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The Trail Boss

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Viewpoint: Improving range science through the appropriate use of statistics

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Abstract

We examined a stratified random sample of articles published over 3 decades of the *Journal of Range Management* to study the applications and changes in statistical methodology employed by range scientists. Our objectives were to characterize the philosophical nature of statistics use in range science and to identify strengths and weaknesses inherent in these approaches. In each article, we examined the research design efficacy and whether the statistical analysis was adeptly used to convey the relevant information. The majority of articles we examined were conducted appropriately. In general, we found more emphasis has been placed on statistical testing than effect size estimation in the last decade. On an average, 82 tests or means comparisons (s.e. = 20) were presented in each article during the 1990's. Articles that reported an effect size via a sample mean frequently did not report an associated standard error. Research designs lacked adequate descriptions in several cases, making it difficult to determine if the appropriate analysis was performed. Improper identification of the experimental or sampling unit and/or the interdependence of observations occurred in all decades. We recommend increased inferential use of confidence intervals and suggest that the practical significance (as opposed to statistical significance) of results be considered more often. Improvements in the 'science' of range science can be made by greater understanding and communication of statistical concepts through consultation with statisticians.

Key Words: effect size, estimation, p-value, repeated measures, Type I error

Resumen

Examinamos una muestra aleatoria estratificada de artículos publicados durante tres décadas en el *Journal of Range Management* para estudiar las aplicaciones y los cambios en la metodología estadística empleada por los científicos de manejo de pastizales. Nuestros objetivos fueron caracterizar la naturaleza filosófica del uso de la estadística en la ciencia de los pastizales e identificar las fortalezas y debilidades inherentes a estas estrategias. En cada articulo, examinamos la eficacia del diseño de la investigación y si el análisis estadístico se uso hábilmente para conducir a información relevante. La mayoría de los artículos que examinamos se condujeron apropiadamente. En general, encontramos que en la última década se ha puesto mas énfasis en las pruebas estadísticas que en el efecto del tamaño de la estimación. En promedio 82 pruebas o comparaciones de medias (s.e. = 20) se presentaron en cada artículo durante la década de 1990. Los artículos que reportaron un efecto de tamaño vía media de la muestra frecuentemente no reportaron un error estándar asociado. En varios casos los diseños de la investigación carecieron de descripciones adecuadas dificultando el determinar si se condujo un análisis estadístico apropiado. La identificación inadecuada de la unidad experimental o de muestreo o la interdependencia de las observaciones ocurrió en todas las décadas. Recomendamos el aumento del uso inferencial de los intervalos de confianza y sugerimos que la significancia práctica (contrario a la significancia estadística) de los resultados debe ser considerada mas a menudo. Se pueden hacer mejoras en la "ciencia" de manejo de pastizales mediante un mayor entendimiento y comunicación de los conceptos estadísticos a través de la consulta con los estadísticos

This paper is motivated by our consulting experience with agricultural, biological, and environmental scientists in the southwest. Combined, we have over 15 years of consulting experience and have worked with dozens of faculty and hundreds of students involved in natural resources. We have found that many students and faculty have an aversion to statistics or a misunderstanding of the role statistics plays in the research process. For example, it is not uncommon for statistical help to be initially solicited after a data set has been collected, leading us to making recommendations that can limit the inferential power of their work (e.g., when randomization was not invoked). As a result, we have been viewed as unrealistic in our desire for scientific rigor and as barriers to publishing research outcomes. This specific study focuses on the use and abuse of statistics in the *Journal of Range Management* over the past 3 decades. Our purpose is not to implicate specific individuals, entire departments or the field of range science. Indeed, our observations apply more generally to many professional fields outside range science, but reviews of statistics use have been made by others in other disciplines (Harlow et al. 1997, Cherry 1998, Anderson et al. 2000).

Anderson et al. (2000) documented the overuse of hypothesis testing in *Ecology* and the *Journal of Wildlife Management*. They concluded that the vast majority of statistical hypothesis tests are conducted on null hypotheses that are clearly false. Nester (1996) suggested several reasons for the indiscriminate use of hypothesis tests. (1) They appear to be objective and exact; (2) they are readily executed with statistical software packages; (3) we are taught

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to use them and everyone seems to use them; (4) some journal editors and supervisors demand them. Anderson et al. (2000) suggest that too much weight is given to statistical tests and that there is not enough emphasis on effect sizes (estimates of magnitudes of effects), directionality of differences, and biological importance. In other words, identifying statistical significance via hypothesis tests, (i.e., reporting of a p-value by itself) provides little information in considering real scientific hypotheses. Furthermore, when statistical hypothesis tests are conducted, the importance of evaluating the assumptions underlying those tests cannot be overstated. Application of statistical methodologies to nonrandom data from observational studies must be clearly described and considered with caution (Cherry 1998).

In evaluating the articles, we asked ourselves 1) Was the research sufficiently described so that it was repeatable? 2) Were randomization, replication and controls or comparisons properly used in experiments? 3) Given a clear description of the study design and treatment arrangement, was an adequate (as opposed to optimal) analysis performed? 4) Were results reported with sufficient detail (e.g., measures of precision, effect size, test statistics, degrees of freedom, etc.). Our evaluation of the range science literature differs from reviews made by others (Cherry 1998, Anderson et al. 2000) in that we examined the experimental and/or sampling designs implemented, methods of analysis, reporting of results and interpretation in both a quantitative and qualitative fashion. We did note when the aforementioned problems in reporting results occurred, but have also attempted to assess all of the statistical machinery underlying range science studies.

The articles we read covered a variety of topics, including habitat use by animals, effects of fire and herbicides on vegetation and soils, food preference studies, nutrient analysis, drought and grazing effects on grasses, evaluation of technology (e.g., pedometers), resource conflicts (e.g., perceived economic damage by ungulates), etc. While we agree with Guthrey et al. (2001) that states the research hypothesis should be given more weight than statistical hypotheses, we have not judged the value or scope of the research itself because we are not range scientists. We excluded technical notes, book reviews, viewpoints, management notes, presidential addresses, comment papers and rebuttals, and invited synthesis papers from the collection we evaluated. As our intent is not to embarrass specific authors or institutions, we refer to specific articles by year only. Exact citations of the examples presented are available upon request.

Methods

We selected a stratified multistage random sample of 54 journal articles from the *Journal of Range Management.* Decades of the 1970s, 1980s, and 1990s served as strata, from which 3 years were randomly selected. We stratified by decade to ensure samples were selected from each decade so that we might identify trends in statistical usage over these time frames. From each of the selected years, 2 issues were randomly selected, from which 3 articles were randomly selected for examination. Simple random samples were selected at each stage using a random number table. Each article was read and evaluated by 1 of us. Quantitatively, we tallied the number of statistical tests or means comparisons, the rate at which appropriate standard errors were reported with means, and the frequency with which P-values were reported without an accompanying test statistic and degrees of freedom.

Evidence of statistical testing was usually indicated in the results section of papers in 1 of 2 manners. Either a declarative statement was made and accompanied with a p-value, or tables of means were presented with superscripts indicating statistical differences. In some articles, the actual number of means comparisons was unclear because the multiple comparison procedure used was unspecified. In such cases, we only recorded the number of means to be compared.

The rate at which standard errors were not reported with means was a frequency measure whereby if an article had at least 1 such occurrence, it was flagged. Only articles that presented at least 1 mean were included in our frequency measure. In a few cases, a single standard error was reported for a collection of means under a complex design structure that would have different variance components. We flagged these instances as failures to report appropriate standard errors.

We use the term 'naked p-value' to indicate values that are reported by themselves without a corresponding test statistic or associated degrees of freedom (e.g., $P = 0.028$). Our definition differs from that used by Anderson et al. (2001b) in which they consider a p-value naked if it lacks an effect size, its direction, and a measure of its precision. Reporting the test statistic and degrees of freedom allows one to evaluate if the test was performed appropriately (e.g., no pseudoreplication occurred). In addition, we noted if only a range was given for the p-value ($P > 0.05$ or $P < 0.10$). We do not wish to perpetuate the misinterpretation of p-values as representing the strength of evidence for the alternative hypothesis or the probability that the null hypothesis is false. However, we believe that knowledge of its exact value more accurately describes the degree of consistency of the data with the null hypothesis (Ellison 1996).

Qualitatively, we determined if the design used was clearly stated and sufficiently detailed so that the study could be replicated. We questioned if the randomization was executed appropriately and replication recognized at the correct level. When statistical tests were used, we determined if they were described adequately and whether or not the practical significance of their result was considered in addition to statistical significance.

Results

The majority of articles we examined were commendable on many measures. Controls or comparisons were used in most experimental studies from all decades. Often, the locations of sampling units were randomized within plots. In several cases, a statistician had been either acknowledged or included as a co-author. However, we found there is room for improvement regarding the statistical components of range science research studies. For example, only occasionally did authors mention that their data met the assumptions underlying the analyses.

The number of means comparisons and/or statistical tests has increased over the past 3 decades, averaging 51 tests per articles in the 1970s (s.e. = 20), 60 tests in the 1980s (s.e. = 15) and 82 tests in the 1990s (s.e. = 20). These results are much higher than those recently reported for other journals. For instance, Anderson et al. (2000) reported that over the period from 1978 to 1997, the average number of p-values per Ecology article ranged from 10 (s.e. = 3) to 44 (s.e. = 8). While some individual articles exceeded 200 p-values, in general more statistical tests are being reported in the *Journal of Range Management.* Statistical testing in the *Journal of Range Management* also exceeds that reported in the *Journal of Wildlife Management*, where the average ranged from 31 (s.e. = 6) to 56 (s.e.= 16) during 1994-1998 (Anderson et al. 2000).

It appears there is a belief that statistical testing is necessary for a study to be scientifically valid (Cherry 1998). Several notable individuals, including statisticians (Yates 1951, Cox 1977) have recognized the overuse of statistical testing in the literature over many years. In contrast, Johnson (1999) notes the lack of use of ordinary confidence intervals, despite being more informative than p-values. We found many articles with large tables of means that were compared within rows and columns. One article from 1992 contained a whopping 328 statistical test results. The potential for Type I error in such cases is extremely large, leading to spurious effects described by Anderson et al. (2001a).

When p-values were reported within an article, they were naked in most cases, although the frequency of such practice appears to be declining (1970s: 80%, 1980s: 69%, 1990s: 58%). In some cases, the effect size or direction was not reported, leaving one to wonder how large the difference or treatment effect was. For example, in a 1978 article, the following results were reported, "Lotebushes used by quail averaged 3.8 m^3 and were significantly ($P < 0.05$) larger than plants randomly chosen". There is no indication of how large randomly chosen plants were and how much variability there was in these sample means.

Sample means were commonly reported in articles (even when no statistical tests were performed), but they were rarely accompanied with a measure of their variability, i.e., a standard error. Standard errors were reported along with means in 6.8% of the articles from the 1970s, 11.6% of the articles from the 1980s and 12.6% of the articles from the 1990s. When standard errors were reported, often there was no mention of evaluating homogeneity of variances, creating a potential for inaccurate values. On many occasions, large tables of means were presented without accompanying standard errors. To be fair, several studies reported the sample mean along with the sample standard deviation, s. Such practice is reasonable if describing the sample is the intention; no inferential process is being initiated. The sample standard deviation is a descriptive statistic whereas the standard error is an inferential statistic (Anderson et al. 2001b). However, when the following combination is reported $\overline{x} \pm s$ there is no meaningful interpretation for this interval as an interval estimator for the true population mean. The standard error or the standard error multiplied by a t-statistic (for a given confidence level) should be used for such constructions.

Qualitative Observations

We noted a variety of misinterpretations of statistics, a listing of which is beyond the scope of our study. We have categorized the most frequent types of mistakes in 3 areas. We noted that several papers lacked an adequate description regarding the treatment application and analysis methodology. For example, in a 1978 article the following statement appears, "Seven treatments and one control were used to evaluate the effect of fire on quail habitat." There is no indication of the design or the treatment structure. Were the treatments randomly assigned? Replication is never mentioned, although it appears there is none. The article then states, "Thirty plants were selected in each of the seven treatment areas plus the control. Fifteen of the lotebushes selected were used by quail and 15 were randomly chosen." One might ask if only lotebushes were sampled from and whether or not the 15 lotebushes used by quail were randomly selected from all lotebushes used by quail. Two of the most basic principles of experimental design appear to have been ignored or at least not adequately described. We refer the reader to Wester (1992) for an excellent discussion about design principles and their use in range science. The first sentence of the last paragraph of the methods states, "Both parametric and nonparametric tests were used to evaluate the data." With the exception of mentioning the use of Spearman's Rho Test for correlating home range size with covey size and woody plant density, no other information is given regarding what testing procedures were used in the study.

Another common mistake made in the papers we examined was the failure to recognize the correlation of observations observed on the same experimental unit over time. Repeated measures designs are often used unknowingly and are not analyzed accordingly, despite a SRM presentation and proceedings paper by Engemen et al. (1986). For example, in a 1989 article, 10 bulls were randomly sampled from 2 cattle herds (one sedentary and the other migratory). Fecal samples were collected biweekly, pooled, and analyzed for fecal nitrogen and fecal acid detergent fiber (ADF). The bulls were weighed on a monthly basis. Average percent weight change and fecal measurements were then correlated without regard to the lack of independence between monthly measurements. Gurevitch and Chester (1986) emphasize that ignoring the correlative structure among observations from the same individual can lead to faulty test results. Furthermore, only under certain conditions (Huynh and Feldt 1970, Milliken and Johnson 1992) can repeated measures data be analyzed via univariate split-plot analysis.

Finally, pseudoreplication issues plagued several papers. Pseudoreplication is a pervasive problem in many scientific areas and has been repeatedly warned against in the ecological literature (Hurlbert 1984, Heffner et al. 1996) and range science literature (Brown and Waller 1986, Wester 1992). Walker and Richardson (1986) clarified the differences between pseudoreplication and true replication in grazing system studies, the key to which lies in identification of the experimental unit. We repeat their plea for proper reporting of results when replication was not achieved due to logistical difficulties. As an example, we refer to the paper on cattle live weight changes described before. Ten bulls were randomly selected from a migratory herd and a sedentary herd. The 10 bulls represent replicates with respect to their specific herds, but do not represent replicates with respect to the 'treatment' of herd type (migratory or sedentary). Furthermore, by pooling fecal samples from the 10 bulls within a herd type, they no longer are useful as replications for their respective herds.

Recommendations

Use of confidence intervals as interval estimators, rather than relying on single point estimators and tests between them, is more informative because it inherently gives the effect size and a measure of its precision. Displaying such values in figures is particularly appealing because of the ease with which one can compare the various responses at different treatment levels. Confidence intervals can still be used to test statistical hypotheses, but they have the added advantages mentioned earlier. The current editor of the *Journal of Wildlife Management* has instructed future authors to present measures of central tendency and dispersion in lieu of excessive use of p-values (Brennan 2001). When reporting the results from a statistical significance test, include the actual p-value (not a range), along with a test statistic and its degrees of freedom. Clearly distinguish between an observational study and an experiment when describing the research, so that p-values under the former can be viewed with a greater degree of skepticism. Additionally, go beyond statistical significance and elaborate on the practical significance of the results. Brennan (2001) suggests more research is needed to determine what effect size has on a meaningful impact on a system. Finally, seek statistical advice at the beginning of a study. The most important time for statistical input is during the planning stages of a study rather than after a data set has been collected.

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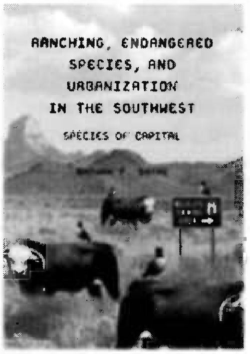

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Research observation: Desert bighorn sheep diets in northwestern Sonora, Mexico

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Abstract

We used microhistological analyses of fresh fecal pellets to determine seasonal diets of desert bighorn sheep (*Ovis canadensis mexicana* Merriam 1901) in northwestern Sonora, Mexico from April 1997 to December 1998. We identified 41 plant species (22 browse, 10 forbs, 5 grasses, and 4 succulents) in diets of bighorn sheep. We found no differences between diets of males and females, and diet diversity between sexes was similar ($P > 0.05$). Diet included: browse (45.7%), forbs (32.0%), succulents (17.8%), and grasses (4.5%). The consumption of succulents was higher during spring, decreased during summer, increased in autumn, and decreased in winter. Consumption of forbs was higher during winter and summer. Globemallow (*Sphaeralceae* spp.), desert agaves (*Agave* spp.), range ratany (*Krameria parvifolia* Benth.), buck-wheatbrush (*Eriogonum* spp.), foothill palo verde (*Cercidium microphyllum* [Torrey] Rose & Johnst.), Engelmann prickly pear (*Opuntia engelmanii* Salm-Dyck), desert ironwood (*Olneya tesota* A. Gray), and elephant tree (*Bursera microphylla* A. Gray) were consumed throughout the study. As biologists identify potential release sites for restoration of bighorn sheep in Mexico, studies of diet composition will provide managers with information for successful translocations.

Key Words: *Ovis canadensis* mexicana, sexual segregation

Diet composition studies for Mexican bighorn sheep (*Ovis canadensis mexicana* Merriam) have been conducted in New Mexico (Elenowitz 1983) and Arizona (Alderman et al. 1989, Krausman et al. 1989, Etchberger 1993). In Mexico, the only formal study of diet composition was for Weem's (*O. c. weemsi* Goldman) and peninsular bighorn sheep (*O.c. cremnobates* Elliot) (Sanchez 1976). Attempts to repopulate areas where bighorns have been extirpated in Sonora, and Baja California Sur have recently been conducted by private organizations and the Mexican government (Jimenez et al. 1996, 1997). In the process of identifying potential release sites, studies of diet composition will provide managers with information essential for successful translocations. The objectives of our study were to identify composition of diets of Mexican bighorn sheep in northwestern Sonora, Mexico and compare diet compositions between sexes and among seasons.

Resumen

Utilizamos análisis microhitological de pelotillas fecales frescas para determinar dietas estacionales de las ovejas del bighorn (*Ovis canadensis* mexicana Merriam 1901) del desierto en Sonora del noroeste, Mexico a parti de abril de 1997 a deiciembre de 1998. Identificamos 41 especies de la planta 22 hojee, 10 forbs, 5 hierbas, y 4 succulents) en dietas de las ovejas del bighron. No encontramos ninguna diferencia entre las dietas de varones y las hembras, y la diversidad de la dieta entre los sexos era similar ($P > 0.05$). Dieta incluida:hojee (45.7%), forbs (32.0%), succulents (17.8%), and hierbas 4.5%). La consumición de succulents era más alta durante el resorte, disminuyó durante el verano, creciente de otoño, y disminuido en invierno. La consumición de forbs era más alta durante invierno y verano. Globemallow (*Sphaeralceae* spp.), agaves del desierto (*Agave* spp.), range ratany (*Krameria parvifolia* Benth.), buck-wheatbrush (Eriogonum spp.), verde del palo de la colina (*Cercidium microphyllum* [Torrey] Rose & Johnst.), pera espinosa de Engelmann (*Opuntia engelamnii* Salm-Dyck), ironwood del desierto (*Olneya tesota* A. Gray), y el árbol del elefante (*Bursera microphylla* A. Gray) era consumidor durante el estudio. Pues los biólogos identifican los sitos potenciales del desbloquear para la restauración de las ovejas del bighorn in Mexico, los estudios de la composición de la dieta proporcionarán a encargado quieren la información para los desplazamientos acertados.

Materials and Methods

This study was conducted in Rancho el Plomito located in the southern portion of Sierra el Viejo about 70 km south of Caborca, northwestern Sonora, Mexico (30° 12' and 30° 20' N, 112° 18' and 112o 22' W) (Fig.1). The privately owned ranch includes 3,576 ha of flat and 4,376 ha of mountainous terrain. Rancho el Plomito contains 9 major canyons and is bordered by private ranches (Fig. 1). There are 2 artificial water tanks (capacity 10,000 liters each) on the ranch and 13 smaller water sources strategically distributed within the ranch to provide water for wildlife. There are also natural water catchments that have been improved for water collection. Livestock were excluded from the ranch in 1994. The ranch is used exclusively for the conservation and management of native wildlife. We selected the study area because of the presence of an indigenous population of Mexican bighorn sheep (N = 300), which is the largest bighorn sheep pop-

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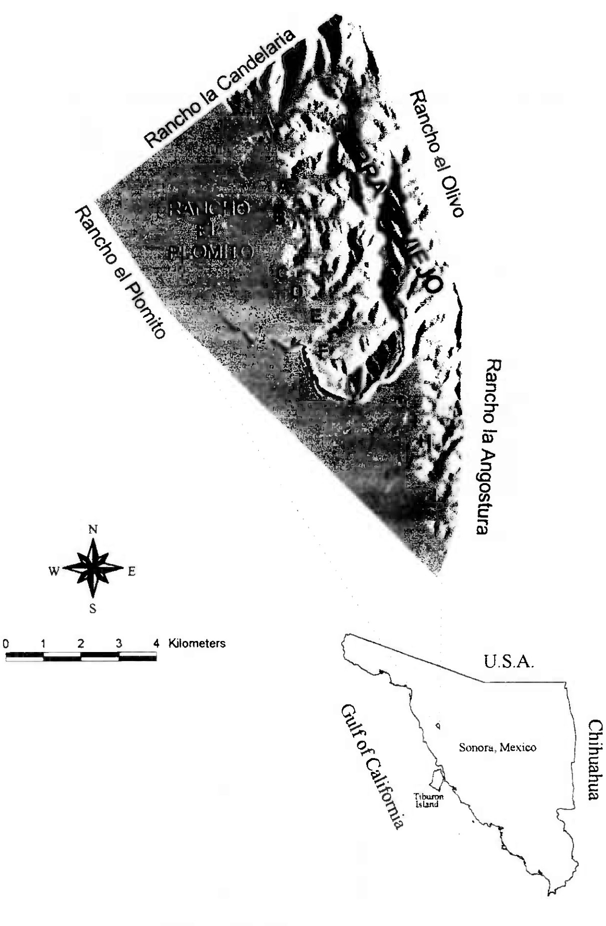

Fig. 1. Rancho el Plomito in Sierra el Viejo, 70 km south of Caborca, northwestern Sonora, Mexico. The mountain range contained 9 major canyons. A, El Serrucho; B, El Recodo; C, El Coliseo; D, El Solitario; E, San Francisco, F, Puerto la Cueva; G, El Colorado; H, El Muro, and I, Dos Minas.

ulation on the mainland of Sonora (Lee and Lopez-Saavedra 1994).

Rancho el Plomito is located in the Sonoran Desert where the terrain is rugged, rocky, and often interspersed by canyons and washes. The area is Sonoran Desert scrub within the subdivision of the Lower Colorado River Valley, which is the largest and most arid subdivision of the Sonoran Desert (Brown 1994).

Elevations ranged from 300 m on flat areas to 1,050 m. The mean daily temperature at 0800 for 1997 and 1998 was 26.2° C and 22.8° C, respectively. The lowest mean minimum temperature for both years occurred in autumn (October–December) (i.e., 12.5° C in 1997 and 7.8° C in 1998), while the highest mean maximum temperature occurred in summer (July– September) (i.e., 41.0° C in 1997 and 41.1° C in 1998). The annual precipitation for 1997 and 1998 was 227.2 and 148.7 mm, respectively and it rained more during summer in both years (i.e., 169.6 mm in 1997 and 110.0 mm in 1998).

Seasons for the study area were determined from the biology of bighorn sheep, bimodal precipitation, and temperature regimes. Seasons were: cold-wet (January –March), hot-dry and peak lambing (April–June), hot-wet (July–September), and cold-dry and rut (October– December). However, for convenience, we named the seasons as winter, spring, summer, and autumn, respectively.

We identified 3 vegetation associations within the study area based on field reconnaissance and following Hernandez (1998). The elephant tree (*Bursera microphylla* A. Gray)-salvia (*Salvia mellifera*)-limber bush (*Jatropha cuneata* Wiggins & Rollins) association (ESL) (2,144 ha) occurs in foothills and mountains on steep slopes. Other dominant plants found within this association are ocotillo (*Fouquieria splendens* Engelm.), brittle bush (*Encelia farinosa* A. Gray), opuntias (*Opuntia* spp.), Mexican jumping bean (*Sapium biloculare* Wats), desert lavender (*Hyptis emoryi* Torr.), mammillarias (*Mammill-aria* spp), hibiscus (*Hibiscus denudatus* Benth), agaves (*Agave* spp.), and foothill palo verde (*Cercidium microphyllum* [Torr.] Rose & Johnst.). The foothill palo verde-desert ironwood (*Olneya tesota* A. Gray) association (FDI) (1,138 ha) is commonly found along bajadas and riparian areas (arroyos and washes) and is accompanied with coursetia (*Coursetia glandulosa* Gray), white-thorn acacia (*Accacia greggii* A. Gray), brittle bush, garabatillo (*Mimosa laxiflora* Benth), limber bush, salvia, wolfberry (*Lycium californicum* Nutt.), range ratany (*Krameria parvifolia* Benth), and helianthus (*Helianthus* spp.). The ocotillo-desert agave (*Agave zebra* Gentry and *A. pelona* Gentry)-hop bush (*Dodonoea viscosa* Jacq.) vegetation association (OAH) (1,094 ha) occurs at high elevations and is commonly found along ridgetops with scattered foothill palo verde and desert ironwood trees. We followed Lehr (1978) for plant nomenclature.

We determined diets of desert bighorn sheep based on fecal pellets collected 2 times each season from April 1997 to December 1998, except winter, which was only sampled in 1998. We systematically traveled the area on foot across washes, ridgetops and cliffs and observed sheep with a pair of 10 x 50 binoculars and a 30 x 16 spotting scope. Sheep were aged and sexed by size and horn development (Geist 1968).

We collected fresh fecal pellets from male and female bighorn sheep within 24 hours of deposition; most pellets were collected within 2 hours following deposition. We avoided disturbing the animals. We collected 10–18 pellets from > 40 pellet groups for each sex/season. Fecal samples were air dried and stored in paper bags until analyses at the Fecal Analyses Laboratory of the University of Arizona. Diets were analyzed by microhistological examination of fecal samples (Sparks and Malecheck 1968). Although some disadvantages related to differential digestibility of forage plants has been reported in the use of this technique (Holechek et. al. 1982, Gill et al, 1983), we assumed that the bias equally affected composition of diets of males and females.

We randomly prepared a composite sample from fecal-pellet samples per sex/season (Holechek and Vavra 1981). Ten slides were prepared and 20 fields were read from each slide (200 fields/season). Frequency for each plant species was recorded and converted to relative density following Fracker and Brischle (1944:285, table 1). We determined percent relative composition by dividing the density of each plant species that occurred on the slide by the total plant density on that slide and multiplied by 100. Plant species found in the diet were classified as browse (perennial shrubs), forbs (annual, herbaceous plants), grasses, or succulents (cacti).

Comparisons of diet between males and females by seasons were made using the Morisita index of overlap (Morisita 1959), as modified by Horn (1966) and Zaret and Rand (1971). Diet overlap indexes were calculated with the following formula (Alcoze and Zimmerman 1973):

$$C = \frac{2\sum_{i=1}^{s} Xi\,Yi}{\sum_{i=1}^{s} Xi^2 + Yi^2}, \qquad (1)$$

Where C is the coefficient value, s is the total number of plant species and Xi and Yi are the proportions of the total diet of males (X) and females (Y). The value of this coefficient ranges from 0 when no plant species are shared to 1 when diets are equal. Diet overlap is significant when the coefficient of overlap is > 0.60. We used this index of overlap because it uses the number of plants that overlap and considers the proportions of those plants in the diet. This index has been previously used in studies of composition of diets of desert bighorn sheep (Krausman et al. 1989, Etchberger 1993). Diversity of diets for males and females by seasons were also identified with the Shannon-Wiener index and tested ($P < 0.05$) for differences between male and female diversity indices (Zar 1996).

Results

The coefficient of overlap (Morisita 1959) of diets of male and female bighorn sheep for the winter, spring, summer, and autumn was 0.970, 0.926, 0.972, and 0.906, respectively. All values indicated significant diet overlap (i.e., > 60) for all seasons. Male and female bighorn sheep in Sonora consumed the same plant species and used them in similar proportions (Table 1). Those species that contributed the highest percentages of combined diets in both years were: globemallow, desert agave, range ratany, buck-wheatbrush, foothill palo verde, sagebrush (*Artemisia* spp.), desert ironwood, elephant tree, and Engelmann prickly pear.

Plant diversity in diets of males and females was very similar among seasons ($P > 0.05$). During winter, spring, summer, and autumn the diversity indices for males were 0.474, 0.512, 0.506, and 0.514, while for females were 0.433, 0.513, 0.497, and 0.545, respectively. Shannon-Wiener diversity indices (Zar 1996) indicated that diets of desert bighorn sheep were less diverse in winter compared to the other seasons. The mean annual composition of categories of forage in diets of males and females was similar (Fig. 1). We identified 41 plant species consumed by desert bighorn sheep from April 1997 to December 1998 in Rancho el Plomito Sonora, Mexico.

Bighorn sheep consumed ≥ 26 different plant species each season (Table 1). However, seasonal diets concentrated on a few plants in all seasons (e.g., in winter 5 plants constituted 69% and globemallow (*Sphaeralcea* spp.) constituted > 37%; spring, 7 plants constituted 58.8% of the diet; summer, 5 plants made up 50.3% of the diet; and autumn 7 plants constituted 60% of the diet) (Table 1).

Table 1 Percent relative composition of plant species in diets of desert bighorn sheep in Rancho el Plomito, Sonora, Mexico.

1997-1998

Species	Winter (Jan.-Mar.)	Spring (Apr.-Jun.)	Summer (Jul.-Sep.)	Autumn (Oct.-Dec.)
	(%)			
Browse				
White-thorn	—	—	0.2	—
Catclaw acacia	—	4.0	3.6	1.1
Ragweed (*Ambrosia ambrosoides* Cav.)	0.4	0.6	0.7	1.9
Sagebrush (*Artemisia* spp.)	—	6.6	5.3	5.3
Fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.)	4.1	0.2	0.2	0.3
Broom baccharis (*Baccharis sarothroides* A. Gray)	0.1	1.7	0.6	0.8
Fairy—duster (*Calliandra eriophylla* Benth.)	0.4	0.5	—	—
Desert hackberry	3.4	0.8	1.4	1.9
Foothill palo verde	7.3	3.9	3.0	8.0
Mormon-tea (*Ephedra* spp.)	0.8	0.6	—	—
Buck-wheatbrush	7.9	5.6	8.1	8.8
Ocotillo	1.1	2.1	1.2	1.9
Snake—weed (*Gutierrezia sarothrae* [Pursh] B. & R.)	2.3	—	—	—
Haploppapus (*Haploppapus tenuisectus* [Greene] Blake)	—	0.5	0.8	—
Range ratany	8.2	12.6	8.1	7.4
Wolf berry *Lycium* spp.	0.2	—	—	—
Desert ironwood	4.4	2.3	3.9	3.7
Elephant tree	1.2	5.4	3.7	4.8
Brittle bush	—	0.6	0.4	—
Velvet mesquite (*Prosopis velutina* Woot.)	0.7	1.8	2.1	0.3
Russian thistle	—	0.1	0.4	—
Jojoba	0.1	0.5	0.1	1.2
No. species	16	19	18	14
Forbs				
Fringed amaranthus (*Amaranthus fimbriatus* [Torr.] Benth.)	0.3	0.1	0.1	0.2
Milk-vetch (*Astragalus* spp.)	—	2.1	2.2	3.7
Borage (*Boraginaceae* spp.)	—	3.3	4.2	4.5
Hyssop spurge (*Euphorbia* spp.)	0.4	—	1.5	0.1
Janusia (*Janusia* spp.)	—	3.9	2.8	3.4
Sida (*Sida* spp.)	—	—	0.5	1.0
Globemallow	37.1	8.2	18.7	13.9
Tidestromia (*Tidestromia lanuginosa* [Nutt] Standl.)	1.4	0.8	0.8	1.7
Trixis (*Trixis californica* Kellogg)	—	0.5	1.5	0.4
Unidentified	2.4	2.8	4.6	—
No. species	≥5	≥8	≥10	≥9
Grasses				
Three-awn (*Aristida* spp.)	—	0.3	1.5	—
Grama grass (*Bouteloa* spp.)	—	2.3	2.9	2.9
Red brome (*Bromus* spp.)	—	0.5	0.5	1.9
Bush muhly (*Muhlenbergia* spp.)	0.1	2.2	0.6	2.1
Drop-seed *Sporobolus* spp.	0.1	0.4	0.2	—
No. species	2	5	5	3
Succulents				
Barrel cactus	—	0.5	0.2	0.8
Prickly pear cactus	4.2	6.7	3.4	6.5
Christmas cactus	4.0	—	—	—
Desert agaves	8.5	15.7	10.1	10.1
No. species	3	3	3	3
Total no. species	26	35	36	29

Desert bighorn sheep consumed desert hackberry (*Celtis pallida* Torr.), foothill palo verde, buck-wheatbrush (*Eriogonum* spp.), ocotillo, range ratany, desert ironwood, elephant tree, globemallow, Engelmann prickly pear (*Opuntia engelmannii* Salm-Dyck.), and desert agave throughout the study (Table 1). However, foothill palo verde, buck-wheatbrush, range ratany, globemallow, and desert agave each occurred in > 5% of the annual diet and constituted 58.0% of the average annual diet (Table 1).

There was seasonal variation in the use of plants by desert bighorn sheep. Consumption of succulents was higher in spring, decreased during summer and winter and increased in autumn (Fig. 2). In the Harquahala and Little Harquahala mountains bighorn sheep consumed more barrel cactus (*Ferocactus acanthodes* [Lemaire] B. & R.) during summer, autumn, and winter (Warrick and Krausman 1989). Weather conditions in the area during spring and autumn are dry. When weather conditions are very dry, bighorn sheep consume barrel cacti and other species of cacti (Sanchez 1976, Alderman et al. 1989, Krausman et al. 1989). Barrel cacti have higher water content than other forage plants and this is a major source of water for bighorn sheep in some areas during dry conditions (Warrick and Krausman 1989). In addition, Etchberger (1993) found that groups of males, females, and mixed groups of bighorn sheep use micro sites with more barrel cacti that random sites. We commonly observed bighorn sheep consuming agaves, prickly pear, and mammillarias. Sheep eat the central portion of the agave by breaking off the spines with their horns and front legs, by hitting, pulling and chewing the leaves until they reach the central portion. Water content in the central stalk of the plant is likely high. Females with lambs occupied areas with higher densities of mammillarias than females without lambs (Tarango 2000). Greater succulent consumption occurred during lambing when lactating females also require more water and energy (Sadlier 1969).

The decrease of succulent plants in the diet of bighorns from spring to summer (rainy season) could be due to the presence of rain water collected in natural catchments (tinajas) that usually lasts for several days. Potholes provided water to bighorn sheep after rains for up to 7 days in western Arizona (Warrick and Krausman 1989). In our study area, bighorn sheep did not drink from man-made catchments. In 1998, during June, July and August (the hottest period of the year), we monitored the use of a artificial water-tank (capacity, 10,000 liters) constructed for the use of wildlife and never recorded use by sheep. It is likely that bighorn sheep in Sierra el Viejo used desert agaves, Engelmann prickly pear, desert Christmas cactus (*Opuntia leptocaulis* DC.), barrel cactus, and mammillarias to fulfill their water requirements. The high consumption of agaves in Sierra el Viejo could be related to their availability also. Agave plants are common in Rancho el Plomito and reach densities of 683 agaves/ha (Tarango 2000). The elephant tree is an important food source for bighorn sheep during hot and dry seasons. This plant is present year round and was the only green forage available to bighorns during the hottest and driest seasons. Other plants that did not occur in the diet analysis, but were observed being eaten by sheep were limber bush (*Jatropha cuneata* Wiggins & Rollins) a plant preferred by lambs, coursetia and salvia by males and females.

Forbs were more important during wet conditions (winter and summer) and less during dry conditions (spring and autumn) (Fig. 2). Content of globemallow in the diet ranged from 5.5 to 38.0% and averaged 19.5%. This forb has also been reported to be an important component of diets of bighorns in other areas (Sanchez 1976, Krausman et al. 1989, Bleich et al. 1992), and in mule deer (Anderson et al. 1965, Leopold and Krausman 1987). In the Santa Catalina Mountains, Arizona, forbs were always higher in protein than browse and grasses throughout the year (Mazaika et al. 1992). Furthermore, Morgart et al. (1986) report that forbs in the spring contained more phosphorus and protein than browse and grasses eaten by bighorns. In addition, in winter, annuals enhanced the physical condition of females during late pregnancy and early lactation (Smith and Krausman 1987).

Forage categories used by bighorn sheep in Rancho el Plomito, Sonora, Mexico were similar to desert bighorn sheep diets in Arizona (Etchberger 1993). Grasses constituted a small portion of diets of bighorn sheep in Rancho el Plomito. Browning and Monson (1980) state that wild sheep of the world are grazers. The preference for browse over grass species is due to their availability rather than preferences (Seegmiller and Ohmart 1982).

Desert bighorn sheep in Sonora exhibited temporal segregation, however, spatial separation by sexes was not clearly defined and consequently differences in composition of diets of males and females during segregation (autumn, winter, spring) were not noticeable. We encountered groups of males and females using the same foraging areas at different times. Furthermore we found no difference of diet diversity for any of the seasons within years and during the nonbreeding period. Males and females in our study area shared most of the plants species throughout the study and used them in similar proportions.

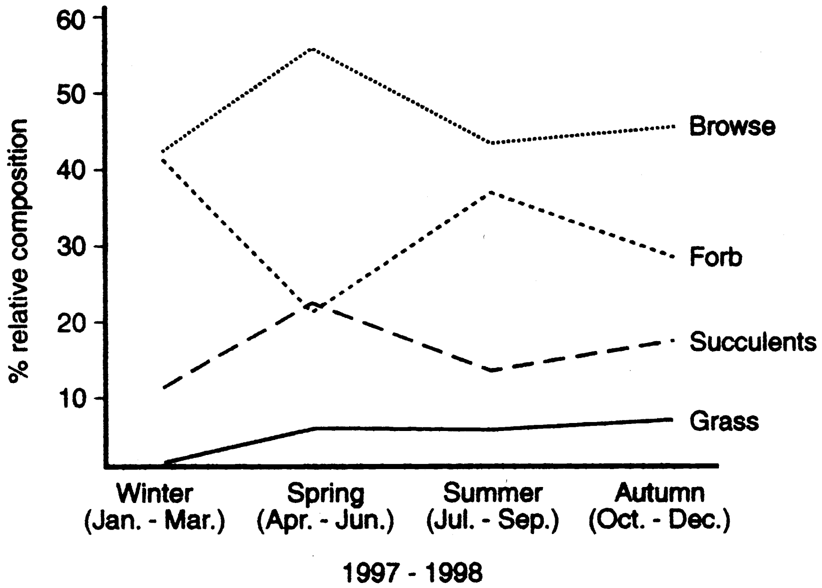

Fig. 2. Consumption of browse, forbs, succulents, and grass by desert bighorn sheep, Rancho el Plomito, Sierra el Viejo, northwestern Sonora, Mexico, 1997–1998.

Management Implications

The diet of males and females was not significantly different and bighorn sheep consumed 41 plant species from April 1997 to December 1998 in Rancho el Plomito, Sonora. These data are important for the successful translocations of bighorn sheep in Mexico. Attempts to repopulate landscapes where bighorn sheep have been extripated, in Sonora and Baja California Sur, are being conducted by private organizations and the Mexican government (Jimenez et al. 1996, 1997). In the process of identifying potential release sites, studies of diet composition will provide managers with information essential for successful translocations. We suggest that studies of translocation sites, including the vegetation resource base, be conducted prior to translocations or habitat alteration.

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Grazing intensity impacts on pasture carbon and nitrogen flow

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Abstract

There is little information on the impact of grazing intensity on productivity and sustainability of intensively managed pastures in the humid, short-season parkland of the Canadian prairies. Our hypothesis was that above-ground productivity of dry matter, carbon, nitrogen, and in vitro digestible organic matter would be reduced proportionately with increasing grazing intensity. The study was conducted on a Typic Haplustoll at Lacombe, Alberta. Paddocks of meadow bromegrass (*Bromus riparius* Rhem.), replicated 4 times, were subjected to heavy, medium and light grazing intensities. Measurements and analyses were carried out for 3 years. Yields of dry matter, carbon, nitrogen, and in vitro digestible organic matter before and after grazing were determined and seasonal pools of above ground production, disappearance and residual were calculated. Concentrations of acid and neutral detergent fiber and lignin were also determined before and after grazing. Increasing grazing intensity tended to increase nitrogen and decrease fiber concentrations for available and residual forage. Heavy and medium grazing intensities produced 83 and 90% as much above ground dry matter and 87 and 90% above ground carbon as the light intensity. All disappearance pools were similar among grazing intensities except in vitro digestible organic matter, where heavy was 116% of light. Heavy grazing reduced the contribution of vegetative dry matter, in vitro digestible organic matter, carbon and nitrogen to the residual to 41, 50, 36, and 52% of that for light grazing. Adding estimated fecal-carbon to the residual significantly increased total residual carbon. Estimated fecal-carbon represented 68, 51, and 42% of all carbon inputs to litter for heavy, medium and light grazing, respectively. Grazing intensity did not affect estimated pools of excreted nitrogen, but increased estimated percent of nitrogen excreted as urine.

Key Words: nutrient flow, productivity, disappearance, residual, pasture, nutritive value

Resumen

Hay poca información sobre el impacto de la intensidad de apacentamiento en la productividad y sustentabilidad de praderas manejados intensivamente en la región de las praderas húmedas de estación corta de Canadá. Nuestra hipótesis fue que la productividad aérea de materia seca, carbón, nitrógeno y materia orgánica digestible sería reducida proporcionalmente al incremento de la intensidad de apacentamiento. Este estudio se condujo en Lacombe, Alberta. Potreros de "Meadow bromegrass" (*Bromus riparius* Rhem.), repetidos 4 veces, se sometieron a intensidades de apacentamiento ligera, moderada y fuerte, las mediciones y análisis se condujeron durante 3 años. Los rendimientos de materia seca, carbón, nitrógeno y la materia orgánica digestible in vitro se determinaron antes y después del apacentamiento y se calcularon las reservas estacionales de la producción aérea, desaparición y del residuo, también se determinaron las concentraciones de fibra neutro y ácido detergente y de lignina. El aumento de la intensidad de apacentamiento tendió a incrementar la concentración de nitrógeno y a disminuir las concentraciones de fibra del forraje disponible y residual. Las intensidades de apacentamiento moderada y fuerte produjeron el 83 y 90% de la materia seca aérea y el 87 y 90% del carbón aéreo producidos con la intensidad ligera. Todas las cantidades de desaparición fueron similares entre las intensidades de apacentamiento, excepto materia orgánica digestible in vitro, la cual con el apacentamiento fuerte fue de 116% con respecto al apacentamiento ligero. El apacentamiento fuerte redujo la contribución de materia seca vegetativa, materia orgánica digestible in vitro, carbón y nitrógeno del residuo en proporciones de 41, 50, 36, y 52% de lo registrado con el apacentamiento ligero. Agregando la estimación del carbón fecal al residual incrementó significativamente el carbón total residual. El carbón fecal estimado representó el 68, 51, y 42% de todas las entradas de carbón en el mantillo, para el apacentamiento fuerte, moderado y ligero respectivamente. La intensidad de apacentamiento no afectó las cantidades estimadas de nitrógeno excretado, pero incrementó el porcentaje estimado del nitrógeno excretado en la orina.

Managed intensive grazing is relatively new in the parkland vegetation zone of the Canadian prairies. The parkland has a short growing season, and is wetter and cooler than the southern prairies (Campbell et al. 1990), but is more productive. Despite

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the potential of intensive grazing, very little basic research has been conducted into its' effect on productivity, and subsequent impact on pasture and soil sustainability. Grazing per se and grazing intensity, in particular, affects productivity and nutritive value of pasture (Briske and Heitschmidt 1991, Wedin 1996), potential for pasture to sequester soil carbon (Schnabel et al. 2001), and for pasture soils to immobilize or mineralize N (Wedin 1996). Studying the flow of C and N through pasture systems in response to varying grazing intensities, should provide information on potential impacts and limitations to long-term pasture sustainability.

Grazing and grazing intensity modify pasture production through effects on leaf area and light interception (Briske and Heitschmidt 1991, Lemaire and Chapman 1996). Generally, productivity is reduced as grazing intensity increases (Parsons et al. 1983, Matches 1992). It follows that the capacity for pastures to accumulate C, N and other nutrients above and below ground may be reduced with increased grazing intensity (Schnabel et al. 2001).

Grazing intensity affects the quantity and quality of organic and mineralized materials that are delivered to the litter and soil as vegetative residues, urine, and feces. As grazing intensifies so does seasonal utilization of pasture dry matter, C and N by livestock (Parsons et al. 1983, Briske and Heitschmidt 1991). Therefore the relative proportion of herbage material that passes directly to the litter via senescence, rather than indirectly via ruminant feces and urine is also affected (Parsons et al. 1983, Whitehead 1995, Lemaire and Chapman 1996).

Grazing also affects the quality of herbage in the sward and this ultimately impacts degradation rate of litter, soil organic matter, and soil nutrient mineralization rates (Wedin 1996). Generally, parameters used to describe nutritive value, such as crude protein and acid detergent fiber (ADF) concentrations have analogous parameters such as C: N ratio and lignin concentration, which are closely related to microbial degradation of litter and soil organic matter (Wedin 1996, Schnabel et al. 2001). Improved grazing efficiency as a result of intensive grazing results in higher leaf to stem ratios (Parsons et al. 1983, Matches 1992) and less dead material left in the sward after grazing (Lemaire and Chapman 1996). Leaves have higher crude protein and lower ADF concentrations than stems at most stages of grass development (Baron et al. 2000), so leafy residues should degrade faster than stemy residues. Dead material has a higher C: N ratio than live material, so residence time of organic-C in litter and soil pools is longer (Holland et al. 1992). Ultimately the quality of vegetative material moving from sward to litter pools affects quantity and residence time of C entering the soil pool (McGill et al. 1981, Holland et al. 1992, Wedin 1996, Schnabel et al. 2001).

Nutritive value of ingested herbage influences the fate of waste materials returned as feces and urine. For example, as N content of the sward increases a greater percentage of ingested-N is excreted as urine (Haynes and Williams 1993, Whitehead 1995), which then becomes susceptible to loss or plant uptake within a short time (McGill et al. 1981, Holland et al. 1992, Wedin 1996).

In this short-season area, plant growth and nutrient uptake is confined to a period of less than 100 days. Grazing can be intensified over shorter periods (within the window of plant growth) or extended to longer periods beyond the period of plant growth (e.g. 160 days). The pattern and intensity of nutrient flow from sward to litter will impact the quantity and quality of litter and the quantity and residence time of C in the soil, which ultimately affects pasture productivity and sustainability. The objectives of this study were: to determine the impact of grazing intensity on relative pool sizes of sward productivity, residual and disappearance dry matter C, and N; to determine the impact of grazing intensity on herbage and residual nutritive value; to estimate the impact of grazing intensity on proportional amounts of dry matter, C and N passed through a ruminant and returned to residual, compared to the vegetative contribution on a rotationally grazed meadow bromegrass (*Bromus riparius* Rhem.) pasture, grown in a short season area.

Materials and Methods

Experiment Establishment

The study was established in 1993 at Lacombe, Alberta, Canada (52° 28' N; 113° 45'W; 847 m) on a Penhold silt loam (Typic Haplustoll) soil. In the spring the experimental area received a broadcast application of 8, 14, 26, and 5 kg ha^{-1} of N, P, K, and S, respectively, followed by a light cultivation and packing. Then 'Paddock' meadow bromegrass was hand broadcast at a rate of 16.8 kg ha^{-1} mixed with 1 kg ha^{-1} of Spredor II alfalfa (*Medicago sativa* L.). Seeding was followed by harrowing and packing. Each paddock was a fenced area of 9 x 30 m. Within each of 4 replicates, 3 paddocks (12 in total) were established for 3 grazing levels. All paddocks were hand weeded during the summer of 1993 and were grazed in late fall, but prior to freezing of the soil. Each spring (1994–1997), fertilizers to supply 100, 22, 42 kg ha^{-1} of N, P, and K, respectively were broadcast over all paddocks. No herbicide was applied to the paddocks. By 1995 almost no alfalfa was present in the grazing treatments.

Grazing Treatments

Paddocks were grazed rotationally by yearling heifers from 1994 until 1997, with 3 grazing levels (GL) represented by different pre-grazing canopy heights. Canopy heights for grazing initiation were determined using the weighted disk method (Bransby et al. 1977). Target pre-grazing heights were 13, 17, and 26 cm for heavy, medium, and light grazing levels, respectively. These heights were used to maintain consistency of grazing treatments, not to predict pasture yield. Grazing parameters are given in Table 1. From 2 to 6 heifers were placed in a paddock at a time and left for a period of no more than 24 hours to bring forage mass down to a desired residual mass for each treatment.

Paddock Sampling.

Detailed sampling for grass productivity and C and N flow was carried out during 1995, 1996, and 1997 on meadow bromegrass paddocks. For randomization of sampling, a grid with 2 x 2 m cells was superimposed on each paddock, with the perimeter of the grid 1 m from the outside on each side of the paddock. Three loca-

Table 1. Grazing management parameters for grazing intensity levels averaged over 1995, 1996, and 1997.

Grazing level	First grazing	Grazing periods	Total animal days	Mean animal days	Mean rest period (days)
		---------(per season) --------		----------(per cycle)----------	
Heavy	28 May	5.3	27.9	5.3	20.3
Medium	01 June	4	16.0	4.0	23.3
Light	12 June	3	14.4	4.8	51.3

tions on the grid were chosen at random for each sampling period with the stipulation that each new sample area be at least 1 grid-square away from the one used in the previous harvest. Within a grid-square, 2 stakes were placed at random to mark sampling areas. Prior to and after grazing periods, a rectangular frame (25 x 50-cm) was placed with one corner against the marker stake and the herbage inside the frame was cut 2.5 cm above the soil surface. All of the harvested herbage from each paddock was bulked, weighed fresh and then subsampled for determination of dry matter, C, N, in vitro digestible organic matter (IVDOM), acid (ADF) and neutral detergent fiber (NDF), and lignin concentrations.

Leaf area index (LAI) was measured before and after grazing periods in 1995 and 1996 using a LAI-2000 plant canopy analyzer consisting of a LAI-2050 optical sensor (Li-Cor Ltd., Lincoln, Nebr.). Ten readings, taken at random, at least 1 m from the edge of each paddock were averaged by the instrument.

Chemical and Biological Composition

Herbage sub-samples (250 g), taken before and after grazing to be used for determination of dry matter concentration were weighed fresh and dried at 80º C for 72 hours. Similar sub-samples (250 g) taken before and after grazing to be used for determination of forage quality and C composition were dried at 50° C for 72 hours. These were ground, first through a Wiley mill (Model no. 4; Arthur H. Thomas Co., Philadelphia, Penn.) equipped with a 2-mm screen and then through a Cyclone mill (Model MS; UD Corporation, Boulder, Colo.) using a 1.0-mm screen, prior to quality determinations. The samples were analyzed for total N concentration by a micro-Kjeldahl technique (Wall and Gerke 1975) and an auto analyzer system (industrial method no. 786-86T. Bran & Luebbe INC, Tarrytown, N.Y., 10591-5097). Crude protein concentration was calculated as 6.25 x N concentration. In vitro digestible organic matter concentration (IVDOM) was measured with direct acidification during a 24 hour second stage pepsin digestion (Marten and Barnes 1980). Neutral detergent fiber, ADF and permanganate lignin (lignin) concentrations were determined sequentially (Van Soest and Robertson 1980). Total C was measured with a Leco Carbon Determinator (Model CN 2000, Leco Corp., St. Joseph, Mich.).

Derived Variables

Available herbage and residual yields were calculated for pre- and post-grazing, respectively. Seasonal pools of above ground productivity, disappearance and the vegetative component of the residual for dry matter, C, N, and IVDOM were determined by a method similar to that described by Singh et al. (1975) as:

$$AP = A_1 + \sum_{i=1}^{n} (A_{i+1} - R_{1}) \qquad \textbf{(1)}$$

$$DP = \sum_{i=1}^{n} (A_1 - R_1) \qquad \textbf{(2)}$$

$$VR = AP - DP \qquad \textbf{(3)}$$

where seasonal above ground productivity (1), disappearance (2), and vegetative residual (3) were calculated from A, available herbage mass, and R, residual, determined before and after each grazing period (i), respectively. Corresponding values for C, N, and IVDOM were determined by multiplying the C, N, and IVDOM concentration at each grazing period for available herbage and residue by the respective paddock dry matter yield and summing over the season as indicated for above ground productivity, disappearance, and vegetative residue.

Fecal C (which is deposited in the litter) was estimated by partitioning disappearance C into digested C and fecal C. Digested C was determined by multiplying the IVDOM concentration of herbage mass at each grazing period by the C disappearance from each grazing period. This was summed over the season as for disappearance. Then fecal C was the difference between disappearance C and digested C.

Excreted N of growing cattle was assumed to be 90% of N disappearance (Whitehead 1995). To partition N excreted in urine and fecal-N, percent N excreted in urine at each grazing period was estimated from the generalized equation below (Whitehead 1995):

$$\text{\% N excreted in urine} = 45 + 14\ \text{x}\ (\text{\%N in herbage mass} - 1.0) \qquad \textbf{(4)}$$

Urine N was estimated by multiplying the fraction times N disappearance for that grazing period, summing over grazing periods within the season. Fecal-N excreted was estimated by subtracting urine N from excreted N for the season.

Statistical Analyses

Data shown for LAI were analyzed as averages over grazing cycles within each paddock and year. Data for chemical and biological composition of available herbage (before grazing) and residual (after grazing) were analyzed statistically as weighted-means of all grazing periods within paddocks and years. Data were subjected to analysis of variance using the SAS GLM procedure (SAS Institute 1989) with a split-plot model. Grazing levels (GL) were main plot effects tested for significance using replication (GL) as the error term, years (repeated measures) were a subplot factor and the interactions were tested with the residual error (Steel and Torrie 1980). Where the F-test indicated a significant ($P \leq 0.05$) effect, means were separated by LSMEANS using the appropriate error mean squares (SAS Institute 1989).

Results and Discussion

Precipitation from April to October was high in all 3 years, ranging from 106% in 1996 to 146% above the long-term average (362 mm) in 1997, although intermittent dry periods occurred as in August of 1996. Long term average mean temperatures for June, July, August, and September are 13.6, 16.1, 16.0, and 14.6° C, respectively. Average mean temperatures for these months were usually average to below average during summers of all 3 years.

Productivity

Heavy, medium, and light grazing intensities were subjected to 5, 4 and 3 grazing periods, respectively per season (Table 1). Average rest periods for light were approximately 2.5 times longer than for heavy. Commercial intensive grazing operations in the area might graze 2 to 3 times and occasionally 4 times under conditions of high pasture growth, rainfall and soil fertil-

Table 2. Seasonal mean leaf area index before and after grazing meadow bromegrass pastures at 3 intensities averaged over grazing periods and 2 years (1995 and 1996).

	Grazing intensity Heavy	 Medium	 Light	 Mean
	($cm^2\ cm^{-2}$)			
Before grazing	3.07c[†]	3.53b	5.04a	3.88
After grazing	1.42a	1.46a	1.52a	1.47

[†] Within rows, values followed by the different letters are significantly different ($P \leq 0.05$) according to LSMEANS test in SAS (SAS 1989).

Table 3. Weighted mean concentrations of in vitro digestible organic matter, neutral detergent fiber, acid detergent fiber, lignin, and protein for available herbage and residual mass from meadow bromegrass pastures grazed at 3 intensities averaged over 3 years (1995, 1996, and 1997).

Grazing intensity	IVDOM[†]	NDF	ADF	Lignin	Protein
	Available Herbage (before grazing) ($g\ kg^{-1}$)				
Heavy	759a[‡]	474b	253b	33.2b	210a
Medium	710b	522a	284ab	37.0ab	182b
Light	688b	535a	301a	41.2a	168b
Mean	720	510	279	37.0	187
	Vegetative Residual (after grazing) ($g\ kg^{-1}$)				
Heavy	694a[‡]	502c	269c	56.7a	169a
Medium	685a	549b	300b	51.4a	164a
Light	650b	575a	322a	53.4a	152b
Mean	676	542	297	53.5	161

[†] IVDOM is in vitro digestible organic matter, NDF is neutral detergent fiber, and ADF is acid detergent fiber.

[‡] Within columns, values followed by different letters are significantly different ($P \leq 0.05$) according to LSMEANS test in SAS.

ity, which occurred in the current study.

Efficient pasture production has been reported on perennial ryegrass (*Lolium perenne* L.) pastures in Europe over a range of LAI between 2 and 4 $cm^2\ cm^{-2}$, when managed under continuous or rotational grazing (Lemaire and Chapman 1996). Despite higher than normal grazing intensities seasonal average LAI prior to grazing ranged from 3.0 to 5.0 $cm^2\ cm^{-2}$ for heavy to light grazing intensities (Table 2). There was no difference among grazing intensities for LAI after grazing. The LAI following grazing would not have been considered low by standards of other studies, where residual LAI were below 1.0 $cm^2\ cm^{-2}$ (Korte et al. 1982, Parsons et al. 1983).

The nutritional qualities of available herbage before and after grazing are shown in Table 3. Available herbage for heavy grazing had greater nutritional value than light for all parameters shown, while medium was intermediate. Also, medium and light grazing intensities were similar for all of these parameters. However, pre-grazing ADF and lignin for medium were similar to both light and heavy grazing treatments. With the exception of weighted-mean lignin concentration nutritive value of residue following grazing was higher for heavy than for light grazing. However, unlike available herbage, residue of the medium intensity had higher IVDOM and protein and lower NDF and ADF concentrations than light (Table 3). Nutritive values for heavy, medium and light intensities, based on weighted-means for available herbage could support average daily gains for growing steers of 1.03, 0.80 and 0.74 kg day^{-1} if consumption was as predicted from NDF concentration of the available forage (NRC 1996).

Above-ground productivity of the heavy and medium grazing treatments were 83% and 90% of the light grazing intensity, respectively for dry matter, and 87% and 90%, respectively for C (Table 4). Above ground productivity of IVDOM and N were similar among grazing intensities (Table 4). The C: N ratio of above ground production was higher for light than other grazing intensities (Table 4).

Magnitudes of above ground productivity of dry matter and C were remarkably close among grazing intensities, even though light and heavy intensities were significantly different ($P \leq 0.05$). The results were in general agreement with those of Parsons et al. (1983) who found shoot and gross photosynthesis increased from heavy to light grazing. Generally, gross production increases with increasing LAI (Lemaire and Chapman 1996). However, in Europe, dry matter production was relatively more efficient per unit LAI when swards were severely defoliated with short rest periods, than when allowed to attain a large LAI over rest periods longer than 20 days (Parsons et al. 1983, 1988, Parsons and Penning 1988).

The weighted mean above ground productivity for N and IVDOM reflect differences among treatments, where the higher N and IVDOM concentrations of the heavy grazing treatment compensate for a lower above ground production of dry matter, with the reverse apparent for the light grazing intensity (Table 3).

Disappearance

Disappearance of dry matter, C, and N, and the C: N ratio were similar among grazing intensities (Table 4). However, this was the result of seasonal utilization of above ground production of dry matter of approximately 83, 73, and 66% for heavy, medium, and light grazing treatments, respectively (data not shown). Ranges among grazing intensities for seasonal utilization of above ground production of N, C, and IVDOM were comparable. By contrast, IVDOM disappearance was significantly higher for heavy compared to light grazing intensity, with medium being intermediate. Parsons et al. (1983) observed greater intakes of dry matter from hard compared to leniently grazed treatments. Defoliation was more severe than in our current study.

Mean utilization rate for specific graz-

Table 4. Seasonal above ground productivity, disappearance and residual dry matter, in vitro digestible organic matter, C and N from meadow bromegrass pastures grazed at 3 intensities averaged over 3 years (1995, 1996, and 1997).

	Grazing intensity			
	Heavy	Medium	Light	Mean
	Above ground productivity ($kg\ ha^{-1}$)			
DM	5862b[†]	6355b	7034a	6399
IVDOM	4458a	4522a	4671a	4547
C	2668b	2746ab	3061a	2819
N	212a	217a	218a	216
C:N	12.6b	12.7b	14.0a	13.0
	Disappearance ($kg\ ha^{-1}$)			
DM	4891a	4661a	4645a	4735
IVDOM	3710a[†]	3302ab	3177b	3396
C	2327a	2102a	2103a	2177
N	182a	160a	159a	167
C:N	12.8a	13.1a	13.2a	13.0
	Vegetative Residual ($kg\ ha^{-1}$)			
DM	972c	1694b	2389a	1665
IVDOM	748b	1220a	1494a	1154
C	341c[†]	645b	958a	643
N	30.0b	57.6a	58.1a	48.6
C:N	11.4b	11.2b	16.5a	13.2

[†] Within rows, values followed by different letters are significantly different ($P \leq 0.05$) according to LSMEANS test in SAS.

DM is dry matter, IVDOM is in vitro digestible organic matter, C is carbon, and N is nitrogen.

Table 5. End of season residual dry matter, carbon (C) and nitrogen (N) mass and C:N ratio left in meadow bromegrass pastures subjected to 3 grazing intensities for 3 years (1995, 1996, and 1997).

	Grazing intensity			
	Heavy	Medium	Light	Mean
	Dry matter (kg ha^{-1})			
1995	452a	908a	1348a	902
1996	1095b†	3034a	2896a	2342
1997	492c	773b	1759a	1430
Mean	680	1572	2001	1558
	C (kg ha^{-1})			
1995	186b	364b	730a	427
1996	481b	1213a	955a	883
1997	260b	321b	864a	482
Mean	309	633	850	597
	N (kg ha^{-1})			
1995	12.9a	21.6a	30.7a	21.7
1996	26.3b	75.7a	62.8a	54.9
1997	11.4b	17.4b	43.1a	24.0
Mean	16.9	38.2	45.5	33.5
	C:N			
1995	14.4b	16.9b	23.8a	18.4
1996	18.3a	16.0b	15.2b	16.5
1997	22.8a	18.4b	20.0ab	20.4
Mean	18.5	17.1	19.7	18.4

†Within rows, values followed by different letters are significantly different ($P \leq 0.05$) according to LSMEANS test in SAS.

ing periods was highly variable (data not shown) over years and grazing intensities. Percent utilization per grazing period was 42% of available herbage dry matter when averaged over years, grazing intensities and grazing cycles. This utilization rate compared favorably with the 40–50% reported by Heitschmidt et al. (1987), although experimental set up was quite different from the current study. The former study found animal density did not consistently affect utilization of available herbage under rotational grazing systems. In the current study, greater grazing frequency for heavy and medium compared to light grazing harvested leaf material before it died and sceneced, resulting in relatively high seasonal dry matter disappearance. There was also little stem formation in these treatments.

Vegetative Component of Residual

Vegetative material moving directly to the litter was calculated from above ground productivity minus disappearance. Grazing intensity affected all fractions of vegetative residue significantly ($P \leq 0.05$), but not identically (Table 4). Vegetatitive residual dry matter, IVDOM, C, and N left after disappearance were 41, 50, 36, and 52% for the heavy compared to the light grazing intensity. One extra grazing cycle (medium) beyond normal (light) reduced dry matter and C residuals to 71% and 80% of the light intensity. Heavy grazing allowed only 13% of above ground production of C and 14% of above ground production of N to move directly to litter compared to 31% of above ground production of C and 27% of above ground production of N for light grazing.

Parsons et al. (1983) reported that reduced residue for hard compared to lenient grazing, was due to removal of a higher percentage of shoot material as it formed, resulting in no tissue death and little accumulation of stem material, which impeded grazing in the lenient grazing treatment. However, under semi-arid range conditions high vs. low stocking density had little impact on grazing efficiency (Heitshmidt et al. 1987).

Year-end residuals, estimated and actual (live and dead standing biomass), determined in the fall, were affected by year x GL interactions (Table 5). However, the same general trends with grazing intensity are evident in both residuals (Tables 4 and 5) for dry matter, C and N pools. Averaged over years, actual, year-end dry matter, C and N residuals (Table 5) are numerically smaller than estimated residuals (Table 4). Heavy grazing dry matter, C and N residues were proportionately smaller than medium and light grazing intensities. Three-year average, actual, year-end residues (Table 5) ranged from 89 to 98 % for C, 69 to 92% for dry matter and 56 to 78% for N compared to estimated counterparts (Table 4). Reasons for differences between estimated and actual residuals are speculative. Error in measurement or estimation of residuals is acknowledged and may have been high. There is evidence in the literature (Wedin 1996, Lemaire and Chapman 1996) to indicate that plant materials of the nature (i.e. high N concentration and narrow C: N ratio) found in the heavily grazed residue may mineralize rapidly. However, there is no certainty that this was the cause for discrepancy between actual and estimated residual pools for the heavy grazing treatment in this study.

Residues from Animal Waste

Animal wastes were not measured directly, but estimates are important because urine and feces are components of C and N flow to litter and soil in a more mineralized form than vegetative material and cycle more rapidly than vegetative material (McGill et al. 1981, Lemaire and Chapman 1996, Wedin 1996). Estimated fecal-C was not affected by grazing intensity. Estimated fecal-C represented 68, 51, and 42% of all residual-C flowing back to litter and soil for heavy, medium, and light grazing intensities respectively, not including root and below ground litter material. However when estimated fecal-C was added to vegetative residue, grazing intensities were significantly different from one another for total residual-C (Table 6). Adding estimated fecal-C to the vegetative residue substantially increased C deposition to the litter. For example, considering only the vegetative residual component, C-inputs to the litter from the heavy and medium grazing intensities were 36 and 67% of the light grazing intensity, respectively. Addition of fecal-C to vegetative residual-C increased C-

Table 6. Estimated annual digested, fecal and residual plus fecal-C from meadow bromegrass pastures grazed at 3 intensities averaged over 3 years (1995, 1996, and 1997).

	Grazing intensity			
	Heavy	Medium	Light	Mean
	(kg ha^{-1})			
Digested-C	1602a	1432b	1419b	1484
Fecal-C	725a	669a	684a	693
Residue + fecal-C	1066c	1314b	1626a	1336

†Within rows, values followed by different letters are significantly different ($P \leq 0.05$) according to LSMEANS test in SAS.

Table 7. Estimates of total annual consumed, excreted and excreted plus residual-N and percentage of excreted-N in urine from meadow bromegrass pastures grazed at 3 intensities averaged across 3 years.

	Grazing intensity			
	Heavy	Medium	Light	Mean
	($kg\ ha^{-1}$)			
Consumed-N	176a	180a	179a	178
Excreted-N	149a	153a	152a	151
Vegetative residue plus excreted N	179a	211a	210a	200
Urinary-N	104a	101a	96a	101
Fecal-N	45a	52a	56a	51
% excreted N in urine	71.2a	64.8b	61.7b	65.9

[†] Within rows, values followed by different letters are significantly different ($P \leq 0.05$) according to LSMEANS test in SAS.

inputs to the litter from the heavy and medium grazing intensities to 66% and 80% of the light grazing intensity, respectively. Increasing grazing cycles beyond 3 resulted in the majority of C deposited to litter as mineralized vs. vegetative.

The literature varies as to percentage of N retained by beef animals. Values range from 5 to 15% for growing animals (Whitehead 1995, Mathews et al. 1996) up to 25% for lactating cows (Whitehead 1995, Mathews et al. 1996). Excreted-N was estimated using a factor of 10% retention by the animal (Whitehead 1995). All categories of N totaled were similar across grazing intensities, except for percent N excreted as urine (Table 7). In the latter case, heavy had higher values than medium and light grazing intensities reflecting higher protein concentrations in available forage for heavy relative to the other grazing intensities (Table 3). Amounts of urine-N excreted per acre would have been double fecal-N. This could affect loss of N as loss of urinary N through volatilization is much greater than fecal-N and dependent on environmental conditions (Whitehead 1995). The proportion of total N returned to the paddock by excretion was 83% for heavy, compared to 73% and 72% for medium and light grazing, respectively. Because excreted N is in more mineralized form than vegetative N, the rate of N cycling through the soil-plant-animal system would likely be greater for the heavy grazing treatment compared to the medium and light treatments.

Summary

The flow of C and N from sward to litter is dictated by the size of above ground productivity and it's partitioning into disappearance, vegetative and animal waste residual products. We hypothesized that the size of above ground productivity, disappearance and vegetative residue would be reduced proportionately as grazing intensity increased. This did not occur. The size of above ground productivity was reduced significantly ($P < 0.05$), but only slightly when meadow bromegrass was exposed to heavy vs. light (5 vs. 3 cycles per season) grazing intensities; disappearance was not reduced by grazing intensity. The consequence was that the vegetative residual component was reduced proportionately more than above ground productivity from light to heavy grazing. In concert with disappearance, fecal-C did not vary with grazing intensity, but when added to vegetative residual-C increased total residual-C substantially. Fecal-C represented a much higher percentage of the total residual-C in the heavy (68%) than in the light (42%) grazing intensity. Percent N, excreted as urine, was higher for heavy than for light grazing. Also the residue ligno-cellulose (ADF) concentration was lower, IVDOM and protein concentrations higher for heavy and medium than light grazing. It is generally accepted that vegetative materials, which move directly to litter degrade and recycle nutrients more slowly than materials that have passed through ruminants on pasture (Briske and Heitschmidt 1991, Holland et al 1992, Haynes and Williams 1993, Whitehead 1995, Lemaire and Chapman 1996, Wedin 1996). Thus, grazing intensity could have large implications to sustainability and productivity in intensive pastures systems in a short-season area.

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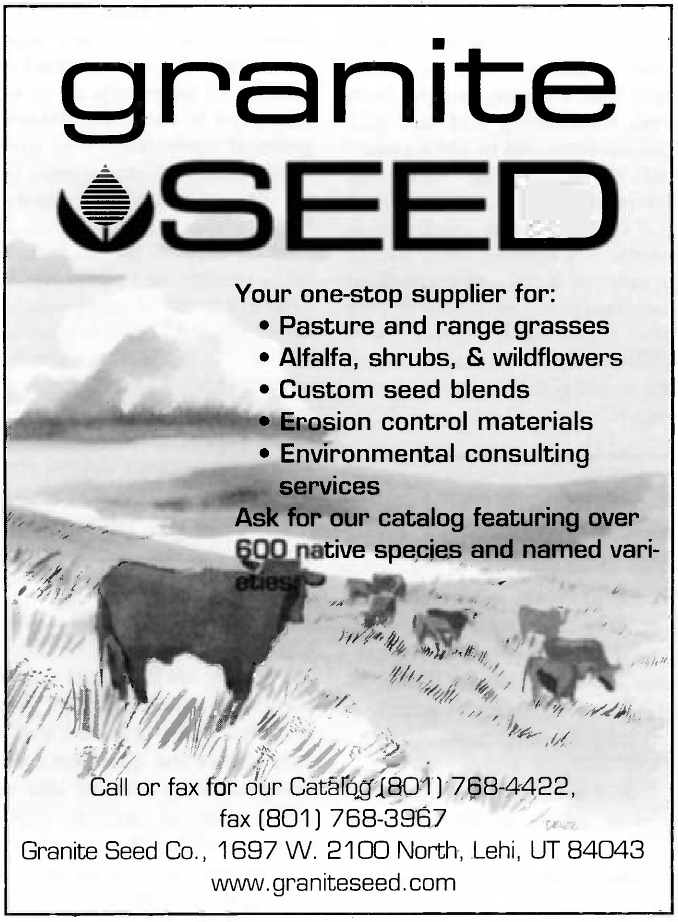

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Stocking rate and cow-calf production on sand sagebrush rangeland

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Abstract

Stocking rate is generally considered to be the most important management factor in sustainable grazing of Great Plains grasslands over management periods of 10 to 20 years or longer. Most studies to determine optimum stocking rates have compared only 2 or 3 discrete stocking rates. Our objective was to determine cow, calf, and economic performance on sand sagebrush (*Artemisia filifolia* Torr.) rangeland as a continuous function of stocking rate. Replicated stocking rates of 0.11, 0.15, and 0.22 head ha^{-1} were studied over an 8-year period. Cow weight declined as stocking rate increased in drought years but was not affected by stocking rate in wetter years. Weaning percentage was not affected by stocking rate but variation within treatment groups was high. Calf birth weight and weaning weight both declined as stocking rate increased. Comparing 0.11 and 0.22 head ha^{-1}, calf production cow^{-1} declined from 206 to 144 kg cow^{-1} as stocking rate increased but calf production ha^{-1} increased from 22.6 to 31.7 kg calf ha^{-1}. Net returns were maximized at \$7.87 ha^{-1} year^{-1} at a stocking rate of 0.172 head ha^{-1}, well within the range of experimental treatments. Net returns were within 5% of maximum between stocking rates of 0.156 and 0.183 head ha^{-1}. The variability of all responses increased as stocking rate increased. Simulation indicated that improved livestock prices and increased animal productivity shifted the economic optimum stocking rate to higher levels, which would put more pressure on the conservation ethic of land managers.

Key Words: *Artemisia filifolia*, mixed prairie, Southern Plains, animal performance, optimum stocking rate

Resumen

La carga animal generalmente es considerada el factor de manejo más importante del apacentamiento sustentable de los pastizales de las Grandes Planicies en periodos de manejo de 10 a 20 años o más. La mayoría de estudios para determinar la carga animal óptima han comparado solo 2 o 3 cargas animal discretas. Nuestro objetivo fue determinar el comportamiento económico de vacas y becerros en un pastizal de "Sand sagebrush" (*Artemisia filifolia* Torr.) Como una función continua de la carga animal. Durante un periodo de 8 años se estudiaron cargas animal repetidas de 0.11, 0.15, y 0.22 cabezas ha^{-1}. En años secos el peso de la vaca disminuyó conforme se incrementó la carga animal, pero en años húmedos no fue afectado por la carga animal. El porcentaje de destete no fue afectado por la carga animal pero la variación dentro de los tratamientos fue alta. Los pesos al nacimiento y al destete disminuyeron al aumentar la carga animal. Comparando las cargas de 0.11 y 0.22 cabezas ha^{-1} se observó que al aumentar la carga animal la producción de becerro vaca^{-1} disminuyó de 206 a 144 kg vaca^{-1}, pero la producción de becerro ha^{-1} se incrementó de 22.6 a 31.7 kg de becerro ha^{-1}. Dentro del rango de tratamientos experimentales, los retornos netos se maximizaron a \$ 7.87 ha^{-1} año^{-1} con una carga animal de 0.172 cabezas ha^{-1}. Los retornos netos estuvieron dentro de 5% del máximo entre las cargas animal de 0.156 y 0.183 cabezas ha^{-1}. La variabilidad de todas las respuestas se incrementó al aumentar la carga animal. La simulación indicó que mejores precios del ganado y una mayor la productividad animal desviaron la carga animal óptima económica a niveles mas altos, los cuales pondrían mayor presión en la conservación ética de los manejadores de tierras.

Stocking rate is generally considered to be the most important management factor in sustainable grazing of Great Plains grasslands over management periods of 10 to 20 years or longer. Numerous studies have reported the impact of stocking rate on livestock production. Weight gain of individual animals generally decreases while weight gain per unit land area increases as stocking rate increases (Vallentine 1990).

While some studies have used 2 or 4 levels of stocking rate (Heitschmidt et al. 1982, Willms et al. 1986), most studies on stocking rates have used 3 stocking rates, often qualitatively described as light, moderate, or heavy grazing. Quantitative stocking rates for each of these qualitative levels vary among regions depending on climate and soils. Moderate stocking rates are usually set at a level estimated to maintain populations of the dominant perennial forage grasses while light and heavy rates are set at some factor below and above moderate grazing. The common use of the qualitative descriptions of light, moderate, and heavy stocking does not take advantage of the continuous, quantitative nature of stocking rates. Development of continuous functions describing the impact of stocking rates on livestock production would allow inferences to be made at stocking rates other than those actually tested in the experiments and is a requirement for conclusive economic analyses (Bransby 1989).

The first objective of this study was to determine the impact of stocking rate as a continuous function on the biological performance of cows and calves grazing sand sagebrush rangeland in the Southern Great Plains. The second objective was to determine

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the response of net returns to stocking rate and to determine the stocking rate that maximized net returns per unit land area. Partial results of this study were first reported by Shoop and McIlvain (1971). This follow-up paper gives a more complete presentation of the results and uses a continuous function for stocking rate rather than only 2 discrete stocking rates.

Materials and Methods

Experimental Pastures

The study was conducted from 1952 through 1961 at the USDA-ARS Southern Plains Experimental Range in northwest Oklahoma (36° 35'N, 99° 35'W, elev. 630 m). The regional climate is continental. Average annual precipitation is 576 mm with 72% falling during the April–September growing season. Average monthly temperature is 2.3°C in January and 28°C in July. Minimum and maximum recorded temperatures are –28°C and 45°C.

Two distinct precipitation periods occurred during the study (Fig. 1). The first 4 years, 1953 to 1956, were characterized by drought. Over this period, annual, winter, and summer precipitation averaged 65, 45, and 74% of the 60-year average (1940 to 2000), respectively. The remaining 5 years received abundant precipitation. Annual and summer precipitation was 110 and 126% of the 60-year average in these later years.

The landscape of the study area consists of undulating, stabilized sand dunes without well-defined drainage patterns. Soils were Pratt loamy fine sands (sandy, mixed thermic Psammentic Haplustalfs) on the lower slopes and more level areas and Tivoli fine sands (mixed, thermic Typic Ustipsamments) on the upper slopes of the dunes. The vegetation was sand sagebrush (*Artemisia filifolia* Torr.)-mixed prairie (Berg 1994). The understory was dominated by a mixture of tall, mid, and short warm-season grasses including sand bluestem [*Andropogon halli* Hack.], little bluestem [*Schizachy-rium scoparium* (Michx.) Nash], sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], and blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths]. Western ragweed (*Ambrosia psilostachya* DC.), camphor weed [*Heterotheca subaxillaris* (Lam.) Britt. & Rusby], and wooly plantain (*Plantago patagonica* Jacq.) were prominent forbs.

Experimental Treatments

This experiment was a continuation of a study initiated in 1942 (Sims and Gillen 1999). The experimental treatments were 3 stocking rates of yearling beef cattle. Stocking levels were 41, 53, and 82 animal-unit-days ha^{-1} (AUD ha^{-1}) over a 320-day grazing season. These stocking rates were selected to bracket the projected sustainable stocking rate for this vegetation type. In 1952 after 10 years of grazing, the livestock class was shifted from yearling cattle to cows and calves. Relative stocking rate treatments were maintained in the respective study pastures but the grazing season was expanded to year-long grazing. Stocking rates in this second phase of the experiment were 45, 60, and 87 animal-unit-days ha^{-1}, an average increase of 9% over the first phase.

A multi-step process was used to calculate the animal unit equivalents in the second phase of the study. First, winter cow weights were calculated by averaging October and April weights. Winter animal-unit-days were then calculated as (winter weight$^{0.75}$/454$^{0.75}$)*winter days (Vallentine 1990). Summer cow weights were calculated by averaging April weights and the weights from the following October. Summer animal-unit-days were then calculated as (summer weight$^{0.75}$/454$^{0.75}$)*summer days*1.35. The factor 1.35 was used to account for greater forage intake when the cow was in lactation and had a grazing calf (Vallentine 1990). Winter and summer AUD's were then summed within a production year (October to October) to arrive at annual AUD's.

The expression of stocking rates as AUD ha^{-1} was necessary to compare stocking rates in the 2 phases of the study since the livestock class was different between phases. However, within a given livestock class it is often more practical to express stocking rates as head ha^{-1} (or ha head^{-1}) and economic analyses are conducted on a per head basis since that is the unit of production and sale. Throughout the remainder of this paper, stocking rates will be expressed as head ha^{-1}. For conversion purposes, each cow-year averaged 408, 404, and 392 AUD for the 45, 60, and 87 AUD ha^{-1} treatments. This resulted in experimental treatments of 0.11, 0.15, and 0.22 head ha^{-1}.

The 3 stocking rate treatments were replicated 2 times for a total of 6 experimental pastures. Both herd size and pasture area were varied to produce the stocking rate treatments. Pastures ranged in size from 43 to 86 ha. All study pastures were contiguous. Herd sizes were initially either 12 or 14 head. Maturation of the cows and drought conditions in the first years of the cow-calf study caused the herd sizes to be reduced from the initial levels. The herds consisted of 10 or 12 head in 1954 and 1955, 8 head in 1956 and 1957, and 9 head from 1958 to 1961. Stocking rates were adjusted over years in an effort to maintain a target forage utilization of 67% at the middle stocking rate at the end of each grazing year, approximately April 20 (Shoop and McIlvain 1971). Livestock numbers were adjusted in all of the treatments to maintain constant treatment ratios.

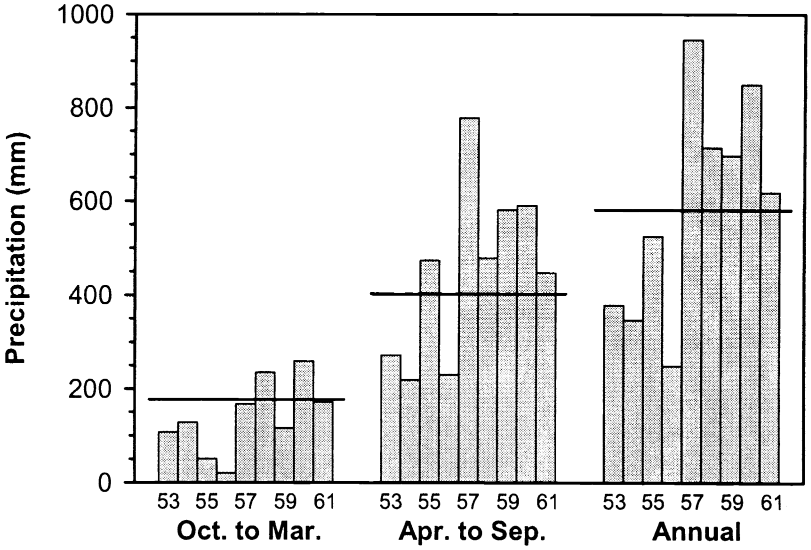

Fig. 1. Seasonal and annual precipitation (mm) from 1953 to 1961 and the long-term averages (1940–1996, straight lines) for each season at the Southern Plains Experimental Range, Fort Supply, Okla.

Livestock Management

The cows used in this study were purchased as weaned heifer calves out of a single commercial herd of Hereford cattle in October 1951. The heifers were vaccinated for blackleg (*Clostridia chauvoei*), malignant edema (*C. septicum*), and brucellosis (*Brucella abortus*) at weaning. The heifers were first allocated to treatment groups on the basis of weight and condition in November 1951. Each group contained 18 heifers with an average weight of 202 kg. During their first winter, the heifers were fed pelleted cottonseed meal containing 41% crude protein at a rate of 0.68 kg head^{-1} day^{-1} from 17 November 1951 until 21 April 1952. They were also fed rolled sorghum grain [*Sorghum bicolor* (L.) Moench] from 11 December 1951 until 9 April 1952 at a rate of 0.9 kg head^{-1} day^{-1}. The heifers were first bred from 10 June until 12 August 1952. Weight at first breeding averaged 302, 298, and 283 kg for the respective treatments. In November 1952, excess heifers were culled leaving either 12 or 14 heifers in each treatment group to begin the main body of the experiment.

The breeding season began on 15 May in 1953 and 30 April to 4 May the remaining years. The length of the breeding season ranged from 65 to 89 days with an average of 72 days. This resulted in calving seasons starting on 24 February in 1954 and 9 February to 13 February the remaining years. Breeding was done by natural service using Hereford bulls. Within stocking rate treatment, cows were gathered into a single herd during the breeding season and moved back and forth between replications at 1 or 2 week intervals. Grazing days were balanced between replications. A single bull was placed with each cow group. Bulls were rotated among all treatment groups every 2 to 3 days. One set of bulls was used from 1952 until 1957 when they were replaced by a new set for the remainder of the study. The bull:cow ratio ranged from 1:25 in 1952 to 1:18 in 1961 as cow stocking rates were reduced over the term of the study.

During the dormant forage period, cows were routinely fed supplemental protein in the form of pelleted cottonseed meal containing 41% crude protein. Rate of feeding was 0.91 kg head^{-1} day^{-1} from 1953 to 1955 and in 1960 and 0.68 kg head^{-1} day^{-1} for the other years. Average dates to start and end feeding were 18 November and 24 April, respectively, for a total feeding period of 162 days. There were 2 exceptions to the routine program and both were due to drought conditions and a shortage of standing forage. First, dormant season feeding began on 28 September for the 1955–56 production year. Second, pelleted cottonseed meal was fed at a rate of 0.91 kg head^{-1} day^{-1} from 11 June to 13 July 1956.

Cows were not routinely fed hay or other roughage. Cows were fed hay for 4, 1, and 9 days in the late winters of 1955, 1957, and 1960, respectively, due to snow cover or cold temperatures. There were 2 major exceptions to this program. First, alfalfa (*Medicago sativa* L.) hay was fed at a rate of 2.3 kg head^{-1} day^{-1} to all cows from 2 March until 18 April 1953. This was just prior to and during their first calving season. Second, alfalfa hay was fed from 4 February to 29 April 1955 in response to drought conditions. The feeding rate was 0, 2.3, and 4.5 kg head^{-1} day^{-1} for cows stocked at 0.11, 0.15, and 0.22 head ha^{-1}, respectively. The differential feeding rates were based on ocular assessments of pasture and livestock conditions. The cows received no other supplements except white block salt which was available free-choice at all times.

Cows remained in a given treatment group for the length of the study. Cows were only replaced if they had to be culled due to injury or if they died. Replacements were taken from cows of similar age and breeding maintained on reserve pastures stocked at the same rates as the treatment pastures.

Cows were weighed at monthly intervals year-round. Weights were taken in early morning after an overnight fast from forage and water. Cows were checked daily during the calving season. Calves were weighed and ear-tagged shortly after birth. At the first weigh date following the close of the calving season, usually in April, calves were hot-branded, dehorned, and vaccinated for blackleg and malignant edema. Male calves were castrated. Calves were then weighed at monthly intervals with the cows until weaning in mid October.

Dates chosen for analysis of cow weights were January (just prior to calving), April (just after calving), August (late growing season), and October (weaning). Calf performance was analyzed using birth and weaning weights.

Statistical methods

The general statistical model used in the analysis was a completely randomized, repeated measures design with stocking rate as the whole plot factor and year as the repeated factor. The stocking rate effect was tested with the pasture-within-stocking-rate error term. Year and stocking rate by year interactions were tested with the residual error term. If the stocking rate by year interaction was significant ($P < 0.05$), analyses were conducted for individual years. Dependent variables were related to stocking rate (head ha^{-1}) by linear regression within year using pasture means as observations. In addition, response data were averaged over years and related to stocking rate by linear regression. Dependent variables included cow weight, weaning percentage, calf birth weight, calf gain, calf weaning weight, calf weaned cow^{-1}, and calf weaned ha^{-1}. Weaning percentage data were transformed using the arcsin transformation before analysis.

To assess the variability of responses, we calculated standard deviations and coefficients of variation for all dependent variables over years. These standard deviations and coefficients of variation were than regressed against stocking rate.

An excess of heifers were bred in 1952 and then culled to arrive at the target group size within treatments. It is not clear from experimental records but it is likely that pregnancy was a criterion for culling since weaning percentage in 1953, the first year of calving, was 100% for all treatments. This may confound the calf production data from this first year so analysis of all treatment responses except cow weight were restricted to the years 1954 to 1961.

Economic methods

The main objective of the economic analysis was to relate net economic returns to stocking rate. A spreadsheet model was developed to calculate net return ha^{-1} based on various input costs, livestock prices, and levels of calf production.

Input costs were entered as total variable costs per cow other than pasture or feed, pasture rental, and supplemental feed and hay. Total non-feed costs were set at $216 cow^{-1} based on data from the Standardized Performance Analysis of 253 cow herds in Texas from 1991 to 1999 (McGrann et al. 2000). Cost of supplemental feed and hay was based on actual feeding rate during the study and a cost of $0.22 kg^{-1} for supplement and $0.067 kg^{-1} for hay. Land costs were set at $16.70 ha^{-1}, the average rental rate for rangeland in this region in 1998 (Doye et al. 1999).

Livestock prices were actual prices from the Oklahoma City National Stockyards (Peel 1996a, 1996b) from the period 1986 to 1995 to encompass a complete price cycle. Prices were indexed to 1995 dollars using the Consumer Price Index. The relationship between calf weight and price kg^{-1} was determined for each year for both steers and heifers using linear regression. Calf weaning weight and weaning percentage over a continuous range of stocking rates were predicted using regression equations developed from the statistical analyses.

Economic returns were calculated as:

$$\text{Gross income cow}^{-1} = (((\text{weaning weight}_s * \text{price kg}^{-1}{}_s) + (\text{weaning weight}_h * \text{price kg}^{-1}{}_h)) / 2) * (\text{weaning \%}/100), \quad (1)$$

where the subscripts s and h refer to steer and heifer, respectively. This assumes a 50:50 ratio between steers and heifers.

Input costs were calculated as:

$$\text{Cost cow}^{-1} = \text{variable cost cow}^{-1} + (\text{ha cow}^{-1} * \text{land cost ha}^{-1}) + (\text{kg supplement cow}^{-1} * \text{supplement cost kg}^{-1}) + (\text{kg hay cow}^{-1} * \text{hay cost kg}^{-1}). \quad (2)$$

Net returns were calculated as:

$$\text{Net return cow}^{-1} = \text{Gross income cow}^{-1} - \text{cost cow}^{-1}. \quad (3)$$

$$\text{Net return ha}^{-1} = \text{net return cow}^{-1}/\text{ha cow}^{-1} \quad (4)$$

Variability in calf prices and calf production were incorporated into the model using the @RISK simulation program[1] (Palisade Software, Newfield, N.Y.). Regression parameters (intercepts and slope coefficients) for prices, weaning percentage, and weaning weight were assumed to be randomly distributed with standard deviations determined from the statistical analyses. Coefficients for weaning percentage and weaning weight were drawn randomly and independently from these distributions for each iteration of the model. Coefficients for steer and heifer prices were linked through the use of correlation coefficients. A different starting point in the cattle price cycle (1986 to 1995) was chosen randomly for each iteration. Once a starting point was determined, prices from consecutive years were used to maintain the general shape of the cycle. This process was repeated for 1,000 iterations. The model calculated net returns for each individual year and then averaged these net returns over the 8-year term of the study. The mean and standard deviation for net return ha^{-1} were then graphed by stocking rate.

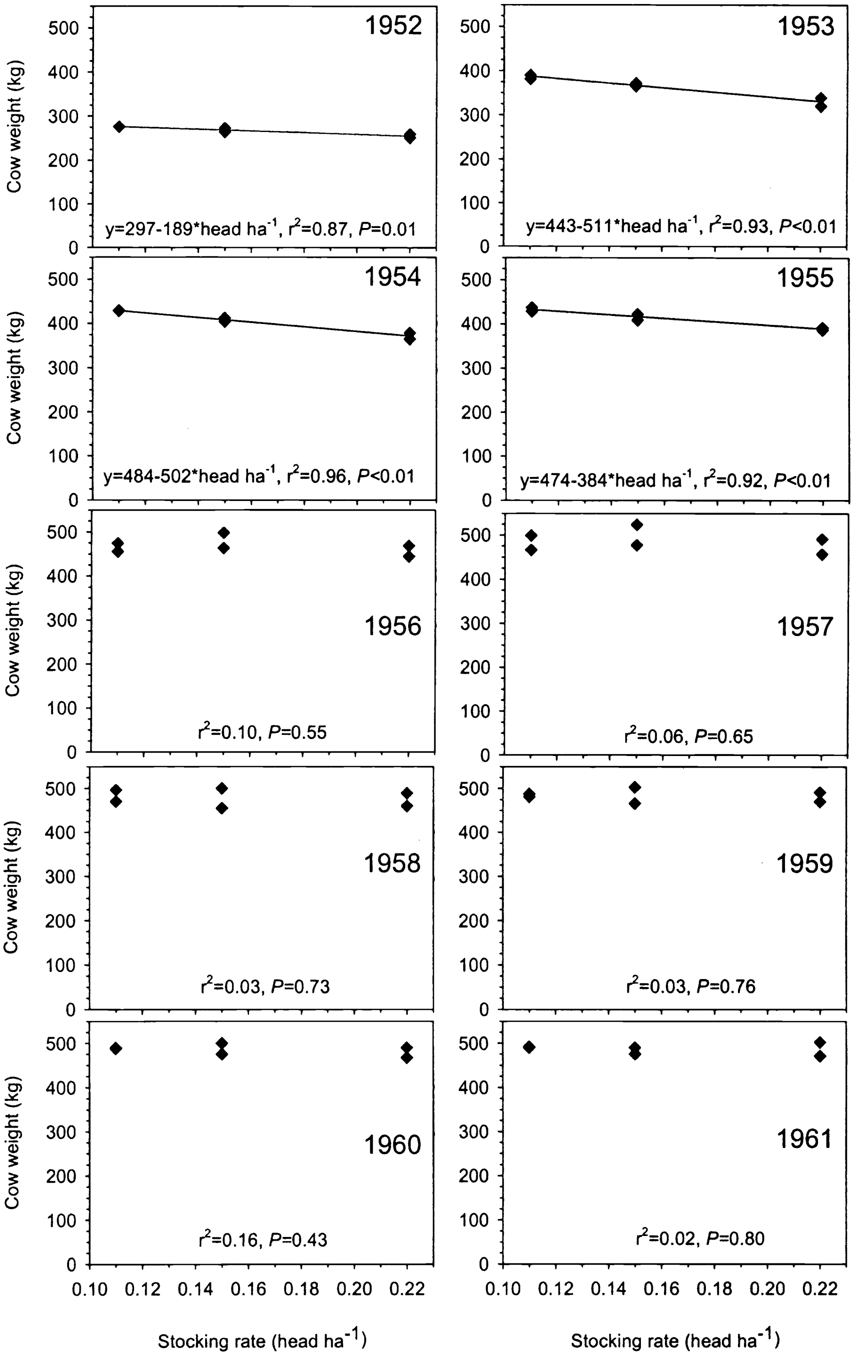

Fig. 2. Average annual cow weight (kg) as affected by stocking rate and year. Regression models only shown for years with significant relationships (P < 0.05).

An alternative analysis was performed in which price and calf production data were first averaged over the 8 years of the study. Single regression equations for price and production were fit to these data. Means and standard deviations for the regression coefficients were entered into the model. The simulation was then repeated for 1,000 iterations and results were graphed.

Finally, the economic model was analyzed for sensitivity to changes of ± 5, 10, or 15% in calf prices, variable cow costs, land costs, and calf production cow^{-1}. Calf prices were varied by changing the intercepts of the regression equations but not the slope coefficients. Calf production was varied by changing the intercepts of the regression equations for weaning percentage or weaning weight. Changing equations for either variable, weaning percentage or weaning weight, gave equivalent results so we discuss changes in calf pro-

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[1] Names are necessary to report factually on available data, however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

Table 1. Weaned calf crop (%) as affected by stocking rate (AUD ha^{-1}) and year.

Stocking rate	1954	1955	1956	1957	1958	1959	1960	1961	Average
(AUD ha^{-1})					(%)				
45	76.5	95.0	80.0	94.0	83.5	83.5	70.0	89.0	84.6
	(9.2)1	(7.1)	(0.0)	(8.5)	(7.8)	(7.8)	(0.0)	(0.0)	(8.8)
60	82.5	91.5	70.0	87.5	94.5	89.0	90.0	94.5	88.1
	(10.6)	(12.2)	(14.1)	(17.7)	(7.8)	(0.0)	(0.0)	(7.8)	(11.4)
87	69.0	74.0	55.0	87.5	89.0	89.0	60.0	72.5	77.1
	(15.6)	(22.7)	(7.1)	(17.7)	(15.6)	(0.0)	(0.0)	(7.8)	(14.4)
Average	76.02	86.8	70.0	89.7	89.0	89.0	78.3	87.2	
	(11.2)	(15.6)	(11.0)	(12.3)	(9.8)	(7.0)	(11.7)	(8.3)	

[1] standard deviation

[2] LSD.05 for year = 12.3; Stocking rate effect non-significant, P = 0.11; Stocking rate by Year effect non-significant, P = 0.44.

duction without specifying whether they are due to changes in weaning percentage or weaning weight.

Results and Discussion

Cow Weights

The cows entered this study as yearling heifers in November 1951. At that time, body weights were 203, 202, and 202 kg for the 0.11, 0.15, and 0.22 head ha^{-1} stocking rate treatments, respectively. By April 1952, weights were different among treatments and inversely related to stocking rate (slope coefficient –1.69, $r^2 = 0.85$, $P < 0.01$). Annual average cow weights for the remainder of the study were affected by the interaction of stocking rate and year ($P < 0.01$, Fig. 2). Average cow weights declined as stocking rate increased for only the first 4 years (Fig. 2). Annual cow weights were similar among stocking rates by 1956 and were not affected by stocking rate through the end of the study (Fig. 2). Within the early years, treatment effects were largest in January and smallest in August and October. Over all treatments, the cows gained weight until they were 5 years old in 1956. Annual average weights fluctuated little the remainder of the study and ranged from 467 to 487 kg.

Previous studies have generally reported a negative effect of stocking rate on cow weight (Lewis et al. 1956, Houston and Woodward 1966, Hughes 1974, Pearson and Whittaker 1974, Heitschmidt et al. 1982, Willms et al. 1986). In these studies, the reduction in cow weight between the heaviest and the lightest stocking rate has ranged from 11 to 45 kg. Huston et al. (1993) reported no effect of stocking rate on annual average cow weights but as stocking rate increased cows lost more weight in winter and gained more weight in summer. Heitschmidt et al. (1990) found no difference between cow weights under moderate and heavy stocking rates over 6 years. In the current study, stocking rate reduced the weights of young cows in dry years but did not affect mature cows in years with above-average precipitation.

Weaning Percentage

The weaned calf crop was variable among stocking rates and years (Table 1). There was no detectable effect of stocking rate on weaning percentage and no stocking rate by year interaction. Year had a significant effect with the lowest weaning percentage, 70%, in 1956 and the highest weaning percentage, 89.7%, in 1957 (Table 1). In the Northern Great Plains, weaning percentage declined with stocking rate (Houston and Woodward 1966). Heitschmidt et al. (1982) and Winder et al. (2000) reported interactions of weaning percentage and year in that higher stocking rates only decreased weaning percentage in drought years. Other studies have reported no impact of stocking rate on weaning percentage (Hughes 1974, Heitschmidt et al. 1990, Pieper et al. 1991).

In the current study, standard deviations were often high within stocking rates (Table 1). This was a result of the low numbers of cows within treatment groups, 8 to 14 depending on treatment and year. One cow failing to wean a calf produced a large change in weaning percentage. The large within-group variation resulted in low statistical power for weaning percentage.

Birth Weight

Calf birth weights were lowest in 1954 with an average of 32.8 kg and highest in 1957 with an average of 36.2 kg. Birth weight declined as stocking rate increased (Fig. 3, $P = 0.01$). Calves at the heaviest stocking rate of 0.22 head ha^{-1} averaged 32.8 kg at birth while calves at the lightest stocking rate of 0.11 head ha^{-1} averaged 35.9 kg at birth. There was no interaction between stocking rate and year ($P = 0.42$).

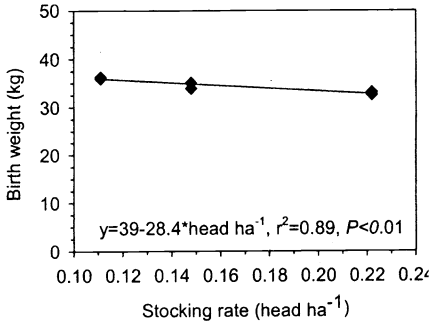

Fig. 3. Birth weight of calves (kg) as affected by stocking rate averaged over year. There was no stocking rate by year interaction (P = 0.42).

The response of birth weight to stocking rate was mixed in other studies. In the Northern Great Plains, birth weights were not affected by stocking rates over 8 years (Woolfolk and Knapp 1949). In the next 9-year period of the same study, birth weights declined 4.1 kg from the lowest to the highest stocking rate (Houston and Woodward 1966). A similar pattern was reported from South Dakota where birth weights were not affected for the first 10 years (Johnson et al. 1951) but declined as stocking rate increased in the following 6 years. In both cases, the vegetation changed dramatically over time and the delayed response of calf birth weight may have been a reflection of the vegetation change. On southern forest range, Hughes (1974) found stocking rate did not affect birth weight.

Weaning Weight

Calf weaning weight, averaged over all stocking rates, ranged from a low of 172 kg in 1954 to highs of 235 kg in both 1957 and 1958. Weaning weight was affected by the interaction of stocking rate and year ($P = 0.01$, Fig. 4). In 6 of 8 years, weaning weight declined as stocking rate increased. In most previous studies, calf weaning weights have consistently declined as stocking rates increased (Woolfolk and Knapp 1949, Johnson et al. 1951, Lewis et al. 1956, Houston and Woodward 1966, Hughes 1974, Pearson and Whitaker 1974, Heitschmidt et al. 1982, Pieper et al. 1991). However, Heitschmidt et al. (1990) and Huston et al. (1993) reported no effect of stocking rate on calf weaning weight.

The negative effect of stocking rate was more pronounced in the drought years, 1954 to 1956 (Shoop and McIlvain 1971).

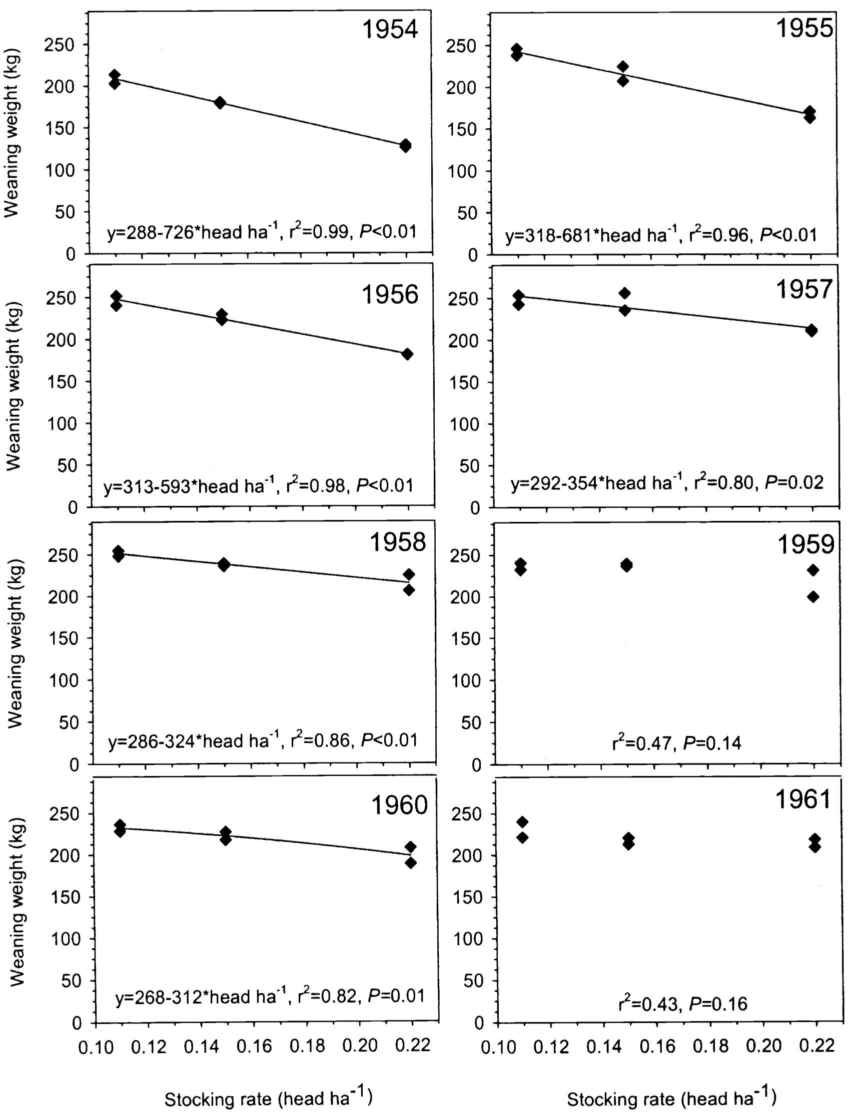

Fig. 4. Weaning weight of calves (kg) as affected by stocking rate and year. Regression models only shown for years with significant relationships (P < 0.05).

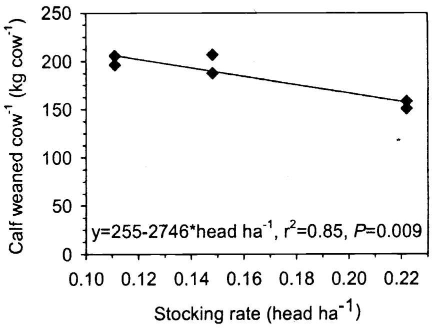

Fig. 5. Calf production cow^{-1} (kg cow^{-1}) as affected by stocking rate averaged over year. There was no stocking rate by year interaction (P = 0.25).

The average slope coefficient relating weaning weight and stocking rate (head ha^{-1}) in non-drought years was –268.8 but in drought years this coefficient was –667.0 (P = 0.01 for non-drought versus drought years). In non-drought years, the difference in weaning weight between a moderate stocking rate of 0.15 head ha^{-1} and a heavy stocking rate of 0.22 head ha^{-1} was 20 kg. In drought years, this same difference was 60 kg. Alternatively, drought reduced weaning weight by 23 kg at 0.15 head ha^{-1} but drought reduced weaning weight by 53 kg at 0.22 head ha^{-1}.

Calf weaning weight is a function of both birth weight and rate of gain. The majority of the decline in weaning weight in this study was attributable to decreased rate of gain because birth weights only varied by 3 kg from between stocking rates of 0.11 head ha^{-1} and 0.22 head ha^{-1} and age at weaning was similar among treatments.

Calf Production

Calf production per cow was affected by year (P < 0.01) and ranged from 132 kg cow^{-1} in 1954 to 210 kg cow^{-1} in 1957, when averaged over stocking rates. Calf production per cow declined as stocking rate increased (P = 0.03, Fig. 5). There was no interaction between stocking rate and year (P = 0.25). Houston and Woodward (1966) reported that calf production declined from 174 to 98 kg cow^{-1} as stocking rate increased from 0.048 head ha^{-1} to 0.084 head ha^{-1}. The effect of stocking rate on calf production cow per cow is not always this large. Heitschmidt et al. (1982) found that calf production declined an average of only 7 kg cow^{-1} as stocking rate increased from 0.132 to 0.196 head ha^{-1} and the difference between stocking rates was present in only 4 of 15 years. Later studies at the same location found no difference in calf production cow per cow (Heitschmidt et al. 1990). Johnson et al. (1951) also reported no difference among stocking rates over the first 8 years of a long-term study.

Calf production per area fluctuated over years from a low of 22.5 kg ha^{-1} in 1954 to a high of 31.0 kg ha^{-1} in 1958. Production over all stocking rates and years was 26.9 kg ha^{-1}. Production per area was affected by the interaction of stocking rate and year (P = 0.05, Fig. 6). Production per area increased as stocking rate increased in 6 of 8 years. Calf production per area was not affected by stocking rate in 1954 and 1956, the driest years of the study. Maximum production per area was achieved within the range of experimental stocking rates in only one year, 1960.

The reduction in calf production per cow was more than offset by the increased number of cows with increasing stocking rate. As a result, calf production ha^{-1} increased as stocking rate increased even though calf production cow^{-1} decreased, a response demonstrated in previous work on cow-calf production (Houston and Woodward 1966, Heitschmidt et al. 1982 1990, Willms et al. 1986,, Pieper et al. 1991) and with the established theory relating livestock production and stocking rate (Vallentine 1990).

Variability

Relative annual variability of the biological responses, as expressed by the coeffi-

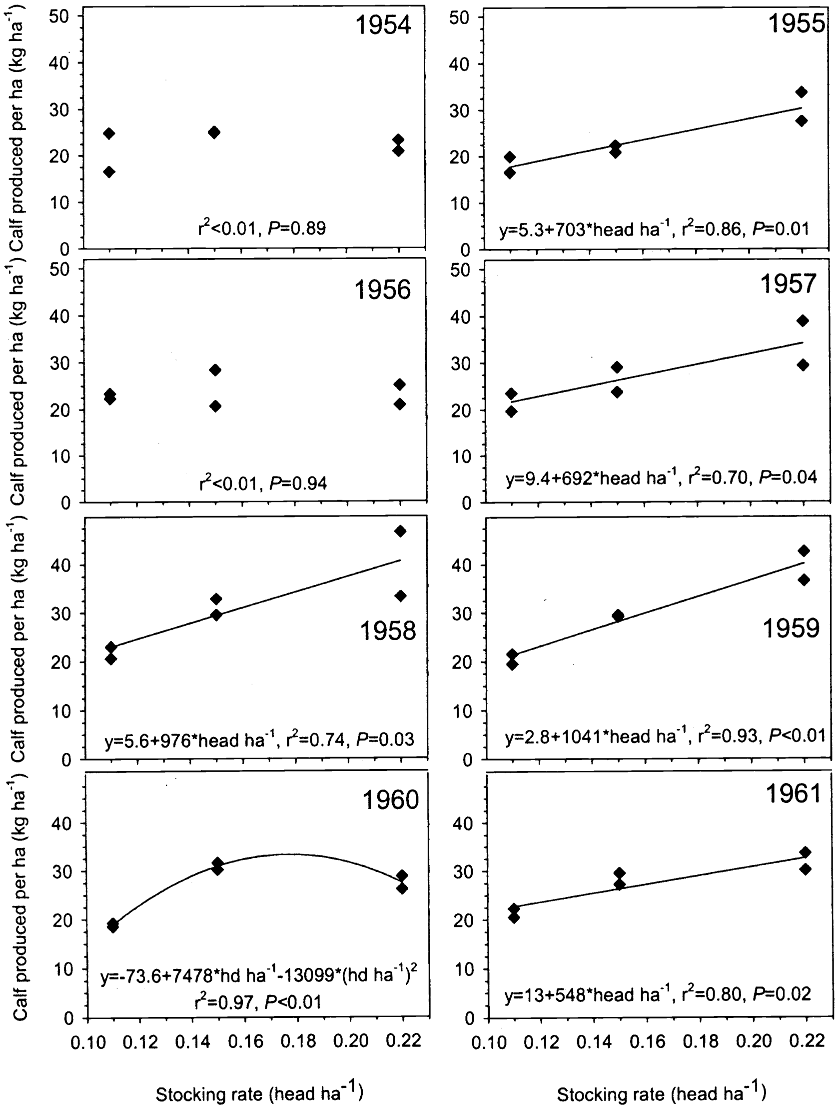

Fig. 6. Calf production ha^{-1} (kg ha^{-1}) as affected by stocking rate and year.

cient of variation, generally increased as stocking rate increased (Fig. 7). Calf birth weight was the least variable of all responses while calf production per cow showed the greatest variability. Previous work has also reported greater variation in livestock production as stocking rate increased. Much of this variation was a result of forced reductions at higher stocking rates due to drought (Johnson et al. 1951, Houston and Woodward 1966, Heitschmidt et al. 1990, Pieper et al. 1991). The current results indicate increased variability as stocking rates increase even when destocking is not required. Relative variability in gains of yearling cattle also increased as stocking rate increased during the first 10 years of this study (Sims and Gillen 1999).

Economic Responses

Within the conditions of this study, net returns were maximized at $7.87 ha^{-1} year^{-1} at a stocking rate of 0.172 head ha^{-1} (Fig. 8A). The curve relating net returns and stocking rate was broad. Returns were within 5% of maximum at stocking rates between 0.156 and 0.183 head ha^{-1}. The width of the 95% confidence band increased as stocking rate increased indicating greater variability in net returns at higher stocking rates. Previous studies have also reported greater income variability as stocking rates increase (Shoop and McIlvain 1971, Whitson et al. 1982, Riechers et al. 1989, Foran and Smith 1991). Based on this analysis, there is no economic incentive to graze at a stocking rate greater than 0.172 head ha^{-1} (5.8 ha head^{-1}). Grazing at a rate below 0.172 head ha^{-1} would sacrifice little net income but would reduce variability of annual returns, reduce impact on the vegetation resource, and leave greater amounts of residual vegetation for site protection and wildlife cover.

Shoop and McIlvain (1971) found higher net returns at moderate stocking, 0.15 head ha^{-1}, compared to heavy stocking, 0.22 head ha^{-1}. The current analysis of the same data found similar results but the maximum net return occurred between the moderate and heavy stocking rates, as defined in the experiment. This illustrates the interpretative value of fitting quantitative response curves rather than comparing discrete stocking rates.

Net returns based on averaged data were maximized at $7.57 ha^{-1} year^{-1} at a stocking rate of 0.158 head ha^{-1} (Fig. 8B). Both of these numbers are lower than the respective amounts based on year-by-year

Table 2. Effect of changes in various inputs on maximum net returns ha^{-1} and the stocking rate that produces those returns.

	Cattle prices		Cow costs (non-feed)		Land costs		Calf production cow^{-1}	
Change	Net return	Stocking rate	Net return	Stocking rate	Net return	Stocking rate	Net return	Stocking rate
(%)	($ ha^{-1})	(head ha^{-1})	($ ha^{-1})	(head ha^{-1})	($ ha^{-1})	(head ha^{-1})	($ ha^{-1})	(head ha^{-1})
–15	-$6.97	0.152	$13.57	0.182	$10.35	0.172	-$.86	0.152
–10	-2.13	0.161	11.64	0.179	9.51	0.172	2.10	0.159
-5	2.84	0.167	9.71	0.175	8.67	0.172	5.02	0.167
0	7.91	0.172	7.91	0.172	7.91	0.172	7.91	0.172
5	13.10	0.175	6.08	0.169	7.02	0.172	10.60	0.175
10	18.24	0.179	4.20	0.167	6.23	0.172	13.24	0.182
15	23.45	0.182	2.45	0.162	5.31	0.172	15.69	0.182

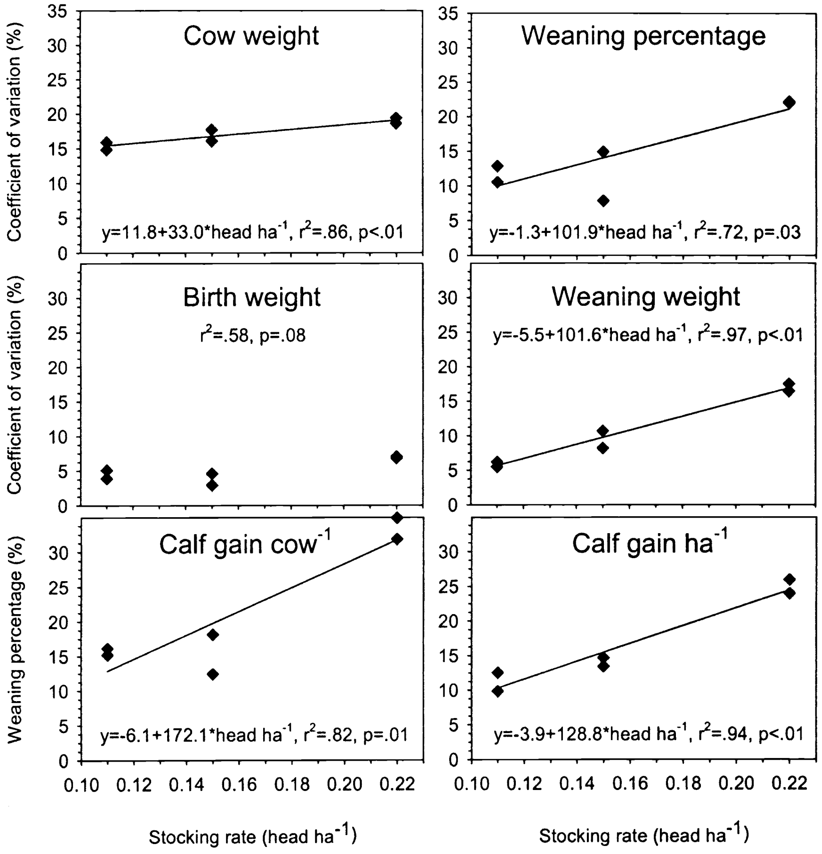

Fig. 7. Coefficient of variation of livestock responses over years as affected by stocking rate. Regression models only shown for years with significant relationships (P < 0.05).

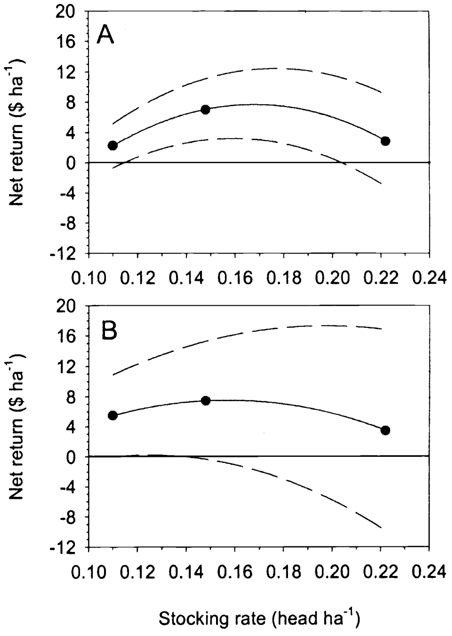

Fig. 8. Economic returns as affected by stocking rate. A) Net returns ($ ha^{-1} year^{-1}) determined from year-by-year livestock performance and prices. B) Net returns determined from average livestock performance over 8 years and average prices. Both results based on 1000 iterations of an economic model. Solid circles indicate stocking rate treatments used in the experiment.

calculations. Returns were within 5% of maximum at stocking rates between 0.140 and 0.179 head ha^{-1}. This translates to a rather broad range of 7.1 to 5.6 ha head^{-1} and encompasses the moderate stocking rate of Shoop and McIlvain (1971). Variability was greater for averaged data than for year-by-year calculations although variability increased as stocking rate increased for both methods. While actual returns and optimum stocking rates vary slightly, conclusions drawn from the use of year-by-year calculations or averaged data are similar. The use of averaged data is more conservative and simplifies the analysis at the expense of some annual detail.

Net returns and the optimum stocking rate were sensitive to changes in inputs to the economic model (Table 2.). As base cattle prices increased, net returns increased and the optimum stocking rate increased. Decreases in non-feed cow costs also increased net returns and the optimum stocking rate. Other authors have also reported that as the ratio between costs and prices decreases, the economic optimum stocking rate increases (Quigley et al. 1984, Wilson and MacLeod 1991). Increasing the amount of calf weaned per cow (either by increasing weaning percentage or weaning weights) increased net returns and the optimum stocking rate. As the production environment became more favorable (cattle prices increased, non-feed cow costs decreased, or calf production increased), net returns increased and the optimum stocking rate also increased.

These results indicate that improved livestock markets and management practices that increase individual animal performance (such as supplementation) favor higher stocking rates. As market structures or animal performance improve, net returns would increase at all stocking rates but returns would be maximized at higher stocking rates. Wilson and MacLeod (1991) reported similar conclusions. However, these theoretical increases in net returns may not be attainable if stocking rates are already at the maximum sustainable level from an ecological perspective. One exception to this trend is the cost of land. As land costs decreased, net returns increased but the optimum stocking rate remained constant.

Conclusions

As stocking rates increased, gains of individual animals generally decreased but total gain ha^{-1} increased. However, the effects of stocking rate were dependent on weather. The negative effects of stocking rate on cow and calf performance were more pronounced during drought years. In other years, favorable weather conditions either reduced or eliminated the influence of stocking rate. Increasing stocking rate also increased the variability of livestock and economic performance.

The stocking rate that generated maximum net returns did not produce maximum calf production cow^{-1} or maximum calf production ha^{-1}. This is in agreement with basic stocking rate (Wilson and MacLeod 1991) and economic theory (Torell et al. 1991). The economic optimum stocking rate in this analysis was higher than that originally determined by Shoop and McIlvain (1971) but the earlier study compared only 2 discrete stocking rates rather than a continuous range of stocking rates. A stocking rate of 0.172 head ha^{-1} appears to be sustainable in the medium to long term. There was no indication of a downward trend in livestock performance after 20 years of study, a criterion that has been suggested as a measure of overgrazing (Wilson and MacLeod 1991).

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Influence of grazing on channel morphology of intermittent streams

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Abstract

Alteration of stream channel morphology by cattle and associated streambank erosion is a concern on rangeland watersheds. The objective of this study was to determine changes in stream channel morphology in response to 5 grazing treatments applied to 0.4 ha pastures and replicated on 3 intermittent streams at the San Joaquin Experimental Range in the central Sierra Nevada foothills of California. Baseline stream channel morphology parameters were determined along 10 transects in each pasture in June 1994. Seasonal grazing treatments (no grazing, wet season moderate, wet season concentrated, dry season moderate, and dry season concentrated) were repeated annually over 4 years beginning in July 1994. Stream channel morphology parameters were measured annually from 1995–1998. When stream morphological responses were averaged across years, there were no detectable effects of grazing on the parameters measured. Year effects and their interaction with grazing were significant, primarily for stream morphological parameters that included channel depth in their measurement or calculation. Channel depth increased significantly in the ungrazed controls, but did not change due to any grazing treatment. These results indicate that grazing had little effect on the morphology of these bedrock limited, intermittent stream channels.

Key Words: grazing effects, streambank erosion, sediment, annual rangelands, California

Resumen

La alteración de la morfología del canal de la corriente por el ganado y la erosión asociada de la vega del río es una preocupación en las cuencas hidrológicas del pastizal. El objetivo de este estudio fue determinar los cambios en la morfología del canal de la corriente en respuesta a 5 tratamientos de apacentamiento aplicados a potreros de 0.4 ha y repetidos en 3 corrientes intermitentes en la Estación Experimental de Pastizales de San Joaquín al pie de monte de la parte central de la Sierra Nevada de California. Los parámetros de base de la morfología del canal fueron determinados a lo largo de 10 transecto en cada potrero, las mediciones se realizaron en Junio de 1994. Los tratamientos de apacentamiento estacional (no apacentamiento, apacentamiento moderado en la época húmeda, apacentamiento concentrado en la época húmeda, apacentamiento moderado en la época seca, apacentamiento concentrado en la época seca) fueron repetidos anualmente durante 4 años, iniciando en Julio de 1994. Los parámetros de la morfología del canal fueron medidos anualmente de 1995 a 1998. Cuando las respuestas morfológicas del canal se promediaron a través de los años no hubo efectos detectables del apacentamiento en los parámetros medidos. El efecto del año y sus interacciones con el apacentamiento fueron significativas, principalmente para los parámetros morfológicos de la corriente que incluyeron la profundidad del canal en sus medidas o cálculos. La profundidad del canal se incrementa significativamente en los controles sin apacentamiento, pero no cambio debido a algún tratamiento de apacentamiento. Estos resultados indican que el apacentamiento tiene poco efecto en la morfología de estos lechos rocosos de canales de corrientes intermitentes.

Most of California's surface water flows through the state's 6.8 million ha of annual rangelands. Sediment is the most prevalent non-point source pollutant in these surface waters (State Water Resources Control Board Staff 1999). Causes of erosion within these rangelands include natural processes and historic land use, as well as anthropogenic activities such as road construction and livestock production (Lewis et al. 2001). Concerns exist throughout California's Sierra Nevada Mountains (Sierra Nevada Ecosystem Project 1996) and the West (Belsky et al. 1999) that livestock grazing increases stream channel erosion via degradation of streambank vegetation and physical damage to the streambank. Several research and case studies have reported livestock induced streambank erosion leading to channel down cutting or widening (Kauffman and Krueger 1984, McDonald et al. 1991, Hall and Bryant 1995, Sierra Nevada Ecosystem Project 1996). Numerous reviews have identified inherent problems associated with studies examining grazing impacts on stream channel properties including: 1) lack of baseline or pre-treatment data, 2)

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inherent variability between and within watersheds or streams, 3) lack of replication across watersheds or streams, 4) inadequate or ambiguous description of grazing treatments, and 5) slow treatment response time of channel morphological parameters (Kauffman and Krueger 1984, Rinne 1988, Fleischner 1994, Larson et al. 1998, Belsky et al. 1999).

Most of California's foothill rangelands are drained by intermittent streams that only flow during the October to May rainy season. In dry years, many intermittent streams in these rangelands do not flow at all. Studies of livestock impacts on stream channels have focused largely on perennial streams and their associated riparian areas (Kauffman and Krueger 1984) with only a few documenting these impacts on intermittent or ephemeral streams (Marlow et al. 1987, Smith et al. 1993).

The objective of this study was to determine changes in stream channel morphology in response to 2 seasons (wet and dry) and 3 intensities (no grazing, moderate, and concentrated) of grazing. Our first hypothesis was that grazing induced bank erosion along the bedrock limited intermittent streams at the San Joaquin Experimental Range would increase stream channel width at bank full compared to that measured in the baseline year or in the ungrazed channel reaches. Our second hypothesis was that bedload deposition was dynamic and would result in yearly fluctuations in stream channel depth. Changes in stream channel depth and/or width may result in changes in channel cross-sectional area and width-to-depth ratio. In an attempt to overcome the problems associated with past livestock - stream channel studies, we: 1) collected baseline data, 2) replicated the study on multiple streams, 3) examined defined grazing treatments, and 4) conducted the study over a 5 year period.

Materials and Methods

Site Description

This study was conducted at the 1,752 ha San Joaquin Experimental Range (SJER) in Madera County, Calif. (37°05'N, 169°45'W) which has been a USDA Forest Service research facility since 1935 (Kie 1990). The SJER lies in the lower central Sierra Nevada foothills in the oak savanna vegetation type (Fig. 1). The station has a Mediterranean climate with annual precipitation ranging from 250 to 800 mm with a mean of 480 mm, coming almost entirely as rainfall between October and April. Mean monthly air temperatures range from 6°C in January to 27°C in July. Elevation ranges from 213 to 518 m. Soils are derived from granitic rocks, and most are less than 0.76 m deep. The Ahwahnee series (coarse-loamy, mixed thermic Mollic Haploxeralf) is common, covering about 96% of the SJER. The Visalia soil series (coarse-loamy, mixed thermic Pachic Haploxeralf) is found on alluvial or swale sites (Ulrich and Stromberg 1962).

Three intermittent tributaries to Cottonwood Creek were selected for study at the SJER (Fig. 1). Cottonwood Creek is a fourth-order stream that drains into the San Joaquin River just below Friant Dam. During this study, stream flow began in early January following 270 to 360 mm of rainfall from October—December. Average pre-treatment bankfull width for channels 1, 2, and 3 was 2.54, 2.48, and 3.56 m, respectively. Average channel depth at bankfull was 20 to 25 cm. Within the study site, most channel cross-sectional profiles are "bowl" shaped with bank angles less than 45 degrees, rather than vertical angles. The stream channels do not have undercut banks. The study reaches are low gradient with less than 2% slope and are Rosgen Class B5 (Rosgen 1996). Stream channels 1, 2, and 3 are 2 to 3 km apart at elevations ranging from 274 to 411 m (Fig. 1).

Granite bedrock underlies all 3 stream channels at 2 to 20 cm, thus limiting channel depth and the potential for down-cutting. Bed material deposits on all 3 stream channels is dominated (> 95%) by large grained sands from decomposed granite. Run off events cause bedload to be entrained and redeposited downstream. Consequently, the depth of transient bed material, and thus channel depth, within a specific stream reach is inherently dynamic from storm-to-storm and year-to-year. While granite rocks, blue oak (*Quercus douglasii* Hook & Arn), interior live oak (*Q. wislizenii* DC), and other woody vegetation provide some stability, the majority of the streambanks are vegetated by shallow-rooted annual grasses and forbs including: wild oats (*Avena fatua* L.), soft chess brome (*Bromus hordaceus* L.), red brome (*B. rubens* L.), ripgut brome (*B. diandrus* Roth.), annual fescue (*Vulpia myuros* L.),

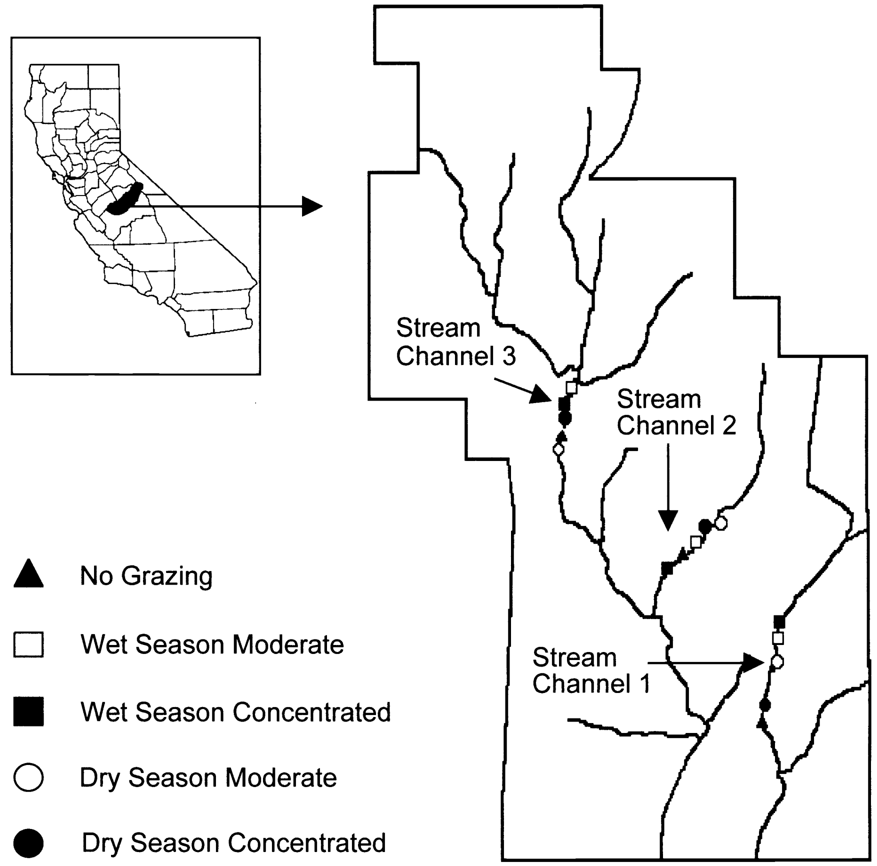

Fig. 1. Location of treatments along stream channels at the San Joaquin Experimental Range in Madera County, Calif.

broadleaf filaree (*Erodium botrys* Bertol.), redstem filaree (*E. cicutarium* L'Her.), popcorn flower (*Plagiobothrys notofulvus* Gray), and turkey mullein (*Eremocarpus setigerous* Hook.). There is no riparian vegetation associated with these intermittent stream channels.

Experimental Design

In this study, the experimental unit was a pasture containing a livestock accessible stream reach of 60 to 70 m in length. We used replication across 3 stream channels to account for inherent differences among streams. We used randomization and buffers between 5 treatment pastures within each stream channel to minimize possible upstream – downstream effects of treatment position(s). Within each stream, the buffer between treatment pastures ranged from 30 to 200 m. The 3 streams represented blocks in a randomized complete block design to which all treatments were randomly applied. Baseline data was collected in 1994 to establish pre-study conditions and was followed by 4 years of treatment application and data collection to capture variability induced by annual rainfall and runoff dynamics.

Grazing Treatments

Grazing treatments representing the range of intensity and season found on these rangelands, as well as a non-grazed control, were selected for implementation. Crossbred beef cows were used to apply the grazing treatments. Beginning in the summer of 1994, five grazing treatments were applied to 5 randomly selected 0.4 ha pastures established for this study along each of the 3 streams (Fig. 1). The 0.4 ha pastures were square with a 60 to 70 m stream segment bisecting each pasture. Portable electric fencing was used to establish the grazed pastures and ungrazed pastures were permanently fenced. Each stream and its five, 0.4 ha pastures was in a different SJER grazing unit. The area of these grazing units is 60, 110, and 47 ha, respectively. There were one or more offsite water troughs in each of these grazing units.

The no grazing (NG) treatment consisted of a 0.4 ha permanently fenced exclosure. The wet season moderate grazing (WSM) treatment was applied by grazing during the wet season so that stubble height averaged 5 to 7.5 cm along the stream channel. The wet season concentration (WSC) treatment consisted of grazing during the wet season so that stubble height along the stream channel averaged less than 5 cm. The dry season moderate grazing (DSM) treatment was applied by grazing during the dry season so that stubble height along the stream channel averaged 5 to 7.5 cm by 1 October. The dry season concentration (DSC) treatment was applied by grazing during the dry season so that stubble height along the stream channel was less than 5 cm by 1 October. The livestock concentration treatments (WSC and DSC) were designed to achieve heavy use as is often associated with a feed or watering station. Each grazing treatment was applied to the same pastures in 1994–95, 1995–96, 1996–97, and 1997–98.

Because grazing is not equally distributed within the topographically diverse SJER grazing units, stocking rate is not an accurate descriptor of grazing treatment effect at the stream segment scale. Therefore, treatments were described in terms of stubble height targets along the stream channels. Because forage growth rate varies within the wet season and between years, a flexible system of grazing application was required to maintain stubble height targets. We achieved stubble height targets in the 0.4 ha pastures by opening and closing access to these pastures by the cows grazing in the surrounding grazing unit. At the beginning of the wet season treatments on 1 February, the grazing units surrounding the treatment pastures were stocked at the density of 1 beef cow per 1.6 ha. To maintain stubble height targets during rapid spring growth, additional cows were added to the grazing units in March up to triple the 1 February stock density. Because the small pastures were readily accessible when open, the moderate grazing treatments were easily maintained by opening and closing the pastures as needed during the grazing season. It was occasionally necessary to close the small pastures during the wet season to avoid exceeding the 5 to 7.5 cm stubble height target in the moderate treatments. The wet season concentrated treatments were never closed during the wet season. To achieve the concentrated grazing treatments, cooked molasses supplement and mineral blocks were placed in the small pasture within 10 m of the channel to attract cattle into the pasture, thus increasing grazing intensity and trampling along the stream channel. Near the end of the dry season, we closed the DSM treatment pastures and increased the stocking rate by 25 to 50% for 1 to 3 days to insure that stubble height targets were met in the DSC treatments.

Stubble height was determined by ocular estimate and confirmed with actual measurements as needed. Stubble height was estimated weekly in the pastures that were being treated that season. Target stubble heights for moderate grazing were achieved throughout the 0.4 ha pasture. Stubble height targets for the concentrated treatments were achieved along a 10 m zone on either side of the stream channel.

Dry season grazing treatments (DSM and DSC) were applied between 1 July and 1 October, a period of little or no rainfall. Typically, the wet season begins in late October or early November and ends by 1 May. This period includes the slow winter growth period and all of the rapid spring growth period of the growing season (George et al. 2001). The soil profile is usually saturated by early January. Wet season treatments (WSM and WSC) were applied starting on 1 February and maintained until surface soil moisture was depleted at the end of the growing season between 15 April and 1 May each year.

Stream Channel Measurements

To determine changes in stream channel morphology, we measured width and depth along stream channel cross-sections which allowed us to calculate various morphological parameters. The width parameters were used to detect streambank erosion. Depth parameters were used to detect annual fluctuations in channel bedload.

Stream morphological measurements were recorded during the first week of June at the beginning of the dry season starting with the baseline year in 1994. Channel cross sections were measured using methods outlined by Bauer and Burton (1993). For each stream reach within a pasture, 10 permanent cross-sectional transects, 6.1 to 9.1 m long, were placed perpendicular to the stream channel at a distance of 1 to 1.5 times the channel width apart (Fig. 2). The transects were marked with permanent stakes and referenced to a permanent benchmark. Stream elevation was determined every 15 cm along the transect using a stretched tape, laser level, and stadia rod. For each transect, width at bankfull (W), distance from the left permanent stake to right and left bank at bankfull height, maximum depth, and depth every 15 cm were measured (Fig. 2). Cross-sectional area (A), channel average depth (A/W), and width-to-depth ratio [W/(A/W)] were calculated. Pasture averages for each morphological parameter were calculated from the 10 transects in each pasture. Cross-sectional area of the channel was determined using bankfull elevations following the methods of Rosgen (1996). Elevation and position readings of the permanent end stakes were checked with benchmark elevations each year.

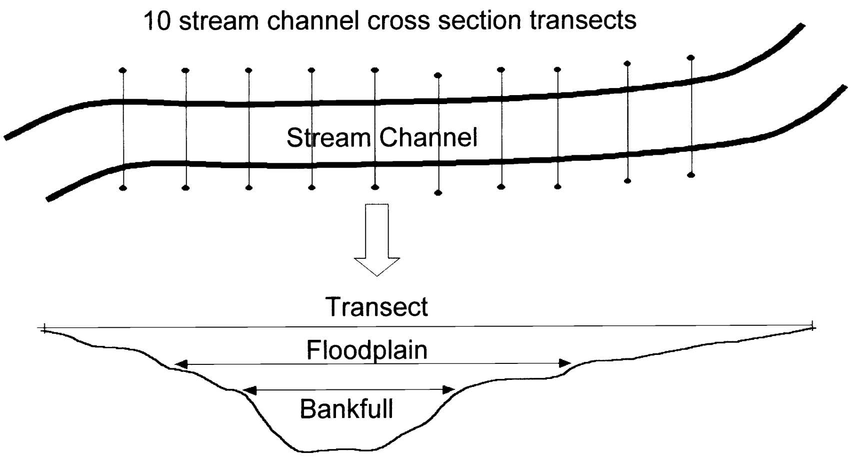

Fig. 2. Layout of stream channel cross-sectional transects.

Data Analysis

Multivariate repeated measures analysis techniques were used to determine how 7 stream morphological parameters were affected by grazing treatment, year, and year x grazing interactions. Profile contrasts were then used to compare successive year-to-year differences among the grazing treatments (Tabachnick and Fidell 1989). Finally, pair-wise comparisons (Khattree and Naik 1999) were used to test for differences between the no grazing treatment and the moderate and concentrated grazing treatments following the 1996–97 water year characterized by above average flow events. All analyses were conducted using SAS Release 6.12 for Open VMS (SAS Institute Inc. 1996).

Results and Discussion

When stream morphological responses to grazing treatments were averaged across years, there were no detectable effects on channel width, distance to right and left bank, maximum depth, mean depth, cross-sectional area, and width-to-depth ratio (Table 1). There was a significant year effect for the depth-based parameters (maximum depth, mean depth, cross sectional area, and width-to-depth ratio). Examination of the yearly means for each treatment (Fig. 3) revealed large changes in several of the depth-based parameters from 1996 to 1997. The year x grazing interaction was significant for the depth-based parameters and for left bank distance when using Roy's maximum root test in the MANOVA. While Roy's test is weaker than other MANOVA tests of significance, other less sensitive (more restrictive) tests increase the risk of overlooking the potential for grazing damage. The profile contrasts indicate that the grazing treatments accounted for significant differences in maximum depth from 1996 to 1997. Examination of the proportional changes in maximum depth and mean depth (Fig. 4) revealed that channel depth in the no grazing (NG) treatment increased over the four years of the experiment. This contributed to the significant pairwise comparison between the wet season moderate grazing (WSM) and the NG treatments.

Channel width and distance to right bank did not change in response to the grazing treatments. Distance to left bank was significant for the year x grazing interaction. There have been conflicting reports on the relationship between grazing along stream channels and sediment loss from streambanks. Buckhouse et al. (1981), Smith et al. (1993), and Kondolf (1993) detected no significant streambank erosion due to grazing. Conversely, several studies comparing exclosures to grazed areas report significant sediment losses from grazed streambanks (Gunderson 1968, Behnke and Zarn 1976, Hedee 1977, Dahlem 1979, Duff 1979, Kauffman et al. 1983, Platts and Nelson 1985, Elmore and Beschta 1987, Marlow et al. 1987, Clary and Webster 1989, 1990, Platts 1991, Myers and Swanson 1994, Swanson and Myers 1994, Trimble 1994). Several of these studies reported that increased channel width was the result of sloughing of undercut banks. The stream channel banks in this study were not undercut and could not achieve this form under any grazing scheme due to substrate type (sand) and dominance by shallow rooted annual vegetation. While most of these studies compared an exclosure to a grazed area, a few studies compared ungrazed areas to several treatments. Siekert et al. (1985) detected changes in stream channel cross-sectional area due to summer and fall grazing treatments along an ephemeral stream in Wyoming. Applying several seasonal grazing treatments, Marlow et al. (1987) detected changes in the stream channel profile due to grazing and trampling of streambanks when streambank soils were moist during the early summer.

We observed grazing and trampling along the stream channel bank by cattle in the treated pastures, yet detected no change in channel width at bankfull. Fine textured and wet streambank soils have been shown to be a factor in vulnerability to erosion (Wolman 1959, Hooke 1979, Marlow and Pogacnik 1985, Marlow et al. 1987, Clary and Webster 1990). The well drained course sands in our study lack the fine particle sizes and have a low water holding capacity which may reduce their vulnerability to streambank erosion. Trimble and Mendel (1995) suggested that watersheds subjected to high intensity, long duration storms generating high stream discharges were more vulnerable to streambank erosion than watersheds that receive relatively equitable flow from

Table 1. Summary of multivariate repeated measures analysis of variance results after Dunn-Šidák familywise adjustments for multiple comparisons.

	Graze	Year	Y x G	Profile Analysis[1]			Pairwise[1]
	(G)	(Y)		95-96	96-97	97-98	1997
Cross-sectional Area	n.s.	**	*	n.s.	n.s.	n.s.	n.s.
Width	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Width-to-Depth Ratio	n.s.	**	*	n.s.	L	n.s.	n.s.
Maximum Depth	n.s.	**	**	n.s.	L,G	n.s.	n.s.
Mean Depth	n.s.	***	*	L[2]	L	n.s.	WSM
Right Bank Distance	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Left Bank Distance	n.s.	n.s.	**	n.s.	n.s.	G	n.s.

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

[1] For $\alpha = 0.10$, a Dunn Sidak family-wise significant p value must be < 0.015 for the profile and pairwise contrasts (Maxwell and Delaney 1990, Sokal and Rohlf 1995).

[2] L indicates a significant linear rend, G indicates a significant grazing treatment effect, ans WSM inicates a significant wet season moderate grazing treatment effect.

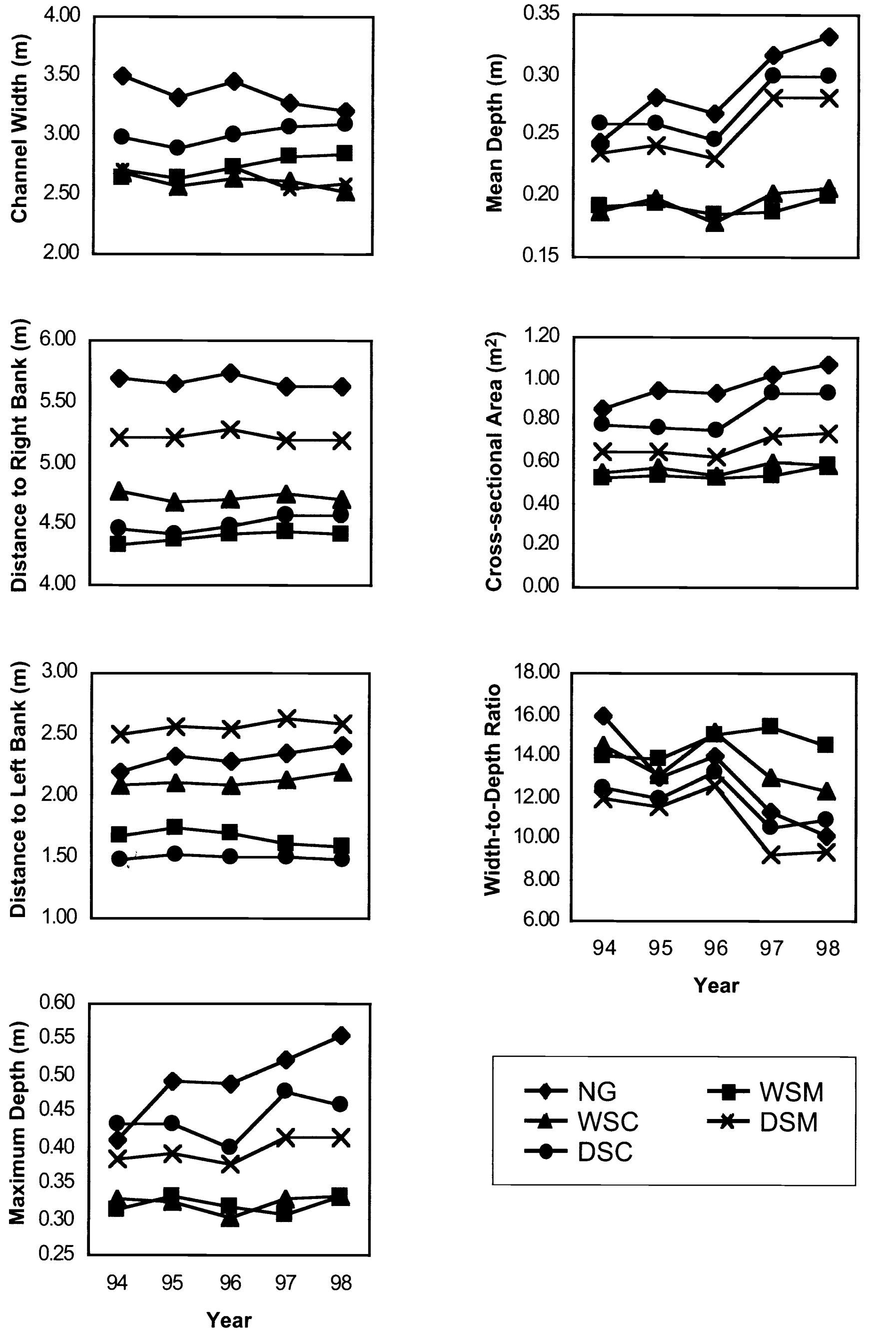

Fig. 3. Yearly treatment means for channel width, distance to right and left bank, maximum depth, mean depth, cross-sectional area, and width-to-depth-ratio.

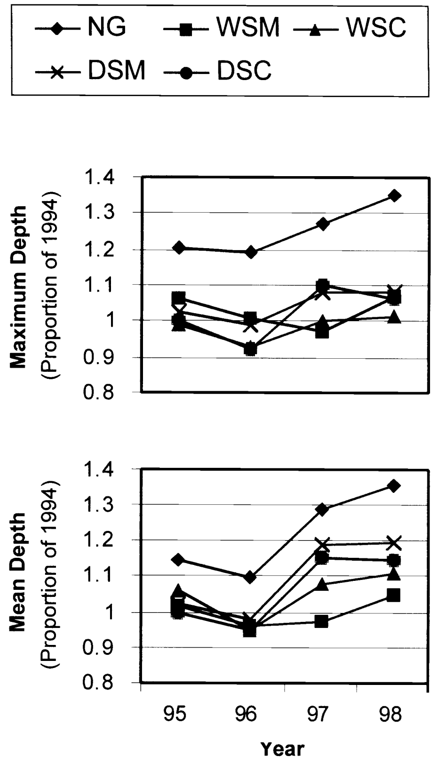

Fig. 4. Yearly proportional change in maximum and mean depth.

snowmelt. During our study, one or more high stream discharges occurred each year lasting for only a few hours during and following a storm. Lack of high intensity rainfall and runoff early in the rainy season may reduce streambank erosion. While intense grazing and trampling can leave unvegetated loose soil at the beginning of the rainy season, low intensity rainfall which is characteristic of the early rainy season results in germination and seedling establishment that stabilizes grazed and trampled soil surfaces before periods of more intense rainfall begin.

Just as grazed stream channels are expected to widen when subjected to grazing, stream channels that are protected from grazing are expected to narrow (McDowell and Magilligan 1997). While not significant, the results of this study suggest that the stream channels in the controls may be narrowing (Fig. 3). Kondolf (1993) reports that recent exclosures (less than 4 years old) have not had time to trap sediment and build bank that results in channel narrowing while differences were more pronounced in older exclosures. Magilligan and McDowell (1997) suggest that streams that lack fine sediment and woody vegetation may take longer to show channel adjustment to protection from grazing. However, the woody vegetation that traps sediment during the bank building process is not present and not known to be within the potential of these oak woodland stream channels.

Seasonal and annual variation in precipitation and resulting run-off could account for the large year effect detected in this study. The 1996–97 rainfall year was characterized by above average stream flow. We observed significant movement of bed material during one or more annual high flow events, usually in January or February, which would have a significant annual effect on channel depth parameters. The significance of year in the results of this study make it difficult to isolate the effect of annual stream flow dynamics from grazing effects on stream channel morphology. We would suggest that stream flow is the largest potential confounder in testing for the effect of grazing on streambank or stream channel morphology. Roath (1980) reported that the actions of streamflow rather than livestock trampling was the cause of streambank erosion in an eastern Oregon study. Buckhouse et al. (1981) reported that most bank cutting was associated with over-winter periods when ice flows and high flow events occurred.

Channel deepening in the control treatments indicates that there was a loss of bedload sediment from the control reaches. Treatment randomization within each stream (block) resulted in the controls being placed at the lowest or next to lowest pasture in the sequence of 5 pastures along each stream. One might expect channel depth in the controls to become shallower if they were influenced by delivery of sediment from upstream grazed treatments, but not for the channel to deepen. While there was no significant change in channel width, Figure 3 suggests a trend toward channel narrowing that may have resulted in increased stream power that could have eroded bedload sediment in the control pastures.

On these stream channels, it was difficult to interpret grazing effects using standard stream morphology parameters (width, depth, area, and width-to-depth ratio). Width did not change significantly and depth parameters were more a reflection of annual flow and bedload dynamics than grazing influences. Distance to left or right bank, an absolute measure from a permanent point, may be more responsive to grazing effects than the standard stream morphology width parameter because changes on one bank may compensate for changes on the opposite bank. We detected a small, weakly significant, change in distance to left bank for the year x grazing interaction during this 5 year study. Over a longer period, if grazing effects accumulated sufficiently, an absolute measure such as distance to right and left bank or distance to cut bank (Buckhouse et al. 1981) may be more responsive than channel width.

Conclusions

In conclusion, we detected no significant streambank erosion, thus we must reject our hypothesis that grazing increases width in these bedrock limited stream channels. We detected a significant increase in depth in the control treatments. Additionally, we found a significant year effect on morphological parameters that included depth in their measurement or calculation, supporting our hypothesis that annual stream flow dynamics have a large effect on depth of the stream channels we studied. The large year effect and weaker year x grazing effect on stream morphology confirms the need for long-term studies to separate natural variation in stream morphological parameters from those caused by land management activities.

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Hydrologic response of diverse western rangelands

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Abstract

There are several generalizations or assumptions concerning rangeland hydrology and erosion relationships found in the literature and in the management arena. These generalizations have found their way into rangeland models, where modelers have assumed that diverse rangeland types can be lumped or averaged together in some way to develop one algorithm or equation to describe a process or relationship across the entire spectrum of rangeland types. These assumptions and modeling approaches based on the universal concept may not be appropriate for diverse rangeland types. This paper presents a comprehensive data set of vegetation, soils, hydrology, and erosion relationships of diverse western rangelands, and utilizes the data to assess the validity of the various assumptions/generalizations for rangelands. The data set emphasizes the difficulty in understanding hydrologic responses on semiarid rangelands, where the relationship between plant/soil characteristics and infiltration/erosion is not well established. When all sites were pooled together, infiltration and sediment production were not correlated with any measured vegetation or soil characteristic. A myriad group of factors determine infiltration and erosion, and is dependent on rangeland type and site conditions. The infiltration and erosion responses and correlation/regression analyses presented highlight the risk of using generalized assumptions about rangeland hydrologic response and emphasize the need to change the current modeling approach. Universal algorithms to represent the response of all rangeland types, such as the pooled multiple regression equations presented, will not provide sufficient accuracy for prediction or assessment of management. We need to develop a rationale to organize rangeland types/vegetation states according to similarities in relationships and responses. These functional rangeland units would assist in the development of more accurate predictive equations to enhance model performance and management of rangelands.

Key Words: rangeland hydrology, infiltration, erosion, hydrologic modeling

Resumen

Hay varias generalizaciones o supuestos concernientes a la hidrología de pastizales y las relaciones de erosión encontradas en la literatura y en la área de manejo. Estas generalizaciones han encontrado su camino dentro de los modelos de pastizales, donde los modeladores han asumido que diversos tipos de pastizales pueden ser agrupados o promediados juntos en alguna manera para desarrollar un algoritmo o ecuación para describir un proceso o relación a lo largo de un espectro de tipos de pastizal. Estas suposiciones o métodos de modelaje basados en un concepto universal pueden no ser apropiados para diversos tipos de pastizales. Este artículo presenta un juego de datos comprensivo de vegetación, suelos, hidrología y relaciones de erosión de diversos pastizales del oeste y utiliza los datos para evaluar la validez de varios supuestos/generalizaciones para los pastizales. El juego de datos enfatiza la dificultad en entender la respuesta hidrológica de los pastizales semiáridos, donde la relación entre las características de planta/suelo e infiltración/erosión no están bien establecidas. Cuando todos los sitios se agruparon, la infiltración y la producción de sedimento no estuvieron correlacionados con ninguna de las características del suelo o planta medidas. Un grupo indeterminado de factores determina la infiltración y erosión y es dependiente del tipo de pastizal y condiciones del sitio. Las respuestas de infiltración y erosión y los análisis de correlación/regresión presentan en forma destacada el riesgo de usar suposiciones generalizadas acerca de la respuesta hidrológica de los pastizales y enfatiza la necesidad de cambiar los métodos actuales de modelaje. Los algoritmos universales para representar la respuesta de todos los tipos de pastizal, tal como se fusionaron en las ecuaciones de regresión múltiple presentadas, no proveerán suficiente certeza para la predicción o evaluación del manejo. Necesitamos desarrollar un fundamento para organizar los estados de tipos de pastizal/vegetación de acuerdo a similitudes en relaciones y respuestas. Estas unidades funcionales de pastizal asistirán en desarrollar ecuaciones predictivas más certeras para mejorar el modelo de comportamiento y manejo de los pastizales.

Rangeland ecosystems are comprised of diverse combinations of vegetation, soils, and climatic conditions. Rangeland managers need an understanding of this complexity to assess system health and apply appropriate management practices. Where direct knowledge of the rangeland system is limited, management decisions are often based on assumptions about how the system may work. Some of the generalizations or assumptions concerning rangeland hydrology and erosion relationships found in the literature are:

1. Rangeland ecological status/similarity index is directly related to hydrologic condition (Ellison 1949, Osborn 1952),
2. Sediment production is highly correlated with amount of infiltration/runoff (Blackburn and Skau 1974, Buckhouse 1984),

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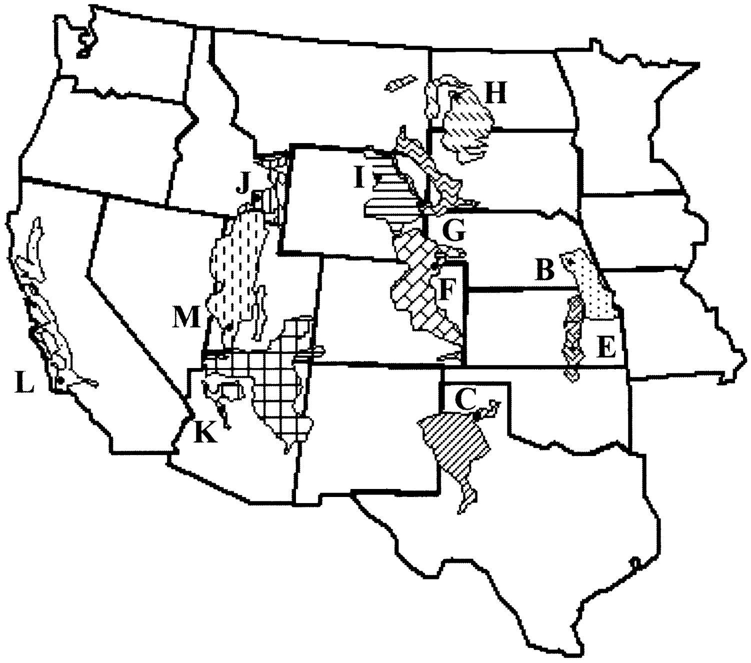
3. Quantity of plant material and litter is positively correlated with infiltration (Gifford 1985, Wilcox et al. 1988),
4. Brush management alters hydrology and erosion (Bedunah and Sosebee 1985, Carlson et al.1990),
5. Vegetation characteristics dominate rangeland hydrology response (Branson et al. 1981, Stoddart et al. 1975, USDA-NRCS 1997).

While numerous examples can be found in the literature to further support these assumptions, little is known about the universality of such assumptions to all rangelands.

This concept of universality has found its way into rangeland models that managers use to assist in the assessment and management of rangelands. Modelers frequently use simplifying assumptions or generalizations to reduce the complexity of model design and system representation. Current rangeland models are based on the following assumptions: 1) algorithms developed from abundant cropland data should apply to rangelands (Foster and Lane 1987) where limited data has hampered rangeland modeling efforts, and 2) site characteristics of diverse rangeland types can be lumped or averaged together to develop 1 algorithm or equation to describe a process or relationship across the entire spectrum of rangeland types (Alberts et al. 1995). This universal approach simplifies the modeling process and broadens the practical application of the rangeland model. These simpler, more generalized models may be easier to use and require fewer resources. However, they may also be unresponsive to, or inaccurate in describing, variable interactions that affect management decisions. They may be unresponsive if the important factors that govern rangeland hydrology on a specific site are not included in the generalized algorithm. They may be inaccurate for a specific site if the relationship or interaction between factors is poorly represented for that site by the generalized algorithm.

Are these assumptions, and modeling approaches based on the universal concept, appropriate for use on diverse rangeland types? This paper presents a comprehensive data set of vegetation, soils, hydrology, and erosion relationships for diverse western rangelands. This initial data summary is used to assess the validity of these assumptions and determine their credibility for rangelands in general.



Site	Location	MLRA	Lat./Long.
⊡ B	Wahoo, NE	M106	41° 3' 58"N, 96° 53'18"W
▨ C	Amarillo, TX	H77	35° 16'30"N, 102° 16'42"W
▩ E	Eureka, KS	H76	37° 38'32"N, 96° 10'48"W
▧ F	Akron, CO	G67	40° 22'26"N, 103° 7' 42"W
▩ G	Newcastle, WY	G60A	43° 45'00"N, 104° 22'30"W
▧ H	Killdeer, ND	F54	47° 25'30"N, 102° 52'45"W
▤ I	Buffalo, WY	G58B	44° 20'32"N, 106° 31'38"W
▥ J	Blackfoot, ID	A13	43° 3' 6" N, 111° 46'40"W
⊞ K	Prescott, AZ	D35	34° 46'41"N, 112° 37'57"W
☐ L	S.L. Obispo, CA	C15	35° 19'46"N, 120° 41'49"W
⊡ M	Cedar City, UT	D28A	37° 43'35"N, 113° 18' 4"W

Fig. 1. Location of sampling sites within the 11 Major Land Resource Areas chosen for study.

Data Set

Background

Process-based models can improve our understanding of system dynamics, and enhance our capability to predict disturbance and management impacts on rangelands. However, these types of endeavors have been hampered by the lack of comprehensive, interdisciplinary data sets for model development and testing. To address this problem, the Agricultural Research Service and the Natural Resources Conservation Service (NRCS) formed the National Range Study Team (NRST) in 1990. This team collected critical interdisciplinary field data pertaining to hydrologic response for a variety of important rangeland soil-vegetation assemblages across the western United States. The data were collected to assist in the development of infiltration and erosion modeling components for WEPP (Water Erosion Prediction Project, Flanagan and Livingston 1995) and similar process-based models and thus further our understanding of the complex soil-vegetation-hydrology interactions that are particular to rangeland ecosystems.

Study Sites

Eleven Major Land Resource Areas (MLRAs) in 10 different western states were evaluated (Fig. 1). Two to 3 contrasting vegetation states within each of these MLRAs were chosen for comparative study based on their relevance to the region and to management (Table 1). Contrasting vegetation states were identified as transition states within the Ecological Site/Range Cover Type, with different ecological status (USDA-NRCS 1997) and/or plant species composition. All study areas were located on native

Table 1. Location and primary features of each study site.

State	Site ID	MLRA, Cover type	Ecological status	Slope	Dominant species
			(%)	(%)	(Descending order of % composition by weight)
NE	B1	NE/KS Loess-Drift Hills (106), Bluestem prairie	11	10	1-Kentucky bluegrass (*Poa pratensis* L.) 2-Dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers) 3-Alsike clover (*Trifolium hybridum* L.)
NE	B2	NE/KS Loess-Drift Hills (106), Bluestem prairie	37	11	1-Primrose (*Primula* spp.) 2-Porcupinegrass (*Stipa spartea* (Trin.) Barkworth) 3-Big bluestem (*Andropogon gerardii* Vitman)
TX	C1	Southern High Plains (77), Blue grama-buffalograss 2-	72	3	1-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 2-Buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.) 3-Prickly pear cactus (*Opuntia polycantha* Haw.)
TX	C2	Southern High Plains (77), Blue grama-buffalograss	62	2	1-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 2-Buffalograss (Buchloe dactyloides (Nutt.) Engelm.) 3-Prickly pear cactus (*Opuntia polycantha* Haw.)
KS	E1	Bluestem Hills (76), Bluestem prairie	7	5	1-Annual broomweed (*Gutierrezia dracunculoides* (Pursh) Britt. & Rusby) 2- Missouri goldenrod (*Solidago missouriensis* Nutt.) 3-Tall dropseed (*Sporobolus asper* (Poir.) Merr.)
KS	E2	Bluestem Hills (76), Bluestem prairie	63	5	1-Little bluestem (*Schizachyrium scoparium* (Michx.) Nash) 2-Big bluestem (*Andropogon gerardii* Vitman) 3-Indiangrass (*Sorghastrum nutans* (L.) Nash)
KS	E3	Bluestem Hills (76), Bluestem prairie	45	3	1-Buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.) 2-Sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.) 3- Little bluestem (*Schizachyrium scoparium* (Michx.) Nash)
CO	F1	Central High Plains (67), Grama-Buffalograss	76	7	1-Blue grama (*Bouteloua gracili*s (Willd. Ex Kunth) Lag. Ex Griffiths) 2-Western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) 3-Buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.)
CO	F2	Central High Plains (67), Grama-Buffalograss	44	8	1-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 2-Sun sedge (*Carex inops* Baily spp. *Heliophila* (Mackenzie) Crins) 3-Bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey)
CO	F3	Central High Plains (67), Grama-Buffalograss	45	7	1-Buffalograss (*Buchloe dactyloide*s (Nutt.) Engelm.) 2 Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 3-Prickly pear cactus (*Opuntia polycantha* Haw.)
WY	G1	Pierre Shale Plains and Badlands (60A), Wheatgrass-Grama-Needlegrass	21	7	1-Prickly pear cactus (*Opuntia polycantha* Haw.) 2-Needle-and-Thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) 3-Threadleaf sedge (*Carex filifolia* Nutt.)
WY	G2	Pierre Shale Plains and Badlands (60A), Wheatgrass-Grama-Needlegrass	22	8	1-Cheatgrass (*Bromus tectorum* (L.) 2-Needle-and-Thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) 3-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths)
WY	G3	Pierre Shale Plains and Badlands (60A), Wheatgrass-Grama-Needlegrass	50	9	1-Needle-and-Thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) 2-Threadleaf sedge (Carex filifolia Nutt.) 3-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths)
ND	H1	Rolling Soft Shale Plain (54), Prairie Sandreed-Needlegrass	60	12	1-Needle-and-Thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) 2-Prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.) 3-Sedge (*Carex* spp.)
ND	H2	Rolling Soft Shale Plain (54), Prairie Sandreed-Needlegrass	43	11	1-Clubmoss (*Lycopodium dendroideum* Michx.) 2-Sedge (*Carex* spp.) 3-Crocus (*Crocus* L.)
ND	H3	Rolling Soft Shale Plain (54), Prairie Sandreed-Needlegrass	52	11	1-Sedge (*Carex* spp.) 2-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 3-Clubmoss (*Lycopodium dendroideum* Michx.)
WY -	I1	N. Rolling high Plains (58B), Sagebrush-Grass Wheatgrass Grama-Needlegrass	33	10	1-Big sagebrush (*Artemisia tridentata* Nutt. ssp wyomingensis Beetle & Young) 2-Prairie junegrass (*Koleria macrantha* (Ledeb.) J.A. Schultes) 3-Western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love)
WY	I2	N. Rolling high Plains (58B), Sagebrush-Grass Wheatgrass-Grama-Needlegrass	40	7	1-Western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) 2-Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) 3-Green needlegrass (*Stipa viridula* (Trin.) Barkworth)
ID	J1	Eastern Idaho Plateau (13), Mountain Big Sagebrush	15	7	1-Big sagebrush (*Artemisia tridentata* Nutt. ssp. *Vaseyana* (Rydb.) Boivin) 2-Letterman's needlegrass (*Achnatherum lettermanii* (Vasey) Barkworth) 3-Sandberg bluegrass (*Poa secunda* J. Presl)
ID	J2	Eastern Idaho Plateau (13), Mountain Big Sagebrush	22	9	1- Letterman's needlegrass (*Achnatherum lettermanii* (Vasey) Barkworth) 2-Sandberg bluegrass (*Poa secunda* J. Presl) 3-Prairie junegrass (*Koleria macrantha* (Ledeb.) J.A. Schultes)

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Table 1. Continued.

State	Site ID	MLRA, Cover type	Ecological status	Slope	Dominant species
			(%)	(%)	(Descending order of % composition by weight)
AZ	K1	CO and Green River Plateaus (35), Grama-galleta	54	5	1-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 2-Goldenweed (*Haplopappus* spp.) 3-Ring muhly (*Muhlenbergia torreyi* (Kunth) A.S. Hithc. ex Bush)
AZ	K2	CO and Green River Plateaus (35), Grama-galleta	36	4	1-Rubber rabbitbrush (*Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird) 2-Blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) 3-Threeawn (*Aristida* ssp.)
CA	L1	Central CA Coast Range (15), Valley grassland	---	11	1-Creatanweed (*Hedypnois cretica* (L.) Dum.-Cours.) 2-Ryegrass (*Lolium* spp.) 3-Burclover (*Medicago polymorpha* (L.) Beauv.)
CA	L2	Central CA Coast Range (15), Valley grassland	---	12	1-Ryegrass (*Lolium* spp.) 2-Purple falsebrome (*Brachypodium distachyon* (L.) Beauv.) 3-Slender oat (*Avena barbata* Pott ex Link)
UT	M1	Great Salt Lake Area (28A), Wyoming big sagebrush	35	3	1-Big sagebrush (*Artemisia tridentata* Nutt. ssp wyomingensis Beetle & Young) 2-Bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) 3-James' Galleta (*Hilaria jamesii* Torr.)
UT	M2	Great Salt Lake Area (28A), Wyoming big sagebrush	24	3	1- James' Galleta (*Hilaria jamesii* Torr.) 2-Arrowfeather threeawn (*Aristida purpurascens* Poir.) 3- Big sagebrush (*Artemisia tridentata* Nutt. ssp *wyomingensis* Beetle & Young)

rangeland (no history of cultivation). Different vegetation states within a MLRA had similar soils and Potential Natural Communities (PNC); differences were assumed to be the result of past and current management. Site selection for each vegetation state within a MLRA was based on the benchmark site concept (Franks et al. 1993) to assure that representative sites integrated the important features of plant community, soils, and management history. Within each representative site, 6 sampling plots with similar slope were randomly selected. A complete description and history of study sites can be found in Franks et al. (1998).

Methods

Rainfall simulation using a rotating boom (Swanson 1965) was conducted simultaneously on two, 3.1 x 10.7 m runoff plots. Detailed description of the rainfall simulation techniques used are presented by Simanton et al. (1987, 1991) and Franks et al. (1998). All 6 runoff plots per site were on undisturbed (not disturbed by farm implement) vegetation and soils. For each of the plots, 2 different rainfall simulation runs were conducted. The first run was conducted on the initial antecedent soil moisture with a target rainfall rate of 63.5 mm hr^{-1} and lasted approximately 1 hour or until steady-state runoff occurred. This was termed the "dry" run. A "wet" run was conducted 24 hours later, utilizing the same target rainfall intensity and lasted until an equilibrium runoff rate was achieved. Runoff was measured continuously using small drop-box weirs equipped with a pressure transducer bubbler gauge. Due to the differences in rainfall application rates typical of rotating boom simulators, actual water application rates and quantities were measured on each plot during the simulation run. Infiltration was calculated as the difference between measured rainfall and measured runoff over each 1 to 2 minute time interval throughout the simulation. Terminal infiltration rate was calculated as the difference between final rainfall intensity and final runoff rate. Sediment samples were collected in bottles at 1 to 2 minute intervals.

Because of the differences between sites in total rainfall application, weighted variables were calculated, in addition to cumulative totals, so that comparison of runoff and sediment could be made on sites with varying amount/duration of rainfall. These normalized variables included runoff/rainfall ratio (mm mm^{-1}), which is the total runoff divided by total rainfall, and sediment/runoff ratio (kg ha^{-1} mm^{-1}), which is the total sediment divided by total runoff.

Five soil pedons from each study site were characterized and sent to the NRCS National Soil Survey Center for analysis. One pedon was selected as representative of the site's soil phase and the others represented the typical range of soil surface characteristics. In addition, 6 to 12 soil bulk density samples were taken outside each plot using either the compliant cavity or the balloon technique (Blake and Hartge 1986). Samples were taken prior to the dry run and after the wet run at 2 different depths (0-2.5 cm, and 2.5-10 cm) below the soil surface. Gravimetric soil moisture samples associated with each plot were collected 30 minutes prior to the dry run, 30 minutes prior to the wet run, and 30 minutes after the wet run. Three samples were collected from 0-5 cm depths, and 3 were collected from 5-20 cm depths (or to the bottom of the wetting front if less than 20 cm). Selected average soil characteristics for each vegetation state within a MLRA are presented in Table 2.

Vegetation canopy and ground cover were evaluated using a point frame (Mueller-Dombois and Ellenberg 1974) with 10 systematic lines of 49 points per runoff plot. First hits were used to determine canopy cover (individual species recorded and standing dead) and ground hits were used to determine ground cover. Random roughness was measured at each pinpoint by determining pin height above/below an arbitrary line. The standard deviation of each of the 10 lines was then averaged for the composite random roughness value. In addition, the standing live and dead biomass (kg ha^{-1}) of individual species/functional groups, and of litter and other surface residue were also measured for each plot by clipping/harvesting after the rainfall simulation, oven drying, and weighing. Root biomass for the surface 0-10 cm of soil was estimated by wet sieving soil cores and drying and weighing remaining roots. Selected average vegetation characteristics for vegetation states within each MLRA are presented in Table 3.

All data were tested for normality, skewness and kurtosis. Normalized distributions were obtained for total sediment, runoff/rainfall ratio and sediment/runoff ratio by using a $\log_{10}$ transformation. An

Table 2. Mean soil characteristics of each study site.

State	Site ID	Soil series, Surface texture	Surface Rough-ness	P_b Dry 0-10 cm	P_b Wet 0-10 cm	Antec. SM[1] Dry Run	Antec. SM[1] Wet Run	Clay 0-8 cm	Sand 0-8 cm	Organic Carbon 0-8 cm	Aggregate Stability
			(m)	(g cm^{-3})	(g cm^{-3})	(%)	(%)	(%)	(%)	(%)	(%)
NE	B1	Burchard, loam	.0099	1.40	1.17	24.2	30.1	32.6	27.3	6.22	67.0
	B2	Burchard, loam	.0101	1.19	1.00	19.9	25.7	27.9	35.9	3.95	81.2
TX	C1	Olton, loam	.0081	1.14	1.14	7.1	23.1	22.8	32.3	2.39	78.2
	C2	Olton, loam	.0072	1.31	1.29	10.9	20.8	23.1	35.9	2.21	54.0
KS	E1	Martin, silty clay loam	.0116	1.10	0.97	18.6	30.1	44.3	4.8	4.23	86.0
	E2	Martin, silty clay loam	.0092	1.04	1.12	34.2	34.0	40.6	11.1	4.36	60.8
	E3	Martin, silty clay loam	.0088	1.01	1.01	18.7	33.6	43.4	2.7	4.34	56.8
CO	F1	Stoneham, loam	.0098	1.10	1.07	5.6	21.7	21.7	51.9	1.45	57.6
	F2	Stoneham, fine sandy loam	.0087	1.34	1.34	4.2	15.7	13.3	55.9	1.75	59.7
	F3	Stoneham, loam	.0125	1.22	1.16	13.5	19.2	18.0	61.9	1.59	53.0
WY	G1	Kishona, v. fine sandy loam	.0165	1.15	1.26	3.2	14.6	11.4	58.1	1.29	34.0
	G2	Kishona, clay loam	.0192	1.21	1.14	6.6	15.5	23.7	47.1	1.76	41.8
	G3	Kishona, v. fine sandy loam	.0207	1.11	1.17	7.1	15.7	13.6	60.1	1.30	11.0
ND	H1	Parshall, sandy loam	.0101	1.25	1.16	6.5	16.3	15.3	61.3	2.70	83.8
	H2	Parshall, fine sandy loam	.0113	1.03	1.09	19.9	19.4	14.4	63.8	3.72	85.3
	H3	Parshall, sandy loam	.0097	1.2	1.31	15.1	19.6	11.3	70.3	3.13	74.0
WY	I1	Forkwood, silt loam	.0269	1.11	1.02	15.9	23.1	23.6	34.9	2.21	17.3
	I2	Forkwood, loam	.0156	1.17	1.10	16.6	24.0	29.5	37.9	1.52	30.0
ID	J1	Robin, silt loam	.0308	0.95	0.82	8.5	25.2	17.4	16.3	5.60	46.8
	J2	Robin, silt loam	.0259	0.93	0.81	7.8	27.5	17.4	14.8	8.06	67.2
AZ	K1	Lonti, sandy loam	.0152	1.36	1.34	8.0	17.2	10.3	53.0	1.26	22.2
	K2	Lonti, sandy loam	.0165	1.14	1.16	6.7	16.5	6.6	56.4	0.72	9.4
CA	L1	Diablo, clay loam	.0162	1.39	1.29	14.6	24.9	37.9	32.7	1.76	69.3
	L2	Diablo, silty clay	.0176	1.35	1.29	12.3	22.6	42.8	15.4	2.39	78.8
UT	M1	Taylors Flat, sandy loam	.0193	0.99	1.20	11.1	18.7	10.7	67.3	0.60	---
	M2	Taylors Flat, sandy loam	.0179	1.45	1.29	8.6	16.3	11.1	65.7	1.17	4.5

[1] Gravimetric antecedent soil moisture

Table 3. Mean vegetative characteristics of each study site.

State	Site ID	Grass Cover	Grass & Forb Cover	Shrub & Cactus Cover	Bare Ground	Litter Cover	Annual Grass Biomass	Perennial Grass Biomass	Shrub Biomass	Litter Biomass	Total Standing Biomass	Root Biomass
		(%)	(%)	(%)	(%)	(%)	(kg ha^{-1})	(kg ha^{-1})	(kg ha^{-1})	(kg ha^{-1})	(kg ha^{-1})	(kg ha^{-1})
NE	B1	9.4	27.3	0	20.4	72.9	12	714	0	575	1100	4798
	B2	10.2	17.4	5.2	11.6	86.0	167	1849	207	763	3443	1653
TX	C1	9.8	10.9	0.5	3.0	83.2	0	1111	101	2383	1331	4695
	C2	8.9	8.9	T[1]	13.3	83.7	0	509	2	1694	510	5532
KS	E1	21.8	54.5	0.2	27.4	70.5	128	269	0	1679	1732	2573
	E2	52.2	58.8	T	23.6	74.3	0	1927	43	1310	2069	8593
	E3	32.2	37.2	0	41.8	55.2	5	404	15	387	508	6651
CO	F1	49.8	50.5	0	4.4	76.9	0	1124	0	2130	1126	4615
	F2	42.0	42.2	0.1	14.4	57.3	0	830	0	1753	831	6357
	F3	27.2	27.4	0.4	17.9	68.6	0	411	15	1789	427	11615
WY	G1	6.0	7.0	3.0	23.2	40.0	27	735	39	423	802	10239
	G2	53.9	54.8	0.7	18.9	77.4	763	1104	7	1047	1879	4021
	G3	27.6	30.1	0.5	53.1	32.1	0	722	4	174	766	8144
ND	H1	48.3	50.7	3.0	3.5	92.0	0	700	4	1534	810	6761
	H2	46.9	63.8	0.5	3.8	64.1	0	692	5	655	1416	7482
	H3	59.6	67.3	1.1	11.6	69.4	0	832	2	1139	1221	4089
WY	I1	19.4	21.0	28.3	38.4	55.6	0	425	494	1103	1730	3413
	I2	41.9	47.8	T	36.5	54.9	29	872	0	796	2246	1881
ID	J1	29.7	30.6	38.9	10.1	84.6	0	297	11	6413	774	3344
	J2	78.6	82.7	3.3	7.4	84.4	0	1194	112	4428	1422	7362
AZ	K1	31.2	45.8	1.6	50.7	28.7	29	474	3	216	782	912
	K2	34.6	39.1	10.6	49.8	26.0	3	566	481	735	1159	759
CA	L1	43.3	96.3	0	50.3	37.4	1171	0	16	177	2621	668
	L2	74.4	77.4	0	6.2	90.1	754	22	0	1730	817	883
UT	M1	3.0	5.1	20.7	59.6	29.5	0	45	405	4936	464	608
	M2	25.3	30.0	1.3	58.2	37.0	1	604	19	2717	3306	1490

[1] Trace amount

Table 4. Differences in cumulative infiltration (mm), terminal infiltration rate (mm hr^{-1}), runoff/rainfall ratio (mm mm^{-1}), total sediment (kg ha^{-1}), and sediment/runoff ratio (kg ha^{-1}) for each study site under dry antecedent soil moisture conditions. Means within a column and within a region/cover type followed by different letters are significantly different ($P < 0.10$).

State	Site ID	Cumulative Infiltration (mm)	Terminal Infiltration Rate (mm hr^{-1})	Runoff/ Rainfall Ratio (mm mm^{-1})	Total Sediment (kg ha^{-1})	Sediment/ Runoff Ratio (kg ha^{-1} mm^{-1})
NE	B1	26.6a	19.1a	0.51b	234.9b	8.8b
	B2	51.3b	49.7b[1]	0.00a	1.3a	1.9a
TX	C1	46.9b	41.7b	0.13a	68.7a	9.8a
	C2	31.2a	14.8a	0.44b	235.6b	10.0a
KS	E1	57.4a	54.5a[1]	0.00a	1.4a	12.1a
	E2	58.1a	58.1a[1]	0.00a	0.3a	2.8a
	E3	55.4a	52.2a	0.04b	17.7b	7.4a
CO	F1	42.4a	32.8a	0.28a	121.7a	8.3a
	F2	38.6a	31.6a	0.33a	119.9a	6.6a
	F3	35.8a	37.8a	0.36a	488.5b	27.2b
WY	G1	46.9b	48.1b	0.04a	21.3a	7.3a
	G2	53.7c	54.3b	0.05a	29.6a	12.7a
	G3	39.6a	32.5a	0.30b	293.1b	17.3a
ND	H1	48.8a	53.5b	0.09a	24.1a	6.9a
	H2	50.4a	53.0ab	0.08a	73.1b	17.4b
	H3	48.3a	49.3a	0.12a	47.5ab	6.9a
WY	I1	52.9a	51.4b	0.05a	77.6a	17.5a
	I2	47.1a	42.5a	0.14a	113.5a	10.2a
ID	J1	50.0a	49.3a	0.08a	28.8a	6.0b
	J2	48.7a	47.8a	0.11a	18.0a	3.5a
AZ	K1	42.8a	39.7a	0.23a	195.7a	11.5a
	K2	38.0a	33.6a	0.31a	158.6a	9.5a
CA	L1	56.7a	56.2a[1]	0.0a	0.3a	1.1a
	L2	60.4b	50.0a	0.02a	6.7a	1.5a
UT	M1	55.3a	53.4a	0.05b	49.2b	20.3b
	M2	56.9a	55.4a	0.01a	7.8a	9.3a

[1] Infiltration rate was greater than application rainfall rate.

analysis of variance was performed on vegetation states within each MLRA, and across MLRAs (with nesting), using SAS (SAS Institute 1999) General Linear Models. Treatment means were separated using the Student-Neuman-Kuels multiple range test with $P \leq 0.10$. The degree of linear association of variables most related to infiltration and erosion were evaluated using SAS Correlation procedures (Pearson correlation matrix). Forward multiple regression analysis ($P \leq 0.15$) identified variables that may estimate infiltration and erosion across MLRAs. Differences discussed in the text are statistically significant at the defined P-values unless indicated otherwise.

Results

Vegetation States Within MLRA

The vegetation states within the tallgrass prairie in Nebraska (B), the shortgrass prairie in Texas (C), and the mixed-grass prairie in Wyoming (G) showed the greatest contrast in cumulative infiltration, terminal infiltration rate, runoff/rainfall ratio, and total sediment under dry conditions (Table 4). Vegetation states of these grasslands had very dramatic differences in vegetation composition (Table 1), and were also the same grassland regions that showed differences in texture and aggregate stability between the vegetation states. The tallgrass prairie in Kansas (E), the annual grassland in California (L), and the mixed-grass prairie in North Dakota (H) showed only slight differences in cumulative infiltration, terminal infiltration rate, or total sediment among the different vegetation states studied. The shrub-steppe rangeland types exhibited few significant differences in cumulative infiltration or terminal infiltration rate. All sagebrush sites in Wyoming (I), Idaho (J), and Utah (M) tended to have greater sediment/runoff ratios for the sites without brush management, but this difference was only significant for Idaho (J) and Utah (M).

Differences in cumulative infiltration, terminal infiltration, and runoff/rainfall ratio between vegetation states were more apparent during the wet runs (Table 5). Only the annual grassland (L) and the Colorado shortgrass prairie (F) did not show significant differences in cumulative infiltration and/or terminal infiltration rate between their respective vegetation states. Vegetation states within grassland sites differed in total sediment and/or sedi-

Table 5. Differences in cumulative infiltration (mm), terminal infiltration rate (mm hr^{-1}), runoff/rainfall ratio (mm mm^{-1}), total sediment (kg ha^{-1}), and sediment/runoff ratio (kg ha^{-1}) for each study site under wet antecedent soil moisture conditions. Means within a column and within a region/cover type followed by different letters are significantly different ($P < 0.10$).

State	Site ID	Cumulative Infiltration (mm)	Terminal Infiltration Rate (mm hr^{-1})	Runoff/ Rainfall Ratio (mm mm^{-1})	Total Sediment (kg ha^{-1})	Sediment/ Runoff Ratio (kg ha^{-1} mm^{-1})
NE	B1	8.4a	17.7a	0.50b	29.6a	3.6a
	B2	25.1b	43.9b	0.07a	21.4a	11.9b
TX	C1	25.4b	40.5b	0.14a	48.3a	11.2b
	C2	15.5a	17.4a	0.46b	78.4a	6.2a
KS	E1	48.0b	50.6b	0.02a	17.2a	10.6b
	E2	56.5b	53.3b[1]	0.00a	0.0a	0.0a
	E3	16.3a	29.2a	0.39b	92.7b	8.9b
CO	F1	19.2a	18.6a	0.49b	81.9a	5.2a
	F2	23.2a	33.5a	0.29a	88.8a	9.7ab
	F3	18.5a	20.8a	0.47b	195.8b	12.8b
WY	G1	44.6b	40.7b	0.10a	75.6b	19.6a
	G2	37.4b	52.1c	0.06a	17.7a	7.6a
	G3	20.9a	24.6a	0.38b	134.5b	10.7a
ND	H1	51.7b	58.3b[1]	0.00a	0.6a	5.4a
	H2	31.1a	36.0a	0.18b	85.3b	10.2a
	H3	25.8a	33.4a	0.22b	67.8b	8.5a
WY	I1	21.5a	42.6b	0.14a	83.8a	17.9a
	I2	20.3a	27.1a	0.36b	113.1a	9.1a
ID	J1	40.6b	44.4a	0.11a	38.8a	7.1a
	J2	33.4a	50.9a	0.07a	8.9a	4.0a
AZ	K1	17.7a	27.1a	0.36a	75.3a	7.2a
	K2	17.2a	28.8a	0.36a	100.6a	10.0a
CA	L1	35.9a	14.0a	0.42a	179.4b	6.8b
	L2	28.7a	7.0a	0.41a	88.3a	4.5a
UT	M1	21.8a	38.1a	0.24a	110.9a	19.4a
	M2	58.8b	45.6a	0.50b	163.0a	17.0a

[1] Infiltration rate was greater than application rainfall rate.

Table 6. **Correlation coefficients for various canopy cover, ground cover, above-ground biomass, root biomass, and soil characteristic variable classes for total (cumulative) infiltration, terminal infiltration rate, total (cumulative) sediment (log10), and sediment/runoff ratio (log 10) on mixed and tall grass study sites. Only the highest correlated variable in each class and run is presented (some sites had few correlated variables). Correlations were performed for each state/region/cover type for both the dry and wet runs.**

State, Region, Cover Type	Hydrologic/Erosion Parameter	Canopy Cover Variables[1]		Ground Cover Variables[2]		Above-ground Biomass Variables[3]		Root Biomass Variables[4]		Soil Variables[5]	
		Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Nebraska, Tallgrass prairie, Bluestem prairie	1. Total Infiltration (mm)	-0.89 (forbs)	-0.95 (forbs)	-0.79 (basal)	-0.75 (basal)	0.85 (p grass)	0.94 (total)		-0.72 (average)	0.87 (ag stab)	0.99 (ag. stab)
	2. Terminal Infiltration Rate (mm hr^{-1})	-0.90 (forbs)	-0.83 (forbs)	0.73 (litter)	-0.56 (basal)	0.88 (p grass)	0.85 (total)	-0.63 (average)	-0.71 (average)	- 0.91 (sm surf)	-0.86 (sm surf)
	3. Total Sediment (kg ha^{-1})	0.93 (forbs)		0.81 (basal)		-0.88 (p grass)	-0.55 (p grass)	0.76 (average)		0.94 (sm surf)	0.64 (sm sub)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})	0.73 (forbs)	-0.78 (forbs)	0.62 (basal)	-0.63 (basal)	-0.73 (a grass)	0.95 (shrubs)	0.74 (average)	-0.53 (average)	0.75 (sm surf)	0.86 (ag stab)
Kansas, Tallgrass prairie, Bluestem prairie	1. Total Infiltration (mm)				0.71 (litter)		0.66 (p grass)		0.60 (surf.)		-0.77 (clay ss)
	2. Terminal Infiltration Rate (mm hr^{-1})				0.80 (litter)		0.74 (total)				-0.78 (clay ss)
	3. Total Sediment (kg ha^{-1})		-0.61 (st dead)	-0.78 (litter)	-0.74 (litter)	-0.57 (total)	-0.71 (total)			0.70 (clay ss)	0.88 (clay ss)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})		-0.82 (grass)	0.59 (basal)		-0.50 (litter)	-0.91 (p grass)		-0.62 (average)		0.94 (clay s)
Wyoming, Mixed grass prairie, Wheatgrass-needlegrass	1. Total Infiltration (mm)		0.70 (cacti)	-0.62 (bare)	-0.65 (bare)			-0.69 (sub)	0.63 (int surf)	0.67 (ag stab)	0.68 (ag stab)
	2. Terminal Infiltration Rate (mm hr^{-1})	-0.58 (forbs)	-0.65 (forbs)	-0.76 (bare)	-0.83 (bare)		0.63 (total)	-0.64 (sub)	-0.61 (sub)	0.80 (ag stab)	0.84 (ag stab)
	3. Total Sediment (kg ha^{-1})	0.60 (forbs)	0.52 (forbs)	0.75 (bare)	-0.62 (litter)	-0.78 (shrubs)			0.51 (average)	-0.62 (ag stab)	-0.69 (OC sub)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})			-0.62 (crypts)		-0.77 (shrubs)					
North Dakota, Mixed grass prairie, Wheatgrass-needlegrass	1. Total Infiltration (mm)		0.92 (st dead)		0.83 (litter)		-0.64 (total std)		0.80 (sub)		-0.75 (sm surf)
	2. Terminal Infiltration Rate (mm hr^{-1})		0.94 (st dead)		0.91 (litter)		-0.63 (total std)	0.52 (average)	0.82 (sub)		-0.75 (sm surf)
	3. Total Sediment (kg ha^{-1})		-0.92 (st dead)		-0.95 (litter)		0.66 (total std)			0.52 (sm surf)	0.77 (sm surf)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})	0.69 (forbs)		0.54 (crypts)	-0.58 (litter)	0.53 (forbs)				0.62 (sm surf)	

[1] st dead=standing dead

[2] crypts=cryptogams, bare=bareground

[3] p grass=perennial grass, a grass=annual grass, total=total yield, tot std=total standing biomass

[4] average=average over soil sampled, surf=surface, sub=subsurface, int surf=interspace surface

[5] ag stab=aggregate stability, sm surf=surface antecedent soil moisture, sm sub=subsurface antecedent soil moisture, clay s=surface clay content, clay ss=subsurface clay content, OC sub=subsurface organic carbon

ment/runoff ratio, although the differences were not well correlated to runoff/rainfall ratios. There were no significant differences in sediment yield or sediment load between any of the vegetation states for shrub sites studied.

The vegetation and soil variables most correlated with infiltration and erosion are presented for tall and mixed grasslands (Table 6), shortgrass and annual grasslands (Table 7), and shrub-steppe rangelands (Table 8). While there were a few variables that were common among some of the rangeland types, they varied widely in their significance. Litter, for example, was highly correlated with terminal infiltration rate (R = 0.91) on the North Dakota mixed grass sites (H, Table 6), but only slightly correlated with terminal infiltration rate (R = 0.53) on the sagebrush sites of Utah (M, Table 8). Some variables were positively correlated on some sites, but negatively correlated on others. For example, shrub biomass on the Nebraska tallgrass sites (B) was positively correlated with sediment loading, but negatively correlated on the Wyoming mixed grass sites (G, Table 6). These correlations demonstrate the extreme diversity of rangelands located in different MLRAs with respect

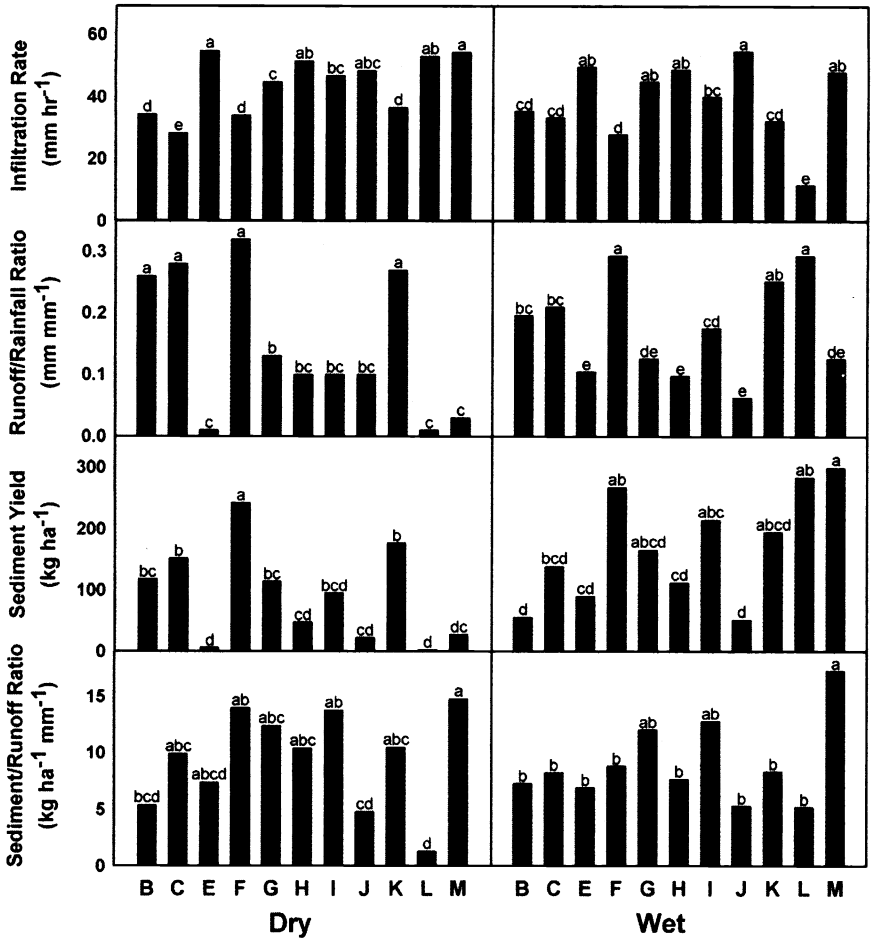

Fig. 2. Average a) terminal infiltration rate (mm hr^{-1}), b) runoff/rainfall ratio (mm mm^{-1}), c) total sediment (kg ha^{-1}), and d) sediment/runoff ratio (kg ha^{-1} mm^{-1}) for dry and wet runs for the 11 region/cover types studied. Values within dry or wet runs followed by a different letter are significantly different (P < 0.10).

to how soil and vegetation properties affect infiltration and erosion processes.

Across MLRAs

The 11 rangeland soil-vegetation assemblages were analyzed to compare differences in hydrologic response across MLRAs, assuming that the vegetation states represented the typical range of vegetation and soil conditions found within MLRAs. For the majority of MLRAs, average terminal infiltration rates for the dry runs ranged from 40 to 55 mm hr^{-1} (Fig. 2a). Slowest terminal infiltration rates occurred on the 3 grassland regions where shortgrass (or sodgrass) predominated. Wet terminal infiltration rates were slightly lower, but exhibited the same general pattern found in dry runs. The 1 exception, however, was annual grasslands. Dry terminal infiltration rates in annual grasslands were among the highest of the MLRAs, but the wet terminal infiltration rates were significantly lower than the other rangeland types. The shrink-swell clayey soils on these sites had extensive sub-surface cracking when dry, and apparently sealed off under wet soil moisture conditions. The runoff/rainfall ratio is a way to compare across sites when differing amounts of total precipitation were applied (but using the same target intensity of 65 mm/hour). Runoff/rainfall ratios (percentage of rainfall lost to runoff, Fig. 2b) basically showed the same general patterns as those observed for terminal infiltration rates.

Colorado shortgrass prairie (F) had the greatest amount of total sediment under dry conditions, followed by the shortgrass site in Texas (C) and the Arizona shrub-steppe (K, Fig. 2c). Under wet antecedent soil moisture conditions, greatest sediment loss occurred from the sagebrush site in Utah (M), the annual grasslands, and the shortgrass prairie site in Colorado (F). The tallgrass prairie regions in Nebraska (B) and Kansas (E), the mountain big sagebrush in Idaho (J), and the mixed grass prairie in North Dakota (H) had among the lowest total sediment production.

The sediment/runoff ratio provides a way to evaluate the erodibility of soil. Rangeland types with greater total sediment were not necessarily the MLRAs with the greatest soil erodibility. Under dry conditions, the Wyoming sagebrush site in Utah (M) ranked the highest for erodibility, and annual grasslands in California (L) the lowest (Fig. 2d). Sediment loading was greater from the 2 Wyoming sagebrush regions in Wyoming (I) and Utah (M) compared to the mountain big sagebrush region in Idaho (J). Under wet conditions, there were few differences between sites in sediment loading. Many rangeland types were actually less erodible during the wet run. These rangelands may be detachment-limited, whereby the majority of erodible material had already been removed the previous day during the dry run.

When all sites were pooled together, infiltration and sediment production were not well correlated with any measured vegetation or soil characteristic (R < 0.5). Forward multiple regression equations for infiltration and erosion variables were developed for both the dry (Table 9) and the wet runs (Table 10). Estimation equations containing 10 or more poorly correlated variables could explain only about 50% (dry condition) to 65% (wet condition) of the variation in infiltration and erosion occurring on all rangeland types. There was a slightly better fit for wet runs because of the removal of antecedent soil moisture as a source of variation. These regression equations were developed only to demonstrate why model dysfunction occurs when using these types of simplistic relationships (pooled data) for rangelands and should not be applied to management decisions.

Discussion

Infiltration and sediment production were differentially affected by vegetation and soil properties on rangeland types throughout the western United States. There were no consistent correlations or variables that affected infiltration or erosion on all sites. When all sites were pooled together, infiltration and sediment production were not well correlated (R < 0.5) with any measured vegetation or soil characteristic. The regression equations illustrate the poor fit that results when including all rangeland types. This type of

Table 7. Correlation coefficients for various canopy cover, ground cover, above-ground biomass, root biomass, and soil characteristic variable classes for total (cumulative) infiltration, terminal infiltration rate, total (cumulative) sediment (log10), and sediment/runoff ratio (log 10) on short and annual grassland study sites. Only the highest correlated variable in each class and run is presented (some sites had few correlated variables). Correlations were performed for each state/region/cover type for both the dry and wet runs.

State, Region, Cover Type	Hydrologic/Erosion Parameter	Canopy Cover Variables[1]		Ground Cover Variables[2]		Above-ground Biomass Variables[3]		Root Biomass Variables[4]		Soil Variables[5]	
		Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Texas, Shortgrass prairie, Blue grama-buffalograss	1. Total Infiltration (mm)	0.89 (st dead)		-0.78 (bare)				-0.72 (sub)		0.94 (ag stab)	0.85 (ag. stab)
	2. Terminal Infiltration Rate (mm hr^{-1})	0.85 (st dead)	0.68 (forbs)	-0.67 (bare)	0.60 (basal)	0.66 (total std)	0.56 (total std)	-0.74 (sub)	-0.55 (sub)	0.94 (ag stab)	0.80 (ag stab)
	3. Total Sediment (kg ha^{-1})	-0.81 (st dead)	-0.51 (st dead)	0.63 (bare)						0.82 (sm sub)	
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})		0.71 (forbs)		-0.61 (bare)		0.61 (forbs)		-0.54 (average)		-0.87 (BD ave)
Colorado, Mixedgrass prairie, Wheatgrass-grama-needlegrass	1. Total Infiltration (mm)						-0.51 (total)			0.65 (sm sub)	
	2. Terminal Infiltration Rate (mm hr^{-1})					-0.61 (forbs)	-0.56 (total)				
	3. Total Sediment (kg ha^{-1})	-0.74 (grass)				-0.51 (p grass)				0.79 (sm surf)	-0.50 (wBD s)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})	-0.69 (grass)				0.57 (shrubs)				0.78 (sm surf)	0.56 (sand s)
California, Annual grassland, Valley grassland	1. Total Infiltration (mm)	-0.86 (forbs)			-0.56 (litter)	-0.80 (total std)	-0.68 (p grass)	0.74 (sub)		0.81 (ag stab)	
	2. Terminal Infiltration Rate (mm hr^{-1})				-0.51 (litter)	-0.68 (p grass)				0.71 (sm surf)	
	3. Total Sediment (kg ha^{-1})		0.58 (forbs)			0.74 (p grass)	0.71 (shrubs)			-0.74 (sm sub)	0.63 (sm sub)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})		0.54 (forbs)		-0.67 (litter)	0.54 (p grass)	-0.65 (litter)			-0.55 (sm sub)	-0.59 (ag stab)

[1] st dead=standing dead

[2] bare=bareground, basal=basal cover

[3] p grass=perennial grass, total=total yield, total std=total standing biomass

[4] average=average over soil sampled, sub=subsurface

[5] ag stab=aggregate stability, sm surf=surface antecedent soil moisture, sm sub=subsurface antecedent soil moisture, BD ave=dry BD averaged over soil sampled, wBD s=surface wet BD, sand s=surface sand content

pooled multiple regression equation is often used in the development of process models (Flanagan and Livingston 1995, Foster and Lane 1987), and the relatively low R^2 value (0.5 to 0.65) illustrates why infiltration and/or erosion estimates are inaccurate for some rangelands. Spaeth et al. (1996a) also found that universal equations representing a wide variety of rangeland plant communities were not as robust compared to equations develop for specific plant communities, due to the unique nature of plant communities. Weltz et al. (2000) also recommend partitioning rangelands according to soil functional units and developing nonlinear predictive equations to estimate infiltration for rangelands based on vegetation and soil characteristics.

Within rangeland types (within MLRA), there were generally an adequate array (Franks et al. 1993) of vegetation and soil characteristics representing the range of typical vegetation states that helped point out the most important factors affecting infiltration and erosion on these soil types. In some cases, it was difficult to identify important variables due to highly variable runoff and erosion responses, especially on arid shrub-steppe rangelands. These rangelands are typified by high microsite variability in the spatial location of shrub coppices and interspaces, leading to greater variability between individual plots (Pierson et al. 1994, Blackburn 1975, Johnson and Gordon 1988).

Generally, dry-run infiltration rates ranged from 40 to 55 mm hr^{-1} for most sites. Those sites with lower infiltration rates (< 40 mm hr^{-1} for the dry runs) were dominated by shortgrasses or sod-forming grasses and this is consistent with the literature (Blackburn 1975, Wood and Blackburn 1981, Knight et al. 1984, Thurow et al. 1986,1988, Thurow 1991, Spaeth et al. 1996a).

Sediment production from all sites was less than 300 kg ha^{-1}. However, greater sediment/runoff ratios for some sites indicate a potential for more sediment loss should large, intense storms produce significant runoff. Under dry conditions, sites in Colorado (F3), Wyoming (G3, I1), North Dakota (H2), and Utah (M1) had greater potentials to produce higher sediment loads with large runoff events. Most of these sites tended to have higher bare soil exposure coupled with less litter and grass cover. Under wet conditions, sites in Wyoming (I1) and Utah (M1) still had a greater erosion potential from large runoff events. In addition, the Utah sagebrush site with brush management (M2) also had

Table 8. Correlation coefficients for various canopy cover, ground cover, above-ground biomass, root biomass, and soil characteristic variable classes for total (cumulative) infiltration, terminal infiltration rate, total (cumulative) sediment (log10), and sediment/runoff ratio (log 10) on shrub-steppe study sites. Only the highest correlated variable in each class and run is presented (some sites had few correlated variables). Correlations were performed for each state/region/cover type for both the dry and wet runs.

State, Region, Cover Type	Hydrologic/Erosion Parameter	Canopy Cover Variables[1]		Ground Cover Variables[2]		Above-ground Biomass Variables[3]		Root Biomass Variables[4]		Soil Variables[5]	
		Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Wyoming, Sage-grass-shrub steppe, Wyoming big sagebrush	1. Total Infiltration (mm)	-0.88 (forbs)	-0.65 (forbs)	0.58 (litter)	0.63 (litter)	0.63 (litter)	0.75 (a grass)	0.64 (int surf)	0.87 (int surf)		-0.75 (sm sub)
	2. Terminal Infiltration Rate (mm hr^{-1})	-0.88 (forbs)	-0.84 (forbs)	-0.68 (rock)	-0.68 (rock)	0.68 (litter)	0.81 (litter)	0.68 (int surf)	0.84 (int surf)	-0.50 (BD ss)	-0.78 (sm sub)
	3. Total Sediment (kg ha^{-1})	0.65 (forbs)	0.54 (forbs)	-0.63 (litter)		-0.67 (litter)	-0.76 (litter)	-0.61 (int ave)	-0.63 (int ave)	0.53 (BD ave)	0.59 (sm sub)
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})	-0.54 (st dead)				-0.63 (p grass)		0.53 (average)		0.54 (BD s)	0.53 (BD s)
Idaho, Sage-grass-shrub steppe, Mountain big sagebrush	1. Total Infiltration (mm)		0.68 (shrubs)				0.76 (forbs)				-0.71 (sm surf)
	2. Terminal Infiltration Rate (mm hr^{-1})				-0.67 (bare)				-0.59 (int sub)		
	3. Total Sediment (kg ha^{-1})	-0.56 (forbs)	0.56 (st dead)								
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})	0.59 (st dead)	0.60 (st dead)							0.59 (sm sub)	
Arizona, Shrub steppe-shortgrass, Grama-galleta	1. Total Infiltration (mm)	0.50 (forbs)		-0.53 (basal)			-0.72 (p grass)		0.56 (int surf)		0.55 (wBD ss)
	2. Terminal Infiltration Rate (mm hr^{-1})	0.56 (forbs)		-0.62 (basal)	0.51 (basal)		-0.85 (p grass)		0.70 (int surf)		
	3. Total Sediment (kg ha^{-1})	0.70 (st dead)	0.52 (st dead)				-0.75 (a grass)		-0.70 (int ave)		
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})		0.65 (st dead)	0.51 (crypts)	0.51 (crypts)	-0.53 (a grass)	-0.67 (a grass)		-0.57 (int ave)		
Utah, Shrub steppe, Wyoming big sagebrush	1. Total Infiltration (mm)		0.86 (grass)	0.52 (litter)	0.74 (litter)		-0.75 (shrubs)		0.73 (average)		0.88 (BD ss)
	2. Terminal Infiltration Rate (mm hr^{-1})			0.59 (litter)	0.53 (litter)		0.55 (forbs)				-0.67 (sm sub)
	3. Total Sediment (kg ha^{-1})	-0.53 (grass)		-0.89 (litter)				-0.52 (average)	0.53 (int ave)	-0.64 (BD s)	
	4. Sediment/Runoff Ratio (kg ha^{-1} mm^{-1})	0.60 (shrubs)		-0.76 (litter)		0.53 (shrubs)		-0.71 (int ave)		0.62 (sm surf)	

[1] st dead=standing dead

[2] crypts=cryptogams, bare=bareground, basal=basal cover

[3] p grass=perennial grass, a grass=annual grass

[4] average=average over soil sampled, int surf=interspace surface, int avg=interspace average

[5] sm surf=surface antecedent soil moisture, sm sub=subsurface antecedent soil moisture, BD s=surface dry BD, BD ss=sub-surface dry BD, BD avg=average dry BD, wBD ss=sub-surface wet BD

a sediment/runoff ratio exceeding 16.0 kg ha^{-1} mm^{-1}, as did the prickly pear cactus-dominated mixed grass prairie site in Wyoming (G1).

Universal Assumptions

The assumptions about hydrology and erosion relationships that were presented in the introduction did not hold true for all rangeland types studied. For every rangeland site in this data set that reinforced the generalized assumptions, there was another rangeland site that refuted them.

Rangeland ecological status/similarity index is directly related to hydrologic condition

Greater ecological status or seral state was not always associated with improved hydrologic condition. For example, the cheatgrass site in Wyoming (G1) had similar infiltration to the late seral site dominated by native mid and short grasses (G3). Differences in bare ground and litter cover were more important than seral state in determining infiltration rates in this case. The same was true for the heavily grazed broomweed site (E1) in Kansas. This site had similar runoff and infiltration rates as compared to site E2 (dominated by mid and tall grasses) despite its early

Table 9. Forward regression equations for dry run infiltration and erosion variables developed across all Major Land Resources Areas (MLRSs).

Variable	Terminal Infiltration Rate (mm hr^{-1})	Total Infiltration (mm)	Runoff/Rainfall Ratio (mm mm^{-1})	Total Sediment ($\log_{10}$) (kg ha^{-1})	Sediment/Runoff Ratio ($\log_{10}$) (kg ha^{-1} mm^{-1})
Intercept	60.06	19.31	-0.23	2.99	1.38
Variable 1	13.73 Grass Cover	9.75 Grass Cover	-5.10 Cacti Cover	-51.80 Cacti Cover	-18.35 Cacti Cover
Variable 2	7.95 Wet Surface Bulk Density	354.25 Surface Roughness	0.53 Basal Cover	-0.63 Dry Surface Bulk Density	-2.89 Slope
Variable 3	-25.92 Dry Sub-surface Bulk Density	10.85 Wet Surface Bulk Density	0.36 Dry Sub-surface Bulk Density	-0.0001 Total Standing Biomass	-0.0001 Perennial Grass Biomass
Variable 4	0.008 Annual Grass Biomass	0.002 Total Standing Biomass	-0.0001 Annual Grass Biomass	0.00005 Root Biomass	0.00003 Root Biomass
Variable 5	0.003 Total Standing Biomass	0.29 Surface Cation Exchange Capacity	-0.00004 Total Standing Biomass	-0.041 Surface Cation Exchange Capacity	-0.017 Surface Cation Exchange Capacity
R^2	0.33	0.38	0.36	0.47	0.30
R^2 Maximum (Complete Model, 10+ variables)	0.48	0.57	0.52	0.56	0.41

seral state, apparently because of equivalent vegetation production, litter cover, and bare soil exposure.

The shortgrass/mixed grass prairie sites in Colorado had contrasting composition, production, and bare soil exposure and differed in their ecological status. Despite these differences, infiltration rate did not differ between the sites during either the dry or wet run. Spaeth et al. (1996b) also found that range ecological status may or may not be correlated to hydrologic condition, depending on the structure and demography of the plant community.

Sediment production is highly correlated with amount of infiltration/runoff

Site characteristics affect infiltration and erosion processes in different ways. Therefore, sediment production may not be well correlated with amount of runoff. For example, total sediment for the wet run did not differ between vegetation states in the tallgrass prairie of Nebraska (B) or the shortgrass prairie of Texas (C) despite large differences in infiltration. Likewise, sites F1 and F3 in the shortgrass prairie of Colorado had similar runoff for the dry and wet runs, but site F1 had a lower sediment load than site F3. Less production of perennial grasses apparently led to greater sediment production from the heavily grazed F3 site. While California annual grassland sites (L1 and L2) did not differ in infiltration or runoff/rainfall ratio during

Table 10. Forward regression equations for wet run infiltration and erosion variables developed across all Major Land Resource Areas (MLRAs).

Variable	Terminal Infiltration Rate (mm hr^{-1})	Total Infiltration (mm)	Runoff/Rainfall Ratio (mm mm^{-1})	Total Sediment ($\log_{10}$) (kg ha^{-1})	Sediment/Runoff Ratio ($\log_{10}$) (kg ha^{-1} mm^{-1})
Intercept	37.62	17.64	0.44	2.20	1.31
Variable 1	60.85 Standing Dead Cover	32.72 Forb Cover	-0.59 Standing Dead Cover	-1.14 Standing Dead Cover	-0.42 Grass Cover
Variable 2	-0.96 Surface Soil Moisture	68.04 Standing Dead Cover	0.015 Surface Soil Moisture	-30.88 Half-shrub Cover	0.50 Cryptogam Cover
Variable 3	0.37 Surface Sand Content	-1.43 Surface Soil Moisture	-0.005 Surface Sand Content	0.021 Surface Soil Moisture	-0.010 Surface Soil Moisture
Variable 4	-19.66 Dry Subsurface Bulk Density	0.26 Surface Sand Content	0.074 Dry Subsurface Bulk Density	-0.0003 Perennial Grass Biomass	0.00005 Forb Biomass
Variable 5	17.52 Subsurface Organic Carbon	17.41 Subsurface Organic Carbon	-0.24 Subsurface Organic Carbon	-0.46 Subsurface Organic Carbon	-0.00008 Perennial Grass Biomass
R^2	0.60	0.54	0.59	0.50	0.24
R^2 Maximum (Complete Model, 10+ variables)	0.66	0.69	0.69	0.56	0.29

the wet run, L1 had twice the sediment yield as L2. L2 had significantly less exposed bare soil and more litter cover than L1. In this case, overland flow velocity was reduced on L2, thus producing less sediment compared to L1.

Quantity of plant material and litter is positively correlated with infiltration

Tallgrass prairie sites in Nebraska (B) represented highly contrasting vegetation states. Site B1 represented a Kentucky bluegrass-dandelion dominated site that had been subjected to heavy season-long use for many years. Site B2 was not grazed (hay meadow) and was dominated by primrose and mid and tall grasses with 3 times the productivity of B1. Cumulative infiltration and infiltration rate for both the dry and wet runs were negatively correlated with basal cover, but positively correlated with total yield. Litter cover and/or biomass were not strongly correlated with infiltration on 5 out of 11 rangeland sites, and total biomass was a correlate on only 4 rangeland types. Individual plant species or overall species composition and the structural component of the plant community may be more important than total cover or biomass (Spaeth et al. 1996a, 1996b). Root morphology, plant growth form and architecture, spatial pattern of plants, soil chemical or physical factors, soil crusts, and micro flora, etc. are attributes of the plant community (associated with individual species or community structure) which can influence infiltration and erosion, but are difficult to measure (Spaeth et al. 1996a).

Brush management alters hydrology and erosion

The Wyoming big sagebrush sites in Wyoming (I) differed in grass and shrub cover due to brush control on site I2 (prescribed burn 3 years prior to study). Infiltration differed slightly for both the dry and wet runs, but total sediment was equivalent for both sites (I1, I2). The mountain big sagebrush sites in Idaho (J) also differed primarily in shrub and grass cover due to brush control on site J2 that reduced shrub cover from 40% to about 5% (chemical control eight years prior to study). Yet infiltration rates and total sediment did not differ between the 2 sites (J1, J2). Both sites had relatively high surface and subsurface organic carbon contents and surface roughness that probably contributed to the good infiltration rates measured on both sites. The Wyoming big sagebrush sites in Utah (M) represented differences between an undisturbed site (M1) and a site that had a history of brush control (chemical control 3 years prior to study)(M2). There were no differences in infiltration rate for the dry or wet run, and only the dry run showed slight differences in total sediment production.

High variability in hydrologic response among plots within a site in some cases made it difficult to discern true differences between vegetation states. This was especially true on the range sites where undisturbed shrub and shrub-converted sites were compared. Soil characteristics and structure associated with shrub-interspace zonation may still exist after conversion (Hester et al. 1997), resulting in similar hydrologic response despite differences in shrub cover. Also, greater variability in soil and vegetation characteristics due to this zonation makes predictive relationships more difficult to ascertain (Pierson et al. 1994).

Vegetation characteristics dominate rangeland hydrology response

Annual grasslands in California (L) had the highest infiltration rates under dry soil conditions, but wet infiltration rates were the slowest measured on any site. These clayey soils (high smectite content) had sub-surface cracking under dry conditions, leading to preferential flow. Once wet, these cracks closed and infiltration rates measured were the lowest for the wet runs. The L1 and L2 sites varied considerably in the amount of bare ground, litter cover, grass cover and biomass, total standing biomass, and litter biomass, yet infiltration and erosion differed very little between the two vegetation states. Vegetation characteristics such as total standing biomass and litter were actually negatively correlated with infiltration. Soil properties, rather than vegetation characteristics, were the predominant factor controlling hydrologic response on these annual grasslands.

Implications

The examples presented above emphasize the difficulty in the "one size fits all" modeling approach in developing universal algorithms to include all rangeland types. While the amount of vegetation and corresponding litter have been found to be the most correlated variables with infiltration (Branson et al. 1981), others have found that the relationship between plant cover/litter and infiltration rates is not well established on semiarid rangelands (Gifford 1968, Blackburn 1975). The amount (biomass and cover) and type of vegetation and litter, canopy structure, rooting patterns, soil physical properties, small-scale spatial variability, bare soil exposure, potential for soil crusting, slope gradient, consumptive water use, and seasonal dynamics can affect hydrology and erosion to varying degrees depending on the plant community type (Rauzi 1960, Johnson 1962, Branson and Owens 1970, Meeuwig 1970, Tromble et al. 1974, Blackburn 1975, Davis and Pase 1977, Branson et al. 1981, Wood and Blackburn 1981, Hibbert 1983, Knight et al. 1984, Thurow et al. 1986, 1988 Johnson and Gordon 1988, Wilcox et al. 1988, Holmstead 1989, Hicks et al. 1990, Thurow 1991, Pierson et al. 1994, Spaeth et al. 1996a, 1996b, Weltz et al. 1998). The NRST data set provides some information as to the degree of influence that various soil and vegetation variables have on infiltration and erosion. However, it also emphasizes the difficulty in determining hydrologic relationships on semiarid rangelands, where infiltration rates are determined from a myriad group of factors that are different (or differ in importance) depending on rangeland type and site conditions.

There are quite a few generalizations or assumptions about the relationships between rangeland soil and vegetation characteristics and infiltration and erosion, and there are examples presented in the NRST dataset that both confirm and refute these generalizations. The regression equations presented highlight the poor fit that results when including all rangeland types. Previous models that have attempted to characterize rangeland infiltration and erosion using similar generalized or generic models/algorithms have not performed well because of this complex interaction of factors that differ from one soil-vegetation assemblage to the next (Pierson et al. 2001). A new paradigm to organize rangeland communities into "functional" units according to similarity in relationships and responses could aid in the development of better models to more accurately predict infiltration and erosion on rangelands.

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Viewpoint: The ecological value of shrub Islands on disturbed sagebrush rangelands

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Abstract

Undisturbed plant communities dominated by shrubs or trees are often left isolated within landscapes otherwise devoid of woody vegetation following large-scale disturbances such as wildfires. We discuss potential ecological benefits associated with these terrestrial vegetation "islands", giving special attention to islands in disturbed shrub systems dominated by big sagebrush (*Artemisia tridentata* Nutt.). Shrub habitat islands provide important refugia for plant and animal species that are associates of shrubs—from those that generally require shrub cover to those that have evolved obligate symbioses with a particular shrub species. Even if islands are not able to support breeding populations, they may provide essential temporary habitat for maintaining a plant or animal metapopulation or for dispersing animals. Habitat islands are likely to enhance local biological diversity of plants and animals, because they harbor species that are lacking in disturbed areas, and because abrupt structural changes from disturbed to undisturbed vegetation provide a habitat mosaic that facilitates high levels of species turnover. A previous study confirmed that small mammal species richness in sagebrush islands is intermediate to the high species richness in undisturbed sagebrush "mainlands" and the low richness associated with burned sagebrush habitats. In re-analyzing some of the data from the latter study, we found that small mammal richness in sagebrush islands increases with time since the surrounding habitat burned. Finally, habitat islands provide more evenly dispersed seed sources for re-establishment of decimated vegetation within disturbed areas, and they may harbor animal species that provide seed dispersal services. Thus, they should accelerate vegetation recovery after disturbance. Managers, fire crews, and others who may influence how disturbance patterns affect habitat heterogeneity should be aware of these ecological benefits of habitat islands.

Key Words: *Artemisia tridentata* Nutt., biological diversity, disturbance, Island Biogeography Theory, succession, terrestrial habitat islands

Resumen

Comunidades vegetales sin disturbio dominadas por arbustos y árboles a menudo se quedan aisladas dentro de los paisajes desprovistos de vegetación leñosa después de ser sujetos a disturbios de gran escala como fuegos naturales. Discutimos los beneficios ecológicos potenciales asociados con esta "islas" terrestres de vegetación, poniendo especial atención a las islas en los sistemas arbustivos disturbados dominados por "Big sagebrush" (*Artemisia tridentata* Nutt.). Las islas de arbustos se proveen un refugio importante para especies de plantas y animales que están asociadas a los arbustos, desde aquellas que generalmente requieren de una cobertura de arbustos hasta aquellas que han evolucionado simbiosis obligadas con especies arbustivas particulares. Aun si las islas no son capaces de soportar poblaciones en reproducción ellas pueden proveer un hábitat temporal esencial para mantener una población de plantas o animales o para animales dispersantes. Los hábitats de las islas probablemente aumentarán la diversidad biológica de plantas y animales porque ellas refugian especies de las que carecen las áreas distrubadas y porque los cambios estructurales abruptos de una vegetación disturbada a una sin disturbio proveen un mosaico de hábitats que facilitan altos niveles de movimiento de especies. Un estudio previo confirmo que la riqueza de especies de pequeños mamíferos en las islas de "Sagebrush" es intermedia entre la alta riqueza de especies de las áreas sin disturbio y la baja riqueza asociada con los hábitats de "Sagebrush" quemados. Al reanalizar los datos del último estudio encontramos que la riqueza de pequeños mamíferos en las islas de "Sagebrush" aumenta con el tiempo a partir de los hábitats quemados que las rodean. Finalmente, los hábitats de las islas proveen fuentes de semilla con una dispersión mas uniforme para el reestablecimiento de la vegetación diezmada dentro de las áreas disturbadas y ellas también pueden refugiar especies animales que pueden dispersar la semilla. Así, ellos deben acelerar la recuperación de la vegetación después de un disturbio. Manejadores, cuadrillas de bomberos y otros quienes pueden influir en como los patrones de disturbio afectan la heterogeneidad de hábitats debe estar alerta de estos beneficios ecológicos de las islas de hábitat.

An alarmingly high proportion of arid western rangelands has been and continues to be converted to weedy monocultures as a result of disturbances that devastate native plant communities. The specific disturbance that has caused this floristic conversion on the most extensive spatial scale is undoubtedly wildfire. Dense understories of non-indigenous, herbaceous weeds among native arid shrub communities have permitted fire to become commonplace in contemporary desert or semi-desert environments, where it was historically infrequent or even virtually absent (Billings 1990, Longland and Young 1995). Although the scale of catastrophic fires can denude the vast majority of an entire landscape

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of native vegetation, patches or "islands" of vegetation are often left isolated within the burned matrix due to natural or human-made firebreaks, changes in wind direction while a fire burns, or other fortuitous causes (Fig. 1). We believe that such islands of unburned native vegetation embedded within an extensive disturbance have potentially great ecological value, and we discuss those values here. Although we focus on fire as a disturbance agent and on shrub habitat islands dominated by big sagebrush (*Artemisia tridentata* Nutt.), the benefits of such islands are applicable to other agents of disturbance and perhaps to islands of native herbaceous vegetation, as well.

Fig. 1. Large (> 37 ha) sagebrush island isolated within a burned landscape near Pyramid Lake, Nev.

Habitat Islands as Refuges

There are several species that are obligate associates of the shrub species that dominate undisturbed sagebrush rangelands. These include understory plant species that utilize shrubs as nurse plants, species that are parasitic on shrubs, herbivores on shrubs, and animal species that require the habitat structure provided by shrubs.

Insect herbivores are often highly specialized on particular plant species, including sagebrush (Christiansen et al. 1989, Wiens et al. 1991). Various species of moths (Hsiao 1986, Strenge and Zack 2001) and beetles (Pringle 1960), for example, are known to impact sagebrush, sometimes causing significant mortality. Any such phytophagous species that feeds specifically on sagebrush will obviously be doomed locally wherever sagebrush has been removed by disturbance. Such specialization is less common and usually less extreme among terrestrial vertebrates than in insects, but it does still occur. Sage grouse (*Centrocercus urophasianus*) and sagebrush voles (*Lagurus curtatus*), for example, require sagebrush in their diets, and would quickly perish where sagebrush has been removed by fire (cf., Nelle et al. 2000). Refugia provided by sagebrush islands could be very important to such species. This has particular practical significance in the case of sage grouse, a species that may be granted threatened status in the near future. Some herbivores that are more generalized, such as mule deer (*Odocoileus hemionus*), frequently include certain subspecies or varieties of sagebrush in their diets (Wambolt 2001, Welch and McArthur 1986), and thus would also be expected to be negatively impacted by sagebrush removal.

There are also many animal species with niche requirements that include some degree of habitat complexity, such as that provided by shrub cover. One such species, the pygmy rabbit (*Sylvilagus idahoensis*), is an obligate associate of sagebrush habitats (Weiss and Verts 1984), and, like the sage grouse, may be given threatened status soon. There are many other examples of small vertebrates that routinely avoid disturbed shrub communities, not because of specialization on sagebrush or some other plant species that is lacking after the disturbance, but because they would be at greater risk of predation due to increased conspicuousness where shrub cover is absent (Longland and Price 1991). These examples illustrate that, in addition to the shrub species that are directly impacted by disturbance, many closely associated species may also persist only within shrub mainland and island habitats following a large-scale disturbance.

Shrub habitat islands provide benefits to dispersing animals as well as residents within the islands. For any shrub-associated species with limited dispersal ability, shrub islands provide "stepping stones" by acting as temporary refuges to facilitate dispersal. Shrub islands may be useful in this regard even when they are too small to retain a breeding population. Similarly, habitat islands can provide essential temporary habitat for transient animals or for the maintenance of a metapopulation, a group of spatially disjunct subpopulations that are interlinked and maintained by occasional dispersal among the subpopulations. For example, certain small mammal species concentrate within sagebrush islands in high densities following fires, and the islands may therefore serve an important function in the persistence of a metapopulation of these species (Bateman 1999). For such species, sagebrush islands can not only maintain metapopulation structure by facilitating recolonization of extinct subpopulations through dispersal; these habitat islands may also serve to reduce local extinction probability, which appears to be relatively more important to metapopulation persistence than an increase in the probability of recolonization (Etienne and Heesterbeek 2001).

Biological Diversity

Island Biogeography Theory (IBT) is a well developed set of ideas that generate predictions concerning how physical attributes of islands should affect the diversity of species occurring on those islands. The theory reasons that the number of species that are able to successfully colonize an island from a mainland source is positively related to the size of the island, because more species can potentially coexist in a larger area, and is negatively related to the distance of the island from the mainland, because successful dispersal is less likely as distance increases. Island Biogeography Theory, as conceived by MacArthur and Wilson (1967), was intended for application to true oceanic islands, but its concepts were soon applied to the insularization of terrestrial environments, such as forested mountains surrounded by desert valleys (Brown 1971). We might expect these areas to represent "biological islands" to the species that are unique to such environments. Island Biogeography Theory may thus provide a useful framework for considering effects of shrub insularization on biological diversity.

One assumption of IBT almost certain to be true of shrub islands isolated by disturbance is that the species occurring in the islands are a subset of those that occur in undisturbed mainland plant communities. Habitat islands may contain the majority of the mainland species, but except for very large islands, they are likely to at least lack uncommon mainland plant species. And, while they may lack certain species that could potentially exist there, these unburned shrub islands certainly harbor species of woody shrubs that are lacking in surrounding burned areas. Like unburned mainland habitats, unburned islands also generally include (albeit in lower densities) the same native herbaceous plants and the same introduced weeds that quickly establish in and dominate the burned areas. By contrast to unburned vegetation associations, early successional vegetation within burned areas is usually composed of just a small subset of the local plant species pool and often approaches a monoculture.

It is clear, then, that for some time during early post-fire succession unburned shrub islands harbor both more plant species and consequently greater floristic genetic diversity than does the surrounding disturbed area. Such measures of diversity within a relatively small patch are often referred to as α-diversity, whereas β- and γ-diversity describe, respectively, the degree of species turnover among different patches in an area and the distinctness of patches across a landscape (Longland and Young 1995). Because entire plant taxa represented in unburned areas are absent from surrounding burns, species turnover between burned and unburned patches is dramatic, and the distinctness of burned versus unburned patches across a landscape is apparent. Thus, unburned vegetation islands enhance floristic β- and γ-diversity at these larger spatial scales, as well as α-diversity within the islands themselves.

In theory, animal biodiversity should also be greater in unburned plant communities than in the more uniform habitats provided by early successional, post-fire vegetation, and there is some empirical evidence that this is so. First, in comparative studies of small mammal species diversity in burned and adjacent unburned sagebrush habitats, species richness and evenness tended to be greater in the unburned, intact shrub communities (Longland 1995, Halford 1981). Second, in an extensive study comparing small mammal communities in burned areas, sagebrush islands within the burns, and in adjacent, continuous sagebrush communities, small mammal species richness typically was greatest in continuous sagebrush, lowest in the burned areas, and intermediate in the islands (Bateman 1999). Furthermore, such beneficial effects of habitat islands may extend to higher trophic levels in a "bottom-up" fashion; by providing refugia for prey species, islands could favor enhanced local diversity of predator species as well (Hixon and Beets 1993).

Another assumption of IBT that is likely to hold true in the context of terrestrial islands isolated by large-scale disturbances, is that island size should be positively related to the number of species inhabiting islands. First, chance inclusions of rare plant or animal species are simply more likely to occur within large islands than smaller islands. Also, larger islands offer more opportunities for heterogeneity in soil types, exposure, topography, and other landscape features that are likely to promote plant species diversity. The greater diversity of plants and physical features in larger islands should also translate into greater animal species diversity. Moreover, larger islands are more likely to include larger animal species, because their home range requirements may exceed the amount of habitat offered by many small islands.

The utility of another assumption of IBT—that the distance an island is isolated from mainland should be inversely related to species diversity harbored by the island—is less clear for terrestrial habitat islands than the assumption concerning island size. When a disturbance, such as fire, leaves behind an isolated island of habitat, there is no reason why the diversity of species contained within the island should be influenced by the distance that the island is left isolated from undisturbed (i.e., mainland) habitat. A distantly isolated island is likely to contain as many species after a fire as an island that is very close to the edge of the burned area. In classical IBT, it is the long-term processes of colonization and extinction of species on islands that leads to the expectation that greater isolation yields lower species diversity. The extinction rate of species is expected to be independent of isolation distance, while colonization is more likely on near than far islands. For terrestrial islands, however, isolation from their mainland species sources is not as difficult to overcome as the isolation of true oceanic islands. Many animal species, especially those with generalized habitat affinities, may be uninhibited from crossing large disturbances to reach habitat islands. Furthermore, the degree of isolation decreases over time for a terrestrial island as the disturbed area that isolates it undergoes succession and becomes more similar to the island and mainland habitats. Thus, the effect of isolation distance in habitat islands may be much greater on a short-lived species, especially one with poor dispersal ability, such as some flightless insects, small mammals, or annual plants, than on longer-lived species, such as woody shrubs. For long-lived taxa, the disturbed habitat surrounding an insularized population may undergo succession rapidly enough that the population is no longer effectively isolated by the time mortality within the island proceeds far enough to cause a risk of local extinction.

If one considers isolation of habitat islands in terms of effects of time and succession, IBT may offer relatively more insight into the value of these islands than it does through the usual considerations of isolation by distance. As an illustration, we reanalyzed Bateman's (1999) data on small mammal species richness in 23 sagebrush islands created by fire versus paired sagebrush "mainlands". Small mammal species richness was reduced in 19 of the islands compared with local species pools; only 4 islands contained all possible species. The mean age (i.e., time since burning) of the latter 4 islands was approximately double that of islands with reduced species numbers (16.0 vs. 8.1 years, respectively), a significant difference based on the 1-tailed expectation of lower species richness resulting from greater isolation (less time for succession, and therefore less similar vegetation between burned and unburned areas; Fig. 2a; 1-tailed $t = 2.01$; $d.f. = 21$, $P = 0.029$). Relaxing the requirement of all species being sampled within the islands, we considered only those 10 sites in Bateman's data with ≤ 5 small mammal species. At 4 of these sites where $\geq 80\%$ of the local small mammal species occurred in sagebrush islands, mean time since the burn which isolated the islands was, again, significantly greater (16.8 years) than at the 6 sites where $< 60\%$ of species were retained in the island habitats (9.2 years; Fig. 2b; 1-tailed $t = 2.78$, $d.f. = 8$, $P < 0.012$).

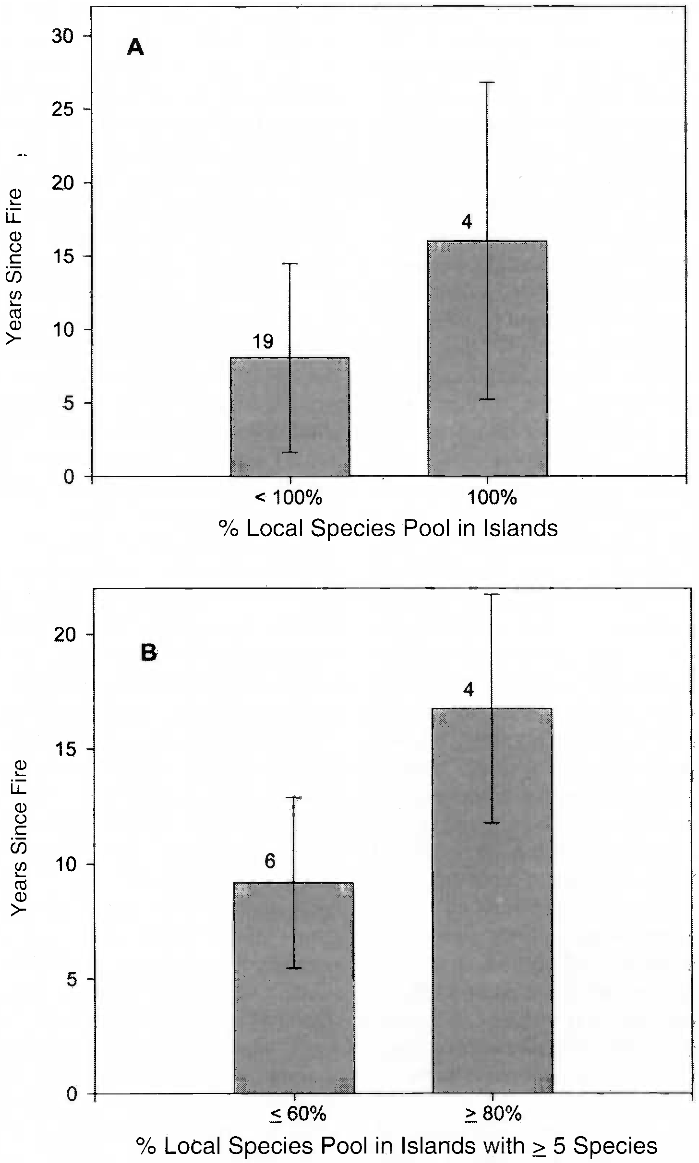

Fig. 2. Effect of time (years) since sagebrush habitat insularization by fire on percentages of local small mammal species pools occurring in habitat islands. A) All habitat islands sampled included—contrasts mean age of islands (± 1 SD) where 100% of small mammal species in local species pool occur in sagebrush islands versus islands with < 100% of species. B) Only includes habitat islands with ≥ 5 small mammal species— contrasts mean age of islands (± 1 SD) with ≥ 80% of species pool versus those with ≤ 60% of species. Numbers above bars are sample sizes of islands included in analyses. Data are from Bateman (1999).

It could be argued that habitat islands lose ecological value with time, because as succession proceeds, burned areas become more similar to the unburned shrub island and mainland areas they separate, effectively reducing isolation. While there is certainly some validity to this argument, Bateman (1999) still found more species in both islands and mainlands than in burns, and this pattern held up in old as well as recently burned sites.

From the above reasoning, if one judges the value of terrestrial islands on the basis of the diversity of natural resources contained within or on conservation value, it is relatively safe to say that "bigger is better". It is not necessarily the case, however, that less isolated islands are more useful than more remotely isolated ones, and, in fact, the exact opposite may sometimes be true. It is certainly possible that failure of some predictions of IBT to account for patterns in isolated sagebrush islands stems from fundamental differences between terrestrial habitat islands and the oceanic islands that motivated early IBT models. For example, traditional IBT assumes that islands are inhabited by colonization (MacArthur and Wilson 1967), whereas in Bateman's (1999) sagebrush islands inhabitation can occur through survival of residual populations within the unburned islands. This is obviously the case for the plant populations occurring in these islands immediately following isolation by fire, but may also explain the presence of certain animal species. Moreover, most previous applications of IBT to terrestrial habitat islands (e.g., Brown 1971) involve habitats that have been insularized for sufficiently long time periods to permit repeated episodes of extinction and colonization to occur. By contrast, in the sagebrush system, plant succession may restore shrubs to the burned areas rapidly enough to make effects of extinction and colonization within isolated habitat islands negligible even for those species that cannot readily disperse across burns. Regardless of these considerations, though, Bateman's (1999) data suggest that at least some predictions of IBT are applicable to sagebrush habitat islands. Furthermore, terrestrial islands of any size or degree of isolation can provide essential habitat for certain species across a fragmented landscape, and they can have important effects on succession within a surrounding disturbed area.

Successional Processes

Although we have already discussed potential effects of post-fire succession on habitat islands, we have not touched on the how the presence of islands may, in turn, affect successional processes. Most woody shrub species that occur in sagebrush environments must reestablish in disturbed areas from seeds; vegetative sprouting from roots following fire is relatively uncommon (Billings 1990). Thus, for successional recovery of a disturbance to proceed, a supply of viable seeds is necessary, and these seeds must find their way to appropriate sites for germination and seedling establishment. A large-scale disturbance that has islands of native vegetation embedded in it provides a more evenly distributed seed source for successional recovery across the disturbed landscape than simply relying on dispersal of seeds from edges of the disturbance (i.e., from the shrub mainland). This, alone, is likely to speed the recovery process for seeds dispersed by either biotic or abiotic agents. It is, perhaps, even more likely to enhance recovery for plant species whose seeds are dispersed by small mammals, which is probably a relatively common phenomenon in arid western shrub environments (Vander Wall 1990). The shrub islands provide not only a ready source of seeds for these animals to harvest, consume, and disperse, but also a refuge for various species that can act as effective seed dispersers. Deer mice (*Peromyscus maniculatus*), and various chipmunks (*Tamias* spp.), ground squirrels (*Spermophilus* spp. and *Ammospermophilus* spp.), and pocket mice (*Perognathus* spp. and *Chaetodipus* spp.), for example, all tend to have strong preferences for shrub-covered over disturbed areas with reduced shrub densities (such as burns), and all are potentially important seed dispersers (Bateman 1999, Halford 1981, Longland 1995). By contrast, kangaroo rats (*Dipodomys* spp.) also disperse the seeds of various desert plants, but they generally increase in abundance in disturbed areas, preferring them to heavy shrub cover. Even in this case, though, shrub islands can provide seed sources that allow these animals to disperse seeds of native plant species into the disturbed habitat matrix.

Management Implications

What practical applications can be gleaned from the above concepts? First and foremost is our central message – that native vegetation islands embedded within otherwise disturbed environments have high potential ecological and conservation value. Thus, these islands should be preserved whenever possible following disturbance. In fact, it may sometimes be possible or even advisable to manage *for* the maintenance or establishment of shrub islands during the planning of prescribed fire or even during the effort to control a wildfire. For example, if an advancing line of fire is too large and/or moving too rapidly to allow establishment of a fire break along the entire advancing front, it may still be possible to use smaller fire breaks to facilitate the creation of unburned shrub islands within the larger burned matrix. We suggest that agency handbooks should address these issues explicitly in cases where policies regarding habitat islands are currently either lacking or ambiguous.

If the agent of vegetation disturbance is under more direct human control than disturbance by fire, such as mechanical shrub removal, it may be possible to intentionally leave established shrub islands or to restore them later as part of the rehabilitation effort. Even in cases where large fires cleanly denude a landscape of shrubs, restoration of native shrub islands within the burn may prove to be an effective means of accelerating natural successional recovery. It is certainly less costly than active revegetation of an entire burned environment, and the result of successional expansion of vegetation islands is likely to yield a closer match to the preburn plant community. The latter approach is being attempted in the Buttermilk Winter Range Restoration Project at the eastern base of the Sierra Nevada Mountains in Round Valley, Calif. In 1995, 2,000 ha of critical mule deer winter range was cleanly consumed by fire in this area, but insufficient funds and concern about the introduction of non-native plant germplasm prohibited attempts to actively revegetate the entire area. Instead, a large number of 10- x 10-m plots have been planted with antelope bitterbrush (*Purshia tridentata* [Pursh] DC) seedlings grown from local seed stocks, and the plots have been made selectively accessible to mule deer and to seed-eating rodents. This project will thus simultaneously evaluate the utility of vegetation islands for restoration and the effects of 2 potential keystone animal taxa on plant succession.

A more general message extending beyond the issue of habitat islands is that theoretical constructs in ecology, conservation biology, or management are more than complications or annoyances that must be overcome during our years as students. They are heuristic tools that can often instruct real life problems. Predictions of Island Biogeography Theory have been tested for a variety of terrestrial habitat island situations, and applied to the optimal design or location of wildlife reserves. Most such examples involve forested habitats isolated by surrounding non-forested lands, but there is no reason why the same principles should not be applicable to arid rangelands. There can be useful, even valuable, empirical lessons hidden in sometimes seemingly esoteric theories.

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Predicting plant community response to picloram

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Abstract

Effective rangeland weed programs require the ability to predict plant community responses to management. Our objective was to develop regression equations to predict the plant community after control with picloram using the pre-treatment plant community. Five transects were established from dense spotted knapweed (*Centaurea maculosa* Lam.) in the center of each patch to an area of low or no spotted knapweed occurrence on the outside of the patch. Transects ended in areas dominated by Idaho fescue (*Festuca idahoensis* Elmer). Twenty permanent plots (20 x 50 cm, spacing along the transect ranged from 1/2 to 2 m) were placed along this gradient. Pre-treatment density and cover of all species were sampled in each plot. Biomass of all species was harvested in plots adjacent to the transect. Picloram (4-amino-3,5,6-trichloropicolinic acid) was applied along each transect at a rate of 0.28 kg a.i. ha^{-1} in October 1996 to each plot. Density, cover, and biomass of all species were re-sampled in August 1998. Regression models were fit using perennial grasses, Idaho fescue, forbs, species richness, and species diversity after treatment as predicted variables. All predicted variables were indigenous species. Regressor variables used were site, transect, and spotted knapweed, a spotted knapweed quadratic component, indigenous perennial grasses, Idaho fescue, indigenous forbs, species richness, and species diversity sampled in the first year (1996) prior to treatment. The best predictive models for assessing post-management indigenous perennial grass, Idaho fescue, and species richness were based on density. The best models predicting post-management forbs and species diversity were based on cover and biomass, respectively. In 4 out of the 5 models, for a given post-management parameter, an important predictor in the model was its pre-management regressor variable. Additionally, pre-management spotted knapweed was a relatively unimportant predictor in most models. The model predicting species diversity based on density (pre-treatment) predicted an increase in species diversity 2 years after management. This study indicated that it may be feasible to use pre-management plant community data to predict post-management plant community response for spotted knapweed-infested rangeland using picloram.

Key Words: Spotted knapweed, predicting plant response, integrated weed management, optimizing herbicide use

Over the past century, loss of indigenous rangeland communities in North America has been related to the invasion of aggressive non-indigenous species (Kedzie-Webb 1999). Ecological impacts attributed to non-indigenous invasions include the dis-

Resumen

Los programas efectivos de control de malezas en los pastizales requieren de la habilidad para predecir las respuestas de la comunidad vegetal al manejo. Nuestro objetivo fue desarrollar ecuaciones de regresión para predecir la comunidad vegetal después del control con picloram usandolo como pre-tratamiento de la comunidad vegetal. Se establecieron 5 transectos desde el centro de cada parche, en donde "Spotted knapweed" (*Centaurea maculosa* Lam.) tenía una alta densidad, hasta un área fuera del parche, donde la densidad de "Spotted knapweed" era baja o no estaba presente. Los transecto terminaron en áreas dominadas por "Idaho fescue" (*Festuca idahoensis* Elmer). Se colocaron 25 parcelas permanentes de (20 x 50 cm, el espaciamiento entre parcelas a lo largo fue de 2 m) a lo largo de este gradiente. La densidad y cobertura de todas las especies se muestreó en cada parcela antes de aplicar los tratamientos. Se cosechó la biomasa de todas las especies en parcelas adyacentes al transecto. En Octubre de 1996, el Picloram (4-amino-3,5,6-ácido tricloropicolinico) se aplicó en cada parcela a lo largo del transecto a una dosis de 0.28 kg i.a. ha^{-1}. La densidad, cobertura y biomasa de todas las especies se muestrearon nuevamente en Agosto de 1998. Los modelos de regresión se ajustaron utilizando como variables predichas los zacates perennes, el " Idaho fescue", las hierbas, la riqueza de especies y la diversidad de especies después del tratamiento. Todas la variables predichas fueron especies nativas. Las variables regresoras utilizadas fueron: sitio, transecto y Spotted knapweed", un componente cuadrático de "Spotted knapweed, zacates perennes nativos, "Idaho fescue", hierbas nativas, riqueza de especies y la diversidad de especies muestreada en el primer año (1996) antes del tratamiento. Los mejores modelos predictivos para evaluar el manejo post-tratamiento de zacates perennes nativos, " Idaho fescue" y la riqueza de especies fueron basados en la densidad. Los mejores modelos para predecir el manejo post-tratamiento de las hierbas y la diversidad de especies se basaron en cobertura y biomasa respectivamente. En 4 de los 5 modelos, para un parámetro post-tratamiento dado, un predictor importante en el modelo fue su variable regresora de pre- tratamiento. Adicionalmente, el manejo pre-tratamiento del " Spotted knapweed" fue un predictor relativamente sin importancia en la mayoría de los modelos. El modelo para predecir la diversidad de especies basado en la densidad (pre-tratamiento) predijo un incremento en la diversidad de especies 2 años después del tratamiento. Este estudio indica que puede ser factible el uso de los datos de la comunidad vegetal pre-tratamiento para predecir la respuesta de la comunidad vegetal después del tratamiento en pastizales infestados de " Spotted knapweed" tratados con Picloram.

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placement of indigenous plant species, declines in biodiversity, and degradation of ecosystem function (Vitousek 1986, Randall 1996). In the western United States, saltcedar (*Tamarix* spp.) (Brotherson and Field 1987), leafy spurge (*Euphorbia esula* L.) (Belcher and Wilson 1989), downy brome (*Bromus tectorum* L.) (Mack 1981, Whisenant 1990), spotted knapweed (*Centaurea maculosa* Lam.), and others have been documented to alter ecosystem function (Tyser and Key 1988). Ecosystem processes threatened by invasive species include primary and secondary productivity, decomposition, nutrient cycles (accumulation or loss), soil development and fertility, and hydrologic cycles (Vitousek and Hooper 1993). In a single, cursory study, Lacey et al. (1989) suggested that surface run-off and sediment yield increased on spotted knapweed-dominated sites under simulated rain events. Spotted knapweed negatively impacts wildlife through forage production loss, habitat modification, or by altering animal-plant interactions (Thompson 1996). Invasion by spotted knapweed into western Montana has reduced winter forage for elk resulting in an estimated loss of 220 elk annually (Spoon et al. 1983). A major economic impact of spotted knapweed invasion is the loss of livestock forage production (Bucher 1984).

Rangeland managers are searching for useful models on which to base their decisions (Archer 1989, Laycock 1991, Schlatterer 1989). The more accurate the predictions, the greater success in developing integrated weed management systems (Schreiber 1982). Coupled with the concept of thresholds, predicting plant community response to regulation may enhance management by providing managers with the information necessary to make thoughtful decisions (Griffith and Lacey 1991).

The overall objective of this study was to determine the potential to predict the post-treatment plant community after a herbicide treatment of spotted knapweed based on the pre-treatment plant community. Specific objectives were to: 1) develop models that predict the post-picloram-treatment plant community composition based on the pre-treatment plant community after a picloram treatment; 2) initiate development of a method to use easily collected field data to predict pre- and post-management biomass; and 3) introduce a method to use predictions to enhance weed management decisions. Since cover data is one of the easiest parameters to collect, using cover to predict biomass may be the most practical and efficient model for decision-making. Although this study was conducted using an herbicide, this method could be used in a similar fashion to predict post-treatment plant community response based on the pre-treatment plant community and application of other management techniques (e.g., grazing, fire, biocontrol, etc.). This research is necessary to improve decision-making abilities and management strategies.

Materials and Methods

This study was conducted on 2 sites from 1996 through 1998 within a Idaho fescue-bluebunch wheatgrass (*Festuca idahoensis-Agropyron spicatum*) habitat type (Mueggler and Stewart 1980). Site 1 was located in Story Hills (45° 42' N, 111° 01' W), four km northeast of Bozeman, Mont. Elevation at this site is 1,478 m. Average annual precipitation is 432 mm. Soil is a clayey-skeletal, mixed Typic Argiborolls. Site 2 was located at Beartrap Canyon, about 45 km east of Norris, Mont. (45° 36' N, 111° 34' W). Elevation is 788 m with an average annual precipitation of 305 mm. Soil at Site 2 is classified as a loamy-skeletal, mixed Aridic Argiborolls.

Five transects, each 20 m long, were established at both sites. Transects radiated from dense spotted knapweed in the center of each patch to an area of low or no spotted knapweed occurrence on the outside of the patch. At each site, all transects radiated from the center of the same patch. The plant community at each transect origin was dominated by spotted knapweed with few or no residual indigenous species growing in association. Transects ended in areas dominated by Idaho fescue (*Festuca idahoensis* Elmer) with a diverse group of associated species. Twenty permanent plots (20 x 50 cm, spacing along the transect ranged from 2 to 2 m) were placed along this gradient of spotted knapweed cover from 0 to 100% (about every 5%). Pre-treatment density (juveniles plus adults) and cover of all species were sampled in each plot. Picloram (4-amino-3,5,6-trichloropicolinic acid) was applied along each transect in a 2 m swath at a rate of 0.28 kg a.i. ha^{-1} in October of 1996 to each plot. Density (juveniles plus adults) and cover of all species were re-sampled in August 1998.

Thirty temporary plots (20 x 50 cm) were also established along the spotted knapweed gradient to sample biomass and soil at each site. Biomass was sampled for all species by clipping plants to ground-level at peak standing crop in August 1996 and 1998. Samples were dried at 60° C to a constant weight and weighed. Soil samples were collected along the transect to determine whether the spotted knapweed gradient was related to differences in soil nutrients. Soil samples were tested for available nitrogen, phosphorous, and potassium using a standardized extraction process (Page and Klute 1982). There were no differences in available soil nutrients, therefore, the data are not presented.

Data Analysis

Data were compiled into tables showing the number of transects in which individual species were present both before and after the picloram treatment (maximum of 5). Plant density, cover, and biomass data were analyzed using a multi-step process. Covariance analysis was conducted to test for sample independence within transects. Analysis indicated independence among all plots, therefore, a step-down linear regression procedure was used to identify the best model (Neter et al. 1985). A combination of P-value, model simplicity, and R^2 values was used to identify the best model for each step-down procedure. Scatter-plots of the residuals versus the standardized predicted values were used to evaluate heterogeneity of variance for each model. Data transformations were conducted where necessary on predicted and/or regressor variables using square-root transformations. Inverse, quadratic, and log transformations were tested, but did not improve the models. Collinearity was evaluated using a SAS tolerance procedure to test for relatedness of predictors (SAS 1990). Collinearity was not a problem in this analysis.

Regression models were fit using density, cover, and biomass after treatment (1998) as predicted variables that include perennial grasses, Idaho fescue, forbs, species richness, and species diversity. All predicted variables were indigenous species. Regressor variables used were site, transect, and density, cover, and biomass of spotted knapweed, a spotted knapweed quadratic component, indigenous perennial grasses, Idaho fescue, indigenous forbs, species richness, and species diversity sampled in the first year (1996) prior to treatment.

Regression models were also fit using density, cover, and biomass of brome species post-treatment as predicted variables. In these models, regressor variables were density, cover, and biomass of pre-treatment brome species, a brome quadratic component, spotted knapweed, and a spotted knapweed quadratic component.

Additionally, regression models were fit to predict production from cover. The predicted variables include: post-treatment indigenous perennial grass, Idaho fescue, forbs, and brome species biomass. Regressor variables used were pre-treatment indigenous perennial grass, Idaho fescue, indigenous forbs, brome species cover, and their respective quadratic components.

All models presented were significant at $P \leq 0.05$. The effects of transects were averaged across sites when significant. Coefficient means and standard deviations for transects are presented. These regression models do not imply causality. Diversity measurements were estimated using Shannon-Weaver's diversity index (Shannon and Weaver 1949).

Results

Presence and Distribution

Nine indigenous grasses, 2 non-indigenous grasses, 9 indigenous forbs, and 3 non-indigenous forbs were present at Site 1. Of the indigenous grasses, bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. & Smith] was found in 3 or more transects, and western wheatgrass (*Agropyron smithii* Rydb.) was present in at least 1 transect along the gradient. Idaho fescue was present in all transects except at 85 and 90% pre-treatment spotted knapweed. All other indigenous grasses were limited in presence after 50% pre-treatment spotted knapweed. Japanese brome (*Bromus japonicus* Thunb.) was present along the entire transect. Kentucky bluegrass (*Poa pratensis* L.) was limited in presence below 30% pre-treatment spotted knapweed. The most abundant indigenous forbs included hairy goldenaster [*Chrysopsis villosa* (Pursh) Nutt.], blazingstar (*Liatris punctata* Hook.) and sagewort cudweed (*Artemisia ludoviciana*). Post-treatment bastard toadflax [*Comandra umbellata* (L). Nutt.] was the most abundant non-indigenous forb present at Site 1.

Seven indigenous grasses, 3 non-indigenous grasses, 5 indigenous forbs and 2 non-indigenous forbs were present at Site 2. Blue grama [*Bouteloua gracilis* (H. B. K.) Lag.] was present along the entire gradient. Idaho fescue was found at all pre-treatment spotted knapweed levels except 70 and 100%. Prairie sandreed (*Calamovilfa longifolia* Hook.) and needle-and-thread grass (*Stipa comata* Trin. & Rupr.) were well represented along the transect except above 60% spotted knapweed. The most abundant forb based on presence in number of transects was the non-indigenous *Berteroa* spp.

Density

Regression models were generated to predict the plant density 2 years after picloram treatment (predicted variables) based on the density of plants sampled prior to treatment (regressor variables) (Table 1). Site was significant when predicting Idaho fescue and forb density, as well as species richness based on density. Estimated effects of site were –8.8, –5.0, and 19.7 for species richness, forbs, and Idaho fescue density, respectively.

For each 1 unit increase in pre-treatment indigenous perennial grass density, predicted post-treatment indigenous perennial grass density increased by about 9.2 tillers m^{-2} (Table 1). For each 1 unit increase in spotted knapweed density, predicted indigenous perennial grass density decreased by 0.1 tillers m^{-2} at Site 1. At Site 2, for each 1 unit increase in spotted knapweed density, predicted indigenous perenni-

Table 1. Regression models predicting post-treatment indigenous species based on pre-treatment density (plants m^{-2}) of regressor variables. Empty cells represent non-significant regressor variables.

				Regressor	variables							
Site	Predicted variables	Intercept	Site	Transect (1)[1]	Perennial grass (0 to 7,280)	Idaho fescue (0 to 3,970)	Forbs (0 to 550)	Species richness (0 to 8)	Species diversity (0 to 2.26)`	Spotted knapweed (0 to 1,170)	Spotted knapweed[2] (0 to 313,290)	R^2
1	Perennial grass[2]	19.2		5.5 [3] (6.8)	9.2					-0.1		0.51
2	Perennial grass	19.2		5.5 (6.8)	9.2					0.4		0.51
1	Idaho fescue	-17.4	0.00			9.5			14.1			0.69
2	Idaho fescue	–17.4	19.7	–2.8		9.5		14.1				0.69
1	Forbs	7.2	0.00	(2.8)	–0.68			2.3				0.34
2	Forbs	7.2	–5.0	–2.8 (2.8)	–0.68			2.3				0.34
1	Species richness	17.8	0.00		1.5			4.4			0.002	0.46
2	Species richess	17.8	–8.8		1.5			4.4			–0.004	0.46
1	Diversity	3.3		–1.0 (1.1)	0.8				1.7			0.30
2	Diversity	3.3		–1.0 (1.1)	0.8				1.7			0.30

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting post-treatment IPG density based on pre-treatment density of PIG and CEMA treatment includes

Site 1; $y = 19.2(B_0)+ 5.5 (B_1)+9.2(B_2)–0.10(B_3)$, where B_0 is the intercept, B_1 is the average of transect, B_2 is the density of the indigenous perennial grass prior to treatment.and B_3 is the density of CEMA at Site 1.

Site 2; $y = 19.2(B_0)+ 5.5 (B_1)+9.2(B_2)+(0.40(B_3)$, where B_0 is the intercept, B_1 is the average of transect, B_2 is the density of the IPG prior to treatment.and B_3 is the density of CEMA at Site 2.

[3] Means represent the average of 10 transects across site with standard deviations are provided below means in table.

Table 2. Regression models predicting post-treatment indigenous species based on pre-treatment cover of regressor variables. Empty cells represent non-significant regressor variables.

				Regressor	variables							
Site	Predicted variables	Intercept	Site	Transect (1)[1]	Perennial grass (0 to 76)	Idaho fescue (0 to 50)	Forbs (0 to 50)	Species richness (0 to 8)	Species diversity (0 to 2.26)`	Spotted knapweed (0 to 100)	Spotted knapweed^2 (0 to 10,000)	R^2
1	Perennial grass[2]	2.12			0.52		–0.19	0.16		–0.009	–0.00005	0.44
2	Perennial grass	2.12			0.52		–0.19	0.16		0.028	–0.0004	0.44
1	Idaho fescue	1.55				0.63				–0.018		0.63
2	Idaho fescue	1.55				0.63				–0.008		0.63
1	Forbs	1.33	0.00	–0.58[3] (4.3)			0.53					0.46
2	Forbs	1.33	-0.94	–0.58 (4.3)			0.53					0.46
1	Species richness	1.61	0.00					0.58				0.40
2	Species richness	1.61	–0.69					0.58				0.40
1	Diversity	0.37					–0.041	0.13		0.007	–0.00008	0.22
2	Diversity	0.37					–0.041	0.13		0.007	–0.00008	0.22

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting IPG cover (after treatment) based on cover of IPG, Forbs, Species Richness, CEMA, and CEMA^2 prior to treatment includes:

Site 1; $y = 21.7(B_0)+ 5.2 (B_1)–0.19(B_2)+0.16(B_3), –0.009(B_4)–0.00005(B_5)$, where B_0 is the intercept, B_1 is the cover of IPG prior to treatment, B_2 is the cover of forbs, B_3 is the species richness, B_4 the cover of CEMA, and B_5 is the cover of CEMA^2 at Site 1;

Site 2; $y = 2.17(B_0)+ 0.52 (B_1)–0.19(B_2)+0.16(B_3)+0.028(B_4)–0.0004(B_5)$, where B_0 is the intercept, B_1 is the cover of IPG prior to treatment, B_2 is the cover of forbs, B_3 is the species richness, B_4 the cover of CEMA, and B_5 is the cover of CEMA^2 at Site 2.

of CEMA at Site 2.

[3] Means represent the average of 10 transects across site with standard deviations are provided below means in table.

al grass density increased by 0.4 tillers m^{-2}. Effect of transect was positively associated with indigenous perennial grass density.

In the model predicting Idaho fescue density, post-treatment Idaho fescue density was positively associated with pre-treatment Idaho fescue density and species diversity (Table 1). Specifically, each 1 unit increase in pre-treatment Idaho fescue density was associated with a 9.5 tillers m^{-2} increase in post-treatment Idaho fescue density. For each 1 unit increase in species diversity, Idaho fescue density increased by 14.1 tillers m^{-2}.

In general, predicted post-treatment indigenous forb density was negatively related to pre-treatment indigenous perennial grass density and positively related to species richness (Table 1). For each 1 unit increase in indigenous perennial grass density, forb density decreased by 0.68 plants m^{-2}. Each 1 unit increase in species richness was associated with a predicted 2.3 plants m^{-2} increase in forb density. Effect of transect was negatively associated with forb density.

For each 1 unit increase in indigenous perennial grass density, predicted species richness increased by about 1.5 plants m^{-2} at both sites (Table 1). For each 1 unit increase in pre-treatment species richness, predicted post-treatment species richness increased by 4.4 plants m^{-2} at both sites. The spotted knapweed quadratic component was associated with an increase in species richness by about 0.002 plants m^{-2} at Site 1 and a decrease of 0.004 plants m^{-2} at Site 2.

Predicted post-treatment species diversity was positively related to both pre-treatment indigenous perennial grass density and species diversity (Table 1). Each 1 unit increase in indigenous perennial grass density was associated with an increase in species diversity by 0.8 Shannon-Weaver's diversity index units. For each 1 unit increase in pre-treatment species richness, post-treatment species diversity increased by 1.7 Shannon-Weaver's diversity index units. Effect of transect was negatively associated with species diversity at both sites.

Cover

Site was significant when predicting forb cover and species richness based on cover. The estimated effects of site were –0.94 and –0.69 for forbs and species richness, respectively (Table 2).

Predicted post-treatment indigenous perennial grass cover was positively related to indigenous perennial grass and species richness, but negatively related to forb cover at both sites (Table 2). Each 1% increase in pre-treatment indigenous perennial grass cover was associated with a 52% increase in post-treatment indigenous perennial grass cover. For each 1% increase in forb cover, indigenous perennial grass cover decreased by 19%. Each 1% increase in species richness based on cover was associated with a predicted increase in indigenous perennial grass cover by 16%. For each 1% increase in spotted knapweed cover, indigenous perennial grass cover decreased by 0.9 % at Site 1 and increased by 2.8% at Site 2. Each 1% increase in the spotted knapweed quadratic component was associated with a decrease in indigenous perennial grass cover by 0.005 and 0.04% for Sites 1 and 2, respectively.

In general, predicted post-treatment Idaho fescue cover was positively related to pre-treatment Idaho fescue cover (Table 2). Each 1% increase in pre-treatment Idaho fescue cover was associated with an increase in post-treatment Idaho fescue cover by 63%. Each 1% increase in spotted knapweed cover was associated with a predicted decrease in Idaho fescue cover

Table 3. Regression models predicting post-treatment indigenous species based on pre-treatment biomass (plants m^{-2}) of regressor variables. Empty cells represent non-significant regressor variables.

				Regressor	variables							
Site	Predicted variables	Intercept	Site	Transect $(1)^1$	Perennial grass (0 to 380)	Idaho fescue (0 to 360)	Forbs (0 to 150)	Species richness (0 to 5)	Species diversity (0 to 2.26)`	Spotted knapweed (0 to 1,280)	Spotted knapweed^2 (0 to 163,840)	R^2
1	Perennial grass^2	14.7					2.7			-0.07	0.0007	0.32
2	Perennial grass	14.7					2.7			0.40	–0.004	0.32
1	Idaho fescue	–1.2			5.4							0.39
2	Idaho fescue	–1.2			5.4							0.39
1	Forbs	3.2		–2.5^3 (7.5)			–5.0	4.0		–0.18		0.38
2	Forbs	3.2		–2.5 (7.5)			–5.0	4.0		0.02		0.38
1	Species richness	32.8								–0.26		0.29
2	Species richness	32.8								–0.12		0.29
1	Diversity	3.1		–3.6 (3.9)	2.2					0.11	–0.0015	0.52
2	Diversity	3.1		–3.6 (3.9)	2.2					0.24	–0.0015	0.52

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting post-treatment IPG biomass based on biomass of Forbs, CEMA, and $CEMA^2$ prior to treatment includes

Site 1; $y = 14.7(B_0) + 2.7\ (B_1) – 0.07(B_2) + 0.0007(B_3)$, where B_0 is the intercept, B_1 is the biomass of forbs prior to treatment, B_2 is the biomass of CEMA, B_3 is the biomass of $CEMA^2$ at Site 1;

Site 2; $y = 14.7(B_0) + 2.7\ (B_1) + 0.38(B_2) – 00004(B_3)$, where B_0 is the intercept, B_1 is the biomass of forbs prior to treatment, B_2 is the biomass of CEMA B_3 is the biomass of CEMA2 at Site 2.

[3] Means represent the average of 10 transects across site with standard deviations are provided below means in table.

by about 1.8 and 0.8% at Sites 1 and 2, respectively.

Predicted post-treatment indigenous forb cover was positively related to pre-treatment indigenous forb cover (Table 2). For each 1% increase in forb cover prior to treatment, forb cover after treatment increased by 53% at both sites. At Site 2, the effect of transect was negatively associated with forb cover.

In the model predicting species richness, post-treatment species richness was positively associated with pre-treatment species richness (Table 2). Specifically, for each 1% increase in species richness, species richness increased by about 58% two years after treatment.

Predicted species diversity was negatively associated with forb cover and the spotted knapweed quadratic component, but positively related to species richness and spotted knapweed cover alone (Table 2). Specifically, each 1% increase in pre-treatment forb cover was associated with a decrease in species diversity by 0.041 Shannon-Weaver's diversity index units. For 1% unit increase in species richness, species diversity increased by 0.13 Shannon-Weaver's diversity index units. For each 1% increase in adult spotted knapweed cover, diversity increased by 0.007 Shannon-Weaver's diversity index units. For each 1% increase in the spotted knapweed quadratic component, diversity decreased by 0.00008 diversity index units.

Biomass

Indigenous perennial grass biomass prior to treatment was positively related to post-treatment forb cover and both positively and negatively related to spotted knapweed (Table 3). For each 1 unit increase in forb biomass, indigenous perennial grass biomass increased by 2.7 g m^{-2}. Each 1 unit increase in spotted knapweed biomass was associated with a predicted 0.07 g m^{-2} decrease in indigenous perennial grass biomass at Site 1. At Site 2, for each 1 unit increase in spotted knapweed biomass, indigenous perennial grass biomass increased by 0.40 g m^{-2}. Each 1 unit increase in the spotted knapweed biomass by spotted knapweed interaction was associated with a predicted 0.0007 g m^{-2} increase in indigenous perennial grass biomass at Site 1 and a 0.004 g m^{-2} decrease at Site 2.

Predicted Idaho fescue biomass was positively related to indigenous perennial grass biomass from year one (Table 3). For each 1 unit increase in indigenous perennial grass biomass, Idaho fescue biomass increased by 5.4 g m^{-2}.

Each 1 unit increase in pre-treatment forb biomass was associated with a predicted 5.0 g m^{-2} decrease in post-treatment forb biomass (Table 3). Each 1 unit increase in species richness based on biomass was associated with an increase in forb biomass by 4.0 g m^{-2} at both sites. Forb biomass was negatively related to spotted knapweed biomass (–0.18 g m^{-2}) at Site 1 and positively related to spotted knapweed biomass (0.02 g m^{-2}) at Site 2. Effect of transect was negatively associated with forb biomass.

Predicted species richness based on biomass was negatively related to spotted knapweed biomass (Table 3). Specifically, each 1 unit increase in spotted knapweed biomass was associated with a decrease in species richness by 0.26 g m^{-2} and 0.12 g m^{-2} at Sites 1 and 2, respectively.

Post-treatment species diversity was positively associated with perennial grass biomass and the spotted knapweed biomass alone, but negatively related to the spotted knapweed quadratic component (Table 3). Each 1 unit increase in indigenous perennial grass biomass was associated with an

Table 4. Regression models predicting post-treatment non-indigenous species based on density (plants m^{-2}) cover, and biomass (g m^{-2}) variables. Empty cells represent non-significant regressor variables.

			Regressor	variables			
Site	Predicted variables (Brome spp.)	Intercept	Brome[1] (0 to 1,950[2] (0 to 12) (0 to 78)	Brome^2 (0 to 38,025) (0 to 144) (0 to 608)	Spotted knapweed (0 to 1,170) (1 to 100) (0 to 1,280)	Spotted knapweed^2 (0 to 313,290) (0 to 10,000) (0 to 163,840)	R^2
1	Density[3]	–633	10.6	–0.006	3.9		0.30
2	Density	–220	1.1	0.00	1.4		0.31
1	Cover	–0.40	1.41	–0.11	0.00		0.13
2	Cover	–0.11	0.00	0.00	0.008		0.10
1	Biomass	43.0	0.05		0.00		0.15
2	Biomass	181	0.00		–2.0	2.5×10^{-5}	0.62

[1] Represents a pre-treatment parameter based on density, cover, and biomass to predict post-treatment Brome density, cover, and biomass, respectively.

[2] Possible range of values for each parameter based on density, cover, and biomass on a m^{-2} basis, respectively.

[3] A a model predicting pre-treatment brome density based on density of Brome, Brome^2, and CEMA, prior to treatment includes:

Site 1; $y = 633\ (B_0)+10.6(B_1)–0.006(B_2)+3.9(B_3)$, where B_0 is the intercept B_1 is the biomass of pre-treatment Brome, B_2 is the biomass of pre-treatment Brome^2, and B_3 is the biomass of CEMA at Site 1;

Site 2; $y = –220(B_0)+1.1(B_1)+1.4(B_2)$, where B_0 is the intercept B_1 is the biomass of pre-treatment Brome, and B_2 is the biomass of CEMA at Site 2.

increase in species diversity by 2.2 Shannon-Weaver's diversity index units. For each 1 unit increase in spotted knapweed biomass, species diversity increased by 0.11 and 0.24 Shannon-Weaver's diversity index units at Sites 1 and 2, respectively. The spotted knapweed quadratic component was related to a decrease of 0.0015 Shannon-Weaver's diversity index units. Indigenous species diversity was negatively related to transect.

Brome species

Density. Regression models were generated to describe density of post-treatment brome species based on pre-treatment brome species (Table 4). For each 1 unit increase in pre-treatment brome density, post-treatment brome increased by 10.6 tillers m^{-2} at Site 1. At Site 2, each 1 unit increase in pre-treatment brome was associated with a 1.1 tillers m^{-2} increase in post-treatment brome. For each 1 unit increase in the brome quadratic component, post-treatment brome decreased by 0.006 tillers m^{-2} at Site 1. Each 1 unit increase in spotted knapweed was associated with a predicted 3.9 tillers m^{-2} increase in brome at Site 1. At Site 2, each 1 unit increase in spotted knapweed was associated with a 1.4 tillers m^{-2} increase in brome.

Cover. For each 1% increase in pre-treatment brome cover, predicted post-treatment brome cover increased by 141% at Site 1 (Table 4). For each 1% increase in the brome quadratic component, post-treatment brome decreased by 11% at Site 1. At Site 2, each 1% increase in spotted knapweed cover was associated with a 0.8% increase in brome.

Biomass. For each 1 unit increase in pre-treatment brome biomass, post-treatment brome biomass increased by 0.05 g m^{-2} at Site 1 (Table 4). At Site 2, for each 1 unit increase in spotted knapweed, post-treatment brome decreased by 2.0 g m-2. Each 1 unit increase in the spotted knapweed quadratic component was associated with a 2.5 x 10-5 g m^{-2} increase in brome.

Predicting Biomass Using Cover

Post-treatment perennial grass biomass was positively associated with pre-treatment indigenous perennial grass cover alone, but negatively associated to the indigenous perennial grass quadratic component (Table 5). For each 1 unit increase in pre-treatment indigenous perennial grass cover, predicted post-treatment perennial grass biomass increased by 57.2 g m^{-2} at both sites. For each 1 unit increase in the pre-treatment perennial

Table 5. Regression models predicting post-treatment biomass (g m^{-2}) indigenous species based on pre-treatment cover of regressor variables. Empty cells represent non-significant regressor variables.

			Regressor	variables									
Site	Predicted variables	Intercept	Perennial grass (0 to 76)[1]	Perennial^2 grass (0 to 5,776)	Idaho fescue ((0 to 50)	Idaho fescue^2 (0 to 2500)	Forb (0 to 50)	Forb^2 (0 to 2500)	Brome (0 to 12)	Brome^2 (0 to 144)	Spotted knapweed (0 to 100)	Spotted knapweed^2 (0 to 10,000)	R^2
1	Perennial grass[2]	571.1	57.2	–0.86									0.35
2	Perennial grass	571.1	57.2	–0.86									0.35
1	Idaho fescue	69.0			53.2	–0.63							0.71
2	Idaho fescue	69.0			53.2	–0.63							0.71
1	Forbs	24.4					24.1						0.13
2	Forbs	24.4					24.1						0.13
1	Brome	–4.74							40.5	–6.5			0.31
2	Brome			Lack	of	Fit							0.00

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting pre-treatment brome density based on density of IPG, and IPG^2 prior to treatment includes:

Sites 1 and 2 $y = –571(B_0)+57.2(B_1)–0.86(B_2)$, where B_0 is the intercept, B_1 is the biomass of pre-treatment IPG, and B_2 is the biomass of pre-treatment IPG^2 at Site 1;.

grass quadratic component based on cover, post-treatment perennial grass biomass decreased by 0.86 g m^{-2} at both sites.

Predicted post-treatment Idaho fescue biomass was positively associated with pre-treatment Idaho fescue cover alone, but negatively associated to the Idaho fescue quadratic component (Table 5). At both sites, each 1 unit increase in pre-treatment Idaho fescue cover was associated with a 53.2 g m^{-2} increase in post-treatment Idaho fescue biomass. For each 1 unit increase in the Idaho fescue quadratic component based on cover, post-treatment Idaho fescue biomass decreased by 0.63 g m^{-2}.

Forb biomass after treatment was positively related to forb cover prior to treatment (Table 5). Each 1 unit increase in pre-treatment forb cover was associated with a 24.1 g m^{-2} increase in post-treatment forb biomass at both sites.

For each 1 unit increase in pre-treatment brome cover, post-treatment brome biomass increased by 40.5 g m^{-2} at Site1 (Table 5). For each 1 unit increase in the pre-treatment brome quadratic component based on cover, post-treatment brome biomass decreased by 6.5 g m^{-2}. Regression analysis showed lack of fit when predicting brome production from brome cover at Site 2.

Biomass Optimization Model

Pre-treatment spotted knapweed cover was used as the regressor variable to predict pre- and post- treatment indigenous perennial grass biomass (Fig. 1). At 0 spotted knapweed cover, predicted pre-treatment grass biomass was about 2,250 kg ha^{-1} and post-treatment grass biomass was about 1,400 kg ha^{-1}. Pre-treatment grass biomass decreased rapidly as pre-treatment spotted knapweed cover increased to about 50%. At that point, predicted grass biomass was about 800 kg ha^{-1}. After that point, predicted grass biomass declined more slowly as spotted knapweed cover increased. The regression model predicted that areas with 95% pre-treatment spotted knapweed cover would produce 200 kg ha^{-1} indigenous perennial grass prior to treatment. Post-treatment grass biomass decreased linearly. Predicted post-treatment grass biomass was about 500 kg ha^{-1} at maximum spotted knapweed cover (95%).

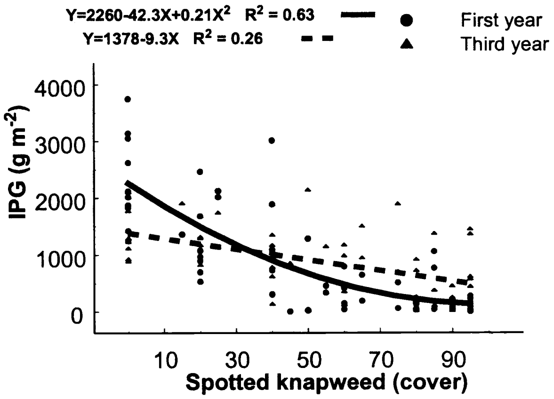

Fig. 1. Models comparing predicted post-treatment grass biomass with predicted pretreatment grass biomass based on pretreatment spotted knapweed cover.

Discussion

Predicting Indigenous Species

Weed managers are searching for useful models on which to base their management decisions (Archer 1989, Laycock 1991, Schlatterer 1989). In agroecosystems, predictive models have been used to assess economic thresholds to better manage a wide range of important crops. For example, Maxwell et al. (1994) developed bioeconomic models to optimize control strategies of wild oats (*Avena fatua* L.) in barley production. Knezevic et al. (1994) determined redroot pigweed (*Amaranthus retroflexus* L.) did not reduce corn production when weed emergence occurred after the corn's 7-leaf stage. However, the use of predictive models to optimize rangeland weed management has been limited. Peat and Bowes (1994) predicted that at biomass above 290 kg ha^{-1} of fringed sagebrush (*Artemisia frigida* Willd.), it becomes economically viable to control this plant using picloram. Keane (1987) developed successional pathway models to predict plant coverage based on treatment and pre-disturbance plant composition.

This study indicated it may be feasible to use pre-management plant community data to predict post-management plant community response for spotted knapweed-infested rangeland using picloram. The best predictive models for assessing post-management indigenous perennial grass, Idaho fescue, and species richness were based on density. The best models predicting post-management forbs and species diversity were based on cover and biomass, respectively. In 4 out of the 5 models, for a given post-management parameter, an important predictor in the model was its pre-management regressor variable. For example, pre-management indigenous grass density was the best predictor of post-management grass density. Additionally, pre-management spotted knapweed was a relatively unimportant predictor in most models. Incorporating environmental factors other than plant community composition into models may enhance their predictive abilities. Although this study was conducted using picloram to control spotted knapweed, other management strategies and/or other weeds could be tested in a similar fashion to predict post-management plant community response.

Species Richness and Species Diversity

The model predicting species diversity based on density indicated an increase in species diversity 2 years after management. However, the species presence data along transect indicated a decrease in 14 out 30 post-management indigenous forb and grass species. Five out of 30 species (16%) were no longer present following the picloram treatment. Four of these species were indigenous forbs. Rice et al. (1997) detected transitory declines in both species richness and diversity in response to picloram. However, this relationship may be an artifact of using Shannon-Weaver's diversity index which sums the proportion of individuals present and provides an "average diversity" (Pielou 1966). Presumably an increase in post-management grass presence (e.g., western wheatgrass, Idaho fescue, needle-and-thread, etc.) may account for this simultaneous gain in species diversity and loss of species richness (number of species) post-management. It is also important to note that different measurements of diversity would likely yield different predictive models.

Biomass Optimization Model

Many land management programs are aimed at maximizing grass production. These weed management programs must use our understanding of the change in grass biomass as a response to management. We attempted to use easily collected pre-treatment data (i.e., spotted knapweed cover) to predict pre- and post-treatment grass biomass. To identify the relative difference in biomass production between years, we compared difference between the predicted pre-treatment and post-treatment biomass. The integration of these models indicated that there would be a decrease in post-treatment grass biomass at spotted knapweed cover below 35%. We suspect that at low spotted knapweed cover, interference between spotted knapweed and indigenous grass was low (Velagala 1996). Therefore, spotted knapweed removal did not result in an increase in grass biomass. We speculate that the decrease in grass biomass was associated with other environmental factors, such as weather. Above 35% spotted knapweed cover, regressions predicted greater post-treatment grass biomass than the pre-treatment biomass. In this case, spotted knapweed may have influenced grass production, and its removal may have favored grasses. In either case, including other environmental factors in the models should improve our ability to predict post-management outcomes based on pre-management conditions. Furthermore, we believe it may be possible to identify the cumulative predictive biomass gain (after treatment) by developing a biomass optimization model for each year of herbicide control. Once the change in biomass is predicted and the predictions verified, economic analysis based on the value of the biomass change may be possible using this method prior to imposing weed management.

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Rangeland health attributes and indicators for qualitative assessment

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Abstract

Panels of experts from the Society for Range Management and the National Research Council proposed that status of rangeland ecosystems could be ascertained by evaluating an ecological site's potential to conserve soil resources and by a series of indicators for ecosystem processes and site stability. Using these recommendations as a starting point, we developed a rapid, qualitative method for assessing a moment-in-time status of rangelands. Evaluators rate 17 indicators to assess 3 ecosystem attributes (soil and site stability, hydrologic function, and biotic integrity) for a given location. Indicators include rills, water flow patterns, pedestals and terracettes, bare ground, gullies, wind scour and depositional areas, litter movement, soil resistance to erosion, soil surface loss or degradation, plant composition relative to infiltration, soil compaction, plant functional/structural groups, plant mortality, litter amount, annual production, invasive plants, and reproductive capability. In this paper, we detail the development and evolution of the technique and introduce a modified ecological reference worksheet that documents the expected presence and amount of each indicator on the ecological site. In addition, we review the intended applications for this technique and clarify the differences between assessment and monitoring that lead us to recommend this technique be used for moment-in-time assessments and not be used for temporal monitoring of rangeland status. Lastly, we propose a mechanism for adapting and modifying this technique to reflect improvements in understanding of ecosystem processes. We support the need for quantitative measures for monitoring rangeland health and propose some measures that we believe may address some of the 17 indicators.

Key Words: Soil stability, hydrologic function, biological integrity, ecosystem status, erosion, infiltration, inventory

Resumen

Un panel de expertos de la "Society for Range Management" y el "National Research Council" propusieron que el estado de los ecosistemas de los agostaderos podría ser determinado evaluando el potencial que un sitio ecológico tiene para conservar recursos del suelo, y por una serie de indicadores de procesos ecológicos y estabilidad del sitio. Utilizando estas recomendaciones como punto de partida, desarrollamos un rápido método cualitativo para evaluar el estado de agostaderos en un punto especifico en el tiempo. Se evaluaron 17 indicadores para asesorar 3 atributos del ecosistema (suelo y estabilidad del sitio, función hidrológica, e integridad biótica) para un sitio especifico. Estos indicadores incluyen riachuelos (canalillos), patrones de escurrimiento, pedestales y terracetas, suelo desnudo, quebradas (carcavas), erosión eólica y áreas de deposición, movimiento de mantillo, resistencia del suelo a la erosión, degradación o perdida de la superficie del suelo, composición vegetal con relación a la infiltración, compactación del suelo, grupos vegetales funcionales y estructurales, mortalidad vegetal, cantidad de mantillo, producción anual, plantas invasivas, y capacidad de reproducción. En este informe, detallamos el desarrollo y evolución de esta técnica. También introducimos una tabla de datos de referencia ecológica modificada que documenta la presencia esperada y la cantidad de cada indicador en el sitio ecológico. En adición, repasamos las aplicaciones apropiadas para esta técnica y clarificamos las diferencias entre evaluación y monitoreo que nos llevaron a recomendar que esta técnica deberá ser utilizada para evaluación de un punto en el tiempo, y no para un monitoreo temporal de el estado de agostaderos. Por ultimo, recomendamos un mecanismo para adaptar y modificar esta técnica para reflejar mejoramientos y entendimiento de los procesos de ecosistemas. Soportamos la necesidad de medidas cuantitativas para el monitoreo de salud de los agostaderos, por lo cual proponemos algunas medidas que creemos que pueden tomarse en cuenta para algunos de los 17 indicadores.

Rangeland assessments in the United States over the past century have relied heavily on the Clementsian view of plant succession that plant communities progress or regress along predictable courses of defined communities in response to changes in disturbance or environmental regimes, including grazing and precipitation (Clements 1920, Dyksterhuis 1949). Rangeland scientists and managers have increasingly questioned the appropriateness

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of this model for making 1 type of rangeland assessment, rangeland condition (Westoby et al. 1989a, 1989b, Friedel 1991, Laycock 1991, Svejcar and Brown 1991). Two panels of experts, National Research Council (NRC 1994) and the Society for Range Management Task Group on Unity in Concepts and Terminology Committee (SRM Task Group 1995), suggested alternative approaches for evaluating rangeland status that relied on factors other than the traditional rangeland condition classification and on similarity of plant species composition to a single climax community. The NRC (1994) experts advocated the evaluation of multiple indicators to assess a site's degree of soil stability and watershed function, integrity of nutrient cycles and energy flow, and presence of functioning recovery mechanisms. The SRM Task Group (1995) recommended that new assessments focus primarily on the soil stability of a site. The Task Group recommended and the SRM adopted the following: (1) that evaluations of a site be based on the expected capability for that land unit (the ecological site) to support a natural range of potential plant communities; (2) that each potential plant community be evaluated for its ability to protect the site from accelerated erosion; and (3) that managers develop objectives for land uses and manage the land to achieve or maintain a desired plant community that protects the site against accelerated erosion.

The U. S. Department of the Interior (USDI), Bureau of Land Management (BLM) and the U. S. Department of Agriculture (USDA), Natural Resources Conservation Service (NRCS) expressed a need for a rapid technique that provides an initial assessment of rangeland health based on a workable set of criteria from a combination of the NRC (1994) and SRM Task Group (1995) reports. These agencies were not seeking a monitoring technique (as defined by SRM Glossary Update Task Group 1998) to determine if their management objectives had been met over time or if significant progress had been made toward meeting these objectives. Rather, they sought a moment-in-time assessment that would be equally effective in estimating the status of most rangeland communities (i.e., from tropical grasslands and coastal marshes to desert and tundra ecosystems) within the United States.

We address 4 objectives in this paper. First, we provide an overview of a technique that satisfies the NRCS/BLM criteria (Pellant et al. 2000). Second, we describe the approach used to develop this technique and introduce an improved technique for developing reference conditions for ecological sites. Third, we define the intended applications of the technique and explain the why we believe this technique may be used to provide a moment-in-time assessment of rangeland health, but not to temporally monitor rangelands. Fourth, we describe a mechanism for adapting the technique for different ecosystems and for ensuring that the technique will continue to reflect improvements in understanding of ecosystem processes.

Rangeland Health

We have chosen to use a definition of rangeland health developed by an ad hoc interagency committee (USDA, NRCS 1997). Rangeland health is the degree to which the integrity of the soil, vegetation, water and air as well as the ecological processes of the rangeland ecosystem are balanced and sustained. Integrity is defined as the maintenance of the functional attributes characteristic of a locale, including normal variability. Although there are a number of problems associated with applying the term "health " to natural ecosystems (Wicklum and Davies 1995, Lackey 1998, Rapport et al. 1998, Smith 1999), we elected to retain it. The NRC (1994) report used the term in the title of its publication. Concurrently, the public has begun to accept this term and to associate it with the status of ecological systems. With Rangeland Reform in 1994, the BLM began developing standards for rangeland health and guidelines for livestock grazing management on BLM rangelands with the assistance of Resource Advisory Councils (USDI, BLM 1994). Although these standards and guidelines differ for each state, they all incorporate language that relates to ecosystem health and have become the BLM policy for assessing public land health and for obtaining or maintaining ecological structure and function on BLM-managed lands (USDI, BLM 2001). Similarly, the NRCS has incorporated the term rangeland health into their latest addition of the National Range and Pasture Handbook and into the inventory phase of the conservation planning process that they conduct with private landowners (USDA, NRCS 1997). By retaining and defining rangeland health, we maintain a connection to the NRC report, to BLM's standards and guidelines for managing rangelands, and to NRCS National Range and Pasture Handbook.

Historical Development

Background. In the mid 1990's, several groups simultaneously advocated that all U.S. governmental agencies with responsibility for managing or reporting rangeland status should coordinate a national assessment of rangelands using common techniques and designs (West et al. 1994, NRC 1994, SRM Task Group 1995). Two of these reports (NRC 1994, SRM Task Group 1995) recommended the development of quantitative techniques for assessing ecosystem status, but both also noted that researchers would need to develop new and efficient techniques to measure many indicators of ecosystem status.

The NRC (1994) and SRM Task Group (1995) also recommended that assessments be used to classify and compare similar combinations of soils and climate that have the capacity to support ecosystems with similar plant communities and production (e.g., ecological sites). New ecological site descriptions (USDA, NRCS 1997), which are in the process of being developed, recognize and portray the multiplicity of vegetation states and transitions among states that are expected with natural or human-induced changes (Westoby et al. 1989a, 1989b, Stringham et al. 2001). These descriptions also use the threshold concept to describe unidirectional changes in ecosystem structure and ecosystem functional processes. When these thresholds are crossed, recovery to original ecosystem states is difficult (Laycock 1991, Friedel 1991, SRM Task Group 1995). When possible, ecosystem assessments should strive to incorporate these concepts as research results refine our understanding of states, transitions and thresholds.

In 1997, agency leaders for the BLM, NRCS, and the USDA Forest Service signed a Memorandum of Understanding (interagency MOU group) that formed a committee responsible for overseeing the development of a common national rangeland assessment technique. This committee is pursuing the development of quantitative assessment indicators and protocols.

While quantitative national assessment techniques are being developed, the BLM and NRCS identified a need for a rapid assessment technique that could provide a preliminary assessment of rangeland health at the management unit or lower level. Additionally, the technique could provide a communication tool with stakeholders regarding the status of ecosystem properties and processes.

Approach used to develop the technique. In 1995, the NRCS and BLM began development of qualitative techniques for the assessment of rangeland health using the NRC (1994) and SRM Task Group (1995) recommendations as a starting point. These efforts resulted in the development of 2 similar protocols. The first 2 versions of this technique were developed separately by the BLM (Pellant 1996) and NRCS (USDA, NRCS 1997). These versions were similar, but not identical. In 1997, we integrated these versions and began a coordinated effort to evaluate each indicator based on the scientific literature and field tests in rangeland ecosystems throughout the United States. Indicators that were not supported by the literature, that could not be consistently applied or interpreted, or that were not sensitive to changes in ecosystem structure or function across a wide variety of ecosystems, were modified, replaced or discarded. For example, repeatability among observers varied using the BLM version that contained only 3 rating categories (properly functioning, functioning at risk, and non-functioning) for 18 indicators divided among a biotic and a physical attribute (Rasmussen et al. 1999). In response, we adjusted the rating categories to 5, the level used in the NRCS version of the technique.

This iterative process involved approximately 500 people participating in over 16 training or testing sessions in 10 states covering 9 of the 36 ecosystem provinces of the humid, temperate and dry domains in the 48 contiguous states in the United States (Bailey et al. 1994). Participants included scientists (federal and university), federal, state, and tribal land managers, ranchers and members of conservation organizations. Over 20 scientists, 25 BLM and NRCS resource specialists, 35 consultants from the Association of Rangeland Consultants, and members of the Western Coordinating Committee on Rangeland Ecological Research and Assessment (WCC-40) reviewed and criticized the final draft of the technique. The technique and the document (Pellant et al. 2000) were improved by incorporating modifications suggested by these peers. For example, training participants found it difficult to provide a single assessment of rangeland health for an evaluation area and that they wanted to be able to generate information relevant to specific attributes. In response, we modified the technique to provide separate ratings for each of the 3 attributes and to eliminate any reference to a single rating of overall status.

Description of the Technique (Methods)

Overview. The technique involves evaluating all locations using the same minimum set of 17 qualitative indicators relative to their potential within an ecological site. We use the Society for Range Management (SRM Glossary Update Task Group 1998) definition of an ecological site being "a kind of land with specific physical characteristics which differs from other kinds of land in its ability to produce distinctive kinds and amounts of vegetation and in its response to management." Site potential for each indicator is defined by that indicator's presence and range of amount in resistant and resilient plant community phases that maximize retention of soil. These may be determined by examining a range of reference areas that describe these phases or they may be defined in or inferred from the ecological site description. Ecological site descriptions describe soil associations (as defined by the Soil Science Society of America 1997) and their physical, hydrological and biological characteristics that produce distinctive kinds and amounts of vegetation. The amount of information included in ecological site descriptions varies depending on when the description was written. Early descriptions, originally called range site descriptions, contained basic descriptions of soils and vegetation. Ecological site descriptions written or revised since 1997 contain additional detail on the variation in plant composition, cover and production for the dynamic set of vegetation states and on hydrologic and soil stability characteristics of the ecological site. The NRCS has committed to a program of revising all previously written range site and ecological site descriptions into this new format (Pers. Comm. G. Peacock, NRCS Grazing Lands Technology Institute, Fort Worth Tex.). All currently approved ecological site descriptions are available at local NRCS offices. In addition, they will be available on the Internet at the PLANTS database homepage (USDA, NRCS 2001) under the Ecological Site Information System (ESIS) heading. If neither reference areas nor an ecological site description exist, then a group of soil and plant experts should define and document their expectations for each of these indicators using their knowledge and data about similar soils and plant communities.

Three overlapping subsets of indicators are used to assess 3 attributes of the site: soil and site stability, hydrologic function, and biotic integrity. We use the term attribute to describe an ecosystem component that cannot be directly measured, but can be approximated by a set of observable indicators of the component. The assessment of these 3 attributes is the final product of the technique. In the remainder of this section, we describe attributes and indicators, outline the technique that is used to evaluate each indicator relative to its potential for a particular site. We include a new method for documenting reference conditions for each indicator and define how the 3 attributes are evaluated based on a combination of indicators to arrive at an assessment of the status of each attribute.

Attributes. Both the SRM Task Group (1995) and the NRC (1994) reports suggested a single rating for the site assessment. The SRM Task Group (1995) emphasized soil conservation in their hypothetical quantitative approach. They proposed the development of a Site Conservation Rating (SCR), "an assessment of the protection afforded a site by the current vegetation against loss of potential." They also proposed that a Site Conservation Threshold (SCT), "the kind, amount, and/or pattern of vegetation needed as a minimum on a given site to prevent accelerated erosion," would provide a mechanism for categorizing a site as "satisfactory or sustainable" or "unsatisfactory or unsustainable." Although this Task Group proposed this new approach for evaluating lands, they clearly stated that criteria for evaluating the SCR and SCT should be objective and quantitative enough to serve as monitoring parameters for assessing the trend in the SCR. However, these criteria "will have to be worked out by research and professional judgment for each ecological site" (SRM Task Group 1995). To our knowledge, few studies have attempted to develop or test quantitative criteria for a SCR (Watters et al. 1996) whereas some development has begun for some indicators of forest and rangeland health or sustainability (de Soyza et al. 1997, 2000, Weltz et al. 2000, Woodley et al. 2000, Herrick et al. 2002).

The NRC (1994) suggested classifying lands into 3 categories using soil and ecological processes as basic elements of site production: (1) those lands that remain above an early warning line where the land produces at its potential for commodities and other values; (2) those that fall below this early warning line and have a reduced ability to produce commodities and support other values, but where this reduction can be reversed through man-

Table 1. Standard indicators included in the rangeland health protocol, attributes to which each indicator applies, and publications used to develop the descriptors and interpretations for each indicator.

Indicators and brief descriptions of characteristics for evaluating the indicator	Attributes			Relevant Literature
	Soil and Site Stability	Hydrologic Function	Biotic Integrity	
1. Rills – the frequency and spatial distribution of linear erosional rivulets.	X	X		Quansah 1985, Morgan and Davidson 1986, Bryan 1987
2. Water Flow Patterns – the amount and distribution of overland flow paths that are identified by litter distribution and visual evidence of soil and gravel movement.	X	X		Morgan and Davidson 1986, Tiscareño Lopez et al. 1993
3. Pedestals and/or Terracettes – the frequency and distribution of rocks or plants where soil has been eroded from their base (pedestals) or areas of soil deposition behind obstacles.	X	X		Anderson 1974, Morgan and Davidson 1986, Satterlund and Adams 1992, Hudson 1993
4. Bare Ground – size and connectivity among areas of soil not protected by vegetation, biological soil crusts, litter, standing dead vegetation, gravel or rocks.	X	X		Smith and Wischmeier 1962, Anderson 1974, Gould 1982, Morgan and Davidson 1986, Benkobi et al. 1993, Blackburn and Pierson 1994, Pierson et al. 1994, Spaeth et al. 1994, Gutierrez and Hernandez 1996, Puigdefábregas and Sánchez 1996, Weltz et al. 1998, Cerda 1999
5. Gullies –amount of channels cut into the soil and the amount and distribution of vegetation in the channel.	X	X		Anderson 1974, Morgan and Davidson 1986, Martin and Morton 1993
6. Wind Scoured, Blowouts and/or Deposition Areas – frequency of areas where soil is removed from under physical or biological soil crust or around vegetation OR frequency of accumulation areas of soil associated with large structural objects, often woody plants.	X			Chepil 1945, Chepil and Woodruff 1963, Anderson 1974, Gillette et al. 1974, Gillette and Walker 1977, Gibbens et al. 1983, Hennessy et al. 1983, Hagen 1984, Hennessy et al. 1986, Morgan and Davidson 1986, Pye 1987
7. Litter Movement – frequency and size of displaced litter by wind and overland flow of water.		X		Thurow et al. 1988
8. Soil Surface Resistance to Erosion – ability of soils to resist erosion through the incorporation of organic material into soil aggregates. It is evaluated by using a modified slake test.	X	X	X	Bond and Harris 1964, Belnap and Gardner 1993, Blackburn et al. 1992, Morgan and Davidson 1986, Goff et al. 1993, Blackburn and Pierson 1994, Fryrear et al. 1994, Pierson et al. 1994, Morgan et al. 1997, Belnap and Gillette 1998, Herrick et al. 2001
9. Soil Surface Loss or Degradation – frequency and size of areas missing all or portions of the upper soil horizons that normally contain the majority of organic material of the site.	X	X	X	Hennessy et al. 1986, Warren et al. 1986, Satterlund and Adams 1992, O'Hara et al. 1993, Karlen and Stott 1994, Wood et al. 1997, Davenport et al. 1998, Dormaar and Willms 1998
10. Plant Community Composition & Distribution Relative to Infiltration & Runoff – the community composition or distribution of species that restrict the infiltration of water on the site.		X		Blackburn 1975, Wood and Blackburn 1984, Johnson and Gordon 1988, Thurow et al. 1988, Blackburn and Wood 1990, Schlesinger et al. 1990, Blackburn et al. 1992
11. Compaction Layer – thickness and distribution of the structure of the soil near the soil surface (=< 15 cm)	X	X	X	Barnes et al. 1971, Webb and Wilshire 1983, Willat and Pullar 1983, Cole 1985, Blake and Hartge 1986, Warren et al. 1986, Wallace 1987, Thurow et al. 1988, Hassink et al. 1993, Larson and Pierce 1993, Chanasyk and Naeth 1995, Hillel 1998
12. Functional/Structural Groups – the number of groups, the number of species within groups, or the rank of order of dominance of groups.			X	Chapin 1993, Dawson and Chapin 1993, Solbrig et al. 1996, Tilman et al. 1997
13. Plant Mortality/Decadence – frequency of dead or moribund (dying) plants			X	Stoddard et al. 1975, Pyke 1995,
14. Litter Amount – deviation in the amount of litter.		X	X	Thurow et al. 1988, Whitford 1988, Whitford 1996, Hester et al. 1997
15. Annual Abroveground Production – amount relative to the potential for that year based upon the climate.			X	Cooper 1975, Whittaker 1975, Rickard and Rogers 1988, Tilman and Downing 1994
16. Invasive Plants – abundance and distribution of invasive plants regardless if they are noxious weeds, exotic species, or native plants whose dominance greatly exceeds that expected at the ecological site.			X	Lacey et al. 1990, Olson 1999, Stohlgren et al. 1999
17. Reproductive Capability of Perennial Plants – evidence of the inflorescences or of vegetative tiller production relative to the potential based upon the current climate.			X	Hanson and Stoddard 1940, Mueggler 1975, Harper 1977, White 1979

Table 2. The 6 steps of the Interpreting Indicators of Rangeland Health (Pellant et al. 2000) are summarized along with the location (evaluation or reference area) where the step is completed, and the recommended worksheets (found in Pellant et al. 2000) that are used when completing each step.

Step	Description	Location	Recommended worksheets
1	Identify the evaluation area and verify soils and ecological site for the area	Evaluation Area	1. Rangeland Health Evaluation Summary, Part 1
2	Develop expected indicator ranges for the ecological site. Visually familiarize yourself with the 17 indicators at an Ecological Reference Area and rate the reference area against the Ecological Reference Worksheet	In the office and at the Ecological Reference Area	1. New Ecological Reference Worksheet (Table 3) 2. Cover 3. Species Dominance 4. Functional/Structural Groups (Potential Dominance)
3	Review or modify descriptors of indicators	Ecological Reference Area	1. Rangeland Health Indicator Evaluation Matrix (Table 4)
4	Characterize the vegetation found at the evaluation area	Evaluation Area	1. Cover 2. Species Dominance 3. Functional/Structural Groups (Actual Dominance)
5	Rate the 17 indicators	Evaluation Area	1. Rangeland Health Evaluation Summary, Part 2 (Table 5) 2. Use Rangeland Health Indicator Evaluation Matrix (Table 4)
6	Determine functional status of the rangeland health attributes	Evaluation Area	1. Rangeland Health Evaluation Summary, Part 3 (Table 6)

agement changes; and (3) those sites with substantial reductions in commodities and values where management changes are not likely to reverse this reduction. They proposed that criteria for rangeland health be defined using multiple indicators in 3 major areas: (1) soil stability and watershed function; (2) the integrity of nutrient cycles and energy flow; and (3) the presence of functioning recovery mechanisms. Although they proposed these criteria, they recognized the lack of quantitative procedures that could be used efficiently and economically in assessments of large amounts of rangelands. They advocated the need for research to develop such quantitative approaches, but in lieu of such techniques, they suggested a series of indicators that could be qualitatively evaluated.

Although a single rating of a site's status is intuitively appealing, we discovered early in the development process of this current approach that some sites might have attributes of ecosystem status that were operating properly while other attributes were not. Initially, we began to look for indicators of nutrient cycling, energy flow and recovery mechanisms that observers could evaluate, but direct linkages between observable quantitative or qualitative measures of these processes were not easy to determine. By blending the NRC and the SRM Task Group approaches and by using an iterative process of field tests and peer reviews by land managers and scientists, we identified 3 attributes of ecosystem status that can be evaluated using multiple indicators:

Soil or Site Stability – The capacity of the site to limit redistribution and loss of soil resources (including nutrients and organic matter) by wind or water;

Hydrologic Function – The capacity of the site to capture, store and safely release water from rainfall, run-on and snowmelt (where relevant), to resist a reduction in this capacity and to recover this capacity following degradation;

Integrity of the Biotic Community – The capacity of the site to support characteristic functional and structural communities in the context of normal variability and to resist loss of this function and structure caused by disturbance, and to recover following each disturbance.

Indicators. We have selected indicators to represent components of attributes that are difficult to measure directly. This use of indicators is similar to the approach used by others in selecting forest or rangeland indicators (Breckenridge et al. 1995, de Soyza et al. 1997, 2000, Whitford et al. 1998, Woodley et al. 2000). We define indicators as observable components of an ecosystem that are related to 1 or more attributes, are easily evaluated, and used in combination with other indicators as an index of the status of that attribute. Each indicator at an evaluation area is assigned to 1 of 5 categories based on its departure from what is expected for that ecological site. The expectation for the ecological site should be derived from the soil survey, the ecological site description or, as a last resort, from expert opinion. Evaluators rate a site using 5 categories that describe a gradient for each indicator associated with each attribute. Indicators were selected if we could provide affirmative answers to 2 successive questions. (1) Did peer-reviewed literature exist to support the association of this indicator with its attribute? (2) Could experienced land managers understand and consistently provide a visual assessment of this indicator?

Currently, we have included 17 indicators for rating the 3 attributes (Table 1). Additional information on the scientific basis for each indicator is included in an interagency technical reference (Pellant et al. 2000). Indicators can be associated with single attributes, such as litter movement's association with hydrologic function and invasive plants' association with biological integrity. Other indicators are associated with 2 or all 3 attributes (Table 1). We recognize that some of these indicators might be related to additional attributes, but we believe the associations that we have selected are the strongest or the best supported by the literature.

Procedure. To rate the 3 attributes at an evaluation area, an evaluator must complete a 6-step process (Pellant et al. 2000, Table 2). **Step 1** requires that evaluators visit an evaluation area to verify the soil and the ecological site of the area. Evaluation areas may be specific sites of concern within a management unit (e.g., a pasture, watershed, allotment or management area) or they may be a representative subsample of strata within a larger management unit (see Intended Applications). Evaluation areas should be within a specific landscape position, include the natural variability of the ecological site, but remain sufficiently small (approximately 0.4 to 2.0 ha or 1 to 5 ac), so that evaluators can easily walk throughout the area and observe the variation in the plant species composition and soil surface features. Since assessments will be made relative to the ecological site description or ecological reference areas on the same ecological site, evaluators must be certain of the evaluation area's landscape position and soils (same ecological site). The eco-

Table 3. Example of an Ecological Reference Worksheet developed for the Limy Ecological Site Description (italics) in the Southern Desert 4 subarea of Southern Desertic Basins, Plains and Mountains Major Land Resource Area (MLRA 42) in New Mexico. This example is based on the Natural Resources Conservation Service Ecological Site Description, unpublished data, and collective knowledge of J. Christensen, B. Call, B. Bestelmeyer, R. Placker, D. Trujillo, L. Hauser, D. Coalson, P. Smith, and J. Herrick.

Indicators. For each indicator, describe the potential for the site. Where possible, (1) use numbers, (2) include expected range of values for poor-good years, when appropriate & (3) cite data. Continue descriptions on separate sheet.

1. **Number and extent of rills:** *None.*
2. **Presence of water flow patterns:** *None, except following extremely high intensity storms, when short (less than 1 m) flow patterns may appear.*
3. **Number and height of erosional pedestals or terracettes:** *None.*
4. **Bare ground from Ecological Site Description or other studies (rock, litter, lichen, moss, plant canopy are not bare ground):** *20 – 30 % bare ground; bare patches should be less than 8-10 inch diameter; occasional 12 inch patches associated with shrubs. Larger bare patches also associated with ant mounds and rodent disturbances.*
5. **Number of gullies and erosion associated with gullies:** *None.*
6. **Extent of wind scoured, blowouts and/or depositional areas:** *None.*
7. **Amount of litter movement (describe size and distance expected to travel):** *Minimal and short, associated with water flow patterns following extremely high intensity storms. Litter also may be moved during intense wind storms.*
8. **Soil surface (top few mm) resistance to erosion (stability values are averages – most sites will show a range of values):** *Stability class (Herrick et al. 2001) anticipated to be 5-6 at surface and subsurface under vegetation and 4-5 at surface and subsurface in the interspaces. These values need verification at reference sites.*
9. **Soil surface structure and SOM content (include type and strength of structure, and A-horizon color and thickness):** *2-4 inch dark brown A horizon with medium granular structure (Otero County Armesa series description refers to platy structure; probably not from a true reference site).*
10. **Effect of plant community composition (relative proportion of different functional groups) & spatial distribution on infiltration & runoff:** *High grass canopy and basal cover and small gaps between plants should reduce raindrop impact and slow overland flow, providing increased time for infiltration to occur. High root density of blue grama can limit infiltration. The more herbaceous vegetation on this site will result in less rain necessary to sustain this site because more water is retained.*
11. **Presence and thickness of compaction layer (usually none; describe soil profile features which may be mistaken for compaction on this site):** *None*
12. **Functional/Structural Groups (list in order of descending dominance by above-ground weight using symbols: >>, >, = to indicate much greater than, greater than, and equal to):** *Blue grama > Black grama > warm season bunchgrasses > Yucca = shrubs >> sub-shrubs = succulents; Forbs 0 – 8 % depending on the year.*
13. **Amount of plant mortality and decadence (include which functional groups are expected to show mortality or decadence):** *Grasses will nearly always show some mortality and decadence.*
14. **Average percent litter cover (_______%) and depth (______ inches).** *20 – 25 % litter cover and 0.25 inch depth.*
15. **Expected annual production (this is TOTAL above-ground production, not just forage production)**
   __________ - __________ pounds/acre or tons/ha (choose one): *650 to 1200 pounds/acre based on ecological site description. Could be even higher on particularly good years.*
16. **Potential invasive (including noxious) species (native and non-native). List species which characterize degraded states and which, after a threshold is crossed, "can and often do continue to increase regardless of the management of the site and may eventually dominate the site":** *Possibly creosote bush which is an invader on similar ecological sites; snakeweed is cyclical, so not regarded as an invasive plant on this ecological site.*
17. **Perennial plant reproductive capability:** *all species should be capable of reproducing.*

logical site will encompass the normal range of variation of successional communities (community phases) with reversible transitions (community pathways) within an ecological state (as defined by Stringham et al. 2001). Since some evaluation areas have crossed thresholds (irreversible transitions) to another ecological state, evaluators must recognize that soils, not plant communities, will be the best aid in identifying the ecological site.

To document soils at evaluation and reference areas, evaluators document the presence and depths of the appropriate diagnostic soil horizons found in each area and provide the corresponding information from the soil survey or ecological site description in the first portion of the Rangeland Health Evaluation Summary (Pellant et al. 2000) and the Ecological Reference Worksheets (Table 3). Evaluators also document the area's location, parent material, slope gradient and topographic position on these same worksheets. Recent weather conditions and cycles should be reported along with disturbances or off-area influences that might affect the assessment.

The objective of the next 2 steps is to define the expected status of each indicator on a healthy site. This process involves examination, and in some cases modification, of the descriptor narratives for the 5 categories for each indicator. We have prepared several worksheets to assist in this process (Table 2).

During **Step 2**, each indicator is described on a new portion of the ecological reference worksheet (Table 3) developed after the publication of Version 3.0 (Pellant et al. 2000). We have found that the most effective way to develop these reference worksheets is to assemble a diverse group of experts regarding the ecological site. Individuals should be included who have extensive, long-term knowledge of the ecological site, in addition to rangeland professionals who understand general soil-climate-vegetation relationships and the relevant literature. These individuals should use all available sources of information, particularly ecological site descriptions and data from potential reference sites. The process is extremely useful for identifying knowledge gaps that require additional research and for helping diverse groups to improve their collective understanding of relationships between soils, vegetation and hydrology. This worksheet is valuable for 3 reasons. First, it is more convenient and therefore more likely to be referred to in the field than a complete ecological site description. Second, the completed reference worksheet can be used to facilitate the development of consensus about each indicator's presence and amount on an ecological site, particularly when no ecological site description is available. Third, and most important, it can increase the consistency with which the method is applied by clarifying the standard that is used to evaluate each indicator. A related use is to compare the description to the "None-Slight" default descriptor in Pellant

Table 4. An example of a series of default descriptions for the bare ground indicator and a hypothetical revision of the descriptions for an ecological site (from Pellant et al. 2000).

Indicator	Degree of Departure from Ecological Site Description and/or Reference Area(s)				
	Extreme	Moderate to Extreme	Moderate	Slight to Moderate	None to Slight
4. Bare Ground (Default description)	Much higher than expected for the site. Bare areas are large and generally connected.	Moderately higher than expected for the site. Bare areas are large and occasionally connected.	Moderately to slightly higher than expected for the site. Bare areas are of moderate size and sporadically connected.	Slightly higher than expected for the site. Bare areas are small and rarely connected.	Amount and size of bare areas matches that expected for the site.
Bare Ground (Revised description)	Much higher than expected for the site. Bare areas are extensive with little ground cover.	Moderately higher than expected for the site. Bare areas are very large and usually connected.	Moderately to slightly higher than expected for the site. Bare areas are large and usually connected.	Slightly higher than expected for the site. Bare areas are of moderate size and usually connected.	Same as default descriptor

et al. (2000) in order to highlight those indicators that are likely to require descriptor revisions.

Once the reference worksheet is developed, evaluators should attempt to locate and visit ecological reference areas (ERA). The ERA's are landscape units that provide visual representations of the characteristics and variability in the ecological site description. These areas do not need to be pristine, historically unused lands (e.g., climax plant communities or relict areas). This concept is similar to that proposed by the Western Regional Coordinating Committee-40 on Rangeland Ecological Research and Assessment of using well-managed rangelands and appropriate relict areas as benchmarks for assessments (West et al. 1994). Since revised ecological site descriptions will include the range of vegetation communities that may exist on an ecological site, the ERA should represent the expected state that would result from natural disturbances such as fire or drought. A single reference area will represent 1 spatial point and temporal moment of this range of variation for that ecological site. Thus, an ERA will represent a single community phase within the ecological state for that ecological site. Evaluators should recognize that vegetation composition within an ecological state may change over time through reversible transitions and should account for this in their interpretation of the ecological site (Stringham et al. 2001).

It is also important to avoid areas that are more productive than anticipated based on the site description, particularly where there is no current or historical explanation for the high productivity. Significantly higher productivity is often due to soil or topographic differences, including differences *within a single soil series*. These differences can also affect the resistance of the site to degradation and recovery. Evaluators should check texture, depth and topographic position, particularly in landscapes where significant runoff or run-on occurs.

To assist evaluators in identification of appropriate ERAs and comparisons with the evaluation area(s), we prepared another set of worksheets (Table 2) to lead them through the process of observation, categorization and documentation of the appropriate information. In the canopy and ground cover worksheet, evaluators estimate broad cover classes for vegetation life forms and ground cover parameters. Species dominance based on cover or biomass is estimated for each major life form group and for the whole site. In the structural and functional groups worksheet, species are placed into structural and functional groups and each group is placed into a dominance class based on the groups relative production or cover. These worksheets assist evaluators to visualize plant species, soil, and hydrological indicators under current weather conditions in this locale. Information from each of these worksheets is used together with additional observations to verify that an ecological reference area agrees with the ecological reference worksheet where soils and the ecological site are verified and where the presence and status of each of the 17 indicators is documented. Photographs, and if possible quantitative data, of ecological reference areas are also recommended to aid in subsequent assessments of similar landscape units.

In some locations and ecological sites, finding an ERA that fits within the range of variation of the ecological site description may be difficult because of site degradation. In those cases, evaluators may elect to only use the ecological site description as the standard of comparison or may elect to use a site as an ERA with limitations. It is still useful, however, to complete worksheets based on the ecological site descriptions and knowledge from local experts.

In Step 3, evaluators compare the series of default narrative descriptions for rating each indicator to the ecological site description and the ERA to determine if default descriptions are adequate for describing the indicator in the ecological site or if a modified description should be written. Each of the 17 indicators has a separate default set of narrative descriptions similar to the default description for bare ground shown in Table 4. All of the narrative descriptors rate indicators at the evaluation area based on that location's degree of departure from ecological site description. Below each default narrative, a blank space is provided for evaluators to write a revised description. These revised descriptions can be written and used immediately, provided that the change is clearly documented in reports or recommendations made based on the assessment, and that consistency can be maintained among assessments made in a particular area or for a particular project. When revised descriptions are necessary, they should be submitted to the NRCS State Rangeland Management Specialist. Each ecological site will have one set of descriptions. This person along with other interested people will discuss and consider the inclusion of the proposed narrative revision in updated ecological site descriptions using accepted NRCS protocols for revisions. Eventually, we hope that each

Table 5. A hypothetical example of a completed Rangeland Health Evaluation Summary Worksheet, part 2 used in the rangeland health assessment for a site. Letters S, W and B under the Attribute column refer to Soil, Water, and Biology and indicate association of the indicator with the respective attributes, Soil or Site Stability, Hydrologic Function, or Biological Integrity. The comments section is used to help evaluators document their rationale for the specific rating of selected indicators.

		Departure from Ecological Site Description/Reference Area(s)				
Attribute	Indicators	Extreme	Moderate to Extreme	Moderate	Slight to Moderate	None to Slight
S,W	1. Rills				√	
Comments						
S,W	2. Water Flow Patterns				√	
Comments						
S,W	3. Pedestals and/or Terracettes			√		
Comments – *Several plants along flowpaths have roots exposed, but site is not prone to frost heaving*						
S,W	4. Bare Ground				√	
Comments						
S,W	5. Gullies				√	
Comments – *One gully visible, vegetation in bottom and on sides; no evidence of headcuts*						
S	6. Wind Scoured, Blowouts and/or Deposition Areas					√
Comments						
W	7. Litter Movement					√
Comments						
S,B,W	8. Soil Surface Resistance to Erosion			√		
Comments – *The majority of soil samples from under canopies of plants tending to fall apart when placed in water*						
S,B,W	9. Soil Surface Loss or Degradation			√		
Comments – *A-horizon missing in interspaces; present under shrubs or larger grasses*						
W	10. Plant Community Composition & Distribution Relative to Infiltration & Runoff			√		
Comments						
S,B,W	11. Compaction Layer			√		
Comments – *Interspaces with platy structure at 2-3 cm depth & roots tending to grow horizontally at this point; No evidence under shrubs*						
B	12. Functional/Structural Groups	√				
Comments – *Tall and short C4 grasses not present; Midgrass C3 grasses restricted to one species; Forb component not present; Shrubs dominate*						
B	13. Plant Mortality/Decadence		√			
Comments – *Many shrubs have died recently*						
B,W	14. Litter Amount		√			
Comments – *Only associated with shrubs; no litter around C3 mid-grasses*						
B	15. Annual Production	√				
Comments – *Site should support 1800 kg/ha, but estimate less than 300 kg/ha*						
B	16. Invasive Plants					√
Comments						
B	17. Reproductive Capability of Perennial Plants	√				
Comments						

ecological site description will include a series of accepted narratives for indicators and attributes.

During this step, evaluators may consider adding indicators that they believe should be included in the assessment. Those indicators might include parameters that may not be important nationally, but may have regional importance. An example of this might be the inclusion of a biological soil crust indicator for specific ecological sites in the Colorado Plateau where these crusts are important for soil stabilization (Belnap and Gardner 1993, Johansen 1993, Warren 2001). Similar to the revised narrative, if an evaluator uses an additional indicator, then they should submit the indicator, the narrative descriptions and the attribute(s) to which it relates along with relevant scientific literature that provide evidence of this relationship to the NRCS State Rangeland Management Specialist who will follow the appropriate NRCS protocol for consideration in future ecological site descriptions. These additional indicators must be ecology-based and not value- or use-based indicators.

Table 6. (a) A hypothetical example of a completed indicator summary, Part 3 of the Rangeland Health Evaluation Summary Worksheet, using the information from Table 5 to show the frequency distribution of indicators for each of the rangeland health attributes and (b) the attribute summary that gives the evaluator's judgment regarding the overall rating for each attribute at the site. Note that italicized text indicates the evaluator's comments regarding the attribute summary.

a) Indicator Summary	Departure from Ecological Site Description/Reference Area(s)					
Rangeland Health Attributes	Extreme	Moderate to Extreme	Moderate	Slight to Moderate	None to Slight	Σ
S – Soil/Site Stability (Indicators 1-6, 8, 9 & 11)			√√√√	√√√√	√	9
W – Hydrologic Function (Indicators 1-5, 7-11 & 14)		√	√√√√√	√√√√	√	11
B – Biotic Integrity (Indicators 8- 9 &11-17)	√√√	√√	√√√		√	9

b) Attribute Summary- Check the category that best fits the "preponderance of evidence" for each of the 3 attributes relative to the distribution of indicator ratings in the preceding "Indicator Summary" table.

Attribute	Extreme	Moderate to Extreme	Moderate	Slight to Moderate	None to Slight
Soil Site Stability Rationale: *Interspaces all show signs of erosion*	☐	☐	☒	☐	☐
Hydrologic Function Rationale: *Water appears to be moving on the surface and low infiltration on the site.*	☐	☐	☒	☐	☐
Biotic Integrity Rationale: *Only invasive plants indicator was rated higher than Moderate*	☐	☒	☐	☐	☐

Evaluators must return to the evaluation area to complete the remaining steps. In **Step 4**, evaluators complete a canopy and ground cover worksheet and a species dominance worksheet similar to those done on the ERA. In addition, evaluators complete the previous structural and functional grouping worksheet by estimating and recording the dominance category of each structural and functional group for the evaluation area. Photographs and quantitative data are again recommended to aid in future interpretations of the site's status.

Step 5 involves rating the 17 indicators using the narrative descriptions for each indicator. These ratings are relative to the ecological site description and the ERA for the specific ecological site. Table 5 includes an example. In **Step 6**, evaluators summarize the indicator ratings for each attribute and provide a summarized attribute rating for the site (Table 6). Indicator and attribute ratings in these last 2 steps are based on their degree of departure from that expected based on the ecological site description or reference areas. We recognize that the relative importance of different indicators varies among ecological sites, but we do not believe indicators can be properly weighted nor do we believe applicability of indicators for each ecological site can be determined for all ecological sites throughout the nation. In the future, this may be possible and these assessments and comments may be helpful in determining such a weighting or application system.

We recognize that this rating system appears to lend itself to numerical values or ranks that could be averaged and weighted. Attempts to create numerical

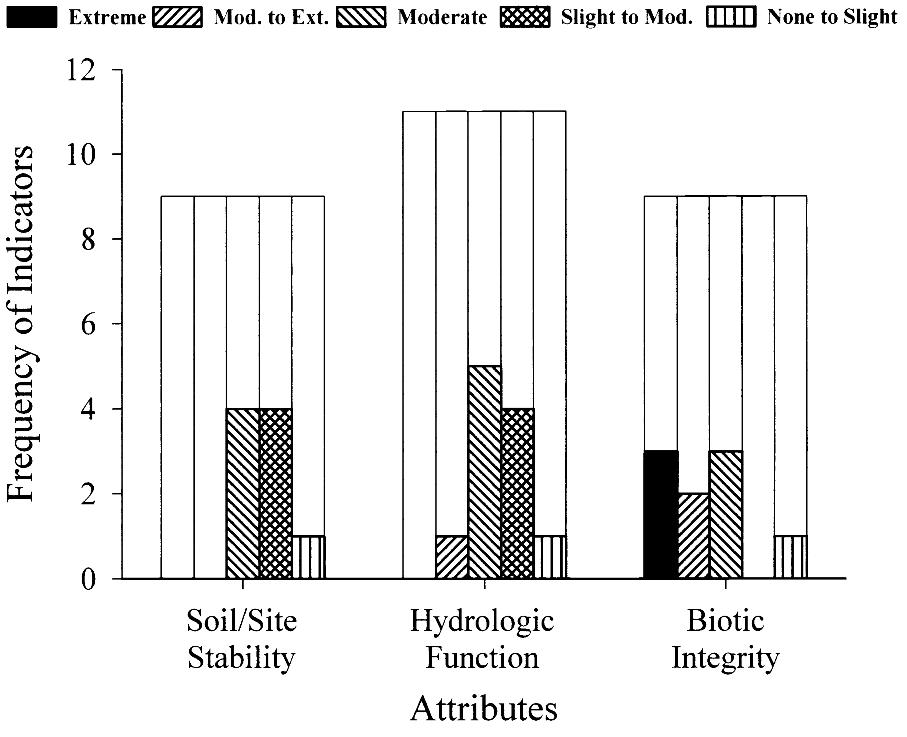

Fig. 1. Example of a histogram used to summarize the indicator categories associated with the 3 rangeland health attributes (adapted from a design by M. Miller, pers. comm.). Open bars indicate the maximum possible frequency for each attribute.

Table 7. Potential quantitative measurements and indicators that we believe relate to the17 rangeland health qualitative indicators from Pellant et al. (2000) each quantitative indicator, we provide a potential explanation (interpretation) of the relationship between the qualitative and quantitative indicators.

Qualitative Indicator	Quantitative Indicator	Measurement	Interpretation
1. Rills	None		
2. Water flow patterns	Percent basal cover	Line-point intercept	Basal cover is *negatively* correlated with water flow patterns because plant bases slow water movement.
	Proportion of basal gaps > 25, 50, 100, 200 cm	Basal gap intercept	Basal gaps are *positively* correlated with water flow patterns because water gains energy as it moves unobstructed across larger gaps.
3. Pedestals and/or terracettes	Standard deviation of pin heights	Erosion bridge (microtopography)	Pedestals and terracettes *can be positively* correlated with pin height standard deviation because increased microtopography is *sometimes* due to pedestals and terracettes.
4. Bare ground	Percent bare ground	Line-point intercept	Bare ground is *positively* correlated with runoff and erosion.
	Proportion of line in canopy gaps > 25, 50, 100, 200 cm	Canopy gap intercept	The bare ground qualitative indicator is also *positively* correlated with canopy gaps because bare ground in large gaps usually has a larger effect on many functions than bare ground in small gaps.
5. Gullies	Width-to-depth ratio and side slope angle	Channel profiles	Lower width-to-depth ratios and higher side slope angles both reflect more severe or active gully erosion.
	Headcut movement	Headcut location	Higher rates of headcut movement reflect greater gully erosion.
6. Wind-scoured areas	None		
7. Litter movement	Proportion of litter cover in interspaces *vs.* under canopies	Line-point intercept	Higher proportions of litter in the interspaces can be *positively* related to litter movement.
	Proportion of basal gaps > 25, 50, 100, 200 cm	Basal gap intercept	Basal gaps can be *positively* related to redistribution or loss of litter.
8. Soil surface resistance to erosion	Average soil surface stability	Soil stability kit (surface)	Surface aggregate stability is *positively* related to soil's resistance to wind and water erosion.
9. Soil surface loss or degradation	Average soil sub-surface stability	Soil stability kit (sub-surface)	Sub-surface soil structure degrades and organic matter declines as surface soil is lost, thus sub-surface aggregate stability is negatively related to soil surface loss or degradation.
10. Plant community composition and distribution relative to infiltration and runoff.	Percent composition	Line-point intercept or production	Changes in species composition can be related to changes in infiltration. For example, root and shoot morphology of tussock *vs.* stoloniferous plants.
	Proportion of basal gaps > 25, 50, 100, 200 cm	Basal gap intercept	Changes in basal gaps can be related to changes plant distributions that relate to infiltration and runoff.
11. Compaction layer	Ratio of penetration resistance in the upper 15 cm (6 inches) between the evaluation and reference area	Impact penetrometer	Ratios of penetration resistance or bulk density above 1 can indicate the presence of a compaction layer.
	Ratio of mass-per-volume of soil in the upper 15 cm between the evaluation and reference area	Bulk density	
12. Plant functional or structural groups	Percent composition by functional or structural group and group richness	Line-point intercept Production	Composition and richness of functional or structural groups are *positively* related to plant functional or structural groups qualitative indicator
13. Plant mortality or decadence	Proportion of live-to-dead canopy	Line-point intercept	The live-to-dead proportion is *positively* related to the plant mortality or decadence qualitative indicator
14. Litter amount	Litter mass	Litter mass	The amount of litter mass and cover per unit area is related to litter amount.
	Litter cover	Line-point intercept	
15. Annual production	Total annual production	Production	Productions relates directly with the qualitative indicator of annual production
16. Noxious and invasive plants	Density of invasive species	Belt tranect	Number of species and their densities or cover will directly relate to the qualitative indicator
	Percent cover of invasive species	Modified Whittaker cover plots	
17. Perennial plant reproductive capability	None		

decision systems and provide weightings for indicators have been proposed (Leininger et al. 1999, Weltz et al. 1999), but since this variation in importance of indicators exists, evaluators should not apply numerical values to indicator categories and determine an average rank for each attribute, nor should they rate the attribute based on the modal category (e.g., the category receiving the greatest number of indicators). Table 6 provides an example of how an evaluator might arrive at a different rating than would be achieved by a rank average. To calculate the average rank, each indicator category is given a whole number-ranked value and the category limits are established as the range of possible ranks divided by the number of categories. In our example, the 5 categories (None-to-Slight to Extreme) are assigned ranks from 1 to 5, respectively. The category limits among the 5 categories would have a 1.0 unit range (the range of 5 if we use 0.5 and 5.49 as the minimum and maximum, divided by the number of categories, 5). Thus, the average rank for each of the 3 attributes would be 2.3 for Soil and Site Stability, 3.6 for Biotic Integrity, and 2.5 for Hydrologic Function. Using the 1.0 category limits, Soil and Site Stability would be in the Slight-to-Moderate category ($1.5 < 2.3 \leq 2.49$), Biotic Integrity in the Moderate-to-Extreme ($3.5 < 3.6 \leq 4.49$), and Hydrologic Function narrowly falling in the Moderate category ($2.5 = 2.5 \leq 3.49$). For Soil and Site Stability, the rank average was one category different than the evaluator's rating. Although this example shows the rank average's summary as being closer to the None-to-Slight category than the evaluator's summary, other examples could illustrate an opposite deviation.

Since indicator weights have not been standardized and since the choice of a weighting system may influence the overall assessment (Weltz et al. 1999), we suggest that evaluators use tick marks or histograms for each category to create a frequency distribution of the indicators within each attribute to assist them in providing their assessment of each attribute (Table 6; Fig. 1). Consequently, the rationale regarding rankings should be recorded on the worksheet (Table 6b) to assist others in interpreting the evaluator's attribute summaries. All worksheets and rating forms should be retained to provide a record of the assessment.

Intended Applications

This approach was developed as a tool for conducting a moment-in-time qualitative assessment of rangeland status and as a communication and training tool for helping land managers and other interested people to better understand rangeland ecological processes and their relationship to indicators. The qualitative nature of this approach is the major reason why only experienced and knowledgeable people should conduct this technique. We believe an adequate knowledge of the ecological site and soils are necessary to interpret many of the indicators. People with experience in other ecosystems will likely require training and several years of experience to understand the appropriate level of occurrence for indicators in new ecosystems.

Analogous to the way rangeland condition provides a snapshot of vegetation similarity to a potential natural community, this approach provides a snapshot of ecosystem status relative to an expected status for lands within the identified ecological site. Management should not be changed **solely** on the findings of this approach, but this approach may be used in conjunction with quantitative monitoring data that do provide a temporal assessment of trend, resource use records (livestock, recreation, etc.) and long-term weather information to identify potential causes of current or historic changes in vegetation and soils.

Others have reported on the potential for using earlier versions of this technique to assess trend of ecosystem status over time (Weltz et al. 1999), but at this moment, we are not recommending that people use this or any earlier version of this approach for measuring rangeland trend, the direction of change in rangeland status over time. Our opposition to such a use is based on 2 factors, our lack of repeated attribute ratings at a single location to determine the year-to-year variation in these ratings, and our belief that quantitative techniques are available that would provide better precision in determining rangeland trend.

Although we oppose the use of this technique for determining rangeland trend, we do believe it is an excellent tool for identifying locations where monitoring should be conducted and for narrowing choices of variables to monitor. Potential candidate locations for establishing quantitative monitoring plots are those locations where the qualitative procedure identified several indicators within an attribute with ratings of Moderate or greater deviation from that expected for the ecological site. At those sites, quantitative measurements for each identified indicator should be considered in a monitoring plan (Table 7). Several documents provide suggestions for quantitative monitoring protocols relating to these indicators as well as other more traditional rangeland monitoring procedures (Bonham 1989, Interagency Technical Team 1996, de Soyza et al. 1997, 2000, Herrick et al. 2002).

This qualitative procedure evolved in part from the NRC (1994) approach that advocated a national assessment of rangelands. However, we do not believe that individual site-specific assessments that are used to evaluate rangelands at a local scale should be combined into state or national assessments without at least combining these qualitative attributes with quantitative data, stratifying the landscape into hierarchical strata (e.g., ecological sites and major land resource areas), and applying a statistically valid sampling method. This does not mean that this qualitative procedure cannot be used to provide a preliminary assessment of a management unit such as a pasture or an allotment. When evaluating a management unit, the manager should stratify the unit into ecological sites and topographic positions. Within each stratum, the manager should evaluate a sample of locations with this protocol. Each stratum should be summarized separately. A manager may use the distribution of attribute ratings within a stratum to develop an interpretation of the attribute's status in that stratum and then use the complete set of strata summaries to write an interpretation of the preliminary management unit status.

Modification and Future Development

We do not believe this technique is final at this stage. The published technical reference indicates that the technique is version 3. The modified ecological reference worksheet presented in this paper documents the next iteration of this technique and we recommend that evaluators who use this modified reference worksheet and cite this paper. Modifications of the technical references will carry later version numbers. This reflects both continuity with earlier versions, and our belief that this technique will be modified in the future as new information is incorporated.

This is not a fault of the technique, but an acknowledgement of the evolution of scientific understanding about rangeland ecosystems.

The method for modifying narrative descriptions of individual indicators is described under Step 3 above. This method allows individuals to adapt the narrative for local conditions. We are also prepared to modify, increase or reduce the indicators that are currently included. The team that developed this approach will continue to solicit input from individuals at training sessions, from trained individuals who are using this approach or from individuals that are conducting research on the technique or on individual indicators. We will also entertain feedback from groups such as the SRM Rangeland Assessment and Monitoring Committee, the Western Coordinating Committee on Rangeland Research and Assessment, and the interagency MOU group that have offered or been given responsibility for coordinating efforts in this area.

We do believe that consistency among observers is extremely important for any assessment program. Consistency varied among observers and teams using versions 1 and 2 (Rasmussen et al. 1999, Lieninger et al. 1999). We are continuing to evaluate consistency among observers and teams using version 3. First-year results indicate less variation among observers and teams than earlier assessments (D.A. Pyke unpublished data). To our knowledge, temporal consistency of assessments among observers has not been tested. Research on this topic may be warranted.

We will attempt to minimize unnecessary changes, but since we have earlier versions and anticipate later versions, we strongly encourage users to cite the version of the technique they use, and to note any modifications to the indicators or the protocol. Federal agencies will use the version approved by their agency. It is our hope that this procedure will stimulate new research and will create knowledgeable discussions to further our understanding of rangeland assessments leading to new versions of this technique or to better assessment techniques for determining ecosystem status.

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Polyethylene glycol affects goats' feeding behavior in a tannin-rich environment

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Abstract

High concentrations of condensed tannins in browse impair brush clearing by goats. We studied the effect of polyethylene glycol (PEG, MW 4000), a polymer that binds condensed tannins, on the feeding behavior of Damascus goats (*Capra hircas*) on a range dominated by tannin-rich lentisk (*Pistacia lentiscus* L.). This was done with or without a nutritious alternative to browse (alfalfa hay) available at pasture. In phase 1, no hay was provided to goats; in phase 2, hay was distributed daily in the field. In both phases, 6 goats had free access to PEG while at pasture, while 6 goats that grazed separately on another paddock did not. All goats received each night an allowance of concentrate (400 g day^{-1} of 40% ground corn grain, 40% ground barley, 17% soybean meal and 3% of a mineral-vitamin premix, and contained as fed 16% crude protein (CP) and 2.66 Mcal kg^{-1} of Metabolizable Energy). The 2 groups of goats alternated daily between paddocks. Goats supplemented with PEG spent more time browsing lentisk than goats in the control group (73 and 41%, respectively, $P < 0.0001$). Goats in the control group spent more time foraging on dry grasses than their PEG-fed counterparts (28 and 12%, respectively, $P < 0.0001$). Goats from the PEG group gained body weight at a higher rate than controls. The daily intake of PEG was 450 g, with an intake rate of 1.2 g sec^{-1}. Supplemental alfalfa hay substituted partly for dry grasses in goats' diets, but did not modify the percent of time goats in either treatment spent browsing lentisk. Our data suggest that PEG has the potential to increase intake of tannin-rich species, even where alternative fodder of better nutritional quality is present. However, self-feeding of PEG may not be the best way to provide PEG because goats may ingest more PEG than needed to annul the aversive effects of tannins on food intake.

Key Words: Mediterranean browse; self-regulation; nutrition

Resumen

Las altas concentraciones de taninos condensados en el forraje ramoneable de los arbustos impide el control de ellos mediante el uso de caprinos. Estudiamos el efecto del polietilen glicol (PEG, MW 4000), un polímero que une a los taninos condensados, en el comportamiento alimenticio de cabras (*Capra hircas*) de Damasco en un pastizal dominado por "Lentisk" (*Pistacia lentiscus* L.), una especie rica en taninos. Esto fue hecho con y sin una alternativa nutritiva (heno de alfalfa) disponible para ramonear en el potrero. En la fase 1 no se suministró heno a las cabras; en la fase 2, el heno se distribuyó diariamente en el campo. En ambas fases, 6 cabras tenían libre acceso al PEG mientras estaban el potrero, en tanto que otras 6 cabras que apacentaban separadamente en otro potrero no tuvieron acceso al PEG. Todas las cabras recibieron cada noche una ración de concentrado (400 g día-1, 40% de grano de maíz molido, 40% de cebada molida, 17% de harina de soya y 3% de una mezcla de vitaminas y minerales, este concentrado tenia un 16% de proteína cruda y 2.66 Mcal kg^{-1} de energía metaboizable). Los 2 grupos de cabras se alternaron diariamente entre los potreros. Las cabras suplementadas con PEG pasaron mas tiempo ramoneando el " Lentisk" que las cabras del grupo control (73 y 41%, respectivamente, $P < 0.0001$). Las cabras del grupo control pasaron más tiempo apacentando zacates secos que las cabras suplementadas con PEG (28 y 12% respectivamente, $P < 0.0001$). Las cabras del grupo con PEG ganaron peso a una mayor tasa que las del grupo control. El consumo diario de PEG fue de 450 g con una tasa de ingestión de 1.2 g seg-1. La alfalfa suplementada substituyó parcialmente los zacates secos de la dieta de las cabras, pero no modificó el porcentaje de tiempo que las cabras de cualquier grupo pasaron ramoneando el " Lentisk" Nuestros datos sugieren que el PEG tiene potencial para incrementar el consumo de especies ricas en taninos, aun donde un alimento alternativo de mejor calidad nutricional este presente. Sin embargo, el autoconsumo de PEG puede no ser la mejor manera de suministrarlo porque las cabras pueden ingerir mas PEG del requerido para anular el efecto aversivo de los taninos en el consumo de alimento.

Efforts are underway to use goats (*Capra hircas*) to reduce the abundance of brush in Mediterranean ecosystems where brush encroachment increases the danger of fire (Perevolotsky and Seligman 1998) and limits recreational value. However, high concentrations of tannin in some species of Mediterranean browse impair browsing. Supplementation with Polyethylene Glycol (PEG), an inert polymer that can bind tannins irreversibly

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(Jones and Mangan 1977), alleviates the aversive effects of tannins on feed intake (Silanikove et al. 1996, 1997).

Given a choice between blackbrush (*Coleogyne ramosissima* Torr.) twigs of different tannin content, PEG-supplemented goats consumed more than unsupplemented goats of the tannin-rich younger twigs, which are more nutritious than the older-growth alternative (Titus et al. 2001). In most farm situations in the Mediterranean area, goats eat numerous feeds differing widely in nutritional quality and tannin content (Kababya et al. 1998). Titus et al. (2000) proposed that tannin neutralization by PEG should lead to an increased intake of tannin-rich browse, provided that the alternative fodder is poorer in nutrients, but did not consider a tannin-free, nutritious alternative. Alfalfa hay is an excellent tannin-free fodder (Broderick and Albrecht 1997) that can be used as sole food for non-productive goats (Morand-Fehr et al. 1991). Goats eat more tannin-free legume hay than tannin-containing browse when offered tannin-free legume hay or tannin-containing browse as a sole food (Perevolotsky et al. 1993). Therefore, given a choice between tannin-free hay and tannin-containing browse, goats may feed mostly on the more nutritious hay, independent of PEG availability.

The different methods proposed for PEG administration involve giving a predetermined dose of PEG (Landau et al. 2000). However, when dietary tannins exert post-ingestive malaise, the best estimator of the effective dose may be the animal itself (Provenza 1996). Lambs fed concentrates differing in concentrations of quebracho tannin showed a close relationship between dietary tannin content and voluntary intake of PEG (Provenza et al. 2000). Self-feeding would be the most convenient way to provide PEG to ranging goats, but it has never been implemented under farm conditions.

The present study evaluated the amount of PEG consumed by goats foraging in a tannin-rich Mediterranean environment, and assessed the change in feeding behavior when alfalfa hay was available as a supplement.

Methods

Animals

Twelve multiparous Damascus goats were allotted to 2 treatments (PEG and C, "control") after weaning of their kids on 2 August 1999. Average body weights were equalized between the PEG and C groups (53.1 and 53.4 kg, SE = 3.7, respectively). Body condition scores were 3.04 and 2.91 (SE = 0.25) and 2.46 and 2.41 (SE = 0.33) at the sternal and lumbar sites, respectively (Santucci et al. 1991). Goats were accustomed to grazing on a Mediterranean shrubland, but had been housed for 3 months before the experiment and fed on alfalfa hay and a commercial concentrate (16% of crude protein, Ambar, Hadera, Israel). Goats were identified using colored plastic bracelets inserted on 2 legs.

Study site

The experiment took place in August in the Sharon Park (32°25' N, 34°52' E), a coastal sand plain located about 30 km North of Tel Aviv, in Central Israel. The area is dominated by lentisk shrubs (*Pistacia lentiscus* L.) and carob trees (*Ceratonia siliqua* L.), featuring 2–3 m high coppice round islets. Isolated bushes of *Ephedra foemina* Forskk., *Retama rateam* Forskk. and *Thymelea hirsuta* L., xerophytes originating from the desert, were also common in the area. Limited amounts of dry annual herbaceous vegetation, including *Carthamus nitidus* Boiss., *Foeniculum vulgare* Miller, *Rubia tenuifolia* Dum., and annual grasses, occurred on the range. An area of 0.215 ha was divided into 2 paddocks (Fig. 1) of 950 m^2 (termed the "Ephedra" paddock) and 1,200 m^2 (termed the "Carob" paddock), using a 5-wire electric fence (RY2 model, 14000 V, Reuven Yoffe Ltd., Kfar Gidon, Israel).

Animal management

Due to high summer temperatures, goats grazed from 0600 to 1000 hours and from 1600 to 1930 hours. No water was available at pasture. Goats were corralled and watered under the shade of a carob tree from 1000 to 1600 hours and from 1930 to 0600 hours. At night, they rested as 1 group and they were group-fed 400 g $head^{-1}$ of a commercial concentrate. The concentrate (Ambar, Hadera, Israel) consisted of 40% ground corn grain, 40% ground barley, 17% soybean meal and 3% of a mineral-vitamin premix, and contained, as fed, 16% crude protein (CP) and 2.66 Mcal kg^{-1} of Metabolizable Energy. Goats from the 2 treatments grazed separately, alternating paddocks each day, to reduce pasture bias. The experiment ran for 3 to 23 August 1999. Flakes of PEG (Molecular Weight 4000) were available ad libitum for the PEG group.

Phase 1: The objective of this phase was to investigate the effect of PEG on feeding behavior when alfalfa hay was not available at pasture. No supplement, apart from PEG, was offered at pasture from day 1 to day 15. Goats were weighed on days 0 and

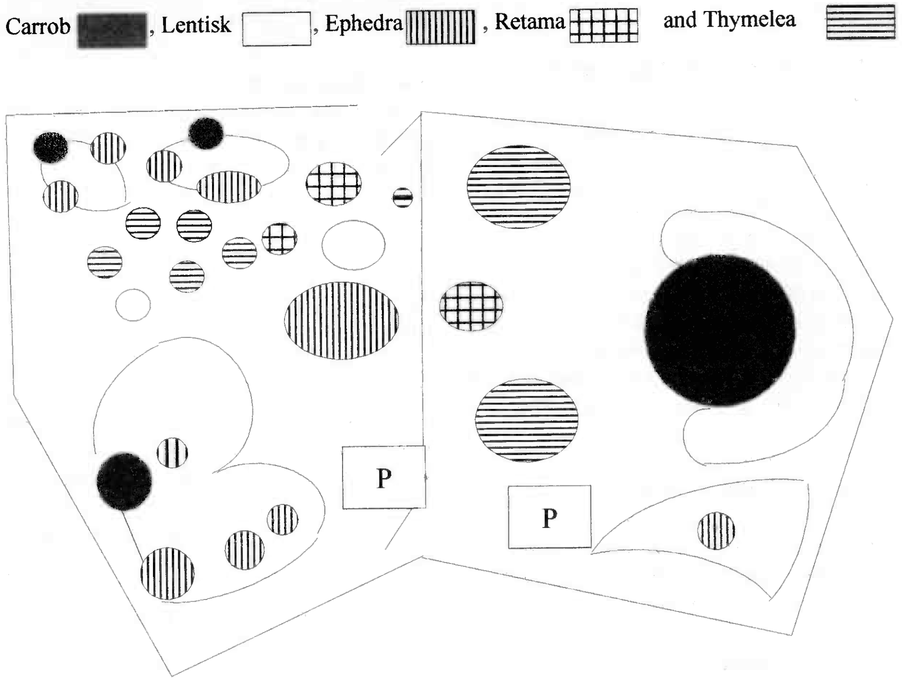

Fig. 1. Grazing paddocks "Carob" (right) and "Ephedra" (left), showing the location of carob trees, and lentisk, *Ephedra*, *Retama*, and *Thymelea* bushes. The location of the PEG trough is indicated by the P box.

14 (to ± 10 g) to evaluate body weight changes.

Phase 2: From days 16 to 20, goats in both groups were offered at pasture the same excellent quality alfalfa hay - containing, on DM basis, 19% CP, 57% neutral detergent fiber (NDF), and 33% acid detergent fiber (ADF) - that was used before the experiment. On those days, intact and partly defoliated lentisk twigs contained, on DM basis: 8.1 and 6.7% of CP, 41 and 65% of NDF, and 29 and 44% of ADF, respectively. Lentisk leaves contained 22% condensed tannins. It was expected that goats would consume most of their diet from hay, rather than the high-tannin foods.

Behavior scanning

The behavior of each goat was recorded by 2 observers every 5 minutes during the morning and evening grazing sessions for 14 days of phase 1, and during 5 days of phase 2, using the scan sampling method (Altmann 1974). Behavior categories were standing, lying (including ruminating, that could not be clearly discerned), playing, eating, searching at a foraging site, consuming PEG (days 1–20) and consuming hay (days 16–20). Within the eating category, some plants were identified to species i.e., carob, lentisk, *E. foemina*, *R. rateam* and *T. hirsuta*, whereas dry herbs were grouped. No details concerning consumed part plants (fruit, leaves, and stems) were recorded.

Individual PEG and hay intake

Polyethylene Glycol (PEG) was provided in a trough placed on a digital scale (Merav 2002, Shekel Scales Ltd., Rosh Haain, Israel), and was available at all times to the PEG group. Hay was provided ad libitum on a similar scale on days 16–20. The scales were fenced to restrict access to only 1 animal at a time. Software included an algorithm devised to weigh objects up to 100 kg with an accuracy of ± 10 g. Weighing occurred automatically 30 times/second and digits were displayed when the SE of weight values reached ± 10 g, i.e., the accuracy of the scale. Every time a goat initiated or ended feeding on PEG or hay, time and scale display were recorded by an observer. This allowed us to calculate the individual eating rate of PEG and hay for each goat.

Total feed intake

Total feed intake was assessed on days 14 and 15 (phase 1) using a modification of the method developed by Penning and Hooper (1985). Intake of forage was determined by the difference in body weight before and after a grazing session, corrected for respiration evaporation losses (insensible weight loss). The method requires that excreta are collected and remain on the animals. To do so, goats were fit with harnesses in which feces and urine were collected on disposable paper diapers. Goats were weighed (± 10 g) before and after grazing sessions of 3 hours. Insensible weight loss per unit of time was calculated for each goat before and after the morning and afternoon grazing sessions in fasting sessions of 30 to 40 minutes. The 12 treatment goats were muzzled as they followed 2 unmuzzled goats while they grazed. Treatment goats were weighed before and after each mock grazing session and insensible weight loss was calculated. Intake was corrected for each grazing session using insensible weight loss per unit of time during the session multiplied by the duration of session.

Table 1. Initial body weight, daily body weight changes (days 1–14), duration of grazing session and the intake of fresh matter (FM) at pasture (days 14–15) in Damascus goats feeding on a Mediterranean shrubland dominated by lentisk and carrob and self-supplemented (PEG) or not (C) with PEG ad libitum (first phase of experiment).

	C	PEG	SEM
Initial body wt. (kg)	53.4	53.1	3.7
Daily body wt. change (kg)[1]	-0.109 a	-0.003 b	0.028
Fresh matter intake (kg)[1]			
Including PEG	0.91 b	2.11 a	0.27
Not including PEG	0.91	1.58	0.24

[1] Within rows means significantly different at P<0.05 have different letters.

Statistical analyses

Changes in body weight (BW) and average daily gain were compared between groups by analysis of variance (GLM of SAS 1989) with treatment (PEG or C) as main effect. Feed intake (days 14 and 15) was compared between groups, using a model that included treatment (PEG or C), day (confounded with paddock), and their interaction.

The effect of paddock on the individual intake of PEG (PEG group only) was established using a repeated measurement procedure. The partition of behaviors (in % of total activities) was calculated for each day, separately for the morning and afternoon grazing sessions, and variances were homogenized by arcsine (square root) transformation.

The repeated measures analyses of variance for the different behavioral categories during phase 1 were carried out on the transformed data, using a model with paddock ("Carob" or "Ephedra"), treatment (PEG or C), and grazing session (morning and afternoon) as main effects, along with their interactions.

The effect of feeding hay (phase 2) on the different behavioral categories, using pooled data from morning and afternoon sessions, was carried out using a model with paddock (" Carob" or " Ephedra"), treatment (PEG or C), and hay (yes or no), as main effects, along with their interactions (GLM of SAS 1989). Goats nested within treatments (PEG or C) was the error term and day was the repeated measure.

Pearson correlation (SAS 1989) was run to assess the relationship between individual values for percent of time spent browsing lentisk and PEG intake.

Results

Phase 1: no hay supplementation at pasture

Effects of PEG on body weight changes and feed intake at pasture

From days 0 to 14, unsupplemented goats lost 109 g day^{-1}, whereas their PEG-fed counterparts nearly maintained body weight (Table 1, P = 0.02).

On days when pasture intake was assessed (days 14 and 15), goats grazed 5.1 (SE = 0.12) hours and 6.2 (SE = 0.25) hours. The total intake at pasture (including PEG) was higher (P < 0.05) for PEG than C animals on both days (Table 1). When the intake of PEG was subtracted from the total intake, the average intake at pasture was still more than 50% greater in PEG-treated animals, but the difference was not significant (P = 0.10) due to small sample sizes and high variability.

Individual PEG intake

Throughout the experiment, intake of PEG by individual goats ranged from 254 to 733 g day^{-1} with an average of 456 g day^{-1} (SE = 44), and did not differ between the carob and "Ephedra" paddocks. There was a small but steady logarithmic increase in PEG intake throughout the

Table 2. Percentages of behaviors recorded in Damascus goats feeding on a Mediterranean shrubland dominated by lentisk and carob and self-supplemented with PEG ad libitum on days when hay was provided ad libitum at pasture. Statistical analyses refer to arcsine (square root) transformed data.

	With Hay		Without Hay	
	PEG	C	PEG	C
	---(% of total activities)---			
Lying	38	38	38	37
Standing	17	18	17	15
Walking, searching	1	1	1	2
Grazing pasture1,2	29^b	29^b	39^a	44^a
Eating Hay	10	12	–	–
Total Foraging	39	41	39	44
Eating PEG	3	–	2	–
Unidentified	2	1	2	1
	---(% of total foraging)---			
Lentisk 1,3	62^{ab}	46^c	73^a	41^c
Dry grasses 1,4	10^b	13^b	12^b	28^a
Carob	1	5	5	11
E. foemina 1,5	0^b	3^b	3^b	11^a
T. hirsuta	1	3	4	4
R. rateam	0	0	2	5
Hay	26	30	–	–

[1] Within rows means significantly different at P <0 .05 have different letters
[2] The only significant effect in the model was hay, P < 0.01.
[3] The only significant effect in the model was treatment, P < 0.001.
[4] Significant effects in the model were treatment, P < 0.0001, hay, P < 0.05 and treatment x hay, P < 0.05.
[5] Significant effects in the model were treatment, P < 0.01 and hay, P < 0.01.

experiment in spite of the high variation (SE ranged from 35 to 85g day^{-1}).

The number of foraging visits to PEG/day was 8.43 (SE = 0.77) (range 1 to 27), with an average intake rate of 1.20 ± 0.03 g sec^{-1} (range 0.25 to 2.23).

Effects of PEG and paddock on feeding behavior

Overall, grazing represented more than 40% of all activities. Eating lentisk was the most frequent foraging activity, and represented a greater share of grazing in PEG than C goats (73% and 41%, respectively P < 0.001; Table 2). In contrast, C goats allocated more time than their PEG counterparts to foraging on dry grasses (28% and 12%, P < 0.0001). Paddock did not affect the response. Goats spent more time lying in the morning than in the afternoon, and there was no effect of paddock or treatment (not shown).

The time spent foraging on carob or *E. foemina* foliage was affected (P < 0.0001) by their abundance on the paddocks. Goats in both groups spent more time browsing carob in the Carob than in the "Ephedra" paddock (16% and 1.4%, respectively). In addition, a strong (P < 0.0001) treatment x paddock effect was noted: Control goats spent more time than PEG goats feeding on carob while grazing in the carob paddock, and more time foraging on *E. foemina* while on the "Ephedra" paddock.

Phase 2: hay supplementation at pasture

There was no interaction between " paddock" and " hay" across days on goats behavior. Thus, the subsequent analyses included the effects of treatment (PEG), hay, and their interaction on behavioral features averaged across paddocks (Table 2).

Feeding hay reduced grazing activity (P < 0.01), but did not affect total foraging activity (including foraging on hay). Hay-supplementation reduced foraging on dry grasses (P < 0.05) and *E. foemina* (P < 0.01) in group C, but not in group PEG. Providing hay did not modify the time spent browsing lentisk in either group. Thus, goats did not substitute hay for tannin-rich lentisk.

The daily intake of hay did not differ between PEG and C (276 and 248 g day^{-1}). Nor did frequency of visits to hay differ between groups. All goats spent approximately 40 minutes/day foraging on hay, but rate of intake was low (0.110 g sec^{-1}), and was not affected by PEG.

Supplemental hay did not modify PEG intake: values for intake, number of visits, and rate of intake were 425 (SE = 48) g day^{-1}, 8.40 (SE = 0.93), and 1.20 (SE = 0.04) g sec^{-1}, respectively.

Phases 1 and 2: Self-regulation of PEG intake

There was no correlation (R = 0.08, P = 0.40) between the individual frequencies (n = 108) of browsing lentisk and the amount of PEG consumed during a grazing session. This suggests that there was no causal relationship between the intake of tannin-rich browse and that of PEG. Including all browse species slightly improved the relationship (R = 0.19, P = 0.04), but not enough for predictive purposes.

Discussion

Even though the intake of PEG by goats was high (456 g day^{-1}, Fig. 2), it had no " bulk" effect, and did not impair intake at pasture (Table 1). The PEG did not modify the share of time (as percent of total activities) spent foraging in either hay-supplemented or non-supplemented goats (Table 2).

When the intake of PEG was subtracted from the total intake, the average intake at pasture was still more than 50% greater in PEG-treated animals, but the difference was not highly significant (P = 0.10) due to small sample sizes and high variability. A limited effect of PEG on total intake at pasture was noted in some studies (Decandia et al. 2000), whereas others working with penned animals restricted in the variety of foods reported increased dry matter (DM) intake (Silanikove et al. 1996, Ben Salem et al. 2000, Titus et al. 2001). The availability of energy may have been affected by PEG, as evidenced by higher body gain during phase 1 of the present study (Table 1). This is consistent with results that PEG has the potential to increase productivity in goats feeding in tannin-rich Mediterranean environments (Gilboa et al. 2000, Decandia et al. (2000).

The high percentage of lentisk browsing by goats reflects the high frequency of lentisk on the range (Perevolotsky et al. 1998, Kababya et al. 1998). Control goats spent about 40% of their foraging time browsing lentisk, and their PEG-supplemented counterparts spent more than 70% of their foraging time browsing lentisk (Table 2). This is consistent with findings for caged goats fed lentisk twigs as the sole diet (Silanikove et al. 1996). Thus, PEG increased intake of lentisk, in accord with Decandia et al. (2000), and this has implications for improving the effectiveness of goats to prevent encroachment of lentisk in Mediterranean environments.

Surveys of chemical composition of Mediterranean species of browse in Israel and Italy show that lentisk is the richest in condensed tannins (Landau et al. 2000). In the present study, control and PEG-supplemented goats consumed 0.91 and 1.58 kg of fresh matter at pasture, respectively

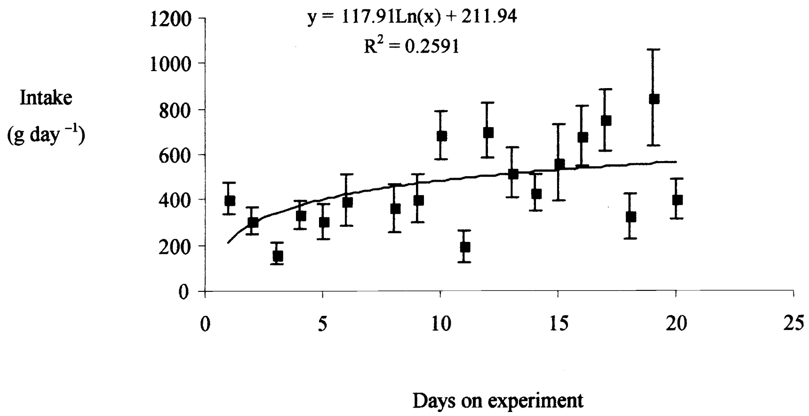

Fig. 2. Individual intake of PEG (g day^{-1}) throughout the experiment: means and SE.

(Table 1). In a previous study, with goats fed lentisk leaves solely, DM intake was increased from 460 to ca. 800 g day^{-1} when PEG was provided at 20 g day^{-1} (Silanikove et al. 1996). No further response in intake was noted when higher doses - 30 or 40 g day^{-1} of PEG were administered. Goats in the PEG group of the present study ingested 456 g day^{-1} PEG on average. Thus, they ingested an amount of lentisk that did not exceed 2-fold that ingested by goats in the study by Silanikove et al. (1996), but they consumed an amount of PEG 10- to 20-fold higher. Thus it can be inferred that intake of PEG in our study was more than needed to maximize the intake of lentisk. Furthermore, the low correlation coefficient found between time spent browsing lentisk and the intake of PEG suggests goats did not self regulate intake of PEG based upon the amount of lentisk consumed. Though one must be cautious when comparing the effects of tannins from different sources (Clausen et al. 1991), a similar result occurred when sheep fed *Acacia cyanophylla* foliage had free access to PEG-containing feed blocks (Ben Salem et al. 2000).

The apparent "overeating" of PEG may be due in part to the aversive effects of tannins on the absorption of nutrients. Low levels of PEG allow DM intake to increase (Silanikove et al. 1996), but higher levels of PEG continue to increase digestibility of crude protein (CP) (Silanikove et al. 1996, Decandia et al. 2000). The high intake of PEG can then be interpreted as a way to maximize the availability of CP, the first limiting factor for goats feeding on Mediterranean browse (Kababya et al. 1998).

Alfalfa hay is excellent fodder and can be used as sole food for non-productive goats (Morand-Fehr et al. 1991). All goats were familiar with alfalfa hay, so one might expect that they would feed mostly on hay, thus cutting the energy expenditure to search for high-tannin shrubs of mediocre nutritional value. In particular, it was anticipated that control goats, not provided with PEG, would switch to hay to a greater extent than PEG-supplemented counterparts. This did not happen. The low preference for alfalfa hay may have been due in part to the nightly allowance of 400 g/goat of concentrate high in crude protein (16%).

Providing tannin-free alfalfa hay ad libitum at pasture reduced the time spent grazing by goats but did not alter their preference for lentisk (Table 2). Even the control goats ate only about 250 g DM of hay and continued to browse. Hay replaced dry grasses and part of the carob and *E. foemina* in the diets, showing again that these species are not considered aversive by goats. This feeding behavior of goats is consistent with previous studies that show goats eat a variety of foods on heterogeneous Mediterranean pastures (Kababya et al. 1998). Interactions between a food's flavor, its nutrient and toxin concentrations and an animal's current nutritional state are likely to cause animals to eat a variety of foods (Provenza 1996). Two consequences of such strategy relevant to the present experiment are that all major species are sampled every day (Meuret 1997), and that the dietary concentration of condensed tannins is kept in a narrow range (Kababya et al. 1998). Therefore, browsing is never discontinued, even when more nutritious feeds are offered. This is in contrast with findings in sheep supplemented with PEG that avoided foods high in quebracho tannins when low-tannin alternatives were available (Titus et al. 2000). Our data suggest that PEG will increase browsing of tannin-rich foliage even when alternative fodder of better nutritional quality is present, and that hay supplementation in periods of fluctuating pasture quality, a common practice in Mediterranean areas, is not incompatible with brush clearing by goats in general, and by PEG-supplemented goats, in particular.

Conclusions

Making PEG available free choice to goats feeding on tannin-rich Mediterranean shrubland resulted in improved body gain. Goats self-supplemented with PEG spend more time browsing tannin-rich species, and less time ingesting species lower in tannins. However, goats may consume amounts of PEG higher than needed to counteract the aversive effects of tannins on DM intake. Feeding hay at pasture does not disrupt browsing activity of unsupplemented goats or of PEG-self-supplemented goats.

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Broom snakeweed control and seed damage after herbicide applications

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Abstract

Broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby) is a major weed problem in the southwestern U.S. because it is toxic to livestock and suppresses forage productivity. In this study, broom snakeweed control, seed production and viability were determined after broadcast spraying in 1997 and 1998 with metsulfuron ({2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl) amino]carbonyl]amino]sulfonyl]benzoic acid}; 0.03 kg a.i. ha^{-1}) and picloram ((4-amino-3, 4, 6-trichloro-2-pyridine-carboxylic acid); 0.28 kg a.i. ha^{-1}). In 1997, plants were sprayed every 2 weeks beginning 1 October when snakeweed was in mid-flower and seed fill and continued until 15 December when seeds were being dispersed. Broom snakeweed control was not different by spray date and averaged 98% with picloram and 77% with metsulfuron. Only plants sprayed on 1 October 1997 with either herbicide had significantly less seed viability than nonsprayed plants, but seed production was not different. In 1998, herbicide applications were repeated at 2 week intervals for 6 weeks beginning on 1 September when snakeweed was in early-flower and seed development. Broom snakeweed control with picloram (average 88%) was consistently high across all spray dates, whereas, control with metsulfuron (average 25%) was always poor. Both herbicides reduced seed production by an average of 99, 95, and 38% when applied on 1 and 15 September 1998 and 1 October 1998, respectively, but seed production was not different among sprayed and nonsprayed plants after these dates. In the spring of 1999, broom snakeweed seedlings were common in all areas previously sprayed in 1997, but few seedlings established in plots sprayed in 1998. In the spring of 2001, the number of newly emerged broom snakeweed seedlings observed in nonsprayed and herbicide-treated areas was the same, irrespective of spray year, herbicide type or date applied. Data indicate that herbicide applications made at flower when seed is in early fill can provide satisfactory plant control and lower seed production. Spraying after seed has reached physiological maturity does not affect seed production or viability. In this study, results were inconclusive for determining if timed herbicide applications in autumn can be used to minimize later broom snakeweed establishment.

Key Words: *Gutierrezia sarothrae*, reproduction, seed production, seed dispersal, seedling emergence, seed viability, herbicide control, metsulfuron, picloram

Resumen

La escobilla de bruja (*Gutierrezia sarothrae* [Pursh] Britt & Rusby) es un problema mayor de maleza en el sureste de EU dado que es tóxica para el ganado y porque suprime la producción de forraje. En este estudio, control de la escobilla de bruja, la producción y viabilidad de la semilla se determinaron después de aspersiones en 1997 y 1998 con metsulfuron ({2-[[[[(4-methoxy-6-metilo-1,3,5-triazin-2-yl) amino] carbonilo] amino] sulfonyl] ácido benzoico}; 0.03 Kg i.a ha^{-1}) y picloram (4-amino-3,4,6-tricloro-2-piridina-ácido carboxílico); 0.28 Kg i.a ha^{-1}). En 1997, las plantas fueron asperjadas cada 2 semanas empezando en Octubre 1 cuando la escobilla de bruja estaba en media floración y en el llenado de la semilla y continuó hasta Diciembre 15 cuando las semillas fueron dispersadas. El control de la escobilla de bruja no fue diferente por fecha de aspersión y promedió 98% con picloram y 77% con metsulfuron. Solamente las plantas asperjadas con cualquiera de los herbicidas en Octubre 1 en 1997 tuvo significantemente menos viabilidad de la semilla que las plantas que no fueron asperjadas, pero la producción de semilla no fue diferente. En 1998, aplicaciones de herbicida fueron repetidas a intervalos de 2 semanas por 6 semanas, empezando en Septiembre 1 cuando la escobilla de bruja estaba en floración temprana y en desarrollo de la semilla. El control de la escobilla de bruja con picloram (promedio 25%) fue consistentemente alto a través de todas las fechas de aspersión, mientras que el control con metsulforon (promedio 25%) fue siempre pobre. Ambos herbicidas redujeron la producción de semilla para un promedio de 99, 95, y 38% cuando se aplicaron en Septiembre 1 y 15 en 1998 y en Octubre 1 en 1998, respectivamente, pero la producción de semilla no fue diferente entre plantas asperjadas y plantas no asperjadas después de esas fechas. En la primavera de 1999, plántulas de escobilla de bruja fueron comunes en todas las áreas previamente asperjadas en 1997, pero pocas plántulas se establecieron en los cuadros asperjados en 1998. En la primavera del 2001, el numero de plántulas de escobilla de bruja recién emergidas observado en áreas sin asperjar y en áreas tratadas con herbicida fue el mismo, indistinto del año de aspersión, del tipo de herbicida o de la fecha de aplicación. Los datos indican que las aplicaciones de herbicida hechas en la flor cuando la semilla esta en llenado temprano puede proveer un control de planta satisfactorio y disminuir la producción de semilla. El asperjado después que la semilla ha alcanzado su madurez fisiológica no afecta la producción o la viabilidad de la semilla. En este estudio, los resultados fueron inconclusos en determinar si las aplicaciones de herbicida programadas en otoño pueden ser usadas para minimizar el establecimiento posterior de la escobilla de bruja.

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Southwestern U.S. rangelands with dense infestations of broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby) are often commercially sprayed by aircraft to promote desired grass growth and to prevent potential livestock health problems from this poisonous plant (McDaniel and Duncan 1987, Strickland et al. 1998). The general commercial spray period for broom snakeweed control in New Mexico and west Texas is October through December (Duncan and McDaniel 1991). In the 1980's, about 600,000 ha were sprayed in this region (McDaniel 1989). In the 1990's, partly because of the success of previous broom snakeweed control activities and partly because the plant population naturally declined in many areas, less than half this area was treated. The majority of treated rangeland was aerially sprayed with picloram (4-amino-3, 4, 6-trichloro-2-pyridine-carboxylic acid) at a rate of 0.28 kg a.i. ha^{-1} whereas less area was treated with metsulfuron ({2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl) amino]carbonyl]amino]sulfonyl]benzoic acid}) at 0.03 kg a.i. ha^{-1} . These herbicides are typically mixed with water and applied at 140 to 240 liters ha^{-1} total spray volume. According to Sosebee (1985, 2000) and Sosebee and Dahl (1991), broom snakeweed increases total nonstructural carbohydrate storage in autumn and this allows herbicides to be more readily translocated to the perennating organs and tissues resulting in optimum plant control.

In New Mexico, commercial aerial applicators usually wait until broom snakeweed completes flowering before spraying (Williams 1990). In its native range from Mexico to Canada, broom snakeweed flowering is photoperiod-sensitive with plants in full bloom earlier and for a shorter duration in northern latitudes (near mid-July) than in southern regions (early September) (Sterling et al. 1999). In New Mexico, broom snakeweed typically begins to flower about 2 weeks earlier in northern portions of the state than southern parts. A study by Wood et al. (1997) closely followed broom snakeweed flower and seed production in central New Mexico and reported that most plants were in full bloom by mid-August and that seed required 6 to 8 weeks to ripen within the inflorescence before dispersal commenced, roughly in mid-October. In the Wood et al. (1997) study, about half the seed dropped to the surface before January and the remainder disseminated by early spring except for a few seeds that were retained within the inflorescence until the next season.

Broom snakeweed relies on seed production for propagation and the number of seeds produced per plant is highly variable depending on plant age, interspecific competition, and seasonal growing conditions (Solbrig 1960, Sterling et al. 1999). Broom snakeweed germination is erratic from year to year, but when specific environmental conditions are met, then prolific propagation occurs, usually in the spring (McDaniel et al. 2000). Broom snakeweed seedling mortality is often high the first year, but surviving propagules generally live for 7 years or longer (Pieper and McDaniel 1989).

Economic returns from broom snakeweed control depend partially on adult plant mortality and the length of time the sprayed area remains weed free (Torell et al. 1989). Uncertainty about future broom snakeweed establishment limits the potential for economic control (Torell et al. 1992). A survey of 65 New Mexico landowners who paid to spray broom snakeweed in the 1980's indicated that 91% of the treatments provided satisfactory initial control (Williams 1990). However, because broom snakeweed reestablished on many areas within 5 years of spraying, only half of those surveyed indicated they would use chemical treatments again (Townsend 1995). Commercial spraying in New Mexico in the 1980's was always conducted when broom snakeweed was in the post-bloom stage (mainly in November and December). Evidence from the rancher surveys (Williams 1990, Townsend 1995) suggested that while herbicide spraying is usually effective in eliminating the current crop of mature broom snakeweed plants, there remains uncertainty regarding treatment effects on later seed germination and plant establishment. Thus, in this study, our objectives were to determine: (1) if picloram and metsulfuron treatments provide consistent broom snakeweed control throughout the autumn spray season, (2) if herbicide treatments damage seed production or seed viability, and (3) if herbicide applications can be timed so as to eliminate parent plants and potential seed progeny.

Materials and Methods

Study Area

Field experiments were initiated in 1997 and 1998 on the New Mexico State University Chihuahuan Desert Rangeland Research Center (CDRRC) about 35 km north of Las Cruces, N.M. (32°34'N, 106°56'). The CDRRC is located on the west mesa of the Rio Grande valley at an elevation of 1,219 m. The experimental site was located on level terrain within a pasture that was lightly grazed with cattle in late winter both years of this study. Rainfall is most common from July through September and averages 236 mm. Low precipitation, warm summers, and mild winters characterize the arid continental climate.

Soils, to a depth of 1.5 m, have sandy loam to sandy texture and are grouped in the Berino-Dona Ana Association (USDA-SCS 1980). Because of eolian origins, these soils are vulnerable to wind erosion leading to constantly shifting coppice dunes throughout the area. Vegetation on the experimental area was once dominated by black grama [*Bouteloua eriopoda* (Torr.) Torr.], but is now predominantly broom snakeweed with occasional mesquite (*Prosopis glandulosa* Torr.). Common grass and forb species include black grama, dropseeds (*Sporobolus* spp.), three-awns (*Aristida* spp.), fluff grass [*Dasyochloa pulchella* (Kunth) Steudel], globe mallow (*Sphaeralcea* spp.), leatherweed croton (*Croton corymbulosus* Engelm.), spectaclepod [*Dimorphocarpa wislizenii* (Engelm.) Rollins], and plains cryptantha [*Cryptantha crassisepala* (Torr. and Gray) Greene]. Mature broom snakeweed were estimated to be at least 3 years old and plant density across the study area ranged from 3 to 7 plants m^{-2}.

Experimental Design and Herbicide Applications

The experimental design was a randomized complete block with an augmented factorial arrangement of treatments replicated 3 times. Experiments conducted in 1997 and 1998 were evaluated separately. Factor A consisted of picloram at a rate of 0.28 kg a.i. ha^{-1} and metsulfuron at a rate of 0.03 kg a.i. ha^{-1}. Picloram was selected because it is the predominant chemical used by commercial aerial applicators for broom snakeweed control in New Mexico. Metsulfuron is presently more expensive than picloram, but is used as an alternative herbicide choice. Factor B included the picloram or metsulfuron application dates presented in Table 1. In 1997, herbicide applications were made 1 and 15 October, November, and December when broom snakeweed phenology ranged from mid flower and seed fill to post flower and seed dispersal. Partially because of treatment effects noted from the 1997 experiment, the herbicide application schedule was moved ahead 1 month for the 1998 experiment. Thus, in 1998, herbicide

Table 1. Application date, timing, and spray conditions for 2 herbicide experiments conducted to control broom snakeweed at the Chihuahuan Desert Rangeland Research Center, Las Cruces, N.M.

Application Date	Application Timing	Air Temp	Soil Temp	Relative Humidity	Wind Speed
		(°C)	(°C)	(%)	(m sec^{-1})
1997					
1 Oct.	Mid flower - mid seed fill	23	21	51	0
15 Oct.	Late flower - late seed fill	21	20	20	0
1 Nov.	Late flower - seed mature	20	13	31	0
15 Nov.	Post flower - seed dispersal	14	4	40	3
1 Dec.	Post flower - seed dispersal	8	8	75	3
15 Dec.	Post flower - seed dispersal	6	2	38	0
1998					
1 Sep.	Early flower - initial seed set	21	18	32	0
15 Sep.	Mid flower - early seed fill	22	22	40	3
1 Oct.	Mid flower - mid seed fill	21	18	34	0
15 Oct.	Late flower - late seed fill	17	16	33	3
1 Nov.	Post flower - seed mature	16	10	43	2
15 Nov.	Post flower - seed dispersal	17	8	34	2

applications began on 1 September when broom snakeweed was in early flower and initial seed set and continued, as presented in Table 1, every 2 weeks for 6 weeks when seeds were being dispersed. A nontreated control was included for comparison.

The potassium salt of picloram and the dry flowable formulation of metsulfuron were applied with a CO_2 pressurized hand held sprayer (3.3-m boom) delivering 200 liters ha^{-1} at 400 kPa to 30- by 30-m plots. The rates were consistent with the recommended commercial application rates of 0.28 kg a.i. ha^{-1} for picloram and 0.03 kg a.i. ha^{-1} for metsulfuron (Duncan and McDaniel 1991). Application dates, broom snakeweed flower and seed development stages, and environmental conditions during spraying in 1997 and 1998 are given in Table 1. Broom snakeweed control was visually estimated by 3 observers comparing treated plots to non-treated rangeland approximately 12 months after treatment (MAT). The data were analyzed separately by experimental year to compare 3 treatments, 3 replications, and 6 spray dates using the GLM procedure of SAS (1989). Data for both experiments were subjected to analysis of variance and means were separated using Fisher's Protected L.S.D. test at the 0.05 level of probability. When significant herbicide by application timing interactions were not detected, data were averaged across herbicide type.

Seed Production

Before experiments commenced in 1997 and 1998, relatively uniform sized mature broom snakeweed plants in each experimental plot were randomly selected and marked with different colored pin flags for later seed harvest from the inflorescence. Pin flags in each plot marked 2 plants (3 replications; 6 total) that were scheduled for seed collection as follows: at spraying and 2, 4, 6, 8, and 10 weeks after spraying. On each collection date, non sprayed plants (6 total) from untreated plots were also harvested. To facilitate seed cleaning, the outer perimeter of each plants canopy containing mostly flower material was clipped and placed separately in paper bags and transported to the laboratory to be oven dried for 24 hours at 50°C. The dried flower material was first hand threshed to shatter achenes (seed) from capitula and to detach the inflorescence from stems. The sample was then sieved with a No. 7 Clipper screen and the remaining sample (fine litter, capitula, and seed) was pulsed twice in a seed scarifier to break apart capitula and to continue dislodging seed. Seeds were separated from litter using 1.18 and 0.6 mm mesh screens, respectively. Finally, remaining chaff was separated from seed using a No. 120 Seedburo. The number of seeds in a 0.2 g subsample of the seed fraction was counted and extrapolated to estimate total seed obtained from the inflorescence. Differences in seed number per plant over the various collection dates and herbicide treatments were analyzed as a completely randomized design with rep by sample date by plant as the error term.

To monitor seed dispersal throughout the duration of each experiment, 2 mature broom snakeweed plants were randomly selected in every experimental plot and a 5- by 25- by 51-cm plastic collection tray (trap) was placed in each plant's seed shadow. Trays were covered with stucco wire to retain seed in the trap and small holes were perforated in the tray bottom to allow rain water to escape using a procedure similar to that described by Wood et al. (1997). Collection of dispersed seed coincided with collections from the inflorescence. All flower material in each trap was emptied into separately labeled paper bags and returned to the lab to be oven-dried and cleaned using the procedure described above. Seeds were counted to determine the number in each trap, and then stored for viability testing.

Seed Viability

Viability tests were conducted shortly after mature seeds were collected from the inflorescences and traps using tetrazolium (TZ) analysis procedures similar to those described by Thill et al. (1985). A subsample of 40 (1997) or 50 seeds (1998) per plant (24 plants per spray date plus controls) were removed from collected material using forceps. If the seed collapsed under normal pressure necessary to pick it up, it was considered immature or deteriorated (fruitless) and not included in the subsample. Seeds were placed in a 5-cm petri dish on double filters saturated with deionized water and imbibed for a minimum of 4 hours. With a dissecting scope, seeds were examined and those with an embryo were dissected near the apical end, below the pappus, and placed in a 1% aqueous solution of TTC (2,3,5-triphenyl tetrazolium chloride) for 8 hours (Tetrazolium Committee of Association of Official Seed Analysts 1970). Following the soaking period, seed with acceptable red-stained embryos were used to calculate percentage net viability (viable seed/total in TZ test X 100). According to analysis of variance, there was no significant difference in the viability of seed collected from either the inflorescence or dispersed in traps by sample date within an experimental year. Therefore, data from both collection procedures were combined by experiment to compare treatment differences for final analysis. Analysis of variance and L.S.D. procedures in SAS (1989) were used to determine viability differences among spray dates and herbicide treatments by experimental year.

Seedling Numbers

Broom snakeweed seedlings were counted in June 1998, 1999, 2000, and 2001 using five, 31.5 by 61 cm permanently marked quadrats located in each experimental plot. These quadrats were placed along 2 diagonal lines across each plot from corner to opposite corner. This allowed a comparison of seedling density after autumn spraying with picloram or

Table 2. **Broom snakeweed control, average seed production, and seedlings established in experimental plots sprayed with 2 herbicides in 1997 at the Chihuahuan Desert Rangeland Research Center, Las Cruces, N.M.**

Spray		Plant Control[1]		Seed Production		1999 Seedlings[2]		2001 Seedlings[3]	
Date	Application Timing	Picloram	Metsulfuron	Picloram	Metsulfuron	Picloram	Metsulfuron	Picloram	Metsulfuron
		(%)		(no. plant^{-1})		(no. m^{-2})		(no. m^{-2})	
1 Oct.	Mid flower - mid seed fill	100 a[4]	81 b	5034	5172	11.1 a	9.3 a	4.3	3.6
15 Oct.	Late flower - late seed fill	94 ab	84 b	4623	4368	40.2 c	16.5 a	2.9	2.2
1 Nov.	Post flower - seed mature	97 a	93 ab	3112	4546	34.8 bc	35.9 bc	2.5	5.7
15 Nov	Post flower - seed dispersal	99 a	79 bc	6326	4309	25.1 b	49.9 cd	1.1	4.7
1 Dec.	Post flower - seed dispersal	100 a	62 c	4177	5724	37.3 c	61.0 d	2.5	5.0
15 Dec.	Post flower - seed dispersal	100 a	65 c	3735	3627	21.5 b	24.0 b	4.3	3.2
Control		0 d		5421 n/s		14.7 a		4.2 n/s	

[1] Plant control evaluated 1 Oct. 1998.
[2] Seedlings counted on 1 July 1999.
[3] Seedlings counted on 1 May 2001.
[4] Means within a category with the same letter are not different ($P < 0.05$); n/s, not significantly different.

metsulfuron in 1997 or 1998. No seedlings emerged in 1998 and 2000; thus, only 1999 and 2001 data are reported. Analysis of variance and L.S.D. mean separation tests were used to determine seedling differences among spray dates, herbicide treatments, experimental years, and collection times.

Results and Discussion

Broom Snakeweed Control

It is difficult to determine precisely when broom snakeweed succumbs to a herbicide after autumn spraying because the plant naturally dies back to its woody base when winter dormant. Typically, broom snakeweed shows epinasty and other effects from picloram within 10 days of herbicide application, but recognizable metsulfuron symptoms may take a month or more (McDaniel and Duncan 1987). An accurate evaluation of broom snakeweed control is best made 9 or more months after herbicide application (Sosebee 1985). Our evaluations of broom snakeweed control were made near the end of the next growing season (about 12 months after treatment) and indicated that picloram was consistently more effective in killing broom snakeweed, irrespective of treatment year or spray date, than was metsulfuron (Tables 2 and 3). Broom snakeweed mortality was less, though not always significantly, when picloram was sprayed near the same dates in 1998 (average 88% control) compared to 1997 (average 98% control). Control with metsulfuron was also higher in 1997 (average 77%) than 1998 (average 24%). McDaniel and Duncan (1987) reported in an experiment conducted in central New Mexico that aerial applications of picloram and metsulfuron gave nearly 100% broom snakeweed control when applied in autumn at the same rates used in this study.

There was little efficacy advantage to application of picloram on earlier spray dates relative to later dates within a treatment year (Tables 2 and 3). Consistent broom snakeweed control with picloram throughout a spray season is an important expectation by aerial applicators and other users of this chemical. Metsulfuron provided relatively higher broom snakeweed control on earlier spray dates than later dates in 1997. However, control with metsulfuron was always poor in 1998 (less than 50%) and this is a major concern because even a minor presence of broom snakeweed can result in significant grass suppression (McDaniel et al. 1993). In general, broom snakeweed control strategies that eliminate less than 85% of the mature plants are regarded as unacceptable (Sterling et al. 1999).

Seed Production and Dispersal

In southern New Mexico, occasional blooms can be found on broom snakeweed throughout the year, but peak flowering generally extends for about 6 to 8 weeks from late summer until a killing frost in autumn (Briede 1990). Broom snakeweed heads usually contain 2 to 7 ray and disk flowers, but only 1 to 3 seeds typically mature from ray florets (Lane 1985). During these experiments, broom snakeweed commenced flowering in early September and ceased flowering by early November when night time air temperatures dropped below freezing (data not shown). A relatively consistent seed supply was collected in traps beneath nonsprayed plants from December through February (Fig. 1). Weather events, such as wind and precipitation, dictated the rate and amount of seed recovered during each 2 week collection period. In this study, we

Table 3. **Broom snakeweed control, average seed production, and seedlings established in experimental plots sprayed with 2 herbicides in 1998 at the Chihuahuan Desert Rangeland Research Center, Las Cruces, N.M.**

Spray		Plant Control[1]		Seed Production		1999 Seedlings[2]		2001 Seedlings[3]	
Date	Application Timing	Picloram	Metsulfuron	Picloram	Metsulfuron	Picloram	Metsulfuron	Picloram	Metsulfuron
		(%)		(no. plant^{-1})		(no. m^{-2})		(no. m^{-2})	
1 Sep.	Early flower - initial seed set	87 ab[4]	8 e	12 a	3 a	3.6 a	0.7 a	4.3	6.5
15 Sep.	Mid flower - early seed fill	96 a	10 e	125 a	154 a	0.0 a	2.2 a	4.7	2.9
1 Oct.	Mid flower - mid seed fill	87 ab	7 e	1763 b	1776 b	3.6 a	1.8 a	2.2	5.4
15 Oct.	Late flower - late seed fill	89 ab	49 c	2897 cd	1461 b	1.1 a	1.4 a	3.2	2.9
1 Nov.	Post flower - seed mature	82 b	46 c	2258 bc	3658 d	0.0 a	0.0 a	2.5	4.7
15 Nov.	Post flower - seed dispersal	84 ab	27 d	2680 c	3166 d	0.7 a	0.4 a	4.3	6.8
Control		0 e		2861 cd		14.7 b		4.3 n/s	

Plant control evaluated 1 Oct. 1998.
[2] Seedlings counted on 1 July 1999.
[3] Seedlings counted on 1 May 2001.
[4] Means within a category with the same letter are not different ($P < 0.05$); n/s, not significantly different.

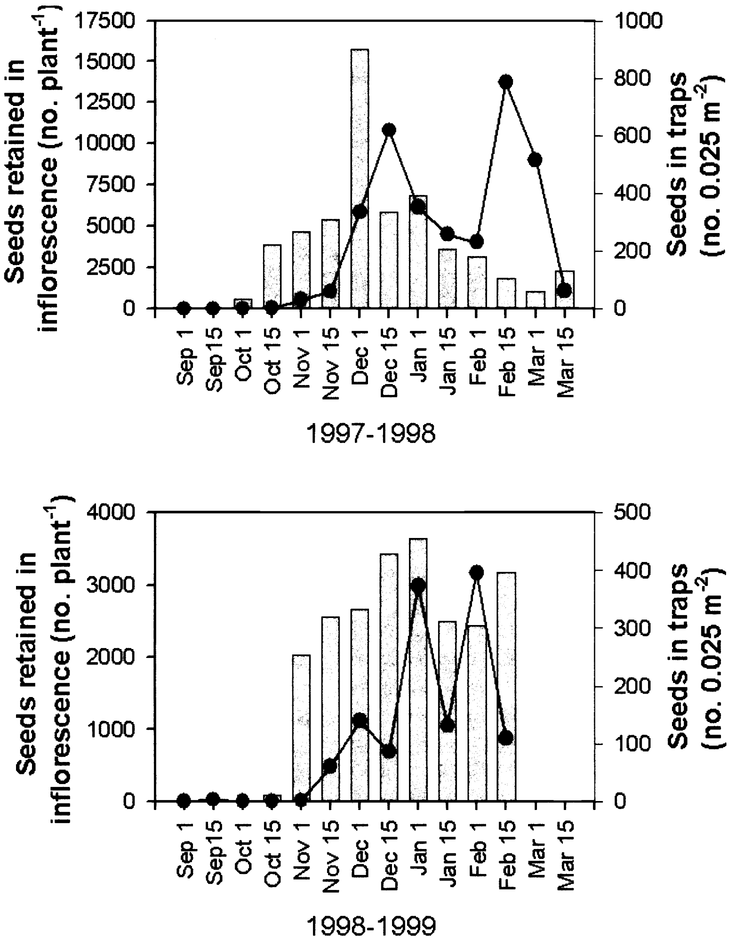

Fig. 1. Average number of broom snakeweed seed recovered from the inflorescence (bar graphs) and from seed traps (line graphs) placed beneath the canopy of nonsprayed plants growing at the Chihuahuan Desert Rangeland Research Center, Las Cruces, N.M. in 1997–1998 and 1998–1999.

stopped collecting seed in March after the majority were dispersed. However, we still found a few seeds on plants until flower parts completely deteriorated in June.

Broom snakeweed seed production can vary greatly from year to year, primarily in response to available soil moisture during flowering (Ragsdale 1969). Under very dry conditions, broom snakeweed typically will not flower, whereas in wetter years, the plant flowers profusely (Pieper and McDaniel 1989). During our study, the average number of seeds per plant counted from the inflorescence of nonsprayed plants was approximately twice as high in 1997 (5,421 seeds per plant) compared to 1998 (2,861 seeds per plant). This difference in seed production between years can largely be attributed to rainfall received during the growing season (April–September) each year. In 1997, growing season rainfall was about 64% above average whereas precipitation in 1998 was about 30% below the 30 yr average of 260 mm. A similar yearly difference in broom snakeweed seed production because of rainfall differences during the growing season was reported by Wood et al. (1997) for plants in central New Mexico.

Irrespective of date sprayed in 1997, there was no significant difference in the average number of mature seed in the inflorescence after applying either picloram or metsulfuron compared to nonsprayed plants (Table 2). Also, the cumulative number of seed dispersed through time from plants sprayed with either picloram or metsulfuron was similar to nonsprayed plants (Fig. 2). In contrast, in 1998, broom snakeweed plants sprayed with either picloram or metsulfuron on 1 and 15 September produced 99 and 95% fewer mature seeds per plant, respectively, compared to nonsprayed plants. Plants sprayed with picloram on 1 October produced about 38% fewer mature seed than nonsprayed plants, whereas plants treated with metsulfuron on 1 and 15 October produced about 43% less mature seed. Several studies have reported that herbicide applications made at or near anthesis can inhibit seed development and reduce germination (Fawcett and Slice 1978, Anderson 1995, Clay and Griffin 2000). How broom snakeweed seed are damaged by picloram or metsulfuron was not investigated in this study, but research is needed to define how these chemicals impede early seed development. Our examination of seed from nonsprayed plants revealed that the seed coat (testa) was generally soft

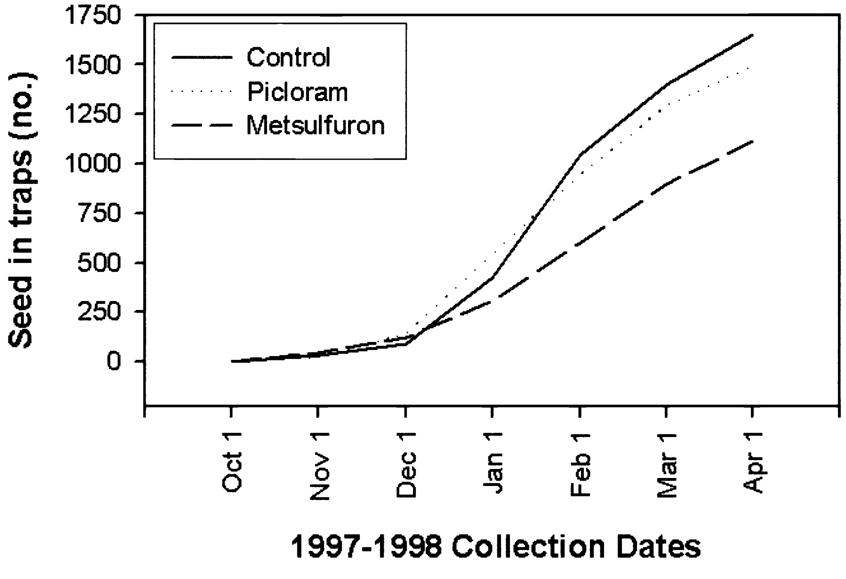

Fig. 2. Cumulative number of seed dispersed into 5- by 25- by 51-cm traps for 22 weeks after spraying on 1 Oct. 1997. Traps were placed beneath 6 broom snakeweed plants per treatment.

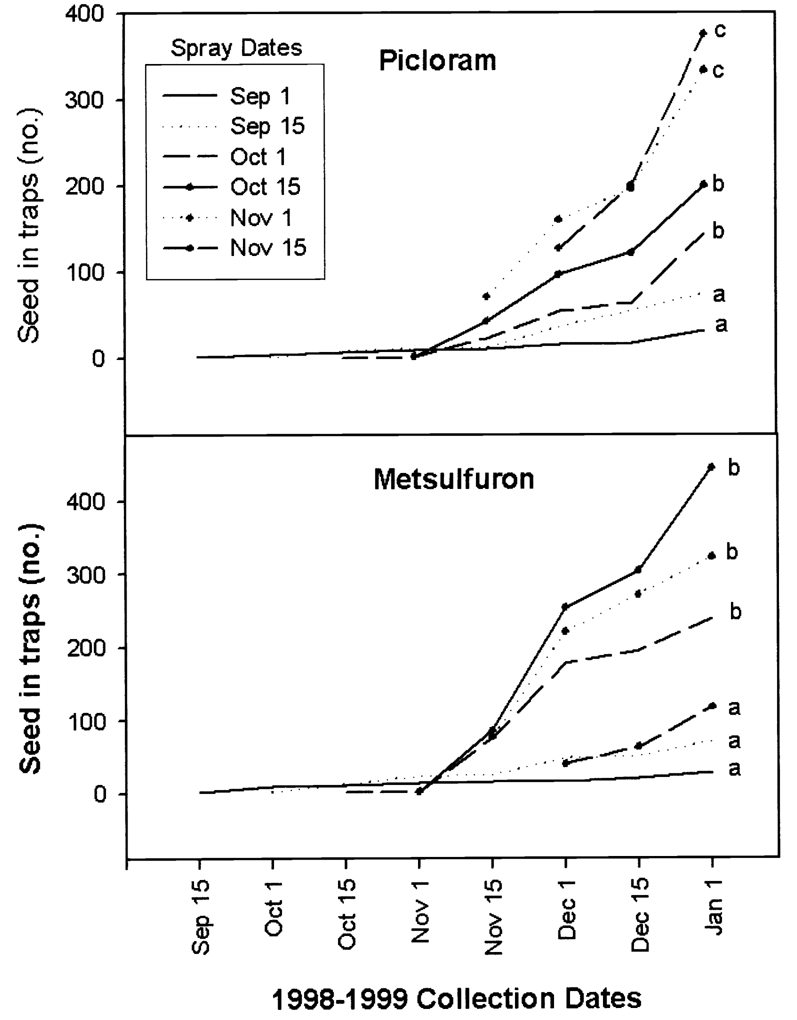

Fig. 3. Cumulative number of seed dispersed into 5- by 25- by 51-cm traps after spraying on 6 dates in 1998. Lines by herbicide type followed by a different letter indicate a difference in the total number of seed collected by 1 Jan. 1999.

(doughy) and embryos remained undeveloped through most of September. We noted that seed in early anthesis remains in a dough stage for 3 to 4 weeks until the testa builds a waxy inner and outer cuticle layer of thickened protective cells that harden around the encased embryo. Because most plants sprayed in early flower with initial to early seed set failed to produce a large quantity of mature seeds, we speculate that a hardened testa provides the protection needed to be impermeable to picloram and metsulfuron. As expected, seed dispersed through time in 1998 was less for plants sprayed on early dates compared to later dates, irrespective of herbicide applied (Fig. 3).

Seed Viability

The average net viability of seed obtained from the inflorescence of nonsprayed broom snakeweed plants was higher for the 1997 (67%) than the 1998 seedlot (49%) (Fig. 4). Wood et al. (1997) also reported annual differences in net viability between broom snakeweed seedlots and indicated that seedlot quality was highly influenced by available soil moisture during flowering. In this study, the number of mature seed needed for viability testing was generally not available from the inflorescence until October, and sufficient mature seed from traps was not available until November. Tetrazolium tests indicated little difference in the viability of seed collected from the inflorescence or recovered in traps beneath sprayed and nonsprayed plants after 1 November 1997 (Fig. 5) or 1998 (data not shown). These data agree with Wood et al. (1997) who reported that mature seed retained within the inflorescence or dropped to the surface remained equally viable after seed matured in autumn through the next spring.

In the 1997 experiment, there was no difference in average net seed viability from plants sprayed with picloram or metsulfuron compared to nonsprayed plants on any date except for those sprayed on 1 October (Fig. 6). On 1 October, only mature seed were tested, but the majority of seed taken from inflorescences were actually in the mid or earlier fill stages. Tetrazolium tests revealed net viability to be low (average 22%) for all seed tested at the time of spraying on 1 October. Two weeks after spraying on 1 October and for the next 20 weeks, seed from metsulfuron treatments had consistently lower net viability (average 26%) than nonsprayed and

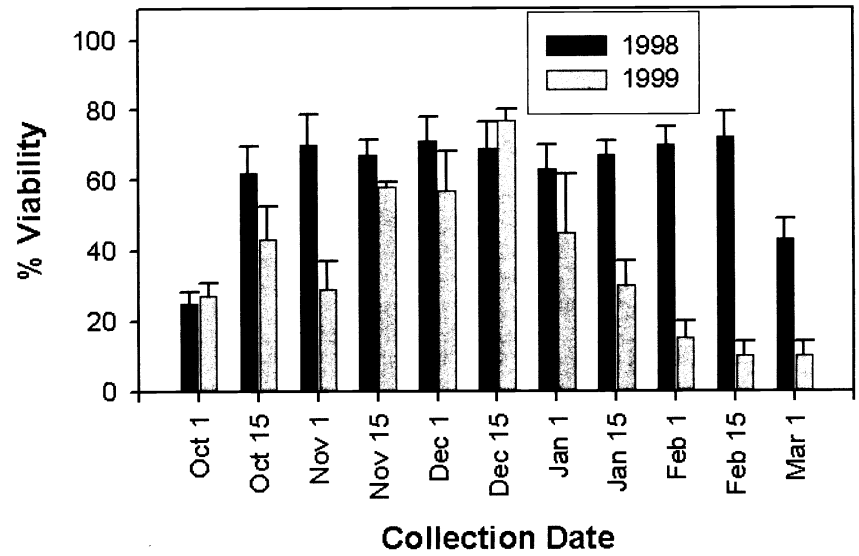

Fig. 4. Percent net viability of seed obtained from nonsprayed broom snakeweed plants on various dates in 1997–1998 and 1998–1999 at the Chihuahuan Desert Rangeland Research Center, Las Cruces, N.M.

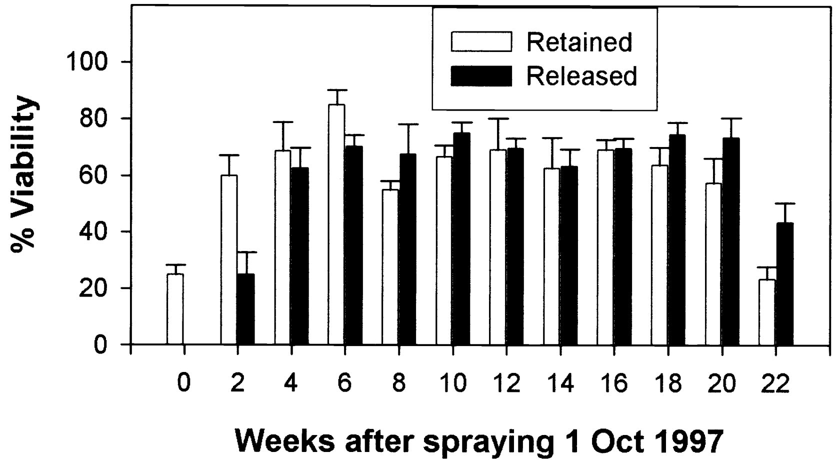

Fig. 5. Percent net viability of nonsprayed broom snakeweed seed retained in the inflorescence or released into traps. Seed collections began on 1 Oct. 1997 and continued every 2 weeks for 22 weeks.

picloram treated plants. Also, net seed viability from picloram treatments (average 45%) was less most weeks after spraying on 1 October compared to nonsprayed plants.

In the 1998 experiment, most seed from broom snakeweed plants sprayed with picloram or metsulfuron in September during initial to early fill stages of development did not mature, thus, there was not the supply of seed necessary to give an accurate estimate of net seed viability through time after spraying. Therefore, to obtain a general average estimate of seed viability after the 1 and 15 September 1998 spray dates, it was necessary to combine mature seed from all collection dates. Tetrazolium tests on the composited samples indicated that net seed viability (average 42%) was not different from nonsprayed plants, irrespective of spray date or herbicide treatment. There was sufficient seed to determine net viability through time after spraying in October and November. However, TZ tests indicated no significant differences in net seed viability through time by spray date or herbicide treatment compared to nonsprayed plants.

Seedling Emergence

Broom snakeweed seed can potentially germinate any time during the year, but optimal propagation occurs under moist conditions with surface soil temperatures ranging between 10 to 25°C (Kruse 1970, Mayeux 1980, Mayeux and Leotta 1981, Wood et al. 1997). Long-term vegetation monitoring on the Chihuahuan Desert Rangeland Research Center indicates that above-average rainfall in the first and second quarter of the year (January–June) is most critical for snakeweed propagation (Beck et al. 1999). In general, under southern New Mexico environmental conditions, snakeweed establishment occurs only once or twice a decade (Barnett 1996). Over this 5 year study (1997 to 2001), broom snakeweed seedlings were only noted in herbicide sprayed and nontreated plots in 1999 and 2001. Rainfall was about twice the winter and spring average in 1999 and 2001, and this is probably what enabled seedlings to establish. When seedlings were counted in 1999, relatively few propagules were noted in the 1998 experimental plots compared to those treated in 1997, irrespective of spray date or herbicide treatment (Tables 2 and 3). Picloram and metsulfuron have soil residual activity that dissipates through time depending on the rate of soil leaching, photo and microbial decomposition, and other processes (Scifres 1980). How long these chemicals remain active in the soil profile is unknown, but we speculate that breakdown of these herbicides within the arid environment of southern New Mexico is slow, requiring 12 months or more. The difference in time after treatment may partially explain why snakeweed germination was retarded the first spring season after 1998 herbicide treatments, and also why seedlings were more common in 1999 in plots sprayed in 1997. In the 1997 experimental plots, seedling numbers in 1999 were equal to or higher in herbicide treated areas, irrespective of spray date, compared to nonsprayed rangeland (Table 2). Conversely, in the 1998 experimental plots, seedling numbers in 1999 were significantly higher in nonsprayed areas than all herbicide plots (Table 3). During the 2001 evaluation, there was no difference in the number of broom snakeweed seedlings that emerged in either the 1997 or 1998 experimental plots compared to nonsprayed rangeland (Tables 2 and 3).

Management Implications

Across 2 autumn spray seasons, picloram at a rate of 0.28 kg a.i. ha^{-1} provided high and consistent broom snakeweed control when applied from mid flower and early seed development through the plant's post bloom and seed dispersal

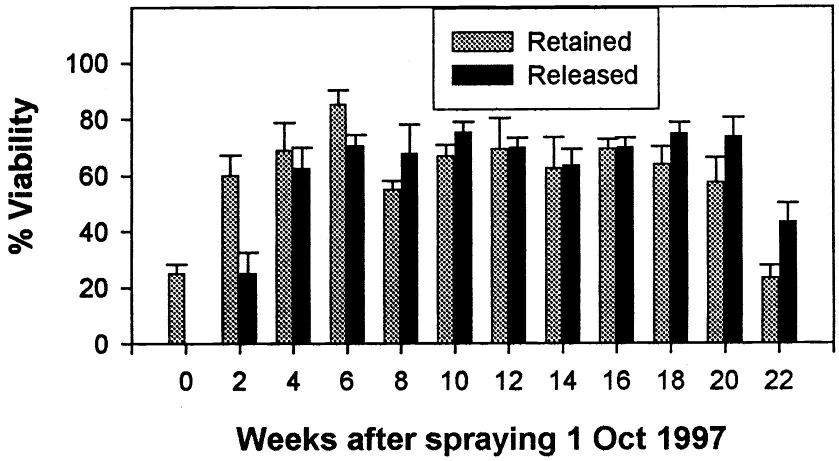

Fig. 6. Percent net viability of broom snakeweed seed collected for 22 weeks after applying herbicides on 1 Oct. 1997 at the Chihuahuan Desert Rangeland Research Center, Las Cruces, N.M.

stages. Metsulfuron at a 0.03 kg a.i. ha^{-1} rate, however, did not provide consistent control results when applied during this same period. Presently, picloram is the principle herbicide used in New Mexico for broom snakeweed control. The majority of commercial aerial spraying of picloram occurs after broom snakeweed has completed flowering and seed is mature. Results from this study suggest that the current spray season can be widened to include an earlier period in which plants are still in flower.

A major objective of this study was to determine if timed herbicide applications could be used to kill the parent plant and its seed crop, and thus reduce the possibility for future broom snakeweed propagation. Picloram and metsulfuron applications made in the 1997 experiment did not lower seed production because spraying did not begin until most seed in the inflorescence had already reached physiological maturity. Two spring seasons after the 1997 treatments, broom snakeweed seedlings were equal or more abundant in all experimental spray plots than in non-sprayed areas, indicating that the herbicides did not impede future propagation. In the 1998 experiment, herbicide applications made in September when broom snakeweed was in flower and early seed development resulted in a near elimination of seed production. The first spring after the 1998 spraying, environmental conditions were suitable for broom snakeweed germination, but few seedlings established in sprayed plots. However, 3 spring seasons after spraying in 1998, seedling numbers were equal in all herbicide and non-sprayed experimental plots, irrespective of spray date. Thus, results from this study were inconclusive for determining if timed herbicide applications could be used to destroy both the parent plant and its seed crop and thereby cause a reduction in future broom snakeweed propagation.

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Selected factors affecting seedling recruitment of dalmatian toadflax

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Abstract

Seedling recruitment of Dalmatian toadflax, (*Linaria genistifolia* ssp. *dalmatica* (L.) Maire and Petitmengin (Scrophulariaceae)), was examined in a 2-year field study in Montana using overseeding and plant/insect exclusion methods, to determine whether it was more limited by seed availability or interspecific plant competition. Overseeding test plots with toadflax seed had no effect on seedling recruitment. Exclusion of plant competition (via herbicide application and pruning) significantly increased total, and cumulative seedling recruitment of Dalmatian toadflax on the last sampling date in 3 of 4, and 2 of 4 cases examined, respectively. Insect exclusion (via insecticide application) significantly increased total seedling recruitment of Dalmatian toadflax on the last sampling date in only 1 of 4 cases examined, and had no effect on cumulative seedling recruitment of Dalmatian toadflax on the last sampling date. We conclude that seedling recruitment in Dalmatian toadflax was more strongly influenced by plant competition than herbivory in our study. Hence, microsite limitation (i.e., competition for "safe sites for germination") rather than seed limitation appears to play a more important role in toadflax seedling recruitment. In light of this, current biological control agents that impact seed production will likely have minimal capabilities of influencing toadflax density. Thus, a premium should be placed on establishing biological control agents that are able to cause significant damage to the stem and root system of Dalmatian toadflax, and in maintaining a healthy plant community that, through interspecific competition, will negatively affect toadflax seedling recruitment.

Key Words: seed limitation, microsite, weed management, biological control, rangeland, ecology, overseeding, *Brachypterolus pulicarius*, plant competition, *Linaria genistifolia*, ssp. *Dalmatica*

Resumen

El establecimiento de plántulas de "Dalmatian toadflax", *Linaria genistifolia* ssp. *dalmatica* (L.) "Maire" y "Petitmengin" (Scrophulariaceae), se examinó en un estudio de campo de 2 años realizado en Montana a través del uso de métodos de sobresiembra y de exclusión a planta/insectos, para determinar si es establecimiento de plántulas fue mas limitado por la disponibilidad de semilla o por competencia interespecifica. La sobresiembra de las parcelas de prueba con semilla de "Toadfax" no tuvo efecto en el establecimiento de plántulas. La exclusión de competencia entre plantas (vía aplicación de herbicidas y poda) incrementó significativamente el establecimiento total y acumulativo de plántulas de "Dalmatian toadflax"en la última fecha de muestreo en 3 de 4 y 2 de 4 casos examinados respectivamente. La exclusión de insectos (vía aplicación de insecticida) incremento significativamente el establecimiento total de plántulas de " Dalmatian toadflax"en la última fecha de muestreo de solo 1 de 4 casos examinados y no tuvo efecto en el establecimiento acumulativo de plántulas de "Dalmatian toadflax"en la última fecha de muestreo. Concluimos, que en nuestro estudio, el establecimiento de plántulas de "Dalmatian toadflax"fue mas fuertemente afectado por la competencia entre plantas que por la herbivoría. Entonces, la disponibilidad limitada de micrositios (esto es, la competencia por sitios seguros para germinación), mas que la disponibilidad limitada de semilla, parece jugar un papel más importante en el establecimiento de plántulas de "Toadflax". A la luz de esto, los agentes de control biológico actuales que impactan la producción de semilla probablemente tendrán un mínima capacidad de influir en la densidad de "Toadflax". Así, se debe poner especial atención en establecer agentes de control biológico que sean capaces de causar un daño significativo al sistema de raíz y tallo del "Dalmatian toadflax"y en mantener una comunidad vegetal saludable, que a través de competencia interespecifica, afectará negativamente el establecimiento de plántulas de "Toadflax".

Dalmatian toadflax, (*Linaria genistifolia* ssp. *dalmatica* (L.) Maire and Petitmengin (Scrophulariaceae)), is an introduced plant of Mediterranean origin that has become a serious weed of recreation and rangelands in Montana and other Northwestern states (Alex 1962, Nowierski 1995, 1996). The plant is characterized by yellow snapdragon-like flowers, spherical seed capsules, glaucous green foliage, a deep taproot, and lateral root system. A single mature plant is capable of producing half a million seeds per growing season (Lajeunesse et al. 1993). Seeds remain viable in the soil for as long as 10 years resulting in high levels of accumulation in the seed bank (Robocker 1970, 1974). In addition to causing disruption of the plant community through displacement of native vegetation, Dalmatian toadflax contains a number of defensive compounds (Jeanneret and Schroeder 1992) and as such is reportedly toxic to livestock and wildlife (Polunin 1969).

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Chemical and cultural management of Dalmatian toadflax has generally been ineffective due to the perennial nature of the weed, its waxy foliage, a deep taproot, and the low economic return associated with recreation and rangelands (Lajenunesse et al. 1993).

Brachypterolus pulicarius (L.) (Nitidulidae) is a biological control agent that directly affects the sexual reproductive capacity of Dalmatian toadflax. The ovary-feeding beetle occurs adventively in North America. *B. pulicarius* larvae feed on pollen, anthers, ovaries, and maturing seed of Dalmatian toadflax, and in the process may cause seed capsule abortion (Nowierski 1996, Grubb 1998). Grubb (1998) has shown that *B. pulicarius* is capable of reducing seed production in Dalmatian toadflax by up to 93%.

At present, it is unclear whether biological control agents that attack reproductive structures of Dalmatian toadflax will have a tangible effect on plant density in established stands. Whether or not Dalmatian toadflax can be managed using natural enemies that attack reproductive tissues likely depends on whether Dalmatian toadflax is a seed-limited versus microsite-limited plant.

Both the availability of seed and the availability of microsites limit the recruitment of new plants into a population (Eriksson and Ehlen 1991). Seed-limited plants generally produce a lower ratio of seeds to microsite, while microsite-limited plants have a higher ratio of seeds to microsite. While recruitment is usually dependent on a combination of both of these factors, in many instances it should be possible to determine which factor plays the dominant role in determining seedling recruitment in specific instances.

For the purpose of this study microsite was defined as a confluence of water, nutrient, and light availability. As Dalmatian toadflax has a tendency to inhabit sites characterized by well-drained soils and this study took place in arid environments, water was quite likely the single most important factor in determining microsites safe for seedling recruitment. Previous studies have shown that Dalmatian toadflax seedling demonstrate poor interspecific competitive ability for soil moisture (Robocker 1970, 1974).

Studies on the effects of inflorescence feeding insects on seedling recruitment of plants have shown that seed predation by insects can have a dramatic effect on seedling recruitment, or little to no effect at all. Extensive experimentation by Louda et al. (1990) and Louda and Potvin (1995) in the Nebraska sand hills prairie has shown that recruitment of the Platt thistle, *Cirsium canescens* (Nutt.), is severely limited by insect seed predators. Seedling recruitment also was found to be limited by seed predation in the perennial shrub *Haploppappus squarrosus* (Hall) (Louda 1982), and in wild parsnip, *Pastinaca sativa* (L.) (Hendrix and Trapp 1989). In contrast, for other plant species such as *Senacio jacoboaea* (L.) and *Cytisus scoparius* (L.), seedling recruitment was not reduced by insect herbivory (Crawley and Gillman 1989), nor by seed predation (Bossard and Rejmanek 1994).

Interspecific plant competition may affect the availability of microsites for seedling emergence, which in turn may effectively limit seedling recruitment. Putwain and Harper (1968) showed that recruitment of *Rumex acetosella* (L.) in established grasslands was entirely dependent on reduced grass competition. Similarly, *Opuntia Fragilis* (Haw.) has been shown to have a higher rate of recruitment when interspecific competition is excluded (Burger and Louda 1995). In another study, initial recruitment of several biennial plants was shown to be inversely correlated with levels of ground cover (Gross and Werner 1982).

Robocker (1970) reported that a single vigorous adult toadflax plant was capable of producing half a million seeds per growing season, 76% of which germinated when between 1–5 years of age and stored at room temperature. In addition to being prolific seed producers mature Dalmatian toadflax plants have been described as possessing an impressive root system consisting both of a taproot as well as lateral roots from which prostrate vegetative stems are produced. Vegetative stems have been described as forming "fairy rings" around parent plants, which may persist after parent plants have dropped out of the population (Vujnovic and Wein 1997).

Given the prolific seed production of Dalmatian toadflax and its ability to reproduce vegetatively we hypothesized that, in situations where seed predation is not a factor and plant competition is negligible, seedling recruitment of Dalmatian toadflax will not be seed limited. Whether or not it might be limited under high levels of seed predation and/or plant competition was a more complex question. Given the poor competitive ability of Dalmatian toadflax seedlings for soil moisture, and under competition from forbs and grasses, it seems reasonable to expect seedling recruitment to be limited by micro-site availability (Robocker 1970, 1974). To test whether or not Dalmatian toadflax was seed limited in the presence or absence of seed predation and interspecific plant competition, a combination of field and experimental studies were carried out during the summers of 1997 and 1998.

Materials and Methods

Experimental design

The field experimental layout for 1997 consisted of a fixed block, split-split plot, factorial design with 4 treatments randomly assigned over 4 blocks at 2 sites in Montana. For the first factor interspecific, above ground plant competition was allowed versus excluded, while insect seed herbivory was allowed or excluded for the second factor.

In 1998 a third factor (overseeded versus non-overseeded) was added to the experimental design at the 2 field sites, resulting in a 3-factor design with 8 treatments and 4 blocks. The 2 sites chosen for this study had received previous releases of *B. pulicarius.* Four blocks were established at the 2 research sites to block against obvious differences in vegetative cover.

Site and block descriptions

The study took place during the 1997 and 1998 growing seasons. The first site was located on the Crow Indian Reservation, 20 km North of Wyola, Big Horn County, Montana, (Latitude 45° 5', Longitude 107° 40', approximate elevation 1,131 meters), hereafter referred to as the Wyola site. The second site was located adjacent to the Canyon Ferry Reservoir approximately 16 km SE of Helena, Broadwater County, Montana (Latitude 49° 39', Longitude 111° 44', approximate elevation 1,211 meters), hereafter referred to as the Canyon Ferry site. Sites were chosen because they reflected different habitat types infested with Dalmatian toadflax and both sites had had previous releases of *Brachypterolus pulicarius* for at least 8 years. The number of *Brachypterolus pulicarius* released at the Wyola site during the summers of 1994, 1995, and 1996 was 100, 675, and 0 individual beetles, respectively. The number of *Brachypterolus pulicarius* released at the Canyon Ferry site during the summers of 1994, 1995, and 1996 was 100, 200, and 300 individual beetles, respectively (Nowierski unpublished data).

Each site consisted of 4 blocks with 8 treatments representing 8 possible combinations of experimental factors. Blocks were fixed previous to treatment assign-

Table 1. Pre-treatment mean (± standard error) Dalmatian toadflax stem counts, Dalmatian toadflax percent cover, other plant species percent cover and bare ground percent cover by blocks at either site 1997.

Block	Number Dalmatian toadflax stems	Dalmatian toadflax cover	Other plant cover	Bare ground
	(No.)	(%)	(%)	(%)
	Canyon Ferry			
1	15.5 ± 1.3	7.9 ± 0.4	85.8± 1.6	6.4 ± 1.6
2	9.4 ± 0.8	20.8± 4.4	72.5 ± 3.9	6.8 ± 1.8
3	14.5 ± 1.0	9.1 ± 1.1	36.4 ± 4.1	54.5 ± 4.6
4	13.8 ± 0.9	7.3 ± 0.5	29.4 ± 2.4	63.4 ± 2.7
	Wyola			
1	25.8 ± 1.7	12.4 ± 1.5	48.9 ± 6.1	38.8 ± 6.1
2	18.3 ± 1.5	11.3 ± 1.1	14.9 ± 1.7	73.9 ± 2.3
3	26.5 ± 1.2	12.9 ± 1.1	49.9 ± 4.1	37.3 ± 3.7
4	19.0 ± 1.1	12.5 ± 1.2	41.6 ± 3.8	45.9 ± 3.7

ment through the use of Dalmatian toadflax stem counts, Dalmatian toadflax percent cover, and total plant cover measurements across a spatial gradient (Table 1). The experiment was laid out in a randomized fashion across the fixed block design, with each treatment occurring once in each block. Replicates of each of the 8 factor/treatment (1998) combinations were positioned within each block through the use of permanent quadrats.

The Wyola site had a higher density of Dalmatian toadflax plants than the Canyon Ferry site in addition to having a long history of cattle grazing. Cattle and horses were present at the Wyola site during both study seasons. The area where the plots were laid out, and where toadflax density was highest was an old unfilled gravel pit. Soil surface texture at the Wyola site ranged from sandy loam to sandy clay loam with a mean organic matter content of 1.29%, and a mean water holding capacity of 9.28% at 15 bars. Blocking was laid out across a basin, up a north-facing slope, along the top of a slight hill, and then down a south-facing slope, with each described region receiving a single block of randomly assigned treatments. Other plants occurring at the study site included downy brome (*Bromus tectorum* L.), yucca (*Yucca glauca* Nutt.), ragweed (*Ambrosia artemisiifolia* L.), western salsify (*Tragopogon dubius* Scop.), and yellow sweet clover (*Melilotus officinalis* (L) Lam).

The site located at Canyon Ferry was markedly different than the Wyola site and consisted of a hillside adjacent to the BLM's Riverside Campground. Grazing pressure at the Canyon Ferry site consisted of only occasional browsing by white-tail and mule deer. Soil surface texture oil at the Canyon Ferry site ranged from sandy clay loam to loam with a mean organic matter content of 3.15%, and a mean water holding capacity of 8.73% at 15 bars. Environmental conditions were somewhat cooler than at the Wyola site with frequent thunderstorms. Blocking was laid across the flat before a hillside and then in 3 progressively decreasing plant cover levels up the hillside. Each described region received a single block of treatments. Other plants occurring at the study site included downy brome, prickly pear (*Opuntia polyacantha* Haw.), yellow sweet clover, leafy spurge (*Euphorbia esula* L.), and spotted knapweed (*Centaurea maculosa* Lam.).

Quadrat frame construction and sampling procedure

Seedling recruitment, plant cover data and seed production rates were collected using 4 blocks of 8, 60 x 60 cm, permanent quadrats at both sites. Thirty-two similar clusters of adult Dalmatian toadflax stems in 4 blocks of 8 treatments per site, were randomly selected for the duration of the study. Adult stem clusters selected for data collection were marked with 2 pieces of rebar at the NW and SE corners of the quadrat. A portable quadrat-frame consisting of a 60 x 60 cm square divided into 9, 20 x 20 cm squares, was used to demarcate the observation arena. The frame had adjustable legs at each corner, which could extend to 30 cm in height to minimize plant disturbance during frame placement and removal.

During data collection, the frame was situated so that it laid between the 2 rebar stakes, with a designated side facing north. Data were collected on a weekly basis during 1997 and on a 7 to 14 day schedule in 1998. Data collected included seedling, stem (data not presented), and seed capsule counts (data not presented). Such data were collected within the 20x20 cm center square and the 4 quadrants located in each cardinal direction. Plant data collected from the 4 quadrants and the 1 center square were averaged to generate mean weekly counts.

Seedlings were sorted into 3 classes of counts to keep track of weekly mortality and emergence events. The first class consisted of seedlings with 1–2 nodes beyond the cotyledon, the second of seedlings 2–5 nodes beyond the cotyledon, and the third of seedlings with more than 5 nodes beyond the cotyledon. Stems were marked with plastic ties to maintain a census through time and to help orient the frame. Two colors of plastic ties were used, 1 for the center square and 1 for each of the 4 squares located in each cardinal position. Finally, seed capsules were harvested from similar plants near each quadrat in 1997 and seeds counted in order to determine a realistic overseeding rate.

Overseeding rate calculation and field application

Experimental plots were supplementary seeded to address the question of whether or not seed abundance was the primary factor limiting Dalmatian toadflax seedling recruitment (Louda et al. 1990, Louda and Potvin 1995, Crawley 1989). Overseeding rate was calculated by averaging the total number of seed capsules from each quadrat at each site and multiplying the resulting mean by the mean number of seeds per capsule. The higher of the 2 site-means was taken and multiplied by a factor of 2 to generate an artificially high seeding rate of 92,192 seeds per quadrat, which was applied to both sites in the Fall of 1997.

Overseeding took place immediately following the last sampling date. Fall 1997 was selected as the overseeding time period so that seeds would be exposed to normal post-dispersal predation and mortality factors. Seeds were collected adjacent to the research plots at the 2 sites in the weeks immediately prior to seeding. Only seeds collected from a given site were used in the experimental treatments for that site. Seeds were scattered by hand from approximately 20 cm above the soil surface, using the quadrat frame as a guide, in an alternating E to W, W to E zigzag running from the N to S sides of the quadrat frame.

A seedling emergence trial was performed in 1999 on seeds collected from either site in 1997 and 1998 to ascertain an approximate seed dormancy figure. Seeds were stored in darkness at room temperature, beginning immediately after collection. In the spring of 1999 seeds were placed on filter paper disks on thermal bars set for 18° C to maximize Dalmatian toadflax seedling emergence (Robocker 1970, 1974, Nowierski, et al. unpublished data). Each bar was equipped with a plexiglass shield and filter paper disks were moistened twice a day with distilled water to maintain constant water availability. Bars were set up with 2 disks per date/site combination with 40 seeds per disk providing 8 total replicates, for each date and site. Seedlings were counted and removed on a daily basis until there were 3 consecutive days without emergence. Temperatures were taken for each disk every 3 days to identify possible temperature effects between disks.

Plant competition exclusion techniques

Interspecific plant competition was excluded from half of the experimental quadrats to ascertain whether or not plant competition had an effect on Dalmatian toadflax seedling recruitment. Plant competition was excluded through a combination of careful pruning and herbicide application. After the quadrats had been mapped out and the frame set in place, Roundup® (N-Phosphonomethylglycine) was applied at the lowest labeled rate to interspecific competitors located around the outside of the quadrat through the use of a paintbrush, with care taken not to paint any toadflax plants. Roundup® was applied in a similar manner to large interspecific competitors (i.e., *O. polyacantha, E. esula, Y. glauca, A. artemisiifolia,* and *M. officinalis*) within the quadrats to more completely remove them. Herbicide application was done only in the 1997 season within the first month (12 May to 15 June, 1997) of initial establishment of the quadrats. Above ground plant competition was further excluded through careful pruning of competitors at the soil surface. Pruning was done at every sampling period to minimize interspecific competition within the plant competition-excluded quadrats. Senescent toadflax stems from prior seasons were removed from all quadrats to facilitate frame placement.

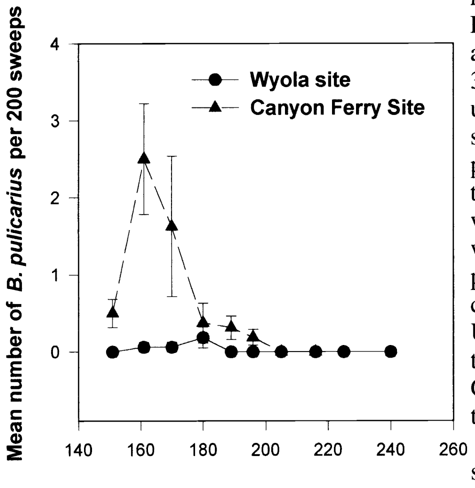

Fig. 1. Mean number of *B. pulicarius* caught per 50 sweeps at the Canyon Ferry and Wyola field sites during 1998. Error bars represent the standard error of the mean.

Natural enemy augmentation, exclusion, and presence measurements

Augmentative releases of *B. pulicarius* were made at each of the 2 research sites to supplement low populations of the beetle and enhance the anticipated negative effects of the beetle on the growth and reproduction of Dalmatian toadflax. Adult B. pulicarius, collected from Dalmatian toadflax in British Columbia, were released at the 2 research sites during the weeks of 7 June 1997 and 10 June 1998. Four hundred adult *B. pulicarius* were released in each beetle treatment plot during 1997 and 1998. Beetle- excluded treatments received no beetles.

An insecticide treatment was applied to the beetle exclusion plots to exclude the effects of *B. pulicarius.* Orthene Isotox® (O,S-dimethyl acetylphos-phoramidothioate) was selected as the insecticide for natural enemy exclusion because it has a systemic residual action, demonstrates a low general phyto-toxicity, and has been used in similar experiments with no demonstrable effects on plant pollination rates (Louda 1982, Louda et al. 1990, Louda and Potvin 1995). Orthene was applied at a rate of 15 ml pesticide per 350 ml of water. Plants were sprayed using a hand-operated squirt bottle type sprayer, and applied from all sides of the plant to runoff. Plants in non-insecticide treatments were sprayed with distilled water in an identical fashion. Pesticide was applied every 14 to 20 days, until plants senesced. A phytotoxicity trial was conducted in the Montana State University Plant Growth Center during the winter of 1998-99 to assess whether Orthene had any effects on Dalmatian toadflax growth and flower production.

During the 1998 growing season insect sweep samples were taken at approximate biweekly intervals in an attempt to quantify the population of *B. pulicarius* at both sites. Sweeps were performed with a standard insect sweep net and consisted of 4 sets of 200 sweeps per block. Samples were taken back to the lab and kept in a freezer until they were processed and mean beetle counts were determined. The mean number of *B. pulicarius* obtained in 1998 from the sweep net samples from the 2 sites is shown in Figure 1.

Analysis

Data were analyzed using a 2 x 2 x 4 factorial ANOVA for the 1997 data and a 2 x 2 x 2 x 4 factorial ANOVA for the 1998 data. The ANOVA focused on 4 measurements related to seedling emergence, recruitment and production. Total seedling counts and cumulative seedling emergence data were transformed using a square root transformation and a natural log transformation ($\ln(x+1)$), respectively, to normalize the data for parametric analysis. Both sites and years were analyzed separately, yielding results from 4 sets of analyses.

The SAS Statistical Package (SAS 1997) was used for all data analyses using the GLM procedure. All ANOVA models were reduced to include only factor effects and 2-way interaction effects with higher order interaction effects included in the overall MSE. Previous analyses indicated that there were no significant 3 or 4-way interactions. Significant 2-way interactions were analyzed using a t-test to compare each possible pairing of 2-way factor combinations.

Results

Total seedling counts on the last sampling date, 1997

Although seeds germinate and produce seedlings over the course of the growing season, only those seedlings that survive until the end of the growing season may contribute to next year's toadflax population. Hence, we restricted the analysis to total seedling counts found among treatments on the last sampling date. The results of ANOVA of the mean total number of Dalmatian toadflax seedlings obtained across treatments on the final sampling date in 1997 for the Canyon Ferry and Wyola sites are presented in Table 2. Factor, block, and 2-way factor interaction means ± standard errors are presented in Table 3 to corroborate the direction of statistically significant results. Significant differences in total seedling counts were found among blocks for both study sites ($P = 0.019$ and $P = 0.033$, respectively; Table 2). Although no differences in total seedling counts were found among treatments for the Canyon Ferry

Table 2. Results of ANOVA of the total seedling count on the last sampling date for the Canyon Ferry and Wyola sites, 1997.[abc]

	Canyon Ferry					Wyola				
Factors	P-value	Blocks				P-value	Blocks			
Block	**0.019**	Block 1	Block 2	Block 3	Block 4	**0.033**	Block 1	Block 2	Block 3	Block 4
	SNK grouping	B	B	A	B	SNK grouping	AB	AB	A	B
Plant competition exclusion	0.932					**0.033**				
Insect exclusion	0.831					**0.008**				
Block x plant competition	0.749					**0.014**				
Block x insect exclusion	0.838					0.095				
Plant competition x insect exclusion	0.940					0.095				

[a] Blocks not sharing the same capital letter below them were significantly different at the 0.05 level using a Student Neuman-Keuls (SNK) mean comparison test.

[b] Data were normalized using a square root transformation.

[c] Bold faced text indicates a significant P-value.

site (P > 0.05), significantly higher seedling counts were found for the Wyola site when either plant competition or insects were excluded (P = 0.033 and P = 0.008, respectively; Table 2). In addition, a significant block x plant competition interaction was found for total seedling counts from the Wyola site (P = 0.014).

Total seedling counts on the last sampling date, 1998

Unlike the previous year, no differences in total seedling counts were found among blocks in 1998 for both the Canyon Ferry and Wyola study sites (P > 0.05; Table 4). As anticipated, plant competition significantly decreased the total seedling counts on the final sampling date for both the Canyon Ferry and Wyola research sites (P = 0.005 and P = 0.010, respectively; Table 4). However, overseeding and insect exclusion were found to have no influence on the total seedling counts obtained on the last sampling date for both research sites (P > 0.05; Table 4). Factor, block, and 2-way factor interaction means ± standard errors are presented in Table 5 to corroborate direction of statistically significant results.

Cumulative seedling counts on the last sampling date, 1997

The results from ANOVA of the mean cumulative number of Dalmatian toadflax seedlings obtained across treatments on the final sampling date in 1997 for the Canyon Ferry and Wyola sites are presented in Table 4. A significant block effect was found for cumulative seedling counts at the Canyon Ferry site in 1997 (P = 0.005), while no differences were found among blocks at the Wyola site in 1997 (P > 0.05; Table 6). Except for a significant block x plant competition interaction at the Wyola site (P = 0.04; Table 6), the exclusion of plant competition and insects had no effects on cumulative seedling emergence (P > 0.05; Table 6). Factor, block, and 2-way factor interaction means ± standard errors are presented in Table 3 to corroborate direction of statistically significant results.

Table 3. Factor means ± standard errors for ANOVA of the total seedling count and cumulative seedling emergence on the last sampling date for the Canyon Ferry and Wyola sites, 1997.[a]

Factors	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Parameter	Total seedling count		Cumulative seedling emergence	
Site	Canyon Ferry	Wyola	Canyon Ferry	Wyola
Block 1	**0.35 ± 0.13**	**0.55 ± 0.33**	**1.40 ± 0.28**	12.83 ± 4.52
Block 2	**0.50 ± 0.21**	**0.40 ± 0.19**	**2.00 ± 0.58**	5.6 ± 2.82
Block 3	**2.6 ± 1.06**	**0.88 ± 0.26**	**8.43 ± 2.50**	7.08 ± 1.05
Block 4	**0.38 ± 0.14**	**0.20 ± 0.08**	**1.88 ± 0.35**	2.58 ± 0.76
Plant competition allowed	1.13 ± 0.58	**0.35 ± 0.15**	3.80 ± 1.46	5.68 ± 1.51
Plant competition excluded	0.79 ± 0.26	**0.65 ± 0.18**	3.05 ± 0.74	8.36 ± 2.52
Insects allowed	0.79 ± 0.27	**0.24 ± 0.07**	1.38 ± 0.81	5.91 ± 1.91
Insects excluded	1.13 ± 0.57	**0.76 ± 0.21**	3.48 ± 1.43	8.13 ± 2.25
Plant comp. allowed x insects allowed	0.75 ± 0.29	0.20 ± 0.09	3.68 ± 1.19	4.20 ± 1.07
Plant comp. allowed x insects excluded	1.50 ± 1.1	0.50 ± 0.29	3.93 ± 2.77	7.15 ± 2.84
Plant comp. excluded x insects allowed	0.83 ± 0.48	0.28 ± 0.11	3.08 ± 1.17	7.63 ± 3.70
Plant comp. excluded x insects excluded	0.75 ± 0.23	1.03 ± 0.30	3.03 ± 1.00	9.10 ± 3.65

[a] Bold faced text indicates a significant factor or interaction ($\alpha = 0.05$).

Cumulative seedling counts on the last sampling date, 1998

As in 1997, significant differences in cumulative seedling numbers were found among blocks for the Canyon Ferry site in 1998 (P = 0.029), but not for the Wyola research site (P > 0.05; Table 7). Significantly higher cumulative seedling counts were found for both the Canyon Ferry and Wyola sites in 1998 when plant competition was excluded (P = 0.021 and P = 0.005, respectively; Table 7). As was found in 1997, insect exclusion had no effect on cumulative seedling numbers at both research sites (P > 0.05). All interactions were nonsignificant (P > 0.05; Table 7). Factor, block, and 2-way factor interaction means ± standard errors are presented in Table 5 to corroborate direction of statistically significant results.

Seedling emergence trial results

Mean temperatures recorded across replicates were statistically similar. Mean percent emergence ± standard error for seed collected from Wyola 1997 (0.71 ± 0.05), Wyola 1998 (0.66 ± 0.05), and Canyon Ferry 1997 (0.69 ± 0.04) were statistically similar (P > 0.05). However mean percent emergence was statistically lower for Canyon Ferry 1998 (0.28 ± 0.05) seed compared to the other 3 seed collections (P = 0.0001).

Discussion and Conclusions

A widely accepted approach for testing seed versus microsite limitation of seedling recruitment is to compare natural seedling population dynamics with situations where unnaturally high quantities of seed are added (Crawley and Nachapong

Table 4. Results of ANOVA of the total seedling count on the last sampling date for the Canyon Ferry and Wyola sites, 1998.[abc]

	Canyon Ferry					Wyola				
Factors	P-value	Blocks				P-value	Blocks			
Block	0.067	Block 1	Block 2	Block 3	Block 4	0.069	Block 1	Block 2	Block 3	Block 4
	SNK grouping	A	A	A	A	SNK grouping	A	A	A	A
Overseeding	0.875					0.281				
Plant competition	**0.005**					**0.010**				
Insect exclusion	0.360					0.431				
Block x overseeding	0.967					0.260				
Block x plant competition	0.204					0.069				
Block x insect exclusion	0.843					0.170				
Overseeding x plant competition	0.695					0.281				
Overseeding x insect exclusion	0.128					0.837				
Plant competition x insect exclusion	0.871					0.431				

[a]Blocks not sharing the same capital letter below them were significantly different at the 0.05 level using a Student Neuman-Keuls (SNK) mean comparison test.
[b]Data were normalized using a square root transformation.
[c]Bold faced text indicates a significant P-value.

1985, Crawley 1988, Louda et al. 1990, Louda and Potvin 1995). However, seedlings do not recruit into an ecological vacuum; seed producing plants, seeds, and seedlings are all subject to plant competition as well as the effects of herbivores, microorganisms, and other factors (Nowierski et al. 1999). In light of this, it is important to understand that seed and microsite limitation are not mutually exclusive; instead they are dependent parts of the weeds biotic and abiotic environment (Eriksson and Ehlen 1991).

Ecological management of rangeland weeds includes the use of natural enemies as predators of weeds as well as the use of more desirable plant species as competitors (Kennett et al. 1992, Sheley et al. 1996, Lym et al. 1997). One biological strategy for managing a target weed is to reduce seed production to a point where adult mortalities cease to be replaced by new recruits. Likewise, plant communities that limit the availability of seedling emergence safe sites or provide heavy competition for resources may be able to limit the recruitment of new seedlings into a weed population (Velagala et al. 1997, Sheley et al. 1999). Both approaches limit the recruitment of the weed albeit by influencing different aspects of the system.

In the case of Dalmatian toadflax, overseeding did not appear to significantly affect seedling recruitment for the first year toadflax population. The enhancement of the seed supply for the 1998 growing season was not a significant factor in last date seedling counts nor cumulative seedling emergence. This suggests that under the field conditions that occurred during our 2-year field study, the Dalmatian toadflax populations at the 2 sites filled most "safe seedling emergence sites". Results obtained from the seedling emergence trial were consistent (66–71%) with results obtained in previous studies for similar aged seeds with the exception of seeds collected in 1998 from Canyon Ferry (Robocker 1970, Nowierski et al. unpublished data). It is therefore possible that a greater portion of seeds added to the Canyon Ferry site may have remained dormant.

It is important to note that belowground interspecific plant competition may have still been a factor in plant competition allowed treatments. While the larger competitors were treated with roundup, the smaller competitors were not, and may have continued to compete for moisture after clipping. However, plant competition was the main factor affecting final seedling counts in 3 of 4 situations examined, suggesting that seedling recruitment of Dalmatian toadflax was limited by interspecific resource competition. Plant competition appeared to play less of a role in the cumulative number of seedlings recorded at the research sites, as significant effects from competition were found in only half of the situations examined.

Herbivory by insects appeared to exert only a minor influence on the final

Table 5. Factor means ± standard errors for total seedling count and cumulative seedling emergence on the last sampling date for the Canyon Ferry and Wyola sites, 1998.[a]

Factors	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Parameter	Total seedling count		Cumulative seedling emergence	
Site	Canyon Ferry	Wyola	Canyon Ferry	Wyola
Block 1	0.40 ± 0.17	0.05 ± 0.05	**3.43 ± 2.29**	6.85 ± 3.77
Block 2	0.53 ± 0.2	0.00 ± 0.00	**4.23 ± 2.59**	7.00 ± 3.22
Block 3	1.93 ± 0.66	0.10 ± 0.0	**12.00 ± 2.4**	6.45 ± 2.26
Block 4	0.68 ± 0.20	0.95 ± 0.76	**2.80 ± 0.76**	16.75 ± 6.60
Non-overseeded	1.00 ± 0.38	0.46 ± 0.39	4.21 ± 1.56	7.99 ± 3.28
Overseeded	0.76 ± 0.18	0.09 ± 0.05	7.01 ± 1.86	10.54 ± 2.93
Plant competition allowed	**0.38 ± 0.13**	**0.00 ± 0.00**	**2.99 ± 1.10**	**2.96 ± 0.87**
Plant competition excluded	**1.39 ± 0.36**	**0.55 ± 0.38**	**8.24 ± 2.01**	**15.56 ± 3.68**
Insects allowed	0.83 ± 0.29	0.46 ± 0.39	6.43 ± 2.00	10.54 ± 3.74
Insects excluded	0.94 ± 0.30	0.09 ± 0.04	4.80 ± 1.44	7.99 ± 2.33
Non-overseeded x plant comp. allowed	0.40 ± 0.16	0.00 ± 0.00	2.13 ± 0.61	2.03 ± 0.61
Non-overseeded x plant comp. excluded	1.60 ± 0.69	0.93 ± 0.76	6.30 ± 2.98	13.95 ± 5.97
Overseeded x plant comp. allowed	0.35 ± 0.20	0.00 ± 0.00	3.85 ± 2.14	3.90 ± 1.62
Overseeded x plant comp. excluded	1.18 ± 0.23	0.18 ± 0.10	10.18 ± 2.71	17.18 ± 4.66
Non-overseeded x insects allowed	0.75 ± 0.52	0.78 ± 0.78	3.63 ± 2.20	11.28 ± 6.43
Non-overseeded x insects excluded	1.25 ± 0.57	0.15 ± 0.08	4.80 ± 2.36	4.70 ± 1.32
Overseeded x insects allowed	0.85 ± 0.32	0.15 ± 0.11	8.45 ± 3.08	7.65 ± 4.43
Overseeded x insects excluded	0.73 ± 0.15	0.03 ± 0.03	3.85 ± 1.15	11.55 ± 4.21
Plant comp. allowed x insects allowed	0.40 ± 0.24	0.00 ± 0.00	2.68 ± 1.60	3.60 ± 1.62
Plant comp. allowed x insects excluded	0.35 ± 0.10	0.00 ± 0.00	3.30 ± 1.60	2.33 ± 0.71
Plant comp. excluded x insects allowed	1.25 ± 0.51	0.93 ± 0.76	10.18 ± 3.24	17.48 ± 6.59
Plant comp. excluded x insects excluded	1.53 ± 0.53	0.18 ± 0.08	6.30 ± 2.40	13.65 ± 3.68

[a]Bold faced text indicates a significant factor or interaction ($\alpha = 0.05$).

Table 6. Results of ANOVA of the cumulative seedling emergence on the last sampling date for the Canyon Ferry and Wyola sites, 1997.[abc]

	Canyon Ferry					Wyola				
Factors	P-value	Blocks				P-value	Blocks			
Block	**0.005**	Block 1	Block 2	Block 3	Block 4	0.052	Block 1	Block 2	Block 3	Block 4
	SNK grouping	B	B	A	B	SNK grouping	A	A	A	A
Plant competition exclusion	0.876					0.424				
Insect exclusion	0.435					0.383				
Block x plant competition	0.900					**0.041**				
Block x insect exclusion	0.905					0.607				
Plant competion x insect exclusion	0.367					0.684				

[a]Blocks not sharing the same capital letter below them were significantly different at the 0.05 level using a Student Neuman-Keuls (SNK) mean comparison test.

[b]Data were normalized using a square root transformation.

[c]Bold faced text indicates a significant P-value.

Table 7. Results of ANOVA of the cumulative seedling emergence on the last sampling date for the Canyon Ferry and Wyola sites, 1998.[abc]

	Canyon Ferry					Wyola				
Factors	P-value	Blocks				P-value	Blocks			
Block	**0.029**	Block 1	Block 2	Block 3	Block 4	0.498	Block 1	Block 2	Block 3	Block 4
	SNK grouping	B	B	A	B	SNK grouping	A		A	A
Overseeding	0.299					0.459				
Plant competition	**0.021**					**0.041**				
Insect exclusion	0.943					0.929				
Block x overseeding	0.940					0.937				
Block x plant competition	0.705					0.434				
Block x insect exclusion	0.875					0.777				
Overseeding x plant competition	0.228					0.992				
Overseeding x insect exclusion	0.246					0.728				
Plant competition x insect exclusion	0.425					0.652				

[a]Blocks not sharing the same capital letter below them were significantly different at the 0.05 level using a Student Neuman-Keuls (SNK) mean comparison test.

[b]Data were normalized using a square root transformation.

[c]Bold faced text indicates a significant P-value

seedling counts, and no influence on final cumulative seedling counts. However, the minimal impact from *B. pulicarius* likely resulted from the extremely low population levels of the beetles present at both sites, even following supplemental releases of the beetle at the sites. Neither site averaged even 1 beetle per sweep in 1998, and peak beetle catches were obtained following supplemental beetle releases at both sites.

Notwithstanding the low *B. pulicarius* populations at the 2 research sites, other studies have documented the relatively negligible effects of herbivory from insects on the reproductive tissues of microsite-limited plants (Crawley 1989, Crawley and Gillman 1989, Eriksson and Ehrlen 1991, Paynter et al. 1996).

Based on the results obtained in this study we conclude that seedling recruitment in Dalmatian toadflax is more commonly limited by interspecific competition for microsites, than by seed availability, which in view of the plant's life history seems plausible. The potential of Dalmatian toadflax for producing large numbers of small seeds, coupled with its vegetative mode of reproduction would seem to limit the importance of individual seedling recruitment in maintaining an established population (Robocker 1970, 1974). The large quantities of seed that the plant produces may also enable the plant to compensate for pre- and post- dispersal seed predation.

Accepting this conclusion means that limiting seed in existing patches of Dalmatian toadflax through the attack of reproductive structures is unlikely to result in a reduction of stand density. Similar conclusions have been reached for tansy ragwort by Crawley and Nachapong (1985) and Crawley and Gillman (1989). Successful management of Dalmatian toadflax will most likely depend on limiting adult stem and lateral root-bud production. This could be accomplished through the establishment of natural enemies that feed on stem or root structures of Dalmatian toadflax, selective herbicide application timed to affect only Dalmatian toadflax stems or over-wintering rosettes, and the encouragement of healthy, desirable plant populations that provide strong competition for resources. Selective herbicides applied at a responsible rate and during appropriate times in the plant and natural enemies' life cycles could potentially augment the effectiveness of biological control. Grazing, in concert with other management strategies, has been shown to have a significant impact on the stand densities of leafy spurge and spotted knapweed (Lacey and Sheley 1996, Lym et al. 1997, Maxwell et al. 1992). Hence, it is conceivable that grazing and cultural control strategies could play an important role in the management of Dalmatian toadflax. In conclusion we believe that the integration of weed management strategies mentioned above, along with the maintenance of a healthy plant community, will likely provide the greatest opportunities for the sustainable management of this troublesome weed in the future.

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The relationship between climate and Rothrock sagebrush colonization patterns

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Abstract

In montane meadows of the southern Sierra Nevada mountains (Calif., USA), Rothrock sagebrush (*Artemisia rothrockii* G.) has expanded into sites once dominated by herbaceous species. We explored the relationship between climate and shrub establishment by estimating Rothrock sagebrush age distributions from growth rings. We compared these age distributions with annual records of spring snowpack and summer precipitation across 4 vegetation types that differed in water table depth, soil moisture, and vegetation cover. In the 2 vegetation types where the water table is consistently deeper than 1 m, Rothrock sagebrush stands were up to 40 years old and had relatively even age structures that showed no strong relationship to climate. In the 2 vegetation types with a shallow water table – but with contrasting soil moisture and herbaceous cover – the majority of shrubs colonized synchronously between 1984 and 1994, a relatively dry period that followed the wet 1982 to 1983 El Niño. These and other published data suggest that initial shrub colonization of new sites is facilitated by wet years, which may increase seed production, germination, and seedling survival. However, once sagebrush stands are established and local seed supply is abundant, its continued recruitment seems independent of climate.

Key Words: *Artemisia rothrockii*, shrub invasion, montane meadows, seedling establishment, Sierra Nevada, Golden Trout Wilderness, demography

Resumen

En las praderas montanas del sur de las montañas Sierra Nevada (California, E.U.A) el "Rothrock sagebrush" (*Artemisia rothrockii* G.) se ha expandido a sitios una vez dominados por especies herbáceas. Exploramos la relación entre el clima y el establecimiento de arbustos mediante la estimación de la distribución de edades del "Rothrock sagebrush" a partir de los anillos de crecimiento. Comparamos estas distribuciones de edad con los registros anuales de acumulación de nieve y precipitación de verano a lo largo de 4 tipos de vegetación que diferían en la profundidad del manto fréatico, humedad del suelo y cobertura vegetal. En los 2 tipos de vegetación en los cuales la profundidad del manto fréatico es consistentemente mayor de 1 m, la población de "Rothrock sagebrush"fue hasta de 40 años de edad, y tenía un estructura de edades relativamente uniforme que no mostró una fuerte relación con el clima. En los 2 tipos de vegetación con manto fréatico poco profundo, pero con humedad del suelo y cobertura vegetal contrastantes, la mayoría de los arbustos colonizó el área sincrónicamente entre 1984 y 1994, un periodo relativamente seco seguido por un periodo húmedo del Niño, que fue de 1982 a 1983. Estos y otros datos publicados, sugieren que la colonización inicial de arbustos en nuevos sitios es facilitada por los años húmedos, lo cual puede incrementar la producción de semilla, la germinación y la sobreviviencia de las plántulas. Sin embargo, una vez que las poblaciones de "Sagebrush"están establecidas y el suministro local de semilla es abundante, el establecimiento de nuevas plántulas parece ser independiente del clima.

Grassland ecosystems throughout the world have experienced shrub encroachment across a wide range of environments (West 1983, Archer 1989, 1995, Vavra et al. 1994, Arnalds and Archer 1999, Van Auken 2000, Roques et al. 2001). Like other semi-arid rangelands of the western United States, large montane meadows (up to ~10 km long) of the southern Sierra Nevada Mountains, Calif. exhibit shrub expansion. In this region, repeat photographs, anecdotal accounts, and pollen data suggest that Rothrock sagebrush (*Artemisia rothrockii* G.), was historically restricted to the dry meadow fringes, and began invading herbaceous meadows after intensive livestock grazing beginning in the mid 1800's (Ratliff 1985, Odion et al. 1988, Menke et al. 1996, Dull 1999). Though cattle continue to graze some meadows in the Sierra Nevada, their numbers are under tighter regulation by the United States Forest Service (USFS), and stocking rates are up to 2 orders of magnitude less today than 100 years ago (Del Hubbs, USFS, personal communication).

Rothrock sagebrush expansion has been attributed to increases in meadow aridity. Grazing and trampling along the stream banks cause channel incision and are associated with the lowering of the water table in adjacent meadows (Platts 1979, Odion et al. 1988, Schoenherr 1995, Knapp and Matthews 1996, Kirchner et al. 1998). Consistent with the notion that sagebrush expansion is a response to increased site aridity, sagebrush is predictably abundant on 'abandoned' meadow terraces in our study sites, along incised stream channels where the water table is deeper than 1 meter (Benedict 1983, Sarr 1995, Berlow et al. in press). However, sagebrush also occurs in moist herbaceous meadows on

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low terraces, where the spring water table is shallow (0.2 to 0.6 m). A lower water table and increased site aridity do not fully explain all the patterns of sagebrush distribution (Berlow et al. in press).

Changes in fire regimes have also been proposed to explain shrub expansion in grassland ecosystems (Milchunas and Lauenroth 1993, Vavra et al. 1994, Van Auken and Bush 1997). However, there is strong evidence that fires in this region were not frequent enough to be an important source of mortality for sagebrush in these montane meadows (Wood 1975, Dull 1999). Others suggest that effects of livestock and stream incision are confounded by significant regional warming in the Sierra Nevada since the end of the 'little ice age' (about 1900), which may have facilitated shrub expansion independent of grazing (Scuderi 1993, Millar and Woolfenden 1999).

Here, our objective is to examine the relationship between climate and Rothrock sagebrush establishment by comparing the age distributions of shrubs to annual variation in precipitation, over the past ~40 years. By comparing the relationship between annual climate and shrub recruitment across 4 contrasting microhabitats we were able to address the following questions:

1) Did Rothrock sagebrush colonize different microhabitats synchronously in response to annual variation in regional climate?

2) Are Rothrock sagebrush establishment events associated with drier (or wetter) than average years, and does this relationship vary spatially among different habitat types?

Materials and Methods

Site Selection

This study was conducted in the Golden Trout Wilderness, located on the Kern Plateau of the southern Sierra Nevada Mountains, Calif., USA (36° N, 118° W). In a series of open basins along the South Fork Kern River and its tributaries, the largest meadows of the entire range (up to 30 km^2) are found at elevations between 2,500 m to 3,000 m. Despite a history of grazing in this area since the late 1800's, the meadow vegetation is almost entirely native. The only common exotic, dandelions (*Taraxicum officinale* G.H. Weber ex Wiggers), comprises less than 0.1% cover in all the vegetation types included in this study (Berlow et al. in press).

These meadows are moist but occur within a semiarid landscape where annual precipitation is about 500 mm (Albert 1982, Odion et al. 1988). They are snow-covered in the winter and snowmelt is the most important source of water for the meadow vegetation. Fluvial processes, including stream channel incision, have created distinct meadow terraces where water table depth increases with vertical distance from the active stream channel. Channel incision has left 'abandoned' meadow terraces that are sometimes more than 2 meters above the level of the stream (Bryant and Nelson 2000).

Data Collection

We collected Rothrock sagebrush stems from Mulkey and Ramshaw meadows (2,806 and 2,597 m elevation, respectively) during 1997 and 1998. Each meadow is about 8 to 10 km long. Rothrock sagebrush occurs in extensive stands on high terraces where the water table is consistently deeper than 1 m. The shrub is patchily distributed on lower terraces, where the early summer water table is 0.2 to 0.6 m deep (Berlow et al. in press). Within these 2 distinct water table regimes, Rothrock sagebrush may be found with an herbaceous understory and fine-textured soil, or with bare, coarse-textured soil and a sparse understory in the inter-shrub spaces (Table 1). We sampled shrubs in 4 vegetation types, hereafter referred to as 'low-terrace Sage-Herb' (low terrace sagebrush with an herbaceous understory), 'low-terrace Sage' (low terrace sagebrush with abundant exposed soil), and 'high-terrace Sage-Herb' (high terrace sagebrush, herbaceous understory), and 'high-terrace Sage' (high terrace sagebrush, exposed soil). Low-terrace Sage, low-terrace Sage-Herb, and high-terrace Sage sites were located in Mulkey Meadow; high-terrace Sage-Herb areas

Table 1. Biotic and abiotic characteristics of the Rothrock sagebrush vegetation types sampled for shrub age distributions (1998–2000).

Vegetation	Meadow	Water Table Depth	Soil Type[1]	Soil Water Content	Total Herb Cover	5 Most Common Herbs[3]
		(m)		(m^{3}m^{-3})[2]	(%)	
High-Terrace Sage-Herb	Ramshaw	>1	Mollisols (Cumulic Haplocryolls)	6-18	35-40	*Carex* spp. *Koeleria macrantha L. Schultes* *Muhlenbergia richardsoni* *Potentilla* spp. *Poa Secunda* ssp. *juncifolia*
High-Terrace Sage	Mulkey	>1	Mollilsols (Cumulic and Pachic Haplocryolls)	4-9	15-20	*Eriogonum umbellatum* *Juncus balticus* *Lupinus* spp. *Muhlenbergia richardsonis* *Poa secunda* ssp. *juncifolia*
Low-Terrace Sage-Herb	Mulkey	0.2-0.6	Mollisols (Aquic Haplocryolls and Typic Cryoaqualls)	15-30	70-80	*Poa secunda* ssp. *juncifolia* *Muhlengergia richardsonis* *Carex* spp. *Eleocharis* spp. *Erigeron Peregrinus*
Low-Terrace Sage	Mulkey	0.2-0.6	Entisols (Oxyaquatic Cryofluvents)	4-9	20-25	*Eriogonum umbellatum* *Muhlengergia richardsonis* *Ivesia capestris* *Poa secunda* ssp. *juncifolia* *Antennaria* spp.

[1] From Bryant and Nelson (2000).
[2] 0 to 30 cm depth measured in mid-summer using Time Domain Reflectometry (TDR) probes.
[3] Listed in order of abundance, based on % canopy cover estimated using 0.5 x 0.5 m point-intercept quadrats during peak flowering. (Berlow et al., unpublished data).

were in Ramshaw meadow. The study area of Ramshaw meadow has been closed to exclude livestock grazing since 1983 (Knapp et al. 1998).

We sampled from each vegetation type at 5, 50 m^2 sites separated by at least 50 m. For each site we selected 25 individuals at random points along a 10 m transect. Since accurate age determination requires that the stem be woody, we did not sample young seedlings (less than ~2 yrs. old) that had not developed a woody stem. In each plot, we also selectively collected at least 1 of the largest individuals to estimate the age of the oldest plants. A total of 502 individuals were sampled. Each plant was excavated from the soil with hand tools and cut at the stem, as close to the roots as possible.

In the laboratory, we followed the techniques suggested by Ferguson (1964) to count growth rings of sagebrush stems. Each stem was cut at its widest point, sanded, and moistened with water to enhance contrasts between the early wood and late wood cells within each ring. Using a dissecting lamp, we counted growth rings of each stem twice along the most visible radius. To acquire data about growth rates, we measured the radius of each stem, using the same axis of rings from which we had determined its age. The centers of sagebrush stems disintegrate as plants age, complicating the counting of growth rings. However, this prevented us from counting rings in less than 1% of the stems we sampled, and primarily in individuals 20 years and older.

In Mulkey and Ramshaw meadows, we also surveyed the entire sagebrush population in each sampling site to estimate its size structure. We divided the population into 4 groups based on appearance and size: small (< 10 cm), medium (10 to 20 cm), large (> 20 cm), and dead. This census allowed us to assess whether there was systematic variation among vegetation types in the proportion of very young (< 2 yrs) and dead individuals, which were necessarily excluded from the ring counting.

We examined annual variation in spring snowpack and summer rains using data gathered by the California Department of Water Resources (CDWR) for over 40 years. The CDWR has recorded the water content of snowpack (cm) at Ramshaw meadow monthly since 1958 (except from 1959 to 1968, and from 1971 to 1972). Peak snowmelt in these meadows occurs between April and early June, with large variations from year to year. We used May snowpack, the last month for which data are reported each year by CDWR, as an indicator of spring and summer water availability. Mulkey Meadow is approximately 200 m higher in elevation than Ramshaw, and is likely to have a later snowmelt date (E. Berlow, personal observation). However, field observations also suggest that Mulkey and Ramshaw show similar annual trends in relative water availability. Thus, this snowpack data are a good relative indicator of annual variation in water availability for the region, rather than an absolute measure of water availability in a given year. For each year that data were available, the May snow water content was standardized relative to the mean of this period (1958 to 1997). In addition to the CDWR data, daily precipitation has been recorded at the USFS weather station in Cottonwood Basin (adjacent to Mulkey and Ramshaw meadows) since 1987. For each year between 1987 and 1997, we calculated the total

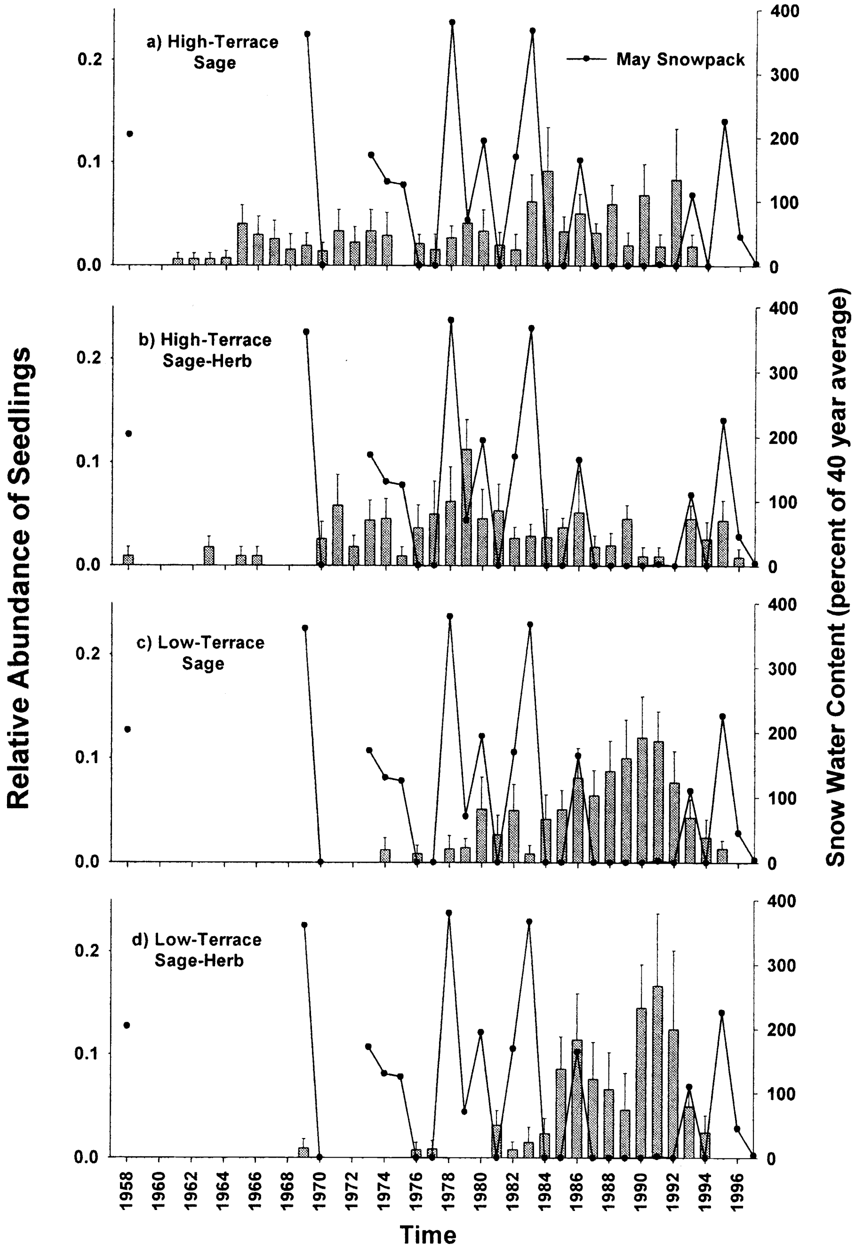

Fig. 1. Relationship between annual recruitment of Rothrock sagebrush seedlings (estimated by counting growth rings) and water content of May snowpack for 4 habitat types. Bar data are relative seedling abundance (the mean + s.e. of 5 sampling sites). The line represents the May snowpack water content (cm) expressed as a percent of the mean snowpack recorded between 1958-1997.

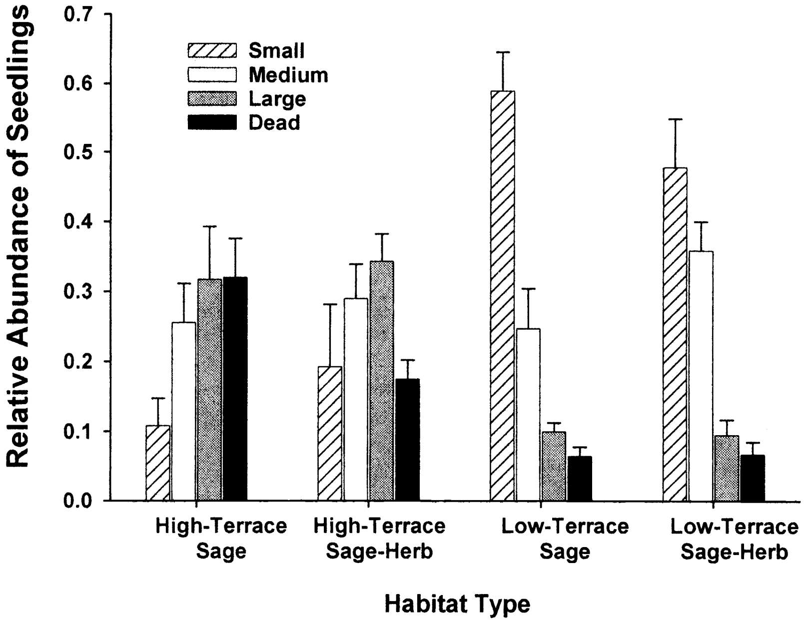

Fig. 2. Size structure of Rothrock sagebrush in 4 vegetation types. Data are the mean (± s.e.) of 5 sampling sites. Size classes are based on the maximum of either height or canopy diameter (whichever was greatest): 'small' (< 10 cm), 'medium' (10-20 cm), and 'large' (> 20 cm).

days of rain and total amount of precipitation over the growing season (1 June to 31 August).

Data Analysis

We used the Pearson Chi-Square to test whether the frequency distribution of shrub ages differed among the 4 vegetation types. Establishment date was the categorical predictor variable and the total counts of individuals established that year served as the response variable. The age distributions differed significantly among all 4 vegetation types ($p < 0.0001$). Therefore, we used separate analyses to test for overall differences between the 2 terrace types ('high-terrace' vs. 'low-terrace'), and to test for differences between 2 vegetation types ('Sage' vs. 'Sage-Herb') within terraces.

We used a 2-way factorial Analysis of Variance (ANOVA) to test for differences among vegetation types in the proportion of dead individuals, and proportions of individuals in each size class ('small', 'medium', and 'large'). The factors for this analysis were 'Terrace' (high vs. low) and 'Vegetation Type' ('Sage' vs. 'Sage-Herb'). Separate ANOVA's were used for each category of plants. Since data were proportions, all data were arcsine square root transformed prior to analysis, which greatly improved variance homogeneity and normality.

We calculated shrub growth rates as the slope of the relationship between age (years) and stem radius (mm). To test for differences in shrub growth rates across 4 vegetation types, we used an Analysis of Covariance (ANCOVA), with stem radius as the response variable, 'Habitat Type' as the categorical predictor variable, and 'Age' as the covariate. Since the interaction of 'Habitat Type' x 'Age' was significant ($p = 0.001$), we used F-protected pairwise comparisons to evaluate differences among habitat types (SAS Institute Inc. 1988).

Results

In both low-terrace vegetation types, less than 50% of the individuals sampled were over 10 yrs. old (Fig. 1). The age distributions of these 2 low-terrace vegetation types were not significantly different, though there was a trend towards a greater number of older individuals in the low-terrace Sage ($p = 0.13$). Most of the low-terrace individuals we sampled colonized between 1984 and 1994 – a relatively dry period that followed the wet 1982 to 1983 El Niño (74 and 85% for low-terrace Sage and low-terrace Sage-Herb, respectively). So, Rothrock sagebrush appears to have only recently colonized the low meadow terraces that we sampled.

The age distributions of the 2 high-terrace vegetation types were significantly different than the low-terrace types ($p < 0.0001$). Compared to the low-terraces, individuals of sagebrush in both high-terrace vegetation types were older and recruited steadily over time (Fig. 1). Recruitment in these terraces appeared independent of annual variations in snowpack. Within high-terraces, the age distributions of sagebrush in the Sage and Sage-Herb vegetation types were significantly different ($p = 0.005$). This difference seems due to: a) early recruitment in the high-terrace Sage in the mid-1960s, b) greater recruitment in high-terrace Sage during the dry period between 1984 and 1992, c) greater recruitment in high-terrace Sage-Herb between 1977 and 1979 (which included the deepest May snowpack on record), and d) greater recruitment in the high-terrace Sage-Herb following the wet winter of 1995 (Fig. 1).

In our general survey of shrub size classes, the relative abundances of small, medium, and large individuals were similar between the low-terrace vegetation types ($p > 0.15$), a pattern consistent with age distribution data (Fig. 1). Small sagebrush seedlings (< 10 cm) were significantly more abundant ($p < 0.001$) in both low-terrace vegetation types than in high-terrace ones (Fig. 2). Large (> 20 cm) and dead shrubs were significantly more abun-

Table 2. Rothrock sagebrush stem growth rates in 4 vegetation types.

Vegetation Type	Growth Rate	R^2	p	Maximum Age/Radius
	(mm • yr^{-1})			(yr • mm^{-1})
High-Terrace Sage-Herb	(0.059 b	0.83	0.001	40/2.8
High-Terrace Sage	0.046 c	0.85	0.001	34/1.9
Low-Terrace Sage-Herb	0.069 a	0.89	0.001	29/1.8
Low-Terrace Sage	0.062 b	0.83	0.001	27/2.4

[1] Estimated from the slope of the linear regression of stem radius (mm) and shrub age (years).

Habitat types with different letters have significantly different slopes ($p < 0.05$ for F-protected pairwise contrasts).

dant in the high-terrace vegetation types ($p < 0.001$). Rothrock sagebrush stem growth rates differed significantly among the 4 vegetation types (Table 2). Compared with high terraces, stem growth was 25% faster in low-terraces. Within each terrace type, growth rates were higher where an herbaceous understory was present, particularly in the high terrace sites.

There were less than 6 total days of rain, on average, during the summer growing seasons between 1987 and 1997. Most of this precipitation comes in the form of brief thundershowers. The mean total summer precipitation during this period was less than 1 mm. Total summer precipitation never exceeded 3 mm, suggesting that it is unlikely to be an important source of water in this system. Our analyses showed no clear relationship between Rothrock sagebrush recruitment and summer precipitation in any of the vegetation types.

Discussion

We did not observe a consistent or region-wide response of Rothrock sagebrush establishment to climatic variation. However, spatial variation in shrub colonization patterns suggests some conditions under which recruitment is sensitive to annual climatic variation. The almost synchronous colonization by Rothrock sagebrush of 2 distinct low-terrace vegetation types from 1984 to 1994 suggests that patch establishment was driven by external climatic factors. One might hypothesize that low-terrace Sage and Sage-Herb types represent different stages in the aridification of formerly moist, herb-dominated sites (e.g., Schlesinger et al. 1990, Vavra et al. 1994). Or these vegetation types might represent different stages in the colonization of gravel bars deposited by the stream. However, our data show that Rothrock sagebrush independently colonized these sites with a priori differences in surface soil conditions. In comparison, Rothrock sagebrush on high meadow terraces were older. Recruitment over the past 20 years in these areas was more steady and appeared to be less related to climate than recruitment in the low-terrace sites (Fig. 1). Together, these patterns suggest that the initial invasion of sagebrush may be related to climate, but once a stand is established, its continued recruitment is independent of climate.

It is unclear from these data alone if the recent colonization of low terrace sites occurred in response to the wet 1982–83 El Niño or to a subsequent string of dry years (1984 to 1994). While shrub expansion in montane meadows is commonly attributed to an increase in meadow aridity (e.g., Schoenherr 1995), other evidence suggests that it may have been the wet conditions that facilitated colonization of new sites. Studies of shrub expansion in other systems have shown that shrub colonization is sometimes associated with periods of increased water availability, even though these species may ultimately be associated with aridification of these habitats (Brown and Archer 1987, 1999, O'Connor 1995, Brown et al. 1997). In a germination experiment conducted in Mulkey meadow (Berlow et al., in press), Rothrock sagebrush had extremely low germination in xeric microhabitats (mean germination percentage was <0.05%), as well as slow growth and low survival rates. The highest observed rates of germination and seedling growth were in moist meadow microhabitats (Berlow et al., in press). While wet years may also suppress colonization by increasing competition from established herbaceous vegetation (e.g., Harrington 1991), seedling emergence, growth, and survival were consistently high in disturbed micro-sites, which are frequently created by burrowing mammals (Berlow et al., in press). Naturally occurring seedlings in moist meadow areas are almost always associated with gopher mounds (Berlow et al., in press).

Whether shrubs are able to colonize these disturbances in moist areas may depend critically on seed supply. While individual plants can produce over 5,000 seeds, maximum observed germination rates in the field were < 1% (Berlow et al. in press). Studies of other *Artemisia* species suggest that most seeds fall within one meter of the shrub (Friedman and Orshan 1975, Wambolt et al. 1989). In our study system, sagebrush seedling density decreased significantly beyond 0.5 m from reproductive shrubs (Berlow et al., in press). Sagebrush seed dispersal is likely limited due to reduced seed pappus and low seed release height (authors' observations). Thus, wet conditions could be important in increasing Rothrock sagebrush seed production and germination rates, which are critical for colonizing new sites given limited dispersal ability of this species. Invasion rates have been shown to increase rapidly following rare long distance establishment events (Nathan and Muller-Landau, 2000). Thus, once the initial colonists have reached reproductive maturity (after approximately 5 to 7 years), further colonization may accelerate rapidly, independent of climatic variation, due to abundant local seed supply.

The age distributions and climate data presented here are consistent with the idea that moist conditions and local seed supply are critical for shrub recruitment. The first shrubs colonized both low-terrace Sage and low-terrace Sage-Herb during or immediately following wetter than average years (e.g., 1973 to 1974 for the former, 1969 for the latter) (Fig. 1c, 1d). Similarly, distinct increases in establishment rates occurred in both areas immediately after the wet 1982 to 1983 El Niño. Furthermore, the time lags between colonization pulses were approximately 6 to 8 years – the time it takes for seedlings to reach reproductive maturity (Fig. 1c, 1d). By 1984, local seed supply may have been sufficient to promote rapid recruitment independent of climate.

There is also some evidence that, in the older high-terrace sage-herb stands, Rothrock sagebrush establishment increased during wet years. For example, 2 distinct increases in recruitment within high-terrace Sage-Herb stands (1970 and 1978) were preceded by years with a spring snowpack 300% of the average (Fig.1). However, there are insufficient climate data to rigorously evaluate the trends of establishment before 1974. After that time, recruitment in high terraces appears continuous and independent of climate. Since the high terrace stands are older and more expansive than low terrace patches, seed supply may not be limiting. Recruitment opportunities may instead depend on the death of adult individuals.

Our growth ring data suggest that the maximum shrub age was 40 years. We assessed whether the age distributions derived from our growth ring data were biased by being based entirely on living individuals. It is possible that individuals died earlier, decomposed, and were not sampled. In aerial photographs taken of Mulkey meadow in 1955 and 1974, Rothrock sagebrush were present in the high-terrace sites but not in the low-terrace sites. These patterns suggest that our age distribution data accurately represent the recent establishment of sagebrush in the low-terrace sites. The aerial photographs, the relative abundance patterns of dead individuals, as well as the size class distributions, suggest that, if anything, we under-estimated the age of the high-terrace Sage stands and under-estimated the abundance of recent recruits in the low-terrace patches (Fig. 2).

Our results are consistent with other studies that suggest it is the interaction of local factors and broader site or climatic conditions that ultimately determine the timing and patterns of shrub encroachment (e.g., Williams and Hobbs 1989, Harrington 1991, Gosz 1993, O'Connor 1995, Miller and Halpern 1998). Our data show that Rothrock sagebrush recently and rapidly colonized meadow areas where the water table is shallow. These and other data suggest that initial colonization of new areas may be facilitated by moist conditions, given a nearby seed source and exposed soil (Berlow et al, in press). In areas where sagebrush cover is already well established, sagebrush will likely continue to recruit independent of climate and grazing regime. Understanding this spatial and temporal variability in the mechanisms of shrub colonization may help land managers identify critical times or places where they might intervene to manage shrub expansion.

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Book Reviews

Ranching, Endangered Species, and Urbanization in the Southwest. Species of Capital. By Nathan F. Sayre. 2002. University of Arizona Press, Tucson. 278 p. US$48.00 cloth. ISBN 0-8165-2158-1.

Long ago in 1975 A.D., as I was completing my B.S. at the University of Arizona, a casual encounter in the university bookstore with the second edition of *Range Management* by L. A. Stoddart and A. D. Smith compelled me to visit the office of Dr. Ervin Schmutz, then Professor of Range Management. The next day, the first of my senior year at Arizona, I enrolled in Dr. Schmutz's introductory range management course as an elective satisfactory to my College of Liberal Arts physics program. On our class field trip that semester, we visited what I saw as a well-financed ranch southwest of Tucson. Although I had not forgotten its impressive purebred Hereford and Brangus cattle, its new livestock sales ring, or its large-scale efforts to control mesquite, I had forgotten, if I had ever realized, that this was the 1970's incarnation of the Buenos Aires Ranch in the Altar Valley chronicled by Dr. Nathan F. Sayre in *Ranching, Endangered Species and Urbanization in the Southwest.* By the time the semester had ended, I had applied for admission at 3 graduate schools, including the University of Arizona's. By spring, Dr. Schmutz had offered me an assistantship involving, as I recall, *quail*, of all things, in the grasslands south of Tucson. Instead, I chose a study at Utah State University involving grazing management and cattle, which I perceived as being more interesting, and more likely to lead to greater career opportunities in research. (I should pause briefly here to allow any underfinanced grazing management researchers who might be laughing at this notion to compose themselves). With Dr. Schmutz's understanding and best wishes for success at his *alma mater*, I headed for Utah State, leaving the quail study behind, and mostly forgotten, until I read Dr. Sayre's book in the past month.

Designed as a Ph.D. dissertation, *Ranching, Endangered Species, and Urbanization in the Southwest* is, as the subtitle suggests, an historical analysis conducted within a theoretical socioeconomic framework. A theoretical discussion of *species of capital* is followed by 6 chapters detailing the pre-settlement history, post-settlement history, ecology, and climate of the Altar Valley in general, and of the Buenos Aires Ranch in particular, until purchase of the latter as a wildlife refuge in 1985. The early chapters show the historical, ecological and economic events related to ranching in the Altar Valley. Historical details are included of manmade landscape features such as Aguirre Lake and the Altar Wash. Dr. Sayre examines the historical challenges of ranching created by variability in climate and exogenous economic conditions beginning with the cattle boom of the 1880s. Chapters 7 and 8 examine the objectives, establishment and behaviors of the Buenos Aires Wildlife Refuge in the past 17 years. The closing chapter evaluates the process of establishing and managing areas such as the Buenos Aires Refuge.

Along the way, Dr. Sayre examines the ecological history of the masked bobwhite quail in southern Arizona, and its description, (although not by Dr. Sayre), as *the most famous bird in Arizona.* He discusses the possible reasons for its disappearance, its elevation to endangered status, its poor to non-existent history of reestablishment, its political utility in acquisition of the Buenos Aires Ranch as a wildlife refuge, and its role as socioeconomic capital in land and power politics. He presents a convincing analysis that southern Arizona is marginal habitat for the masked bobwhite, is at the northern extreme of its historical range, and may be too ecologically altered to provide habitat for a population in the present or future. Subtly at first, gradually less subtly, but convincingly, he implies that little evidence exists that livestock grazing *per se* is incompatible with masked bobwhites, and that misinformation and dishonesty have linked bobwhite disappearance with cattle grazing. He describes the inadequacies of sampling methods, and raises such issues as confounding, a concept of importance in grazing research. He explains the ineffectiveness of sampling masked bobwhite survival and reproduction while continuing to release birds, and convincingly questions whether reestablishment of the masked bobwhite, ostensibly the reason for establishment of the Buenos Aires Wildlife Refuge, has succeeded at all. At closing, he suggests that the objectives in establishing such refuges should be more honest, and that the endangered species concept, as a political construct, is "a narrow and distorting lens through which to view the challenges ahead."

The book's historical narrative, immersed in socioeconomic theory, is analytical and self-assured. It shows simplicity in wording, patience in presentation, a strong sense of direction, and considerable literary skill. Although the theoretical discussions show dissertation–style forcing in a few places, Dr. Sayre's attempts to integrate history and theory are mostly successful. The theoretical interpretations, though arguably simple by sociological standards, do contain socioeconomic jargon and quasi-jargon, sometimes alarmingly well disguised as colloquial words. Dr. Sayre shows disciplined consistency in the use of this jargon, but readers unfamiliar with socioeconomic jargon, even those armed with conventional dictionaries, may find the precise meanings of some of these words as elusive as masked bobwhites in the Altar Valley.

Ultimately the historical narrative, as much as the theoretical framework, gives structure and continuity to Dr. Sayer's book. His skill as a storyteller is apparent. In the first 6 chapters of *Ranching, Endangered Species, and Urbanization in the Southwest*, he shows how to begin, develop and end each chapter in ways that further his historical narrative while leaving the reader wanting more. The book reads its best when theory flavors the history rather than *vice-versa.* But throughout the book Dr. Sayre's phrasing is always sound, consistently interesting, and frequently outstanding.

The last 3 chapters deal mostly with recent and ongoing activities on the Buenos Aires Wildlife Refuge, and include lengthy discussions of secondary topics such a *signs* and *birding*. The historical narrative that carries the first two-thirds of the book cannot carry the last one-third, and the book fragments slightly in these closing chapters. A reader needn't be an ornithologist to recognize odd ducks; the disproportionately long sections on signs and birding, while analytical and relevant, seem eccentric non-sequiturs which, for continuity, might have been either abbreviated, or relegated to appendices. Here, as throughout the book, Dr. Sayre shows little desire to judge technical details of range management. He is concerned with larger matters. From a posture of analytical neutrality, he witholds emotional criticism of the Wildlife Refuge even while he skillfully unmasks it with understated, incisive analysis. Ultimately it is all very convincing, and the author escapes with his scientific objectivity intact.

The closing discussion on enhancing the future of the Altar Valley seems abbreviated. Like an experienced consultant, Dr. Sayre closes wisely, and leaves the reader with the impression that he has still more to offer to address the current situation in the Alter Valley. Had I such judgment in 1975, I might today be conducting well-supported systems research on avian endangered species, and probably wouldn't be looking at snow tires.

Last week I decided to test the assertion (again, not by Dr. Sayre) that the masked bobwhite was in fact *the most famous bird in Arizona*. In the last question of their weekly quiz, I asked the 65 students in my introductory natural resources class at Washington State University to name the bird that they think of when they think of Arizona. Nearly 20 birds received votes. Although no student listed the masked bobwhite by name, one did write *quail*. In Natural Resources Sciences 100, the most famous bird in Arizona was the *cardinal* (12 votes), a species best known for playing football. Running a close second (9 votes) was a bird that comes to mind if you tap twice on the horn of a *Volkswagen*. Three students listed the *phoenix*, and one showed his savvy by adding, "*even though I know it doesn't really exist.*" Sure it does pal. And if you wander the bottomlands of the Buenos Aires Wildlife Refuge among all of those *Wildlife Viewing Area* signs, you may see one sooner or later.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

The Economics of Biological Invasions. Edited by Charles Perrings, Mark Williamson, and Silvana Dalmazzone. 2000. Edward Elgar, Cheltenham, UK. 249p. US$95.00 hardbound. ISBN 1-84064-378-1.

Researchers now typically agree that there are 2 principal causes for the global diminution of biological diversity. The first cause is the loss of habitat stemming from, *inter alia*, the continuance of economic activities such as agriculture and the development of land. Habitat loss is a particularly serious problem in areas of high endemism. The second cause is the introduction of species or, put differently, the problem of biological invasions. This edited book is about the economics of biological invasions. The 12 chapters of this book are divided into 3 parts. The first part contains largely theoretical analyses of issues such as the economic factors that influence susceptibility to biological invasions, infectious diseases as invasives in human populations, and risk reduction strategies against biological invaders. The second part consists of case studies of biological invasions in regions such as Australia, South Africa, and the lakes of Africa. Finally, the solitary chapter comprising the third part of this book summarizes the key points made in the individual chapters and offers concluding comments. In the rest of this review, I shall sample selectively from these 3 parts. This should give the reader a good idea of the scholarly contributions of this book.

Chapter 3 contains a useful account of the nature of infectious diseases as invasives in human populations. This chapter's particular interest is on the manner in which a particular economy interacts with the invasive disease on a global scale. On a related note, this chapter is also interested in studying "how the invasive disease can be controlled and whether public policy is necessary to implement the control" (p. 31). The authors model the underlying epidemiological process with 2 differential equations and they then proceed to analyze the ways in which vaccination, a cure for the disease, and economic growth affect the steady state properties of this 2 equation system. The authors show that when the infectious disease is very strong, the infected and the vulnerable groups of the population eventually become extinct. On the other hand, under alternate conditions, although the disease is not entirely eliminated, "it reaches a low endemic level in the population and the susceptibles keep multiplying" (p. 53). These are useful points and they deserve to have been made. Even so, because the authors work with a very specific epidemiological model, there is some question about the robustness of their conclusions. Moreover, this chapter would have profited from an optimization-based analysis of alternate disease control mechanisms.

The purpose of Chapter 4 is to use the economic theory of endogenous risk to develop an analytical model "which frames the ecological and economic tradeoffs with undesirable invasive species" (p. 56). Specifically, this chapter makes 3 pertinent points. First, it points out that the question of the risk of unwanted invasive species is both an economic and an ecological question. Second, it notes that endogenous risk affects how we measure the benefits of risk reduction. Finally, it remarks that a higher risk of invasive species immediately increases adaptation. Although these are interesting points, the chapter's discussion of these and related points is often a little too terse. For instance, on p. 64 it is noted that mitigation "efforts create a threshold in a person's preferences for risk reduction." Why does this threshold arise? What are the implications of the existence of this threshold for the valuation of risk reduction? Unfortunately, these sorts of questions receive inadequate attention in this chapter.

Chapter 8 argues that although biologically diversity-rich areas have salient direct use, functional, and option values, it is important to recognize that they also have a supplemental existence value. To drive home this central point, the author concentrates on the case of *Maesopsis eminii*, an invasive tree species in the submontane rain forests of the east Usambara mountains of eastern Tanzania. It is first noted that logging in the east Usambara forests has provided the *Maesopsis* with a habitat. This invasive species is present in the nearby plantations and, as a result, it has easily invaded this new found habitat. The chapter then goes on to say that although there have—most likely—been functional changes in the forests as a result of *Maesopsis* invasions, "the main economic concern is that of loss of existence value due to a change in the floristic composition of the forests, with a loss of endemic species resulting from disturbance" (p. 140). So far so good but the chapter is distinctly laconic in its discussion of the ways in which one might monetize this existence value. In addition, there are sentences like the following one: "The difficulty of including environmental values in cost-benefit decisions has led to the development of a variety of techniques to monetize non-market values *in an attempt to avoid market failure*" (p. 145, emphases added). At the very least, the part of the sentence I have emphasized needs to be rephrased.

The physical and the economic effects of the introduction of the Nile perch, the Tilapiine species, the Tanganyika sardines, and the water hyacinth into African lakes and rivers are examined in the well written Chapter 10. In particular, this chapter makes 3 worthwhile points. First, it points out that although the introduction of the Nile perch has resulted in increased catches, this increase in catch has contributed to "the extinction of numerous endemic species in the target lakes—a cost which may outweigh the benefits" (p. 204). Second, we are told that in lakes with low fish diversity, introduced fish species can increase productivity and not cause much ecological damage. However, in lakes with high fish diversity, such introductions can be costly. Finally, it is noted that water weeds such as the water hyacinth have "low use value but high economic costs" (p. 205).

In conclusion let me say that although this book makes a few errors of commission and omission, it does contain some useful analysis. In particular, the book rightly tells policymakers that the "probability that any one introduced species will establish and become a pest or pathogen is very low, but the costs to society if it does can be very high" (p. 234). Further, it should not go unsaid that this book treads over territory that is largely uncharted. As such, I recommend this book to all readers who wish to learn more about the economic aspects of biological invasions.—*Amitrajeet A. Batabyal*, Rochester Institute of Technology, Rochester, New York.

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