exclude grazing. Stocking rates were 2.9 AUM ha⁻¹ in the tallgrass prairie pastures and 1.6 AUM ha⁻¹ in the mixed prairie pastures. Conservative stocking rates are considered to be 2.2 AUM ha⁻¹ and 0.9 AUM ha⁻¹ for the tallgrass and mixed grass prairies, respectively. Corners of grazed plots were marked with wooden stakes driven to near-ground level. Ungrazed plots were fenced with wire panels and a 1-m strip was maintained between the panels and subplots within the enclosure. Grazed and ungrazed plots were 4 meters apart. Plots were divided into 21 subplots each measuring 1 x 1m. Fifteen of these subplots were sampled. Standing herbage levels were visually similar for grazed and ungrazed plots when the study began since plots were randomly selected from within grazed pastures. We removed standing dead herbage in both plots between the first and second years of the study to minimize any possible effects of dead herbage accumulation in the ungrazed plots. In early March of the second year, while vegetation was dormant, all plots were cut to a height of 14 cm with a rotary mower. The cut herbage was scattered over the plots by the mower and was not removed. Density of western ragweed was determined by counting all emerged shoots in the subplots in early June, mid-July and early September. Standing crops for western ragweed, other forbs, and grasses were determined by separately hand-clipping each component from 0.1 x 1-m quadrats placed within the subplots in September. Quadrats were clipped to ground level. In the second year, height and weight were determined for 1 shoot of western ragweed clipped near the center of

each subplot. All herbage was oven-dried 5 days at 48°C. All variables were averaged over subplots within plots for further analyses. In a separate series of measurements, shoots of western ragweed were collected in each vegetation type to develop growth curves. A transect, open to grazing, was established in a north-south orientation within 50 meters of each pair of plots. The transect was paced at 2-week intervals from mid-May through early October in the second year. At each pace, the height of the shoot of western ragweed located nearest to the toe of the technician was measured. The shoot was then clipped at ground level, oven-dried, and weighed in the laboratory. Twenty shoots were sampled on each transect for a total of 80 shoots in each vegetation type for each sample date. Only ungrazed shoots were collected.

Analysis

Analysis-of-variance was used to determine the effect of vegetation type and year on standing crops of all vegetation components (SAS Institute 1985). Regression models were then constructed to determine the relationships between standing crops of western ragweed and other vegetation components. Separate regression models were constructed for the independent variables of standing crop and density of western ragweed. Dependent variables were standing crops of grasses, forbs (other than western ragweed), and the combination of grasses and forbs.

Density of western ragweed was analyzed with a repeated measures analysis-of-variance. The model contained terms for vegetation type, grazing treatment, year, sample date, and all interactions. Year and sample date were considered repeated variables. A square root transformation was applied to the density data because of heterogeneity of variances. Changes in shoot density were further analyzed by expressing July and September densities as a percentage of the initial density in June. These percentages were then analyzed with a repeated measures analysis-of-variance containing terms for vegetation type, grazing treatment, year, month, and all interactions.

Regression models were constructed to relate western ragweed height, weight, and weight:height ratios to day of year. The models included terms for vegetation type, day of year, and their interactions. Both linear and quadratic terms were included for day of year. Vegetation type was a qualitative variable coded as 0 for mixed prairie and 1 for tallgrass prairie (Neter

and Wasserman 1974). The full model was fitted and then terms were deleted until all remaining terms were significant ($P = 0.05$).

End-of-season western ragweed stem height, weight, and weight:height ratios were analyzed by analysis-of-variance. The model contained terms for vegetation type, grazing treatment, and their interaction. A square root transformation was applied to all of the dependent variables because of heterogeneity of variances.

Where differences occurred in any analysis-of-variance, means were separated by the least significant difference. Unless noted otherwise, an alpha level of 0.05 was used for all hypothesis testing.

Results and Discussion

Precipitation

Precipitation was favorable during the May to September growing period at both locations and in both years (Fig. 1). Precipitation during this period was particularly high at the mixed prairie location with 193% and 169% of normal received in 1994–95 and 1995–96, respectively. At the tallgrass prairie location, precipitation from May to September was 146% and 109% of normal for the 2 study years. Winter-spring drought (November to April) was severe at both study locations in 1995–96. Precipitation in that period was 17% of average at the mixed prairie location, a record low, and 30% of average at the tallgrass prairie location.

Standing Crop Relationships

Standing crop of grasses was lower in mixed prairie than in tallgrass prairie (2,820 and 5,170 kg ha⁻¹). Standing crop of western ragweed and other forbs was not affected by vegetation type. Standing crop of grasses and western ragweed was similar across years, but the standing crop of other forbs was greater in 1995 than in 1996 (630 and 250 kg ha⁻¹). Based on these results, data used to develop regression models were pooled over years within vegetation type (except for other forbs).

In mixed prairie, standing crop of western ragweed ranged from 40 to 620 kg ha⁻¹. These levels of standing crop were positively correlated with grass and grass-forb standing crops (Fig. 2). No relationships existed between the standing crops of grass and other forbs ($P > 0.65$) or the standing crops of grass and total forbs ($P > 0.12$). Total forb standing crop ranged from 250 to 1,350 kg ha⁻¹. Western ragweed densities between 6 and 41 shoots m⁻² were also

Fig. 1. Study period and long-term mean precipitation received by month at each study location.

positively correlated with grass and grass-forb standing crops (Fig. 3).

Launchbaugh (1967) concluded forb

standing crop, almost entirely western ragweed, had to exceed 1,230 kg ha⁻¹ before grass production was reduced on clay

Fig. 2. Relationships of grass (open symbols) and grass-forb (closed symbols) standing crops with western ragweed standing crop in ungrazed mixed prairie.

Fig. 3. Relationships of grass (open symbols) and grass-forb (closed symbols) standing crops with western ragweed density in ungrazed mixed prairie.

uplands. On sandy sites, grass standing crop increased up to 1 kg with control of each kilogram of forbs (Dahl et al. 1989). The forb component was dominated by western ragweed. However, shinnery oak (*Quercus havardii* Rydb.) was also controlled in the test plots and this may have influenced the release of grasses. Our study and the threshold established by Launchbaugh (1967) indicate relatively large amounts of western ragweed have no effect on the standing crop of grasses in mixed prairie.

One reason for the positive correlation between biomass of western ragweed and

grasses was that western ragweed tended to be more abundant on plots dominated by midgrasses, mainly sideoats grama, and less abundant on plots dominated by shortgrasses, mainly buffalograss. Plots dominated by midgrasses also tended to have higher standing crops of grasses. It is likely that water relations were more favorable for plant growth on the midgrass plots. On the same soil, water infiltration and grass production is higher on midgrass-dominated sites compared to shortgrass-dominated sites (Wood and Blackburn 1981, Dormarr et al. 1994). Shortgrass roots form a dense mat in the

Fig. 4. Relationships between standing crop and density of western ragweed in ungrazed tallgrass (open symbols) and mixed (closed symbols) prairies.

upper soil layers (Weaver 1958). Western ragweed may be more abundant on midgrass areas because of the improved water relations and reduced root competition. Second, forbs may alter the microenvironment to favor increased grass production by providing shade and reducing wind speeds, which in turn reduce evapotranspiration (Launchbaugh 1967, Whitham 1971). Finally, high levels of precipitation during the study may have reduced the impact of soil moisture as a limiting factor for plant growth.

In tallgrass prairie, no relationship existed between the standing crop of grasses and the standing crop of western ragweed when the latter ranged between 30 and 1,030 kg ha⁻¹ (Fig. 4). The only significant relationship for tallgrass prairie was between density of western ragweed and standing crop of western ragweed (Fig. 5). Simple coefficients of determination of 0.85 and 0.75 indicate densities of western ragweed shoots provided a reasonable estimate of western ragweed standing crop in tallgrass and mixed prairie, respectively. On loamy prairie ecological sites with forb standing crops similar to ours, grass production increased about 1 kg for every kilogram of forbs controlled by herbicides (Rice and Stritzke 1989, Powell et al. 1982). Grass standing crop increased 0.7 to 0.9 kg with each kilogram of forbs controlled on claypan sites (Powell et al. 1982). However, these results are confounded by the varying degrees that forbs other than western ragweed were reduced by the herbicide. The presence of other forbs, such as heath aster [*Aster ericoides* L.], in both of these studies makes it difficult to determine which forb species are most associated with grass response following forb removal.

On another loamy prairie ecological site, above and below-ground standing crop of big bluestem was 56 and 54% lower, respectively, in the presence of western ragweed at 753 kg ha⁻¹ and 65 shoots m⁻² (Dwyer 1958). This appeared to be the result of direct plant competition because the site had had no grazing or major disturbance for many years. However, this relationship may have been a result of sampling methodology. Quadrats were selectively placed to include only big bluestem or combinations of big bluestem and western ragweed. With selective sampling, it is impossible to determine if the relationship of big bluestem and western ragweed is due to plant competition, inherent soil factors, animal disturbance, or some other unmeasured environmental influence.

Density of Western Ragweed

Western ragweed density decreased from early June to early September (Table 1) even with favorable precipitation.

Table 1. Western ragweed density by month averaged over grazing treatment and years.

Vegetation type	Sample Date		
	1 Jun.	15 Jul.	1 Sept.
	----- (Shoots m ⁻²) -----		
Mixed prairie	20 ^{cd1}	17 ^{de}	15 ^e
Tallgrass prairie	36 ^a	24 ^b	21 ^{bc}

¹Means with different letters are significantly different at $P < 0.05$.

Density of western ragweed was always higher in tallgrass prairie but the difference between vegetation types narrowed as the growing season progressed. Western ragweed density was not affected by year, averaging 24 shoots m⁻² in 1995 and 28 shoots m⁻² in 1996. The density of western ragweed averaged 31 shoots m⁻² on ungrazed plots and 20 shoots m⁻² on grazed plots but this difference was not significant.

Elder (1951) observed a 63% reduction in density of western ragweed following 3 years of rest. The lack of grazing or year effects or a grazing by year interaction in our study may reflect the above-average precipitation. Initial conditions were also different for the 2 studies. The sites studied by Elder were described as "weedy" at the start of his experiment while our study sites were in a high seral stage. There was probably more potential for change on the "weedy" site. Finally, Elder allowed dead herbage to accumulate over 3 years while we removed standing dead herbage during the dormant season.

Survival of shoots of western ragweed was higher in mixed prairie (81%) compared to tallgrass prairie (63%). We suggest this is a result of greater light competition in tallgrass prairie. The difference is not likely explained by soil moisture since the tallgrass prairie site received greater precipitation.

Survival to mid July (77%) was significantly greater than survival to early September (67%). This indicates that mortality was twice as high during the early portion of the growing season.

Survival of western ragweed tended to be greater in ungrazed plots (76%) compared to grazed plots (68%, $P = 0.09$) for both locations. This suggests some shoots were trampled or grazed. We found 5 and 13% of the shoots had the terminal portions removed by the end of June in mixed

Fig. 5. Relationships between standing crop and density of western ragweed in ungrazed tallgrass (open symbols) and mixed (closed symbols) prairies.

and tallgrass prairies, respectively. However, we cannot specifically attribute this grazing to cattle. Cattle graze young western ragweed but it is not a preferred forage plant (Elder 1951). By mid-July, the heavier grazing pressure of intensive-early stocking reduced forb standing crop, mostly western ragweed, to 54% of that in pastures stocked season-long in tallgrass prairie (McCollum et al. 1990).

Growth and Morphology

The rate of height increase for western ragweed was not affected by vegetation type ($p = 0.30$, Fig. 6). A simple time expression, day of year, accounted for

nearly all of the variation in rate of height increase ($r^2 = 0.97$, $p < 0.01$). Rainfall events had little discernable influence, but the plants were not exposed to prolonged soil drought during our study.

Vegetation type affected the rate of change in shoot weight (Fig. 7a) as well as the weight:height ratio (Fig. 7b). Shoots of western ragweed in mixed prairie gained weight more rapidly and weighed more per unit of height throughout the growing season than shoots in tallgrass prairie. Shoots of western ragweed in tallgrass prairie were less robust and had fewer branches and leaves on the lower portions of the shoots.

Fig. 6. Growth curve for western ragweed height. Models do not differ by vegetation type.

Table 2. Height, weight, and weight:height ratio of shoots of western ragweed at the end of the grazing season as affected by grazing treatment averaged over vegetation type.

Management	Treatment	
	Grazed	Ungrazed
Height (cm)	24*	30
Weight (mg)	1,290	860
Weight:height ratio (mg cm ⁻¹)	56*	29

*Indicates means within row are significantly different at $P < 0.05$.

Grazing also affected the morphology of western ragweed shoots. Near the end of the grazing period, shoots of western ragweed in grazed plots were shorter than those in ungrazed plots (Table 2). Shoot weight was not influenced by grazing treatment, but western ragweed shoots in grazed plots weighed nearly twice as much per unit of height as those in ungrazed plots. These differences were consistent over vegetation types. Previous

work in tallgrass prairie found that western ragweed shoots were taller and lighter in ungrazed plots compared to grazed plots (Fahnestock and Knapp 1993).

Competition for light is a limiting factor for growth of western ragweed in tallgrass prairie (Fahnestock and Knapp 1993). Competition for light is also an important factor in explaining the affect of vegetation type and grazing on the morphology of western ragweed shoots in this study. Plants with the least available light often have elongated internodes and less branching. Competition for light should be higher in tallgrass compared to mixed grass prairie and should also be higher in ungrazed versus grazed sites. Our results are consistent with these relationships, especially with respect to the weight:height ratio. Because of greater light availability in areas with lower standing crops of grasses, robust western ragweed plants are likely a result of, rather than the cause of, lower grass standing crop.

Management Implications

Western ragweed has long been considered an aggressive competitor, but the results of our study question this conventional wisdom. The density of western ragweed decreases throughout the growing season and shoot morphology changes as grasses reduce the availability of light. Western ragweed's prominence in the forb component has likely led to the assumption that the majority of grass response to forb control is due to reduction of western ragweed.

Our study supports Launchbaugh (1967) who reported a positive relationship between grass standing crop and western ragweed standing crop below 1,230 kg ha⁻¹ in mixed prairie. An economic threshold for western ragweed control in mixed prairie has not been proposed, but our results suggest standing crops of at least 600 kg ha⁻¹ can be tolerated before control should be considered.

Western ragweed thrives where grass vigor has declined from grazing or drought in tallgrass prairie (Elder 1951, Bovey et al. 1966). Shoots of western ragweed are shorter in grazed environments but have more weight per unit of height. An abundance of western ragweed in tallgrass prairie likely indicates that grasses are over-utilized. However, in such cases, high levels of western ragweed are a result of, not a cause of, lower vigor of the grasses. If a reduction in western ragweed is desired, attention should first be directed toward improved grazing management. Future research should focus on determining competitive and economic thresholds for western ragweed in tallgrass and mixed prairies.

Fig. 7. Growth curves for western ragweed weight ($R^2 = 0.98$ for system of equations) and weight:height ratio ($R^2 = 0.99$ for system of equations). Models are significantly different between vegetation types.

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Age-stem diameter relationships of big sagebrush and their management implications

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Abstract

Decisions to control big sagebrush (*Artemisia tridentata* Nutt.) on North American rangelands are traditionally based on morphological characteristics (e.g., cover) rather than more ecologically based community successional criteria. Big sagebrush stand age is a critical component for evaluating successional status, but has been difficult to obtain under field conditions. Assessing big sagebrush plant age based on stem diameter would provide resource managers with an efficient field tool to make management decisions based on ecological principles. For each of 3 subspecies of big sagebrush, between 75–80 stem cross-sections were collected within each of 9 stands situated at 3 regionally dispersed locations across Wyoming. Maximum basal stem diameters were measured and plant age determined from annual growth-ring assessments. Regression analysis (95% confidence interval) relating maximum basal stem diameter to plant age produced coefficients of determination (r^2) of 0.70, 0.64, and 0.61 for Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle and Young) in each of 3 regional locations; 0.53, 0.69, and 0.64 for mountain big sagebrush (*A. tridentata* ssp. *vaseyana* [Rydb.] Beetle); and 0.50, 0.62, and 0.44 for basin big sagebrush (*A. tridentata* ssp. *tridentata*). Combined regional data for each subspecies produced r^2 values of 0.54 for Wyoming big sagebrush, 0.52 for mountain big sagebrush, and 0.50 for basin big sagebrush. Results indicate that maximum basal stem diameter can be used to assess the age of big sagebrush subspecies, thus, providing land managers with an ecologically based alternative method for justifying big sagebrush management decisions.

Key Words: big sagebrush, annual growth-rings, succession

All 3 subspecies of big sagebrush, basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*), mountain big sagebrush (*A. tridentata* subsp. *vaseyana* [Rydb.] Beetle), and Wyoming big sagebrush (*A. tridentata* subsp. *wyomingensis* Beetle and Young) are dominant constituents of many rangeland communities. Intensive livestock grazing during the first half of this century, periodic drought and recent wildfire suppression efforts have allowed big sagebrush to dominate more than 100 million acres of North American rangelands (Miller et al. 1994, Pieper 1994). Decisions to control big sagebrush are generally based on either the subjective condition of “when sagebrush stands are dense and tall” or the more quantitative condition

Resumen

Las decisiones de controlar la artemisa grande (*Artemisia tridentata* Nutt.) en las praderas norte americanas tradicionalmente están basadas en las características morfológicas (e.g., la tapa) más bien que el criterio comunitario sucesivo que es más basada en la ecología. La edad situada de la artemisa grande es un componente crítico para evaluar el estatus sucesivo, pero ha sido difícil en obtener bajo de las condiciones del campo. Amillarar la edad de la artemisa grande a base del diámetro del tallo les proveería a los gerentes de recursos con una ventaja eficaz para hacer decisiones basadas en los principales ecológicos. Por cada una de las 3 subespecies de la artemisa grande, fueron coleccionados entre 75–80 tallos cuadrículados dentro de cada de las 9 plataformas situadas en 3 lugares regionalmente dispersados por Wyoming. Los diámetros máximos de los tallos basales fueron medidos y la edad de la planta fue determinada por el amillarar de los anillos anuales del crecimiento. El análisis regresado (de intervalo de confianza a 95%) relacionando el diámetro máximo del tallo basa a la edad de la planta produjo coeficientes de determinación (r^2) de 0.70, 0.64, y 0.61 para la artemisa grande de Wyoming (*A. tridentata* ssp. *wyomingensis* Beetle y Young) en cada de los tres lugares regionales; 0.53, 0.69, y 0.64 para la artemisa grande de la montaña (*A. tridentata* ssp. *vaseyana* [Rydb.] Beetle); y 0.50, 0.62 y 0.44 para la artemisa grande de la cuenca (*A. tridentata* ssp. *tridentata*). La data combinada de cada subespecie produjo los valores de r^2 de 0.54 para la artemisa grande de Wyoming, 0.52 para la artemisa grande de la montaña y 0.50 para la artemisa grande de la cuenca. Los resultados indican que el diámetro máximo del tallo basa se puede usar para amillarar la edad de las subespecies de la artemisa grande, entonces, les provee a los gerentes de la tierra con una manera alternativa basada ecológicamente para justificar las decisiones administrativas en cuanto a la artemisa grande.

“when sagebrush makes up more than one-half of the total plant cover,” (Pechanec et al. 1954).

Recently, several rangeland ecologists have advocated the development and implementation of successional models that contain the concepts of multiple stable states, thresholds, and/or transition states, allowing opportunistic management strategies to be utilized in the manipulation of plant communities (Smith 1978, Archer et al. 1988, Westoby et al. 1989, Friedel 1991,

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Laycock 1991, and SRM Task Group on Unity in Concepts and Terminology 1995). Within these new models, the successional state of a given plant community is usually identified in terms of recovery time since the occurrence of some disturbance. Fire is one important disturbance process that drives successional changes in grassland/shrubland ecosystems (Wright and Bailey 1982). Fire suppression has been practiced since European settlement in almost all areas where grassland systems occur. On this basis, increased fire-return intervals have been cited as a primary cause of invasion and encroachment of fire-sensitive woody species into grasslands (Kucera 1981, Bock and Bock 1984, Wright and Bailey 1982, Fisher et al. 1987, Steinaur and Bragg 1987).

We believe that decisions to implement big sagebrush control practices should be based on ecological principles. A comparison of the age of a big sagebrush stand and the characteristic fire-return interval is an ecological approach related to the successional state of a given plant community. For example, if a particular stand of big sagebrush is 50 years old and the characteristic fire-return interval is 10 years, control practices should be implemented irrespective of the amount of big sagebrush cover.

Several investigators have used stem diameter to quickly predict the age of individuals or stands of woody plants. Hinchman and Birkeland (1995) developed age-stem diameter relationships for Fremont cottonwoods (*Populus fremontii* S. Wats.) in Utah and Arizona, to aid in dating fluvial surfaces such as channel bars in riparian environments. Brotherson et al. (1983) developed age-stem diameter relationships for 8 tree species in the Navajo National Monument, Arizona. These species included: box elder maple (*Acer negundo* L.), Utah juniper (*Juniperus osteosperma utahensis* [Torr.] Little), pinyon pine (*Pinus edulis* Engelm.), Fremont cottonwood, quaking aspen (*Populus tremuloides* Michx.), Douglas fir (*Pseudotsuga taxifolia* [Loudon] Britton), Gamble oak (*Quercus gambelii* Nutt.), and salt cedar (*Tamarisk ramosissima* Ledeb.). In another study, Brotherson et al. (1984) investigated age-stem diameter relationships of salt cedar in central Utah to assess invasion dynamics. Brotherson et al. (1980) also developed age-stem diameter relationships for 2 species of mountain mahogany (*Cercocarpus montanus* [Raf.] and *Cercocarpus ledifolius* [Nutt.]) from populations in Utah, Oregon, Nevada, and Wyoming. In each case, investigators found reasonable age-stem diameter rela-

tionships for individuals within stands. However, the regression models were not consistent across stands or differing site potentials. Age-stem diameter relationships have not been developed for any subspecies of big sagebrush.

Ferguson (1964) demonstrated that annual growth-rings in big sagebrush were easily identified and reliable as a chronologic device. Given this characteristic, the purpose of this study was to determine if the age of big sagebrush plants could be predicted from maximum stem diameters. If big sagebrush plant or stand age can be quickly and accurately determined from maximum stem diameter, land managers will have a new method for identifying areas that are in a stable ecological state requiring sagebrush control. This is a more ecologically centered approach based on succession and fire frequency parameters rather than morphologic characteristics (e.g., cover) of big sagebrush plants.

Our specific objectives were: 1) determine if an accurate age to maximum basal stem diameter relationship existed for the 3 subspecies of big sagebrush; 2) determine if the relationship was stand specific within the same geographic region; and 3) determine if the relationship was consistent across a larger geographic area.

Table 1. GPS coordinates and elevations for all big sagebrush stands.

Subspecies and location	latitude	longitude	elevation (m)
<i>wyomingensis</i>			
Northeast WY	43° 34' 20.439"N	105° 10' 24.033"W	1538
	43° 35' 20.184"N	104° 52' 02.262"W	1384
	43° 28' 51.262"N	105° 03' 04.094"W	1355
Central WY	43° 08' 40.000"N	106° 34' 40.591"W	1866
	43° 10' 02.433"N	106° 35' 46.319"W	1864
	43° 04' 21.831"N	106° 34' 52.492"W	1899
Southwest WY	42° 52' 07.327"N	109° 57' 53.668"W	2295
	42° 51' 41.114"N	109° 57' 21.097"W	2289
	42° 51' 23.230"N	109° 57' 36.580"W	2359
<i>vaseyana</i>			
Southcentral WY	41° 42' 13.681"N	106° 34' 14.926"W	2244
	41° 42' 19.279"N	106° 34' 03.639"W	2247
	41° 42' 38.414"N	106° 33' 26.978"W	2269
Central WY	43° 55' 30.500"N	106° 45' 30.500"W	2530
	43° 51' 15.144"N	106° 35' 45.100"W	2591
	43° 30' 10.500"N	106° 28' 30.575"W	2743
Southwest WY	43° 00' 24.997"N	110° 00' 36.117"W	2361
	42° 59' 26.545"N	110° 00' 05.645"W	2323
	42° 68' 12.283"N	110° 00' 12.478"W	2350
<i>tridentata</i>			
Central WY	44° 59' 04.103"N	108° 15' 37.742"W	1500
	44° 01' 25.918"N	108° 00' 40.873"W	1276
	44° 02' 44.150"N	108° 04' 02.211"W	1222
Southwest WY ¹	42° 53' 32.871"N	110° 08' 10.433"W	2232
	42° 47' 24.146"N	110° 01' 02.187"W	2151
	42° 45' 13.367"N	110° 03' 39.924"W	2229
Southwest WY ²	42° 47' 30.161"N	109° 57' 49.956"W	2104
	42° 47' 57.983"N	109° 57' 48.782"W	2119
	42° 48' 02.694"N	109° 57' 46.575"W	2108

¹West slope of the Green River Basin

²East slope of the Green River Basin

Methods

Big sagebrush stands having a variety of cohorts, similar soil characteristics and topography, and relatively free from herbivory disturbance were selected for this study. Sites were selected to minimize microsite effects that increase or decrease supplemental moisture conditions. This approach minimized variations in growth rates between sites (Bonham et al. 1991).

Stem sections for subspecies *wyomingensis* were collected from 3 stands in northeast Wyoming near Rochelle; 3 stands in the South Fork of the Powder River watershed, northwest of Casper in central Wyoming; and 3 stands in southwest Wyoming near Pinedale. Stem sections for the subspecies *tridentata* were collected from 3 stands near Pinedale; 3 stands near Worland, on the west slope of the Bighorn Mountains; and 3 stands near Farson, in southwest Wyoming. Stem sections for the subspecies *vaseyana* were collected from 3 stands near Pinedale; 3 stands near Buffalo, on the east slope of the Bighorn Mountains; and 3 stands west of Laramie, near Elk Mountain in south central Wyoming. The 3 stands in each regional grouping were located within a 15 mile radius. All stand locations were permanently recorded with a Global Positioning System, and latitude/longitude coordinates and elevations are listed in Table 1.

A stratified, random sampling method was used to collect stem cross-sections from each sagebrush stand. A permanent baseline transect 100 m long was located within each sagebrush stand, and ten, 100 m long perpendicular transects were established at randomly selected points along the baseline transect. Along each perpen-

dicular transect, 8 random points were selected, and the closest individual big sagebrush plant was selected for sampling. If the closest individual was not suitable for aging (e.g., damaged stem), another random point was selected until a suitable individual was encountered.

Stem cross-sections were obtained by sawing the plant off below ground level (Ferguson 1964) to ensure that the pith and first annual growth ring were included. The stem was then cut approximately 10 cm from the bottom, providing a 10 cm long stem section. Sampling was conducted during the summer of 1997. Between 75 and 80 stem sections were collected from each stand (Cawker 1980).

In the laboratory, the bottom portion of each stem section was sanded sequentially with 60, 80, 320, and 400 grit sanding belts. Annual growth-rings were examined using a 10 power stereo microscope, and enumerated once by 2 different technicians for a total of 2 observations per sample.

Basal stem diameters were measured at the widest point across the face of each cross-section. Maximum basal stem diameter was designated the dependent variable, and age the predictor variable in simple linear regression analyses (Steel and Torrie 1980).

Regression models were constructed at 3 geographic scales. A model was constructed for each subspecies stand and for each group of 3 stands within the same relative geographic region. A comprehensive model for each subspecies was also constructed by combining all stands of the same subspecies to assess statewide consistency. All regression analyses were performed with the Microsoft Excel Version 7.0 Statistics Module.

Results and Discussion

Annual growth rings were easily identified making crossdating unnecessary. False rings have never been encountered in big sagebrush in northern latitudes and at higher elevations (Diettert 1938, Moss 1940, Ferguson 1964). Global position and elevation of Wyoming fulfill both of these criteria. Locally absent rings do occur, however complete absence of rings are almost never encountered due to the unique nature of annual ring formation in big sagebrush.

The annual growth-ring in big sagebrush is formed by an interxylary cork layer rather than increasing cell density bands as in most tree species. By nature, this makes the creation of interannual bands impossible. "This cork layer is produced during the growing season, between the new annual wood ring and that of the previous year. With the beginning of growth in the spring a single layer of meristematic cells (the interxylary cork cambium) remains between the last-formed xylem of the previous year and the newly forming xylem tissue. With the onset of hot and dry weather, the innermost layer of these cells becomes suberized" (Ferguson 1964).

Simple linear regression of the number of annual growth-rings against maximum basal stem diameter yielded significant equations ($p < 0.0001$) for all 27 individual stands, all 9 regional stand combinations, and all 3 statewide combinations. The coefficient of determination for individual stands ranged from 0.22 to 0.73; 0.44 to 0.70 for regional stand combinations; and 0.50 to 0.54 for statewide combinations (Table 2). Ranges and means for maximum diameter and age by subspecies are listed in Table 3. The residuals for each regression model had normal distributions.

Table 2. Age prediction equations for each individual big sagebrush subspecies by regional stand locations along with coefficients of determination (r^2), sample numbers (n), and p-values.

Subspecies and Location	Age prediction equation	r^2	n	p-value	95%CI
<i>wyomingensis</i>					
Northeast WY	Age = $5.6910 + 0.6744(\text{diameter})$	0.70	220	0.0001	± 0.12
Central WY	Age = $16.6392 + 0.9404(\text{diameter})$	0.64	199	0.0001	± 0.20
Southwest WY	Age = $5.4648 + 0.8514(\text{diameter})$	0.61	181	0.0001	± 0.29
<i>vaseyana</i>					
Southcentral WY	Age = $1.4846 + 0.6819(\text{diameter})$	0.53	211	0.0001	± 0.18
Central WY	Age = $5.6688 + 0.4430(\text{diameter})$	0.69	229	0.0001	± 0.08
Southwest WY	Age = $7.8955 + 0.8830(\text{diameter})$	0.64	191	0.0001	± 0.19
<i>tridentata</i>					
Central WY	Age = $6.3189 + 0.3783(\text{diameter})$	0.50	229	0.0001	± 0.10
Southwest WY ¹	Age = $4.9916 + 0.3543(\text{diameter})$	0.62	223	0.0001	± 0.07
Southwest WY ²	Age = $6.1918 + 0.3020(\text{diameter})$	0.44	212	0.0001	± 0.09

¹West slope of the Green River Basin

²East slope of the Green River Basin

$$6.810 + 0.7194(\text{diameter}), r^2 = 0.73$$

Fig. 1. A representative scatter plot for subspecies *wyomingensis* at the individual stand scale.

All samples including those which seemed to be outliers were included in the analyses. The effect of outliers is insignificant considering the large sample sizes incorporated in each model. Inclusion of potential outliers also provides models that are similar to conditions actually encountered in the field. A representative scatter plot for subspecies *wyomingensis* at the stand scale is shown in Fig. 1. Differences in intercept values were generally small between individual stands, regional stand combinations, and statewide combinations within the same subspecies, and ranged from 1 to 17 years. Confidence intervals (95%) around the population means ranged from ± 0.10 to ± 0.48 for individual stands; ± 0.07 to ± 0.29 for regional stand combinations; and ± 0.06 to ± 0.14 for statewide combinations. Coefficient of determination values indicate that maximum stem diameter can predict the age of big sagebrush plants. The relationship was stronger for Wyoming and mountain big sagebrush than for basin big sagebrush at the stand and regional combination scales. However, 2 individual stands of basin big sagebrush showed very strong relationships (0.75 and 0.71 coefficients of determination). We believe that because basin big sagebrush often occurs in areas where groundwater can be relatively shallow, some individual plants may be accessing a reliable groundwater source deep in the soil profile resulting in differen-

tial growth rates from plants not able to access the additional moisture. In areas where this additional moisture is not available, the age-stem diameter relationship appears to be similar to the other 2 subspecies.

The relationships are almost identical at the statewide scale. At this large spatial scale, coefficient of determination values were 0.54 for Wyoming big sagebrush, 0.52 for mountain big sagebrush, and 0.50 for basin big sagebrush. This is a predictable response when combining data sampled from areas that have significant variations in precipitation timing and amount, and growing season temperatures and lengths. Our models demonstrated efficacy at the stand and regional stand combination scales, however, inter-stand variations do exist. Our method has limitations similar to estimating aboveground biomass production with Robel et al. (1970) or other vegetation height-weight relationship methods. An initial regression model must be constructed before application to larger geographic areas. Once initial baseline models are generated for an area, maximum stem diameter measurements could serve as a useful tool for predicting big sagebrush stand ages.

Results from this study have several implications for management. Based on our developed regression models, land managers could quickly assess the age of big sagebrush stands by measuring maxi-

mum basal stem diameter of the largest individual plants in a stand. Stand age could then be compared with fire frequency information to determine if control practices should be implemented. This ecologically based assessment provides stronger justification for management decisions. Likewise, this approach will clarify the successional state (if stable state successional models are applicable) of any big sagebrush stand for satisfying land use management objectives in any situation.

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Table 3. Ranges and means for maximum stem diameter and age by subspecies.

Subspecies	Diameter			Age		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
	----- (mm) -----			----- (years) -----		
<i>wyomingensis</i>	3	75	27.6	3	75	31.7
<i>vaseyana</i>	5	82	27.3	3	79	23.4
<i>tridentata</i>	2	145	29.5	3	54	16.0

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Characterization of Siberian wheatgrass germplasm from Kazakhstan (Poaceae: Triticeae)

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Abstract

Siberian wheatgrass [*Agropyron fragile* (Roth) Candargy] is known for its establishment and persistence on sandy soils under severe water limitations. Morphology, cytology, and forage and seed characteristics were studied on 59 accessions (JA) of Siberian wheatgrass collected on sandy soils in the desert areas of western Kazakhstan. Plants were grown at Nephi, Ut., from 1993 to 1996 and compared with the check cultivars of Vavilov and P-27 Siberian wheatgrass, and Nordan crested wheatgrass [*A. desertorum* (Fisch. ex Link) Schultes]. All JA-accessions were autotetraploids, $2n = 4x = 28$. The most frequently observed meiotic association was 6 bivalents + 4 quadrivalents. The JA-accessions were morphologically diverse, ranging from short to tall in stature and from dark-green, glaucous to blue-green, strongly pubescent. Mean forage yield, crude protein, and dry matter digestibility were generally lower in the JA-accessions than the check varieties. Entry $\times$ year interactions were nonsignificant ($P > 0.05$) for all measured forage variables. Entries were significantly ($P < 0.01$) different for dry matter production. Seed weight of Vavilov and mean seed weight of JA-accessions were significantly ($P < 0.01$) greater than that for the check cultivars P-27 and Nordan. Entries that were highly pubescent had the heaviest seed and greatest capacity to emerge from a 7.6-cm planting depth. Seed yield plant⁻¹ was significantly ($P < 0.01$) lower in the JA-accessions than cultivars Vavilov, P-27, and Nordan. Sufficient variations exist for seed yield, seed weight, seedling vigor, and forage yield within the JA-accessions to allow for the development of an agronomically suitable, drought tolerant Siberian wheatgrass through selection.

Key Words: Crested wheatgrass, morphology, meiosis, chromosome pairing, taxonomy, forage and seed characteristics

The Siberian form of crested wheatgrass [*Agropyron fragile* (Roth) Candargy] is an important forage grass with a natural distribution in the Steppe regions of European Russia and southwestern Siberia. In its native habitat, the Siberian form of crested wheatgrass is more drought tolerant than either standard (cv Nordan) or fairway types of crested wheatgrass [*A. desertorum* (Fisch. ex Link) Schultes and *A. cristatum* (L.) Gaertner, respectively] and is better adapted to sandy soils that receive only 200 to 450 mm of annual precipitation (Asay et al. 1995). There are only 2 cultivars of Siberian wheatgrass, Vavilov and P-27. Both cultivars are adapted to similar environments, however, on sandy

Resumen

El zacate "Siberian wheatgrass" [*Agropyron fragile* (Roth) Candargy] es conocido por su establecimiento y persistencia en suelos arenosos bajo severas limitaciones de agua. Se estudio la morfología, citología y características del forraje y semilla de 59 accesiones (JA) de "Siberian wheatgrass" obtenidas de suelos arenosos de las áreas desérticas del oeste de Kazakhstan. Las plantas se cultivaron en Nephi, Ut de 1993 a 1996 y se compararon con los cultivares testigo Vavilov y P-27 de "Siberian wheatgrass" y Nordan de "Crested wheatgrass" [*A. desertorum* (Fisch. Ex. Link) Schultes]. Todas las accesiones de JA fueron autotetraploides, $2n = 4x = 28$. La asociación meiótica mas frecuentemente observada fue 6 bivalentes + 4 cuadrivalentes. Las accesiones de JA fueron morfológicamente diversas, la estatura vario de corta a alta y de verde oscuro, glaucoso a azul-verde y muy pubescente. Las medias de rendimiento de forraje, proteína cruda y digestibilidad de la materia seca fueron generalmente mas bajas que las de los cultivares testigo. Las interacciones accesión $\times$ año no fueron significativas ($P > 0.05$) para ninguna de las variables de forraje que se evaluaron. Las accesiones fueron significativamente ($P < 0.01$) diferentes en producción de forraje. El peso de la semilla de Vavilov y la media de peso de semilla para las accesiones de JA fueron significativamente ($P < 0.01$) mayores que la de los cultivares testigo P-27 y Nordan. Las colectas muy pubescentes tuvieron la semilla mas pesada y la mayor capacidad de emerger cuando se sembraron a una profundidad de 7.5 cm. El rendimiento de semilla por planta de las accesiones de JA fue significativamente ($P < 0.01$) menor que el de los cultivares Vavilov, P-27 y Nordan. Entre las colectas de JA existen suficientes variaciones respecto al rendimiento de semilla, peso de semilla, vigor de plántula y rendimiento de forraje lo que permite, mediante selección, el desarrollo de un cultivar del "Siberian wheatgrass" tolerante a sequía y agrónomicamente adecuada.

soils Vavilov out yields P-27 and has increased seedling vigor (Asay et al. 1995).

Under the current taxonomic treatment (Dewey 1984, Love 1984), the genus *Agropyron* is restricted to 10 species, commonly referred to as the crested wheatgrass complex. *Agropyron fragile* is synonymous with the more traditional name, *A. sibiricum* (Willd.) P. Beauv. Tzvelev (1976) described 2 botanical varieties within *A. fragile*: (1) var. *fragile* (plants with pubescent leaf sheaths) and (2) var. *sibiricum* (plants with glabrous leaf sheaths). Siberian wheatgrass is characterized by long, linear spikes. Most narrow-spiked crested wheatgrasses introduced to North America, including the cultivars P-27 and Vavilov, have glabrous leaf sheaths and fall under *A. fragile* var. *sibiricum*.

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Fifty-nine accessions of Siberian wheatgrass recently obtained from western Kazakhstan (JA-accessions) were compared with Siberian wheatgrass cultivars P-27 and Vavilov, and the crested wheatgrass cultivar Nordan. Objectives were to determine: (1) the morphological variation and taxonomic placement among the accessions, (2) the chromosome number and pairing within the accessions, and (3) the potential of these accessions to improve seedling vigor, productivity, and forage quality in a breeding program of Siberian wheatgrass growing under dry conditions.

Materials and Methods

Plant materials

Fifty-nine accessions of narrow-spiked Siberian wheatgrasses from Kazakhstan were obtained in 1992 by Drs. D. A. Johnson and K. H. Asay (JA-accessions). The 59-accessions were collected from desert areas of Kazakhstan that receive between 100 to 300 mm of annual precipitation. Check cultivars included Siberian wheatgrass P-27 and Vavilov, along with Nordan crested wheatgrass.

Field plot design

Field plots were located 121 km south of Salt Lake City, Ut., at the Utah State University Nephi Field Station at an elevation of 1,615 m. The soil type is Nephi silt loam (fine-silty, mixed, mesic Calcic

Argixerolls). No supplemental irrigation was used. Long-term (1903 to 1996) annual precipitation is 324 mm with about one-third occurring in March, April, and May. Total precipitation received from October through September was 486 and 249 mm for 1995 and 1996, respectively. Seedlings from original seed lots of JA-accessions were established in the greenhouse prior to transplanting in the field on 12 April 1993. Each field plot (1 x 10 m) consisted of 10 plants, planted on 1-m centers. Field plot design was a randomized complete block with 4 replicates.

Morphology

Eighteen morphological characters were evaluated (Table 1) on 58 of the 59 JA-accessions plus the cultivars Vavilov, P-27, and Nordan. A total of 10 to 12 operational taxonomic units (1 operational taxonomic unit = 1 complete, mature, flowering culm, with intact leaves and inflorescence) were collected from each of the 58 JA-accessions and check cultivars across replicates. Leaf measurements were taken on the first leaf below the flag leaf. Spikelet and flower part measurements were taken from spikelets collected mid spike. During data collection of operational taxonomic units, JA-85 was inadvertently not included. Operational taxonomic units were measured between 5 to 9 June 1995 at Nephi, Ut. Multivariate analysis of the data was conducted on 700 operational taxonomic units comprised of 58 JA-accessions, (10 to 12 operational

taxonomic units per accession; 664 total operational taxonomic units), and cultivars Vavilov, P-27, and Nordan (1 population and 12 operational taxonomic units per cultivar). Data for the characters listed in Table 1 were standardized according to the Standard Program on NT-SYS (Rohlf 1993). All principal components were derived using correlation matrices. Principal component analysis explains the variation observed between and within populations by creating linear combinations and character weights from the original variables. All cluster analyses were performed using unweighted pair-group mathematical average algorithms on the distance matrices to provide a distance phenogram. The distance coefficient was defined as the average taxonomic distance computed by NT-SYS (Rohlf 1993).

Mitotic analysis

Somatic cells of the 59 JA-accessions were prepared from root tips of potted seedlings grown from original seeds collected in Kazakhstan in a greenhouse. Root tips were treated in an aqueous solution containing 0.05% colchicine plus 0.025% 8-hydroxyquinoline and 25 drops 100 ml⁻¹ of dimethylsulfoxide (DMSO) for 2 to 3 hours at room temperature in darkness. They were then fixed and stained in 2% aceto-orcein at 40°C for a minimum of 3 days. The meristematic portion of the root tip was squashed in 45% acetic acid.

Table 1. Morphological characters in Siberian wheatgrass accessions (JA) from Kazakhstan, Siberian wheatgrass cultivars Vavilov, and P-27, and the crested wheatgrass cultivar Nordan.

Character	Mean	JA ¹		Species/Cultivar Vavilov ²		P-27 ²		Nordan ²		LSD
		SD	Range	Mean	SD	Mean	SD	Mean	SD	
Plant height (cm)	58.2	10.2	43.3-72.3	65.7	5.5	64.5	4.9	61.8	5.6	7.0
Leaf length (cm)	12.2	3.6	9.1-17.1	15.0	4.8	16.1	3.3	13.0	3.7	2.5
Leaf width (mm)	5.9	1.2	5.0-7.7	5.8	0.9	6.1	1.1	7.7	2.4	0.9
Spike length (cm)	13.0	2.2	7.6-13.8	10.7	1.5	10.4	2.0	5.9	0.8	1.6
Spike width (mm)	6.3	1.5	4.9-7.9	9.1	2.5	8.1	1.3	13.0	2.9	1.1
Spike Length/width (cm/cm)	18.5	6.1	7.0-41.2	12.9	5.4	13.2	3.4	4.9	1.5	4.2
Spikelet length (mm)	12.9	2.3	11.1-16.8	10.4	2.0	11.1	1.4	7.5	1.6	1.7
Spikelet width (mm)	4.1	0.7	3.7-4.9	4.7	1.1	4.3	0.6	3.7	0.6	0.5
First glume length (mm)	6.4	1.2	5.3-7.6	8.0	1.6	6.5	1.0	5.3	1.3	0.9
Width (mm)	1.1	0.2	1.0-1.3	1.0	0.2	1.1	0.1	0.6	0.2	0.1
Awn length(mm)	1.5	0.9	0.3-2.6	3.1	1.5	2.2	0.7	2.0	0.8	0.6
Second glume length (mm)	6.8	1.3	5.6-8.0	8.1	1.7	6.6	1.1	5.6	0.9	0.9
Width (mm)	1.2	0.2	1.1-1.4	1.0	0.2	1.1	0.2	0.8	0.3	0.2
Awn length (mm)	1.6	1.0	0.2-2.8	2.9	1.6	1.8	1.1	2.2	0.7	0.7
First lemma length (mm)	7.5	1.2	6.2-9.1	8.5	1.9	7.0	1.0	7.4	0.9	0.9
Width (mm)	1.3	0.2	1.1-1.4	1.1	0.1	1.2	0.2	0.9	0.1	0.4
Awn length (mm)	1.0	1.0	0.0-2.4	1.5	1.4	0.7	0.8	2.2	0.6	0.7
Palea length (mm)	5.8	0.6	5.3-6.3	6.1	1.0	5.6	0.3	4.5	0.6	0.4

¹Mean based on between 628 to 664 operational taxonomic units.

²Mean based on 12 operational taxonomic units.

Meiotic analysis

Pollen mother cells from 6 randomly selected accessions were preserved in Carnoy's fixative (6 parts absolute alcohol: 3 parts chloroform : 1 part glacial acetic acid) for 24 to 48 hours, transferred to 70% ethanol, and stored in a refrigerator until analyzed. Squashed preparations of the pollen mother cells were stained with 2% acetocarmine. Chromosome pairing was analyzed at metaphase I.

Seed characteristics

Seed yield and 100-seed weight were obtained in 1995 and 1996 from open-pollinated JA-accessions and checks at Nephi, Ut. The first 5 plants in each plot were harvested for seed yield and 100-seed weight. Seedling vigor on open pollinated seed produced in 1995 and 1996 was assessed based on the ability of the seedling to emerge from a 7.6-cm seeding depth (Asay and Johnson 1980) and measured by the rate of emergence (Maguire 1962).

Forage characteristics

Following several years of establishment in 1993, the plants were harvested 1 to 2 weeks post-anthesis with a sickle-bar mower from the remaining 5 plants in the 10-plant plot on 20 and 21 June 1995 and 18 June 1996. Dry matter production (kg plot⁻¹) were measured on a subsample from each plot. Subsamples were dried at 60°C in a forced-draft oven, and then first ground by a Wiley mill and then a Cyclone mill to pass through a 1-mm screen. Dry matter digestibility and crude protein were determined by near-infrared-reflectance spectroscopy on a dry matter basis according to procedures described by Marten et al. (1989). Validation of the calibration equation within the NIRS ($R^2 = 0.93$) for crested and Siberian wheatgrass was reported in Mayland et al. (1992).

Data analysis

Data were analyzed across years as a split-plot-in-time design with a general linear model (SAS 1985) using plot means. Single degree of freedom contrasts tested the overall mean for the JA-accessions with the check cultivars for forage yield, quality, and seed characteristics. For the combined analysis, entry x block was used as the error term to test entry effects, and year effects were tested with year x block interaction. Due to a significant ($P < 0.01$) year x entry interaction for total seed yield, data were also analyzed within years. A protected LSD test was used to separate entry means within and across years.

Table 2. Chromosome pairing in selected (JA) accessions of Siberian wheatgrass and related crested wheatgrasses

Species	Chromosome No. (2n)	Chromosome associations (No. cell ⁻¹)					No. cells
		I	II		II	IV+	
			Ring	Rod	Total		
<i>A. fragile</i>							
JA-accessions	28	0.27 1	6.04	1.08	7.17	0.17	3.14
		0-3 2	3-11	0-5	3-12	0-2	0-5
<i>A. desertorum</i>	28	2.06	4.13	4.84	8.97	0.62	1.62
(Asay et al. 1992)		0-6	0-8	0-9	4-14	0-3	0-5
<i>A. cristatum</i> X	28	0.97	9.85	0.63	1.66	---	---
<i>A. desertorum</i> ('Hycrest')		0-7	---	---	4-15	0-4	0-4
(Asay et al. 1986)							155

¹Configuration mean number of chromosomes.

²Configuration range of number of chromosomes.

Results and Discussion

Morphology

It appears that genetic introgression has occurred between Siberian and standard forms in nature. This introgression is evident in the Siberian cultivars, P-27 (Alderson and Sharp 1994) and Vavilov (Asay et al. 1995) (Fig. 1), by the morphological cline that exists between the long, narrow spike of Siberian wheatgrass and the shorter, wider spike of standard forms of crested wheatgrass.

Based on the 18 characters (Table 1), principal components of all operational taxonomic units accounted for 82% of the variation in the first 4 axes (data not shown). Within the first principal component, 6 of the 18 morphological characters were weighted greater than 0.80. The characters and their weights were: spike

length (0.82), spike length/spike width (0.81), first glume awn length (0.93), second glume awn length (0.95), lemma length (0.92), and lemma awn length (0.95). The first component accounted for 40% of the variation observed. The second and third components accounted for 32% of the variation, but were much less diagnostic with no characters weighted more than 0.80. Cluster analysis had a cophenetic correlation of 0.88, which is considered a good fit (Rohlf 1993).

Examination of the 1st, 2nd, and 3rd principal components suggests a clear separation among the JA-accessions and the check cultivars P-27, Vavilov, and Nordan (data not shown). In most cases, the glumes and lemma awns were longer in the check cultivars than in the JA-collections (Table 1). The narrow-shaped (linear) spike compared to the broad (pectinate) spike was the most discriminating

Fig. 1. Spike morphology of Standard crested wheatgrass 'Nordan' (A), Siberian wheatgrass JA-accessions (B), Siberian wheatgrass 'Vavilov' (C), and Siberian wheatgrass 'P-27' (D).

morphological character (Fig. 1). This is consistent with Tzvelev (1976) who distinguished between the broad-shaped spike of crested wheatgrass types [*A. cristatum* and *A. desertorum*] and the narrow-shaped spike types of Siberian wheatgrass [*A. fragile* and *A. mongolicum*] based on the length and width of the spike. The ratio of spike length/width proved highly diagnostic when separating the Siberian wheatgrass collections from the standard crested wheatgrass cultivar Nordan (Fig. 1, Table 1). The spike shape for Nordan is typically more pectinate at the base than is Siberian wheatgrass as evidenced by the spike length/width ratio ranging from 3.2 to 8.2 for Nordan compared to 7.0 to 41.3 in the JA-accessions. This relationship was observed by Asay et al. (1992), who found that spike length/width ratio within *A. mongolicum* (a diploid Siberian wheatgrass) was 12.0 compared to 3.6 and 6.0 for *A. cristatum* and *A. desertorum*, respectively. This ratio was less definitive in separating the JA-accessions from P-27 and Vavilov. However, the average spike length/width ratio within the JA-accessions was 18.5 compared to 12.9 for Vavilov and 13.2 for P-27. The spike length/width ratio ranged from 7.8 to 24.9 for Vavilov and 9.7 to 21.6 for P-27. These data suggest that during the development of Siberian wheatgrass cultivars P-27 (Alderson and Sharp 1994) and Vavilov (Asay et al. 1995), genetic introgression occurred between the broad-spiked types (probably *A. desertorum*) and narrow-spiked types.

JA-accessions 48, 49, 52, 58, 84, and 85 had a blue-green leaf color and densely pubescent (pilose) leaves, leaf sheaths, and spikes, which corresponds to Tzvelev's (1976) description of *A. fragile* var. *fragile*. All other JA-accessions had green leaf color in varying shades and glabrous leaves, leaf sheaths, and spikes. These latter accessions would be classified as *A. fragile* var. *sibiricum* according to Tzvelev (1976). Plant growth habit within the population ranged from strongly caespitose to moderately rhizomatous in JA-66.

Cytology

The crested wheatgrasses occur in an autopolyploid series of diploid ($2n = 2x = 14$), tetraploid ($2n = 4x = 28$), and hexaploid ($2n = 6x = 42$) species with tetraploids occurring most frequently (Dewey and Asay 1975). Hybridization among the various crested wheatgrass taxa across all ploidy levels supports the premise that this complex is based on the 'P' genome (Asay and Dewey 1979), and should be treated

Table 3. Mean squares from analysis of variance for JA-accessions of Siberian Wheatgrass from Kazakhstan, 'Vavilov' and 'P-27' Siberian wheatgrass, and 'Nordan' crested wheatgrass for forage production and quality and seed characteristics.

Character	Entry	Year	Entry x Year
Seed yield (g plant ⁻¹)			
1995	1651.2**1		
1996	234.6**		
1995-96	976.0**	15646.8**	756.5**
100-seed weight (g)			
1995	0.014**		
1996	0.011**		
1995-96	0.025**	0.127**	0.00
Rate of emergence (seedlings day ⁻¹)			
1995	0.494		
1996		0.745**	
1995-96	0.552**	0.402	0.358
Dry matter production (kg ha ⁻¹)			
1995	7308268.6**		
1996	1691761.4**		
1995-96	7750158.2**	19527354.7**	1251452.9
Crude protein (g kg ⁻¹)			
1995	86.3		
1996	180.0		
1995-96	88.7	69867.3**	17.9
Dry matter digestibility (g kg ⁻¹)			
1995	361.5		
1996	169.4		
1995-96	22.8	809028.5**	508.2

¹ *, ** indicate significant differences at $P < 0.05$ and $P < 0.01$, respectively.

as one gene pool (Asay and Dewey 1983).

Root tip chromosomes of all 59 JA-accessions were tetraploids with a chromosome number of $2n = 4x = 28$. The 6 randomly selected JA-accessions did not differ in pairing behavior. Thus, the pairing data were bulked across accessions (Table 2). The most common associations were 6 bivalents + 4 quadrivalents or 8 bivalents + 3 quadrivalents (Fig. 2a), which occurred in 25 and 23% of the metaphase I cells observed, respectively. Multivalents, usually quadrivalents (Fig.

2bc), formed in more than 70% of the metaphase-I cells. Average chromosome associations per cell were 0.27 univalents + 7.17 bivalents + 0.17 trivalents + 3.14 quadrivalents-plus (Table 2). These values are similar to those reported for other autotetraploid crested wheatgrasses (Dewey 1984, Asay et al. 1992). The high frequency of quadrivalents is also consistent with previous reports (Asay and Dewey 1979) that indicate that crested wheatgrasses and now Siberian wheatgrass are true autotetraploids.

Fig. 2. Chromosome pairing at late diakinesis/early metaphase I in Siberian wheatgrass (JA-accessions): (a) 8 II (small arrows) + 3 IV, (b) 2 II + 4 IV (small arrows) + 1 VIII (large arrows), and (c) 4 II (large arrows) + 5 IV (small arrows).

Table 4. Means and ranges for total seed yield, 100-seed weight, and rate of seedling emergence for 59 JA-accessions of Siberian wheatgrass (SWG) from Kazakhstan, 'Vavilov' and 'P-27' Siberian wheatgrass (SWG), and 'Nordan' crested wheatgrass (CWG).

Entry	Seed yield			100-Seed weight			Rate of emergence		
	1995	1996	1995-96	1995	1996	1995-96	1995	1996	1995-96
	----- (g plant ⁻¹) -----			----- (g) -----			----- (seedlings day ⁻¹) -----		
JA - SWG									
Mean	22.25	11.87	17.04	0.25	0.21	0.23	0.32	0.75	0.54
Range	8.3-37.4	5.2-20.0	7.8-26.8	0.21-0.31	0.18-0.26	0.19-0.27	0.03-1.1	0.23-1.7	0.14-1.12
Vavilov - SWG									
Mean	48.30	12.19	30.24	0.26	0.25	0.25	0.37	0.89	0.63
P-27 - SWG									
Mean	49.72	14.36	30.54	0.22	0.19	0.20	0.63	0.58	0.61
Nordan - CWG									
Mean	21.09	4.61	12.85	0.15	0.13	0.14	0.16	0.03	0.10
LSD	17.5	6.15	8.83	0.04	0.04	0.03	0.45	0.48	0.25
<u>Contrasts:</u>									
JA- vs. Vavilov	** ¹	—	**	—	*	*	—	—	—
JA- vs. P-27	**	—	**	—	—	*	—	—	—
JA- vs. Nordan	—	**	—	**	**	**	—	**	**

¹*, ** indicate significant differences at P 0.05 and P 0.01, respectively.

Based on chromosome pairing in hybrids between the narrow spiked diploid, *A. mongolicum* Keng from Mongolia, and the broad spiked diploid, *A. cristatum* from Eurasia, Dewey (1984) and Asay et al. (1992) concluded that both groups are comprised of the same basic genome "P". Most if not all *A. mon-* *golicum* accessions are diploids and appear to be a smaller strain of the tetraploid Siberian wheatgrass (Dewey 1984, Asay et al. 1992)

Seed characteristics

The entry x year interaction was not significant (P > 0.05) for 100-seed weight and rate of seedling emergence; however, it was significant (P < 0.01) for total seed yield plant⁻¹ (Table 3). This significance was due to a rank change between cultivars P-27 and Vavilov and JA-accessions from 1995 to 1996. The overall 100-seed weight declined with reduced annual precipitation received during 1996, which was 77% of normal compared to 150% of normal in 1995. However, the ability of seedlings to rapidly emerge from a 7.6-cm depth was not affected by the different levels of annual precipitation between 1995 and 1996 (Table 4).

The Siberian wheatgrass cultivars P-27 and Vavilov produced significantly more seed than the JA-accessions and the crested wheatgrass cultivar Nordan (Table 4). However, within the entire JA-collection, individual accessions (JA-96, 42, 95, 80, and 42) were not significantly (P > 0.05) different from the Siberian wheatgrass checks (data not shown), suggesting that

sufficient variations exist within the JA-accessions for improvement in seed production.

The cultivar Vavilov and the mean of the JA-accessions had significantly (P < 0.01) heavier seeds (100-seed weight) than P-27 and Nordan (Table 4). Within Siberian wheatgrass, no correlation (r = 0.03) was apparent between seed yield plant⁻¹ and individual seed weight (data not shown). Accessions JA-48, 46, 51, 98, 47, 50, and 49 had heavier seeds than Vavilov. Morphologically, densely pubescent plants produced heavier seeds. Differences in seed weight were reflected in results from

seedling vigor trials. Of the 10 accessions with the heaviest seeds, 6 had higher rates of emergence (JA-48, 45, 98, 46, 51, and 47). During the 1996 drought, JA-accessions 42, 43, 96, 75, and 95 exceeded the check cultivars with a total seed yield greater than 16 g plant⁻¹, suggesting that under harsh environments with limited water, total seed yield can be improved through selection within the JA-accessions.

Forage characteristics

Entries differed significantly (P < 0.01) for dry matter production between the JA-

Table 5. Means and ranges for dry matter production, crude protein, and dry matter digestibility for 59 JA-accessions of Siberian wheatgrass (SWG) from Kazakhstan, 'Vavilov' and 'P-27' Siberian wheatgrass (SWG), and 'Nordan' crested wheatgrass (CWG). Data were combined across years.

Entry	Dry matter production	Crude protein	Dry matter digestibility
	(kg ha ⁻¹)	(g kg ⁻¹)	(g kg ⁻¹)
JA - SWG			
Mean	1362	115.6	569.2
Range	869-1823	104.8-126.7	536-583.2
Vavilov - SWG			
Mean	2539	111.6	570.5
P-27 - SWG			
Mean	2130	111.4	568.9
Nordan - CWG			
Mean	2400	115.5	571.8
LSD	522	17.2	27
<u>Contrasts:</u>			
JA- vs. Vavilov	** ¹	nsns	
JA- vs. P-27	**	ns	ns
JA- vs. Nordan	**	ns	ns

¹*, ** indicate significant differences at P 0.05 and P 0.01, respectively.

accessions and checks; however, differences were relatively consistent across years as indicated by the nonsignificant entry x year interaction (Table 3). The mean dry matter production for the 59 JA-accessions was significantly ($P < 0.01$) lower than Vavilov, P-27, and Nordan checks. None of the individual JA-accessions had greater dry matter production than the checks. The mean range of dry matter production among the JA-accessions averaged across years, 869 to 1,823 kg ha⁻¹ (Table 5), indicated that substantial variation was available to select for genetic improvement in this trait. Because of the difference in annual precipitation between 1995 (486 mm) and 1996 (249 mm), a significant ($P < 0.01$) year effect was observed for dry matter production (Table 3).

Differences between the JA-accessions and check cultivars were nonsignificant ($P > 0.05$) for crude protein and dry matter digestibility (Tables 3 and 5). The entry x year interaction was also nonsignificant ($P > 0.05$). Similar to dry matter production, crude protein and dry matter digestibility varied significantly between years ($P < 0.01$), possibly a result of the large variation in annual precipitation between 1995 and 1996.

Mean dry matter production increased in the JA-accessions and the check cultivar P-27 in 1996 under dry conditions. Even though dry matter production within the JA-accessions was still significantly ($P \leq 0.05$) lower than the check cultivars, their ability to produce more, rather than less, forage and seeds under drought suggests that they may be better adapted and subsequently survive longer in extreme environments. In their native environment of western Kazakhstan, the smaller statured Siberian wheatgrass accessions occupy sandy soils that receive between 100 to 300 mm of annual precipitation per year, while *A. cristatum* and *A. desertorum* are typically found in regions of higher rainfall and better soils.

Conclusions and Implications

Morphological analysis suggests that, at present, no Siberian wheatgrass cultivars are available with true narrow-shaped spikes. Based on spike shape, cultivars P-27 and Vavilov appear to have gene(s) from the broader-shaped (more pectinate) spike, which is characteristic of *A. cristatum* and *A. desertorum*. Cytologically, the JA-accessions have the same chromosome number ($2n = 4x = 28$) and behave cytologically as true autotetraploids.

When developing new cultivars that are capable of establishing and persisting under environments with very low rainfall, characters such as seedling vigor and persistence are more important than forage yield and quality. Our results suggest that there are sufficient variations for seed yield, seed weight, seedling vigor, and forage yield within the JA-accessions of Siberian wheatgrass germplasm to allow for the development of an agronomically suitable, drought-tolerant Siberian wheatgrass through breeding and selection. Variations in forage quality were much less than that observed for other traits so that prospects for improving forage quality are considerably less.

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Soil properties and species diversity of grazed crested wheatgrass and native rangelands

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Abstract

Crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) is an introduced grass used extensively for rangeland revegetation in the semiarid and arid regions of western North America. The long-term effects of crested wheatgrass on soil properties and plant community were evaluated on 5 grazed sites in the southern interior of British Columbia, Canada. Each site included plant communities of native bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith) and 14- to 60-year-old stands of crested wheatgrass. Soil samples and plant data were collected in June 1997. Species numbers were similar for native and crested wheatgrass rangelands, while the diversity index of crested wheatgrass rangeland was lower due to lower evenness. Crested wheatgrass and native grasses were observed to produce similar amounts of root biomass. Most soil properties were similar under the 2 rangelands. One of the exceptions was soil carbon at 0–7.5 and 7.5–15 cm depths, which was higher on crested wheatgrass than native rangeland. Soil nitrogen at 15–30 cm depth was also higher on crested wheatgrass rangeland. Greater soil penetration resistance was observed at 7.5 and 9 cm depths on crested wheatgrass than native rangeland. Higher soil compaction was caused by grazing of crested wheatgrass earlier in the season when soils are wetter relative to the native rangeland. The results of this study indicate that seeding of crested wheatgrass combined with the long-term grazing by cattle did not result in the degradation of soil properties, but plant diversity was reduced relative to grazed native, bluebunch wheatgrass rangeland.

Key Words: Soil C, soil N, penetration resistance, aggregate stability, root biomass, bluebunch wheatgrass

Crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), a drought- and cold-tolerant grass from the steppes of central Asia, has been seeded on about 5 million hectares in western North America (Gomm 1981). It is an important cool-season grass, providing nutritious, early spring forage that is converted into increased livestock gains. Although advantages of crested wheatgrass as a seeded forage grass are well known, data are lacking

Resumen

El zacate "Crested wheatgrass" (*Agropyron cristatum* (L.) Gaertn.) es una especie introducida utilizada ampliamente para revegetar pastizales de las regiones áridas y semiáridas del oeste de Norteamérica. Se evaluaron los efectos a largo plazo del "Crested wheatgrass" en las propiedades del suelo y la comunidad vegetal, la evaluación se llevó a cabo en 5 sitios con apacentamiento localizados en el interior de Columbia Británica, Canadá. Cada sitio incluía comunidades del zacate nativo "Bluebunch wheatgrass" (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith) y poblaciones de "Crested wheatgrass" de entre 14 y 60 años de edad. Las muestras de suelo y los datos de las plantas se colectaron en junio de 1997. Los números de especie fueron similares para los pastizales nativos y de "Crested wheatgrass", mientras el índice de diversidad del pastizal de "Crested wheatgrass" fue mas bajo debido a su uniformidad. Se observó que los zacates nativos y el "Crested wheatgrass" producen cantidades similares de biomasa de raíz. La mayoría de las propiedades del suelo fueron similares en los dos tipos de pastizal. Una de las excepciones fue el carbón del suelo a las profundidades de 0–7.5 y 7.5–15 cm, el cual fue mayor en el pastizal de "Crested wheatgrass" que en los pastizales nativos. El contenido de nitrógeno del suelo a la profundidad de 15–30 cm fue también mayor en el pastizal de "Crested wheatgrass". En el pastizal de "Crested wheatgrass" la resistencia de penetración del suelo en las profundidades de 7.5 y 9 cm fue mayor que la registrada en los pastizales nativos. La mayor compactación del suelo la causó el apacentamiento del "Crested wheatgrass" a inicios de la estación cuando los suelos estaban mas húmedos en relación a los suelos de los pastizales nativos. Los resultados de este estudio indican que la siembra de "Crested wheatgrass" en combinación con el apacentamiento con ganado doméstico a largo plazo no resulta en la degradación de las propiedades del suelo, pero la diversidad de especies vegetales fue reducida en relación con pastizales nativos de "Bluebunch wheatgrass" bajo apacentamiento.

regarding its long-term effects on physical and chemical properties of the soil.

Past studies comparing crested wheatgrass seedings to adjacent native rangeland have shown that crested wheatgrass is a strong competitor and usually produces a monoculture for 40 to 50 years (Looman and Heinrichs 1973, Anderson and Marlette 1986). When a native *Stipa-Bouteloua* community in the semiarid regions of southern Alberta was altered to a crested wheatgrass monoculture, soil quality declined as a result of decreasing root biomass,

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accompanied with less stable soil organic matter, lower aggregate stability, and higher bulk density (Smoliak et al. 1967, Dormaar et al. 1978, Dormaar et al. 1995).

Most of the previous work in Canada considering impacts of crested wheatgrass on the soil was done in southern Alberta, and no information is available for British Columbia (BC). Southern Alberta and southern interior of BC have somewhat similar climate and soil types, although the latter region is characterized by a greater summer water deficit. In addition, lower elevation native rangelands in the southern interior of BC are dominated by bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith) and big sagebrush (*Artemisia tridentata* Nutt.), while native rangelands in southern Alberta are dominated by needle-and-thread (*Stipa comata* Trin. & Rupr.) and blue grama (*Bouteloua gracilis* (HBK.) Lag.).

The objective of this study was to assess soil chemical and physical properties and plant community on long-term grazed stands of crested wheatgrass and adjacent stands of native rangeland dominated by bluebunch wheatgrass.

Materials and Methods

Site Description

Five sites (Table 1), each including adjacent plant communities of crested wheatgrass and native bluebunch wheatgrass, were selected in the Thompson-Nicola region of BC about 150 km north from the Canada-US border. Soils at all sites were classified as Dark Brown Chernozem (Typic Haploboroll). The semiarid climate of the region is characterized by hot, dry summers (average temperature for June-September is 18.6°C) and relatively cold winters (average temperature for November-February is -1.8°C). An average annual precipitation of 300 mm is bimodally distributed with peaks in

May-June and December-January (Environment Canada 1998).

Sampling and Analyses

Plant and soil samples were collected during 3-10 June 1997. Species number and foliar cover of each plant species on crested wheatgrass and native rangeland were determined within 0.25 x 0.5 m frames located at every meter along 3 randomly selected transects (Daubenmire 1959). These transects were 25 m long and oriented along similar slopes on crested wheatgrass and native rangelands. Species-cover data were used to calculate a diversity index (Shannon and Weaver 1949) and evenness (Pileou 1966) within both rangelands. The simplest indicator of species diversity is species richness, representing the number of species encountered in a sample area. Species diversity can also be described by diversity indices, which balance species richness with another component—evenness. The evenness describes how the measure of abundance (such as cover in this study) is shared among species. Maximum evenness occurs when species abundance is equally shared between 2 species, but this may not give a high diversity index because few species are present. The Shannon-Weaver-diversity index was used since it is sensitive to changes in the abundance of less dominant species in a community (De Jong 1975).

Four soil and root sampling units were randomly selected within crested wheatgrass and native rangelands. A double-cylinder, drop-hammer sampler (with a core of 7.5 x 7.5 cm) was used to collect root samples from 0-7.5 and 7.5-15 cm depths. Two cores were taken at each of the 4 sampling units and mixed to make a composite root sample. Root samples were washed, sieved through a 1-mm sieve, dried at 65°C for 48 hours, and weighed. Ash content of roots was determined by ignition at 550°C for 4 hours and root bio-

mass is reported on an ash-free, oven-dry basis. Carbon and N concentrations of root samples were determined by automated combustion analyzer (Carlo Erba, Milan, Italy) and calculated on an ash-free basis.

Soil samples for chemical properties were taken at 0-7.5, 7.5-15, and 15-30 cm depths, air-dried, and ground to pass a 2.0-mm sieve. One sample was taken per sampling unit. Total soil C and N were determined by a dry combustion method (Nelson and Sommers 1982) using an automated analyzer (Carlo Erba, Milan, Italy). Content of total soil polysaccharides was determined by the phenol-sulfuric acid method of Dubois et al. (1956) as modified by Dautre et al. (1978). Light fraction was isolated by flotation on sodium iodide at a density of 1.7 g cm⁻³ (Gregorich and Ellert 1993). Total soil P was determined by the Parkinson and Allen (1975) method, while available P was determined on a sodium bicarbonate (NaHCO₃) extract (Olsen et al. 1954). Soil cation exchange capacity (CEC) and exchangeable cations (Ca, Mg, K, and Na) were determined by the ammonium acetate (pH 7) method (Soil Survey Laboratory Staff 1992). Soil pH was determined on a 1:2 (v/v) soil to 0.01 M CaCl₂ slurry (McLean 1982).

Three soil samples were taken from the 0-7.5 cm depth on each of the 4 randomly selected sampling units and mixed to make a composite sample for aggregate stability analysis. The soil structural stability was assessed using a variation of the wet sieving method (Yoder 1936). Moist samples collected from the field were sieved using a 6-mm sieve and collected on a 2-mm sieve. The pre-sieved 2-6 mm moist sample (of about 10 g) was placed on the top of a nest of sieves with openings of 2.00, 1.00, and 0.25 mm and wetted in a humidifier for 1 hour to minimize disruption caused by air trapping. This was done immediately before wet sieving. Wet sieving was performed for 10 minutes

Table 1. Location, site characteristics, and time of crested wheatgrass seeding on 5 sites in Thompson-Nicola region of British Columbia.

Description	Site				
	Tranquille ranch	Dewdrop ranch	Quilchena ranch	Harper ranch	Guichon ranch
Longitude	120° 30'W	120° 33'W	120° 29'W	120° 09'W	120° 26'W
Latitude	50° 43'N	50° 45'N	50° 09'N	50° 40'N	50° 15'N
Elevation (m)	450	600	650	500	700
Precipitation for May-Sep (mm)	125	125	150	175	150
Parent material	fluvial	fluvial	glaciofluvial	lacustrine	glaciofluvial
Coarse fragments, i.e. diameter >2 mm (%)	1	8	13	0	9
Soil texture	sandy loam	loam	silt loam	silt loam	loam
Clay (%)	8	21	17	10	13
Sand (%)	62	38	29	13	48
Crested wheatgrass seeded	1937	1968	1937	1982	1983

in a motor-driven mechanical device with a vertical stroke of 2.5 cm at a rate of 30 strokes per minute. The motion of the system had both a vertical stroke and an oscillating action through an angle of 30°. After sieves were removed from water, the proportion of material retained on each sieve was oven dried at 105°C for 24 hours, weighed, and expressed as a percentage of the total soil. The results were expressed as the mean weight diameter, which represents the sum of the mean diameter of each size fraction (D_i) and the proportion of the sample weight occurring in the corresponding size fraction (W_i) (Van Bavel 1949). The mean weight diameter was summed over all 4 size fractions, including the one that passed the 0.25-mm sieve

$$(MWD = \sum_{i=1}^4 W_i D_i)$$

Corrections were made for the coarse fraction retained on each sieve to avoid biased interpretations of water stable aggregates.

Intact soil samples were taken with a double-cylinder, drop-hammer sampler (with a core of 7.5 x 7.5 cm) for bulk density determination (Blake and Hartge 1986). One core was taken per sampling unit from 0–7.5, 7.5–15, and 15–30 cm depths on Tranquille, Dewdrop, and Harper sites, while stoniness restricted soil coring below 15 cm on Guichon site and below 7.5 cm on Quilchena site. Soil samples for bulk density determination were dried at 105°C for 48 hours in a forced-air oven. Coarse fragments (diameter >2 mm) within the sample were screened out and weighed. Volume of mineral coarse fragments was determined from dry mass and assumed to have a particle density of 2.65 Mg m⁻³. Soil bulk density was calculated as the mass of dry, coarse, fragment-free mineral soil per volume of field-moist soil, where volume is also calculated on a coarse fragment-free basis.

Soil penetration resistance (Bradford 1986) was measured to 30 cm depth on Tranquille, Dewdrop, and Harper sites, to 12 cm depth on Guichon site, and to 10.5 cm depth on Quilchena site. Different depths determined were the result of soil stoniness. Measurements were recorded at depth intervals of 1.5 cm, using a hand-pushed 13-mm diameter cone (30°) penetrometer with data logger (Agridry Rimik PTY Ltd., Toowoomba, QLD, Australia). Three soil profiles were recorded on each of the 4 randomly selected sampling units.

Rate of water infiltration in the field was determined using a double-ring infiltrometer (Bouwer 1986). One measurement was done per sampling unit. Hence, at each site a total of 8 sets of cylinders (with an outer

cylinder—56 cm diameter by 30 cm height and inner cylinder—30 cm diameter by 30 cm height) were used. The cylinders were nested and pounded 5 cm into the ground forming a watertight seal. The change in water depth of the inner cylinder was measured over a period of 2 hours at time intervals of 5, 10, 15, 20, 30, 40, 50, 60, 75, 90, 105, and 120 minutes. A head of 5–10 cm was maintained and readings were taken with a floating gauge. Conditions for the measurement of unsaturated hydraulic conductivity were assumed to occur after 20 minutes.

Statistical Analyses

Species cover, diversity index, evenness, and species number data were analyzed as randomized, complete block design with 5 replications (i.e., sites). Soil and root samples taken at consecutive depths from the same hole are dependent on each other. Hence, soil and root data were analyzed separately for each depth of sampling as a randomized, complete block design with 5 replications. The general linear model procedure in the SAS package (SAS Institute Inc. 1989) was used.

Results

Vegetation

Total plant cover and bare ground were similar for crested wheatgrass and native

rangelands (Table 2). Cover of grasses was greater on crested wheatgrass than native rangeland, while the opposite was true for shrub cover. Forb cover was similar for the 2 rangelands.

Predominant species on native rangeland were big sagebrush, bluebunch wheatgrass, needle-and-thread, Sandberg's bluegrass (*Poa secunda* Presl.), and dwarf pussytoes (*Antennaria dimorpha* Nutt. T. & G.). Crested wheatgrass was the most abundant species on seeded rangeland with 23% of the total plant cover, while Sandberg's bluegrass, needle-and-thread, dwarf pussytoes, and big sagebrush together contributed 8% to total plant cover (Table 2). Species number was similar for crested wheatgrass and native rangelands, but diversity of crested wheatgrass rangeland was lower due to lower evenness.

Seeding of crested wheatgrass did not lead to reduction of root biomass relative to native rangeland (Table 3). Root biomass was similar for crested wheatgrass and native grasses at both 0–7.5 and 7.5–15 cm depths. In addition, roots of the 2 grass communities contained similar amounts of C and N (Table 3).

Soil

Most soil properties were not affected by crested wheatgrass, although there were several exceptions. Soil C and N were marginally greater under crested wheatgrass than native grasses at the 2

Table 2. Botanical composition (% cover) on crested wheatgrass and native rangelands.

Species	Rangeland		P
	Crested wheatgrass	Native grasses	
	------(%)-----		
Grasses			
Bluebunch wheatgrass	0.5	6.8	0.038
Crested wheatgrass	23.4	1.1	0.000
Sandberg's bluegrass	2.3	3.4	0.512
Needle-and-thread	1.4	6.7	0.116
Junegrass	0.4	2.2	0.349
Other grasses	0.3	1.7	0.024
Total grasses	28.3	21.9	0.028
Forbs			
Dwarf pussytoes	1.7	2.1	0.806
Other forbs	1.2	3.7	0.075
Total forbs	2.9	5.8	0.174
Shrubs			
Big sagebrush	1.4	7.8	0.109
Pasture sage	0.7	1.1	0.493
Rabbit-brush	0.8	1.5	0.332
Total shrubs	2.9	10.5	0.034
Total cover	34.5	37.6	0.493
Bare ground	58.1	52.6	0.332
Diversity index	0.98	1.70	0.010
Evenness	0.37	0.76	0.002
Species number per 9.4 m ²	14.0	17.0	0.470

lower depths, i.e. 7.5-15 and 15-30 cm, (Table 4). Light fraction C was also greater with crested wheatgrass than native rangeland (Table 4). Total soil P at 15-30 cm depth was greater on native than on crested wheatgrass rangeland (Table 5). Available soil K at 0-7.5 cm depth was greater on crested wheatgrass than native rangeland (Table 5).

Soil aggregate stability parameters were not affected by crested wheatgrass seeding (Table 6). On both crested wheatgrass and native rangeland the smallest, <0.25-mm fraction, was the most dominant size fraction by making up about 50% of total soil aggregates. The largest, 2-6-mm size fraction, made up 26 to 30% of total soil aggregates on both rangelands.

Soil bulk density was similar under crested wheatgrass and native grasses at all 3 depths (Fig. 1a). Soil penetration resistance was also similar for the 2 grass communities with an exception at the 7.5 and 9 cm depths where it was greater on crested wheatgrass rangeland (Fig. 1b). No difference in the rate of water infiltration was observed between crested wheatgrass and native rangeland (Fig. 2).

Discussion

Low plant cover of both crested wheatgrass and native rangeland resulted from high utilization by cattle and limited soil water available for plant growth. Although native and crested wheatgrass rangelands were adjacent, the cover of crested wheatgrass was low on native rangeland (Table 2). This indicates that crested wheatgrass is not highly invasive on these rangelands. Crested wheatgrass did not deter reestablishment of native species to the degree reported in a mixed prairie of southern Alberta, dominated by *Stipa-Bouteloua* community, (Dormaar et al. 1978) or a sagebrush zone of southeastern Idaho (Marlette and Anderson 1986). The competitive ability of crested wheatgrass in our study was most likely reduced by heavy grazing allowing native species to establish. Native species, such as big sagebrush, Sandberg's bluegrass, needle-and-thread, and dwarf pussytoes, which established in crested wheatgrass rangeland, all have a high tolerance to grazing by cattle. On the other hand, establishment of bluebunch wheatgrass, which is not grazing tolerant, was restricted. In 2 earlier studies in Idaho (Hull and Klomp 1966, Marlette and Anderson 1986), big sagebrush was also one of the most abundant native species invading crested wheatgrass rangeland.

Table 3. Root biomass and root C and N contents of crested wheatgrass and native grasses.

Rangeland				
Root	Depth (cm)	Crested wheatgrass	Native grasses	P
----- (t ha ⁻¹) -----				
Biomass	0-7.5	2.4	2.6	0.874
	7.5-15	1.2	1.0	0.882
----- (kg ha ⁻¹) -----				
C content	0-7.5	412	533	0.387
	7.5-15	210	226	0.818
N content	0-7.5	22	25	0.723
	7.5-15	8	9	0.719

Table 4. Soil properties of crested wheatgrass and native rangelands.

Soil property	Rangeland			<i>P</i>
	Depth (cm)	Crested wheatgrass	Native grasses	
	----- (kg m ⁻²) -----			
Total C	0-7.5	18.7	16.9	0.267
	7.5-15	14.6	12.4	0.072
	15-30	12.6	10.2	0.028
Total N	0-7.5	1.7	1.5	0.133
	7.5-15	1.4	1.2	0.088
	15-30	1.2	1.0	0.053
	----- (%) -----			
C as polysaccharides	0-7.5	0.83	0.63	0.998
	7.5-15	0.59	0.52	0.202
Light fraction C	0-7.5	4.26	3.97	0.013
Light fraction N	0-7.5	1.08	1.09	0.904

Table 5. Soil pH, total and available phosphorus, exchangeable cations, and cation exchange capacity (CEC) on crested wheatgrass and native rangelands.

Soil property	Depth (cm)	Rangeland		P
		Crested wheatgrass	Native grasses	
pH (CaCl ₂)	0-7.5	6.4	6.4	0.914
	7.5-15	6.6	6.5	0.520
	15-30	6.7	6.6	0.399
----- (%) -----				
Total P	0-7.5	0.08	0.09	0.399
	7.5-15	0.07	0.07	0.289
	15-30	0.07	0.09	0.031
----- (mg kg ⁻¹) -----				
Available P	0-7.5	14.7	12.3	0.214
	7.5-15	13.9	12.6	0.711
	15-30	13.3	14.1	0.857
----- (cmol _c kg ⁻¹) -----				
Ca	0-7.5	8.45	7.94	0.563
	7.5-15	9.16	8.34	0.523
	15-30	10.13	9.66	0.854
Mg	0-7.5	6.46	6.06	0.482
	7.5-15	7.68	6.93	0.348
	15-30	8.75	7.29	0.136
K	0-7.5	1.79	1.57	0.041
	7.5-15	1.48	1.48	0.956
	15-30	1.30	1.37	0.614
Na	0-7.5	0.10	0.08	0.568
	7.5-15	0.16	0.11	0.246
	15-30	0.24	0.14	0.225
CEC	0-7.5	25.03	22.90	0.331
	7.5-15	25.51	23.69	0.315
	15-30	25.93	22.50	0.159

Fig. 1. Soil bulk density (a) and soil penetration resistance (b) on crested wheatgrass and native rangelands. Error bars represent standard error of the mean ($n = 20$) and they are shown on graph (b) only on means that are significantly different ($P < 0.05$).

Several researchers (Wilson 1989, Lesica and DeLuca 1996) suggested that seeding with crested wheatgrass results in a less diverse plant community. Our study shows no reduction in species number on crested wheatgrass compared to native rangeland (Table 2), indicating that crested wheatgrass has not reduced plant diversity. Since crested wheatgrass was the most dominant species, while the remaining species were less abundant on the seeded rangeland than on the native rangeland, the Shannon-Weaver-diversity index

was a better indicator of species diversity than species number. The diversity index was lower on crested wheatgrass rangeland indicating a less diverse plant community than on native rangeland. Nevertheless, crested wheatgrass did not completely prevent the establishment of grazing tolerant native species.

We found similar root biomass at both 0-7.5 and 7.5-15 cm depths with long-term grazing of crested wheatgrass and bluebunch wheatgrass rangeland (Table 3). In contrast, Smoliak et al. (1967) and

Dormaer et al. (1995) found that crested wheatgrass rangeland contained less root biomass than native rangeland dominated by blue grama and needle-and-thread in southern Alberta. Major cause for this disagreement is a difference in native grass species between southern Alberta and interior of BC. Different plant species composition in the 2 regions is, on the other hand, caused by different distribution of precipitation.

Higher total soil C at 7.5-15 and 15-30 cm depths (Table 4) in crested wheatgrass compared to native rangelands was probably due to the higher number of shrubs on native rangeland. Shrubs, having coarser roots than grasses, contribute less to the addition of total soil organic matter.

Long-term grazing, especially at high stocking rates, reduces soil structural stability and increases soil compaction (Warren et al. 1986, Dormaer and Willms 1998). Sites sampled during this study were grazed for more than a century before the seeding of crested wheatgrass and for 14 to 60 years after seeding. Hence, potential effects of crested wheatgrass seeding on soil aggregate stability and compaction were confounded by grazing. Soil bulk density, water infiltration rate, and most of the soil penetration resistance measurements were similar for crested wheatgrass and native rangelands (Fig. 1 and 2). Despite the fact that all these sites were grazed, differences in soil penetration resistance were observed at 7.5 and 9 cm depths, where it was greater on crested wheatgrass than native rangeland. Greater soil compaction on crested wheatgrass rangeland can be a result of earlier

Fig. 2. Rate of water infiltration on crested wheatgrass and native rangelands. Error bars represent standard error of the mean ($n = 20$).

Table 6. Soil aggregate stability parameters on crested wheatgrass and native rangelands at 0-7.5 cm depth.

Species	Rangeland		P
	Crested wheatgrass	Native grasses	
	------(%)-----		
2-6 mm	26.2	29.7	0.455
1-2 mm	8.8	7.7	0.471
0.25-1 mm	13.6	9.9	0.370
<0.25 mm	51.5	52.7	0.799
	------(mm)-----		
Mean weight diameter	1.3	1.4	0.546

grazing of crested wheatgrass occurring under wetter soil conditions relative to grazing of native grasses.

This study shed some light on the impact of crested wheatgrass on rangeland soil and plant composition in the southern interior of British Columbia. Our findings show that seeding of crested wheatgrass did not lead to a monoculture, although the diversity of plant community was reduced relative to native rangeland. In addition, crested wheatgrass introduction accompanied with long-term grazing did not significantly change soil properties relative to the grazed native rangeland dominated by bluebunch wheatgrass. Responses of the rangeland soil to introduction of exotic grass species are strongly dependent on the rangeland vegetation and consequently they should be studied together to achieve sustainable range management.

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Book Review

Shinners and Mahler's Flora of North Central Texas. By George M. Diggs, Jr., Barney L. Lipscomb, and Robert J. O'Kennon. 1999. Botanical Research Institute of Texas, Ft. Worth, Texas. 1626 p. US\$89.95cloth. ISBN 1-889878-01-4.

If some travelers who have motored in daylight through North Central Texas have found the landscape uninspiring by Western standards, the same would likely not be said of Shinners and Mahler's *Flora of North Central Texas*, an impressive new flora of the cross timbers and prairies areas of lone star land. A compilation of the work of a number of botanists who have studied the region, the voluminous volume combines elements of botanical history, community ecology, and floristic taxonomy with attractive graphics and a readable text. The authors present it all in a stylish, efficient format that makes the book pleasantly functional compared with many other *floras*, even while it inspires admiration of its scope and detail.

More than just *briefly summarizing* all of the contents of *The Flora of North Central Texas* would be a significant undertaking. The book begins with about 15 pages of its own summary information on design and use of the flora. Matters such as nomenclature, sources of information, summary data on the flora, and threatened and endangered taxa are addressed here. Following this summary, a 60-page introduction to the natural features of North Central Texas introduces the user to the geology, soils, climate, botanical history, and vegetation areas of the region. Included are a number of black and white maps, several color maps, several historical drawings of early vegetation, and some drawings and black and white photographs of early botanists who worked in the area. Thirty pages of color photographs, 4 or 5 to a page, of some of the more attractive flowering species follow the introduction. You can be sure that Texas bluebonnet (*Lupinus texensis*) is among them.

The preceding 3 sections would make an attractive, informative book in themselves, but the over 1,200 pages of the taxonomic key to, and botanical descriptions of the flora of the region which follow expand the book to Texan proportions. Both the keys and descriptions are admirably formatted, making this flora one of the most inviting to use that I have encountered. The text is abbreviated in the manner of a flora, but the abbreviations are rarely cryptic, allowing the taxonomic text to be read comfortably. Most species descriptions are accompanied by hand-drawn illustrations, on adjacent pages, 4 to 9 to a page.

Following the keys and taxonomic descriptions are no fewer than 15 appendices covering topics such as lists of endemic species, lists of conservation organizations, sources of native plants, collecting herbarium specimens, grass phylogeny, larval host plants of Lepidoptera, and 9 other topics. These appendices contain a wealth of information for the professional or amateur botanist. An extensive glossary of taxonomic terms, an illustrated glossary of morphological terms, 75 pages of literature citations, and a 100-page index nearly com-

plete the book, but not without formal printing credits, credits to authors and institutions, and a final map. The entire production is admirably detailed and polished in a kind of Texas tradition, reminding me of the high degree of dedication and professionalism I have observed in many recent and historical natural scientists of that state. It represents the work of many contributors, and the book's attractive format showcases their efforts.

Many of the species described in this book are found in other parts of Texas, and in adjoining states, so that the book should be of interest somewhat beyond the area named in its title. Researchers, teachers, managers, students and amateur botanists of North Central Texas, centered around Dallas-Ft. Worth, will certainly want this floristic survey of this often sultry sub-state of Texas on their shelf. Like the summer nights in North Central Texas, the stylish *Flora of North Central Texas* is, at least for a flora, hotter than it is dry.—*David L. Scarneccchia*, Washington State University, Pullman, Washington.

INSTRUCTIONS FOR AUTHORS (from revised *Handbook and Style Manual*)

Eligibility

The *Journal of Range Management* is a publication for reporting and documenting results of original research and selected invitational papers. Previously published papers are unacceptable and will not be considered for publication. Exceptions to this criterion are research results that were originally published as department research summaries, field station reports, abstracts of presentations, and other obscure and nontechnical handout publications. Manuscripts submitted to the *JRM* are the property of the *Journal* until published or released back to the author(s). Manuscripts may not be submitted elsewhere while they are being considered for this journal. Papers not accepted for publication are automatically released to the authors.

Kinds of Manuscripts

Journal Articles report original findings in Plant Physiology, Animal Nutrition, Ecology, Economics, Hydrology, Wildlife Habitat, Methodology, Taxonomy, Grazing Management, Soils, Land Reclamation (reseeding), and Range Improvement (fire, mechanical chemical). *Technical Notes* are short articles (usually less than 2 printed pages) reporting unique apparatus and experimental techniques. By invitation of the Editorial Board, a *Review* or *Synthesis Paper* may be printed in the journal. *Viewpoint* articles or *Research Observations* discussing opinion or philosophical concepts regarding topical material or observational data are acceptable. Such articles are identified by the word *viewpoint* or *observations* in the title.

Manuscript Submission

Contributions are addressed to the **Editor, Gary Frasier, *Journal of Range Management*, 7820 Stag Hollow Road, Loveland, Colorado 80538**. Manuscripts are to be prepared according to the instructions in the *Journal's Handbook and Style Manual*. If the manuscript is to be one of a series, the Editor must be notified. Four copies of the complete manuscript, typed on paper with numbered line spaces are required. Authors may retain original tables and figures until the paper is accepted, and send good quality photocopies for the review process. Receipt of all manuscripts is acknowledged at once, and authors are informed about subsequent steps of review, approval or release, and publication.

Manuscripts that do not follow the directives and style in *Journal* handbook will be returned to the authors before being reviewed. A manuscript number and submission date will be assigned when the paper is received in the appropriate format.

Manuscript Review

Manuscripts are forwarded to an Associate Editor, who usually obtains 2 or more additional reviews. Reviewers remain anonymous. These reviewers have the major responsibility for critical evaluation to determine whether or not a manuscript meets scientific and literary standards. Where reviewers disagree, the Associate Editor, at his discretion, may obtain additional reviews before accepting or rejecting a manuscript. The Associate Editor may also elect to return to the author those manuscripts that require revision to meet format criteria before the *Journal* review.

The Associate Editor sends approved manuscripts, with recommendations for publication, to the Editor, who notifies the author of a projected publication date. Manuscripts found inappropriate for the *JRM* are released to the author by the Associate Editor. Manuscripts returned to an author for revision are *returned to the Associate Editor for final acceptability of the revision*. Revisions not returned within 6 months, are considered terminated. Authors who consider that their manuscript has

received an unsatisfactory review may file an appeal with the Editor. The Editor then may select another Associate Editor to review the appeal. The Associate Editor reviewing the appeal will be provided with copies of an correspondence relating to the original review of the manuscript. If the appeal is sustained, a new review of the manuscript may be implemented at the discretion of the Editor.

Authors should feel free to contact the Associate Editor assigned to their manuscript at any stage of the review process: to find out where the paper is in the process; to ask questions about reviewer comments; to ask for clarification or options if a paper has been rejected.

Page Proofs

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Authors should have manuscripts thoroughly reviewed by colleagues in their own institution and elsewhere before submitting them. Peer review before submission insures that publications will present significant new information or interpretation of previous data and will speed *JRM* review process.

Particular attention should be given to literature cited: names of authors, date of publication, abbreviations or names of journals, titles, volumes, and page numbers.

It is not the task of Associate Editors or *Journal* reviewers to edit poorly prepared papers or to correct readily detectable errors. Papers not properly prepared will be returned to the author.