Journal of Range Management


The Trail Boss

TABLE OF CONTENTS: VOL. 55, NO. 3, May 2002

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

INDIVIDUAL SUBSCRIPTION is by membership in the Society for Range Management.

LIBRARY or other INSTITUTIONAL SUBSCRIPTIONS on a calendar year basis are $95.00 for the United States postpaid and $112.00 for other countries, postpaid. Payment from outside the United States should be remitted in US dollars by international money order or draft on a New York bank.

BUSINESS CORRESPONDENCE, concerning subscriptions, advertising, reprints, back issues, and related matters, should be addressed to the Managing Editor, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228.

EDITORIAL CORRESPONDENCE, concerning manuscripts or other editorial matters, should be addressed to the Editor, Gary Frasier, 7820 Stag Hollow Road, Loveland, Colorado 80538. Page proofs should be returned to the Production Editor, 3059A Hwy 92, Hotchkiss, CO 81419-9548..

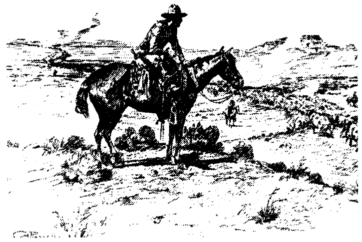
INSTRUCTIONS FOR AUTHORS appear on the inside back cover of most issues. *THE JOURNAL OF RANGE MANAGEMENT* (ISSN 0022-409X) is published bimonthly for $56.00 per year by the Society for Range Management, 445 Union Blvd., Ste 230, Lakewood, Colorado 80228. PERIODICALS POSTAGE paid at Denver, Colorado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

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

Symposium Papers

Book Reviews

PRINTED IN USA



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

The objectives for which the corporation is established are:

—*to properly take care of the basic rangeland resources of soil, plants, and water;*

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

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

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

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

—*to promote professional development of its members.*

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

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

In Cooperation With: Some of the articles appearing in *The Journal of Range Management (JRM)* are presented in cooperation with The American Forage and Grassland Council (AFGC). This cooperation consists of *JRM* acceptance of professional papers in forage grazing management and related subject areas from AFGC members and the appointment of 2 AFGC affiliated associate editors to *JRM*'s Editorial Staff. The American Forage and Grassland Council Offices: P.O. Box 94, Georgetown, Texas 78627; Larry Jeffries, President; Dana Tucker, Executive Secretary.

Contribution Policy: The Society for Range Management may accept donations of real and/or personal property subject to limitations set forth by State and Federal law. All donations shall be subject to management by the Executive Vice President as directed by the Board of Directors and their discretion in establishing and maintaining trusts, memorials, scholarships, or other types of funds. Individual endowments for designated purposes can be established according to Society policies. Gifts, bequests, legacies, devises, or donations not intended for establishing designated endowments will be deposited into the SRM Endowment Fund. Donations or requests for further information on Society policies can be directed to the Society for Range Management, Executive Vice-President, 445 Union Blvd., Suite 230, Lakewood, Colo. 80228-1259. We recommend that donors consult Tax Advisors in regard to any tax consideration that may result from any donation.

J. Range Manage.
55: 210-216 May 2002

Response of the mixed prairie to protection from grazing

WALTER D. WILLMS, JOHAN F. DORMAAR, BARRY W. ADAMS, AND HARRIET E. DOUWES

Walter D. Willms, Johan F. Dormaar, and Harriet E. Douwes are Range Ecologist, Soil Scientist (emeritus), and Range Technician, respectively, Agriculture and AgriFood Canada, PO Box 3000, Lethbridge, Alberta, Canada T1J 4B1; Barry W. Adams is Range Specialist, Alberta Agriculture, Food and Rural Development, #100, 5401 - 1ST Ave. S., Lethbridge, Alberta, Canada T1J 4V6.

Abstract

The Mixed Prairie plant communities developed with the influences of fire and grazing. Available evidence suggests that removal of these disturbances could cause succession toward a more mesic type with the accumulation of litter or loss in productivity as nutrient turnover is delayed. Exclosures constructed in 1927 in a semiarid Mixed Prairie community provided an opportunity to examine the effects that protection had on vegetation and soils. Fifteen exclosures were selected for detailed examination; of these, 11 were located on Chernozemic soil and 4 on Solonetzic soil. We measured plant and soil variables both inside and outside the exclosures in a test of the hypothesis that protection from grazing will lead to a loss of production potential of the semi-arid. Mixed Prairie communities in the Northern Great Plains of southeastern Alberta. We found little evidence that 70 years of protection from large animal disturbance reduced the production potential of the plant communities. Conversely, most evidence suggested a neutral effect or an improvement as reflected in an increased cover of *Pascopyrum smithii* Rydb. (Löve) ($P = 0.049$) and increased annual net primary production ($P = 0.047$). The effect of protection appeared largely driven by the accumulation of litter mass that primarily benefits soil and plant indices of quality on the Chernozemic soil type. Although protection tended to reduce species diversity ($P = 0.097$) among native plants on the Chernozemic soil type, evenness and richness were not affected ($P > 0.10$). The potential effect that reduced diversity might have on reducing production stability appears more than compensated for by increased litter mass.

Key Words: Soil nitrogen, soil depth, botanical composition, plant biomass, plant nitrogen

Resumen

Las comunidades de plantas de la Pradera Mixta se han desarrollado bajo la influencia del fuego y del pastoreo. Las evidencias disponibles sugieren que la remoción de estos disturbios podrían causar una sucesión hacia tipos de comunidades con más humedad disponible, con la acumulación de residuos o pérdidas en productividad debido al retraso en el reciclado de nutrientes. Parcelas aisladas en 1927 en una comunidad semiárida de Pradera Mixta brindaron la oportunidad de examinar los efectos de la protección sobre la vegetación y los suelos. Quince parcelas aisladas fueron seleccionadas para un exámen más minucioso; de éstas, once fueron localizadas en suelos Chernozémicos y cuatro en suelos Solonetzicos. Se midieron variables relacionadas con plantas y suelo, dentro y fuera de las parcelas aisladas, en una investigación experimental en que la hipótesis era que la protección contra el pastoreo llevaría a una pérdida potencial de producción en las comunidades de la zona semiárida de la Pradera Mixta en las Grandes Llanuras del Norte en el sudeste de Alberta. Se encontró poca evidencia que en setenta años de protección contra disturbios causados por grandes animales se redujera el potencial de producción de las plantas de la comunidad. Por el contrario, los resultados sugirieron que el efecto sería neutral o incluso se produciría una mejora como se reflejó en el incremento en la cobertura de *Pascopyrum smithii* Rydb. (Love) ($P = 0,049$) y un incremento en la producción primaria neta anual ($P = 0,047$). El efecto de la protección pareció en mayor medida influenciado por la acumulación de masa de cama de paja que beneficia primeramente los índices de calidad de suelo y plantas en el suelo Chernozémico. Si bien la protección tendió a reducir la diversidad de las especies ($P = 0,097$) entre las plantas nativas en el tipo de suelo Chernozémico, la uniformidad y la riqueza no fueron afectadas ($P > 0,10$). El efecto potencial que la reducción en la diversidad tendría sobre la reducción de la estabilidad productiva parece estar más que compensado por el incremento en la acumulación de residuos.

The Northern Great Plains developed under a system of periodic use by bison and occasional fire. Fire prevention has effectively eliminated the greatest disturbance that prevented litter build-up and arrested succession to more mesic conditions. Presently, the primary means of disturbance is from grazing by cattle. Without disturbance, the mesic grasslands are encroached upon by shrubs and eventually trees, while on drier sites the communities become more representative of those found in less arid conditions (Lauenroth et al. 1994) as soil moisture retention improves with litter accumulation. Grazing can enhance species diversity on grasslands but that response appears linked to the moisture regime of the site (Milchunas and Lauenroth 1993).

Since the Mixed Prairie developed under the influence of grazing by large animals, the proposition seems reasonable that grazing impact is required to maintain it (Savory 1983). Unfortunately, we have no way of ascertaining the pre-European conditions but we can assess the effects that protection from grazing has on the plant community. Protection from grazing has been recognized as a strategy to improve range condition although

The authors wish to thank Mr Allan Ross, who was manager of the Onefour substation at the time of the study, for help in facilitating the research.

Manuscript accepted 17 Aug. 01.

under specific conditions, i.e. grasslands with a long evolutionary history, low annual net primary production, and few years of grazing treatment (Milchunas and Lauenroth 1993). The construction of exclosures in 1927, within the most arid portion of the Northern Great Plains in Canada, provided an opportunity to study the effects of long-term protection from large animal impact on the ecology of the grassland in a study to test the hypothesis that protection from grazing is detrimental to the health of the Mixed Prairie community. In this study, vegetation and soil characteristics were compared between ungrazed paddocks and paddocks stocked at light to moderate stocking rates (Wroe et al. 1988). The objective was to compare the effects that protection from grazing had on soil and vegetation properties on 2 common soil types.

Materials and Methods

The study was conducted at the Agriculture and AgriFood Canada substation at Onefour in southeastern Alberta (49° 07', 110° 28') at 935 m elevation. Long-term average annual precipitation and average daily temperature was 332 mm and 4.6° C, respectively, while the long-term average precipitation and daily average temperatures for the period from April to September was 226 mm and 13.8° C, respectively. In 1996 and 1997, precipitation from April to September was 245 and 219 mm, respectively, while average daily temperatures were 13.9 and 14.4°C, respectively. While the predominant plant community is representative of the *Stipa-Bouteloua* faciation on Orthic Brown Chernozemic (Aridic Haplustoll) soil, another important type is the *Agropyron smithii* [ie *Pascopyrum smithii* Rydb. (Löve)] consocies on Brown Solodized Solonetzic (Aridic Natrustoll) soil (Coupland 1950).

In 1927, when the Onefour substation was established, at least 26, 11 x 11 m exclosures were constructed on various grassland types throughout an area of 5 x 10 km. Fencing of the current paddocks began in 1927 and all were in place by 1938 when they appear on the earliest available map of the area. A preliminary examination of the exclosures in 1995 revealed that 15 were suitable for inclusion in the study. Exclosures were eliminated from the study if the plant community in, or around them, had been compromised by invasion with crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) or were located on a knob or in a depression that created a habitat type not represented in the immediate vicinity.

A history of grazing management was not available until 1992 when records began to be kept of stocking rates in the various paddocks. However, early studies, begun in 1931 at the substation, established an acceptable stocking rate of about 0.5 AUM ha^{-1} (Smoliak and Peters 1952) but that could vary from 0.35 to 0.62 AUM ha^{-1} (Clarke et al. 1942), and 0.43 AUM ha^{-1} was considered to be "very moderate" (Clarke et al. 1947). The targeted stocking rate was 0.43 AUM ha^{-1} from 1949 to 1964 (Smoliak, Personal Communication) and was believed to be the goal since then. Later published stocking rates recommended 0.37 to 0.74 AUM ha^{-1} (Wroe et al. 1988), depending on the condition of the grassland. From 1992 to 1997 the average stocking rates ranged from 0.25 to 0.67 AUM ha^{-1} and the onset of grazing was mostly in late summer (Table 1) and completed by December. The original recommended stocking rates were designed to utilize an average of 55% of standing crop (Clarke et al. 1942) while long-term estimates of production were 388 kg ha^{-1} (Smoliak 1986) measured from 1930 to 1983.

Sampling

Soil and vegetation were sampled inside and outside each exclosure. Sampling inside the exclosure occurred in the center, either along a transect or at a central point, that were paired with equivalent samples taken 5 m outside the exclosure. The proximity of the outside transect to the exclosure ensured minimal spatial variation while avoiding a potential edge-effect produced by livestock distribution. We saw no evidence of increased animal activity, expressed by trails, fecal loading, or increased grazing pressure, immediately adjacent to the exclosures.

Soil

A soil survey was carried out in August 1993 by describing the landform and a single pedon in the center and outside of each exclosure. A physical description of soil in the Ah horizon included the depth, stoniness, color, texture, and alkalinity. Soils were sampled in July and September, 1997, for moisture and in September, 1997, for chemical analyses. The Ah (=A1) horizons were sampled in 3 subplots, spaced about 7 m apart, that were pooled giving 1 composite sample each for inside and outside the exclosure. The soils were screened (2-mm sieve) to remove the macro-organic matter, dried, and ground to pass a 0.5-mm sieve. Moisture content was determined gravimetrically. Bulk density of the Ah was estimated in September, 1998, by extract-

Table 1. Location and soils of 15 exclosures and their grazing management over 6 years from 1992 to 1997.

Field	Field size	Soil type	Grazing period (month, yr.)[1] Starting	Ending	Stocking rate[2]
	(ha)				(AUM ha^{-1})
Chernozemic					
A	1765	Orthic Brown	Aug. (1); Sept. (5)	Oct. (1); Nov. (5)	0.25
A	1765	Orthic Regosol	Aug. (1); Sept. (5)	Oct. (1); Nov. (5)	0.25
A	1765	Orthic Brown	Aug. (1); Sept. (5)	Oct. (1); Nov. (5)	0.25
A	1765	Brown Solod	Aug. (1); Sept. (5)	Oct. (1); Nov. (5)	0.25
A	1765	Orthic Brown	Aug. (1); Sept. (5)	Oct. (1); Nov. (5)	0.25
B	1330	Orthic Brown	May (2); Aug. (4)	Oct. (2); Nov. (4)	0.48
B	1330	Orthic Brown	May (2); Aug. (4)	Oct. (2); Nov. (4)	0.48
C	696	Orthic Brown	Sept. (3); Oct. (3)	Oct. (2); Nov. (4)	0.32
C	696	Orthic Brown	Sept. (3); Oct. (3)	Oct. (2); Nov. (4)	0.32
D	170	Orthic Brown	May (3); June (3)	Sept. (2); Oct. (4)	0.67
E	344	Orthic Brown	May (2); June (4)	Oct. (2); Nov. (4)	0.57
Solonetzic					
A	1765	Bn Solod. Solon.[3]	Aug. (1); Sept. (6)	Oct. (1); Nov. (5)	0.25
A	1765	Bn Solod. Solon.	Aug. (1); Sept. (6)	Oct. (1); Nov. (5)	0.25
B	1330	Bn Solod. Solon.	May (2); Aug. (4)	Oct. (2); Nov. (4)	0.48
B	1330	Bn Solod. Solon.	May (2); Aug. (4)	Oct. (2); Nov. (4)	0.48

[1]Month when grazing started or ended and the number of years (out of 6) when action was implemented.
[2]The recommended stocking rate for range in good condition is 0.61 AUM ha^{-1} (Wroe et al. 1988).
[3]Brown Solodized Solonetz.

ing undisturbed samples (15-mm dia.) to the depth of the Ah horizon. The cores were oven-dried, their mass obtained and their bulk densities calculated. Previous tests had shown that the 15-mm core diameter provided a similar estimate of bulk density as the 3-cm core providing the soil was stone-free (Unpublished data, Dormaar).

Soil pH was measured in 0.01M $CaCl_2$ (solution:soil ratio of 2:1). Total C and N were determined by dry combustion in a Carlo Erba NA 1500 Analyzer while total P was determined as per Na_2CO_3 fusion outlined by Jackson (1958). Available P (N_aHCO_3-soluble phosphorus) was determined as described by Olsen et al. (1954). Particle size distribution was determined by the hydrometer method as per Sheldrick and Wang (1993). Total C and N were calculated in tonne ha^{-1} for the depth of the surface horizon using the formula: concentration x bulk density x soil volume.

Vegetation

Herbage biomass and species cover were sampled along a single permanent, 10-m transect established both inside and outside each exclosure. Twenty, 20 x 50-cm quadrats were placed along the transect at 0.5-m intervals (beginning 0.5 m from one end) but alternately staggered on either side to increase the effective separation. Ten alternate quadrats were sampled in 1996 and the remainder in 1997. Species cover was sampled according to Daubenmire (1959) but due to time constraints, only 7 exclosures were sampled in 1996 and the remaining 8 in 1997. Estimates of foliar cover were made in alternate quadrats at each site and were aided with the use of a 100 cm^2 template that provided a standard. Standing biomass and fallen litter were harvested at ground level in all quadrats after plant cover was estimated as well as in those exclosures where cover estimates were not made. This ensured that biomass estimates were made in all exclosures in both years. Moss, lichen, and bare ground cover were estimated after the standing biomass and fallen litter had been removed. Therefore, percent bare ground represented: 100% - (% area of moss + % area of lichen + % basal area of live vegetation).

Standing biomass was partitioned into annual net primary production and standing litter by pooling the standing biomass of 10 quadrats in each experimental unit, mixing the herbage and subsampling at least 10% of the total mass. The subsampled herbage was hand-sorted into current annual production and previous years' production. The proportion of these components was applied to the pooled total to estimate annual net primary production and standing litter. Each component was dried, weighed, and ground to pass a 100-mesh screen (149 μm) in preparation for chemical analyses. A representative subsample of herbage was analyzed for total C and N concentrations by an automated dry combustion technique (Carlo Erba^{TM}, Milan, Italy).

Vegetation was sampled from 4 July to 27 July in 1996 and from 16 June to 20 July in 1997. In 1996, grazing had begun in paddocks containing 2 exclosures by the time of sampling. In those cases, the quadrats were examined and discarded if evidence of grazing in the current year was found. This resulted in 1 quadrat being deleted from the data.

Categorizing exclosures

Each exclosure was categorized into 1 of 2 types based primarily on soil and verified by an independent examination of species composition using De-trended Correspondence Analysis (Gauch 1982) to establish similarity or dissimilarity in plant communities by transect. The ordination scores were plotted in 3 dimensional "species space" and differences in community types were inferred from their eigenvalues. As a result, 11 exclosures were placed in the Chernozemic soil type and 4 in the Solonetzic soil type (Table 1).

Statistical analyses

Diversity statistics were calculated for each transect including species numbers, evenness and the Shannon index for both native species only and all species. The Shannon index (H') is defined as $-\Sigma$ [Pi x ln(Pi)] where Pi is the importance probability in element i. Richness is an estimate of the number of species present while evenness = H'/ln(Richness) (Pielou 1977). Soil and biomass indices were analyzed using mixed effects ANOVA (SAS Institute Inc. 1999) for an unbalanced design with block (n = 11 or 4) as the random variable nested in soil type (n = 2) as a fixed effect with grazing treatment (n = 2). Year was also included as a fixed effect in an analysis of biomass components. Where necessary, paired means were compared with single degree of freedom contrasts. Foliar cover of selected species, and species indices, were analyzed as a randomized complete block design for each soil type across sampling years. Pooling across years was justified because the grazing effect was blocked by each exclosure and the treatment effect could be considered stabilized after 70 years. Plant cover was first normalized by the arcsine square root transformation (Steel and Torrie 1980) before analysis.

Species richness, evenness, and diversity were related to site physical and chemical characteristics (total phosphorus, available phosphorus, percent clay, percent sand, depth of Ah horizon, soil bulk density, soil carbon concentration, soil nitrogen concentration, bare ground, surface litter mass, and percent cover of *Selaginella densa* Rydb) with stepwise regression analyses (SAS Institute Inc. 1999) where the probability of any variable needed for inclusion was less than 0.15. The analyses were made separately for both grazed and protected areas but across soil type.

Results

The effect of protection from grazing on annual net primary production, standing litter, and standing crop was dependent on soil type (Table 2). Protection resulted in greater herbage yields ($P < 0.05$) on the Chernozemic soil type but had no effect ($P > 0.10$) on the Solonetzic soil type. Standing crop across all soil types averaged 160 and 130 g m^{-2} in 1996 and 1997, respectively (Data not shown). The effect of protection on standing crop was different between years ($P = 0.023$). In 1996 and 1997 the protected treatment yielded 175 and 141% of the grazed treatment, respectively (Data not shown).

The response of annual net primary production and standing litter to grazing were affected by soil type ($P = 0.056$ and 0.045, respectively). Although the trends in relation to grazing were the same on each type, the magnitude of response was less on the Solonetzic soil type than on the Chernozemic soil type (Table 2).

Nitrogen concentration in plant tissue of annual net primary production and standing litter was not affected by protection ($P > 0.10$) but it was greater ($P < 0.001$) in 1997 than in 1996. The standing crop was sampled 1 to 2 weeks earlier in 1997 than in 1996 that might have resulted in less senescent herbage having a greater nitro-

Table 2. Herbage biomass after 70 years of protection from livestock grazing in Mixed Prairie plant communities on Chernozemic and Solonetzic soils.

Factors	ANPP[1]	Standing litter	Fallen litter	Standing crop[2]
	(g m^{-2})			
Chernozemic (n = 11)				
Grazed	92 a	28 a	67 a	120 a
Ungrazed	129 b	94 b	184 b	223 b
Solonetzic (n=4)				
Grazed	78 a	26 a	72 a	104 a
Ungrazed	79 a	53 a	133 a	132 a
	Probabilities			
Soil	0.033	0.028	0.471	0.028
Graze	0.047	<0.001	0.005	0.002
Soil x Graze	0.056	0.045	0.301	0.044
Year	0.399	0.001	0.877	0.002
Soil x Year	0.579	0.918	0.161	0.666
Graze x Year	0.064	0.120	0.534	0.023
Soil x Graze x Year	0.533	0.919	0.915	0.744

[1]Annual net primary production.
[2]ANPP + standing litter.
[a,b]Means with the same letter within subset of columns are not significantly different (P > 0.05) as tested by single degree of freedom contrasts.

gen concentration. The net effect of nitrogen concentration and standing crop biomass resulted in greater (P = 0.002) nitrogen mass on protected than on grazed sites (Table 3) although the effect was modified by year (P = 0.048). Nitrogen mass was marginally different between soil types (P = 0.073). In annual net primary production and standing litter, the concentration of carbon was greater on the Chernozemic soil type than on the Solonetzic soil type (P = 0.056 and 0.002, respectively). The C:N ratio of standing litter was influenced by an interaction between grazing and soil type (P = 0.041).

On the Chernozemic soil type, protection from grazing resulted in an increase in the cover of *P. smithii* (P = 0.049) and *Tragopogon dubius* Scop., and in a decrease of *Bouteloua gracilis* (H.B.K.) Lag ex Steud. (P = 0.004) and *Poa sandbergii* Vasey (P = 0.009, Table 4). Species cover differences were not detected (P > 0.10) on the Solonetzic soil type. We could not detect any grazing effect (P > 0.10) on species richness and evenness on either soil type and only diversity among native species on the Chernozemic soil type tended (P = 0.096) to decline with protection.

Species richness, evenness, or diversity were not related (P > 0.10) to any tested physical or chemical soil variable on the protected areas. On grazed areas, species richness was related to the mass of ground litter (b = 0.077, r^2=0.27, P = 0.049), concentration of available phosphorus (b = 1.03, r^2 = 0.20, P = 0.053), and percent cover of *Selaginella densa* (b = 0.046, r^2 = 0.11, P = 0.116). For the model, R^2 = 0.58 (P = 0.018). Species diversity was related to soil bulk density (b = -0.47, r^2 = 0.46, P = 0.005) and the concentration of total available phosphorus (b = -2.02, r^2 = 0.12, P = 0.096). For the model, R^2 = 0.58 (P = 0.006). Species evenness was related only to soil bulk density (b = -0.16, r^2 = 0.45, P = 0.006).

Of the soil properties measured in the Ah horizon, only soil moisture was affected (P < 0.050) by protection while only depth of Ah and bulk density were affected (P = 0.020 and < 0.001, respectively) by soil type (Table 5). The effects of protection were similar (P > 0.10) for all measured properties on each soil type.

Table 3. Carbon and nitrogen concentrations of herbage biomass, their C:N ratios, and mass of nitrogen after 70 years of protection from livestock grazing in Mixed Prairie plant communities on Chernozemic and Solonetzic soils.

Factors	ANPP[1]			Standing Litter			Standing Crop[2]
	Nitrogen	Carbon	C:N	Nitrogen	Carbon	C:N	Nitrogen
Chernozemic (n = 11)	(-mg g^{-1})			(mg g^{-1})			(mg m^{-2})
Grazed	15.0	453	31	10.3	446	44	1662
Ungrazed	15.2	455	32	9.4	450	49	2716
Solonetzic (n = 4)							
Grazed	14.7	448	31	9.3	430	47	1421
Ungrazed	15.6	449	28	10.2	431	42	1804
1996							
Grazed	13.6	449	33	9.2	434	49	1451
Ungrazed	14.2	449	32	9.8	435	45	2456
1997							
Grazed	16.4	452	28	10.4	442	43	1633
Ungrazed	16.2	455	29	9.9	446	46	2064
	Probabilities						
Soil	0.137	0.056	0.098	0.879	0.002	0.532	0.073
Graze	0.797	0.301	0.701	0.878	0.073	0.830	0.002
Soil x Graze	0.118	0.731	0.162	0.053	0.344	0.041	0.101
Year	<0.001	<0.001	0.004	0.007	<0.001	0.167	0.453
Soil x Year	0.072	0.601	0.100	0.030	0.092	0.232	0.497
Graze x Year	0.545	0.225	0.535	0.030	0.093	0.034	0.048
Soil x Graze x Year	0.558	0.502	0.342	0.143	0.185	0.351	0.903

[1]Annual net primary production.
[2]Annual net primary production plus standing litter.

Discussion

Protection from grazing after 70 years did not produce substantive effects among measured variables that would indicate deterioration of the plant or soil in 2 Mixed Prairie communities. Evidence that might be interpreted to indicate deterioration was a marginally depressed species diversity compared with grazed areas. Nevertheless, species richness was not affected by protection, suggesting that grazing did not affect the presence of a species but rather the abundance of the species; an observation that is reflected by shifts in plant cover particularly of *P. smithii, B. gracilis,* and *P. sandbergii* (Table 4).

Community changes appear to have occurred on the Chernozemic sites, since the exclosures were constructed in 1927, with a marked reduction in the composition of *B. gracilis* from about 55% in 1929 as determined by basal area (Clarke et al. 1947) to about 8 and 21% as determined by cover on protected and grazed treatments, respectively (calculated from Table 4). The high proportion of *B. gracilis* in 1929 may indicate previous heavy grazing pressure, drought, or both as these condi-

Table 4. Properties of a Mixed Prairie plant community after 70 years of protection from livestock grazing on Chernozemic and Solonetzic soils.

Factors	Chernozemic (n = 11)			Solonetzic (n = 4)		
	Grazed	Protected	Probability[1]	Grazed	Protected	Probability
Graminoids	--Foliar cover (%)--			--Foliar cover (%)--		
Pascopyrum smithii[2]	8.6	17.6	0.049	32.0	34.6	0.766
Bouteloua gracilis	25.2	9.2	0.004	6.4	0.4	0.215
Carex spp.	14.6	16.0	0.881	6.4	6.4	0.879
Koeleria macrantha	4.8	5.2	0.857	8.5	3.5	0.613
Poa sandbergii	9.1	4.4	0.009	6.9	4.0	0.196
Stipa comata	16.0	25.8	0.111	2.4	0	0.171
Forbs						
Artemisia frigida	3.7	5.7	0.941	5.9	3.8	0.804
Eurotia lanata	1.4	1.5	0.870	0.4	0.4	0.946
Tragopogon dubius	0.2	1.2	0.006	0	0.4	0.356
Other						
Selaginella densa	28.8	24.2	0.445	16.2	25.6	0.737
Lichen	4.6	5.1	0.679	8.2	16.5	0.506
Bare ground[3]	25.8	35.4	0.211	57.9	41.6	0.473
Indices	--------Index-------			--------Index-------		
Native species only						
Richness	12.0	11.5	0.681	11.2	11.5	0.791
Evenness	0.70	0.64	0.330	0.62	0.45	0.353
Diversity H'	1.73	1.53	0.096	1.48	1.11	0.393
All species						
Richness	13.1	13.4	0.820	12.0	13.0	0.267
Evenness	0.69	0.63	0.262	0.62	0.50	0.478
Diversity H'	1.77	1.60	0.186	1.51	1.28	0.569

[1]Probabilities for percent plant cover were determined on data transformed by the arcsine square root before analyses.
[2]Nomenclature follows Moss (1983).
[3]Estimated as: 100% - (% area of moss + % area of lichen + % basal area of live vegetation).

tions favor *B. gracilis* in the Mixed Prairie and disadvantage the larger C_3 grasses. Weather records prior to 1929 from Medicine Hat (49° 03', 110° 40') show a 28-year average annual precipitation of 295 mm (Unpublished data) but records of stocking rates were not available.

Grazing by large herbivores is the greatest disturbance imposed on these grasslands since fires were controlled. While the impact of protection from cattle grazing on soil enzymes and N constituents can be detected within 5 years (Dormaar et al. 1997), perhaps the most significant effects of protection are observed through litter accumulation. Litter can influence diversity by suppressing the establishment and growth of some species while favoring others. Therefore, adding straw on an arid Mixed Prairie community promoted *P. smithii* and reduced *P. sandbergii* and *S. densa* (Smoliak 1965). Protection from grazing for almost 80 years apparently caused the elimination of *B. gracilis* (Frank et al. 1995). The influence of litter is expressed through shading, conserving soil moisture, and modifying establishment potential from seed (Facelli and Pickett 1991). Nevertheless, in our study litter did not impede species richness but appeared to enhance the establishment of *T. dubius*, a biennial that depends on seedling establishment for survival.

Annual net primary production is responsive to litter biomass (Willms et al. 1993) that conserves soil moisture (Table 5). While litter mass can inhibit production in mesic associations such as the Fescue (Willms unpublished data) or Tallgrass Prairies (Weaver and Rowland 1952, Penfound 1964), there is no evidence that litter accumulation can reach masses that impair production on the more arid region of the Mixed Prairie. Schuman et al. (1999) reported similar live aboveground biomass within exclosures and lightly grazed Mixed Prairie grassland that had 2,870 and 1,650 kg ha^{-1} litter. Smoliak (1965) applied straw at rates of 11,000 kg ha^{-1} on a *Stipa-Bouteloua* community and found immediate suppression of herbage yield; but 1 year after application the treatment produced almost 200% more biomass than the control.

Nitrogen mass in the standing crop was directly related to biomass as its concentration was similar in each herbage type ($P > 0.10$). Consequently the protected site had the greatest mass of N aboveground. This suggests that N mineralization was greater in protected sites, to supply the increased demand for growth, since total N was similar on both protected and grazed sites. This might be achieved by a more mesic soil environment enhanced by the greater mass of litter. However, this proposed mechanism disagrees with the observations of Shariff et al. (1994) who report greater soil N mineralization with moderate vs no grazing on a Mixed Prairie site in North Dakota.

Table 5. Soil properties of the Ah horizon after 70 years of protection from livestock grazing in Mixed Prairie plant communities on Chernozemic and Solonetzic soils.

Factors	P_{total}	$P_{available}$	Nitrogen		Carbon		pH	Ah		Soil moisture	
								Depth	Bd[2]	July 9	Sept. 11
Chernozemic (n = 11)	(g kg^{-1})	(mg kg^{-1})	(mg g^{-1})	(t ha^{-1})[1]	(mg g^{-1})	(t ha^{-1})		(cm)	(g cm^{-3})	--(%)--	
Grazed	0.36	6.17	1.62	1.39	16.6	14.0	6.03	6.6	1.32	5.0	2.5
Ungrazed	0.37	6.21	1.78	1.52	17.3	14.7	6.05	7.1	1.19	9.2	3.5
Solonetzic (n=4)											
Grazed	0.32	5.75	1.44	0.94	13.4	8.7	6.52	3.2	2.29	7.0	4.1
Ungrazed	0.33	5.98	1.38	1.66	13.2	15.7	6.41	4.0	2.33	9.5	5.2
Effects											
Soil	0.253	0.725	0.240	0.696	0.152	0.565	0.107	0.020	<0.001	0.632	0.166
Graze	0.363	0.889	0.399	0.184	0.618	0.194	0.200	0.375	0.790	0.050	<0.001
Soil x Graze	0.884	0.920	0.095	0.344	0.460	0.290	0.090	0.825	0.636	0.576	0.886

[1]The mass is expressed for the volume defined by the depth of the Ah horizon.
[2]Bulk density.

Within a common environment the rates of litter decomposition between grazed and protected sites are expected to be comparable based on similar ($P > 0.10$) C:N ratios (Table 3, Taylor et al.1989) and composition of the most productive forage species (Table 4). However, trampling by cattle may enhance decomposition by compacting the litter and increasing its contact with the soil, thus exposing it to a potentially more humid and microbial-rich environment. Presumably the discrepancy in litter mass between grazed and protected areas was determined by the effects of trampling and differences in primary production.

As a component of the cryptogamic crust, lichen cover was expected to be greatest with protection from livestock grazing (Anderson et al. 1982) as trampling can fragment the mass. The role of lichen in the arid grassland is generally viewed as positive in stabilizing the soil, fixing nitrogen by blue-green algae, and enhancing water infiltration. However, it may impair seedling establishment (McIlvanie 1942), a function that is likely unimportant in an established community. In the present study, lichen cover did not increase significantly ($P > 0.10$) with protection (Table 4).

The effect of protection on species diversity appears to be dependent on the moisture conditions of the site with diversity decreasing on relatively mesic sites and increasing on more arid sites (Milchunas and Lauenroth 1993). According to this generalization, diversity in the present study should increase with protection, but this failed to materialize. Bai et al. (2001) also report lower diversity with protection on semiarid sites in the Northern Great Plains.

With a few exceptions, the effects of protection on plant variables produced similar trends on both Chernozemic or Solonetzic soil types although significant ($P < 0.10$) effects tended to be found only on the Chernozemic soil type. The most significant difference between the soil types was a greater response to protection of annual net primary production on the Chernozemic than the Solonetzic soil type. The cause of this effect is not clear but one might speculate on the lower production potential of the Solonetzic soil type produced by greater physical and chemical limitations of the soil that impedes root growth and reduces water availability. Also, the Solonetzic soil type does not support *S. comata*, 1 of the more productive grass species on the Chernozemic soil type that also decreases with grazing pressure. Therefore, the opportunity for impacting annual net primary production is greater on the more productive Chernozemic soil type.

Marginal differences ($P = 0.095$) in the response of soil N to grazing between the Chernozemic and Solonetzic soil types may also reflect greater forage utilization of the former by cattle. Total soil N can decrease with grazing if the N removed is not completely replaced by atmospheric inputs. Frank et al. (1995) reported greater total soil N in an exclosure in a Mixed Prairie community that had been protected from grazing for almost 80 years than on grazed areas. On shortgrass steppe, Lauenroth and Milchunas (1991) estimate that atmospheric inputs are greater than all losses, resulting in a net annual N gain. Therefore, since the productivity of Solonetzic soil is less than the Chernozemic soil, and removal through utilization might follow a similar pattern, an interaction of soil type and grazing treatment might be expected.

Conclusion

We found little evidence that 70 years of protection from large animal disturbance had any detrimental effect on plant communities or soil quality of the Chernozemic or Solonetzic soil types. Conversely, most evidence suggested a neutral or beneficial effect as reflected in soil chemistry, cover of preferred native grasses, and annual net primary production. The effect of protection appeared largely driven by the accumulation of litter mass that benefits primarily the Chernozemic soil type. Lack of effect on the Solonetzic soil type does not indicate degradation but rather a non-response due to protection.

Literature Cited

Anderson, D.C., K.T. Harper, and R.C. Holmgren. 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. J. Range Manage. 35:180–185.

Bai, Y., Z. Abouguendia, and R.E. Redmann. 2001. Relationship between plant species diversity and grassland condition. J. Range Manage. 54:177–183.

Clarke, S.E., J.A. Campbell, and J.B. Campbell. 1942. An ecological and grazing capacity study of the native grass pastures in southern Alberta, Saskatchewan, and Manitoba. Publ.738, Tech. Bull. 44, Dept. Agr., Ottawa, Ont.

Clarke, S.E., E.W. Tisdale, and N.A. Skoglund. 1947. The effects of climate and grazing practices on short-grass prairie vegetation in southern Alberta and southwestern Saskatchewan. Publ. 747, Tech. Bull. 46, Dept. Agr., Ottawa, Ont.

Coupland, R.T. 1950. Ecology of Mixed Prairie in Canada. Ecol. Mono. 20:272–315.

Daubenmire, R.F. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43–64.

Dormaar, J.F., B.W. Adams, and W.D. Willms. 1997. Impacts of rotational grazing on mixed prairie soils and vegetation. J. Range Manage. 50:647–651.

Facelli, J.M. and S.T.A. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. Bot. Rev. 57:1–32.

Frank, A.B., D.L. Tanaka, L. Hofmann, and R.F. Follet. 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. J. Range Manage. 48:470–474.

Gauch, H. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press. Cambridge, England.

Jackson, M.L. 1958. Soil chemical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Lauenroth, W.K. and D.G. Milchunas. 1991. Short-grass steppe. p. 183–226. *In:* R.T. Coupland (ed), Natural Grasslands: Introduction and Western Hemisphere. Ecosystems of the World Vol 8A, Elsevier Press, New York, N.Y..

Lauenroth, W.K., D.G. Milchunas, J.L. Dodd, R.H. Hart, R.K. Heitschmidt, and L.R Rittenhouse. 1994. Effects of grazing on ecosystems of the Great Plains, p. 69–100. *In:* Martin Vavra, William A. Laycock, and Rex D. Pieper (eds.), Ecological implications of livestock herbivory in the West. Soc. for Range Manage., Denver, Colo.

McIlvanie, S.K. 1942. Grass seedling establishment and productivity—overgrazed vs protected range soils. Ecol. 23:228-231.

Milchunas, D.G. and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Mono. 63:327–366.

Moss, E.H. 1983. Flora of Alberta. 2nd Ed., Univ. Toronto Press, Toronto, Ont.

Olsen, S.R., C.V. Cole, F.S. Watanabe, and L.A. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA, Circ. 939, U.S. Government Printing Office, Washington, D.C.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley & Sons, Toronto, Ont.

Penfound, W.T. 1964. Effects of denudation on the productivity of grassland. Ecol. 45:838–845.

Savory, A. 1983. The Savory Grazing Method or Holistic Resource Management. Rangelands 5:155-159.

SAS Institute Inc. 1999. SAS/STAT Users Guide. Version 8, SAS Institute Inc., Cary, N.C.,

Shariff, A.R., M.E. Biondini, and C.E. Grygiel. 1994. Grazing intensity effects on litter decomposition and soil nitrogen mineralization. J. Range Manage. 47:444–449.

Sheldrick, B.H. and C. Wang. 1993. Particle size distribution, p. 499-511. *In:* M.R. Carter (ed), Soil Sampling and methods of analysis. Lewis Publishers, Boca Raton, Fla.

Schuman, G.E., J.D. Reeder, J.T. Manley, R.H. Hart, and W.A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9: 65–71.

Smoliak, S. 1965. Effects of manure, straw and inorganic fertilizers on Northern Great Plains ranges. J. Range Manage. 18:11–14.

Smoliak, S. 1986. Influence of climate conditions on production of Stipa-Bouteloua prairie over a 50-year period. J. Range Manage. 39:100–103.

Smoliak, S. and H.F. Peters. 1952. Range and livestock management in the shortgrass prairie region of southern Alberta and Saskatchewan. Publ. 876. Dept. Agr., Ottawa, Ont.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and Procedures of Statisitics: A Biometrical Approach. 2nd ed., McGraw-Hill Book Co. N.Y.

Taylor, B.R., D. Parkinson, and W.F.J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. Ecol. 70:97–104.

Weaver, J.E. and N.W. Rowland. 1952. Effects of natural mulch on development, yield, and structure of native grassland. Bot. Gazette 114:1–19.

Willms W.D., S.M. McGinn, and J.F. Dormaar. 1993. Influence of litter on herbage production in the Mixed Prairie. J. Range Manage. 46:320–324.

Wroe, R.A., S. Smoliak, B.W. Adams, W.D. Willms, and M.L. Anderson. 1988. Guide to stocking rates for Alberta grasslands 1988. Alberta Forest. Lands and Wildl., Public Lands, Edmonton, Alberta.

J. Range Manage.
55: 217-221 May 2002

Establishment of silver sagebrush in the Northern Mixed Prairie

J.T. ROMO AND R.W. GRILZ

Authors are respectively Professor, Department of Plant Sciences, 51 Campus Drive, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5A8 and Habitat Professional, Ducks Unlimited Canada, 603 45th Street West, Saskatoon, SK S7L 5W5.

Abstract

Interest has been expressed in using silver sagebrush (*Artemisia cana* Pursh ssp. *cana*) in restoring the Northern Mixed Prairie in Saskatchewan. The objectives of this study were to determine the effects of seedbed manipulation treatments and autumn or spring sowing on establishment of silver sagebrush on sites previously seeded to native, perennial grasses. Seeds (achenes) were sown by broadcasting at 20 pure live seeds m^{-2}. Seedling emergence ranged from 5 to 6% of seeds sown. Most seedlings emerged in May and June; no seedlings emerged after July or in the second year after planting. Seventy-four to 84% of emerging seedlings survived the first growing season with 96 to 98% of these seedlings establishing. On upland sites, seedling emergence (1.1 seedlings m^{-2} SE ± 0.1) and establishment (0.9 seedlings m^{-2} SE ± 0.1) were similar between autumn and spring sowing and among seedbed manipulation treatments. On lowland sites, seedling emergence (1.4 seedlings m^{-2} SE+0.2) and establishment (0.8 seedlings m^{-2} SE ± 0.2) were similar between autumn and spring seeding. Density of seedlings establishing was greatest when the seedbed was tilled. Establishment of silver sagebrush appears primarily limited by low numbers of seedlings emerging, indicating very specific safe site requirements for this shrub. Drastic disturbance of the seedbed is not required to establish silver sagebrush in established stands of perennial grasses. Sowing silver sagebrush in late autumn when temperatures are consistently below 0°C or in early spring immediately after snowmelt is recommended.

Key Words: *Artemisia cana* ssp. *cana*, ecological restoration, seedling establishment, seedbed ecology

Resumen

Se ha expresado el interés de utilizar el "Silver sagebrush" (*Artemisia cana* Pursh ssp. *cana*) en restaurar la Pradera Mixta del Norte en Saskatchewan. Los objetivos de este estudio fueron determinar los efectos de tratamientos de manipulación de la cama de siembra y las siembras de otoño y primavera en el establecimiento de "Silver sagebrush" en sitios previamente sembrados con zacates perennes nativos. Las semillas (aquenios) fueron sembradas al voleo a razón de 20 Semillas Puras Viables m^{-2}. La emergencia de plántulas vario de 5 a 6% de las semillas sembradas. La mayoría de las plántulas emergieron en Mayo y Junio; no emergieron plántulas después de Julio ni en el segundo año después de la siembra. De 74 a 84% de las plántulas emergidas sobrevivieron la primer estación de crecimiento y un 96 a 98% de ellas se establecieron. En los sitios altos la emergencia de plántulas (1.1 plántulas m^{-2} ES ± 0.1) y el establecimiento (0.9 plántulas m^{-2} ES ± 0.1) fueron similares entre las siembras de otoño y primavera y entre los tratamientos de manipulación de la cama de siembra. En los sitios bajos la emergencia de plántulas (1.4 plántulas m^{-2} ES ± 0.2) y establecimiento (0.8 plántulas m^{-2} ES ± 0.2) fueron similares entre las siembras de otoño y primavera. La densidad de plántulas establecidas fue mayor cuando la cama de siembra fue labrada. El establecimiento de "Silver sagebrush"parce ser limitado principalmente por el bajo número de plántulas que emergen, indicando que este arbusto tiene requerimientos de sitio seguro muy específicos. En lugares donde se tienen establecidos zacates perennes no se requiere un disturbio drástico para establecer el "Silver sagebrush". Se recomienda sembrar el "Silver sagebrush"a fines de otoño, cuando las temperaturas están consistentemente bajo 0°C o a inicios de primavera, inmediatamente después de que la nieve se derrite.

Most Northern Mixed Prairie in Canada has been drastically disturbed since the arrival of European settlers in the late 1800s. In Saskatchewan, about 82% of native prairie has been cultivated for growing annual crops (Saskatchewan Agriculture and Food 1998). Ecological consequences of this conversion are a concern and, over the past decade, effort has been placed on restoring plant communities with native, perennial plants.

A common approach in restoration is to seed a simple mixture of native, perennial grasses to stabilize the site (Wark et al. 1995). Establishing perennial grasses enables restoration specialists to use herbicides to control unwanted early seral plants. Later, additional forb and grass species are sown to increase diversity. Interest has also been expressed in including silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*) and other shrubs in restoration because of their importance in many aspects of the structure and functioning of ecosystems (Miller 1987, Allen 1988, Call and Roundy 1991, Pyke and Archer 1991).

Silver sagebrush is common throughout the Northern Great Plains and occupies early to late successional communities on a variety of soils (Beetle 1960). In the Northern Mixed Prairie of Canada, silver sagebrush is most abundant in the *Bouteloua-Stipa* faciation, and is less abundant in *Stipa-Bouteloua, Stipa-Bouteloua-Agropyron, Bouteloua-Agropyron*, and *Stipa-Agropyron* faciations (Coupland 1950, 1961). Even though silver

Thanks are extended to Dr. Y. Bai for useful comments on an earlier version of this manuscript.
Manuscript accepted 7 Sept. 01.

sagebrush is an important component of natural plant communities of the Northern Mixed Prairie, little research has been completed on establishing this shrub. The objective of this study was to determine effects of seedbed manipulation treatments and autumn or spring sowing on establishment of silver sagebrush on sites previously seeded to native, perennial grasses.

Materials and Methods

Seed Source

Silver sagebrush seeds (achenes) were collected in mid-October 1994 and 1995 near Outlook, Saskatchewan (51°29'N, 107°03'W, elevation 518 m). The collection site, a naturally revegetated roadcut, was dominated by silver sagebrush, western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve), and needle-and-thread (*Stipa comata* Trin. & Rupr.). Inflorescences were cut from plants, placed in large paper bags, and air-dried in a laboratory at room temperature for about 5 days. Inflorescences were rubbed by hand to remove seeds, and seeds were then cleaned with a Clipper desktop thresher. Cleaned seeds were stored in paper envelopes in darkness at 5°C until used.

Seeding trials

Three lowland and 2 upland sites were selected for seeding trials in 1994–95 and 1995–96 in south-central Saskatchewan. All sites are in the Mixedgrass Prairie Ecodistrict of the Grassland Ecoregion (Harris et al. 1983), and were within 85 km of the site where the seeds were collected. Two lowland sites, South Lucky Lake and North Lucky Lake, were located on the west edge of Luck Lake Heritage Marsh about 11 km north of Lucky Lake in the Beechy Hills ecological landscape (Padbury and Acton 1994). The third lowland site was 8 km south of Clavet in the Elstow Plain landscape. Lucky Lake sites are on a lacustrine plain and the Clavet site is on a fluvial plain (Acton 1977). Lucky Lake soils are Birsay fine-sandy loam whereas Clavet soils are loamy alluvium complexes (Ellis et al. 1968b). In 1995–96, new plots were located adjacent to those seeded in 1994–95. All sites had been cultivated and annual crops produced for several years before restoration was begun. A mixture of native, perennial grasses including western wheatgrass, northern wheatgrass (*Elymus lanceolatus* [Scribn. & Smith] Gould), slender wheatgrass (*Elymus trachycaulus* [Link] Gould ex Shinners), and green needlegrass (*Nassella viridula* [Trin.] Barkworth) was seeded in 1989.

Upland sites were located in the Allan Hills and Coteau Hills ecological landscapes (Padbury and Acton 1994). They are hummocky, knob-and-kettle landscapes formed from glacial moraines; Weyburn loam soils predominate (Ellis et al. 1968a, 1968b). In 1994–95, the Allan Hills site was 27 km south of Allan and, in 1995–96, the site was 7 km further south. The Coteau Hills site was 24 km north and 41 km northwest of Lucky Lake in 1994–95 and 1995–96, respectively. Sites used for the 1994–95 trial were seeded in the spring of 1994 to the same mixture of native, perennial grasses seeded on lowland sites, and sites for the 1995–96 trial were seeded in the spring of 1995. These sites had been cultivated for annual crop production for many years before being seeded to perennial grasses.

Of the weather stations in Saskatchewan, Beechy is nearest the Lucky Lake and Coteau Hills sites, Watrous is closest to Allan Hills, and Saskatoon is nearest to Clavet. Annual temperatures within the area of study range from 1.9 to 4.7°C (Table 1). Average monthly temperatures

Table 1. Mean monthly temperatures and precipitation in 1994–1997, and normal temperatures and precipitation at Beechy, Watrous, and Saskatoon, Saskatchewan (Environment Canada 1998).

Station	Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
		Temperature (°C)											
Beechy	1994	-18	-19	0.1	6	12	16	19	18	15	7	-3	-7
	1995	-12	-8	-3	2	11	17	18	17	12	5	-8	-14
	1996	-20	-9	-8	4	9	17	19	20	11	4	-10	-17
	1997	-17	-8	-6	3	11	17	19	19	15	6	-2	-3
	Normal	-14	-4	5	5	11	16	19	18	12	5	-5	-12
Watrous	1994	-21	-20	-1	5	11	16	18	17	14	6	-4	-12
	1995	-14	-13	-6	1	11	18	18	16	12	5	-9	-15
	1996	-22	-12	-11	2	8	16	18	19	11	3	-12	-19
	1997	-21	-11	-8	2	10	17	18	18	14	4	-4	-5
	Normal	-17	-13	-6	4	11	16	18	17	11	4	-6	-14
Saskatoon	1994	-21	-21	-3	5	11	15	18	17	14	6	-5	-14
	1995	-15	-13	-6	1	10	17	17	15	12	5	-10	-17
	1996	-25	-14	-11	3	8	16	18	18	10	2	-13	-20
	1997	-21	-11	-10	2	10	17	18	18	14	4	-4	-6
	Normal	-18	-14	-7	4	11	16	19	17	11	5	-6	-15
		Precipitation (mm)											
Beechy	1994	47	9	2	8	63	65	9	40	19	41	4	3
	1995	14	3	20	19	52	50	45	84	18	29	47	21
	1996	19	7	14	20	97	93	57	21	68	14	43	41
	1997	13	5	37	21	56	75	12	47	33	38	1	1
	Normal	16	11	16	20	46	67	62	39	30	17	14	16
Watrous	1994	26	12	11	10	61	112	49	81	12	30	14	18
	1995	21	16	52	57	30	73	29	153	3	60	13	14
	1996	6	15	11	31	55	94	64	24	59	27	22	31
	1997	28	4	16	31	65	106	18	64	98	31	1	2
	Normal	17	12	17	29	51	74	68	52	43	28	14	19
Saskatoon	1994	25	11	3	8	116	54	42	64	1	19	12	10
	1995	12	13	30	34	15	33	81	85	1	35	16	22
	1996	14	12	12	30	59	101	114	18	40	6	23	17
	1997	16	5	19	36	26	53	25	50	55	21	3	5
	Normal	16	13	16	20	44	63	58	37	32	17	14	17

are below freezing from November through March, with January the coldest month. Monthly temperatures are above freezing from April through October, peaking in July. Most precipitation is received during the growing season, with 78 to 81% of total annual precipitation received from April through October (Table 1).

Seedbed manipulation treatments were selected primarily for ease of application based on consultation with vegetation management specialists of Ducks Unlimited Canada. Manipulation treatments at the lowland sites included: 1) control—undisturbed sward; 2) mowing the sward to a 15-cm height; 3) haying—mowing+removal of phytomass; 4) haying followed by application of Glyphosate at 6.75 liters ha^{-1} in the autumn after grasses had grown new leaves, and; 5) haying followed by tillage of the soil to a 10–15 cm depth with a rotovator. Seedbed manipulation treatments on uplands consisted of the above except the haying treatment was not included and Glyphosate was applied after mowing. Plots were 5 by 5 m and seedbeds were manipulated in mid- to late September 1994 or 1995. Plots on the upland sites were located on upper slopes and knoll tops, positions where silver sagebrush stands are naturally located in this landscape.

Immediately after cleaning, 12 replicates of 50 silver sagebrush seeds were placed in Petri dishes containing 1 layer of #4 Whatman filter paper moistened with distilled water. Petri dishes were enclosed in clear plastic bags and incubated for 12 days at 10°C with 12-hours darkness and 12-hours light (220 μmol m^{-2} sec^{-1}), and germinated seeds counted. Total germination averaged 96% (SE±1.3) for 1994 seeds and 80% (SE±1.6) for 1995 seeds. Ten replicates of 100 pure live seeds (PLS) seeds were counted, weighed, and seeds g^{-1} calculated. Seeds for autumn and spring sowing were weighed and placed in paper envelopes to provide 20 PLS m^{-2} for each plot. During sowing, seeds were mixed with about 100 g of 'Redi-earth' potting mix and broadcast in plots on 4 November 1994, 21 April 1995, 5 November 1995, and 6–7 April 1996. Seeds sown in the spring were stored in darkness at 5°C over the winter. Autumn seeding was done just before snow began accumulating whereas seeds were sown about 10 days after snow had melted in the spring.

Four permanent 50- by 50-cm quadrats were placed 1 m apart along a transect through the center in each plot to monitor seedling emergence and establishment. Data from the 4 quadrats were pooled (1 m^2) in each replicate for statistical analysis. During the first growing season, newly emerged seedlings in quadrats were marked with colored, chicken leg bands every 2 weeks from 1 May to 30 June, in mid-July, and in late August. Seedling survival was also recorded at each counting period. In 1995–96, seedling emergence and survival were recorded in mid-May, June, July, and August 1996. Second-year seedling establishment was determined in late August of the second growing season after planting.

In June of the first growing season after seeding, cover of litter and bare ground was estimated in each replicate of each plot using point intercept (n = 100 points per treatment replicate) (Cook and Stubbendieck 1986). In mid-August of the first growing season, vegetation was clipped to ground level in one, 50- by 50-cm quadrat in each replicate of seedbed manipulations. Phytomass was sorted into perennial grasses, annual grasses, and forbs. Litter, dead phytomass on the soil surface, was also collected. Samples were dried at 80°C for 48 hours and weighed.

Seedbed manipulation treatments and season of sowing were factorially applied in a randomized-complete-block design (Snedecor and Cochran 1980) with 4 replicates per site at lowlands and 5 replicates on uplands. Sites were treated as random effects in analysis of variance. Treatment effects on phytomass, cover of litter, bare ground, seedling emergence, seedling survival, and seedling establishment from lowland and upland sites were analyzed separately because of differences in landscapes, history of management, and seedbed manipulation treatments. Means were compared with Tukey's HSD (Snedecor and Cochran 1980). Regression analysis (Snedecor and Cochran 1980) was used to relate seedling emergence and establishment. Statistical significance was presumed at P ≤ 0.05 in all cases.

Table 2. Phytomass determined in August of the first growing season on upland and lowland sites in which seedbeds were manipulated.

Sites	Seedbed Manipulation Treatment	Plant Group: Perennial Grasses	Annual Grasses	Forbs	Total	Litter
		(g m^{-2})				
Uplands	Control	125a[1]	0.9a	24a	149a	8a
	Mowing	147a	4a	14a	164a	2a
	Glyphosate	27b	17a	16a	59b	21a
	Tillage	46b	19a	19a	85b	1a
	SE	22	4	5	17	4
Lowlands	Control	197a	0.1a	8a	206a	271a
	Mowing	169a	0.7a	13a	183a	182a
	Haying	200a	0.1a	7a	207a	88b
	Glyphosate	73b	6.0b	66b	144a	81b
	Tillage	94b	7.5b	36b	137a	22c
	SE	28	2	11	13	29

[1] Means followed by the same letter within a site and plant group are not significantly different (P > 0.05) using Tukey's HSD.

Table 3. Seedling emergence and establishment (mean ± SE) of silver sagebrush each month from autumn or spring sowing averaged over sites, years, and seedbed manipulation treatments for upland and lowland sites.

Site	Time of sowing	Month of Emergence: May	Jun.	Jul.
		Emergence (% of total seedlings)		
Upland	Autumn	36 ± 10	38 ± 6	27 ± 6
	Spring	35 ± 9	58 ± 8	5 ± 3
Lowland	Autumn	64 ± 5	33 ± 5	3 ± 1
	Spring	64 ± 8	15 ± 5	20 ± 6
		Establishment (% of seedlings emerging each month)		
Upland	Autumn	46 ± 10	84 ± 6	100 ± 0
	Spring	68 ± 3	90 ± 6	100 ± 0
Lowland	Autumn	51 ± 6	96 ± 2	100 ± 0
	Spring	89 ± 5	100 ± 0	92 ± 8

Results

Upland Sites

Application of Glyphosate and the tillage treatment reduced total phytomass and that of perennial grasses on upland sites, but mass of annual grasses, forbs, and litter was similar among seedbed manipulation treatments (Table 2). Cover of litter (33%, SE ± 2.9, P = 0.317) and bare ground (63%, SE ± 3.7, P = 0.307) was similar among seedbed manipulation treatments.

Averaged across season of sowing and seedbed manipulation treatments, seedling emergence was 5.3% (SE ± 0.7) of seeds sown. Most seedlings emerged in May and June (Table 3); no seedlings of silver sagebrush emerged after July or in the second year after planting. A trend of increasing establishment with emergence occurring at a later date was also apparent (Table 3).

Eighty-four percent of emerging seedlings survived the first growing season (Surviving seedlings m^{-2} = 0.01+0.84 X Emerged seedlings m^{-2}, $R^2 = 0.89$, $P < 0.001$). Seedlings established in the second growing season were correlated with emergence (Established seedlings m^{-2} = 0.01+ 0.82 X Emerged seedlings m^{-2}, $R^2 = 0.89$, $P < 0.001$), indicating 82% survival of emerging seedlings. Of seedlings that survived the first year, 96% survived through August of the second growing season (Established seedlings m^{-2} = 0.01+0.96 X Seedlings surviving m^{-2}, $R^2 = 0.96$, $P < 0.001$). Emergence (1.1 seedlings m^{-2}, SE ± 0.1), survival (0.9 seedlings m^{-2}, SE ± 0.1), and establishment (0.9 seedlings m^{-2}, SE ± 0.1) were similar between autumn and spring sowing and among seedbed manipulation treatments.

Lowland Sites

On lowland sites, Glyphosate and tillage reduced phytomass of perennial grasses, but that of annual grasses and forbs increased with the same treatments (Table 2). Haying, Glyphosate, and tillage reduced litter mass because plant material was removed from plots in all 3 treatments (Table 2). However, litter cover was greatest with mowing and applying Glyphosate, intermediate in control, haying, or mowing, and least with tillage (Table 4). Tillage created nearly 5-fold more bare ground than the remaining manipulation treatments (Table 4).

Seedling emergence decreased from May through July of the first growing season (Table 3) and averaged 6.4% (SE ± 0.8) of seeds sown. Establishment of later emerging seedlings was greater than earlier emerging ones (Table 3). On average, 74% of seedlings survived the first growing season (Surviving seedlings m^{-2} =0.001+0.74 X Emerged seedlings m^{-2}, R^2=0.81, $P < 0.001$) and 72% of emergent seedlings established (Established seedlings m^{-2}=0.01+0.72 X Emerged seedlings m^{-2}, R^2=0.79, $P < 0.001$). Of the seedlings that survived the first growing season, 98% established (Established seedlings m^{-2} =0.01+ 0.98 X Seedlings surviving m^{-2}, R^2=0.97, $P < 0.001$). Emergence (1.4 seedlings m^{-2}, SE ± 0.2), survival (1.0 seedlings m^{-2}, SE ± 0.1), and establishment (0.8 seedlings m^{-2}, SE ± 0.2) were similar between autumn and spring seeding. Emergence and survival during the first growing season varied among seedbed manipulations and were generally greatest in tillage and control (Table 5). Density of establishing seedlings was greatest when the seedbed was tilled.

Table 4. Cover of litter and bare ground determined in June of the first growing season on lowland sites in 5 seedbed manipulation treatments.

	Seedbed Manipulation Treatment				
Cover Category	Control	Mowing	Haying	Glyphosate	Tillage
	(%)				
Litter	69ab[1]	86b	66ab	88b	51a
Bare ground	17a	3a	8a	10a	47b

[1]Means followed by the same letter within a cover category are not significantly (P > 0.05) different using Tukey's HSD.

Discussion

As predicted from germination studies on silver sagebrush (Romo and Eddleman 1995, Romo and Young 2002), most seedlings emerged early in the growing season. This pulse in seedling emergence corresponds with the June peak in precipitation received in Northern Mixed Prairie (Table 1). Most seedlings of fringed sagebrush also emerge in May and June in the Northern Mixed Prairie (Bai and Romo 1996). Early emerging seedlings of silver sagebrush are more vigorous (Hou and Romo 1998a) and tolerant of freezing temperatures than later emerging ones (Hou and Romo 1998b). On the other hand, seedlings emerging too early in the spring may be killed by freezing temperatures or desiccation (Hou and Romo 1997, 1998b).

Emergence of shrubs with after ripening requirements (Booth and Schuman 1983, Haferkamp et al. 1990, Shaw et al. 1994) is greater from autumn than spring seeding because dormancy is broken by exposing seeds to cool, moist conditions. Silver sagebrush seeds are not dormant and emergence of seedlings was similar between autumn and spring sowing. Seedling populations were primarily limited by low emergence. Only 5 to 6% of the seeds sown produced seedlings. Less than 8% of seeds sown in southeastern Montana resulted in emergent seedlings (Eddleman 1980, Walton 1984). The fate of the remainder of the seeds sown in the present study is unknown, however, there are several explanations for limited seedling emergence.

First, seeds may have germinated, but seedlings did not emerge. Second, seeds were broadcast, thus some were likely buried at various soil depths. Emergence of silver sagebrush is greatest from about the 2- (Harvey 1981) to 5-mm depth (Walton 1984), and no seedlings emerge from depths greater than 25 mm (Walton 1984). Thirdly, if seedlings emerged, they may have perished before being counted in the spring or they may have emerged and died between seedling counts. Another possibility is that predators may have gathered or consumed seeds. The

Table 5. Effects of seedbed manipulation treatments on seedling emergence, survival, and establishment of silver sagebrush on lowland sites.

	Seedbed Manipulation Treatment				
Variable	Control	Mowing	Haying	Haying + Glyphosate	Tillage
	(Seedlings m^{-2})				
Seedling Emergence	1.9ab[1]	0.6c	1.2bc	0.7c	2.3a
Seedling Survival[2]	1.3ab	0.4b	1.0ab	0.4b	1.9a
Seedling Establishment[3]	0.8b	0.3b	0.7b	0.4b	1.7a

[1]Means followed by the same letter are not significantly (P > 0.05) different using Tukey's HSD.
[2]Survival is the density of seedlings alive in August of the first growing season.
[3]Establishment is the density of seedlings alive in August of the second growing season.

importance of predation on seeds and seedlings of silver sagebrush is not known, but ants are a significant predator on seedlings of fringed sagebrush (Bai and Romo 1996). Some seeds may have entered secondary dormancy or lost viability as they were exposed to many wetting-drying cycles and wide fluctuations in temperatures in the field. However, no evidence exists that exposing seeds to environmental conditions encountered in the field causes secondary dormancy in silver sagebrush, but seeds of silver sagebrush loose viability rapidly when exposed to field environments (Romo and Young 2002). Low emergence of seedlings is interpreted to indicate that this shrub has very specific safe site requirements. Safe sites were apparently present in all seedbeds with most being created with tillage on lowland sites. Reduced competition caused by tillage or the increased amount of bare soil likely favored establishment of silver sagebrush. Competition from grasses also reduces establishment of Wyoming big sagebrush (Schuman et al. 1998), and establishment of fringed sagebrush is greater in disturbed than undisturbed swards (Bai and Romo 1996).

Identifying criteria for gauging success of establishing plants is key to selecting, evaluating, developing, and improving restoration practices. In naturally occurring silver sagebrush stands in Saskatchewan, shrub densities range from 0.3 to about 1.0 m^{-2} (Coupland 1950,1961, Romo unpub. data), and stem densities can reach 5 m^{-2} (Hulett et al. 1966, Lawrence and Romo 1994). If these densities are used as the ecologically-based standards for judging seeding success, establishment of silver sagebrush was successful in this study for densities fell within the range encountered in natural communities. In all seedings, plants produced seeds in the fourth year of growth (J.T. Romo pers. obser.) potentially leading to more plants establishing through natural regeneration.

Silver sagebrush appears to be a useful species for restoration in the Northern Mixed Prairie. Seeds can be easily collected from wildlands, seed processing is simple, and seeds are not dormant. Drastic disturbance of the seedbed is not required to establish this shrub in stands of perennial grasses, but greater densities can be expected on tilled sites or sites disturbed by burrowing animals. Sowing silver sagebrush in autumn after temperatures are consistently below 0°C or in spring immediately after snowmelt is recommended because seedling emergence, survival, and establishment were equivocal in autumn and spring seeding.

Literature Cited

Acton, D.F. 1977. Landscapes of southern Saskatchewan. Department of Energy, Mines and Resources, Ottawa, Ont.

Allen, M. F. 1988. Belowground structure: A key to reconstructing a productive arid ecosystem, p. 113–135. *In:* E.B. Allen (ed.), The reconstruction of disturbed arid lands-An ecological approach. Westview Press, Boulder, Colo.

Bai, Y. and J.T. Romo. 1996. Fringed sagebrush response to sward disturbances: Seedling dynamics and plant growth. J. Range Manage. 49:228–233.

Beetle, A.A. 1960. A study of sagebrush: The section *Tridentatae* of *Artemisia.* Wyoming Agr. Exp. Sta. Bull. 368. Laramie, Wyo.

Booth, D.T. and G.E. Schuman. 1983. Seedbed ecology of winterfat: Fruit versus threshed seeds. J. Range Manage. 36:387–390.

Call, C.A. and B.A. Roundy. 1991. Perspectives and processes in revegetation of arid and semi-arid rangelands. J. Range Manage. 44:543–549.

Cook, C.W. and J. Stubbendieck. 1986. Range research: Basic problems and techniques. Soc. Range Manage. Jostens Pub., Broomfield, Colo.

Coupland, R.T. 1950. Ecology of Mixed Prairie in Canada. Ecol. Monogr. 20:273–315.

Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. J. Ecol. 49:135–167.

Eddleman, L.E. 1980. Coal mine reclamation with native plants, p.80-90. *In:* Proc. 1980 Symposium on Watershed Manage. Boise, Ida.

Ellis, J.G., D.F. Acton, and H.C. Moss. 1968a. The soils of the Last Mountain Lake map area. Ext. Division, Univ. Saskatchewan, Saskatoon, Sask.

Ellis, J.G., D.F. Acton, and H.C. Moss. 1968b. The soils of the Rosetown map area. Ext. Division, Univ. Saskatchewan, Saskatoon, Sask.

Environment Canada. 1998. Climate data supplied by the Saskatoon, Saskatchewan office upon special request.

Haferkamp, M.R., D.C. Ganskopp, K.L. Marietta, and B.W. Knapp. 1990. Environmental influences on germination of utricles and seedling establishment of immigrant forage kochia. J. Range Manage. 43:518–522.

Harris, W. C., A. Kabzems, A.L. Kosowan, G.A. Padbury, and J.S. Rowe. 1983. Ecological regions of Saskatchewan. Saskatchewan Parks and Renewable Resources Tech. Bull. No. 10. Regina, Sask.

Harvey, S.J. 1981. Life history and reproductive strategies in Artemisia. M.S. Thesis, Montana State Univ., Bozeman, Mont.

Hou, J.Q. and J.T. Romo. 1997. Growth and freezing tolerance of winterfat seedlings. J. Range Manage. 50:165-169.

Hou, J.Q. and J.T. Romo. 1998a. Seed weight and germination time affect growth of two shrubs. J. Range Manage. 51:699–703.

Hou, J.Q. and J.T. Romo. 1998b. Cold-hardiness of silver sagebrush seedlings. J. Range Manage. 51:704–708.

Hulett, G.K., R.T. Coupland, and R.L. Dix. 1966. The vegetation of dune sand areas within the grassland region of Saskatchewan. Can. J. Bot. 44:1307–1331.

Lawrence, D.L. and J.T. Romo. 1994. Tree and shrub communities of wooded draws near the Matador Research Station in southern Saskatchewan. Can. Field Natur. 108:397–412.

Miller, R.M. 1987. Mycorrhizae and succession, p. 205–219. *In:* W.R. Jordan III., M.E.Gilpin, and J.D. Aber (eds.), Restoration ecology-A synthetic approach to ecological research. Cambridge Univ. Press, New York, N.Y.

Padbury, G.A. and D.F. Acton. 1994. Ecoregions of Saskatchewan. Minister of Supply and Services, Ottawa, Ont.

Pyke, D.A. and S. Archer. 1991. Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland. J. Range Manage. 44: 550–557.

Romo, J.T. and L.E. Eddleman. 1995. Use of degree-days in multiple-temperature experiments. J. Range Manage. 48:410–416.

Romo, J.T. and J.A. Young. 2002. Temperature profiles and the effects of field environments on germination of silver sagebrush. Native Plants J. 3:5–13.

Saskatchewan Agriculture and Food. 1998. Agricultural statistics 1998. Saskatchewan Agr. and Food, Statistics Branch, Regina, Sask.

Schuman, G.E., D.T. Booth, and J.R. Cockrell. 1998. Cultural methods for establishing Wyoming big sagebrush on mined lands. J. Range Manage. 51:223–230.

Shaw, N.L., M.R. Haferkamp, and E.G. Hurd. 1994. Germination and establishment of spiny hopsage in response to planting date and seedbed environment. J. Range Manage. 47:165–174.

Snedecor, G.W. and W.G. Cochran. 1980. Statistical methods. Iowa State Univ. Press. Ames, Iowa.

Walton, T.P. 1984. Reproductive mechanisms of plains silver sagebrush *Artemisia cana cana* in southern Montana. M.S. Thesis, Montana State Univ., Bozeman, Mont.

Wark, D.B., W.R. Poole, R.G. Arnott, L.R. Moats, and L. Wetter. 1995. Revegetating with native grasses. Ducks Unlimited Canada, Stonewall, Man.

J. Range Manage.
55: 222-228 May 2002

Steer nutritional response to intensive-early stocking on shortgrass rangeland

KENNETH C. OLSON, JOHN R. JAEGER, JOHN R. BRETHOUR, AND THOMAS B. AVERY

Authors are former Associate Professor, former Research Assistant, and Professor, Agricultural Research Center-Hays, Kansas State Univ., 1232 240th Avenue, Hays, Kans. 67601-9228, and Professor (deceased), College of Vet. Med., Kansas State Univ., Manhattan, Kans. 66506. Olson is currently Associate Professor, Animal, Dairy, and Veterinary Sciences Dept., Utah State Univ., Logan, Utah 84322-4815. Jaeger is currently Research Assistant, Eastern Oregon Agricultural Research Center, Oregon State Univ., Union, Ore. 97883.

Abstract

Steer nutritional response to vegetation conditions created by 4 grazing treatments was evaluated during the final 2 years (1987–88) of a 9-year grazing trial. Treatments were season-long stocking (treatment 1) at a moderate stocking rate and intensive-early stocking at 3 stocking rates: equal to season-long stocking by using twice as many steers for the first half of the season-long stocking grazing season (double-stocked-intensive-early stocking, treatment 2), and 2 rates greater than season-long stocking made by stocking at 2.5 or 3 times the stocking density of season-long stocking (2.5X- and triple-stocked-intensive-early stocking, treatments 3 and 4). Each treatment was replicated twice in a randomized-complete block. Three esophageally fistulated steers were placed in each pasture to collect diet samples for nutritional analyses, including crude protein and cell wall constituents. Total feces were collected from 3 steers in each pasture to estimate fecal output and calculate forage intake. Diet digestibility was estimated using alkaline-peroxide lignin as an internal marker. Three or 4 sampling periods were conducted during each grazing season. Herbage availability and dietary crude protein were similar among treatments in 1987, but both declined as stocking density increased in 1988. Cell wall constituents generally increased as stocking density increased in 1987, but were similar among treatments in 1988. Digestibility and forage intake were unaffected by grazing treatments in both years. Steer average daily gain declined as stocking density increased in both years. Seasonal changes in diet quality and forage intake reflected the precipitation pattern with improved nutrition whenever precipitation caused growth of the warm-season shortgrasses. Nutrient intake was reduced by stocking rates greater than that employed under season-long stocking, but was generally similar between season-long stocking and double-stocked-intensive-early stocking.

Key Words: grazing systems, beef cattle, stockers, diet quality, forage intake

Resumen

La respuesta nutricional de novillos a condiciones de vegetación creadas por 4 tratamientos de pastoreo fue evaluada durante los últimos dos años (1987–88) de una prueba de pastoreo que duro 9 años. Los tratamientos fueron uno de temporada larga (SLS, por sus siglas en inglés, tratamiento 1) con carga animal moderada y otro con carga animal intensiva temprana (IES por sus siglas en inglés), a tres rangos de carga animal: igual a SLS, usando el doble de novillos para la primera mitad de la temporada de pastoreo SLS (2X-IES, tratamiento 2), y dos rangos mayores que SLS compuestos por 2.5 o 3 veces la densidad de carga animal de SLS (2.5X- y 3X-IES, tratamientos 3 y 4). Cada tratamiento fue repetido dos veces en un bloque completo al azar. Tres novillos fistulados vía esofágica fueron puestos en cada lugar de pastoreo para recolectar muestras para análisis nutricional, incluyendo proteína cruda y constituyentes de pared celular. Heces totales fueron recolectadas de tres novillos en cada lugar para estimar la descarga fecal y calcular el consumo de forraje. La digestibilidad de la dieta fue estimada usando lignina peroxido-alcalina como un marcador interno. Tres o cuatro periodos de muestra fueron conducidos durante cada estación de pastoreo. La disponibilidad de pasto y de proteína cruda dietética fueron similares entre los tratamientos en 1987, pero ambos declinaron conforme la densidad de ganado incrementó en 1988. Los constituyentes de pared celular generalmente se incrementaron conforme la densidad de ganado incrementó durante 1987, pero fueron similares entre tratamientos en 1988. La digestibilidad y el consumo de forraje no fueron afectados por los tratamientos de pastoreo en ambos años. La ganancia de peso diaria promedio (ADG por sus siglas en inglés) de los novillos declinó conforme la densidad de ganado se incrementó en ambos años. Cambios estacionales en la calidad de la dieta y el consumo de forraje reflejaron el patrón de precipitación con nutrición mejorada cada vez que la precipitación provocó el crecimiento de los zacates cortos de temporada cálida. El consumo de nutrientes se redujo por los rangos de ganado mayores que el empleado bajo SLS, pero fue generalmente similar entre SLS y 2X-IES.

Intensive-early stocking is a grazing management practice intended to improve efficiency of converting vegetation to livestock products while sustaining the natural resource. Under intensive-early stocking, stocker cattle are placed on rangeland in the spring at double the number recommended for season-long stocking, but removed at the midpoint of the season-long stocking grazing season. The result is doubled stocking density (animal units ha^{-1}) during the grazing season, but a stocking rate [animal unit-months (AUM) ha^{-1}] equivalent to season-long stocking. The purposes are to concentrate grazing during the period of highest nutritional quality of the forage, thus increasing livestock production, and to allow a late-season rest so that desirable species enter the dormant season in high vigor. Although this practice is highly successful at increasing livestock production and improving vegetation at up to 3 times the number of cattle recommended for

Contribution 98-214-J from the Kansas Agricultural Experiment Station.
The authors thank H. Jansonius for technical assistance.
Manuscript accepted 7 Sept. 01.

season-long stocking on tallgrass prairie (Owensby et al. 1988, McCollum et al. 1990), we reported that intensive-early stocking only maintained steer performance and vegetation characteristics at double-stocked-intensive-early stocking, and both responses decreased at triple-stocked-intensive-early stocking on shortgrass plains (Olson et al. 1993).

During the final 2 years of a long-term experiment comparing intensive-early stocking to season-long stocking (Olson et al. 1993), we evaluated steer nutritional responses to pasture conditions created by the intensive-early stocking grazing treatments. The objective was to compare dietary nutritional quality and forage intake by steers among season-long stocking, double-stocked-intensive-early stocking, 2.5X-intensive-early stocking, and triple-stocked-intensive-early stocking. Our hypothesis was that nutrient intake would decline at higher stocking rates of intensive-early stocking (2.5X- and triple-stocked-intensive-early stocking) based on previously observed reductions in animal performance and herbage biomass.

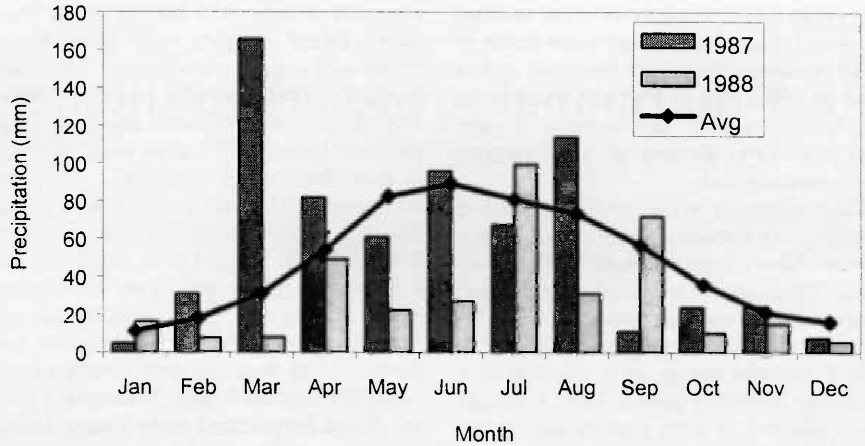


Fig. 1. Monthly precipitation during each year of study and long-term mean monthly precipitation.

Materials and Methods

Study Site

The study was conducted on the Kansas State University Agricultural Research Center-Hays, located in west-central Kansas (38.9°N 99.3°W). The climate is semiarid with a long-term mean annual precipitation of 571 mm, of which 77% occurs during April through September. Annual precipitation was 687 and 363 mm in 1987 and 1988, respectively. These amounts were 120 and 64% of average, respectively. Monthly precipitation was above average in most months of 1987 and below average in most months of 1988, especially before and during the growing season (Fig. 1).

The vegetation was typical of shortgrass plains. Dominant species were western wheatgrass [*Pascopyrum smithii* (Rydb.) Löve], buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], and blue grama [*Bouteloua gracilis* (HBK.) Lag. ex Steud.]. Subdominant species were Japanese brome (*Bromus japonicus* Thunb.) and western ragweed (*Ambrosia psilostachya* DC.). Olson et al. (1993) described the study area in detail.

Grazing Treatments

The original study was initiated in 1980 and continued through 1988. At initiation of the trial, 4 grazing treatments were assigned to 8 pastures in a randomized-complete-block design with 2 blocks. The blocking factor was range site composition in the pastures. Each treatment remained on the same pastures throughout the study. The control was season-long stocking at 1.4 ha steer^{-1} for a 5-month grazing season (1 May to 1 Oct.). Previous long-term research indicated this stocking rate was sustainable on this site (Launchbaugh 1957). The second and third treatments were intensive-early stocking at 2 stocking densities, 0.7 ha steer^{-1} for double-stocked-intensive-early stocking and 0.5 ha steer^{-1} for triple-stocked-intensive-early stocking, for a 2.5-month grazing season (1 May to 15 July). Double-stocked intensive-early stocking yielded a stocking rate equal to season-long stocking (0.4 ha AUM^{-1}) and triple-stocked-intensive-early stocking yielded a stocking rate of 0.28 ha AUM^{-1}. The fourth treatment from initiation of the original grazing trial through 1983 was triple-stocked-intensive-early stocking supplemented daily with 1.8 kg of sorghum grain. This was in addition to the triple-stocked-intensive-early stocking treatment that was not supplemented. It was apparent by 1984 that triple-stocked-intensive-early stocking was not sustainable, so the supplemented triple-stocked-intensive-early stocking treatment was changed to 2.5X-intensive-early stocking (without supplement) from 1984 through 1988 to evaluate a stocking rate between double-stocked- and triple-stocked-intensive-early stocking. The 2.5X-intensive-early stocking treatment yielded a stocking density of 0.6 ha steer^{-1} and a stocking rate of 0.33 ha AUM^{-1}. Thus, the 4 grazing treatments used from 1984 through the experiment reported herein were season-long stocking, double-stocked-intensive-early stocking, 2.5X-intensive-early stocking, and triple-stocked-intensive-early stocking. Pastures were 12.5 ha (block 1) or 14.6 ha (block 2), so steer numbers per pasture were 9 or 10, 18 or 20, 23 or 25, and 27 or 31 for blocks 1 or 2 of season-long stocking, double-stocked-intensive-early stocking, 2.5X-intensive-early stocking, and triple-stocked-intensive-early stocking, respectively. Grazing was initiated on 30 Apr. 1987 and 28 Apr. 1988. Intensive-early stocking was terminated on 16 Jul. 1987 and 29 Jun. 1988, and season-long stocking was terminated on 2 Oct. 1987 and 7 Sept. 1988. Both intensive-early stocking and season-long stocking grazing seasons were shortened in 1988 because drought limited forage.

Experimental Livestock

Yearling steers (12 to 14 months of age) of British breeding (Hereford or Hereford × Angus) with mean initial weights of 308 and 342 kg were used in 1987 and 1988, respectively. Twenty-four contemporaries of the 1987 steers were tamed and esophageally fistulated in Mar. 1987. Three fistulated steers were assigned randomly to each treatment pasture as part of each treatment group described above. The same fistulated steers were used as 2-year-olds in 1988 rather than fistulate a new group of steers. Steers had continuous ad-libitum access to water and salt throughout the experiment. Steers that were not fistulated or used for fecal collections (see below) were weighed after a 16 to 18 hour fast at initiation of grazing and termination of intensive-early stocking grazing to calculate average daily gain (ADG).

Data Collection and Analysis

Nutritional sampling was conducted in 4 and 3 periods in 1987 and 1988, respectively, during the early-summer period that both season-long stocking and intensive-early stocking pastures were stocked (Table 1). Sampling periods were fewer in 1988 because steers were removed earlier than in 1987. Sampling was conducted during 3 periods in late summer of each year when only season-long stocking pastures were stocked.

Diet samples were collected from esophageally fistulated steers shortly after sunrise. Steers were not fasted before sampling. Two samples were collected in each pasture during most sampling periods. To accomplish this, samples were collected in 2 to 4 pastures during each morning of a weeklong sampling period. Only 1 sample was collected in each pasture during the first 3 sampling periods of 1988 because of labor constraints. Samples were frozen immediately after collection and stored frozen until freeze-dried. Dried samples were ground in a Wiley mill to pass a 1-mm screen. Ground samples were analyzed for dry and organic matter (DM and OM, AOAC 1984). Crude protein (CP) was determined as Kjeldahl N (AOAC 1984) × 6.25. Neutral and acid detergent fiber (NDF and ADF) and acid detergent lignin (ADL) were determined using the non-sequential procedures of Goering and Van Soest (1970), except sodium sulfite and decahydronapthalene were eliminated from the NDF and ADF extractions and asbestos was eliminated from the ADL extraction. Hemicellulose was calculated as the difference between NDF and ADF, and cellulose was calculated as the percentage weight loss during incubation in 72% H_2SO_4. All results were converted to an OM basis.

Forage intake was estimated by fecal output/diet indigestibility. Fecal output was estimated using total fecal collections. Each year, 24 intact yearling steers were tamed and trained to wear fecal bags. Thus, 3 trained steers were assigned randomly to the treatment group in each pasture. Feces were collected in all sampling periods except the first in 1987. Feces were collected for 4 consecutive days during each sampling period. Fecal bags were changed once daily. Each daily fecal collection was weighed and sampled. Samples were stored frozen until dried to a constant weight in a forced air oven at 60°C. Dried samples were ground in a Wiley mill to pass a 1-mm screen and analyzed for DM and OM (AOAC 1984). Digestibility was estimated using alkaline-peroxide lignin (APL) as an internal marker according to the PRE-APL procedure described by Cochran et al. (1988), except that 0.5 g rather than 1 g samples were used. The technique was validated for native range forage grown on the research center in a separate experiment (Olson and Sunvold 1991). The APL procedure was performed on feed and fecal samples composited within each steer × sampling period. Fecal output and daily forage intake were expressed as OM on a percentage of body weight (BW) basis.

Total herbage availability was estimated using a disk meter (Sharrow 1984, Karl and Nicholson 1987) in a double-sampling procedure. Each pasture was sampled during each nutritional sampling period except the first in 1988. Sampling involved measuring disk height at 25 locations in each pasture and clipping every fifth plot. Plots were clipped at ground level and all plant material from each plot was placed in a bag. Samples were dried to a constant weight in a 100°C oven. We evaluated the best predictive relationship between disk meter height and sample weight based on scatter plots of height versus weight and regression statistics from various regression relationships. Including grazing treatment as a class effect in an analysis of covariance approach indicated that the relationship between weight and height did not vary among grazing treatments. However, when date of sampling was included as a class effect, results indicated that intercept and slope both varied among dates. Consequently, we developed separate regressions for each sampling period by regressing weight on the natural log of height. R-squared values ranged from 0.68 to 0.90 in 1987 and 0.67 to 0.83 in 1988. Plot weights were then predicted from height readings and converted to kg ha^{-1} for subsequent statistical analysis.

Statistical Analysis

All dependent variables were analyzed using the General Linear Models procedure of the Statistical Analysis System (SAS 1988). Pasture was the experimental unit for all analyses. Data were analyzed separately for each year because of the different number of sampling periods. Nutritional data collected while animals were in season-long stocking and intensive-early stocking treatments were analyzed using a randomized-complete block design with a split-plot treatment structure. Grazing treatment was in the main plot with block × treatment used as the error term. Sampling period and grazing treatment × sampling period were in the subplot with the residual used as the error term. To evaluate changes over time throughout the entire season-long stocking grazing season (particularly during the period when intensive-early stocking treatments were not grazed), data from the season-long stocking treatment were used in a randomized-complete block design with sampling period as the main effect. To evaluate steer performance during these 2 years of the overall performance trial (Olson et al. 1993), ADG was analyzed using a randomized-complete block design with a split-plot treatment structure. Year was in the main plot and block × year was the error term. Grazing treatment and year × grazing treatment were in the subplot with the residual used as the error term. Least squares means and standard errors for split-plot designs were calculated (Cochran and Cox 1957). Following significant F tests, main effect means were separated using single-degree-of-freedom contrasts. Contrasts were pair-wise comparisons of all possible grazing treatment pairings. When grazing treatment and sampling period interacted, grazing treatment means were separated within each sampling period using the same contrasts. Grazing treatment and sampling period rarely interacted, so only significant interactions are indicated herein. All tests were considered significant at $P \leq 0.10$.

Table 1. Periods when nutritional sampling was performed.

	Period	1987	1988
Season-long	1	11-19 May	2-6 May
stocking and	2	1-12 Jun.	23-27 May
intensive-early	3	22-26 Jun.	13-17 Jun.
stocking	4	6-10 Jul.	
Season-long	1	3-7 Aug.	11-15 Jul.
stocking only	2	31 Aug.-4 Sep.	1-5 Aug.
	3	28 Sep.-2 Oct.	29 Aug.-2 Sept

Results and Discussion

Herbage availability did not vary among grazing treatments in 1987 ($P = 0.25$, Table 2), but decreased as stocking rate increased in 1988 ($P = 0.08$). Numeric differences among grazing treatments were large in 1987, with the triple-stocked-intensive-early stocking mean being only 60% of the season-long stocking mean in Table 2. However, large variability and limited replication among experimental units precluded the power to statistically detect differences. We (Olson et al. 1993) previously reported that plant species composition shifted from mixed grass to shortgrass domination and herbage biomass decreased as stocking rate increased during the entire 9 years of this grazing study. The difference in species composition and herbage availability among grazing treatments was visually apparent. Herbage availability increased ($P < 0.01$) from May through July during 1987 (Table 2), and then declined ($P < 0.01$) during September in the season-long stocking treatment (Table 3). This pattern reflected the above-average precipitation (Fig. 1) and good growing conditions experienced during the growing season of 1987. Herbage availability declined ($P < 0.01$) during intensive-early stocking grazing in 1988 (Table 2), and then was similar across sample periods in the season-long stocking treatment during July and August (Table 3). Drought severely reduced herbage availability during 1988, particularly during the intensive-early stocking season. Above-average precipitation during July 1988 stabilized herbage availability during July and August.

Table 2. Herbage biomass (kg ha^{-1}) available during each year under season-long stocking (SLS) or intensive-early stocking (IES) at 2, 2.5, or 3 times the stocking density of SLS (2X, 2.5X, or 3X, respectively) and during each sampling period.

Year	Grazing treatment				
	SLS	2X-IES	2.5X-IES	3X-IES	SE
	(kg ha^{-1})				
1987	3109	2906	2103	1850	566
1988	2868[c]	2626[bc]	1991[ab]	1598[a]	322
	Sampling period				
	1	2	3	4	SE
	(kg ha^{-1})				
1987	1808[a]	2506[b]	2580[b]	3074[c]	141
1988	—[1]	2663[b]	1878[a]	—[2]	146

[1]Data not collected.
[2]Livestock removed from intensive-early stocking treatments before fourth sampling period.
[abc]Means within a row lacking a common superscript differ ($P < 0.10$).

Table 3. Herbage availability, dietary nutrient density, and daily forage intake by steers grazing shortgrass plains during each sampling period of the last half of the season-long stocking grazing season.

Variable	1987				1988			
	5 Aug.[1]	2 Sep.	30 Sep.	SE	13 Jul.	3 Aug.	31 Aug.	SE
	(kg ha^{-1})							
Herbage availability	3524[b]	3465[b]	3141[a]	102	2033	1754	1872	127
	(% of OM)							
Crude protein	9.34[b]	10.40[b]	6.95[a]	0.58	9.19[a]	13.72[b]	9.85[a]	0.34
Neutral detergent fiber	72.3	73.2	76.1	3.92	70.9	69.1	67.8	1.13
Acid detergent fiber	38.4	39.2	42.9	2.57	39.9[b]	37.9[ab]	36.6[a]	1.00
Acid detergent lignin	5.89	6.04	6.64	0.65	5.53[b]	3.76[a]	4.45[a]	0.34
Hemicellulose	33.8	34.0	33.2	1.74	31.1	31.2	31.3	1.36
Cellulose	29.0	30.2	31.3	1.88	31.75[b]	30.25[ab]	29.48[a]	0.54
Digestibility	32.8	47.3	30.8	6.89	43.9	46.1	60.1	6.81
	(% (OM) of body weight day^{-1})							
Forage intake	1.31[a]	1.65[b]	1.64[b]	0.11	1.59	1.13	1.60	0.21
Fecal output	0.864[a]	0.862[a]	1.130[b]	0.071	0.826[b]	0.592[a]	0.638[a]	0.025

[1]Median date of each sampling period.
[ab]Means within a row and year lacking a common superscript differ ($P < 0.10$).

During 1987, dietary crude protein displayed a grazing treatment × sampling period interaction ($P = 0.03$, Table 6). The interaction occurred because crude protein did not vary among grazing treatments during the first 2 sampling periods, but varied during the last 2. Dietary crude protein was higher under double-stocked-intensive-early stocking than the other 3 treatments during the third sampling period, and was higher under double-stocked- and triple-stocked-intensive-early stocking than season-long stocking and 2.5X-intensive-early stocking during the fourth sampling period. Dietary crude protein did not change during August and early September under season-long stocking, but declined by the end of the season-long stocking grazing season ($P < 0.01$, Table 3). During 1988, dietary crude protein declined with increasing stocking density ($P = 0.02$, Table 4) and with advancing time ($P < 0.01$, Table 5). Dietary crude protein rebounded and then declined again during late summer under season-long stocking ($P < 0.01$, Table 3). Dietary crude protein was similar to that reported by Vavra et al. (1973) for shortgrass rangeland and Wallace et al. (1972) for sandhills rangeland, both in eastern Colorado, but was slightly less than that reported by McCollum et al. (1985) for shortgrass rangeland in eastern New Mexico. Vavra et al. (1973) reported that dietary crude protein was similar among low and high grazing intensities. Likewise, Malechek (1984) indicated dietary crude protein was similar among low and high grazing intensities in a review of 4 studies on arid rangelands in Utah. These were in contrast with our results wherein crude protein was higher under some intensive-early stocking treatments late in the intensive-early stocking grazing season of 1987, and inversely related to stocking density during 1988. Perhaps the additive influences of grazing treatment and drought conditions during 1988 reduced herbage availability below the point that would allow adequate selectivity. Wallace et al. (1972), Vavra et al (1973), and McCollum et al. (1985) all reported crude protein declined as the growing season progressed and forage matured. Generally, we found a similar response, except when only season-long stocking was stocked in 1988. Apparently, the lapse in drought conditions during July 1988 (Fig. 1) allowed a spurt of growth by the warm-season shortgrasses: buffalograss and blue grama. Blue grama does not have a smooth growth curve, and actually grows in spurts, anytime moisture is available during the growing season (Bement 1969). We observed that buffalograss follows the same pattern. This weather-event driven improvement in forage conditions likely caused the rebound in dietary crude protein under season-long stocking during that period.

During 1987, NDF, ADL, hemicellulose, and cellulose responded ($P = 0.06$, 0.10, 0.01, and 0.01, respectively), and ADF tended to respond ($P = 0.11$) to grazing treatment (Table 4). In general, these cell wall constituents increased in the diet as stocking rate increased. The exception was cellulose, which was lower in diets of steers grazing double-stocked- and triple-stocked-intensive-early stocking than steers grazing season-long stocking and 2.5X-intensive-early stocking. During 1988, none of the cell wall constituents responded to grazing treatment ($P > 0.29$, Table 4), but ADF and ADL displayed

Table 4. Dietary nutrient density and daily forage intake by steers grazing shortgrass plains under season-long stocking (SLS) or intensive early stocking (IES) at 2, 2.5, or 3 times the stocking density of SLS (2X, 2.5X, or 3X, respectively) during each of 2 years.

	1987					1988				
Variable	SLS	2X-IES	2.5X-IES	3X-IES	SE	SLS	2X-IES	2.5X-IES	3X-IES	SE
	(% of OM)									
Crude protein	10.84	12.77	10.88	11.76	0.96	10.72[c]	9.93[b]	10.52[bc]	8.90[a]	0.28
Neutral detergent fiber	69.55[ab]	68.53[a]	72.42[c]	71.40[bc]	0.85	67.2	68.8	67.4	69.3	1.04
Acid detergent fiber	36.25[de]	34.98[d]	37.46[e]	36.24[de]	0.64	35.3	37.9	35.9	38.0	2.04
Acid detergent lignin	4.77[a]	5.22[b]	5.20[b]	5.03[ab]	0.13	5.02	5.80	5.42	5.81	0.57
Hemicellulose	33.31[a]	33.54[a]	34.96[b]	35.16[b]	0.27	31.9	30.8	31.5	31.3	1.50
Cellulose	30.20[b]	27.65[a]	30.52[b]	28.96[a]	0.37	27.6	29.5	27.8	28.9	1.20
Digestibility	51.7	46.2	49.6	49.9	2.2	64.9	56.0	57.7	55.1	2.9
	(% (OM) of body weight day^{-1})									
Forage intake	1.11	1.18	1.20	1.23	0.17	1.87	1.73	1.90	1.76	0.22
Fecal output	0.547	0.618	0.609	0.594	0.067	0.661	0.754	0.788	0.777	0.047

[abc]Means within a row and year lacking a common superscript differ (P < 0.10).
[de]Means within a row and year lacking a common superscript tend to differ (P = 0.11).

grazing treatment X sampling period interactions (P = 0.08 and 0.07, respectively, Table 6). Acid detergent fiber was higher under triple-stocked-intensive-early stocking than the lower stocking densities during the first sampling period, but was similar across grazing treatments during the remaining sampling periods. Acid detergent lignin was similar among grazing treatments during the first 2 sampling periods, but varied during the final period, being lower for 2.5X-intensive-early stocking than triple-stocked-intensive-early stocking, with season-long stocking and double-stocked-intensive-early stocking similar and intermediate to other grazing treatments. Overall, cell-wall components generally increased in steer diets as grazing intensity increased, indicating that increased grazing pressure (more animal units per amount of available herbage) reduced the steers' ability to graze selectively, forcing them to consume herbage that was more mature. Wallace et al. (1972), Vavra et al. (1973), and McCollum et al. (1985) reported similar values for NDF and cellulose, but slightly higher values for ADF and lignin. These authors all oven dried their fistula samples, which causes formation of artifact lignin, thus artificially elevating ADF and lignin values (Burritt et al. 1988). Vavra et al. (1973) reported that ADF increased with grazing intensity during some sampling periods, but did not respond consistently, which was similar to our observations. Inconsistency in steer diet response to grazing intensity in all studies may result from the temporally dynamic nature of herbage availability and quality response to grazing treatments, weather events, and their interaction. For example, precipitation events may sometimes induce growth in all grazing treatments, allowing steers in all grazing treatments to be selective, but at other times, high quality forage may be depleted in treatments with high grazing intensity, or perhaps sometimes these treatments cannot respond to precipitation events because of shifts in vegetation composition or reductions in plant vigor. Vavra et al. (1973) also found that lignin did not respond to grazing intensity, in contrast to our results throughout 1987 and during the final sampling period in 1988. Malechek (1984) indicated that dietary lignin increased with grazing intensity in the 4 grazing studies conducted in Utah. Vavra et al. (1973) and Malechek (1984) reported mixed effects of grazing intensity on dietary cellulose, and Malechek (1984) suggested this was dependent upon changes among life forms of vegetation in the botanical composition of the diet.

During 1987, NDF, ADF, ADL, and cellulose increased as the intensive-early stocking grazing season progressed (P < 0.01 for NDF, ADF, and ADL, and = 0.05 for cellulose, Table 5). None of these cell wall constituents changed during the remainder of the season-long stocking season after the intensive-early stocking season had ended (P > 0.22, Table 3). During 1988, NDF, ADF, hemicellulose, and cellulose varied across sampling periods (P = 0.04, < 0.01, = 0.06, and < 0.01, respectively, Table 5). Responses varied among the cell wall constituents that did not display an interaction with grazing treatment. Neutral detergent fiber increased during May and decreased in June, hemicellulose decreased in June from similar levels during both May sampling periods, and cellu-

Table 5. Dietary nutrient density and daily forage intake by steers grazing shortgrass plains during each sampling period during each of 2 years.

	1987					1988			
Variable	15 May[1]	6 Jun.	24 Jun.	8 Jul.	SE	4 May	25 May	15 Jun.	SE
	(% of OM)								
Crude protein	13.83[c]	10.41[a]	10.48[a]	11.53[b]	0.59	12.31[b]	9.19[a]	8.50[a]	0.51
Neutral detergent fiber	66.0[a]	71.3[b]	71.6[b]	73.0[b]	1.50	66.7[a]	70.1[b]	67.8[a]	1.09
Acid detergent fiber	32.88[a]	36.33[b]	37.56[bc]	38.16[c]	0.73	34.53[a]	38.09[b]	37.78[b]	0.57
Acid detergent lignin	4.26[a]	5.31[b]	5.28[b]	5.36[b]	0.25	5.42	5.69	5.43	0.16
Hemicellulose	33.13	34.98	34.00	34.87	0.95	32.17[b]	31.96[b]	30.02[a]	0.84
Cellulose	27.30[a]	28.86[ab]	30.13[b]	30.02[b]	0.99	25.96[a]	29.89[b]	29.43[b]	0.84
Digestibility	—[2]	52.4	51.4	44.2	4.9	62.5[b]	58.5[ab]	54.4[a]	2.6
	(% (OM) of body weight day^{-1})								
Forage intake	—[2]	1.03	1.21	1.31	0.12	1.63[a]	1.78[a]	2.03[b]	0.11
Fecal output	—[2]	0.484[a]	0.575[b]	0.718[c]	0.043	0.597[a]	0.736[b]	0.902[c]	0.030

[1]Median date of each sampling period.
[2]Feces not collected during this sampling period.
[abc]Means within a row and year lacking a common superscript differ (P < 0.10).

Table 6. Nutritional responses to grazing treatment × sampling period interactions.

Sampling period	SLS[1]	2X-IES	2.5X-IES	3X-IES
		1987		
		Crude protein, % of OM[3]		
15 May[2]	14.6	13.6	14.3	12.8
6 Jun.	10.8	10.1	9.8	11.0
24 Jun.	8.5[a]	13.5[b]	9.7[a]	10.3[a]
8 Jul.	9.5[a]	13.9[b]	9.7[a]	12.9[b]
		1988		
		Acid detergent fiber, % of OM[4]		
4 May	31.2[a]	35.4[a]	34.2[a]	37.2[b]
25 May	37.0	39.7	36.4	39.3
15 Jun.	37.9	38.7	37.1	37.5
		Acid detergent lignin, % of OM[5]		
4 May	4.72	5.66	5.67	5.62
25 May	5.33	5.95	5.89	5.61
15 Jun.	5.00[ab]	5.80[ab]	4.71[a]	6.19[b]
		Digestibility, % of OM[6]		
4 May	70.3[b]	62.8[ab]	54.2[a]	62.5[ab]
25 May	61.5	55.4	58.1	59.0
15 Jun.	62.9[b]	50.0[a]	60.9[b]	43.7[a]
		Forage intake, % of BW[7]		
4 May	1.58	1.80	1.40	1.76
25 May	1.74	1.72	1.85	1.82
15 Jun.	2.28[ab]	1.69[a]	2.45[b]	1.71[a]

[1]2X, 2.5X, and 3X refer to stocking density of intensive-early stocking (IES) relative to season-long stocking (SLS).
[2]Median date of each sampling period.
[3]Standard error (SE) = 1.19 for sampling periods within grazing treatments and 1.41 for sampling periods across grazing treatments.
[4]SE = 1.15 for periods within treatments, 2.24 for periods across treatments.
[5]SE = 0.33 for periods within treatments, 0.63 for periods across treatments.
[6]SE = 5.3 for periods within treatments, 5.2 for periods across treatments.
[7]SE = 0.21 for periods within treatments, 0.28 for periods across treatments.
[ab]Means within a row lacking a common superscript differ (P < 0.10).

lose increased in May but did not change in June. Acid detergent fiber, ADL, and cellulose decreased across time during the last half of the season-long stocking grazing season (P = 0.02, 0.10, and < 0.01, respectively, Table 3). Wallace et al. (1972), Vavra et al (1973), and McCollum et al. (1985) reported that cell wall components generally increased as vegetation matured. The only exceptions were that Vavra et al. (1973) reported that cellulose was unaffected by maturity, and McCollum et al. (1985) reported that NDF decreased with maturity. The latter authors attributed this to increased forbs in the diet as the growing season progressed. Our results during 1987 fit the expectation that cell walls increase as plants mature. Variable results during 1988 were probably the result of spurts of new growth following precipitation events during the drought, as described previously.

Digestibility did not respond to the grazing treatment main effect during 1987 or 1988 (P = 0.26 and 0.12, Table 4), but displayed a grazing treatment × sampling period interaction during 1988 (P = 0.10, Table 6). During the early May sampling period of 1988, digestibility was higher under season-long stocking than 2.5X-intensive-early stocking, with double-stocked- and triple-stocked-intensive-early stocking being intermediate and similar to all treatments. This relationship among treatments changed in late May, with no difference among grazing treatments, and changed again in June, with season-long stocking and 2.5X-intensive-early stocking being similar and higher than double-stocked and triple-stocked-intensive-early stocking, which were similar. Digestibility was similar to that reported by Wallace et al. (1972), Vavra et al. (1973), Malechek (1984), and McCollum et al. (1985) for diets collected during the growing season. Vavra et al. (1973) reported small and inconsistent differences in in vitro dry matter digestibility among grazing intensities, with digestibility being greater under lower grazing intensity when differences existed. Malechek (1984) observed that digestibility generally was depressed by heavy grazing in the 4 Utah studies. He further indicated that a small depression in digestibility could severely impact animal performance because of its concomitant influence on forage intake. It was surprising that we did not detect depressed digestibility as stocking density increased in light of negative changes observed in dietary chemical composition. However, the standard error of treatment means was larger for digestibility than chemical components during both years (Table 4). Thus, high variability made detection of differences among treatment means difficult.

Digestibility did not vary across sampling periods during 1987 (P = 0.25, Table 5), but declined as the season progressed during 1988 (P = 0.04). During both years, digestibility was similar among sampling periods during the last half of the season under season-long stocking (P > 0.16, Table 3). Wallace et al. (1972) and McCollum et al. (1985) both reported that digestibility declined as vegetation matured, and Vavra et al. (1973) reported that digestibility responded inconsistently as the grazing season progressed, but the general tendency was for digestibility to decrease as the season progressed. Digestibility would be expected to decline as crude protein declines and cell wall components increase in response to increasing plant maturity, but inconsistencies should be expected in shortgrass-dominated vegetation types wherein spurts of growth can increase diet quality, as previously discussed. Digestibility values were particularly low under season-long stocking during the early August and September sampling periods of 1987. These were times when precipitation events had not occurred to initiate new growth, so the animals were selecting from typical, late-season mature herbage. Steers only gained 0.32 kg day^{-1} during this period (Olson et al. 1993). However, when precipitation occurred late in the season-long stocking grazing season of 1988, digestibility values were higher. As a result, steers gained 0.47 kg day^{-1} during this same period in 1988 (Olson et al. 1993).

Forage intake did not respond to the grazing treatment main effect during either year (P > 0.84, Table 4), but displayed a grazing treatment by sampling period interaction during 1988 (P = 0.04, Table 6). In this interaction, forage intake did not respond to grazing treatments during the first 2 sampling periods, but was lowest under double-stocked- and triple-stocked-intensive-early stocking, highest under 2.5X-intensive-early stocking, and season-long stocking was intermediate and similar to all intensive-early stocking treatments during the final sampling period. Apparently, neither forage quality nor quantity differences among grazing treatments influenced forage intake, because neither digestibility nor fecal output (P > 0.20, Table 4) responded to grazing treatment. This was in contrast to Vavra et al.

(1973) and Malechek (1984), who reported depression of forage intake at heavier grazing intensities. Depression of forage intake would be expected because increased grazing intensity reduces availability of forage, which in turn limits the animal's ability to select a nutritious diet and restricts its ability to consume to its ruminal capacity.

Forage intake did not vary with time during 1987 (P = 0.14, Table 5), but increased as the season progressed during 1988 (P = 0.02). Forage intake increased (P = 0.03) during the last half of the season-long stocking season of 1987 (Table 3), but did not change (P = 0.53) during this period in 1988. McCollum and Galyean (1985) found that intake declined as forage matured, and suggested it was limited by forage quality, because forage intake was related directly to digestibility. In their study, fecal output did not vary among sampling periods, which indicated their steers were able to eat to a constant rumen fill. In our study, forage intake responses generally were similar to fecal output responses, which increased during the intensive-early stocking grazing season of both years (P < 0.02, Table 5) and the last half of the season-long stocking grazing season of 1987 (P < 0.01, Table 3), but decreased (P < 0.01) during the same period of 1988. Therefore, forage intake appeared to be limited by quantity rather than quality of forage because differences in fecal output suggest an inability to eat to a constant rumen fill. This was not supported by seasonal changes in total herbage availability, though, which was not always proportional to fecal output (Tables 2, 3, and 5). However, it is impossible to ascertain what portions of total herbage were considered acceptable as forage by the cattle and how this may have affected their ability and desire to maintain rumen fill.

Steer ADG responded to grazing treatment (P = 0.01) and year (P = 0.07). Average daily gains were 0.80, 0.63, 0.55, and 0.47 kg d^{-1} (SE = 0.068) for season-long stocking, double-stocked-, 2.5X-, and triple-stocked-intensive-early stocking, respectively. Gain was greater under season-long stocking than all intensive-early stocking treatments and greater under double-stocked-intensive-early stocking than triple-stocked-intensive-early stocking, with 2.5X-intensive-early stocking intermediate and similar to both other intensive-early stocking treatments. Vavra et al. (1973) also reported improved performance at lower grazing intensity. They attributed it to greater digestibility and its influence on forage intake. In this study, it appears that the influence of forage availability on quality of the diet selected and ability of the steers to maintain gastrointestinal fill and concomitant fecal output were influential in determining steer ADG.

Steer ADG was greater in 1987 than 1988 (0.66, 0.56, and 0.01 for 1987, 1988, and SE, respectively). This difference was likely a response to drought conditions during 1988, despite the fact that we removed animals earlier than planned to avoid extreme forage shortages.

Conclusions and Implications

Inferior vegetation characteristics created by grazing shortgrass rangeland for 9 years at 2.5X- and triple-stocked-intensive-early stocking decreased the quality of diets that steers selected during the final 2 years of the study. Collectively, these data supported our hypothesis that nutrient intake would decline at higher stocking rates of intensive-early stocking (2.5X- and triple-stocked-intensive-early stocking). Nutritional quality typically was similar among diets collected from season-long stocking and double-stocked-intensive-early stocking. These results substantiated our previous conclusion (Olson et al. 1993) that intensive-early stocking can be sustained at the same stocking rate as season-long stocking, but cannot be sustained at higher stocking rates. Furthermore, dietary nutritional quality and forage intake did not decline dramatically during the latter half of the season-long stocking grazing season. This supported our previous evidence that this vegetation type is not as suited to intensive-early stocking as types that lose substantial nutritional value as they mature, such as tallgrass prairie. In fact, nutritional quality actually can be relatively high during late summer if precipitation events keep the shortgrasses green and actively growing.

Literature Cited

AOAC. 1984. Official Methods of Analysis (14th Ed.). Assoc. of Official Anal. Chem, Washington, D.C.

Bement, R.E. 1969. A stocking-rate guide for beef production on blue-grama range. J. Range Manage. 22:83–86.

Burritt, E.A., J.A. Pfister, and J.C. Malechek. 1988. Effect of drying method on the nutritive composition of esophageal fistula forage samples: Influence of maturity. J. Range Manage. 41:346–349.

Cochran, W.G. and G.M. Cox. 1957. Experimental designs. Wiley and Sons, New York, N.Y.

Cochran, R.C., E.S. Vanzant, and T. DelCurto. 1988. Evaluation of internal markers isolated by alkaline hydrogen peroxide incubation and acid detergent lignin extraction. J. Anim. Sci. 66:3245–3251.

Goering, H.K. and P.J. Van Soest. 1970. Forage fiber analysis (apparatus, reagents, procedures, and some applications). USDA-ARS Agr. Handb. 379. Washington, D.C.

Karl, M.G. and R.A. Nicholson. 1987. Evaluation of the forage-disk method in mixed-grass rangelands of Kansas. J. Range Manage. 40:467–471.

Launchbaugh, J.L. 1957. The effect of stocking rate on cattle gains and on native shortgrass vegetation in west-central Kansas. Kansas Agr. Exp. Sta. Bull. 394. Manhattan, Kan.

Malechek, J.C. 1984. Impacts of grazing intensity and specialized grazing systems on livestock response, p. 1129–1158. *In:* Developing Strategies for Rangeland Management. Westview Press, Boulder, Colo.

McCollum, F.T. and M.L. Galyean. 1985. Cattle grazing blue grama rangeland. II. Seasonal forage intake and digesta kinetics. J. Range Manage. 38:543–546.

McCollum, F.T., M.L. Galyean, L.J. Krysl, and J.D. Wallace. 1985. Cattle grazing blue grama rangeland. I. Seasonal diets and rumen fermentation. J. Range Manage. 38:539–543.

McCollum, F.T., R.L. Gillen, D.M. Engle, and G.W. Horn. 1990. Stocker cattle performance and vegetation response to intensive-early stocking of Cross Timbers rangeland. J. Range Manage. 43:99–103.

Olson, K.C. and G.D. Sunvold. 1991. Predicting digestibility of mixed cool- and warm-season grass diets with internal markers. Proc. West. Sec. Amer. Soc. Anim. Sci. 42:197–200.

Olson, K.C., J.R. Brethour, and J.L. Launchbaugh. 1993. Shortgrass range vegetation and steer growth response to intensive-early stocking. J. Range Manage. 46:127–132.

Owensby, C.E., R. Cochran, and E.F. Smith. 1988. Stocking rate effects on intensive-early stocked Flint Hills bluestem range. J. Range Manage. 41:483–487.

SAS. 1988. SAS/STAT™ User's Guide (Release 6.03). SAS Inst. Inc., Cary, N.C.

Sharrow, S.H. 1984. A simple disc meter for measurement of pasture height and forage bulk. J. Range Manage. 37:94–95.

Vavra, M., R.W. Rice, and R.E. Bement. 1973. Chemical composition of the diet, intake and gain of yearling cattle on different grazing intensities. J. Anim. Sci. 36:411–414.

Wallace, J.D., J.C. Free, and A.H. Denham. 1972. Seasonal changes in herbage and cattle diets on sandhill grassland. J. Range Manage. 25:100–104.

J. Range Manage.
55: 229-234 May 2002

Drought and grazing: II. Effects on runoff and water quality

WILLIAM E. EMMERICH AND R. K. HEITSCHMIDT

Authors are Soil Scientist, USDA Agricultural Research Service, Southwest Watershed Research Center, 2000 E. Allen Rd., Tucson, Ariz. 85719 and Supervisory Rangeland Scientist USDA Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301.

Abstract

Understanding the interacting effects of drought and grazing on runoff, erosion, and nutrient transport is essential for improved rangeland management. Research was conducted at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. using 12, non-weighing lysimeters for 3 years. During years 1 and 3, no drought treatment was imposed. For year 2, one half of the lysimeters were covered to implement a drought treatment. The 3 grazing treatments were ungrazed, grazed during but not after drought, and grazed during and after drought. Runoff, sediment yield, and an array of nutrients in the runoff water were measured from the lysimeters. First year base line data with no grazing or drought treatments applied indicated no significant differences among lysimeters. Below normal precipitation occurred during year 2, resulting in no runoff from the drought treatment and negated the "non-drought" control. This prevented a direct assessment of the interaction among the drought and grazing treatments for this year. The drought treatment did produce significant reductions in water, sediment, and nutrient yield. No grazing impact was observed during year 2. The third year with more normal precipitation, there was a trend toward increased runoff, sediment, and nutrient yield from the second year drought treatment lysimeters. In the third year, both grazing treatments showed significantly greater runoff, sediment, and nutrient yield than the ungrazed treatment. Runoff and sediment yield tended to increase from the combination of drought and grazing treatments. The observed increases in runoff and sediment and reduced water quality from the drought and grazing treatments were measured against controls and when compared to the natural variability and water quality standards, they were concluded to be minimal.

Key Words: erosion, sediment yield, nutrient transport, great plains

Resumen

Entender los efectos al interactuar la sequía y el apacentamiento en el escurrimiento, erosión y transporte de nutrientes es esencial para un mejor manejo de pastizales. La investigación se condujo en el laboratorio de Investigación en Pastizales y Ganado Fort Keogh localizado cerca de Miles, Montana, tuvo una duración de 3 años y se utilizan 12 lisímetros que no se pesan. Durante los años 1 y 3 no se impusieron tratamientos de sequía, en el año 2, una mitad de los lisímetros se cubrieron para implementar el tratamiento de sequía. Los 3 tratamientos de apacentamiento fueron: sin apacentamiento, apacentamiento durante, pero no después, de la sequía y apacentamiento durante y después de la sequía. De los lisímetros se midió el escurrimiento, la producción de sedimento y el arrastre de nutrientes en el agua del escurrimiento. El primer año, los datos iniciales de los tratamientos sin apacentamiento o sequía no indicaron diferencias significativas entre lisímetros. En el año 2 la precipitación que ocurrió fue abajo de lo normal, lo que resulto en que no hubiera escurrimiento en los tratamientos con sequía y se anulara el tratamiento control de no-sequía; esto evito que ese año se realizara la evaluación directa de la interacción entre los tratamientos de sequía y apacentamiento. El tratamiento de sequía produjo reducciones significativas en la producción de agua, sedimento y nutrientes. El impacto de no apacentar se observó durante el año 2. En el tercer año, en el que se presentó una precipitación arriba de lo normal, hubo una tendencia a incrementar el escurrimiento y la producción de sedimento y nutrientes en los lisímetros del tratamiento del segundo año de sequía. En el tercer año ambos tratamientos de apacentamiento mostraron un escurrimiento y una producción de sedimentos y nutrientes significativamente mayor que el tratamiento sin apacentamiento. El rendimiento de sedimento y el escurrimiento tendió a incrementarse en los tratamientos de la combinación de sequía y apacentamiento. Los incrementos observados en el escurrimiento y sedimento y la reducida calidad del agua de los tratamientos de sequía y apacentamiento se compararon contra los controles, y cuando se compararon con la variabilidad natural y los estándares de calidad de agua, se concluyó que son mínimos.

Many factors, such as grazing, topography, and type and intensity of precipitation, influence amounts of runoff, erosion, and nutrient transport from rangelands. Excessive runoff, erosion, and nutrient transport degrades water quality, production capacity, and ranch profitability. Of serious concern is the potential for heavy grazing and drought to interact and accelerate runoff, erosion, and nutrient transport. Such knowledge is critical for developing management strategies to maintain and/or improve rangeland health.

The effects of grazing on runoff, erosion, and nutrient transport have been examined by many (Gifford and Hawkins 1978, McGinty et al. 1979, Robbins 1979, Wood and Blackburn 1981, Jawson et al. 1982, Schepers and Francis 1982). As grazing intensity increases, water quality decreases and nutrient transport increases (Wood and Blackburn 1981, Schepers et al. 1982).

Authors thank Dr. Gary Richardson for assistance in statistical analysis, and Cheryl Murphy and Charmaine Verdugo for field and laboratory assistance. This research was conducted under a cooperative agreement between USDA-ARS and the Montana Agric. Exp. Sta. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Montana Agric. Exp. Sta., or the authors and does not imply its approval to the exclusion of other products that may also be suitable. USDA Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer and all agency services are available without discrimination.

Manuscript accepted 2 Sept. 01.

Sometimes the response is not linear and frequently there is a critical point where dramatic changes occur (Thurow 1991). The response arises from the direct impacts that grazing animals have on rangeland resources; those being increased concentrations of pollutants via deposition of animal wastes, decreased vegetation cover and aboveground plant biomass via consumption and trampling, and increased soil bulk density from trampling of the soil surface (Robbins 1979, Dadkhah and Gifford 1980, Wood and Blackburn 1981). The amount of bare soil surface is linked closely to runoff and erosion amounts (Hofmann et al. 1983) because raindrop impact alters soil structure and reduces aggregate stability directly, which in turn increases runoff and erosion (Thurow et al. 1986). Trampling also reduces water infiltration rates by destroying desired soil structure and increasing bulk density (Hanson et al. 1970, McGinty et al. 1979, Dadkhah and Gifford 1980, Warren et al. 1986b).

Drought can be defined in many different ways (Thurow and Taylor 1999). The Society for Range Management Glossary (Kothmann 1974) uses the meteorological-based definition of "prolonged dry weather, generally when precipitation is less than three-quarters of the average annual amount". A detrimental effect of drought on infiltration and erosion can occur under intensive rotational grazing (Warren et al. 1986a). This effect was related to reductions in vegetation cover and aboveground plant biomass. In another study, drought caused the greatest changes in erosion and nutrient transport even when compared to where fire had removed all vegetation (White and Loftin 2000). Our hypothesis was that drought and grazing together would substantially increase runoff, erosion, and nutrient transport during storms that occurred after drought compared to non-drought conditions. The objective of this study was to evaluate the interaction effects of drought and grazing sequences on runoff, erosion, and nutrient transport in a northern Great Plains rangeland setting.

Materials and Methods

Study Area

Research was conducted during the 1993–1995 growing seasons at the 22,000 ha, Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. (46°22'N 105° 5'W). The study area was ungrazed by livestock from 1988 to the start of the study. Regional topography ranges from rolling hills to broken badlands with small intermittent streams that flow into large perennial rivers meandering through broad, low-gradient valleys. The regional natural vegetation is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mixed grass plant community (Kuchler 1964). Average annual precipitation is 341 mm and highly variable with about 60% received during the 150 day, mid-April to mid-September growing season (Fig. 1). Soil erosive precipitation events occur primarily from spring to summer as intense, short-duration thunderstorms. Other runoff events can occur with precipitation on frozen soil or during snow melt. Average daily temperatures range from a low of –10° C in January to a high of 24° C in July with daily maximum temperatures occasionally exceeding 37° C during summer and daily minimums occasionally falling below –40° C during winter.

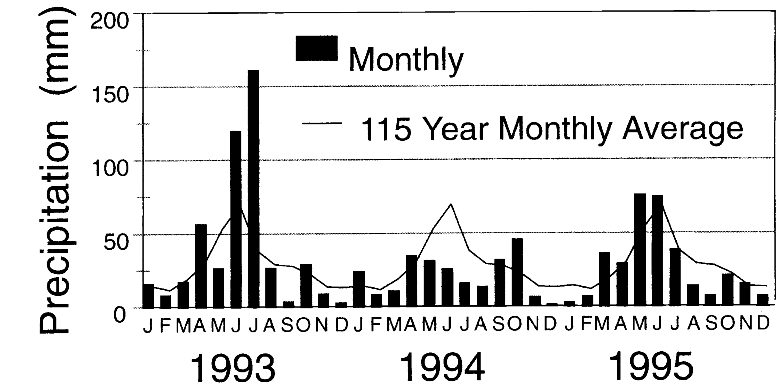


Fig. 1. Monthly precipitation (mm) from January 1993 through December 1995 and long-term monthly averages at Miles City, Mont. (NOAA 1996).

Study Lysimeters

Twelve, non-weighing lysimeters, 5 m wide by 10 m long were installed in 1992. Lysimeter walls were constructed by filling 12 cm wide by 2 m deep perimeter trenches with urethane foam insulation. Twenty cm wide wooden walls extending 15 cm above the soil were placed on top of the trenches and supported a metal v-notched cap to drain off any rainfall landing on the wall. At the lowest elevation point in each lysimeter, a concrete collection basin 2,100 cm^2 in size was constructed and fitted with a drain and below-ground piping to transport water and sediment to fiberglass collection tanks. The storage tanks were each fitted with 20-liter plastic canisters to collect and accurately measure small runoff volumes. For larger volumes, the canisters overflowed into the tank and the combined volumes used. Total tank capacity was calculated to be of sufficient size to measure a 100-year, 24 hour, runoff event (Hershfield 1961).

Vegetation within the lysimeters was a mixed grass dominance of western wheatgrass [*Pascopyrum smithii* Rydb. (Love)], a cool-season, perennial midgrass; blue grama [*Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths], a warm-season, perennial shortgrass; and Japanese brome [*Bromus japonicus* Thunb. ex Murr.], a cool-season, annual midgrass (Heitschmidt et al. 1999). Soil was a Kobase silty clay loam (Fine, montmorillonitic, frigid, Aridic Ustochrept). Soil samples from the lysimeters had an average pH of 7.5, 3.5% organic matter, and a cation exchange capacity of 26 meq/100 g of soil. Average soil particle size was 19, 61, and 20% sand, silt, and clay, respectively, with no rock fragments (>2 mm). Slope was southern and 4%. Lysimeters were arranged perpendicularly along a 65-m transect in 2 groups of 6 lysimeters with a 5-m space between groups.

Treatments

The drought treatment was imposed only during the second year (1994) of the 3-year study (1993–1995) from late May to mid-October. The drought treatment was intended to reduce growing season precipitation by 80%, with precipitation early and late in the growing season producing runoff. A 12 x 35-m automated, metal-framed, rainout shelter was mounted on wheels and rails about 75 cm above the soil surface of 1 of the two, 6-lysimeter sets, hereafter referred to as the drought treatment lysimeters. Rails extended from the top edge of the lysimeters to 25 m below the bottom edge. Rails were located directly over lysimeter borders. It was equipped with a moisture sensitive conductance plate that, when wetted, activated a small electric motor and its associated drive system to move the shelter over the lysimeters.

Three grazing treatments, twice replicated, were imposed randomly on both non-drought and drought treatment lysimeters. Grazing treatments were: 1) graze both the year of (i.e., 1994) and the year after (i.e., 1995) imposed drought, hereafter referred to as the 94–95 grazed treatment; 2) graze during the year of drought (i.e., 1994) and rest the year after, hereafter referred to as the 94 grazed treatment; and 3) rest for all 3 years (i.e. 1993-95), hereafter referred to as the ungrazed treatment. The grazing treatments were applied by placing 6 ewes and their twin lambs in each lysimeter for 1 day in early June and early July, which represented before and during peak standing biomass for the growing season. Grazing continued until an estimated 50% of the standing biomass was removed to achieve a heavy grazing treatment. In 1994, 40% of the standing plant biomass was removed during each grazing event and 50% in 1995 (Heitschmidt et al. 1999). Average year-end standing biomass was 1,000 kg ha^{-1} in 1994 and 500 kg ha^{-1} in 1995 which represented 35 and 30% of the ungrazed treatment, respectively.

Sampling Procedures

Soil chemical and physical properties were characterized by collecting eight, 4-cm deep soil samples at stratified locations in each lysimeter in May 1993. Samples within each lysimeter were composited for analysis. Saturation extracts (Richards 1954) were used to determine pH, electrical conductivity (EC), and soluble nutrient ion concentrations of Ca, Mg, K, Na, NO_3, NH_4, PO_4, Cl, SO_4, and HCO_3. The PO_4, Cl, SO_4, HCO_3, NO_3, and NH_4 concentrations were determined using Technicon AutoAnalyzer II[1] standard procedures and the Ca, Mg, K, and Na concentrations with a Perkin-Elmer 5000[1] atomic absorption spectrophotometer. Triplicate subsamples were digested according to Technicon procedure No. 376-75W/B and analyzed for total N and P with the Technicon AutoAnalyzer II using method No. 329-74W/B (Technicon 1977). Soil texture was determined by the hydrometer method (Day 1965) and organic matter content was determined using the Walkley-Black procedure (Nelson and Sommers 1982). Cation exchange capacity was estimated using ammonium acetate extraction (Bower et al. 1952).

[1]Mention of trade names or proprietary products does not indicate endorsement by USDA, and does not imply its approval to the exclusion of other products that may also be suitable.

Storm rainfall was measured on site from 1 May to 31 October using plastic rain gauges. Runoff and sediment samples were collected from each lysimeter between 1 May and 31 October for every runoff event. In all instances, water and sediment were channeled into the collection system located inside the large storage tanks. Runoff volume was estimated by weighing collected runoff samples and converting weight to volume, ignoring the weight of the sediment. Total sediment yield was estimated for all events by allowing the sediment in collected runoff to settle over time before decanting, centrifuging, drying at 65° C, and weighing. Following all 1994 and 1995 runoff events, a 250-ml aliquot sub-sample was collected from the runoff/sediment sample, centrifuged to remove any suspended sediment, and analyzed for ions using the same procedures as the soluble ions extracted from the soil. This 250-ml sub-sample was not collected in 1993 and no data is available for that year. The dried sediment was then analyzed for total N and P concentrations (sed-N and sed-P, respectively) using the same procedures and methods as the soil samples. Volume of runoff, soluble ion, sediment, and sed-N and sed-P concentrations were used to calculate mass transport for each event. Total annual runoff, sediment, and nutrient yield were estimated by summation of individual events for each lysimeter.

Analysis

The experimental design was a 2 x 3 factorial completely randomized by grazing treatment. Total annual data were statistically analyzed using within years analysis of variance models. Main effects were drought and grazing treatments. The error term for testing for drought effects was replication (i.e., lysimeter) within drought treatment. The model residual was used to test for the main effect of grazing treatment and the drought by grazing treatment interaction effect. Main effects of drought and grazing were either pooled or separated depending on significance of the interactions ($P \leq 0.05$). The potential for non-homogeneity of the variances with the small number of lysimeters within treatments was compensated for by evaluating the data and determining that a log transformation was most appropriate. For treatments with zeros because of no runoff, small values (i.e., 0.01-0.00001) were added to all the data to permit the transformation. The value was chosen to distinguish the zero value from the next larger value in the data set for each variable. The LSD test was used to separate means for treatment effects ($P \leq 0.05$).

Results and Discussion

Predrought (1993)

Runoff and erosion are the major processes that transport nutrients and should be most affected by the drought and grazing treatments. Total precipitation during 1993 was 519 mm, 52% above the long-term average of 341 mm (Fig. 1). The abundance of April through September growing season precipitation was fortunate because it provided an opportunity to clearly identify any inherent, pretreatment differences between lysimeters before treatments were applied for runoff and sediment yield. The lysimeters were analyzed as if all treatments had been applied. There were no significant differences ($P \leq 0.05$) among treatments for runoff or sediment yield (Table 1). The above normal precipitation produced the highest annual runoff and sediment yield values observed during the study. The trend toward more runoff and sediment yield on the non-drought lysimeters may have been related to vegetation composition differences among lysimeters reported by Heitschmidt et al. (1999). Average cool-season perennial grasses on the drought lysimeters was 572 vs. 1,237 kg ha^{-1} for the non-drought and 1,446 vs 1,094 kg ha^{-1} for warm-season perennial grasses, respectively. Although vegetation type and amount can influence runoff and erosion (Warren et al. 1986a), its influence in our study was not large enough to produce significant differences, therefore, any future effects were considered to be related to the treatments and not the vegetation.

Analyses of soil revealed no significant differences among lysimeters in either soil texture, soil organic matter content, cation exchange capacity, total-N, total-P, or soluble nutrient ion concentrations other than chlorine (data not shown). Chlorine concentrations were significantly greater in the non-drought lysimeters than drought (6 vs 3 $\mu g\ g^{-1}$ soil), but the values were so

Table 1. Effect of drought and non-drought treatments on runoff, sediment yield, and nutrient transport from 1 May to 31 October for 1993–1995. No runoff occurred from drought lysimeters in 1994, the year drought was applied. Values are averages across grazing treatments.

Variable	1993 Non-Drought	1993 Drought	1994[1] Non-Drought	1995[2] Non-Drought	1995[2] Drought
	(g ha^{-1})				
Ca	–[3]	–	10.0 (2.9)[4]	11.8a (5.3)	27.0a (9.9)
Mg	–	–	4.1 (1.2)	3.2a (1.6)	4.8a (1.9)
K	–	–	6.4 (1.7)	7.5a (3.8)	11.4a (4.8)
Na	–	–	2.4 (0.4)	5.8a (2.4)	4.7a (1.7)
NO_3-N	–	–	3.3 (1.9)	0.9a (0.5)	1.1a (0.5)
NH_3	–	–	1.8 (0.5)	0.6a (0.4)	0.9a (0.5)
PO_4-P	–	–	0.24 (0.06)	0.23a (0.15)	0.46a (0.26)
Cl	–	–	4.1 (1.2)	3.0a (1.6)	5.1a (2.5)
SO_4	–	–	2.2 (0.1)	4.5a (1.9)	11.0a (4.4)
HCO_3	–	–	20.9 (4.9)	30.1a (12.8)	46.1a (16.8)
Sed-N[5]	5.2 (1.4)	2.7 (0.9)	2.8 (1.2)	8.9 (5.0)	14.9 (8.4)
Sed-P[5]	1.2 (0.3)	0.6 (0.2)	0.5 (0.2)	1.5 (0.9)	2.9 (1.7)
Sediment[5]	19,403 (5,086)	9,689 (3,519)	664 (278)	2,548 (1,539)	5,889 (3,643)
	(mm)				
Runoff	2.6 (0.6)	0.9 (0.2)	0.10 (0.03)	0.22a (0.11)	0.33a (0.15)

[1]All 1994 non-drought means significantly different from zero at P ≤ 0.05.
[2]Means from 1995 within rows with the same letter are not significantly different at P ≤ 0.05.
[3]Not determined.
[4]Values in parentheses are standard errors.
[5]Sed-N, Sed-P, and Sediment in 1995 had a two-way grazing by drought interaction P ≤ 0.05.

small, it was not possible to attribute any environmental significance. Although runoff water quality analyses were not done, the soil is the dominant source of nutrients for transport in runoff water and sediment. The minimal soil differences and the absence of significant runoff and sediment yield differences indicated that future significant differences would be due to treatment effects.

Drought (1994)

Annual precipitation during 1994 was 256 mm, 25% below normal, with below typical growing season precipitation (Fig. 1). Precipitation from May through October was 163 mm as compared to the long-term average of 271 mm. This produced the situation where a drought treatment was imposed in what turned out to be a below normal precipitation year. Drought treatment precipitation from 1 May through 31 October was 23 mm with 0 precipitation from 15 June to 15 October which produced no runoff from the drought treatment. Similar severe droughts have occurred in recent history. For example, there was only 34 mm of precipitation that fell between 15 May and 15 September 1988.

Runoff, sediment yield, and nutrient transport were all significantly greater from the non-drought than the drought treatment lysimeters because all were greater than zero (Table 1). The absence of runoff from drought treatment lysimeters eliminated the opportunity to statistically examine the interaction effects of drought and grazing during 1994. There were no differences between grazed and ungrazed treatments relative to any measured variable. We suspect this was largely because the total amount of runoff and sediment production was very limited in this study regardless of treatment. The ungrazed treatments did have more runoff (0.14 vs 0.08 mm) and the grazed treatment had more sediment yield (914 vs 163 g ha^{-1}). Our results should not be perceived as being in conflict with the generally accepted conclusion that grazing generally increases both surface runoff and sediment production (Dadkhah and Gifford 1980, Thurow et al. 1988, Thurow 1991). The results should be viewed as reflecting the reality that grazing in an arid environment with limited high intensity precipitation events, produces limited runoff and sediment production, at least for the period of this study.

Post-drought (1995)

Total precipitation during 1995 was 284 mm with above average spring rainfall (Fig. 1). Analyses of the post-drought 1995 data indicated no significant drought effect. The 1994 drought treatment did increase the runoff, sediment, and nutrient yield from the drought lysimeters in 1995 when compared to the non-drought (Table 1). This was largely because of the carry-over effect of reduced standing plant biomass from the drought treatment. Heitschmidt et al. (1999) reported the standing plant biomass during 1995 averaged 1,259 and 1,673 kg ha^{-1} in drought and non-drought treatment lysimeters, respectively, as compared to averages of 1,735 and 2,084 kg ha^{-1} during 1994. A larger impact of the 1994 imposed drought may have been observed in 1995, if 1994 had not been a below normal precipitation year. Carry-over of the drought treatment effects to the following year are in agreement with other studies that have shown post-drought vegetation recovery varies in part as a function of drought severity and grazing intensities, and as such, so do hydrological recovery rates (Thurow et al. 1988).

The 94 grazed and 94–95 grazed treatments had significantly more runoff, sediment, and nutrient yield in 1995 than the ungrazed treatment (Tables 2 and 3). Nutrient yields were greater from the 94-95 grazed than 94 grazed treatments, but only significantly so for NH_3 and PO_4-P. For sediment, sed-N, and sed-P yields, there were significant drought by grazing treatment interactions (Table 3). These interactions showed that sediment, sed-N, and sed-P yields were: 1) significantly less on the ungrazed treatment with no runoff from the ungrazed non-drought treatment; 2) significantly greater on the non-drought 94–95 grazed treatment than the non-drought 94 grazed treatment; and 3) similar on the drought 94–95 grazed and drought 94 grazed treatment. An increase in sediment yield with increasing grazing has been related to aboveground biomass (Thurow et al. 1986). The average aboveground standing biomass was 782 kg ha^{-1}

Table 2. Effect of drought and non-drought treatments on runoff, sediment yield, and nutrient transport from 1 May to 31 October 1995. Lysimeters were either ungrazed, grazed only in 1994, or grazed both in 1994 and 1995. Values are averages across drought and non-drought treatments.

Variable	Ungrazed	94 Grazed	94–95 Grazed
		($g\ ha^{-1}$)	
Ca	0.5a[1]	25.2b	32.5b
	(0.4)[2]	(10.3)	(4.1)
Mg	0.1a	4.8b	7.1b
	(0.04)	(1.9)	(1.2)
K	0.2a	10.1b	17.8b
	(0.2)	(3.6)	(4.1)
Na	0.2a	5.9b	9.6b
	(0.2)	(1.4)	(1.6)
NO_3-N	0.01a	0.96b	2.08b
	(0.004)	(0.20)	(0.59)
NH_3	0.01a	0.47b	1.75c
	(0.004)	(0.33)	(0.52)
PO_4-P	0.001a	0.31b	0.73c
	(0.001)	(0.17)	(0.36)
Cl	0.1a	4.5b	7.6b
	(0.04)	(2.0)	(2.2)
SO_4	0.2a	8.5b	14.6b
	(0.2)	(2.7)	(3.8)
HCO_3	1.3a	46.9b	66.1b
	(1.1)	(16.0)	(6.0)
Sed-N[3]	0.2	12.9	22.6
	(0.2)	(7.9)	(6.8)
Sed-P[3]	0.03	2.19	4.35
	(0.03)	(1.36)	(1.54)
Sediment[3]	31	3,972	8,652
	(25)	(2,650)	(3,553)
		(mm)	
Runoff	0.007a	0.359b	0.470b
	(0.006)	(0.162)	(0.098)

[1]Values within rows with the same letter are not significantly different at $P \leq 0.05$.
[2]Values in parentheses are standard errors.
[3]Sed-N, Sed-P, and Sediment had a two-way grazing by drought interaction $P \leq 0.05$.

for the 94-95 grazed, 1,422 kg ha^{-1} for the 94 grazed, and 2,196 kg ha^{-1} for the ungrazed treatments (Heitschmidt et al. 1999). The sediment yield and standing biomass data agrees with other studies that have shown good correlations between them (Thurow et al. 1986, Warren et al. 1986a). Although not large, the combination of drought and gazing did produce a trend toward increased runoff and sediment yield (Tables 1, 2, and 3).

The drought and grazing treatment impacts were small and the potential increase in water yield from the treatments was small (Tables 1 and 2). This small impact was surprising in light of other studies showing dramatically accelerated runoff and erosion (e.g., see reviews by Blackburn 1984 and Thurow 1991). Most of these studies were conducted in regions experiencing much greater intensity of rainfall and/or results derived from simulated, high intensity rainfall events. The conditions of this study were much different in that annual precipitation was low and individual rainfall events were generally small. For example, there were 104 precipitation events during 1993, 1994, and 1995 between 1 May and 31 October. Of these events, 79 were <10 mm in magnitude and only 6 were >20 mm with the largest being 61.2 mm (7 Jun 1993).

Table 3. Effects of drought and grazing on sediment nitrogen (Sed-N), sediment phosphorus (Sed-P), and total sediment transport from 1 May to 31 October 1995. Lysimeters were either ungrazed, grazed only in 1994, or grazed both in 1994 and 1995.

Drought Treatment[1]	Grazing Treatments: Ungrazed	94 Grazed	94–95 Grazed
		($g\ ha^{-1}$)	
		Sed-N	
Non-Drought	0a[2]	3.9b	22.9c
	(0)[3]	(1.8)	(8.3)
Drought	0.4a	21.9b	22.4b
	(0.4)	(19.1)	(18.7)
		Sed-P	
Non-Drought	0a	0.6b	3.9c
	(0)	(0.3)	(1.4)
Drought	0.1a	3.8b	4.8b
	(0.1)	(3.4)	(4.3)
		Sediment	
Non-Drought	0a	875b	6,768c
	(0)	(443)	(2,871)
Drought	61a	7,068b	10,536b
	(61)	(6,624)	(9,915)

[1]The two-way grazing by drought interaction was significant at $P \leq 0.05$.
[2]Values within rows with the same letter are not significantly different at $P \leq 0.05$.
[3]Values in parentheses are standard errors.

Runoff from the lysimeters averaged about 20 mm during this event. The 7 June event was long in duration with a maximum rainfall rate of 6.6 mm per hour and represented a 1 in 10 year, 12-hour rainfall event (Hershfield 1961). These data emphasize that erosive rainfall events are rare in this region and that the yearly variability in precipitation was a larger factor in runoff than any of the treatments, as shown by 1993, an above average year, and 1994 a below normal year (Fig. 1, Table 1). As a result, runoff from this range site was low and quality was generally better than EPA (1976) standards. The sediment and nutrient levels realized in this study are in close agreement with those of Owens et al. (1983) and Barros et al. (1995), and specifically by Neff (1982) for an analogous Montana rangeland soil.

Summary and Conclusions

The absence of runoff from the drought treatment lysimeters during the 1994 below normal precipitation year prevented a direct assessment of drought and grazing interactions. However, 1 year after the drought treatment (1995), the hypothesized substantial increase in runoff, sediment, and nutrient transport from the combined effects of drought and grazing did not materialize, only an increasing trend for runoff and sediment yield. After the drought treatment, runoff and sediment yields increased and water quality was reduced. Grazing produced significant increases in runoff and sediment yield and decreases in water quality compared to no grazing. These increases were concluded to be minimal under the drought and grazing conditions evaluated in this study when compared to the yearly natural variability at the site.

Literature Cited

Barros, M.C., M.J.M. Mendo, and F.C.R. Negrao. 1995. Surface water quality in Portugal during a drought period. Sci. Total Environ. 171:69–76.

Blackburn, W.H. 1984. Impacts of grazing intensity and specialized grazing systems of watershed characteristics and responses, p. 927–983. *In:* Developing Strategies for Rangeland Management. Nat. Res. Counc., Nat. Acad. Sci., Westview Press, Boulder, Colo.

Bower, C.A., R.F. Reitemeirer, and M. Fireman. 1952. Exchangeable cation analysis of saline and alkali soils. Soil Sci. 73:251–261.

Dadkhah, M. and G.F. Gifford. 1980. Influence of vegetation, rock cover, and trampling on infiltration rates and sediment production. Water Resour. Bull. 16:979–986.

Day, P.R. 1965. Particle fractionation and particle-size analysis. *In:* C.A. Black (ed.), Methods of soil analysis. Part I. Agron. 9:545–576.

EPA. 1976. Quality criteria for water. U.S. Environ. Protection Agency, Washington, D.C.

Gifford, G.F. and R.R. Hawkins. 1978. Hydrologic impact of grazing on infiltration: A critical review. Water Resour. Res. 14:305–313.

Hanson, C.B., H.G. Heinemann, A.R. Kuhlman, and J.W. Neuberger. 1970. Grazing effects on runoff and vegetation on western South Dakota rangeland. J. Range Manage. 23:418–420.

Heitschmidt, R.K., M.R. Haferkamp, M.G. Karl, and A.L. Hild. 1999. Drought and grazing: I. Effects on quantity of forage production. J. Range Manage. 52:440–446.

Hershfield, D.M.. 1961. Rainfall frequency atlas of the United States for duration from 30 minutes to 24 hours and return periods for 1 to 100 years. Tech. Paper No. 40 U.S. Dept. of Commerce Weather Bureau. Washington D.C.

Hofmann, L., R.E. Ries, and J.E. Gilley. 1983. Relationship of runoff and soil loss to ground cover of native and reclaimed grazing land. Agron. J. 75:599–602.

Jawson, M.D., L.F. Elliott, K.E. Saxton, and D.H. Fortier. 1982. The effect of cattle grazing on nutrient losses in a pacific Northwest setting. J. Environ. Qual. 11:628–631.

Kothmann, M.M. 1974. A glossary of terms used in range management. Soc. Range Manage., Denver, Colo.

Kuchler, A.W. 1964. Potential natural vegetation of the coterminous United States. Amer. Geogr. Soc. Spec. Pub. 36, New York, N.Y.

McGinty, W.A, R.E. Smeins, and L.B. Merrill. 1979. Influence of soil, vegetation, and grazing management on infiltration rate and sediment production of Edwards Plateau rangeland. J. Range Manage. 32:33-37.

National Oceanic and Atmospheric Administration. 1996. Climatological data Montana annual summary. National Climatic Data Center, Asheville, N.C.

Neff, E.L. 1982. Chemical quality and sediment content of runoff water from southeastern Montana rangeland. J. Range Manage. 35:130–132.

Nelson, D.A. and L.P. Sommers. 1982. Total carbon, organic carbon, and organic matter. *In:* A.L. Page et al. (eds.), Methods of soil analysis, Part II, 2nd ed. Agron. 9:539-579.

Owens, L.B., W.M. Edwards, and R.W. Van Kwuren. 1983. Surface runoff water quality comparisons between unimproved pasture and woodland. J. Environ. Qual. 12:518–522.

Richards, L.A. 1954. Diagnosis and improvement of saline and alkali soils. Agr. Handb.. 60. USDA-ARS, Washington D.C.

Robbins, J.W.D. 1979. Impact of unconfined livestock activities on water quality. Trans. ASAE. 22:1317–1323.

Schepers, J.S. and D.D. Francis. 1982. Chemical water quality of runoff from grazing land in Nebraska: I. Influence of grazing livestock. J. Environ. Qual. 11:351–354.

Schepers, J.S., B.L. Hackes, and D.D. Francis. 1982. Chemical water quality of runoff from grazing land in Nebraska: II. Contributing factor. J. Environ. Qual. 11:355–359.

Technicon Industrial Systems. 1977. Industrial method No. 376-75W/B and 329-74W/B. Tarrytown, N.Y.

Thurow, T.L. 1991. Hydrology and erosion. p. 141–159. *In:* R.K. Heitschmidt and J.W. Stuth (eds.), Grazing management: An ecological perspective. Timber Press, Portland, Ore.

Thurow, T.L. and C.A. Taylor, Jr. 1999. Viewpoint: The role of drought in range management. J. Range Manage. 52:413–419.

Thurow, T.L., W.H. Blackburn, and C.A. Taylor, Jr. 1986. Hydrologic characteristics of vegetation types as affected by livestock grazing systems, Edwards Plateau, Texas. J. Range Manage. 39:505–509.

Thurow, T.L., W.H. Blackburn, and C.A. Taylor, Jr. 1988. Infiltration and interrill erosion responses to selected livestock grazing strategies, Edwards Plateau, Texas. J. Range Manage. 41:296–302.

Warren, S.D., W.H. Blackburn, and C.A. Taylor, Jr. 1986a. Effects of season and stage of rotation cycle on hydrologic condition of rangeland under intensive rotation grazing. J. Range Manage. 39:486–491.

Warren, S.D., M.B. Nevill, W.H. Blackburn, and N.E. Garza. 1986b. Soil response to trampling under intensive rotation grazing. Soil Sci. Soc. Amer. 50:1336–1341.

White, C.S. and S.R. Loftin. 2000. Response of 2 semiarid grasslands to cool-season prescribed fire. J Range Manage. 53:52–61.

Wood, M.K. and W.H. Blackburn. 1981. Sediment production as influenced by livestock grazing in the Texas rolling plains. J. Range Manage. 34:228–231.

J. Range Manage.
55: 235-241 May 2002

Evaluation of a technique for measuring canopy volume of shrubs

MARK S. THORNE, QUENTIN D. SKINNER, MICHAEL A. SMITH, J. DANIEL RODGERS, WILLIAM A. LAYCOCK, AND SULE A. CEREKCI

Authors are Graduate Research Assistant, Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, Colo, Professors, Assistant Professor, and Professor Emeritus, Department of Renewable Resources, University of Wyoming, Laramie, Wyo., and Project Engineer, Ministry of Agriculture and Rural Affairs, Eastern Anatolia Watershed Rehabilitation Project, Turkey. At the time of research, the senior author was a Graduate Research Assistant, Department of Renewable Resources, University of Wyoming, Laramie, Wyo.

Abstract

Cover methods quantify vegetative communities in only 2 dimensions. The addition of height measurements to cover data, resulting in canopy volume estimates, provide a more practical level of description for shrub communities. We evaluated a technique to estimate canopy volume of shrubs that used a formula [2/3πH (A/2 x B/2)] derived from the basic ellipsoid volume formula. Objectives of this study were to determine if there were significant differences among means of repeated observations on sample units: (1) among observers; (2) within observers; and (3) between sample periods when using this technique. At 2 locations in Wyoming, 10 planeleaf willow (*Salix planifolia* var. *planifolia* Pursh) plants along each of 5 randomly established transects were sampled during 2 consecutive periods by 4 observers. Differences among observers were significant at both sites ($P < 0.05$). However, within observer variation between sample periods was not significant ($P > 0.05$) at either site. Mean canopy volume did not vary significantly ($P > 0.05$) between sample periods when averaged across observers. Estimated sample sizes ranged between 2 and 31 transects depending on the desired sampling precision and confidence level. The average time per transect among all observers decreased from 13 minutes (SD = 3.7) in sample period 1 to 9 minutes (SD = 1.3) in sample period 2. Using this method, managers can better describe and monitor trends in the structural diversity of shrub communities. This canopy volume technique can be applied with minimal training and is precise, efficient, and repeatable.

Key Words: willow (*Salix* spp.), measurement variability, sampling techniques, sample size

Resumen

Los métodos de cobertura cuantifican las comunidades vegetativas en solo 2 dimensiones. La adición de mediciones de altura a los datos de cobertura resultan en estimaciones del volumen de la copa y proveen un nivel más práctico de descripción de las comunidades de arbustos. Evaluamos una técnica para estimar el volumen de copa de los arbustos que utiliza una fórmula [2/3πH (A/2 x B/2)] derivada de la fórmula básica para calcular el volumen de un elipsoide. Los objetivos de este estudio fueron determinar si hubo diferencias significativas entre las medias de observaciones repetidas en unidades de muestreo: (1) entre observadores; (2) dentro de observadores y (3) entre periodos de muestreo cuando se utiliza esta técnica. En 2 localidades de Wyoming, 10 plantas de "Planeleaf willow" (*Salix planifolia* var. *planifolia* Pursh), situadas a lo largo de cada uno de 5 transecto establecidos aleatoriamente, se muestrearon por 4 observadores durante 2 periodos consecutivos. Las diferencias entre observadores fueron significativas en ambos sitios ($P < 0.05$). Sin embargo, la variación dentro de observadores entre los periodos de muestro no fue significativa ($P > 0.05$) en ningún sitio. Cuando la media del volumen de la copa se promedio entre observadores esta no varió significativamente ($P > 0.05$) entre los periodos de muestreo. Los tamaños de muestra estimados variaron entre 2 y 31 transecto, dependiendo de la precisión de muestreo y nivel de confianza deseados. El tiempo promedio por transecto entre todos los observadores disminuyó de 13 minutos (DS = 3.7) en el periodo de muestreo 1 a 9 minutos (DS = 1.3) en el periodo de muestreo 2. Usando este método los manejadores pueden describir y monitorear mejor las tendencias en la diversidad estructural de las comunidades de arbustos. Esta técnica de volumen de copa puede ser aplicada con un entrenamiento mínimo y es precisa, eficiente y repetible.

Early researchers realized that temporal changes in plant cover were often a reflection of management practices and developed appropriate techniques to quantify those changes (Nelson 1930, Pickford and Stewart 1935, Bauer 1936, Parker 1951, Cooper 1957, Daubenmire 1959). Other investigators noted that plant cover estimates varied between methods, observers, and vegetation types (Smith 1944, Johnston 1957, Heady et al. 1959, Kinsinger et al. 1960, Fisser 1961). Despite problems with precision, repeatability, and efficiency, these methods remain in common use.

Cover methods quantify vegetative communities in only 2 dimensions. Daubenmire (1968) noted that the omission of the vertical dimension was the largest limitation to cover data. He also pointed out that, since height was a structural parameter, it could be used to determine and compare dominance of plant species in a community. Zamora (1981) modified Daubenmire's

Research was funded in part by the Wyoming Water Resources Center, the Hyatt Ranch, the Pitchfork Ranch, the WesMar Grazing Management Trust Fund, and the SRM Hyatt Trust. Authors wish to thank Dr. Robert S. Cochran of the Statistics Department at the University of Wyoming for assistance in statistical analyses. We would also like to thank Dr. J. Brummer and 2 anonymous reviewers for their insightful comments and suggestions on drafts of this manuscript.

Manuscript accepted 22 Aug. 01.

(1959) quadrat frame with the addition of a vertical dimension and suggested that it could be used to quantify canopy volume in shrub communities. Recently, Myers (1989) suggested that the addition of height measurements might be a more practical level of description for riparian shrub communities. In addition, canopy volume estimates have been used for predicting biomass or current-year twig production of shrubs (Lyon 1968, Peek 1970, Rittenhouse and Sneva 1977, Uresk et al. 1977, Bryant and Kothmann 1979, Creamer 1991).

More recently, several investigators have used canopy volume to quantify other attributes of shrub communities. For example, Taylor (1986) used canopy volume to define nesting habitat suitability for passerine birds in willow (*Salix* spp.) communities along the Blitzen River in Oregon. Manoukian (1994) used canopy volume to describe seasonal changes in Montana willow communities subjected to wildlife and livestock herbivory.

Although prior studies have focused on estimating plant volume, all used different measures of the volume components. Likewise, a variety of mathematical formulas have been used to calculate volume. Therefore, comparing canopy volume estimates among different studies and management programs is difficult. Since canopy volume is an important attribute in shrub communities and its estimation is becoming more common, it may be appropriate to standardize an approach to measure it. It would also be convenient to use a mathematical formula that is elastic in its ability to absorb a wide range of canopy shapes. Several factors could define the usefulness of a standard method of measuring canopy volume such as ease of application, efficiency, precision, and repeatability.

Ease of application is related to the simplicity of the methodology. Efficiency is a function of the time it takes to make a precise and repeatable estimate where as, precision and repeatability of an estimate are controlled by the inherent variation in the vegetative community and error caused by the method and observer. Error imposed by the method and variation in the vegetative community are uncontrollable. Since vegetative communities are the object of study, controlling this source of variation in the estimate is only desirable for sources not related to the community or temporal factors of interest. Conversely, error in accuracy imposed by a method designed to measure vegetative attributes is always undesirable. If a method (assuming no observer error) continuously over- or underestimates an attribute of interest, then it is a less desirable technique.

Canopy Volume Formula

In estimating plant canopy volumes, the largest source of methodological error lies in the volume formula. Lyon (1968), Peek (1970), Creamer (1991), and Manoukian (1994) used mathematically equivalent formulas for an elliptical cylinder to estimate canopy volume of different shrub species. The elliptical cylinder formula, V = π(H)[Major axis/2 x Minor axis/2], where H is the plant height, assumes right angles at both the base and crest of the shape for which volume is being estimated. This formula may overestimate plant canopy volume because it does not integrate changing radial distances along the vertical axis of the plant. Shrub canopy volume estimates have also been calculated using the rectangular volume formula (H x W x L) reported by Uresk et al. (1977). Since plants tend to be bounded by a spherical or elliptical form, the rectangular volume formula may overestimate plant canopy volume by a factor of π. Conversely, the conical volume formula reported by Bryant and Kothmann (1978), V = (π r^2 H)/3, where H is the plant height, may underestimate canopy volume. The conical formula assumes that the junction of the central vertical axis and the widest radial plane is a right angle, and that the radial distances are equal across all horizontal axes. Most plants, even when severely hedged, would not meet these requirements, and averaging unequal radial distances of the horizontal axes forces the plant into a contrived canopy shape thus altering the estimate of volume.

The ellipsoid volume formula [2/3πH (A/2 x B/2)] used in this study is not subject to the limitations described above (Fig. 1). Changing radial distances along the vertical axes are accounted for within the formula. The formula is elastic and accurately accommodates a wide range of plant shapes and sizes. Specifically, the formula can absorb plant shapes that are non-concentric about the horizontal axis and either compressed or elongated along the vertical axis. Thorne (1998) found that the ellipsoid volume formula was sensitive to changes in plant dimensions over time. Importantly, growth, utilization, and twig death do not affect the application of the formula. Because the ellipsoid form "adjusts" to the varying sizes and shapes of plants, consecutive observations closely reflect what has been gained or lost over time.

The purpose of this study was to describe and evaluate the efficiency, precision, and repeatability of a technique to estimate canopy volume of shrubs. The objectives were to determine if there were significant differences among means of repeated observations on sample units: (1)

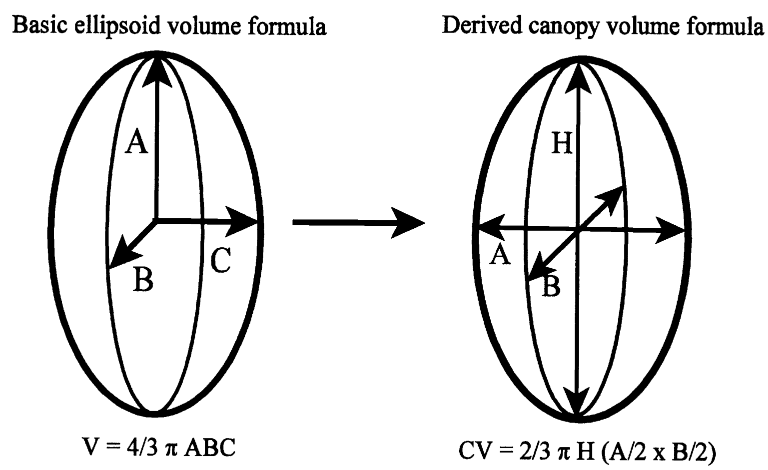


Fig. 1. The canopy volume formula used in this study was derived from the basic ellipsoid volume formula. In the canopy volume (CV) formula, H is substituted for A and is the height of the plant from the base to the top of the photosynthetically active material. Both A and B in the CV formula are diameter readings taken at 50% of the plant height across the plane of photosynthetically active material. Because height and diameter meaurements are used, it is necessary to divide the components of the basic volume formula by 2 so that volume will be properly estimated.

among observers, (2) within observers, and (3) between sample periods (means pooled across observers). Secondarily, we asked; could the variability be reduced if observers were trained and the plants were well defined and easy to distinguish?

Materials and Methods

Study Areas

This study was conducted in a planeleaf willow (*Salix planifolia* var. *planifolia* Pursh) community located on the Paintrock Grazing Allotment (Willow Swamp; 44°21' N, 107° 21' W), Paintrock District, Bighorn National Forest, Wyo. in July 1997. The allotment was approximately 24 km east of Hyattville, Wyo. and ranged in elevation from 2,150 m to over 3,700 m. Annual precipitation ranged from 380 mm at the lower elevations to 1,020 mm at the higher elevations. The shrub component of Willow Swamp (elev. 2,675 m) was actually dominated by bog birch (*Betula glandulosa* Michx.), but a substantial amount of planeleaf willow was present (Meiman 1996).

A second set of observations were taken among potted planeleaf willows in August 1997 in a common garden at the Greenhouse Facility of the University of Wyoming (41°19' N, 105°35' W). All plants used in this study were established from stem cuttings of planeleaf willow collected from Willow Swamp in May 1994 for a frequency of clipping study (Thorne 1998).

The observations taken at the Willow Swamp site represented a "worst case" scenario where observers were not trained and the plants were not easily distinguishable. At this site, willows and bog birch grew in close proximity to each other, often with branches intertwined. In other cases, 2 or 3 separately rooted willow plants grew on the same hummock making it difficult to separate plants for the purpose of estimating canopy volume. The observations taken at the garden site represented a "best case" scenario where the plants were easily distinguishable and the observers were more familiar with the technique. Since the plants at the garden were potted separately (i.e., 1 plant per pot) on a 1 x 2 m grid, distinguishing between plants was not a problem. Further, the same observers were used for both sites and, in effect, had become trained at Willow Swamp for the observations at the Garden site.

Experimental Design

A completely randomized, repeated measures sample design was used at both sites. At the Willow Swamp site, a base line was established from the northeast corner of a U. S. Forest Service wildlife and livestock exclosure and continued eastward for 100 m. Along the base line, 5 perpendicular sub-transects were established at random distances running south to north. From each sub-transect, one measurement transect was randomly established that ran east to west if the distance up the sub-transect from the base line was an even value or west to east if the value was odd. Along each of the measurement transects, 10 random distances between 0 and 35 m were selected. Pin flags were placed in the vicinity of each plant along each transect to assist in locating plants during observations. Canopy volume was estimated on the willow nearest to each pin flag along each of the 5 measurement transects.

At the Garden site, five, 10 plant transects were randomly selected from a pool of all possible 10 plant combinations among 200 potted willows. This was done to provide continuity in sampling design between the Garden and Willow Swamp sites.

At both sites, canopy volume measurements along the set of transects, 1 through 5, were taken twice (sample periods 1 and 2) by each of 4 observers (A, B, C, and D). Each of the 5 transects was considered an observation. Both sample periods were conducted on the same day at both the Willow Swamp and Garden sites on their respective sampling dates. To estimate technique efficiency, the amount of time for each observer to complete a transect was recorded for sample periods 1 and 2 at the Willow Swamp site.

Canopy volume components were measured by taking the height and 2 diameter readings at 50% of the willow height. Willow height was defined as the distance from the base of the mainstem to the tallest extent of photosynthetically active plant material. Diameter readings were defined as the widest extent of photosynthetically active plant material that intersected a plane passing horizontally through the plant at 50% of the plant height. The 2 diameter readings were taken at right angles to each other (one parallel and the other perpendicular to the transect line). Willow canopy volume was estimated by applying the height and 2 diameter measurements to a derivative of the basic ellipsoid volume formula, Canopy Volume = $2/3\pi$ Height (A/2 x B/2), where Height is the distance from the base of the plant to the tallest photosynthetically active material and A and B are the diameter readings taken at 50% of plant height with B perpendicular to A (Fig. 1).

The experiment was analyzed using a repeated measures analysis of variance (AOV) with plants as the subject, transects as the within-subject term, and observers and sample period as the between-subject factors (Vonesh and Chinchilli 1997). The model included 2- and 3-way interactions of observers, transects, and sample periods. Plants and transects were random terms. Observer was tested using the transect x observer interaction as the error term. Sample period was tested with the transect x sample period error term. Observer x sample period was tested with the error term from the transect x observer x sample period interaction. Transect x observer x sample period, observer x plant within transect, and sample period x plant within transect were tested with the residual error term. Since transects were randomly selected, the error terms testing transect, plant within transect, transect x observer, and transect x sample period were estimated using the appropriate expected mean squares (Dowdy and Wearden 1991, Vonesh and Chinchilli 1997). Duncan's New Multiple Range (DNMR) Test was used to compare means among and within observers and sample periods (Duncan 1955, Dowdy and Wearden 1991) when appropriate. All mean separations were conducted with an overall α of 0.05 and 12 degrees of freedom.

To compare the consistency and precision among and within observers, coefficients of variation were calculated by sample period for each observer. Since the coefficient of variation is a measure of the internal variability of an estimate, differences among sequential coefficient values for the same sample unit reflect a shift in the degree of observer error. Thus, smaller coefficient of variation values were interpreted to indicate greater precision in an estimate. Consistency across sample periods was considered to be explained by the degree of similarity in coefficient of variation values when AOV indicated non-significance.

Sample size calculations were conducted to estimate the number of 10 plant transects required to achieve a sampling precision (E) of ± 10, 20, or 30% of the mean total canopy volume of the willow population at the study sites with confidence intervals of 80, 90, or 95%. Desired sample sizes were estimated using the average coefficient of variation for each of the 4 observers estimated for sample periods 1 and 2 at each study site. The formula used to estimate sample size was: $n = t^2\ CV^2/E^2$ where t is the critical t-value evaluated at $\alpha/2$ and ∞ degrees of freedom; CV is the coefficient of variation; and E is the desired sampling precision (Zamora 1981).

Results

Willow Swamp Site

At the Willow Swamp site, differences among transects, and transect x observer, observer x sample period, and transect x observer x sample period interactions were not significant (P = 0.296, 0.846, 0.151, and 0.069, respectively). Observer A's estimate of mean canopy volume increased by 19% between sample periods 1 and 2, while the coefficients of variation changed from 26 to 29%, respectively (Table 1). Conversely, estimated mean canopy volume decreased by 3, 19, and 6% between sample periods 1 and 2 for observers B, C, and D, respectively (Table 1). Coefficients of variation also increased between sample periods 1 and 2 for observers B, C, and D (Table 1).

Observers varied significantly (P = 0.009) in their estimates of canopy volume at the Willow Swamp site. However, while the average canopy volume estimated by observer B was significantly different from the other observers, estimates among observers A, C, and D were not different (Table 1). The transect x sample period interaction was not significant (P = 0.493) for Willow Swamp. When mean canopy volume was pooled across observers, sample period 1 (81,043 ± 6,626 cm^3 SE; n = 20) did not vary (P = 0.814) from sample period 2 (79,599 ± 7,786 cm^3 SE; n = 20).

The average time to measure canopy volume along a transect decreased from sample period 1 to 2 for all observers. Observer D had the largest decrease averaging 17.2 minutes (SD = 5.07) per transect during sample period 1 compared to 9.3 minutes (SD = 1.3) during sample period 2. Observers A, B, and C averaged 11.1 ± 1.03, 8.4 ± 2.1, and 13.2 ± 3 minutes per transect to measure canopy volume during sample period 1, respectively. During sample period 2, the average time per transect decreased to 9.4 ± 0.5, 7.6 ± 2.1, and 9.6 ± 0.5 minutes for observers A, B, and C, respectively. The average time per transect among all observers for sample period 1 was 12.5 minutes (SD = 3.7) and decreased to 9.3 minutes (SD = 1.3) in sample period 2.

Garden Site

At the garden site, differences among transects, and transect x observer, observer x sample period, and transect x observer x sample period interactions were not significant (P = 0.493, 0.604, 0.06, and 0.163, respectively). Mean canopy volume decreased between sample periods 1 and 2 by 2, 10, and 5% for observers A, B, and D, respectively (Table 2). Conversely, the estimated mean canopy volume increased by nearly 17% for observer C. Coefficients of variation at the Garden site remained constant at 23% for observer A, increased for observers B and D, and decreased for observer C.

Observers varied significantly (P < 0.001) in their estimate of canopy volume for the Garden site (Table 2). Mean canopy volume estimates of observers A and D were similar and significantly different from the average volume estimates of observers B and C which were also similar. At the Garden site, the transect x sample period interaction was not significant (P = 0.854). When canopy volume estimates were pooled across observers, sample period 1 (159,187 ± 24,993 cm^3 SE; n = 20) did not vary (P = 0.510) from sample period 2 (157,512 ± 21,060 cm^3 SE; n = 20).

Table 1. Mean canopy volume (cm^3) for each observer by transect and sample period for measurements taken at Willow Swamp, 17 Jul. 1997.

Observer	Sample Period	Transect[1] Mean Canopy Volume ± SE: 1	2	3	4	5	Canopy Volume, Sample Period[2]: x̄ ± SE	Coeff. Var.	Observer[3]: x̄ ± SE
		(cm^3)							
A	1	76,826	75,905	50,636	84,105	107,286	78,952	26%	88,296
		± 17,825	± 21,055	± 14,503	± 15,879	± 26,689	± 9,069		± 9,344[a]
	2	88,857	85,140	62,487	133,232	118,486	97,640	29%	
		± 21,915	± 25,937	± 16,806	± 40,219	± 34,098	± 12,590		
B	1	65,459	66,388	52,663	67,793	63,250	63,111	10%	62,183
		± 17,801	± 17,813	± 17,225	± 19,129	± 12,330	± 2,714		± 928[b]
	2	56,877	59,143	44,918	59,519	85,821	61,256	24%	
		± 11,132	± 14,320	± 12,144	± 15,040	± 23,156	± 6,697		
C	1	99,156	105,055	62,701	107,102	83,739	91,550	20%	82,786
		± 26,219	± 25,649	± 16,437	± 18,446	± 20,383	± 8,293		± 8,764[a]
	2	58,617	76,876	38,861	56,929	138,830	74,022	52%	
		± 15,913	± 22,547	± 11,770	± 12,192	± 38,427	± 17,283		
D	1	96,663	72,403	53,774	106,905	123,054	90,560	30%	88,018
		± 25,884	± 18,692	± 11,272	± 34,089	± 40,370	± 12,335		± 9,482[a]
	2	93,565	67,966	40,864	107,008	117,976	85,476	36%	
		± 25,923	± 15,828	± 9,885	± 40,450	± 31,139	± 13,932		

[1]Transect mean canopy volume ± standard error of the mean (cm^3), n = 10; within observer means at transect level were not significantly different (P > 0.05).
[2]Sample period mean canopy volume ± standard error of the mean (cm^3), n = 5 (average of 5 transects); within observer means at the sample period level were not significantly different (P > 0.05)
[3]Mean canopy volume ± standard error of the mean (cm^3) by observer, n = 2 (average across sample periods); means among observers were significantly different (P < 0.05), likelettered means were not different using Duncan's New Multiple Range Test.

Table 2. Mean canopy volume (cm^3) for each observer by transect and sample period for measurements taken at the Garden site, 29 Aug. 1997.

Observer	Sample Period	Transect[1] Mean Canopy Volume ± SE: 1	2	3	4	5	Canopy Volume: Sample Period[2] $\bar{x}$ ± SE	Sample Period[2] Coeff. Var.	Observer[3] $\bar{x}$ ± SE
		(cm^3)							
A	1	282,806 ± 53,441	230,968 ± 35,356	174,950 ± 35,720	184,659 ± 66,488	165,855 ± 42,750	207,848 ± 21,837	23%	205,553 ± 2,295[a]
	2	271,511 ± 56,615	232,722 ± 35,080	65,315 ± 35,364	182,117 ± 70,017	164,624 ± 41,469	203,258 ± 21,101	23%	
B	1	160,323 ± 31,968	14,6618 ± 20,589	113,723 ± 20,561	144,915 ± 66,937	110,990 ± 31,588	135,314 ± 9,755	16%	128,469 ± 6,845[b]
	2	155,606 ± 24,166	14,7924 ± 21,111	82,162 ± 16,269	129,592 ± 43,554	92,840 ± 26,022	121,625 ± 14,656	27%	
C	1	153,231 ± 27,646	117,285 ± 21,431	73,947 ± 14,282	87,502 ± 31,367	71,479 ± 17,624	100,689 ± 15,457	34%	111,251 ± 10,563[b]
	2	132,352 ± 26,530	122,082 ± 19,896	110,457 ± 24,824	139,246 ± 47,126	104,932 ± 29,579	121,814 ± 6,438	12%	
D	1	249,283 ± 49,388	215,189 ± 34,561	163,514 ± 33,032	193,525 ± 45,405	142,970 ± 35,725	192,896 ± 18,752	22%	188,124 ± 4,772[a]
	2	243,754 ± 34,398	201,612 ± 29,208	173,541 ± 38,460	168,758 ± 53,373	129,091 ± 32,075	183,351 ± 19,020	23%	

[1]Transect mean canopy volume ± standard error of the mean (cm^3), n = 10; within observer means at transect level were not significantly different (P > 0.05).
[2] Sample period mean canopy volume ± standard error of the mean (cm^3), n = 5 (average of 5 transects); within observer means at the sample period level were not significantly different (P > 0.05).
[3]Mean canopy volume ± standard error of the mean (cm^3) by observer, n = 2 (average across sample periods); means among observers were significantly different (P < 0.05), like lettered means were not different using Duncan's New Multiple Range Test.

Sample Size

The average coefficient of variation among both sample periods for all observers was 28% (± 12.25 SD) for Willow Swamp and 22.5% (± 6.61 SD) for the Garden site. Our estimates of sample size were evaluated with the variation based on 5 transects comprised of 10 plants each. Consequently, the sample sizes reported here should be considered as the minimum estimated number of transects with 10 plants each required to meet experimental design restrictions. At Willow Swamp, sample sizes ranged between 2 and 31 transects depending on the level of desired precision and confidence level (Table 3). For the Garden site, the largest estimated sample size was 20 transects required to obtain an estimate within ± 10% of the population mean at the 95% confidence level (Table 3). The minimum viable number of transects estimated to be required at the Garden site was 2 (one transect does not provide an estimate of variability and, thus, is not a viable sample size).

Discussion

At Willow Swamp, 3 of the 4 observers did not have experience with this technique before taking measurements. Training included only a brief introduction on the identification of: a) the measurement plant, b) its photosynthetically active material, and c) where to place the measuring rods. Sampling error was compounded when several willows occurred on the same hummock together or with bog birch plants. Consequently, it was possible for an observer to mistakenly measure more or less plant, or a different plant at the second sample period. At the Garden site, these sources of observer error were controlled. Observers had gained experience from the Willow Swamp measurements and plant identification problems were eliminated.

Consistency, Precision, and Efficiency

The lack of significance in the AOV among the interaction terms at both sites indicated that observers were consistent in their estimates of mean canopy volume between sample periods. Observer consistency was also reflected by the degree of similarity in their respective canopy volume estimates and coefficients of variation across sample periods. Although mean canopy volume estimates within observers remained similar, there was an increase in the coefficients of variation between sample periods for all observers at Willow Swamp. While difficulty in identifying the same plant or the amount of plant measured between sample periods may have contributed to these differences, fatigue may have been an important factor as well. For example, observer C became ill during the second sample period possibly contributing to the larger difference

Table 3. Estimated number of transects of 10 plants each required to achieve sampling precision (E) of ± 10, 20, and 30% of the mean total canopy volume of the willow populations at the Willow Swamp and Garden sites at confidence levels of 80, 90, and 95%.

Site	Sampling Precision	Confidence Level 80%	90%	95%
Willow Swamp (CV = 28% ± 12.35)[1]	(%)	(Sample Size)		
	± 10	13	22	31
	± 20	4	6	8
	± 30	2	3	4
Garden (CV = 22.5% ± 6.61)				
	± 10	9	14	20
	± 20	3	4	5
	± 30	1[2]	2	3

[1]CV = coefficient of variation; coefficients presented in this table are the average CV of observers for both sample periods at each site (n = 8).
[2]Note that 1 transect does not provide an estimate of variability and, thus, is not a viable sample size.

between mean estimates (19%) and the increase in coefficients of variation (20–52%) for this observer.

At the Garden site, the within observer consistency and precision improved for all observers. Coefficient of variation values were lower at the Garden site than at Willow Swamp in 5 of 8 observations among observers. More importantly, differences in coefficient of variation values between sample periods for observers B, C, and D were smaller than at Willow Swamp. For observer A, however, coefficient of variation values remained constant at 23% between sample periods at the Garden site.

Efficiency is a function of both the precision and time required to obtain a reliable estimate. As the variation in the experimental material and observer error increases, sample size must increase rapidly to bring the precision of the estimate to within a desired percentage of the population mean at a given level of confidence. The more samples required to achieve a desired level of precision, the more time required to obtain the estimate. We found, under difficult conditions for estimating canopy volume, that the average coefficient of variation was about 28%. With this level of precision, we estimated between 2 and 31 transects would be required depending on the level of desired precision (± 10, 20, and 30%) and confidence (80, 90, and 95%). These are not unreasonably large sample sizes given that the average time estimated to complete a transect was between 9 and 13 minutes. Consider also, that the precision increased and the estimated sample size decreased when the shrubs were well defined and easily distinguishable.

Other techniques commonly used to estimate shrub cover or volume do not appear to be as precise or efficient by comparison. For example, coefficients of variation for shrub cover estimated by the line-intercept method in different community types have ranged from 18.5 to 86.8% (Heady et al. 1959, Kinsinger et al. 1960). Estimated sample sizes for the line-intercept method have varied between 14 and 290 transects (Heady et al. 1959, Kinsinger et al. 1960) with each transect requiring, on average, 16 minutes to complete (Heady et al. 1959). Zamora (1981) proposed a method using a 3-m^3 frame to estimate canopy volume based on midpoint averages of eight volume size classes. He reported coefficients of variation of 63 to 168% for shrub communities in 3 different grand fir [*Abies grandis* (Douglas ex D. Don in Lambert) Lindley] clear cuts in north-central Idaho. Subsequently, he estimated that between 1,084 and seven, 3-m^3 plots were required to achieve a desired level of precision and confidence (± 10 and 30% of the mean at 95 and 80% confidence level, respectively). Although Zamora (1981) did not estimate time per plot directly, he did report that, under highly diverse composition and complex structure, 50 plots required 3 man hours to complete.

Differences Among Observers

In most cases, while not desirable, observers frequently vary in estimates of the same sample unit. Our results confirm that observers can vary in their mean estimates. However, observer differences were not as pronounced at Willow Swamp as they were at the Garden site. Specifically, at Willow Swamp, mean estimates by observers A, C, and D were within 0.3 to 6% of each other and were not statistically different. Observer B, however, differed by 30, 29, and 25% from observers A, D, and C, respectively. Thus, observer B accounted for most of the differences among observers at Willow Swamp. Conversely, at the Garden site, mean estimates of willow volume by pairs of observers who were not statistically different were more divergent. For example, observers B and C were 13% different from each other while observers A and D were less than 9% different.

The divergence of agreement on the mean canopy volume estimates among observers may have been the result of training. Smith (1944) found that differences among observers were greater after a week's training. He suggested that this was caused by a general inclination among observers to become more conservative as a result of discussion and comparison of estimates. This may well have been a factor in our study. Although effort was made to restrict comparisons among mean estimates at both sites, discussion among observers was inevitable. Note, however, that although training seemingly contributed to a greater divergence in mean estimates among observers at the Garden site, within observer mean estimates were less variable and were not significantly different between sample periods.

Importantly, there was no transect by sample period interaction among observers. Moreover, the estimate of mean canopy volume pooled across observers did not vary between sample periods. This suggests that canopy volume estimates can be made by an individual managing a local area, or by a team of individuals sampling over a large geographical area with the same level of precision.

Conclusions

Conclusions are: a) Willow canopy volume estimates will likely vary between individuals using this technique. b) Estimates of canopy volume made by a single individual will be consistent and precise. Moreover, differences in canopy volume estimates made by a single individual appear to decrease with training. c) When observations of each individual are pooled, estimates of canopy volume appear to be reliable and precise supporting a team concept to monitoring broad geographical areas using this technique. Mean canopy volume did not vary significantly across sample periods when estimates were pooled among observers.

Management Implications and Recommendations

In using the canopy volume method described here, it is recommended that managers first clearly define management objectives for a site or sites. This will help define the desired sampling intensity required to monitor trends toward meeting stated objectives. Permanent transects should be placed randomly throughout the community. Plants along the transects should be randomly located and permanently marked for identification. The basal perimeter of each plant should be clearly defined. This can be accomplished by wrapping colored wire or plastic ties around the outside basal stems of the shrub (Thorne 1998). Permanently marking the location and basal perimeter of each plant should improve the precision of consecutive canopy volume estimates.

Using this method, managers can better describe and monitor trends in the structural diversity of shrub communities. This canopy volume technique appears to be sensitive to changes in plant size over short time intervals (Thorne 1998), so it can be used to evaluate annual impacts to shrub communities such as herbivory, disease, drought, and various land uses. Other uses might include evaluating wildlife habitat quality and forage production (Taylor 1986, Manoukian 1994).

In monitoring our rangeland resources, a methodology that is efficient, precise, and repeatable is clearly desirable. This canopy volume technique can be applied with minimal training and is precise, efficient, and repeatable. It can also be consistently applied by an individual observer as well as by a team of observers to sample larger geographical areas.

Literature Cited

Bauer, H.L. 1936. Moisture relations in the chaparral of the Santa Monica Mountains, California. Ecol. Monogr. 6:409–454.

Bryant, F.C. and M.M. Kothmann. 1979. Variability in predicting edible browse from crown volume. J. Range Manage. 32:144–146.

Creamer, W.H. IV. 1991. Prediction of available forage production of big sagebrush. M.S. Thesis, Montana State Univ., Bozeman, Mont.

Cooper, C.F. 1957. The variable plot method for estimating shrub density. J. Range Manage. 10:111–115.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43–64.

Daubenmire, R. 1968. Plant communities-a textbook of synecology. Harper and Row, N.Y.

Dowdy, S., and S. Wearden. 1991. Statistics for research. 2nd ed. John Wiley & Sons, N.Y.

Duncan, D.B. 1955. Multiple range and multiple F tests. Biometrics 11:1–42.

Fisser, H.G. 1961. Variable plot, square foot plot, and visual estimate of shrub crown cover measurements. J. Range Manage. 14:202–207.

Heady, H.F., R.P. Gibbens, and R.W. Powell. 1959. A comparison of the charting, line intercept, and line point methods of sampling shrub types of vegetation. J. Range Manage. 12:180–188.

Johnston, A. 1957. A comparison of the line interception, vertical point quadrat, and loop methods as used in measuring basal area of grassland vegetation. Can. J. Plant Sci. 37:34–42.

Kinsinger, F.E., R.E. Eckert, and P.O. Currie. 1960. A comparison of the line-interception, variable-plot and loop methods as used to measure shrub-crown cover. J. Range Manage. 13:17–21.

Lyon, J.L. 1968. Estimating twig production of serviceberry from crown volumes. J. Wildl. Manage. 32:115–119.

Manoukian, M.E. 1994. Evaluation of tall willows (*Salix* Spp.) within a livestock grazing allotment in southwest Montana. M.S. Thesis, Montana State Univ., Bozeman, Mont.

Meiman, P.J. 1996. Effects of large ungulate herbivory on willow (*Salix*) in mountain rangelands of northern Wyoming. M.S. Thesis, Univ. Wyoming, Laramie, Wyo.

Myers, L.H. 1989. Riparian area management: Inventory and monitoring riparian areas. U.S. Dept. Int., Bur. Land Manage.,TR 1737-3 Denver, Colo.

Nelson, E.W. 1930. Methods of studying shrubby plants in relation to grazing. Ecol. 11:764–769.

Parker, K.W. 1951. A method for measuring trend in range condition on national forest ranges. U.S. Forest Serv., Washington, D.C.

Peek, J.M. 1970. Relation of canopy area and volume to production of three woody species. Ecol. 51:1098–1101.

Pickford, G.D., and G. Stewart. 1935. Coordinate method of mapping low shrubs. Ecol. 16:257–261.

Rittenhouse, L.R. and F.A. Sneva. 1977. A technique for estimating big sagebrush production. J. Range Manage. 30:68–70.

Smith, A.D. 1944. A study of the reliability of range vegetation estimates. Ecol. 25:441–448.

Taylor, D.M. 1986. Effects of cattle grazing on passerine birds nesting in riparian habitat. J. Range Manage. 39:254–258.

Thorne, M.S. 1998. Effects of large ungulate herbivory on willow (*Salix*) canopy volume on mountain rangelands of northern Wyoming. M.S. Thesis, Univ. Wyoming, Laramie, Wyo.

Uresk, D.W., R.O. Gilbert, and W.H. Rickard. 1977. Sampling big sagebrush for phytomass. J. Range Manage. 30:311–314.

Vonesh, E.F., and V.M. Chinchilli. 1997. Linear and nonlinear models for the analysis of repeated measurements. Marcel Dekker, Inc. New York, N.Y.

Zamora, B.A. 1981. An approach to plot sampling for canopy volume in shrub communities. J. Range Manage. 34:155–156.

J. Range Manage.
55: 242-252 May 2002

White-tailed deer habitats in the central Black Hills

CHRISTOPHER S. DEPERNO, JONATHAN A. JENKS, STEVEN L. GRIFFIN, LESLIE A. RICE, AND KENNETH F. HIGGINS

Authors are Deer Project Leader, Minnesota Department of Natural Resources, Farmland Wildlife Populations and Research Group, Madelia, Minn. 56062; Professor, Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, S.D. 57007; Wildlife Biologist, South Dakota Department of Game, Fish and Parks, 3305 W. South Street, Rapid City, S.D. 57702: Retired Senior Wildlife Biologist, South Dakota Department of Game, Fish and Parks, 3305 W. South Street, Rapid City, S.D. 57702: Professor, South Dakota Cooperative Fish and Wildlife Research Unit, USGS-BRD, South Dakota State University, Brookings, S.D. 57007.

Abstract

White-tailed deer (*Odocoileus virginianus dacotensis* Zimm.) numbers in the central Black Hills have declined since the middle 1970s. Population status has been documented by a decline in hunter success, deer reproductive success, and fawn survival. Most management agencies believe habitat deterioration is the primary cause of population decline in the Black Hills. We evaluated habitat selection for a white-tailed deer herd in the central Black Hills of South Dakota and Wyoming. From July 1993–July 1996, 73 adult and yearling doe and 12 adult and yearling buck white-tailed deer were radiocollared and visually monitored. Habitat information was collected at 4,662 white-tailed deer locations and 1,087 random locations. During winter, white-tailed deer selected ponderosa pine- (*Pinus ponderosa* P. & C. Lawson) deciduous and burned pine cover types. Overstory-understory habitats selected included pine/grass-forb, pine/bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), pine/snowberry (*Symphoricarpos albus* L.), burned pine/grass-forb, and pine/shrub habitats. Structural stages selected included sapling-pole pine stands with > 70% canopy cover, burned pine sapling-pole and saw-timber stands with < 40% canopy cover. During summer, white-tailed deer selected pine-deciduous, aspen (*Populus tremuloides* Michx.), aspen-coniferous, spruce (*Picea glauca* (Moench) Voss), and spruce-deciduous cover types. Overstory-understory habitats selected included pine/juniper (*Juniperus communis* L.), aspen/shrubs, spruce/juniper, and spruce/shrub habitats. Structural stages selected included pine, aspen, and spruce sapling pole stands with all levels (0–40%, 41–70%, 71–100%) of canopy cover. Results supported low habitat quality as a factor involved with the decline of the deer population. We recommend that habitat management techniques, such as aspen regeneration and prescribed burns, be used to improve the habitat base in the central Black Hills.

This study was supported by Federal Aid to Wildlife Restoration Fund, Project W-75-R through the South Dakota Department of Game, Fish and Parks (Study Numbers 7563 and 7564). D. Flory, J. McCormick, D. Knowlton, S. Clark, B. Bol, D. Beck, and B. A. Hippensteel provided field assistance. We thank L. D. Flake, M. K. Johnson, G. E. Larson, and J. Vandever for their review of this manuscript. T. Klinkner and J. Giudice provided editorial assistance. We wish to thank the USDA, Forest Service, Pactola and Harney Ranger Districts and all landowners that allowed access to their property throughout this study.

Manuscript accepted 7 Sep. 01.

Resumen

El número de venados cola blanca (*Odocoileus virginianus dacotensis* Zimm.) del área central de Black Hills ha disminuido desde mediados de la década de los 70's. El estado de la población ha sido documentado por una reducción en el éxito de la cacería, la reproducción exitosa del venado y la sobrevivencia de los cervatos. La mayoría de las agencias de manejo creen que el deterioro del hábitat es la causa principal de la disminución de la población en Black Hill. Evaluamos la selección de hábitat por un hato de venados cola blanca en la región central de Black Hill en South Dakota y Wyoming. De Julio de 1993 a Julio de 1996, a 73 hembras adultas y juveniles y 12 machos adultos y juveniles de venado cola blanca se les coloco un radiotransmisor y se monitorearon visualmente. La información del hábitat se colectó en 4,662 localidades de venado cola blanca y 1,078 localidades aleatorias. Durante el invierno, el venado cola blanca seleccionó los tipos de cobertura de pino ponderosa (*Pinus ponderosa* P. & C. Lawson) deciduo y quemados. Los hábitats con cobertura superior/inferior seleccionados incluyeron pino/zacate-hierba, pino/ "Bearberry"(*Arctostaphylos uva-ursi* (L.) Spreng.), pino/ "Snowberry" (*Symphoricarpos albus* L.), pino quemado/zacate-hierba y pino/arbusto. Las etapas estructurales seleccionados incluyeron poblaciones de plántulas de pino con una cobertura de copa mayor al 70%, poblaciones de plántulas de pino quemado y poblaciones de pino aserrado con menos del 40% de cobertura. Durante el verano, el venado cola blanca seleccionó coberturas del tipo pino-deciduo, álamo (*Populus tremuloides* Michx.), álamo-coníferas, pícea (Picea glauca (Moench) Voss) y pícea-deciduo. Los hábitats de cobertura alta-baja seleccionados incluyeron hábitats de pino/enebro (*Juniperus communis* L.), álamo/arbustos, pícea/enebro y pícea/arbustos. Los niveles estructurales seleccionados incluyeron poblaciones de plántulas de pino, álamo y pícea con todos los niveles (0–40%, 41–70%, 71–100%) de cobertura de copa. Los resultados apoyan la baja calidad del hábitat como un factor involucrado en la disminución de la población de venados. Recomendamos que técnicas de manejo del hábitat, tales como la regeneración del álamo y los fuegos prescritos, sean utilizadas para mejorar el hábitat base en la región central de Black Hills.

Key Words: aspen regeneration, Black Hills, habitat quality, habitat selection, *Odocoileus virginianus dacotensis*, prescribed burns, South Dakota, white-tailed deer, Wyoming

White-tailed deer (*Odocoileus virginianus dacotensis* Zimm.) are an important economic resource within the Black Hills of South Dakota and throughout North America. Williamson and Doster (1981) estimated that each white-tailed deer in North America generates about $1,657 per year through consumptive and non-consumptive uses. Restaurants, lodges, convenience stores, and gas stations receive income from visitors attempting to observe white-tailed deer (Martin and Gum 1978, Wallace et al. 1991). Annually, the Black Hills deer herd generates over $2 million dollars, in addition to license fees (Richardson and Peterson 1974), with each resident hunter spending approximately $372/year (United States Fish and Wildlife Service 1993).

White-tailed deer numbers in the central Black Hills have declined since the middle 1970's (Griffin et al. 1992, Griffin 1994) and DePerno (1998) estimated this population declined by 10–15% per year from 1993–1996. Population status has been documented by a decline in hunter success (McPhillips and Rice 1991), deer reproductive success (Rice 1984, Hauk 1987, McPhillips 1990), and fawn survival (Rice 1979). Additionally, because reproductive and recruitment rates have not increased with herd reductions, it appears that deer carrying capacity in the central Black Hills has declined (DePerno et al. 2000). Griffin et al. (1992) reported that most management agencies believe the low productivity affecting the central Black Hills deer herd was directly related to long-term habitat deterioration.

We evaluated habitat selection by white-tailed deer in the central Black Hills of South Dakota and Wyoming. Habitats are differentiated by tree size and amount of overstory cover present; characteristics that represent age and structural class of vegetation within forested areas (Smith 1962). Documentation of habitat use by bucks and does during winter and summer is necessary to develop area-specific strategies for maintaining deer populations. For example, in the northern Black Hills, many habitats used by white-tailed deer differ from their relative availability on summer and winter ranges (Kennedy 1992). During winter, Moen (1968, 1976) concluded that dense pine stands are important to deer; these stands minimize energy expenditures for thermoregulation by reducing windchill and radiant heat loss (Parker and Gillingham 1990). During spring and summer, because condition and type of cover used for fawning may influence the survival rate of fawns, does seek isolation in areas where hiding cover is abundant (King and Smith 1980, Fox and Krausman 1994). We hypothesized that white-tailed deer in the central Black Hills select habitats on summer range that contain abundant forage (stands with low overstory cover and significant shrub biomass) and cover (stands with high overstory cover and significant shrub biomass) necessary to enhance reproductive success, while selecting habitats on winter range that contain abundant forage and cover necessary to reduce thermal stress.

Study Area

The Black Hills is an isolated mountainous area in western South Dakota and northeast Wyoming that extends approximately 190 km north to south and 95 km east to west (Petersen 1984). Elevation of the Black Hills ranges from 973–2,202 m above mean sea level (Orr 1959, Turner 1974). Annual mean temperatures are typical of a continental climate and range from 5–9° C with extremes of –40–44° C (Thilenius 1972). Mean annual precipitation ranges from 45–66 cm (Orr 1959) and yearly snowfall may exceed 254 cm at higher elevations (Thilenius 1972).

The central Black Hills study area (43° 52' N to 44° 15' N–104° 07' W to 103° 22' W) includes Pennington and Lawrence counties of South Dakota and Crook and Weston counties of Wyoming (Fig. 1). The study area is composed of separate winter and summer ranges used by migratory white-tailed deer (DePerno 1998, DePerno et al. 2000, Griffin et al. 1995, 1999). In the central Black Hills, typical autumn migration for white-tailed deer is in a southeast direction from high elevation summer ranges to low elevation winter ranges and generally occurs between August and February (DePerno 1998, Griffin et al. 1999). Typical spring migration is in a northwest direction from low elevation winter ranges to high elevation summer ranges and generally occurs between 17 and 23 May (DePerno 1998, Griffin et al. 1999). Public land within the study area is managed by the United States Department of Agriculture Forest Service, within the Pactola, Harney, and Elk Mountain Ranger Districts, primarily for timber production and livestock grazing (1 June–31 October).

Winter range consists primarily of monotypic stands of ponderosa pine (*Pinus ponderosa* P. & C. Lawson) interspersed with stands of burned pine, quaking aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.) (McIntosh 1949, Orr 1959,

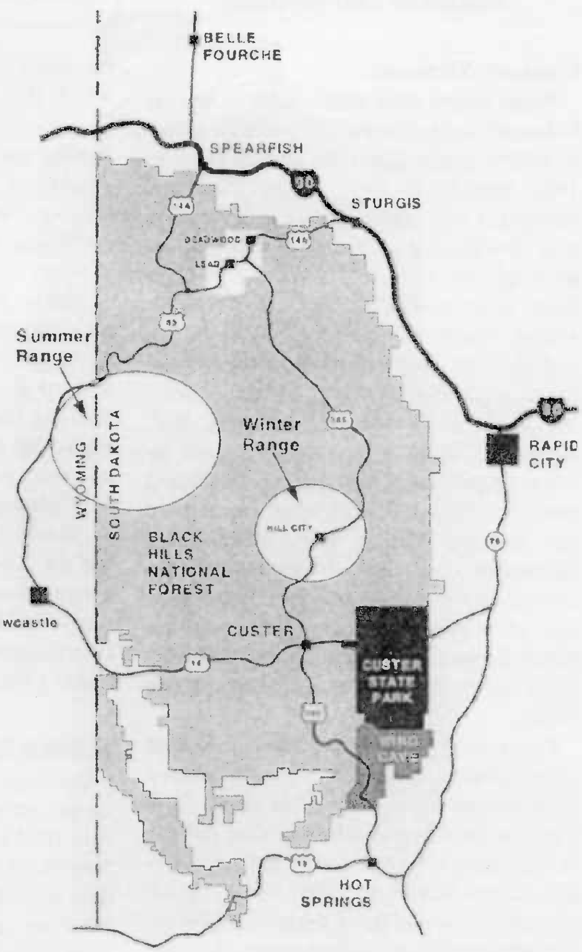


Fig. 1. Location of winter and summer ranges of white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Thilenius 1972, Richardson and Petersen 1974, Hoffman and Alexander 1987). Primary understory vegetation on winter range is characterized by snowberry (*Symphoricarpos albus* L.), spiraea (*Spiraea betulifolia* Pallas), serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex. M. Roemer), woods rose (*Rosa woodsii* Lindl.), bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), and cherry species (*Prunus* spp.). Summer range consists primarily of ponderosa pine and white spruce (*Picea glauca* (Moench) Voss) interspersed with small stands of quaking aspen (McIntosh 1949, Orr 1959, Thilenius 1972, Richardson and Petersen 1974, Hoffman and Alexander 1987). Understory vegetation on summer range is characterized by Oregon grape (*Berberis repens* Lindl.), juniper (*Juniperus communis* L.), bearberry, snowberry, spiraea, and serviceberry.

Appendix A. Common and scientific names of trees and shrubs included in the 'other shrubs' category.

Bearberry	*Arctostaphylos uva-ursi* ((L.) Spreng.)
Cherry species	*Prunus* spp.
Currants	*Ribes* spp.
Fleshy hawthorn	*Crataegus succulenta* (Shrad. ex Link)
Juniper	*Juniperus communis* (L.)
Leadplant	*Amorpha canescens* (Pursh)
Mountain balm	*Ceanothus velutinus* (Dougl. ex Hook.)
Mountain meadowsweet	*Spiraea betulifolia* (Pallas)
Oregon grape	*Berberis repens* (Lindl.)
Paper birch	*Betula papyrifera* (Marsh.)
Ponderosa pine	*Pinus ponderosa* (P. & C. Lawson)
Quaking aspen	*Populus tremuloides* (Michx.)
Red raspberry	*Rubus idaeus* (L.)
Russet buffaloberry	*Shepherdia canadensis* ((L.) Nutt.)
Serviceberry	*Amelanchier alnifolia* ((Nutt.) Nutt. ex M. Roemer)
Snowberry	*Symphoricarpos albus* (L.)
Wartleberry	*Vaccinium scoparium* (Leib ex Coville)
White spruce	*Picea glauca* ((Moench) Voss)
Willow	*Salix* spp.
Woods rose	*Rosa woodsii* (Lindl.)
Yellow rose	*Potentilla fruticosa* ((Pursh) A. Love)

Materials and Methods

Capture Methods

White-tailed deer were captured during February and March 1993–1996 using modified, single-gate Clover traps (Clover 1956) baited with fresh alfalfa (*Medicago sativa* L.) hay. Deer were captured on 4 trap sites located northeast, northwest, and west of Hill City, S.D., on the McVey Burn deer winter range (Griffin et al. 1995). Adult and yearling doe (n = 73) and buck (n = 12) white-tailed deer were fitted with radiocollars (Telonics Inc., Mesa, Ariz.; Lotek Engineering, Inc. Ontario, Canada), ear-tagged, aged by lower incisor wear, and released. Captured fawn white-tailed deer were ear-tagged and released (Griffin et al. 1995). Each radiocollar used in this study contained a mercury tip switch that enabled determination of head-up and head-down position based upon signal intensity and differing pulse intervals (Beier and McCullough 1988).

From July 1993–July 1996, individual radiocollared deer were visually located from the ground 1–3 times per week. Deer were radiotracked at different time periods to maximize observations of diurnal activities (Kernohan et al. 1996) and to obtain adequate sample sizes without violating the assumption of independent observations (White and Garrott 1990). Kernohan et al. (1996) demonstrated no differences between diurnal and 24-hour habitat use for white-tailed deer. Within the central Black Hills, steep hills, deep draws, and long migration distances limited data collection activities to diurnal, visual observations of deer and prevented the use of other techniques (e.g., triangulation) for obtaining radiolocations. Furthermore, because of the terrain and inaccessibility of many areas, attempts at spotlighting radiocollared deer to obtain nocturnal data were inefficient and represented a bias toward deer that were more accessible. Activity (feeding and bedding) was determined by radio signal intensity and speed of the pulse intervals (Beier and McCullough 1988, Hansen et al. 1992, Weckerly 1993). Deer locations were plotted on 7.5-minute USGS topographical maps (scale, 1:24,000) and assigned Universal Transverse Mercator (UTM) coordinates (Edwards 1969, Grubb and Eakle 1988).

Habitat Selection

Because separate winter and summer ranges are used by migratory white-tailed deer (DePerno 1998, DePerno et al. 2000, Griffin et al. 1995, 1999), we stratified data according to seasonal elevation shifts made by each individual each year (Apps et al. 2001) and classified each deer location and the corresponding habitat information as either winter or summer range. Habitat information was collected from 400-m^2, circular plots centered on each deer observation site (providing the location of the radiocollared deer was visually determined without disturbing the animal) and, to obtain a measure of relative habitat availability, at computer generated random locations (i.e., sampled throughout the study area) (Marcum and Loftsgaarden 1980, Kennedy 1992). General information recorded at each location included: UTM location (north and east), and dominant overstory tree species along with the most prominent understory vegetation. If $\geq$ 2 tree species provided canopy cover, the species that provided the largest amount of cover was recorded as the primary forest species; remaining species were recorded as secondary species.

Additional habitat characteristics recorded at each location included: overstory canopy cover (%), basal area (m^2/ha), diameter at breast height (DBH) (cm), habitat association (pine, spruce, aspen), and vegetation structural stage. Percent overstory canopy cover was measured using a spherical densiometer (Lemmon 1956). Basal area, the cross sectional area of trees at breast height, was determined using a 10-factor angle gauge (Hovind and Reick 1970). Diameter at breast height of each tree included in the basal area count was measured, 1.37 m above the ground (Ford-Robertson 1971), to the nearest centimeter using a diameter tape. Vegetation structural stage units,

Table 1. Percent forest type availability and use by doe and buck white-tailed deer during winter and summer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Forest Type	Winter			Summer		
	Does (n = 1319)	Bucks (n = 146)	Availability (90 % CI) (n = 533)	Does (n = 1496)	Bucks (n = 181)	Availability (90% CI) (n = 563)
Pine	68.5	68.5	72.8 (67.6 – 77.4)	44.7 –	54.7	58.1 (52.7 – 63.2)
Pine/Deciduous	14.3 +[1]	10.1	8.4 (5.6 – 11.8)	20.9 +	15.5 +	9.4 (6.5 – 12.9)
Aspen	2.3	1.3	2.1 (0.8 – 4.1)	5.4 +	3.9	2.3 (1.0 – 4.3)
Aspen/Coniferous	2.0	2.0	2.6 (1.2 – 4.8)	8.8 +	7.2 +	3.6 (1.8 – 5.9)
Spruce	0.1 –	0.0 –	0.8 (0.1 – 2.2)	13.2 +	11.6	8.9 (6.1 – 12.2)
Spruce/Deciduous	0.0 –	0.0 –	0.6 (0.0 – 1.9)	5.2 +	6.6 +	1.1 (0.3 – 2.6)
Burned Pine	6.4 +	16.8 +	1.1 (0.3 – 2.8)	0.1	0.0	0.0 (0.0 – 0.8)
Meadow	6.4 –	1.3 –	11.6 (8.4 – 15.5)	1.8 –	0.6 –	16.7 (12.9 – 20.9)

[1]A positive sign (+) indicates significant habitat selection and a negative sign (-) indicates significant habitat avoidance. Significant levels for 90% confidence intervals were determined using the Bonferroni method (Neu et al. 1974, Byers et al. 1984).

which followed the Black Hills National Forest inventory system, were based on dominant overstory tree species, percent overstory canopy cover, and average DBH (Buttery and Gillam 1983, Rumble and Anderson 1992, 1993). Dominant tree species included ponderosa pine, spruce, and aspen. Meadow and burned pine habitats also were included. Pine, burned pine, spruce, and aspen stands were categorized based on stand age (Buttery and Gillam 1983). Structural stage categories included: 1 = grass/forb - 0 cm DBH; 2 = shrub/sapling - < 12.7 cm DBH; 3 = pole-timber - 12.7 - 22.8 cm DBH, and 4 = saw-timber - > 22.8 cm DBH. Structural stage categories 3 and 4 were further separated by percent canopy cover into: A = 0 - 40%, B = 41–70%, and C = 71–100% (e.g., A3B represents an aspen pole-stand with 41–70% canopy cover) (Kennedy 1992, DePerno 1998).

The overstory-understory relationships for pine, spruce, and aspen associations were determined by combining overstory characteristics (i.e., dominant tree species present, percent overstory canopy cover, basal area, average DBH) with dominant understory species present. Dominant understory species were determined in 15, 1-m^2 plots systematically spaced within the 400-m^2 area surrounding and including plot center (Daubenmire 1959, Kennedy 1992). Percent ground cover of grass, forbs, and shrubs < 1 m in height was visually estimated for each plot using the midpoint method as described by Daubenmire (1959).

Analytical Methods

Forest type, overstory-understory habitat, and structural stages were pooled across individuals, years, and activities by season. Deer locations were pooled for all

Fig. 2. Burned pine habitat on winter range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Fig. 3. Aspen habitat on summer range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Fig. 4. Aspen/coniferous habitat on summer range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Fig. 5. Burned pine/litter habitat on winter range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

years of the study because of high seasonal site fidelity (Progulske and Baskett 1958, Ozoga et al. 1982, Tierson et al. 1985, Kennedy 1992, Nelson 1995, Griffin et al. 1999). Because sufficient observations per animal ($\bar{x} = 52.96 \pm 5.20$) were recorded (Alldredge and Ratti 1986, 1992) and because habitat availability was assumed to be equal for all radiocollared animals, a chi-square test of homogeneity was used to determine differences between expected and observed distributions of forest type, overstory-understory habitat, and structural stage (Jelinski 1991, Kennedy 1992, McClean et al. 1998). Selection for a particular cover type, overstory-understory habitat, or structural stage was defined as use significantly greater than availability, while avoidance was defined as use significantly less than availability (Neu et al. 1974, Byers et al. 1984, Kennedy 1992). Significance levels for 90% confidence intervals were determined using the Bonferroni method (Neu et al. 1974, Byers et al. 1984). All analyses were performed using SYSTAT (Wilkinson 1990).

Results

Between July 1993 and July 1996, 4,089 and 573 radiolocations were obtained for does and bucks, respectively. To obtain a measure of relative habitat availability, habitat information was collected at 1,087 computer generated random locations sampled throughout the study area. Excluded from analyses were data on 1 radiocollared buck that remained on winter range throughout the year and 1 radiocollared doe that demonstrated an abnormal migration pattern (DePerno et al. 1997).

Forest Type

Forest type availability varied between winter and summer ranges ($\chi^2 = 68.56$, df = 7, $P < 0.001$), and use of forest types (Table 1) differed for does and bucks compared to forest type availability during winter ($\chi^2 = 66.59$, df = 7, $P < 0.001$, $\chi^2 = 72.03$, df = 7, $P < 0.001$) and summer ($\chi^2 = 238.77$, df = 7, $P < 0.001$, $\chi^2 = 30.32$, df = 7, $P < 0.001$).

During winter, pine/deciduous and burned pine forests (Fig. 2) were selected ($P < 0.05$), whereas spruce, spruce/deciduous, and meadows were avoided ($P < 0.05$) by does; remaining habitats were used in proportion to their availabilities. Buck use of burned pine forest was nearly 3-times that of does and buck use of pine/deciduous habitat was less ($P < 0.05$) than does and not significantly different from its availability. During summer, pine/deciduous, aspen (Fig. 3), aspen/coniferous (Fig. 4), spruce, and spruce/deciduous habitats were selected ($P < 0.05$), whereas pine and meadow habitats were avoided ($P < 0.05$) and burned pine was used in proportion to its availability by does. Bucks selected ($P < 0.05$) pine/deciduous, aspen/coniferous, and spruce/deciduous habitats, while avoiding ($P < 0.05$) meadows; remaining habitats were used in proportion to their availabilities. Overall, deer selected forest types that comprised only 10% of the winter range and 25% of the summer range.

Overstory/Understory Type

Availability of overstory-understory types differed ($\chi^2 = 58.89$, df = 14, $P < 0.001$) between summer and winter range. Overstory/understory use differed (Table 2) for does compared to availability during winter ($\chi^2 = 116.16$, df = 14, $P < 0.001$)

Table 2. Percent overstory-understory availability and use by doe and buck white-tailed deer during winter and summer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Forest Type	Winter Does (n = 1000)	Winter Bucks (n = 124)	Winter Availability (90 % CI) (n = 470)	Summer Does (n = 1387)	Summer Bucks (n = 177)	Summer Availability (90% CI) (n = 466)
Pine/Grass/Forb	45.3 +[1]	37.9 +	14.9 (10.7 – 19.7)	22.5 –	32.8	37.1 (31.0 – 43.3)
Pine/Bearberry	2.0 +	11.3 +	0.2 (0.0 – 1.6)	5.8 –	9.0	9.4 (6.1 – 13.6)
Pine/Juniper	0.0	0.8	0.0 (0.0 – 1.1)	24.3 +	16.4 +	6.7 (3.8 – 10.3)
Pine/Snowberry	10.1 +	1.6 +	0.2 (0.0 – 1.6)	0.7	0.6	0.6 (0.0 – 2.4)
Burned Pine/Grass/Forb	6.8 +	17.7 +	0.0 (0.0 – 1.1)	0.1	0.0	0.0 (0.0 – 1.1)
Burned Pine/Litter	25.4 –	22.6 –	78.7 (73.0 – 83.5)	12.0 –	6.8 –	25.8 (20.3 – 31.5)
Pine/Other Shrubs[2]	5.4 +	4.0 +	0.2 (0.0 – 1.6)	2.3	5.1 +	0.9 (0.1 – 2.7)
Aspen/Grass/Forb	2.3	2.4	3.0 (1.2 – 5.7)	8.6	7.9	5.4 (2.9 – 8.7)
Aspen/Litter	0.5	0.8	1.5 (0.3 – 3.6)	1.0	0.6	0.4 (0.0 – 2.0)
Aspen/Other Shrubs[2]	2.1	0.8	1.1 (0.2 – 3.0)	3.8 +	2.8 +	0.4 (0.0 – 2.0)
Spruce/Grass/Forb	0.1	0.0	0.0 (0.0 – 1.1)	7.6	7.4	5.8 (3.2 – 9.3)
Spruce/Juniper	0.0	0.0	0.0 (0.0 – 1.1)	4.2 +	4.0 +	0.9 (0.1 – 2.7)
Spruce/Wartleberry	0.0	0.0	0.0 (0.0 – 1.1)	3.1	1.7	2.2 (0.7 – 4.6)
Spruce/Litter	0.0	0.0	0.2 (0.0 – 1.6)	2.2	1.7 –	4.3 (2.1 – 7.4)
Spruce/Other Shrubs[2]	0.0	0.0	0.0 (0.0 – 1.1)	2.0 +	3.4 +	0.2 (0.0 – 1.6)

[1]A positive (+) sign indicates significant habitat selection and a negative sign (-) indicates significant habitat avoidance. Significance levels for 90% confidence intervals was determined using the Bonferroni method (Neu et al. 1974, Byers et al. 1984).
[2]See Appendix A for a list of other shrubs.

and summer (χ^2 = 203.11, df = 14, P < 0.001), and for bucks during winter (χ^2 = 65.31, df = 14, P < 0.001). During summer, overstory-understory habitats used by bucks did not differ (χ^2 = 10.39, df = 14.0, P = 0.73) from habitat availability.

During winter, pine/grass/forb, pine/bearberry, pine/snowberry, burned pine/grass/forb, and ponderosa pine/other shrubs (Appendix A) were selected (P < 0.05), whereas burned pine/litter (Fig. 5) was avoided (P < 0.05) by does and bucks;

Table 3. Percent structural stage availability and use by doe and buck white-tailed deer during summer and winter in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Habitat[1]	Winter Does (n = 477)	Winter Bucks (n = 47)	Winter Availability (90% CI) (n = 532)	Summer Does (n = 786)	Summer Bucks (n = 99)	Summer Availability (90% CI) (n = 562)
P3A	9.6	4.3 –	8.5 (5.3 – 12.4)	7.3	10.1 +	5.9 (3.3 – 9.2)
P3B	15.9	36.2 +	13.7 (9.6 – 18.4)	10.8	13.1 +	7.7 (4.7 – 11.3)
P3C	22.2 +[2]	25.5 +	14.7 (10.5 – 19.5)	10.4 +	12.1 +	4.8 (2.5 – 7.9)
P4A	10.9	10.6	9.2 (5.9 – 13.3)	17.2	23.2 +	14.2 (10.2 – 18.9)
P4B	12.4 –	8.5 –	17.1 (12.6 –22.2)	12.9 –	9.1 –	22.1 (17.1 – 27.4)
P4C	9.2 –	0.0 –	19.2 (14.4 – 24.4)	7.0 –	3.0 –	11.9 (8.2 – 16.3)
A2	0.6	0.0 –	0.8 (0.1 – 2.5)	1.3	0.0	0.2 (0.0 – 1.4)
A3A	0.6	0.0 –	0.6 (0.0 – 2.2)	2.5 +	4.0 +	0.5 (0.0 – 2.1)
A3B	0.6	0.0 –	1.1 (0.2 – 3.1)	4.6 +	2.0	1.4 (0.3 – 3.4)
A3C	2.1	0.0 –	2.1 (0.7 – 4.4)	2.8 +	2.0	0.9 (0.0 – 2.6)
A4A	0.4	4.3 +	0.2 (0.0 – 1.5)	1.2	0.0 –	0.9 (0.0 – 2.6)
A4B	0.4	0.0 –	0.2 (0.0 – 1.5)	1.3	0.0 –	0.9 (0.0 – 2.6)
A4C	0.0	0.0 –	0.4 (0.0 – 1.8)	0.6	2.0	0.5 (0.0 – 2.1)
S3A	0.0	0.0 –	0.0 (0.0 – 1.1)	1.7	2.0	0.7 (0.1 – 2.4)
S3B	0.0	0.0 –	0.0 (0.0 – 1.1)	2.9 +	3.0 +	0.4 (0.0 – 1.7)
S3C	0.0	0.0 –	0.0 (0.0 – 1.1)	3.7 +	7.1 +	0.4 (0.0 – 1.7)
S4A	0.0	0.0 –	0.0 (0.0 – 1.1)	4.6 +	0.0 –	2.1 (0.7 – 4.5)
S4B	0.0	0.0 –	0.0 (0.0 – 1.1)	3.4	3.0	3.9 (1.9 – 6.8)
S4C	0.0	0.0 –	0.0 (0.0 – 1.1)	2.0	3.0	3.6 (1.6 – 6.3)
MD	9.0	4.3 –	11.3 (7.8 – 15.7)	1.9 –	1.0 –	17.1 (12.7 – 22.0)
BP3A	3.4 +	2.1	1.1 (0.2 – 3.1)	0.0	0.0	0.0 (0.0 – 1.0)
BP3B	0.6	2.1 +	0.0 (0.0 – 1.1)	0.0	0.0	0.0 (0.0 – 1.0)
BP3C	0.0	0.0 –	0.0 (0.0 – 1.1)	0.0	0.0	0.0 (0.0 – 1.0)
BP4A	1.7 +	2.1 +	0.0 (0.0 – 1.1)	0.0	0.0	0.0 (0.0 – 1.0)
BP4B	0.2	0.0 –	0.0 (0.0 – 1.1)	0.0	0.0	0.0 (0.0 – 1.0)
BP4C	0.0	0.0 –	0.0 (0.0 – 1.1)	0.0	0.0	0.0 (0.0 – 1.0)

[1]P = Pine; A = Aspen; S = Spruce; MD = Meadows; BP = Burned Pine.
Significance levels for 90% confidence intervals was determined using the Bonferroni method (Neu et al. 1974, Byers et al. 1984).
2 = < 2.5 cm DBH; 3 = 12.7 – 22.9 cm DBH; 4 = > 22.9 cm DBH.
A = 0 – 40% canopy cover; B = 41 – 70% canopy cover; C = 71 – 100% canopy cover.
[2]A positive sign (+) indicates significant habitat selection and a negative sign (-) indicates significant habitat avoidance.

Table 4. Percent availability and use of habitats with and without shrubs selected by doe and buck white-tailed deer during winter and summer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

	Does		Bucks	
	Winter	Summer	Winter	Summer
With Shrubs				
Forest Type				
n	1319	1496	146	181
availability (%)	9.6	25.2	9.6	25.2
use (%)	20.8	53.5	26.9	44.8
Overstory/Understory				
n	1000	1387	124	177
availability (%)	15.5	9.0	15.5	9.0
use (%)	69.6	36.6	72.6	31.7
Structural Stage				
n	477	786	47	99
availability (%)	29.7	38.3	29.7	38.3
use (%)	44.2	66.8	72.4	76.8
Without Shrubs				
Forest Type				
n	1319	1496	146	181
availability (%)	11.6	74.8	11.6	74.8
use (%)	6.4	46.5	1.3	55.3
Overstory/Understory				
n	1000	1387	124	177
availability (%)	78.7	76.6	78.7	76.6
use (%)	25.4	42.4	22.6	50.3
Structural Stage				
n	477	786	47	99
availability (%)	61.1	52.8	61.1	52.8
use (%)	35.2	24.2	17.0	13.1

remaining habitats were used in proportions to their availabilities. During summer, pine/juniper (Fig. 6), aspen/other shrubs, spruce/juniper, and spruce/other shrubs were selected ($P < 0.05$), whereas burned pine/litter was avoided ($P < 0.05$) by does and bucks; pine/grass/forb and pine/bearberry was avoided ($P < 0.05$) by does and spruce/litter was avoided by bucks. All other habitats were used in proportion to their availabilities. Regardless of season, deer of both sexes selected understory range similarly and used types that comprised only 15% of the landscape on winter range and 9% of the landscape on summer range.

Structural Stage

Availability of structural stages differed ($\chi^2 = 49.70$, df = 25, $P < 0.001$) between winter and summer ranges. During winter, structural stage use for does ($\chi^2 = 3.86$, df = 25, $P = 1.00$) and bucks ($\chi^2 = 21.26$, df = 25, $P = 0.68$) did not differ from habitat availability (Table 3). During summer, structural stage use differed for does ($\chi^2 = 49.63$, df = 25, $P < 0.001$) and bucks ($\chi^2 = 39.75$, df = 25, $P < 0.001$) compared to habitat availability.

During winter, deer of both sexes spent > 80% of their time in pine stands (Fig. 7) and selected medium to older age trees with medium to heavy forest canopies. Does spent twice as much time as bucks in meadows and both sexes spent small amounts of time in burned pine stands. During summer, deer spent > 60% of their time in pine stands, primarily in stands of medium age with medium to heavy canopies. Most of the remaining time was spent in stands of aspen and spruce (Fig. 8) regardless of canopy cover. Overall, deer selected structural stages that comprised only 30% of the winter range and 38% of the summer range.

Discussion

Clearly, in the central Black Hills, deer spent most of their time in and were primarily supported by pine forested range, which dominates the landscape. However, the structural stage classification of the Black Hills National Forest Inventory System does not lend itself to clearly explaining deer/habitat relationships. Selection of specific habitats by deer was much better explained by the availability of understory plant communities, which provides, thermal cover, escape cover, and food. Therefore, we more closely examined these relationships by comparing deer use of habitats in relation to the presence/absence of shrubs (Table 4). On winter range, deer use of forested stands with shrubs was 1.5 to 4.7 times greater than the availability of those habitats. On summer range, the relative difference between habitats containing shrubs selected by deer compared to the availability of those habitats ranged from 1.8 to 4.1 times greater than those habitats without shrubs.

Because hunter success (McPhillips and

Fig. 6. Pine/juniper habitat on summer range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Fig. 7. Pine habitat on winter range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

Rice 1991), deer reproductive success (Rice 1984, Hauk 1987, McPhillips 1990, Hippensteel 2000), and fawn survival (Rice 1979, Benzon 1998) have not increased with herd reductions, Griffin et al. (1992) reported that most management agencies believe the long term population decline and low productivity affecting central Black Hills white-tailed deer are directly related to habitat deterioration. In the central Black Hills, Hippensteel (2000) determined that winter range diets of white-tailed deer were composed of approximately 40% ponderosa pine, 30% grass, 20% shrub, and 5% forbs, which supports the contention that poor quality habitat is responsible for the long term population decline of white-tailed deer in the central Black Hills.

Winter Range

During winter, pine habitats that contained a shrub component were selected by white-tailed deer. We believe these pine stands were selected because of the thermoregulatory benefits they provide (Kennedy 1992). As air temperature declines, heat loss from the animal's surface increases due to convection (Moen 1968). Therefore, deer may be experiencing a physiological benefit by occupying habitats on winter range that contain understory and overstory vegetation; habitats with high thermal cover characteristics (Moen 1976, Parker and Gillingham 1990). In addition to thermoregulatory benefits, we believe deer are selecting areas that contain shrubs (i.e., bearberry, juniper, and snowberry) because they are important sources of forage necessary to winter survival of deer in the central Black Hills (Hill 1946, Schneeweis et al. 1972, Schenck et al. 1972). This is further supported because pine habitats dominated by snowberry, juniper, and bearberry are relatively rare in this region of the Black Hills but were sought out and selected by deer. Additionally, habitats with shrubs were selected at levels 1.5 to 4.7 times greater than the availability of those habitats. Results indicate that approximately 80% of the habitat in the central Black Hills does not contain shrubs and thus, is not acceptable for deer.

Burned pine forests were selected by white-tailed deer during winter but not during summer (burned habitats are rare on summer range). Burning speeds organic matter decomposition rates and releases nutrients into the environment, promoting the production of forage higher in protein (Einarsen 1946, Swank 1956, Sieg and Severson 1996). Similarly, researchers have concluded that burning in an unthinned ponderosa pine stand removed the litter component, initially increased the nutrient value of the herbaceous vegetation, and stimulated growth of grasses, forbs, and shrubs, thereby increasing the quality of the vegetation (Krefting 1962, Pearson et al. 1972, Harestad and Rochelle 1982). However, most larger burned areas within the central Black Hills are > 40 years post-burn. Browse production increases for 3–5 years following a burn before returning to pre-burn levels (Lay 1957, Taber and Dasmann 1957, Pearson et al. 1972). Consequently, deer use of burned areas may have been detected because forage species (e.g., bearberry, snowberry, and juniper) important to deer (Hill 1946, Schneeweis et al. 1972, Schenck et al. 1972) are essentially absent in the dominant unburned pine communities of the central Black Hills.

Fig. 8. Spruce habitat on summer range in the central Black Hills, South Dakota and Wyoming, 1993–1996.

On winter range, does selected open burned pine and pine deciduous habitats, whereas bucks selected closed pine stands and avoided meadows. Interestingly, does were located feeding (52%) and bedding (48%) similar proportions of time, whereas bucks were located bedding (64%) more often than feeding (36%). Additionally, doe home ranges were about twice as large on winter (202.9 ha) range compared to summer (130.9 ha) range (Griffin et al. 1999). Larger winter home ranges and increased time spent foraging by does compared to bucks may be a function of the does requirement for greater quantities of forage during winter gestation, whereas bucks have lower energy demands during this period and spend more time loafing. Although, white-tailed deer normally reduce food intake during winter (Short et al. 1969, Schultz et al. 1993), we believe that adequate forage is limited (Spalinger et al. 1993) in this region. For example, on winter range, aspen stands represent < 5% of the available habitat, understory shrubs (i.e., bearberry, juniper, and snowberry) and forbs represent < 30%, and litter comprises 57% of the available ground cover (DePerno 1998, DePerno et al. 2000). Furthermore, > 90% of the forest stands lack significant understory vegetation or tall shrub saplings (DePerno 1998, DePerno et al. 2000). Poor quality habitat and limited availability of deciduous and shrub habitats (DePerno 1998), high doe mortality in early spring (i.e., 53.2% of radiocollared doe mortality occurred in spring, DePerno 1998, DePerno et al. 2000), an adult reproductive rate of 1.33 fawns/doe, and a winter range diet of 40% ponderosa pine (Hippensteel 2000) indicate that does are nutritionally stressed on winter range in the central Black Hills.

Summer Range

During summer, deer selected deciduous forests that contained shrubs. Hill (1946) concluded that aspen and associated shrubs were important and highly palatable to white-tailed deer during summer in the northern Black Hills. Aspen areas have been determined to be important for both escape cover and forage for white-tailed deer throughout the Black Hills (Kranz 1971, Schneeweis et al. 1972, Schenck et al. 1972, Kranz and Linder 1973, Kennedy 1992, Stefanich 1995). However, habitats dominated by deciduous cover (< 12%) are limited on summer range in the central Black Hills (DePerno 1998, DePerno et al. 2000). Furthermore, grass and forbs composed < 30% of ground cover and shrubs composed < 21% of the available ground cover. These data coupled with approximately 48% litter cover indicate that grass, forb, and shrub forages are lacking on summer range in the central Black Hills (DePerno 1998, DePerno et al. 2000). Additionally, tall shrub sapling densities were nearly three times lower in the central Black Hills (1113.03 + 321.07 stems/ha) compared to the northern Black Hills (3246.84 + 164.87 stems/ha; Hippensteel 2000), which suggests the central Black Hills lack sufficient understory vegetation and escape cover that are important for white-tailed deer (DePerno 1998). Furthermore, habitats with shrubs were selected at levels 1.8 to 4.1 times greater than the availability of those habitats, suggesting that much of the habitat in the central Black Hills does not contain shrubs and is not acceptable habitat for deer.

During summer, structural stages with 71–100% canopy cover, were selected by white-tailed deer. Dense overhead canopy cover provides a cool environment, which may allow deer to avoid heat stress (Bunnell et al. 1986, Hoffman and Alexander 1987) and reduce cutaneous water loss (Parker and Robbins 1984). Additionally, deer selected the relatively open aspen and spruce stands, suggesting that habitats containing understory vegetation were important. Deciduous habitats and habitats with shrubs were likely selected because they are important sources of forage and provide horizontal cover for predator avoidance (DePerno 1998).

In the central Black Hills, spring migration of white-tailed deer from low elevation winter ranges to high elevation summer ranges generally occurs between 17 and 23 May (DePerno 1998, Griffin et al. 1999). This is about 3 weeks prior to the peak date of parturition, which occurs approximately 11 June (Benzon 1998). On summer range, does selected deciduous habitats that provide horizontal cover (DePerno 1998) and an abundant supply of forage for fawning (Smith and LeCount 1979, King and Smith 1980, Bowyer and Bleich 1984, Riley and Dood 1984, Huegel et al. 1986, Loft et al. 1987, Fox and Krausman 1994, Main and Coblentz 1996, Uresk et al. unpublished data). Horizontal cover is important to fawns; does seek isolation in areas where hiding cover and forage are abundant (King and Smith 1980, DePerno 1998). Interestingly, does were located feeding (37%) more than bucks (14%). Therefore, we postulate that in the central Black Hills, does migrate from winter to summer range just prior to parturition to give birth in areas that provide thermal cover, maximum forage characteristics, and concealment cover for fawns, whereas bucks migrate to sites with high quality forage on summer range to maximize body condition.

Summary and Management Implications

Results of this study indicate that deciduous cover types and habitats with understory vegetation were important to white-tailed deer in the central Black Hills. Sieg and Severson (1996) hypothesized that white-tailed deer densities in the Black Hills have been reduced due to the regeneration of ponderosa pine stands, prevention of natural fires, and elimination of man-made fires. Absence of fire has substantially increased ponderosa pine while hindering new growth with negative consequences for habitat diversity, wildlife, and livestock interests (Richardson and Petersen 1974, Sieg and Severson 1996). Reducing coniferous overstory vegetation in and around aspen stands could increase understory vegetation and forage diversity, which would enhance opportunities for herbivores to encounter higher quality plants or plant parts (Ffolliot and Clary 1982, McConnell and Smith 1970, Severson and Uresk 1988). Furthermore, if areas are logged first and then burned, forbs and shrubs will increase and sprout growth of some species (e.g., chokecherry, snowberry, and willow; Wright and Bailey 1982) may be doubled (Krefting 1962, Harestad and Rochelle 1982). We recommend that agencies responsible for habitat manipulation/management in the central Black Hills give consideration to habitat treatments or modifications of on-going management (e.g., aspen regeneration, logging, prescribed burning) that benefit white-tailed deer by significantly increasing deciduous habitats and understory vegetation on both winter and summer ranges in the central Black Hills.

Elk and livestock interests may be contributing to deer decline in the central Black Hills (DePerno 1998, DePerno et al. 2000) through competition for forage

(Jenks et al. 1996, Hippensteel 2000), habitat disturbance (Loft et al. 1987), displacement (Crawford 1984, Loft et al. 1987, Loft 1988, Kie at al. 1991), survival (Smith 1982), and length of time on grazing allotments. Low to moderate cattle regimes may be beneficial to elk and deer (Skovlin et al. 1968). However, high dietary overlap between deer and elk (49%), high pine consumption by deer (Hippensteel 2000), and length of cattle grazing (i.e., in the central Black Hills livestock grazing occurs from 1 June to 31 October) suggest the cattle grazing regime presently practiced in the Black Hills is excessive and incompatible with improving the white-tailed deer herd in the central Black Hills. We recommend the Forest Service re-evaluate their current grazing allotment (e.g., number of cattle and length of time) system as it relates to availability of deciduous and shrub habitats for white-tailed deer in the central Black Hills.

Literature Cited

Alldredge, J. R. and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 50:157–165.

Alldredge, J. R. and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 56:1–9.

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. J. Wildl. Manage. 65:65–77.

Beier, P. and D. R. McCullough. 1988. Motion-sensitive radio collars for estimating white-tailed deer activity. J. Wildl. Manage. 52:11–13.

Benzon, T. A. 1998. Mortality and habitat use of white-tailed deer fawns in the central Black Hills, South Dakota 1994-1998. Pittman-Robertson Game Rep. W-75-R-34. S. D. Dept. of Game, Fish and Parks, Pierre, S.D. 43pp.

Bowyer, R. T. and V. C. Bleich. 1984. Effects of cattle grazing on selected habitats of southern mule deer. Calif. Fish and Game. 70:240–247.

Bunnell, F.L., K.L. Parker, L.L. Kremsater, and F.W. Hovey. 1986. Thermoregulation and thermal cover of deer and elk on Vancouver Island: problem analysis. British Columbia Ministries of Environment and Forests. IWIFR-28. Victoria, British Columbia.

Buttery, R. F. and B. C. Gillam. 1983. Forest ecosystems. pp 34–71 *In*: R. L. Hoover and D.L. Wills, eds. Managing forested lands for wildlife. Colo. Div. of Wildl. in cooperation with USDA Forest Serv., Rocky Mountain Region, Denver, Colo.. 459 pp.

Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050–1053.

Clover, M. R. 1956. Single-gate deer trap. Calif. Fish and Game. 42:199–201.

Crawford, H. S. 1984. Habitat management. Pages 629–646 in L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole, Harrisburg, Penns., USA.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43–64.

DePerno, C. S. 1998. Habitat selection of a declining white-tailed deer herd in the central Black Hills, South Dakota and Wyoming. Ph.D. Diss., S. Dak. State Univ., Brookings, S. Dak. USA.

DePerno, C. S., S. L. Griffin, J. A. Jenks, and L. A. Rice. 1997. Unusual migration by a white-tailed deer fawn. Prairie Nat. 29:93–97.

DePerno, C. S., J. A. Jenks, S. L. Griffin, and L. A. Rice. 2000. Female survival rates in a declining white-tailed deer population. Wildl. Soc. Bull. 28:1030–1037.

Edwards, R. L. 1969. Archaeological use of the Universal Transverse Mercator grid. American Antiquity 34:180–182.

Einarsen, A. S. 1946. Crude protein determination of deer food as an applied management technique. Trans. North Amer. Wildl. Conf. 11:309–312.

Ffolliot, P. F. and W. P. Clary. 1982. Understory-overstory vegetation relationships: an annotated bibliography. USDA For. Serv. Gen. Tech. Rep. INT-136. Intermtn. For. and Range Exp. Sta., Ogden, Utah. 33pp.

Ford-Robertson, F. C., Ed. 1971. Terminology of forest science technology practice and products: English language version. Multilingual For. Term. Ser. 1. Soc. Amer. For., Washington D.C. 349pp.

Fox, K. B., and P. R. Krausman. 1994. Fawning habitat of desert mule deer. Southwest. Nat. 39:269–275.

Griffin, S. L. 1994. Seasonal movements and home range of white-tailed deer in the central Black Hills, South Dakota, 1993. Pittman-Robertson Report W-75-R-35. South Dakota Dept. of Game, Fish and Parks, Pierre, S. Dak. 13pp.

Griffin, S. L., J. F. Kennedy, L. A. Rice, and J. A. Jenks. 1992. Movements and habitat use of white-tailed deer in the northern Black Hills, S. Dak., 1991. Pittman-Robertson Report W-75-R-33. South Dakota Dept. of Game, Fish and Parks, Pierre, S. Dak. 21pp.

Griffin, S. L., L. A. Rice, C. S. DePerno, and J. A. Jenks. 1999. Seasonal movements and home ranges of white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993–97. S. Dak. Dept. of Game, Fish and Parks, Pittman-Robertson Game Rep. W-75-R-34, Pierre, S. Dak., USA.

Griffin, S. L., C. S. DePerno, J. A. Jenks, L. A. Rice, and D. A. Flory. 1995. Capture success of white-tailed deer in the central Black Hills, South Dakota. S. Dak. Acad. Sci. 74:71–76.

Grubb, T. G. and W. L. Eakle. 1988. Recording wildlife locations with the Universal Transverse Mercator (UTM) Grid System. USDA For. Serv. Res. Pap. RM-483. Rocky Mt. For. and Range Exp. Sta., Ft. Collins, Colo.. 3pp.

Hansen, M. C., G. W. Garner, and S. G. Fancy. 1992. Comparison of 3 methods for evaluating activity of Dall's sheep. J. Wildl. Manage. 56:661–668.

Harestad, A. S., and J. A. Rochelle. 1982. Old-growth forests and black-tailed deer on Vancouver Island. Trans. North Amer. Wildl. Nat. Resour. Conf. 47:363–373.

Hauk, R. W. 1987. Deer management surveys, 1987. Pittman-Robertson Rept. W-95-R-22. S. Dak. Dept. of Game, Fish and Parks, Pierre, S. Dak. 40pp.

Hill, R. R. 1946. Palatability ratings of Black Hills plants for white-tailed deer. J. Wildl. Manage. 10:47–54.

Hippensteel, B. A. 2000. Factors affecting nutritional condition of white-tailed deer in the central Black Hills, South Dakota. M.S. Thesis, S. Dak. State Univ., Brookings, S. Dak., USA.

Hoffman, G. R. and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. USDA Res. Pap. RM-276. Rocky Mt. For. and Range Exp. Sta., Fort Collins, Colo. 48pp.

Hovind, H. J. and C. E. Reick. 1970. Basal area and point sampling: interpretation and application. Wis. Dept. Nat. Res. Tech. Bull. 23. 52 pp.

Huegel, C. N., R. B. Dahlgren, and H. L. Gladfelter. 1986. Bedsite selection by white-tailed deer fawns in Iowa. J. Wildl. Manage. 50:474–480.

Jelinski, D. E. 1991. On the use of chi-square analyses in studies of resource utilization. Can. J. For. Res. 21:58–65.

Jenks, J.A., D.M. Leslie, Jr., R.L. Lochmiller, M. A. Melchiors, and F. McCollum, III. 1996. Competition in sympatric white-tailed deer and cattle populations in southern pine forests of Oklahoma and Arkansas, USA. Acta Theriologica 41:287B306

Kennedy, J. F. 1992. Habitat selection by female white-tailed deer in the northern Black Hills, South Dakota and Wyoming. M.S. Thesis, South Dakota State Univ., Brookings, S. Dak. 65pp.

Kernohan, B. J., J. A. Jenks, D. E. Naugle, and J. J. Millspaugh. 1996. Estimating 24-h habitat use patterns of white-tailed deer from diurnal use. J. Environ. Manage. 48:299–303.

Kie, J. G., C. J. Evans, E. R. Loft, and J. W. Menke. 1991. Foraging behavior by mule deer: the influence of cattle grazing. J. Wild. Manage. 55:665–674.

King, M. M. and H. D. Smith. 1980. Differential habitat utilization by the sexes of mule deer. Great Basin Nat. 40:273–281.

Kranz, J. J. 1971. A comparison of aspen and pine communities in the northern Black Hills. M.S. Thesis, South Dakota State Univ., Brookings, S. Dak. 52 pp.

Kranz, J. J. and R. L. Linder. 1973. Value of Black Hills forest communities to deer and cattle. J. Range Manage. 26:263–265.

Krefting, L. W. 1962. Use of silvicultural techniques for improving deer habitat in the lake states. J. For. 60:40–42.

Lay, D. W. 1957. Browse quality and the effects of prescribed burning in southern pine forests. J. For. 55:342–347.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2:314–320.

Loft, E. R. 1988. Habitat and spatial relationships between mule deer and cattle in a Sierra Nevada forest zone. Diss., Univ. of California, Davis, Calif., USA.

Loft, E. R., J. W. Menke, J. G. Kie, and R. C. Bertram. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. J. Wildl. Manage. 51:655–664.

Main, M. B. and B. E. Coblentz. 1996. Sexual segregation in Rocky Mountain mule deer. J. Wildl. Manage. 60:497–507.

Marcum, C. L. and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. J. Wildl. Manage. 44:963–968.

Martin, W. E. and R. L. Gum. 1978. Economic value of hunting, fishing, and general rural outdoor recreation. Wildl. Soc. Bull. 6:3–7.

McClean, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. J. Wildl. Manage. 62:793–801.

McConnell, B. R., and J. G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. J. Range Manage. 23:208–212.

McIntosh, A. C. 1949. A botanical survey of the Black Hills of South Dakota. Black Hills Engin. 28:1–74.

McPhillips, K. 1990. Deer management surveys, 1989. Pittman-Robertson Report W-95-R-24. South Dakota Department of Game, Fish and Parks, Pierre, S. Dak. 40pp.

McPhillips, K. and L. A. Rice. 1991. Deer management surveys, 1991. South Dakota Department of Game, Fish and Parks, Pittman-Robertson Game Report W-95-R-25, Pierre, S. Dak. 49 pp.

Moen, A. N. 1968. Surface temperatures and radiant heat loss from white-tailed deer. J. Wildl. Manage. 32:338–344.

Moen, A. N. 1976. Energy conservation by white-tailed deer in winter. Ecol. 57:192–198.

Nelson, B. E. 1995. Use of a Geographic Information system for determining white-tailed deer habitat use in the Northern Black Hills of South Dakota and Wyoming. M.S. Thesis, South Dakota State Univ., Brookings, S. Dak. USA.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541–545.

Orr, H. K. 1959. Precipitation and streamflow in the Black Hills. USDA Station Pap. 44. Rocky Mt. For. and Range Exp. Station, Fort Collins, Colo. 25pp.

Ozoga, J. J., L. J. Verme, and C. S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. J. Wildl. Manage. 46:1–11.

Parker, K. L. and M. P. Gillingham. 1990. Estimates of critical thermal environments for mule deer. J. Range. Manage. 43:73–80.

Parker K. L., and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. Can. J. Zool. 62:1409–1422.

Pearson, H. A., J. R. Davis, and G. H. Shubert. 1972. Effects of wildfire on timber and forage production in Arizona. J. Range Manage. 25:250–253.

Petersen, L.E. 1984. Northern Plains. pp. 441–448 *In:* L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Penn. 870pp.

Progulske, D. R. and T. S. Baskett. 1958. Mobility of Missouri deer and their harassment by dogs. J. Wildl. Manage. 22:184–192.

Richardson, A. H., and L. E. Peterson. 1974. History and Management of South Dakota Deer. South Dakota Dept. Game, Fish and Parks Publ. Bull. No. 5. Pierre, S. Dak. 113pp.

Riley, S. J. and A. R. Dood. 1984. Summer movements, home range, habitat use, and behavior of mule deer fawns. J. Wildl. Manage. 48:1302–1310.

Rice, L. A. 1979. Mortality rates of fawn age class in South Dakota deer populations, 1978–1979. Pittman-Robertson Report W-75-R-21. S. Dak. Department Game, Fish and Parks, Pierre, S. Dak. 17 pp.

Rice, L. A. 1984. Fawn mortality rates in South Dakota deer populations, 1977–1981. Pittman-Robertson Report W-75-R-26. S. Dak. Dept. Game, Fish and Parks, Pierre, S. Dak. 45pp.

Rumble, M. A. and S. H. Anderson. 1992. Stratification of habitats for identifying habitat selection by Merriam's Turkeys. Great Basin Nat. 52:139–144.

Rumble, M. A. and S. H. Anderson. 1993. Habitat selection of Merriam's turkey (*Meleagris gallopavo merriami*) hens with poults in the Black Hills, S. Dak. Great Basin Nat. 53:131–136.

Schenck, T. E., III, R. L. Linder, and A. H. Richardson. 1972. Food habits of deer in the Black Hills, Part II: Southern Black Hills. South Dakota Agr. Exp. Sta. Bull. 606, S. Dak. State Univ., Brookings S. Dak. 35pp.

Schneeweis, J. C., K. E. Severson, and L. E. Petersen. 1972. Food habits of deer in the Black Hills, Part I: Northern Black Hills. South Dakota Agr. Exp. Sta. Bull. 606, South Dakota State Univ., Brookings, S. Dak. 35 pp.

Schultz, S. R., M. K. Johnson, and A. E. Hindrichs. 1993. Effects of spring/summer body mass gain and sex ratio on fall/winter body mass loss of adult, male white-tailed deer. Small Rum. Res. 10:183–188.

Severson, K. E. and D. W. Uresk. 1988. Influence of ponderosa pine overstory on forage quality in the Black Hills, South Dakota. Great Bas. Nat. 48:78–82.

Short, H. L., J. D. Newsom, G. L. McCoy, and J. F. Fowler. 1969. Effects of nutrition and climate on southern deer. Trans. North Amer. Wildl. Conf. 34:137–146.

Sieg, C. H. and K. E. Severson. 1996. Managing habitats for white-tailed deer in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. USDA For. Serv. Gen. Tech. Rep. RM-GTR-274. Rocky Mt. For. and Range Exp. Station, Fort Collins, Colo. 24pp.

Skovlin, J. M., P. J. Edgerton, and R. W. Harris. 1968. The influence of cattle management on deer and elk. Trans. of the North Amer. Wildl. and Nat. Res. Conf. 33:169–181.

Smith, D. M. 1962. The practice of silviculture, 7th edition. John Wiley and Sons, Inc. New York, N.Y. 578 pp.

Smith, W. P. 1982. Status and habitat use of Columbian white-tailed deer in Douglas County, Oregon, Diss., Oregon State Univ., Corvallis, Ore., USA.

Smith, R. H. and A. LeCount. 1979. Some factors affecting survival of desert mule deer fawns. J. Wildl. Manage. 43:657≠665.

Spalinger, D. E., C. T. Robbins, and T. A. Hanley. 1993. Adaptive rumen function in elk (*Cervus elaphus nelsoni*) and mule deer (*Odocoileus hemionus hemionus*). Can. J. Zool. 71:601–610.

Stefanich, M. R. 1995. Movements and habitat use of white-tailed deer in the northwestern Black Hills of Wyoming and South Dakota. M.S. Thesis, Univ. of Wyo., Laramie, Wyo. 46 pp.

Swank, W. G. 1956. Protein and phosphorous content of browse plants as an influence on southwestern deer herd levels. Trans. North Amer. Wildl. Conf. 21:141–158.

Taber, R. D. and R. F. Dasmann. 1957. The dynamics of three natural populations of the deer *Odocoileus hemionus columbianus*. Ecol. 38:233–246.

Thilenius, J. F. 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. USDA For. Serv. Res. Pap. RM-91. Fort Collins, Colo. 28 pp.

Tierson, W. C., G. F. Mattfield, R. W. Sage, Jr., and D. F. Behrend. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. J. Wildl. Manage. 49:760–769.

Turner, R. W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. Misc. Publ. Mus. Nat. Hist. University of Kansas. 178 pp.

United States Fish and Wildlife Service. 1993. National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. U.S. Govern. Printing Off., Washington D.C. 41 pp.

Wallace, M. S., H. L. Stribling, and H. A. Clonts. 1991. Effects of hunter expenditure distribution on community economics. Wildl. Soc. Bull. 19:7–14.

Weckerly, F. W. 1993. Intersexual resource partitioning in black-tailed deer: a test of the body size hypothesis. J. Wildl. Manage. 57:475–494.

White, G. C. and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, N.Y. 383 pp.

Wilkinson, L. 1990. Systat: the system for statistics. Systat, Inc. Evanston, Ill. 750 pp.

Williamson, L. L. and G. L. Doster. 1981. Socioeconomic aspects of white-tailed deer diseases. pp 434–439 *In:* W.R. Davidson, ed. Diseases and parasites of white-tailed deer. Tall Timbers research Station, Tallahassee, Fla. 472 pp.

Wright, H. A. and A. W. Bailey. 1982. Fire Ecology. John Wiley & Sons, New York, N.Y. 501pp.

J. Range Manage.
55: 253-259 May 2002

Nutritional quality of forages used by elk in northern Idaho

MATHEW W. ALLDREDGE, JAMES M. PEEK, AND WILLIAM A. WALL

Authors are Ph.D. candidate, Biomathematics Program, Statistics Department, North Carolina State University, Raleigh, N.C. 27695; professor, Department of Fish and Wildlife Resources, University of Idaho, Moscow, Ida. 83844; and Wildlife Biologist, Safari Club International, Herndon, Virg. 20170. At the time of the research the senior author was Research Assistant, Department of Fish & Wildlife Resources, University of Idaho, Moscow, Ida.

Abstract

The nutritional quality (digestible energy, crude protein, and minerals) of 7 known elk (*Cervus elaphus* Linnaeus) forages was assessed at 4 different time periods from May to November. Species evaluated were elk sedge (*Carex geyeri* Boott), Kentucky bluegrass (*Poa pratensis* Linnaeus), western goldthread (*Coptis occidentalis* Nuttall), clover (*Trifolium repens* Linnaeus), serviceberry (*Amelanchier alnifolia* Nuttall), redstem ceanothus (*Ceanothus sanguineus* Pursh), and Scouler willow (*Salix scouleriana* Barratt). Mineral concentrations generally met estimated requirements for elk in all seasons, except sodium remained below requirements in all seasons. Crude protein in most plant species sampled was adequate for adult gravid or lactating cows throughout the year, although concentrations in graminoids fell below requirements during August. Forage provided adequate digestible energy for gravid or lactating cows only during May, indicating potential deficiencies in summer and autumn. Elk must be selective of plant parts, plant taxa, and foraging habitat to gain adequate nutrition. In this area, summer and fall forage quality may be critical to lactating cow elk.

Key Words: **Elk, *Cervus elaphus*, forage quality, nutrition, Idaho**

Resumen

Se evaluó la calidad nutricional (energía digestible, proteína cruda y minerales) de 7 especies forrajes que se sabe que el alce (Cervus elaphus Linnaeus) las consume, la evaluación se realizó en 4 diferentes periodos de tiempo de Mayo a Noviembre. Las especies evaluadas fueron: "Elk sedge" (*Carex geyeri* Boott), "Kentucky bluegrass" (*Poa pratensis* Linnaeus), "Western goldthread" (*Coptis occidentalis* Nuttall), "Clover" (*Trifolium repens* Linnaeus), "Serviceberry" (*Amelanchier alnifolia* Nuttall), "Redstem ceanothus" (*Ceanothus sanguineus* Pursh) y "Scouler willow" (*Salix scouleriana* Barratt). Las concentraciones de minerales generalmente satisfacen los requerimientos estimados para el alce en todas las estaciones, excepto sodio el cual permanece abajo de los requerimientos en todas las estaciones. A través de todo el año la proteína cruda de la mayoría de las especies de plantas muestreadas fue adecuada para las hembras preñadas o lactantes, sin embargo, en Agosto, las concentraciones de proteína cruda de las gramíneas cayó por abajo de los requerimientos. El forraje proveyó de energía digestible adecuada para las hembras adultas preñadas o lactantes solo en Mayo, indicando deficiencias potenciales en verano y otoño. Para tener una nutrición adecuada el alce debe ser selectivo de las partes de la planta que consume, el género de planta y el hábitat de forrajeo. En esta área la calidad del forraje en verano y otoño puede ser critica para las hembras lactantes de alce.

Industrial forests in northern Idaho managed primarily for timber production contain substantial populations of elk. These forests contain a mixture of age classes of trees in a diverse mosaic of successional patterns. However, they do not provide large blocks of mature timber for security cover and road densities are high, causing them to fall outside of the suitable criteria for elk habitat developed by Leege (1984).

Elk presumably select habitats that have high quality, abundant forage, or provide cover (Patton 1974, Edge et al. 1988, Thomas et al. 1979). Nutritional quality of available forages may change with phenological stage, between vegetation classes, aspect, and overstory structure (Irwin and Peek 1979). Nutrition is assumed to be a primary factor influencing elk distribution, abundance, and productivity (Cook in press). However, few studies have described forage quality and attempt to relate this to the nutritional levels that elk experience.

We examined nutritional quality of primary elk forages in an industrial forest. We build on the substantial number of elk habitat use investigations in northern Idaho showing the importance of seral shrub communities as foraging areas. Substantial knowledge of food habits and responses of forage plants to logging and burning is also available for this area to pursue the analyses. Specific objectives were to (1) assess the variability in digestible energy, crude protein, and mineral concentrations of known elk forages across seasons and topographical aspect; (2) determine seasonal trend in nutritional quality by species and vegetation class; and (3) compare nutritional quality of representative forage species with the daily nutritional requirements of elk.

Study Area

The study area was located west of the Dworshak Reservoir in the North Fork of the Clearwater River drainage, in Clearwater County, Ida. (45°N, 116.15°W). Mild summers and long-cold

Authors wish to thank J. G. Cook , P. J. Heglund, R. K. Steinhorst , and C. J. Williams for their advice. K.L. Launchbaugh extended use of her lab for the nutritional analysis. J. Scott and B. Knapton provided invaluable field assistance. Research was funded by Potlatch Corporation, Rocky Mountain Elk Foundation, and the University of Idaho. This is University of Idaho, College of Natural Resources Journal Series Paper Number 956.

Manuscript accepted 7 Sept. 01.

winters characterize the climate in the area (Hansen et al. 1989). Annual precipitation is 93.6 cm with the majority falling as snow from November through February. Western Red Cedar-Pachistima (*Thuja plicata* Donn-*Pachistima myrsinites* Rafinesque) habitat type dominates the area (Daubenmire and Daubenmire 1968). Alldredge et al. (2001), Cooper et al. (1987), Crookston and Stage (1999), Irwin and Peek (1979), Moeur (1985), and Stage (1973) have described the successional patterns, species composition, and productivity of this habitat type in northern Idaho.

Logging since the 1920's has created a variety of seral stands from clearcuts to closed-canopy forests. Approximately 14% of the area is a recently cut, grass/low shrub community. Kentucky bluegrass (*Poa pratensis* L.), elk sedge (*Carex geyeri* Boott), pearly everlasting (*Anaphalis margaritacea* L.), fireweed (*Epilobium angustifoliums* L), senecios (*Senecio triangularis* Hooker), pentstemons (*Pentstemon* spp Mitch.), pinegrass (*Calamagrostis rubescens* Buck.), wild strawberry (*Fragaria vesca* L.) were common forbs and graminoids. Clover (*Trifolium repens* L.) commonly occurred along access routes that had been reseeded. A tall shrub/grass community occupied 36% of the study area. Mountain maple (*Acer glabrum* Torrey), redstem ceanothus (*Ceanothus sanguineus* Pursh), serviceberry (*Amelanchier alnifolia* Nuttall), and Sitka alder (*Alnus sinuata* Rydberg) were common shrubs, with similar graminoids and forbs. Open-canopy conifer communities comprised 21% of the area, with Douglas fir (*Pseudotsuga menziesii* Franco) being the most common tree. Understories were more sparse, and shade tolerant species including mountain maple, thimbleberry (*Rubus parviflorus* Nuttall), Scouler willow (*Salix scouleriana* Barratt), pachistima, huckleberries (*Vaccinium membranaceum* Douglas, *V. globulare* Rydberg), and menziesia (*Menziesia ferruginia* Smith) were common. Common understory species included western goldthread (*Coptis occidentalis* Nuttall), twinflower (*Linneaea borealis* L.), Solomon seal (*Smilacina stellata* L.), and bedstraw (*Gallium triflorum* Michx). Closed-canopy forests containing very sparse understories of shade-tolerants comprised 29% of the area.

Potlatch Corporation managed 40.6%, Idaho Department of Lands 32.1%, and U.S. Forest Service 18.8% of the area. The study area received over 30,000 hunter-days use in recent years (Idaho Department of Fish and Game 1999). Alldredge (1999) reported that elk foraged in areas that had been logged within the past 20 years, except during the rifle hunting season, when they switched to mature conifer cover, confirming the general pattern observed by Hash (1973), Hershey and Leege (1984), Irwin and Peek (1983b, McLean (1972), and Unsworth et al. (1998) in northern Idaho.

Methods

Collections

We selected graminoids, forbs, and shrubs known to be important in the elk diet in the area (Irwin and Peek 1983a, Kingery et al. 1996, Leege 1969, Leege and Godbolt 1985, Nelson and Leege 1982, Young and Robinette 1939). Elk sedge, Kentucky bluegrass, western goldthread, clover, serviceberry, redstem ceanothus, and Scouler willow were collected to represent the variety of species used by elk and abundant in the study area.

Collections for all of these species were made on 3 sites in 6 areas in mid-June, mid-August, and mid-November, 1997–1998 and May 1998. Clover became completely desiccated and unavailable in November. Plants were collected on north and south aspects to represent different light and moisture conditions, in the cedar-pachistima habitat type.

Current year's growth of shrubs, and above-ground portions of graminoids and forbs were collected for analysis. The entire twig of current year's growth, including leaves except in November was collected for shrubs, and graminoids and forbs were clipped to within 1 cm of the ground. Approximately 200 g per species per site were collected. Samples also consisted of collections from multiple plants to account for variation between plants.

Forage Analysis

Samples were oven-dried at 40ºC for 48 hours, ground with a Wiley Mill through a 1 mm screen, and stored until analysis. This temperature was selected to ensure that fermentable carbohydrates were retained, at the risk of reduction of cell solubles (Wolf and Carson 1973). Analyses included in-vitro-dry-matter-digestibility (IVDMD), gross energy content, and macro- and micro-element concentrations.

The IVDMD was determined using the Tilley and Terry (1963) technique as modified by Pearson (1970). Ancom filter bags were used to contain the material during fermentation. In-vitro-dry-matter-digestion was terminated after 48 hours for all trials. To reduce variability in the lab procedure, rumen inoculum was obtained from a single Hereford cow maintained on a constant alfalfa diet and all analyses were done within a 2 month period.

Estimates of gross energy were determined for 2 samples for each species within each time period using bomb calorimetry. Digestible energy was determined for all samples collected by approximating digestible energy as the product of digestibility and gross energy (Hobbs et al. 1982, Robbins 1983). Crude protein was estimated as 6.25 times the percent nitrogen content (A.O.A.C. 1984).

The organic and mineral composition of the 7 selected forage species was estimated across seasons and years. Organic constituents of carbon (C), nitrogen (N), and sulfur (S), were determined using a combustion technique (McGeehan and Naylor 1988). Atomic emission spectroscopy (Anderson 1996) was used to determine concentrations of aluminum (Al), cadmium (Cd), calcium (Ca), chromium (Cr), cobalt (Co), copper (Cu), iron (Fe), lead (Pb), molybdenum (Mo), potassium (K), phosphorus (P), magnesium (Mg), manganese (Mn), sodium (Na), nickel (Ni), sulfur (S), vanadium (V), and zinc (Zn).

We used multiple analysis of variance (MANOVA) to assess the variability in nutrient quality by aspect, time, species, and vegetation class. Vegetation class (graminoids, forbs, shrubs) was examined because these differences could affect cover type use. Trends in nutritional quality of each forage species were examined to determine if they met the requirements of elk. Crude protein and digestible energy concentrations by species and vegetation class were compared to estimated daily requirements of an elk (Cook in press), across time periods, using a t test. Estimates of digestible energy and crude protein were based on an adult cow, gravid in spring and lactating through mid-autumn, with average consumption rates, daily activities, and metabolic demands. Mineral concentrations were also compared to mineral requirements for cattle (National Research Council 1996), using a t-test.

Results

A total of 114 and 160 vegetation samples were collected during 1997 and 1998. Seasonal collections were made within 2 days of the same date each year. No significant differences in energy, mineral concentrations or protein were related to aspect.

Minerals

Mineral concentrations in all species were variable with no predictable seasonal patterns (Table 1). Molybdenum, Co, and Ni concentrations were below detectable limits. Significant differences were detected ($P < 0.001$) for time*species and time*vegetation class interactions, indicating a high degree of variability in mineral concentrations. Forage species provided sufficient concentrations of required minerals above levels necessary to meet animal requirements for all seasons ($t > 2.92$, $P < 0.02$), with the exception of Na. The highest Na level in any forage species was 91 $\mu g/g$, well below estimated minimum Na requirement for cattle of 600 $\mu g/g$.

Some forage species, including Mg and K, provided concentrations of some minerals above the maximum tolerable limits during certain time periods. No mineral exceeded the tolerable limits for elk across all forage species during any single time period. Elements toxic to animals, such as Cd and Pb, were present at low levels throughout all seasons in all forage species.

Crude Protein

Crude protein levels in all species declined from May through November (Table 2). In May crude protein concentrations in all 3 shrubs and clover were over 24%, higher than other species across all collection periods, except western goldthread in November. Crude protein in western goldthread was lower than all other species early in the year but smaller declines throughout the year relative to other species resulted in high levels in November.

A similar pattern was observed in levels of crude protein by vegetation class (Table 2). Protein concentrations in graminoids were lower than in other vegetation classes. Shrubs had higher levels than forbs in May and June, were similar in August, and lower than forbs in November. Significant differences in crude protein concentrations were detected within species and vegetation classes between collection periods ($P < 0.05$, Table 2).

All species provided adequate protein for elk in May, but only redstem ceanothus, Scouler willow, serviceberry, and clover met requirements in June. By August crude protein of redstem ceanothus and clover exceeded requirements, as did western goldthread in November. Protein levels in forbs and shrubs met requirements for elk in all seasons except for shrubs in November. Levels of protein in graminoids met elk requirements only in May. In August crude protein levels in graminoids, elk sedge, and Kentucky bluegrass were significantly lower than elk requirements ($t > 3.4$, $P = 0.01$, $P = 0.01$, and $P < 0.0001$, respectively). Crude protein concentrations in Kentucky bluegrass and redstem ceanothus were significantly below requirements during November ($t > 2.83$, $P < 0.0001$ and $P = 0.04$, respectively).

Digestible Energy

Digestible energy declined from May through November, with some species increasing from August to November (Table 3). Western goldthread showed the largest increase in digestible energy between August and November, but Scouler willow, redstem ceanothus, and serviceberry also increased between these times. Western goldthread had the highest levels of digestible energy for all seasons. Scouler willow had the lowest levels for all periods except November, where it had one of the highest concentrations. Elk sedge and Kentucky bluegrass had the

Table 1. High and low mineral concentrations found in forage species and estimated elk requirements (Cook in press, National Research Council 1984) of macro and micro elements (bdl = below detectable levels, and N/A = not available). Concentrations reported in µg/g. Values are averages of mineral concentrations within a given time period. MANOVA detected significant differences (P < 0.001) for *timespecies and time* vegetation class interactions. All centrations of required minerals except Na were above required levels for all seasons (t > 2.92, P < 0.02). Co, Mo, and Ni concentrations were below detectable limits.

	Required	Clover	Goldthread	Elk sedge	Bluegrass	Redstem	Serviceberry	Scouler Willow
					($\mu g/g$)			
Al	N/A	52-338	66-302	65-505	72-255	71-191	25-308	201-715
Cd	N/A	0.2-0.5	0.1-0.3	0.04-0.9	0.2-1.7	0.1-0.4	0.1-1.3	0.1-1.3
Ca	1600-5800	9,683-13,780	2,467-13,750	5,608-11,367	2,983-10,217	7,167-13,200	3,450-8,950	12,000-14,283
Cr	N/A	Bdl-0.3	0.1-1.0	0.1-0.8	0.3-0.8	0.1-0.5	bdl-0.4	0.5-0.7
Co	0.07-0.11	bdl[c]-0.4	bdl[c]-0.2	bdl[c]-0.2	0.1-2.8	bdl[c]-0.1	bdl[c]-0.2	0.6-1.7
Cu	4-10	5.0-12.9	6.0-7.1	4.6-7.2	4.0-9.8	3.6[c]-9.6	6.0-8.1	6.5-12.7
Fe	50-100	111-220	113-321	111-230	98-163	107-195	10[c]-110	29-201
Pb	N/A	6-56	11.5-234	17-150	29-245	1.1-39	3.3-111	0.9-19
Mg	500-2500	2,500-3,708	1,562-3,267	1,228-2,217	1,267-2,717	1,231-2,842	1,333-1,650	2,100-4,467[b]
Mn	20-50	241-414	78-195	205-493	300-413	748-143	143-453	97-302
Mo	6[a]	Bdl-0.2	0.3-1.1	Bdl-1.3	bdl	bdl-0.4	bdl-2.0	bdl-0.2
Ni	N/A	0.06-1.8	0.1-1.3	0.3-2.4	0.2-4.1	bdl-1.3	0.2-3.5	1.6-3.8
K	5000-7000	9,867-26,750	11,408-31,500[b]	11,408-19,833	7,308-16,417	9,392-20,083	5,217-31,500[b]	10,092-32,833[b]
P	1700-3900	3,267-5,633	2,375-3,817	1,260[c]-4,525	970[c]-5,258	1,273[c]-3,250	1,633[c]-2,733	1,767-3,000
Na	600-1000	19[c]-45[c]	32[c]-92[c]	30[c]-71[c]	27[c]-63[c]	25[c]-50[c]	27[c]-39[c]	20[c]-81[c]
S	800-1500	857-2,142	1,588-2,258	1,143-2,358	913-3,133	880-1,983	663[c]-2,075	1,382-2,083
V	N/A	0.1-1.3	0.3-2.3	0.1-2.7	0.1-1.8	0.2-2.3	0.5-2.5	0.4-3.5
Zn	20-40	37-58	28-100	27-39	21-136	18[c]-73	22-42	30-109

[a]no specified requirement, but a maximum tolerable value was known.
[b]concentrations of the given element exceed the maximum tolerable limit.
[c]concentrations of the given element do not meet the minimum requirements.

Table 2. **Crude protein concentrations (percent) for all species and vegetation classes across all time periods, with corresponding 95% confidence intervals. Required levels from Cook (in press).**

Species/ Vegetation Class	May	June	August	November
	(%)			
Forbs	18.7 ± 13.2[N]	15.8 ± 10.7	12.5 ± 5.3	8.7 ± 1.8
Clover	24.3 ± 2.6[A]	19.7 ± 8.1	14.3 ± 3.5	N/A
Western goldthread	13.0 ± 3.9	11.8 ± 6.2	11.0 ± 5.0	8.7 ± 1.8
Graminoids	17.8 ± 6.5[A,N]	11.6 ± 6.9	5.83 ± 3.4	4.7 ± 3.8
Elk sedge	16.0 ± 4.7[A,N]	11.2 ± 7.2	6.8 ± 3.4	5.9 ± 3.6
Kentucky bluegrass	19.7 ± 6.7[A,N]	12.0 ± 7.5	4.9 ± 2.4	3.5 ± 2.1
Shrubs	26.5 ± 8.3[N]	20.5 ± 9.2[N]	12.6 ± 7.0	6.1 ± 1.8
Redstem ceanothus	29.5 ± 6.5[A,N]	23.9 ± 5.8[N]	15.1 ± 6.0	5.6 ± 1.3
Scouler willow	24.2 ± 8.0[A,N]	19.8 ± 6.7[N]	11.2 ± 3.5	6.8 ± 1.24
Serviceberry	25.9 ± 10.3[N]	14.9 ± 9.8	11.3 ± 8.8	6.1 ± 2.2
Requirements	7.5	15	12	7.5

[A]Estimate significantly different than estimate in August ($P < 0.05$)
[N]Estimate significantly different than estimate in November ($P < 0.05$).

lowest levels of digestible energy of all species in November. Levels of digestible energy were more similar for all species during August. Significant differences in digestible energy were detected within species between collection periods ($P < 0.05$) (Table 3).

Seasonal trends in digestible energy levels by vegetation class were similar (Table 3). Graminoids declined from 3,100 kcals/kg to 1,450 kcals/kg between May and November. Digestible energy of shrubs was highest in May at 3,200 kcals/kg, lowest in August at just over 1,800 kcals/kg, and moderate (2,000 kcals/kg) in November. Forbs also declined through the seasons from almost 3,500 kcals/kg in May to slightly over 1,900 kcals/kg in August. Western goldthread, the only forb measured during November, contained about 3,300 kcals/kg digestible energy. Between mid-June and mid-August, digestible energy content in graminoids fell below shrubs. Significant differences in digestible energy concentrations were detected within vegetation classes between collection periods ($P < 0.05$, Table 3).

All species and vegetation classes met estimated digestible energy requirements of elk during May. Digestible energy levels for all species and vegetation classes were significantly below requirements ($t > 3.61, P < 0.05$) during June, August, and November, except for western goldthread in November.

Table 3. **Digestible energy levels (Kcal/kg of forage) for all species and vegetation classes across all time periods, with corresponding 95% confidence intervals. Required levels from Cook (in press).**

Species/ Vegetation Class	May	June	August	November
	(Kcal/kg))			
Forbs	3,454 ± 182[J,A,N]	2,385 ± 177[A,N]	1,910 ± 285[N]	3,286 ± 42
Clover	3,236 ± 195[J,A]	2,146 ± 184	1,673 ± 473	N/A
Western goldthread	3,672 ± 188[J,A,N]	2,567 ± 105[A,N]	2,147 ± 377[N]	3,286 ± 42
Graminoids	3,141 ± 120[J,A,N]	2,337 ± 105[A,N]	1,681 ± 144	1,456 ± 136
Elk sedge	2,980 ± 143[J,A,N]	2,298 ± 139[A,N]	1,761 ± 175	1,578 ± 04
Kentucky bluegrass	3,301 ± 57[J,A,N]	2,375 ± 160[A,N]	1,601 ± 226	1,334 ± 160
Shrubs	3,195 ± 246[J,A,N]	1,915 ± 156	1,779 ± 187	2,007 ± 76
Redstem ceanothus	3,497 ± 146[J,A,N]	2,013 ± 181	1,740 ± 223	1,897 ± 114
Scouler willow	2,601 ± 423[J,A,N]	1,565 ± 261[N]	1,623 ± 317	2,073 ± 154
Serviceberry	3,488 ± 93[J,A,N]	1,973 ± 129	2,092 ±404	2,049 ± 109
Requirements	2,200	3,000	2,700	2,400

[J]Estimate significantly different than estimate in June ($P < 0.05$)
[A]Estimate significantly different than estimate in August ($P < 0.05$)
[N]Estimate significantly different than estimate in November ($P < 0.05$).

Discussion

The high degree of variability in mineral concentrations observed in this study might be expected. Differences between vegetation classes are typical due to different cell-wall components (Short 1981). Other studies have documented a high degree of variability in plant mineral concentrations associated with soil type, precipitation, and weather conditions (Poole et al. 1989, Beaver 1999). Spring weather conditions can affect the timing of growth initiation. This, along with subsequent weather conditions could affect the phenological stage of plants throughout the growing season. Favorable growing conditions may be conducive to greater mineral absorption (Beaver 1999).

The importance of minerals to the proper biological function of animals is well recognized (Underwood 1977, Robbins 1983, Van Soest 1994), but often neglected in studies of large herbivores (Cook in press). Results from this study indicate that elk mineral requirements are generally provided for. Mixing of forage species probably compensates for deficiencies and for concentrations in certain species that are too high.

Sodium, which averaged only 1/10 or less of the daily nutritional requirements (estimates for beef cattle), is the cation of the extracellular environment, it is important for regulation of body fluid volume and osmolarity, acid-base balance and tissue pH, muscle contraction, and nerve impulse transmission (Robbins 1983). Thus, without sufficient amounts of sodium, elk growth and reproduction could be depressed. However, elk may be obtaining sodium from other sources than forage consumption, such as mineral licks and water (Weeks and Kirkpatrick 1976, Robbins 1983).

Toxic elements were also found in the forage analyzed. Detrimental effects of toxic elements, such as lead and cadmium, are related to the magnitude of the concentration within the body. Cadmium levels appear quite low and are similar to levels that are in domestic animal feeds (Underwood 1977). However, lead concentrations were much higher and were similar to levels reported from pastures rich in lead or areas near lead mines (Underwood 1977). Whether these levels would produce a toxic effect was not determined.

Percent crude protein in forage species

steadily declined from May through November, a commonly reported pattern (Cook in press). We also found that shrubs had higher concentrations of crude protein than graminoids. This may be an area-specific relationship as Urness et al. (1983) reported higher levels of protein in graminoids than shrubs, but others have reported the opposite (Everitt and Gonzalez 1981, Meyer et al. 1984). Hobbs et al. (1981) reported that grasses typically had lower concentrations of crude protein than shrubs during winter. However, our results indicate that crude protein in graminoids is significantly lower than in shrubs during August, but only slightly lower in November.

During summer, elk forage in open areas where abundant new-growth provides ample nutrients (Martinka 1969, Edge et al. 1988, Leege 1984). McLean (1972) and Hash (1973) reported elk using shrubfields throughout late summer and fall in northern Idaho. Movement to security areas of closed-canopy cover types during hunting seasons is evident in other areas as well (Morgantini and Hudson 1980, Unsworth and Kuck 1991, Hurley 1994).

Estimates of crude protein levels from May through November generally provided for the requirements of elk. Small deficiencies could be overcome via selective foraging. For example, elk could select leaves and terminal ends of twigs to overcome small deficiencies (Blair and Epps 1967, Dietz 1972). However, the higher the level of selective foraging to meet requirements results in a greater proportion of total forage that is "unavailable." Significant deficiencies, such as those observed for all graminoids in August, might not be overcome by diet selection.

By August, crude protein of graminoids was so low that losses of endogenous body protein associated with digesting them would equal or exceed any gain (Hobbs et al. 1982). The crude protein deficiencies we observed for graminoids in August indicate that elk could not restrict their diet to them and maintain endogenous body protein. Maintenance of dietary mixes is a means of achieving energy and protein requirements (Hobbs et al. 1981, Otsyina et al. 1982). Low crude protein levels in graminoids coincide with the period when elk have shifted from grass/low shrub areas to areas dominated by shrubs (Alldredge 1999).

Digestible energy levels of forage declined steadily from May through November, failed to provide for elk requirements after May, and were most deficient in graminoids after mid-summer. These patterns suggest elk should shift from grass/low shrub areas to areas with greater shrub development as seasons progress. In Colorado grasses provided more digestible energy on winter range than shrubs (Hobbs et al. 1981). However, our results for November suggest that shrubs provide more digestible energy during this period.

Estimates of digestible energy indicate that requirements of gravid cow elk are provided for in May, but moderate to severe deficiencies exist for lactating cow elk during the entire summer. Studies with captive elk indicate that lactating cow elk cannot be maintained (J.G. Cook personal communication) nor can elk calves grow (Cook et al. 1996) on diets with the low levels of digestible energy we report. Digestible energy is commonly a limiting component of ungulate diets from mid-summer through winter on many western large-ungulate ranges (Cook, in press, Parker et al. 1999). Loss of condition on winter range is expected as nutritional levels of winter forage decline below the requirements for maintenance (Hobbs et al. 1981, Cook in press).

Nutritional deficiencies can have serious effects on the reproductive capabilities of elk. Thorne et al. (1976) related poor condition to low birth weight, which resulted in a low probability of calf survival. Poor condition has resulted in delayed ovulation and breeding (Verme 1969), failure to ovulate, resorption of ovum, and failure to conceive (Trainer 1971). Failure to breed as a result of poor condition was reported for caribou (*Rangifer tarandus,* Cameron 1994) and elk (Trainer 1971, Cook 2000). Pregnancy rates of elk as low as 70% in some areas of Idaho (Gratson and Zager 1999) and 55% in western Oregon (Stussy 1993) have been reported. These low pregnancy rates are probably due to inadequate nutrition on summer and autumn ranges. Low levels of digestible energy reported in our study could result in reproductive pauses, slow calf growth over summer and autumn, and increased winter mortality because condition in autumn may be relatively poor, especially as the effects of low nutrition accumulate across years.

Foraging efficiency is an important factor influencing cover type use (Collins et al. 1978, Irwin and Peek 1983b). Both quantity and quality of forage are factors influencing cover type use patterns (Hanley et al. 1989). Several studies have demonstrated that both natural and man-made openings in forest canopies result in dramatic increases in forage production (Patton 1974, Lyon and Jensen 1980, Riggs et al. 1990). Maximum annual shrub biomass productivity occurs between 7 and 14 years after overstory removal (Alldredge 1999) and total shrub biomass was greatest 10 to 14 years following harvests within the cedar-hemlock zone of northern Idaho (Irwin and Peek 1979). Changes in habitat use from early summer to fall indicate that forage quality may be a factor driving habitat selection as areas used in both periods have large quantities of forage.

Many studies indicate that elk habitat use should switch during the fall to areas with conifer over-stories because vegetation in these areas remains succulent (Stehn 1973, Biggins 1975, Schoen 1977, Irwin and Peek 1983b, Wisdom and Cook 2000). However, forage quantity in conifer stands is very low. Graminoids and forbs are rare and total annual shrub productivity, including unpalatable species, is only 50 kg/ha, 5 to 10 times lower than early successional areas (Alldredge 2001). Such low forage biomass may limit foraging efficiency as instantaneous intake rates decrease and travel rates are elevated (Wickstrom et al. 1984). Low foraging efficiency may account for avoidance of conifer- dominated habitats as key foraging areas (Collins and Urness 1983) because lactating cow elk would not be able to consume sufficient forage to meet daily nutritional requirements (Cook in press).

Management Implications

Our nutrition data indicate that elk forages provide adequate levels of minerals and probably protein over the summer and autumn. However, digestible energy deficiencies over an extended period of time warrants concern, especially in relation to potential effects on herd productivity. Our data only provide a measure of the digestible energy available to elk, and does not indicate actual digestible energy content of diets. Thus, conclusions about the effects on their nutritional condition and productivity are avoided. At the least, the data indicate that elk must be highly selective of plant parts, plant taxa, and habitats where they forage, if they are to achieve adequate digestible energy intake. Therefore, we speculate that much of the forage available to them is of little value, and "carrying capacity" is probably considerably lower than would be predicted based only on forage biomass. Our data also suggest a nutritional environment that is marginal in its ability to provide for the summer-fall digestible energy needs of cow-calf pairs. We would predict relatively strong density-dependent relations in such an environment, because a potentially small portion of the forage base apparently is actually of value to elk. Further, we would predict that under these marginal conditions that landscape-scale forest management practices that influence forage quality and quantity will have substantial long-term influences on these elk. Although causes are unknown, elk herds of the Clearwater basin in north-central Idaho have experienced declines in calf recruitment and subsequently declines in herd size of about 25% over the last decade (Gratson and Zager 1999). Our data suggest that nutrition, perhaps via density dependent mechanisms, should be suspected as a potential contributor to these declines.

Our data support the contention that a diversity of habitats providing forages that vary in nutritional levels through time is an important factor in maintaining high-quality habitat for elk. These include forests that provide security and late-maturing forage as well as seral communities that provide forage throughout the year. We suggest that winter range may also be limiting, but diversity of summer and fall forage should be considered in management plans.

Literature Cited

Alldredge, M. W. 1999. Elk habitat relationships on an industrial forest in northern Idaho. M. S. Thesis, Univ. of Idaho, Moscow, Ida.

Alldredge, M.W., J. M. Peek, and W.A.Wall. 2001. Shrub community development and annual trends over a 100 year period on an industrial forest of Idaho. Forest Ecol. and Manage. 152:259–273.

Anderson, K. A. 1996. Micro-digestion and ICP-AES analysis for the determination of macro and micro elements in plant tissues. Atomic Spectroscopy 1:30–33.

Association of Official Analytical Chemists (A.O.A.C.). 1984. Official methods of analysis. 14th ed. Assoc. of Official Chemists, Washington D.C.

Beaver, D. E. 1999. Habitat use and patch selection by mule deer in a sagebrush-steppe environment of southeast Idaho. M. S. Thesis, Univ. of Idaho, Moscow, Ida.

Biggins, D. E. 1975. Seasonal habitat relationships and movements of the Spotted Bear elk herd. M. S. Thesis, Univ. of Montana, Missoula, Mont.

Blair, R. M. and E. A. Epps, Jr. 1967. Distribution of protein and phosphorus in spring growth of rusty blackhaw. J. Wildl. Manage. 31:188–190.

Cameron, R. D. 1994. Reproductive pauses by female caribou. J. Mammal.75:10–13.

Collins, W. B. and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manage. 47:646–663.

Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. J. Wildl. Manage. 42:799–810.

Cook, R. A. 2000. Nutritional influences on breeding dynamics in elk. M.S. Thesis, Univ. of Idaho, Moscow, Ida.

Cook, J. G. In press. Nutrition and food habits. pp 000-000 *In* D. E. Toweill and J. W. Thomas, (ed.), Elk of North America: Ecology and Management. 2nd ed. Smithsonian Inst. Press, Washington, D.C..

Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. J. Wildl. Manage. 60:528–541.

Cooper, S.V., K.E. Neiman, R. Steele, and D.W. Roberts. 1987. Forest habitat types of northern Idaho: a second approximation. U.S. D. A. For. Ser. Gen. Tech. Rep. INT 2136.

Crookston, N.L. and A. R. Stage. 1999. Percent canopy cover and stand structure statistics from the forests vegetation simulator. USDA For. Ser. Gen. Tech. Rep RM/RS GTR 24.

Daubenmire, R. and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. State Univ. Agr. Expt. Sta. Tech. Bull.60. Pullman, Wash.

Dietz, D. R. 1972. Nutritive value of shrubs. pp 289-302 *In* C. M. McKell, J. P. Blaisdell, and J. R. Goodin, (ed.), Wildland Shrubs—their biology and utilization. USDA For. Serv. Gen. Tech. Rep. INT-I.

Edge, W. D., C. L. Marcum, and S. L. Olson-Edge. 1988. Summer forage and feeding site selection by elk. J. Wildl. Manage. 52:573–577.

Everitt, J. H. and C. L. Gonzalez. 1981. Seasonal nutrient content in food plants of white-tailed deer on the south Texas plains. J. Range Manage. 34:506–510.

Gratson, M. W., and Zager, P. 1999. Study IV: Factors influencing elk calf recruitment. Idaho Dept. of Fish and Game, Project W-160-R-25, Subproject 31. Job progress report. Boise, Ida.

Hanley, T. A., C. T. Robbins, and D. E. Spalinger. 1989. Forest habitats and the nutritional ecology of Sitka black-tailed deer: A research synthesis with implications for forest management. USDA For. Ser. Gen. Tech. Rep. PNW-GTR-230.

Hansen, H. J., R. C. Martin, and G. A. Meuleman. 1989. Phase II, wildlife protection, mitigation, and enhancement planning, Dworshak Reservoir. Contract, DI-I79-88BP92631, Draft report, Idaho Dept. Fish and Game, Boise, Ida.

Hash, H. S. 1973. Movements and food habits of Lochsa elk. M. S. Thesis, University of Idaho, Moscow, Ida.

Hershey, T.J. and T.A. Leege. 1984. Elk movements and habitat use on a managed forest in northcentral Idaho. Idaho Dept. of Fish & Game Wildl. Bull. 10.

Hobbs, N. T., D. L. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Manage. 45:156–171.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. J. Wildl. Manage. 46:12–21.

Hurley, M. A. 1994. Summer-fall ecology of the Blackfoot-Clearwater elk herd of western Montana. M. S. Thesis, Univ. of Idaho, Moscow, Ida.

Idaho Dept. Fish and Game. 1999. Statewide surveys and inventory. Federal Aid in Wildl. Restoration Project, W-170-R-22 progress report. Boise, Ida.

Irwin, L.L., and J. M. Peek. 1979. Shrub production and biomass trends following five logging treatments within the cedar-hemlock zone of northern Idaho. Forest Sci. 25:415–426.

Irwin, L.L., and J. M. Peek. 1983a. Elk, *Cervus elaphus*, foraging related to forest management and succession in Idaho. Canad. Field-Nat. 97(4): 443–447.

Irwin, L.L., and J. M. Peek. 1983b. Elk habitat use relative to forest succession in Idaho. J. Wildl. Manage. 47:664–672.

Kingery, J. L., J. C. Mosley, and K. C. Bordwell. 1996. Dietary overlap among cattle and cervids in northern Idaho forests. J. Range Manage. 49:8–15.

Leege, T.A. 1969. Burning seral brush ranges for big game in northern Idaho. Proc. North Amer. Wildl. and Nat. Res. Conf. 34: 429–438.

Leege, T. A. 1984. Guidelines for evaluating and managing summer elk habitat in northern Idaho. Idaho Dept. Fish and Game Wildl. Bull. 11. Boise, Ida.

Leege, T. A. and G. Godbolt. 1985. Herbaceous response following prescribed burning and seeding of elk range in Idaho. Northwest Sci. 59:134–143.

Lyon, L. J. and C. E. Jensen. 1980. Management implications of elk and deer use of clear-cuts in Montana. J. Wildl. Manage. 44:352–362.

Martinka, C. J. 1969. Population ecology of summer resident elk in Jackson Hole, Wyoming. J. Wildl. Manage. 33:465-481.

McGeehan, S. L. and D. V. Naylor. 1988. Automated instrumental analysis of carbon and nitrogen in plant and soil samples. Comm. in Soil Sci. and Plant Anal. 19:493–505.

McLean, S. 1972. Movements and migrations of the Lochsa elk herd. M. S. Thesis, Univ. Idaho, Moscow, Ida.

Meyer, M. W., R. D. Brown, and M. W. Graham. 1984. Protein and energy content of white-tailed deer diets in the Texas coastal bend. J. Wildl.Manage. 48:527–534.

Moeur, M. 1985. COVER: a user's guide to the Canopy and SHRUBS extension of the Stand Prognosis Model. USDA For. Ser. Gen. Tech. Rep. INT-GTR- 190.

Morgantini, L. E., and R. J. Hudson. 1980. Human disturbance and habitat selection in elk. pp 132–139 *In:* M. S. Boyce and L. D. Hayden-Wing, (ed.), North American elk: ecology, behavior and management. Univ. Wyoming. Laramie, Wyo.

National Research Council. 1996. Nutrient requirements of cattle. Seventh edition, National Academy Press, Washington D. C.

Nelson J.R, and T.A Leege. 1982. Nutritional requirements and food habits. pp 219–277 *In:* J. W. Thomas and D. E. Toweill, (ed.), Elk of North America: ecology and management. Stackpole Books, Harrisburg, Penn.

Otsyina, R., C. M. McKell, and G. Van Epps. 1982. Use of range shrubs to meet nutrient requirements of sheep grazing on crested wheatgrass during fall and early winter. J. Range Manage. 35:751–753.

Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in natural forest environment. Wildl. Monogr. 163.

Patton, D. R. 1974. Patch cutting increases deer and elk use of a pine forest in Arizona. J. Forest. 72:764–766.

Pearson, H. A. 1970. Digestibility trials: in vitro techniques. pp 85-92 *In* H. A. Paulsen, Jr., E. H. Reid, and K. W. Parker, (ed.), Range and wildlife habitat evaluation-a research symposium. USDA For. Serv. Misc. Publ. 1147.

Poole, S. C., V. R. Bohman, and J. A. Young. 1989. Review of selenium in soils, plants, and animals in Nevada. Great Basin Nat. 49:201–213.

Riggs, R. A., J. G. Cook, L. L. Irwin, and J. L. Spicer. 1990. Relating timber management to cover for big game on interior northwest winter range: some thoughts on reducing conflict. pp 18–36 *In:* R. L. Callas, D. B. Kock, and E. R. Loft, (ed.), Proc. Western States and Provinces Elk Workshop. Calif. Dept. of Fish and Game, Sacramento, Calif.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, Inc., Orlando, Fla.

Schoen, J. W. 1977. The ecological distribution and biology of wapiti (*Cervus elaphus nelsoni*) in the Cedar River Watershed, Washington. Ph.D. Diss., Univ. Washington, Seattle, Wash.

Short, H. L. 1981. Nutrition and metabolism. pp 99-127 *In* O. C. Wallmo, (ed.), Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln, Neb.

Stage, A. R. 1973. Prognosis model for stand development. USDA For. Ser. Res. Pap. INT 137.

Stehn, T. 1973. Daily movements and activities of cow elk in the Sapphire Mountains of western Montana during summer and fall. M. S. Thesis, Univ. Montana, Missoula, Mont.

Stussy, R. 1993. The effects of forage improvement practices on Roosevelt elk in the Oregon Coast range. M.S. Thesis, Oregon State Univ., Corvallis, Ore.

Thomas, J. W., H. Black, Jr., R. J. Scherzinger, and R. J. Pedersen. 1979. Deer and elk. pp104-127, *In* J. W. Thomas (ed.), Wildlife habitats in managed forests the Blue Mountains of Oregon and Washington. USDA For. Ser., Agr. Handb. No. 553.

Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. J. Wildl. Manage. 40:330–335.

Tilley, J. M. A., and R. A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. J. British Grassl. Soc. 18:104–111.

Trainer, C. E. 1971. The relationship of physical condition and fertility of female Roosevelt elk (*Cervus canadensis roosevelti*) in Oregon. M.S. Thesis, Oregon State Univ., Corvallis, Ore.

Underwood, E. J. 1977. Trace elements in human and animal nutrition. Fourth ed. Academ. Press, New York.

Unsworth, J. W. and L. Kuck. 1991. Bull elk vulnerability in the Clearwater Drainage of north-central Idaho. pp 85–88 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers. Proc. of the elk vulnerability symposium. Montana State Univ., Bozeman, Mont.

Unsworth, J.W., L. Kuck, E. O. Garton, and G. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. J. Wildl. Manage. 62:1255–1263.

Urness, P. J., D. D. Austin, and L. C. Fierro. 1983. Nutritional value of crested wheatgrass for wintering mule deer. J. Range Manage. 36:225–226.

Van Soest, P. J. 1994. Nutritional ecology of the ruminant. Second edition. Cornell University Press, Ithaca, N.Y.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildl. Manage. 33:881–887.

Weeks, H. P. Jr. and C. M. Kirkpatrick. 1976. Adaptations of white-tailed deer to naturally occurring sodium deficiencies. J. Wildl. Manage. 40:610–625.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48:1285–1301.

Wisdom, M. J. and J. G. Cook. 2000. North American elk. pp 694–735 *In:* S. Demarais and P. R. Krausman, (ed.), Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, N.J.

Wolf, D.D. and E.W. Carson. 1973. Respiration during drying of alfalfa herbage. Crop Sci. 13. 660.

Young, V.A. and W.L. Robinette. 1939. A study of the range habits of elk on the Selway game Preserve. Univ. Idaho School of Forest. Bull. No. 9.

J. Range Manage.
55: 260-265 May 2002

Irrigation impact on harvest efficiency in grazed Old World bluestem

W.R. TEAGUE AND S.L. DOWHOWER

Authors are Associate Professor and senior Research Associate, Texas Agricultural Experiment Station, P.O. Box 1658, Vernon, Tex. 76385.

Abstract

In 1992 and 1993, pastures of WW-Spar Old World bluestem (*Bothriochloa ischaemum* L.) were maintained at 2 levels of soil water, rainfall and rainfall plus 25 mm/week of supplementary irrigation. At both moisture levels the grass was maintained at 2 levels of standing crop, averaging 1,548 and 2,154 kg ha^{-1}, using continuous variable stocking. Measurements were made to determine how different levels of soil moisture interacted with grazing intensity to change leaf area index, leaf-stem and live-dead ratios, tiller density, and the proportion of gross leaf production that was grazed (harvest efficiency). The proportions of live to dead, and leaf and stem biomass, remained constant under the different levels of soil water content. Soil water content alone had no effect on leaf area index, tiller density and the proportion of live or dead, leaf and stem. Winter tiller survival was significantly higher in the pastures with higher soil water content. Increasing soil water content and increasing grazing intensity interacted to reduce the proportion of dead leaf, increase production of new tillers, and increase the proportion of leaf grazed by decreasing leaf that died and was not grazed. This study indicates that if continuously grazed Old World bluestem was maintained at a standing crop of 1,500 kg ha^{-1}, harvest efficiency would be higher in wet years or under irrigation than if standing crop was higher.

Key Words: *Bothriochloa ischaemum,* continuous variable stocking, herbage allowance

Resumen

En 1992 y 1993 poteros de WW-Spar "Old World bluestem" (*Bothriochloa ischaemum* L.) se mantuvieron en dos niveles de humedad del suelo, humedad proveniente de la lluvia y humedad producto de la lluvia mas 25 mm/semana de irrigación suplementaria. En ambos niveles de humedad el zacate se mantuvo en 2 niveles de cosecha en pie, 1,548 y 2,154 kg ha^{-1} en promedio, para lo cual se utilizo una carga animal continua variable. Las mediciones se hicieron para determinar como los diferentes niveles de humedad del suelo interactuaron con la intensidad de apacentamiento para cambiar el indice de área foliar, las relaciones tallo-hoja y biomasa viva-muerta, la densidad de hijuelos y la proporción de producción total de hojas que fue apacentada (eficiencia de cosecha). Las proporciones de biomasa viva-muerta y tallo-hoja permanecieron constantes bajo los diferentes niveles de humedad del suelo. El contenido de humedad del suelo solo no tuvo efecto en el indice de área foliar, la densidad de hijuelos y las proporciones de biomasa viva-muerta y tallo-hoja. La sobrevivencia de los hijuelos en invierno fue significativamente mayor en los potreros con alto contenido de agua en el suelo. El aumento del contenido de agua en el suelo y la intensidad de apacentamiento interactuaron para reducir la proporción de hojas muertas, incrementar la producción de nuevos hijuelos e incrementar la proporción de hojas apacentadas al disminuir las hojas muertas y no fueron apacentadas. Este estudio indica que si las praderas de "Old World bluestem" apacentadas continuamente se mantuvieran con una biomasa en pie de 1,500 kg ha^{-1}, la eficiencia de cosecha sería mayor en los años húmedos o bajo irrigación que si la cosecha en pie fuera mayor.

Old World bluestem (*Bothriochloa ischaemum* L.) pastures are widely used to enhance production and profitability of range-based beef systems in the southern plains of North America (Sims and Dewald 1982, Coyne and Bradford 1985). This species is easy to establish, drought hardy, resistant to defoliation and produces moderate quality forage in spring and summer, but forage quality in late summer through winter is very low (Eck and Sims 1984, Dabo et al. 1987). Diet quality, intake, and animal performance of animals grazing Old World bluestem are particularly sensitive to the proportion and density of green leaf mass and the leaf to stem ratio (Forbes and Coleman 1986, Teague et al. 1996).

Under continuous grazing, the rapid turnover of leaves on tillers has meant that maximizing yield per hectare (amount harvested by grazing) does not depend on maximizing photosynthesis and the gross rate of tissue production, since such management also results in high rates of leaf senescence. Maximum yield per hectare is achieved when the pasture is maintained at a relatively low leaf area index (LAI), which is usually at lower gross tissue production (Grant et al. 1983, Parsons et al. 1983a, 1983b). Lower LAI increases harvest efficiency, since a greater percentage of leaf is consumed before it dies and different pasture structure provides the grazing animal greater leaf densities and a diet

We gratefully acknowledge the facilities and livestock made available to us by Dr. Marvin Sharp and the financial support of the E. Paul and Helen Buck Waggoner Foundation, Inc. We thank Jeff Estes, Paula Martinez, Chad Sosolik and Jan Worrall for technical support. David Briske, Jerry Cox, Mort Kothmann, Don Robinson and Darek Malinowski kindly reviewed this manuscript.
Manuscript accepted 22 Aug. 2001.

proportionally greater in leaf and nutrients (Grant et al. 1983, Parsons et al. 1983a, 1983b). Photosynthetic rates are greater in younger leaf and the respiratory burden and shading of older plant material is avoided (Johnson and Parsons 1985, Parsons et al. 1988, Murphy 1990). In addition, production is enhanced through more rapid nutrient cycling (McNaughton 1979). These factors all result in more growth, an extended growing season and greater levels of water-use-efficiency in pastures that are grazed to maintain relatively low leaf area indices.

This study examines the leaf and tiller dynamics and harvest efficiency of Old World bluestem pasture under different levels of soil water and intensities of continuous stocking. In an adjacent study, Old World bluestem was maintained at 1,500, 1,900 and 2,400 kg ha^{-1} with continuous variable stocking during 1992 and 1993 with normal rainfall (Teague et al. 1996). This concurrent study with irrigation was conducted to determine if a higher level of soil moisture would alter parameters influencing the proportion of leaf produced that is harvested (harvest efficiency). We hypothesize that under continuous stocking of Old World bluestem, increasing soil water level and grazing intensity will increase the leaf to stem and live to dead ratios, increase tiller density, and increase harvest efficiency. This basic information is needed to determine if grazing management to sustain efficient pasture and animal productivity needs to be different in dry compared to wet years or under irrigation.

Grazing was used in this study since estimates of the seasonal pattern of grass production, using intermittent cutting at regular intervals, differ substantially from those generated by studying the pasture under grazing (Barnes 1972, Coughenour et al. 1984, Blackburn and Kothmann 1989).

Materials and Methods

Study Site

The study was conducted on a 4-year-old, weed-free pasture of WW-Spar Old World bluestem (*B. ischaemum* (L.) Ken var *ischaemum* (WW-573). The study was located at a site 5 km east of Vernon (34° 10' N, 100° 16' W) in north-central Texas. The climate is continental with an average 220 frost-free, growing days. Mean annual precipitation is 550 mm, varying from 490 mm to 1,000 mm, that is bimodally distributed with peaks in May (102 mm) and September (81 mm). Evaporation averages 1,835 mm per annum (607 mm diameter pan). Rainfall was recorded on-site and temperature was recorded 15 km NW at the Vernon airport. Annual mean monthly temperature is 17.4° C ranging from 36.4° C in July to –2.3° C in January. Elevation is 390 m at the research site and slope is 1–3%.

Soil was a Wichita clay loam (fine, mixed, thermic Typic Paleustalf) with an 'A' horizon permeability of 5–12 mm hr^{-1} (USDA 1997). These soils are moderately alkaline (pH = 7.8-8.5) and at the beginning of the experiment had no measurable nitrogen, moderate levels of phosphorus (12 ppm), high potassium (290 ppm), high calcium (4,540 ppm), high magnesium (600 ppm), no salinity, and very low sodium (< 10 ppm) and sulphur (< 1 ppm) based on dry soil weights.

Pasture Management

Two levels of soil moisture were maintained within each of 2 grazing intensity treatments outlined below, between May and August in both 1992 and 1993. These levels were: a control receiving incoming rainfall, and an irrigated treatment receiving rainfall plus 25 mm per week. Water was applied in 1 application per week using an overhead sprinkler irrigation system at a rate of approximately 12 mm/hour. Each irrigation treatment had 2 replicates allocated at random. Grazing intensity was not replicated. Within each grazing intensity area the irrigation plots were not separately fenced off. Each irrigated replicate plot was 4 x 4 m. Soil moisture was monitored volumetrically each week using a neutron probe to a depth of 1.2 m at intervals to the following depths 15, 30, 60, 90, and 120 cm. The access tube was located in the center of each moisture level plot.

The 2 different grazing intensities were maintained using continuous, variable stocking. Each area was 0.25 ha in size. Stock numbers on the grazed pastures were adjusted weekly following pasture height measurement using a pasture disc-meter (Bransby et al. 1977). The number of steers per pasture ranged from 3 to 8. The target disc-meter heights were 35–40 mm (heavy) and 46–55 mm (light). The mean stocking rates for the treatments were 2.1 AUD/ha (heavy), and 1.4 AUD/ha (light). Average standing crops were 1,548, and 2,154 kg ha^{-1} for the heavy and light pastures, respectively. A multiple regression model was developed, including disc-meter height and the percentage of live and dead leaf and culm to describe the relations between standing crop and disc-meter height. The R^2 values were 0.93 and 0.92 for heavy and light pastures, respectively (Teague et al. 1996).

In 1992, the pastures were fertilized with 112 kg ha^{-1} of nitrogen, as urea, in 2 equal dressings prior to expected rainfall in late April and late June. In 1993, only the April fertilizer application (56 kg ha^{-1}) was applied since the trial was terminated at the end of July. To remove residual standing crop from the previous season, all pastures were either burned (1992) or mowed (1993) in late winter. The pastures were stocked with steers on 4 May 1992 and 19 May 1993.

Tiller Density and Leaf Area Index

In 1992, dry weight, leaf and sheath area and number of tillers per unit ground area in the pastures were measured weekly on each treatment replicate by clipping 20 randomly located quadrats (100 cm^2) at ground level. Lamina area was measured with an area meter (LiCor LI-3000, Lincoln, Nebr.). Samples were separated after drying into live or dead, lamina and stem (reproductive). To record possible winter mortality differences after these treatments, a total tiller count was made on 20 tufts in each treatment replicate in the fall of 1992. The tillers on these tufts were counted again after green-up in spring.

Turnover and Fate of Leaves

In 1993, leaf extension and death were measured in each of the treatment replicate plots. Tillers were marked with colored wire ties and measured weekly for a period of 6 weeks from 30 June 1993. A total of 40 tillers were marked per replicate. These were located 10 per line at random along 4 line transects radiating out from the center to each plot corner. Tillers with 5 to 6 leaves were chosen, 2 of which were usually fully expanded. At each randomly located point, the nearest tiller with 5 to 6 leaves was selected. Each lamina on each tiller was measured weekly to record lamina extension, lamina defoliation, lamina senescence, the emergence of a new leaf or the emergence of a daughter tiller. The same parameters were recorded for each daughter tiller that appeared on any mother tiller.

Leaf senescence occurred on the older leaves and proceeded progressively from the tip towards the lamina base and finally the leaf sheath. Defoliation occurred on the younger, more elevated leaves and was noted by a clean removal of a part of the lamina. In most cases, these younger defoliated laminae continued to expand for a week or 2. Recent defoliations were easy to distinguish from week-old or older defoliations, owing to the development of a dry necrotic edge on the end of the defoliated laminae.

Data Analysis

Since irrigation but not grazing intensity was replicated, the significance of the main effects for irrigation and the irrigation by grazing intensity interaction were tested as a split plot with the soil moisture replicate as split plot error. Data were analyzed using ANOVA for soil moisture, standing crop, LAI and tiller density, and repeated measures analysis of variance for lamina extension, lamina defoliation and lamina senescence. For analysis of plant parts, standing crops and tiller survival, a General Linear Model (GLM) was used, with tiller density (tillers cm^{-2}) as a covariant. Percentage values covered a wide range and did not require transformation. All analyses were carried out using the SAS statistical package (SAS 1988). Least significant difference tests (Steel and Torrie 1960) were used to separate means.

Results and Discussion

Climate and Soil Moisture

The temperatures in the 1992 growing period were slightly lower than the long-term means but 1993 temperatures were very close to the long-term means (Fig. 1). Evaporation in 1992 was similar to the long-term mean while that in 1993 was somewhat greater, particularly in July. Precipitation prior to growth in May 1992 and 1993 was above average. May was drier but June was wetter than average in 1992. In 1993, both May and June precipitation were slightly above average. July through September precipitation was average in both years.

Over the period that plant growth was measured in both 1992 and 1993, the non-irrigated control had significantly lower ($P < 0.05$) soil moisture than the irrigated treatment (Fig. 2). Differences in soil moisture in all treatments in the top 60 cm of soil, where 90% of old world bluestem roots occur (Coyne and Bradford 1986), showed similar differences and levels of significance as illustrated for the full 120 cm profile presented in Fig. 2. In both years, soil moisture was lower in the lightly grazed treatment than the heavily grazed treatment ($P < 0.10$), probably due to the higher leaf area and live biomass in the lightly grazed treatment (Teague et al. 1996).

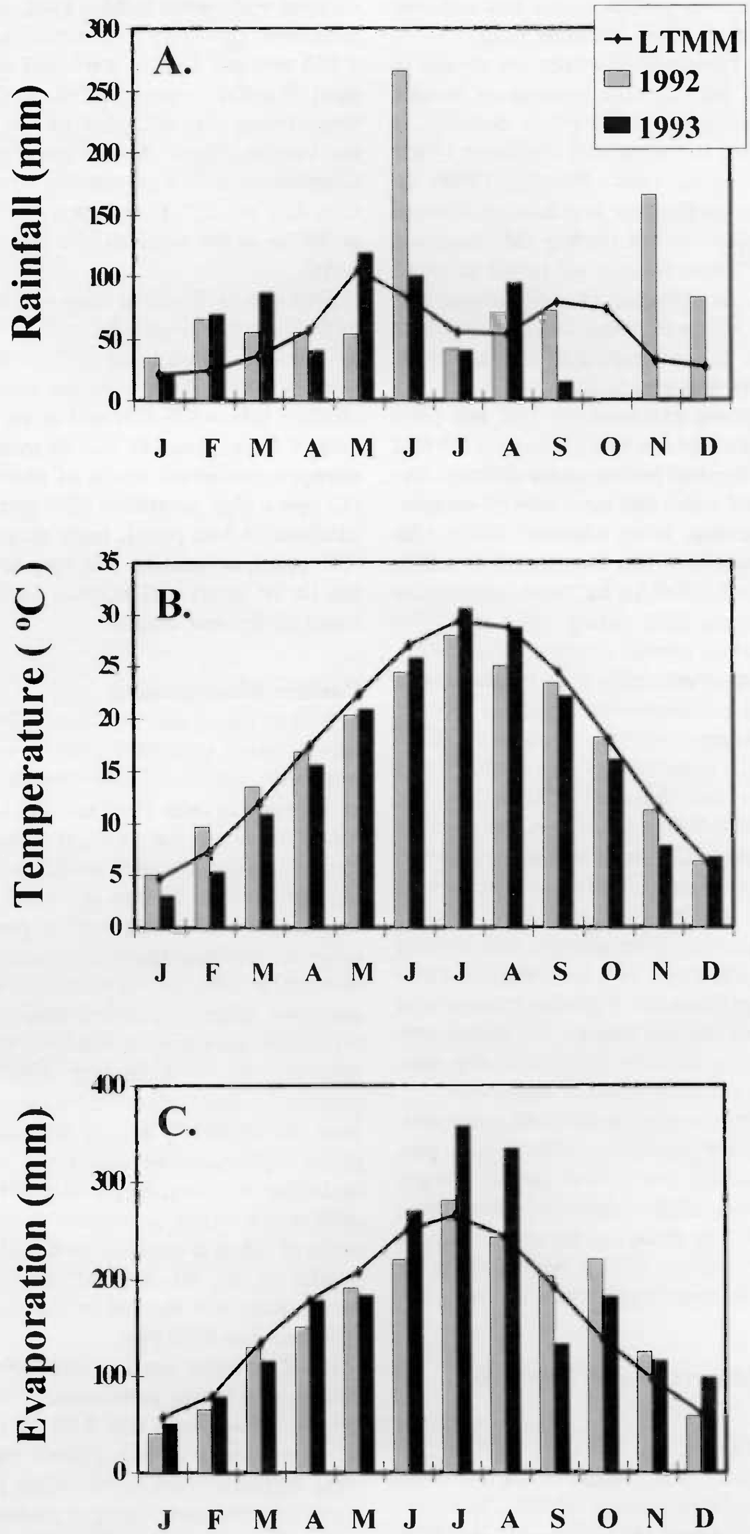


Fig. 1. Mean monthly weather data at the experimental site for 1992 and 1993 compared to long-term mean monthly (LTMM) data. (A) rainfall, (B) temperature, and (C) evaporation.

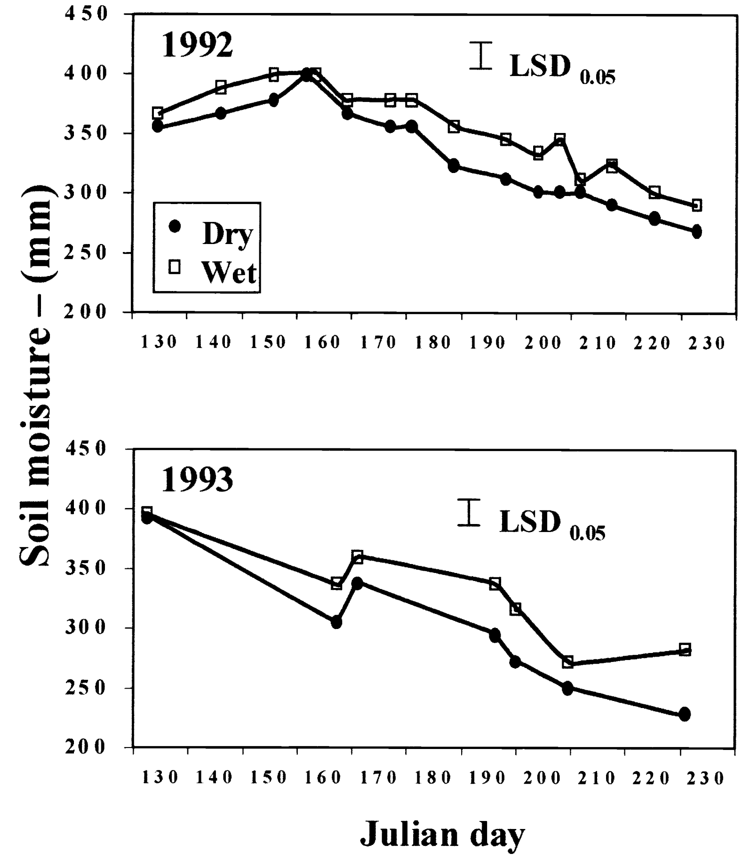


Fig. 2. Total soil moisture (mm) to 1.2 m depth for the irrigated treatment and non-irrigated control from mid May to the end of August for 1992 and 1993.

Leaf and Stem Proportions, Tiller Density and Leaf Area Index

Although the proportion of live and dead, leaf and stem was different at different dates during the experiment ($P < 0.05$), there was no overall difference in proportions of these plant organ categories due to soil moisture per se ($P > 0.10$) (Table 1) and no interaction between soil moisture and grazing intensity ($P > 0.10$) regarding live and dead organ proportions. Tiller densities and leaf area index were not different between irrigation treatments ($P > 0.10$) (Table 2), and there were no interactions between soil moisture and grazing intensity regarding tiller density and leaf area index ($P > 0.10$).

Winter tiller survival was significantly higher ($P < 0.05$) in the irrigated treatments (Table 2) in a winter that was average for the area regarding temperature and soil moisture. However, there was no interaction between moisture level and grazing intensity ($P > 0.10$) regarding winter tiller survival.

Harvest Efficiency

Increasing soil moisture significantly increased overall plant height and total live leaf extension ($P < 0.10$)(data not shown). Additional soil moisture also stimulated total leaf extension ($P < 0.10$) but it had no measurable effect on the proportion of dead leaf ($P > 0.10$) even though the number of dead leaves per tiller was higher with increasing soil moisture ($P < 0.10$) (Table 3). However, a greater percentage of total leaf (length) died in the low soil moisture treatment ($P < 0.10$) so decreasing soil moisture had the effect of increasing the proportion of leaf that died and was not grazed, resulting in a lower harvesting efficiency. The amount of leaf (length) that was grazed increased with increasing soil moisture ($P < 0.10$), but the percentage of total leaf grazed was similar at different soil moisture levels ($P > 0.10$). Increased soil moisture had no effect on the number of new leaves per tiller ($P > 0.10$) (Table 3).

There were interactions between soil moisture and grazing treatments regarding length of live leaf and dead leaf produced (data not shown). Increasing soil moisture interacted with increasing grazing pressure to increase live leaf production ($P < 0.01$). High soil moisture and heavier grazing also interacted to reduce the proportion of dead leaf ($P < 0.10$) and increase production of new tillers ($P < 0.05$).

The low level of response by Old World bluestem to the irrigation treatments is surprising since there was a significantly lower level of soil moisture in the non-irrigated control compared to the irrigated treatment. It is possible that the close to average precipitation during this study, resulted in insufficient water stress in the lower moisture treatment to cause significant differences, since a response to different levels of soil moisture is probably contingent upon differences in moisture stress exceeding a certain level (Busso and Richards 1995). However, grass response to irrigation alone may be smaller than other treatments and the greatest increases in plant growth occur when irrigation is combined with other treatments (Risser et al 1981).

Table 1. Contribution of different plant organs to standing crop of Old World bluestem pastures at 2 levels of soil moisture in 1992.

Moisture Level	Standing crop: Live leaf	Dead leaf	Live stem	Dead stem	Total
	($g\ m^{-2}$)				
Wet[1]	94.0[a]	25.1[a]	48.9[a]	7.8[a]	175.8[a]
Dry	94.0[a]	24.2[a]	48.7[a]	8.7[a]	175.6[a]
Pooled s.e.	3.5	1.9	3.6	0.6	7.5

[1]Means within columns with same subscripts are not significantly different ($P > 0.05$).

Table 2. Density of primary tillers (cm^{-2}) and leaf area index during the 1992 growing season at 2 levels of soil moisture and the number of tillers (cm^{-2}) surviving winter in Old World bluestem pastures.

Moisture level	Wet	Dry	Pooled s.e.
Tiller density[1]	3.81[a]	3.82[a]	0.56
Leaf area index	1.22[a]	1.14[a]	0.06
Tiller survival	2.03[a]	1.70[b]	0.065

[1]Means within rows with different subscripts are significantly different ($P < 0.05$).

Table 3. The effect of different levels of irrigation on plant stature and the turnover and fate of leaves on Old World bluestem pastures.

Moisture level	Dry	Wet
Total leaf extension (mm)[1]	149[a]	259[b]
Total leaf death (mm)	261[a]	253[a]
Total leaf grazed (mm)	159[a]	237[a]
Dead leaf as % of total leaf	66[a]	45[b]
Grazed leaf as % of total	40[a]	47[a]
Number of new leaves per tiller	2.7[a]	3.6[a]
Number of dead leaves per tiller	4.4[a]	5.3[b]
Number of leaves grazed per tiller	1.4[a]	2.4[a]

[1]Means within rows with different subscripts are significantly different (P < 010).

In a species such as Old World bluestem, which is adapted to a semi-arid environment (Sims and Dewald 1982), an inherent ability to maintain a low density of tillers may increase survival and fitness. A feature of Old World bluestem in the field is that there are distinctive tufts surrounded by bare ground, resulting in the low tiller densities and LAIs reported here. There may be adaptive significance to having lower tiller densities and less or slower growth to survive and compete successfully under more stressful and variable conditions. Lower densities of perennial grasses are believed to be more competitive with invading grass species in semi-arid environments (Buman et al. 1988, Pyke and Archer 1991).

Species differ markedly in how they respond above and below ground to different levels of herbivory (Briske 1993). Those that have demonstrated the ability to withstand severe herbivory and prosper, generally require a high level of resources, i.e. water and nutrients, to do so (Maschinski and Whitham 1989, Holland et al. 1992, Briske 1991). Nitrogen fertilizer levels in this study were moderately low (Taliaferro et al. 1975, Teague et al. 1996) and nitrogen was, therefore, probably moderately limiting. Coyne and Bradford (1986, 1987) report that with Old World bluestem, greater levels of nitrogen increase photosynthetic efficiency per unit leaf area and maintain a higher and more constant growth rate. Nitrogen deficiency also reduced growth and competitive ability in a number of other species by slowing leaf appearance rate and limiting tillering capacity (Wilson and Brown 1983, Thomas et al. 1990, Tallowin and Brookman 1996). It is possible that low nitrogen may have resulted in low tiller densities and the lack of response to the irrigation treatment in this study.

Conclusions

Maximizing the amount of secondary productivity per hectare involves balancing the efficiency of capturing incoming solar radiation and forage production with forage quality and harvesting efficiency. Leaf area index and tiller density influence capture of solar radiation and forage production per hectare, while density of live leaf and the ratios of live to dead, and leaf and stem, influence diet quality and harvesting efficiency. In the companion, rain fed study where Old World bluestem was maintained at 1,500, 1,900, and 2,400 kg ha^{-1}, the shorter pastures had a greater proportion of leaf, live stem, percentage of crude protein, and weight gain per hectare (Teague et al. 1996). The results of this study indicate that increasing soil moisture level and grazing intensity interacted to increase the proportion of leaf produced that was harvested (harvest efficiency), reduce the proportion of dead leaf, and increase production of new tillers and winter tiller survival. However, increasing soil water level did not increase tiller density during the summer growing period. In addition, increasing soil water level did not increase the leaf to stem and live to dead ratios as hypothesized. This study indicates that if continuously grazed Old World bluestem is maintained at a standing crop of 1,500 kg ha^{-1}, harvesting efficiency is higher in wet years or under irrigation than if standing crop is higher.

Literature Cited

Barnes, D.L. 1972. Defoliation effects on perennial ryegrass—continuing confusion. Proc. of the Grassl. Soc. of Southern Africa 7:138–145.

Blackburn, H.D. and M.M. Kothmann. 1989. A forage dynamics model for use in range or pasture environments. Grass and Forage Sci. 44: 283–294.

Bransby, D.I., A.G. Matches, and G.F. Krause. 1977. Disc meter for rapid estimation of herbage yield in grazing trials. Agron. J. 69:393–396.

Briske, D.D. 1991. Developmental morphology and physiology of grasses, p. 85–108. *In*: R.K. Heitschmidt and J.W. Stuth, (eds.), Grazing management: an ecological perspective. Timber Press, Portland, Ore.

Briske, D.D. 1993. Grazing optimization: a plea for a balanced perspective. Ecol. Appl. 3:24–26.

Buman, R.D. S.B. Monsen, and R.H. Abernethy. 1988. Seedling competition between mountain rye, 'Hycrest' crested wheatgrass and downy brome. J. Range Manage. 41:30–34.

Busso, C.A. and J.H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. J. Arid Environ. 29:239–251.

Coughenour, N.B., S.J. McNaughton, and L.L. Wallace. 1984. Modelling primary production of perennial graminoids. Ecol. Model. 23:101–134.

Coyne, P.I. and J.A. Bradford. 1985. Some growth characteristics of four Old World bluestems. J. Range Manage. 38:27–32.

Coyne, P.I. and J.A. Bradford. 1986. Biomass partitioning in `Caucasian' and `WW-Spar' Old World bluestems. J. Range Manage. 39:303–310.

Coyne, P.I. and J.A. Bradford. 1987. Nitrogen and carbohydrate partitioning in `Caucasian' and `WW-Spar' Old World bluestems. J. Range Manage. 40:353–360.

Dabo, S.M., C.M. Taliaferro, S.W. Coleman, F.P. Horn, and P.L. Claypool. 1987. Yield and digestibility of Old World bluestem grasses as affected by cultivar, plant part and maturity. J. Range Manage. 40:10–15.

Eck, H.V. and P.L. Sims 1984. Grass species adaptability in the Southern High Plains—36-year assessment. J. Range Manage. 37:211–217.

Forbes, T.D.A. and S.W. Coleman. 1986. Herbage intake and ingestive behavior of grazing cattle as influenced by variation in sward characteristics, p. 141–152. *In*: F.P Horn, (ed.), Grazinglands research at the plant animal interface. Winrock Int., Morrilton, Ark.

Grant, S.A., G.T. Barthram, L. Torvell, J. King, and K. Smith. 1983. Sward management, lamina turnover and tiller population density in continuously stocked *Lolium perenne* dominated swards. Grass and Forage Sci. 38:333–344.

Holland, E.A.W., W.J. Parton, J.K. Detling, and D.L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. American Naturalist 142:685–706.

Johnson, I.R. and A.J. Parsons. 1985. Use of a model to analyze the effects of continuous grazing managements on seasonal patterns of grass production. Grass and Forage Sci. 40:449–458.

Maschinski, J. and T.G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. Amer. Natur. 134:1–19.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Ameri. Natur. 113:691–703.

Murphy, B. 1990. Pasture Management, p. 231–262. *In*: C.A. Francis, C.B. Butler and L.D. King, (eds.), Sustainable Agriculture in Temperate Zones. Wiley-Interscience, New York.

Parsons, A.J., I.R. Johnson, and A. Harvey. 1988. Use of a model to optimize the interaction between frequency and severity of intermittent defoliation and to provide a fundamental comparison of the continuous and intermittent defoliation of grass. Grass and Forage Sci. 43:49–59.

Parsons, A.J., E.L. Leafe, B. Collett, and W. Stiles 1983a. The physiology of grass growth under grazing. I. Characteristics of leaf and canopy photosynthesis of continuously grazed swards. J. Appl. Ecol. 20:117–126.

Parsons, A.J., E.L. Leafe, B. Collett, P.D. Penning, and J. Lewis. 1983b. The physiology of grass growth under grazing. II. Photosynthesis, crop growth and animal intake of continuously grazed swards. J. Appl. Ecol. 20:127-139.

Pyke D.A. and S. Archer. 1991. Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland. J. Range Manage. 44:550–557.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton and J.A. Wiens. 1981. Ecosystem responses to stress, p. 332-436. *In*: P.G. Risser, E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton and J.A. Wiens, (eds). The True Prairie Ecosystem, US/IBP Synthesis Series 16.

Sims, P.L. and C.L. Dewald. 1982. Old World bluestems and their forage potential for the Southern Great Plains. USDA Agr .Res. Serv., Agr. Revi. and Manuals, ARM-S-28.

SAS Institute. 1988. SAS/STAT User's Guide. SAS Institute Inc., Cary, N.C.

Steel, R.G.D. and Torrie, J.H. 1960. Principles and procedures of statistics, McGraw-Hill, New York.

Taliaferro, C.M., F.P. Horn, B.B. Tucker, R. Totusek, and R.D. Morrison. 1975. Performance of three warm-season perennial grasses and a native range mixture as influenced by N and P fertilization. Agron. J. 67:289–292.

Tallowin, J.R.B. and S.K.E. Brookman. 1996. The impact of differences in nitrogen content, nitrogen utilization and loss from laminae on competition between four grasses in an old pasture. J. Agr. Sci. 126:25–35.

Teague, W.R., S.L. Dowhower, W.E. Pinchak, D.R. Tolleson and L.J. Hunt. 1996. Increasing utilization efficiency of continuously grazed Old World bluestem pasture. J. Range Manage. 49:535–540.

Thomas, R.J., K.A.B Logan, A.D. Ironside, and G.R. Bolton. 1990. The effects of grazing with and without excretal returns on the accumulation of nitrogen by ryegrass in a continuously grazed upland sward. Grass and Forage Sci. 45:65–75.

USDA. 1997. USDA-NRCS Official Soil Series Description 6/97. Available online at - http://www.statlab.iastate.edu/cgi-bin/osd/osdname.cgi.

Wilson, J.R. and R.H. Brown. 1983. Nitrogen response of *Panicum* species differing in CO_2 fixation pathways. I. Growth analysis and carbohydrate accumulation. Crop Sci. 23:1148–1153.

J. Range Manage.
55: 266-269 May 2002

Water stress and triclopyr on clopyralid efficacy in honey mesquite

ANDREA R. ROCHE, RODNEY W. BOVEY, AND SCOTT A. SENSEMAN

Authors are Analytical Chemist, BASF Corp., Agricultural Research Center, 26 Davis Drive, Research Triangle Park, N.C. 27709-3528; Adjunct Professor Department of Rangeland Ecology and Management, Texas A&M University, College Station Tex., 77843-2126; and Associate Professor, Department of Soil and Crop Sciences, Texas A&M University, College Station, Tex. 77843-2474.

Abstract

Water stress may affect herbicide efficacy in herbaceous and woody plants. Chamber studies were conducted to evaluate the influence of water stress (–1.3 to –2.8 MPa) and triclopyr on the absorption and translocation of clopyralid in greenhouse-grown honey mesquite (*Prosopus glandulosa* Torr.). Xylem water potential was determined in honey mesquite at time of herbicide application. Absorption and translocation of clopyralid was determined at low (–1.3 MPa), medium (–2.2 MPa), and high (–2.8 MPa) water stress at 4 h after application for 1.5-mo-old plants, while only translocation was determined at either a low (–1.4 or –1.6 MPa) or a high (–2.4 MPa) water stress treatment at 24 hours after herbicide application for 3-mo-old plants. Water stress did not affect ($P < 0.05$) absorption or translocation of clopyralid alone in either study. With 1.5-mo-old plants, the addition of triclopyr to clopyralid increased ($P < 0.05$) clopyralid absorption in leaves at low (63 µg) and medium (54 µg) water stress compared to high water stress (33 µg) but did not affect ($P > 0.05$) translocation at 4 hours after application. On 3-mo-old plants, triclopyr decreased ($P < 0.01$) clopyralid translocation 24 hours after treatment at high water stress. The reasons for reduced uptake and 24 hours post-treatment translocation of clopyralid when applied with triclopyr at high water stress are unclear, but have implications for field applications.

Resumen

El estrés hídrico puede afectar la eficacia de los herbicidas en las plantas herbáceas y leñosas. Se condujeron estudios en cámaras para evaluar la influencia del estrés hídrico (–1.3 to –2.8 MPa) y el triclopir en la absorción y translocación de clopiralid en mezquite (*Prosopus glandulosa* Torr.) desarrollado en invernadero. El potencial del agua del xilema se determinó en el mezquite al momento de la aplicación del herbicida. La absorción y translocación del clopiralid se determinó 4 h después de la aplicación en plantas de 1.5 meses de edad sujetas a un estrés hídrico bajo (–1.3 MPa), medio (–2.2 MPa) y alto (–2.8 MPa), mientras que en plantas de 3 meses de edad, sometidas a estrés hídrico bajo (–1.4 or –1.6 MPa) o alto (–2.4 MPa), solo se determino la translocación 24 h después de la aplicación. En ningún estudio estrés hídrico afectó ($P < 0.05$) la absorción o translocación del clopiralid aplica solo. En plantas de 1.5 meses de edad, la adición de triclopir al clopiralid incrementó ($P < 0.05$) la absorción de clopiralid en los niveles de estrés hídrico bajo (63 µg) y medio (54 µg) comparado con el estrés hídrico alto (33 µg), pero no afectó ($P > 0.05$) la translocación a las 4 h después de la aplicación. En plantas de 3 meses de edad, en el tratamiento de estrés hídrico alto, el triclopir disminuyó ($P < 0.01$) la translocación del clopiralid 24 h después de la aplicación. Las razones para la reducida absorción y la translocación del clopiralid 24 h después de tratadas los plantas, cuando se aplica con triclopir, no son claras, pero tienen implicaciones para las aplicaciones en campo.

Key Words: *Prosopis glandulosa,* herbicide, growth chamber, xylem water potential, gas chromatographic analysis

The monoethanolamine salt of clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) is a highly effective herbicide for honey mesquite (*Prosopis glandulosa* Torr.) control when used alone or in mixtures with the butoxyethyl ester of triclopyr {[(3,5,6-trichlor-2-pyridinyl) oxy]acetic acid} (Bovey et al., 1988, Bovey and Whisenant 1991, Jacoby et al. 1981). Davis et al. (1968) studied the effect of water stress on two other auxin-type herbicides, picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) and 2,4,5-T [(2,4,5-trichlorophenoxy)acetic acid]. They found that water stress reduced foliar uptake of picloram but not 2,4,5-T in honey mesquite. However, water stress sufficient to slow growth markedly reduced the translocation of both herbicides. Clopyralid, however, may be less sensitive to water stress since it has been effective on honey mesquite during periods of drought. Bovey and Meyer (1986) detected high clopyralid concentrations in stem phloem and xylem when applications were made during drought or fall months. Kloppenburg and Hall (1990a) found that the absorption and translocation of the acid and ester formulations of clopyralid were not reduced in water stressed wild buckwheat (*Polygonum convolvulus* L.) but absorption of the monoethanolamine and potassium salt formulations were reduced.

The objectives of this study were to determine the effect of plant water stress on the absorption and translocation of the monoethanolamine salt of clopyralid alone and in mixtures with the butoxyethyl ester of triclopyr in greenhouse-grown honey mesquite.

Manuscript accepted 7 Sept. 01.

Materials and Methods

Growth environment

Honey mesquite were grown from seed in the greenhouse under natural light in pots (12.7-cm diam x 12.7-cm deep) containing a mixture of Bleiblerville clay (fine montmorillontic Udic Pellusterts), sand, and peat moss (1:1:1, v/v/v) from March to June 1990. Daytime temperature was 35° C and night temperature was 25° C. Two plants were grown per pot, and each had a single woody stem. Plants treated at 1.5-mo old averaged 20-cm tall with approximately 8 to 10 leaves per plant. Plants treated at 3-mo old averaged 36-cm tall with approximately 17 leaves per plant. Pots were watered daily to saturation.

Plants were transferred to a growth chamber 2 weeks prior to initiating water stress. Chamber temperature was set at a day/night regime of 35/30° C with a 16-hour day length and relative humidity of 75%. Light irridiance of the Na/Hg lamps ranged between 600 to 700 μmol m-2 sec^{-1} at the plant apex. Water content of the soil at field capacity was determined by weighing the pots after watering to saturation and allowing the pots to drain.

Stress measurements

Xylem water potential in the honey mesquite was determined by the Scholander apparatus (Scholander et al. 1965). A separate batch of plants were grown along with the test plants to establish water stress categories. Water was withheld from selected sets of plants at staggered times coincidentally with selected sets of the test plants. Various plants were measured for xylem potential from these selected sets of extra plants until a clear separation of water stress categories emerged. At the time of treatment, 1 of the 2 plants in each pot was cut with a razor blade 1 cm from the soil level. The cut stem was inserted through the lid of the pressure bomb with the cut end exposed to detect negative hydrostatic pressure in the xylem of honey mesquite. Stem diameter varied from 1.5 to 2.0 mm in 1.5-mo old plants to 3 to 4 mm in 3-mo old plants. The pressure at which liquid first wet the cut surface was recorded. Based on these measurements, 3 stress categories were created that represented low (–1.3 MPa), moderate (–2.2 MPa), and high (–2.8 MPa) water stress. Each pressure stress category represented the mean xylem potential ± 0.2 MPa. The average xylem potentials for each stress category ranged from –1.3 to –2.8 MPa.

Absorption and Translocation 4 hours After Herbicide Application

The paired, uncut honey mesquite plants (1.5-mo old) in every pot were treated with 60 μg $plant^{-1}$ of the monoethanolamine salt of clopyralid in 20 μl aqueous solution or 60 μg $plant^{-1}$ of clopyralid plus 20 μg $plant^{-1}$ of the butoxyethyl ester of triclopyr. Commercial formulations were used. The final treating solutions contained 0.025% (v/v) surfactant[1]. Surfactant concentration of 0.025% had little biological activity but was necessary for application of the aqueous solution on the leaf cuticle. Herbicides were applied to the two youngest mature leaves at the apex in 10 μl aqueous solution (30 μg clopyralid) $leaf^{-1}$ of a plant that consisted of approximately 8 to 10 leaves. Honey mesquite seedlings were treated at each stress category based on xylem potential readings as described previously.

Plants were harvested 4 hours after treatment. Samples included washed treated leaves, treated leaf washes, and stem which included the entire plant minus treated leaves and roots. The leaf wash was accomplished by washing the detached leaves 2 times in 50 ml basic water (1 ml concentrated NH_4OH 1 $liter^{-1}$ distilled H_2O) for 30 sec.

To extract clopyralid from plant samples, samples were ground in a Waring blender with acidified acetone [(0.5 ml HCl $liter^{-1}$ acetone and water mixture (7:1 v/v)]. Samples were then filtered through a Büchner funnel and 5 ml NH_4OH were added to the filtered solution.

The acetone was evaporated at room temperature and the H_2O fraction was adjusted to pH 12 with concentrated NH_4OH and extracted once with ether. The ether fraction was discarded, and the H_2O fraction was adjusted to pH 2 with HCl and saturated with approximately 12 g of NaCl to assist in the extraction. This fraction was then extracted 3 times with 50 ml of ether. Ether fractions were passed through an anhydrous Na_2SO_4 column to remove moisture, then combined and completely dried. A 50-ml portion of the leaf wash was adjusted to pH 2 with HCl, saturated with NaCl (12 g) and extracted in the same manner as the H_2O fraction. A butyl ester derivative of the clopyralid was formed by adding 1 ml 1-butanol and 6 drops H_2SO_4 to the residue and heating for 30 min in boiling water (Cotterill 1978). The mixture was cooled and 20 ml H_2O and 5 ml hexane were added to the test tube. The mixture was shaken for 1 min, and the hexane layer was dispensed.

The hexane fraction was analyzed by a gas chromatograph (GC) using a 2-m long glass column packed with 3% OV 210 on 80 to 100 mesh Supelcoport[2]. The GC was equipped with an electron capture detector and GC settings were: column-160°C, injector-290°C, and detector-300°C. Herbicide concentration was determined by comparing samples to a standard of known concentration. Treating solutions were also analyzed by preparing a derivative of a 10-μl aliquot. Percent recovery for the entire procedure was also determined by fortifying untreated plant samples with known amounts of clopyralid (3 μg and 30 μg). Clopyralid recovery was approximately 80% and was easily detected to 0.05 μg g^{-1}. Triclopyr was not determined in these experiments because it had been previously determined that it did not interfere in extraction and analysis of clopyralid as determined by analysis of fortified plant material with clopyralid alone and clopyralid with triclopyr.

The experiment utilized a completely randomized design. Four plants were used per replication with 4 replications. The entire experiment was repeated. Data were subjected to analysis of variance (SAS 1989). Means for the herbicide amount (μg) and concentration (μg g^{-1}) for the 2 herbicide treatments were compared using Fisher's protected LSD at the 5% level (Steel and Torrie 1980).

Translocation 24 hours After Herbicide Application

Three-mo-old honey mesquite plants were sprayed with 0.28 kg ha^{-1} of the monoethanolamine salt of clopyralid or clopyralid at 0.28 kg ha^{-1} plus 0.14 kg ha^{-1} of the butoxyethyl ester of triclopyr. Herbicides were applied in water with 0.025% surfactant1 (v/v) of the spray solution at the equivalent volume of 93.5 $liter^{-1}$ ha^{-1} with a laboratory spray chamber (Bouse and Bovey 1967). Plant growth environment and water stress measurements were similar to those in previous experiments except that plants were treat-

[1]Surfactant WK (trimethylnonylpolyethoxyethanol) E.I. duPont de Nemours and Co., Inc., Walkers Mill. Barley Mill Plaza, Wilmington, Del. 19898.

[2]Supelco Inc., Supelco Park, Bellefonte, Penn. 16823.

ed at only 2 stress levels: low (–1.4 or 1.6 MPa) and high (–2.4 MPa). The upper canopy was sprayed while the lower 10 cm of canopy and stem were protected by fitting split styrofoam cups and cotton over the lower plant and soil surface to prevent herbicide contact. The cup and cotton were removed after spraying. Plants were harvested 24 hours after treatment since previous studies showed that maximum clopyralid translocation occurred by this time (Bovey et al. 1987, 1989, et al. 1990). Plants were analyzed for clopyralid content in the lower canopy only. Three replications with 3 plants per replication were used in a completely randomized design. The entire experiment was repeated. Data were subjected to analysis of variance and means were compared using Fisher's protected LSD at the 5% level (Steel and Torrie 1980).

Results and Discussion

Absorption and Translocation 4 hours After Herbicide Application

Data were pooled for presentation since no interaction between date and treatment were found. Also, there was no herbicide treatment X moisture stress interaction for leaf wash, treated leaves, or stem. When clopyralid was applied alone, clopyralid amounts were higher in the leaf wash under high (–2.8 MPa) than at low (–1.3 MPa) moisture stress levels 4 hours after treatment (Table 1). There was also a higher fresh weight concentration of clopyralid at the high versus low stress level (data not shown). However, there were no differences in clopyralid content absorbed by the treated leaf or translocated to the lower stem.

Clopyralid remaining in the plant tissue represented 63 to 77% of the original amount applied 4 hours after treatment after adjusting for the percent recovery of the method, however, the roots were not analyzed (Table 1). Data were consistent with other studies that indicated rapid translocation of clopyralid to the lower stem and roots of plants within 4 hours or more after treatment (Bovey et al. 1987, 1988, 1989, 1990; Bovey and Mayeux 1980, Devine and Vanden Born 1985, Kloppenberg and Hall 1990a, O'Sullivan and Kossatz 1984). Although movement is rapid, some clopyralid may be lost by metabolism (Hall and Vanden Born 1988). Devine and Vanden Born (1985) found that after 144 hours, 29% of the 14°C-clopyralid was recovered in roots and developing root buds of Canada thistle [*Circuim arvense* (L.) Scop.] plants. O'Sullivan and Kossatz (1984) using 14°C-clopyralid in Canada thistle only recovered about 85% of the radioactivity after harvesting the entire plant 2 days after treatment. Based on this earlier work, the discrepancy in the amount of clopyralid remaining was probably due to translocation to the root tissue within the first 4 hours.

When clopyralid was combined with triclopyr, more clopyralid was detected in the treated leaves at low and medium stress compared to high stress (Table 1). However, no differences occurred in clopyralid recovered among water stress levels in the leaf wash or the amount of clopyralid translocated to the stem 4 hours after application of the clopyralid:triclopyr mixture (Table 1).

Data in this report agree with field research which indicated more clopyralid was detected in leaves when triclopyr was combined with clopyralid (0.28 + 0.28 kg ha^{-1}) than when clopyralid was applied alone at 0.28 kg ha^{-1} 4 hours after treatment (Bovey et al. 1988). After 24 hours, more clopyralid was detected in the upper stem phloem when combined with triclopyr than when applied alone (Bovey et al. 1988).

Translocation 24 hours After Herbicide Application

Data were pooled for presentation since no date by treatment interaction occurred. However, a herbicide treatment X moisture stress interaction was present (Table 2). There was no difference in clopyralid translocation to the lower stem when applied alone in 3-mo-old honey mesquite 24 hours after treatment at low and high stress levels (Table 2). However, there was less clopyralid detected in both amount and concentration in high stress plant stems when applied with triclopyr (Table 2). The reason for reduced translocation of clopyralid when combined with triclopyr at high stress is not clear. Kloppenburg and Hall (1990b) found that acid forms of clopyralid and triclopyr and the butoxyethyl ester of triclopyr readily partitioned through chemically isolated cuticular membranes into agar but ester formulations of clopyralid were retained by the cuticular membrane. However, they did not look at the influence of one herbicide on the behavior of another herbicide (Kloppenburg and Hall 1990b). Bovey et al. (1983) found that triclopyr was readily

Table 2. Clopyralid detected in the lower stem 24 hours after spray application of clopyralid on 3-mo-old, greenhouse-grown honey mesquite.

Herbicide[1]	Water potential	Amount	Concentration
	(-MPa)	(μg)	($\mu g\ g^{-1}$)
Clopyralid	1.6	4.2 a[2]	3.5 a
	2.4	4.6 a	3.8 a
Clopyralid + triclopyr	1.4	6.5 a	5.1 a
	2.4	2.6 b	2.2 b

[1]Monoethanolamine salt of clopyralid (0.28 kg ha^{-1}). Study was done with 3 plants/replication and 3 replications.
[2]Values within columns and herbicide followed by the same letter are not significantly different at the 5% level using Fisher's protected LSD.

Table 1. Clopyralid detected in leaf wash, treated leaves and stem 4 hours after application of clopyralid or clopyralid + triclopyr mixture on 1.5 mo-old, greenhouse-grown honey mesquite.

		Plant part					
	Water	Leaf wash		Treated leaves[1]		Stem[2]	
Herbicide	potential	Amount	Conc.	Amount	Conc.	Amount	Conc.
	(-MPa)	(μg)	($\mu g\ g^{-1}$)	(μg)	($\mu g\ g^{-1}$)	(μg)	($\mu g\ g^{-1}$)
Clopyralid	1.3	154 b[3]	416 b	27 a	73 ab	2.6 b	1.0 a
	2.2	120 ab	368 ab	28 a	78 ab	2.5 ab	1.0 a
	2.8	222 c	659 c	23 a	69 a	3.1 b	1.4 b
Clopyralid + triclopyr							
	1.3	89 a	229 a	63 b	165 c	2.4 ab	0.9 a
	2.2	99 ab	231 a	54 b	117 b	2.3 ab	0.8 a
	2.8	129 ab	381 ab	33 a	101 ab	1.5 a	0.8 a

[1]Monoethanolamine salt of clopyralid and the butoxyethyl ester of triclopyr applied at 60 μg and 20 μg, respectively, to the 2 youngest mature leaves of each plant. Four plants/replication were treated and 4 replications were included in the study.
[2]Plant minus treated leaves and roots.
[3]Values in columns followed by the same letter are not significantly different at the 5% level using Fisher's protected LSD. The values represent mean total amounts and concentrations from 4 plants per replication.

absorbed from either ester or amine formulations and that triclopyr translocation was rapid in greenhouse-grown honey mesquite. As indicated earlier, certain rates of clopyralid plus triclopyr are synergistic in controlling honey mesquite (Bovey and Whisenant 1991), but the benefit of adding triclopyr to clopyralid may not always be attained when plants are under high water stress.

Conclusion

From these data, we concluded that clopyralid absorption and translocation in honey mesquite plants is not altered by water stress extremes when evaluated 4 or 24 hours after treatment. Data from the field supports these conclusions since high concentrations of clopyralid were detected in upper and basal stem phloem and xylem both 3 and 30 days after treatment during periods of water stress that ranged between –3.1 and –1.9 MPa during midday (Meyer and Bovey 1986).

In the field, even during periods of high water stress at midday, predawn water stress in honey mesquite may be < –1.0 MPa (Meyer and Bovey 1986, Haas and Dodd 1972) and may permit significant clopyralid translocation. In these studies, water stress was constant, and clopyralid uptake and transport was not reduced under high water stress. It is evident that clopyralid is highly stable and mobile within honey mesquite plants. Absorption through the symplast and translocation through the phloem are essential for activity. The uptake of clopyralid has been classified as nonfacilitated diffusion by Devine et al. (1987). An ion-trap mechanism was shown to be responsible for retaining the undissociated herbicide in the cytoplasm. Since clopyralid was reversibly bound, it can easily be moved into the phloem for transport.

The reasons are unclear for reduced uptake of clopyralid when applied with triclopyr at high water stress. This mechanism should be investigated since clopyralid:triclopyr mixtures are sometimes synergistic in controlling honey mesquite plants and similar mechanisms may exist for other weeds and herbicides.

Literature Cited

Bouse, L. F. and R. W. Bovey. 1967. A laboratory sprayer for potted plants. Weeds 15:89–91.

Bovey, R. W. and H. S. Mayeux, Jr. 1980. Effectiveness and distribution of 2,4,5-T, triclopyr, picloram and 3, 6-dichloropicolinic acid in honey mesquite (*Prosopis juliflora* var. *glandulosa*). Weed Sci. 28:666–670.

Bovey, R. W. and R. E. Meyer. 1986. Concentration of 2,4,5-T, triclopyr, picloram and clopyralid in honey mesquite (*Prosopis glandulosa*) stems. Weed Sci. 34:211–217.

Bovey, R. W. and S. G. Whisenant. 1991. Control of honey mesquite with clopyralid, triclopyr, or other clopyralid:triclopyr mixtures. J. Range Manage. 44:52–55.

Bovey, R. W., H. Hein, Jr., and R. E. Meyer. 1983. Absorption and translocation of triclopyr in honey mesquite (*Prospsis juliflora* var. *glandulosa*). Weed Sci. 31:807–812.

Bovey, R. W., H. Hein, Jr., and R. E. Meyer. 1988. Phytotoxicity and uptake of clopyralid in honey mesquite (*Prosopis glandulosa*) as affected by adjuvants and other herbicides. Weed Sci., 36:20–23.

Bovey, R. W., H. Hein, Jr., and F. N. Keeney. 1989. Phytotoxicity, absorption and translocation of five clopyralid formulations in honey mesquite (*Prosopis glandulosa*). Weed Sci. 37:19–22.

Bovey, R. W., H. Hein, Jr., R. E. Meyer, and L. F. Bouse. 1987. Influence of adjuvants on the deposition, absorption and translocation of clopyralid in honey mesquite (*Prosopis glandulosa*). Weed Sci. 35:253–258.

Bovey, R. W., H. Hein, Jr., F. N. Keeney, and S. G. Whisenant. 1990. Phytotoxicity and transport of clopyralid from three formulations in honey mesquite. J. Plant Growth Regul. 9:65–69.

Cotterill, E. G. 1978. Determination of 3,6-dichloropiclonic acid residues in soil by gas chromatography of the 1-butyl ester. Bull. Environ. Contamin. Toxicol. 15:471–474.

Davis, F. S., M. G. Merkle and R. W. Bovey. 1968. Effect of moisture stress on the absorption and transport of herbicides in woody plants. Bot. Gaz. 129:183–189.

Devine, M. D. and W. H. Vanden Born. 1985. Absorption, translocation and foliar activity of clopyralid and chlorsulfuron in Canada thistle (*Cirsium arvense*) and perennial sowthistle (*Sonchus arvensis*). Weed Sci. 35:524–530.

Devine, M. D., H. D. Bestmann, W. H. Vanden Born. 1987. Uptake and accumulation of the herbicides chlorsulfuron and clopyralid in excised pea root tissue. Plant Physiol. 85:82–86.

Haas, R. H. and J. D. Dodd. 1972. Water-stress patterns in honey mesquite. Ecol. 53: 674–680.

Hall, J. C. and W. H. Vanden Born. 1988. The absence of a role of absorption, translocation, or metabolism in the selectivity of picloram and clopyralid in two plant species. Weed Sci. 36: 9–14.

Jacoby, P. W., C. H. Meadors, and M. A. Foster. 1981. Control of honey mesquite (*Prosopis juliflora* var. *glandulosa*) with 3,6-dichloropiclonic acid. Weed Sci. 29:376–381.

Kloppenburg, D. J. and J. C. Hall. 1990a. Effects of formulation and environment on absorption and translocation of clopyralid in *Cirsium arvense* (L.) Scop. and *Polygonum convolvulus* L. Weed Res. 30:9-20.

Kloppenburg, D. J. and J. C. Hall. 1990b. Penetration of clopyralid and related weak acid herbicides into and through isolated cuticular membranes of *Euonymus fortunei.* Weed Res. 30: 431–438.

Meyer, R. E. and R. W. Bovey. 1986. Influence of environment and stage of growth on honey mesquite response to herbicides. Weed Sci. 34:287–289.

O'Sullivan, P. A. and V. C. Kossatz. 1984. Absorption and translocation of ^{14}C-3, 6-dichloropicolinic acid in *Circium arvense* (L.) Scop. Weed Res. 24:17–22.

Statistical Analysis Systems [SAS]. 1989. The SAS System for Windows. Version 6.12. Cary, NC: Stat. Anal. Systems Instit.

Scholander, P. F., H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Sci. 148:339–348.

Steel, R. G. D. and J. H. Torrie. 1980. Principles and Procedures of Statistics, a Biometrical Approach, 2nd Ed. McGraw-Hill Book Co., New York.

J. Range Manage.
55: 270-276 May 2002

Do most livestock losses to poisonous plants result from "poor" range management?

JERRY L. HOLECHEK

The author is Professor, Dept. of Animal and Range Sciences, New Mexico State Univ., Las Cruces, N.M. 88003.

Abstract

In recent years livestock death losses from poisonous plants in the western United States have averaged about 2–3% annually. A review of 36 grazing studies in North America shows poisonous plant availability and death losses of livestock from poisonous plants are closely associated with grazing intensity. Across studies, livestock death losses to poisonous plants average about 2.0% under moderate grazing compared with 4.8% under heavy grazing intensities. Sheep and goat losses from poisonous plants appear to be increased more by heavy stocking than those from cattle. Impacts of poisonous plants on livestock reproductive success are difficult to quantify, but probably reduce calf and lamb crops, even when grazing intensities are conservative. Increased poisonous plant consumption may explain in part why calf and lamb crops average about 7% lower under heavy compared to moderate grazing. With the exception of 1 Texas study, rotation and continuous/season long grazing systems show little differences in livestock death losses under comparable stocking rates. Certain plants, such as locoweeds (*Astragalus* sp.) and larkspur (*Delphinium* sp.), can elevate livestock death losses, even when grazing intensities are moderate or conservative. Special management programs that involve careful timing of grazing, aversive conditioning, and creation of locoweed (or larkspur)-free pastures can reduce problems with these plants. Use of adapted livestock is a critical part of minimizing poisonous plant problems. However, on some rangelands, such as those with infestations of locoweed and larkspurs, naive livestock may be less affected by poisonous plants than familiar livestock. Knowledge of poisonous plant identification, conditions of toxicity, and affects on the animal, in conjunction with conservative grazing, will in most cases avoid excessive death and productivity losses from poisonous plants. In some cases livestock can be conditioned or trained to not consume poisonous plants. It can be concluded that most livestock losses from poisonous plants are caused by poor management.

Key Words: Cattle, sheep, goats, grazing, poisonous plants, economics

Resumen

En años recientes, en el oeste de Estados Unidos las perdidas por muerte de ganado debido a plantas tóxicas ocurridas promedian anualmente del 2–3%. Una revisión de 36 estudios de apacentamiento realizados en Norte América muestran que la disponibilidad de plantas tóxicas y las perdidas por muerte de ganado a causa de este tipo de plantas están estrechamente asociadas con la intensidad de apacentamiento. Los estudios revisados muestran que bajo apacentamiento moderado las perdidas por muerte de ganado debido a plantas tóxicas promedian aproximadamente 2.0%, comparado con 4.8% bajo intensidades de apacentamiento fuerte. El apacentamiento fuerte parece incrementar mas las perdidas por plantas tóxicas de caprinos y ovinos que de bovinos. Los impactos de las plantas tóxicas en el éxito reproductivo del ganado es difícil de cuantificar, pero probablemente reducen la cosecha de becerros y corderos, aun bajo intensidades de apacentamiento conservadoras. El aumento en el consumo de plantas tóxicas puede explicar en parte porque la cosecha de becerros y corderos es aproximadamente 7% menos bajo el apacentamiento fuerte que bajo el apacentamiento moderado. Con excepción de 1 estudio en Texas, los sistemas de apacentamiento rotacionales y continuo/estación larga, con cargas animal comparables, presentaron pocas diferencias en las perdidas por muerte de ganado por plantas tóxicas Ciertas plantas como "Locoweeds" (*Astragalus* sp.) y "Larkspur" (*Delphinium* sp.) pueden aumentar las perdidas por muerte de ganado, aun en intensidades de apacentamiento que son moderadas o conservadoras. Programas especiales de manejo que involucran el apacentar en el tiempo correcto, el acondicionamiento aversivo y la creación de potreros libres de "Locoweed" o "Larkspur" pueden reducir los problemas con estas plantas. El uso de ganado adaptado es una parte critica para minimizar los problemas de plantas tóxicas. Sin embargo, en algunos pastizales, tales como aquellos con infestaciones de "Locoweed" y "Larkspur", el ganado no familiarizado puede ser menos afectado por las plantas toxicas que el familiarizado. El conocimiento en la identificación de las plantas tóxicas, condiciones de toxicidad y los efectos en el animal en conjunto con un apacentamiento conservador, evitara, en muchos casos, perdidas excesivas de productividad y muertes por plantas tóxicas. En algunos casos el ganado puede ser acondicionado o entrenado para no consumir plantas tóxicas. Se puede concluir que la mayoría de las perdidas de ganado por plantas tóxicas son causadas por un manejo pobre.

This paper was supported by the New Mexico Agr. Exp. Sta., Las Cruces, NM 88003 and was part of project 1-5-27474.
Manuscript accepted 16 Aug. 01.

Poisonous plants have been an important problem for livestock producers using rangelands in the United States since the first pioneers from Europe began settlement of the country in the 1600's (James et al. 1992). Through the early history of range management, beginning in the late 1800's to the present, grazing practices have been closely linked with the magnitude of livestock losses from poisonous plants (Smith 1899, Stoddert and Smith 1943, Holechek et al. 2001). Presently poisonous plants are considered to be important impediments to profitable ranching on roughly 400 million hectares of rangeland in the United States (James et al. 1992).

The issue of whether or not economically significant livestock losses from poisonous plants are a result of "poor" range management practices has long been a point of controversy among ranchers and range scientists. Some 30 long term grazing studies reviewed by Vallentine (1990), Heady and Child (1994), and Holechek et al. (2001) provide insight into this issue. More recently, several studies have evaluated how timing and intensity of livestock grazing can be manipulated to minimize losses from poisonous plants such as larkspurs and locoweeds.

In this review consideration will be given to what the various long term studies on grazing intensities and grazing systems have shown regarding poisonous plant losses. Personal observations regarding livestock losses from poisonous plants on Oregon and New Mexico rangelands will be incorporated into the discussion. Consideration will also be given to special grazing approaches to deal with poisonous plants such as locoweeds and larkspurs that may be readily consumed by livestock even when non-poisonous forage species are available. Finally, the practicality of conditioning livestock to avoid poisonous plants will be examined.

Magnitude of Poison Plant Losses

Economic losses due to livestock poisoning can be divided into 2 parts: (1) direct losses and (2) indirect losses (James 1978). Direct losses of livestock involve the effects of poison plants on livestock productivity and health. Indirect losses include those activities or costs that are incurred by a livestock operation to prevent losses or costs from poisonous plants (James et al. 1992).

It has always been difficult to quantify actual dollar losses to livestock operations from poisonous plants. This is because separation of disease, accident, and predator losses from poisonous plant losses can be difficult. Low reproductive performance and weight gains can be caused by disease and inadequate nutrition as well as poisonous plants. Some adverse effects of poisonous plants such as birth defects occur long after poisonous plant ingestion. Nevertheless, various attempts have been made to quantify economic impacts of poisonous plants on the range livestock industry.

Based on a 1% death loss in cattle, a 3.5% death loss in sheep, and a 1% decrease in calf and lamb crops due to poisonous plants, Nielsen and James (1991) estimated total annual economic losses at $340,000,000 in the 17 western states. They used 1989 livestock numbers and prices. Based on 1999 livestock prices and livestock numbers, the estimate would be $503,000,000. In New Mexico annual experiment station reports based on rancher interviews have shown cattle death losses to average 3–4% and sheep death losses to average 4–6% for the 1987 to 1996 period (Torell et al. 1998). At least half of these losses are believed to be caused by poisonous plants. Gay and Dwyer (1967) suggested that over the entire western range, death losses were 2 to 3%. The USDA (1968) estimated countable death losses in the western United States were 3-5%. It is believed that losses in reproduction and weight gains from animals poisoned that do not die exceed those from death loss (Gay and Dwyer 1967).

Regardless of how estimates of livestock losses from poisonous plants are derived, poisonous plants are one of the most important causes of economic loss to the livestock industry. However, averages are somewhat misleading in that they do not take into account management. An important question is how much could economic losses from poisonous plants be reduced with improved grazing management? This issue will be explored.

Grazing Management and Poisonous Plant Availability

Grazing Intensity

Poisonous plant abundance on rangelands has been linked with overgrazing from the beginning of scientific range management in the late 1800's. Smith (1895, 1899) in west Texas, Colville (1898) in Oregon, Nelson (1898) in Wyoming, and Wooton (1915) in New Mexico all commented that overstocking caused a decline in palatable forage plants and an increase in unpalatable poisonous plants. Through the years various papers have described how and why retrogression from palatable to unpalatable plant species occurs under heavy or severe grazing pressure (Ellison 1960, Cronin et al. 1978, Laycock 1978, Molyneuax and Ralphs 1992). The processes were summarized by Holechek et al. (2001) as follows:

> "Under moderate or light grazing levels the poisonous, unpalatable plants are at a competitive disadvantage because they invest part of their products from photosynthesis in poisonous compounds (alkaloids, oxalates, glycosides, etc.) and appendages (spines, thorns, stickers, etc.) that discourage defoliation rather than contribute to growth...In contrast the palatable plants use their photosynthetic products mainly for growth in the form of roots, leaves, stems, rhizomes, stolons, seeds, and so forth. Under heavy defoliation levels the photosynthetic capacity of the palatable plants is reduced to the point that they are unable to produce enough carbon compounds for maintaining root systems, regeneration of leaves, respiration and reproduction. Over time, they shrink and die, and gradually are replaced with the unpalatable plants that are able to defend themselves against defoliation."

Various long-term grazing studies in North America support the above statement (Table 1). The concept advanced by Dyksterhuis (1949) that the more palatable species increase and least palatable species decrease under light to moderate grazing pressure is well supported by the literature (Table 1). On the other hand, the literature consistently shows species that are unpalatable or low in palatability tend to increase under heavy grazing pressure. The only major exception was the California annual grassland type where vegetation compositional changes were not greatly affected by grazing pressure.

Another minor exception was the study by Burzlaff and Harris (1969) in the shortgrass prairie of Nebraska. However, Vallentine (1990) noted that this study was conducted under favorable precipitation conditions. After the study was reported, 2 years of severe drought occurred that reduced the tallgrasses and midgrasses under all grazing intensities. However, the deleterious effects of the drought on the forage stand, including wind erosion, were much more severe under the heaviest stocking rate.

Table 1. Summary of studies evaluating influence of grazing intensities and grazing systems on long-term trend in palatable, unpalatable, and poisonous plant levels on North American rangelands.

Range Type/ Location	Livestock Type	Number of Years	Grazing Intensities: Grazing Intensity	Grazing Intensities: Forage Use Level	Change in Proportion of Palatable Plants	Relative Poison Plant Availability	Reference
				(%)			
Deserts							
Salt Desert (Utah)	Ewe-Lamb	13	Heavy Moderate Light	60 35 25	No Change Large Increase Large Increase	Highest Intermediate Lowest	Hutchings and Stewart 1953
Chihuahuan Desert (New Mexico)	Cow-Calf	22	Heavy Moderate	60 35	Decrease Large Increase	Highest Lowest	Holechek et al. 1994
Grasslands							
Shortgrass (Colorado)	Yearling-Cattle	55	Heavy Moderate Light	54 37 21	Decrease Increase Increase	No definite difference	Klipple and Costello 1960, Hart and Ashby 1998
Tallgrass (Kansas)	Yearling-Cattle	5	Heavy Moderate Light	Not Given	Decrease Increase Increase	Not Evaluated	Gillen et al. 1998
Sandhills (Colorado)	Yearling-Cattle	12	Heavy Moderate Light	64 44 30	Decrease Decrease Stable	No definite differences	Sims et. al. 1976
Shortgrass (Wyoming)	Yearling-Cattle	13	Heavy Moderate Light	45 36 25	Decrease Stable Increase	No definite differences	Manley et al. 1997
Mixed Prairie (South Dakota)	Cow-Calf	9	Heavy Moderate Light	63 46 37	Decrease Stable Increase	No definite differences	Johnson et al. 1951
Mixed Prairie (Montana)	Cow-Calf	10	Heavy Moderate Light	51 38 29	Decrease Stable Increase	Highest Intermediate Lowest	Houston and Woodward 1966
Mixed Prairie (Texas)	Cow-Calf	16	Heavy Moderate	50 40	Decrease Increase	No definite differences	Kothmann et al. 1978
Mixed Prairie (Alberta)	Ewe-Lamb	19	Heavy Moderate Light	68 53 45	Decrease Stable Increase	No definite differences	Smoliak 1974
Tallgrass Prairie (Kansas)	Yearling-Cattle	7	Heavy Moderate Light	58 52 29	Decrease Decrease Increase	No definite differences	Herbel and Anderson 1959
Shortgrass (Nebraska)	Yearling-Cattle	10	Heavy Moderate Light	74 58 53	Stable Stable Stable	No definite differences	Burzlaff and Harris 1969
Shortgrass (Wyoming)	Ewe-Lamb	10	Heavy Moderate Light	Not Given	Decrease Small Decrease Increase	No definite differences	Lang et al. 1956
Shortgrass (Kansas)	Yearling-Cattle	20	Heavy Moderate Light	66 48 39	Decrease Increase Large Increase	No definite differences	Launchbaugh 1967
Annual Grassland (California)	Cow-Calf	14	Heavy Moderate Light	Not Given	No definite changes	No definite differences	Bently and Talbot 1951
Bunchgrass (Oregon)	Cow-Calf	12	Heavy Moderate Light	53 35 20	Decrease Small Increse Large Increase	Highest Intermediate Lowest	Skovlin et al. 1976
Woodland							
Pinyon-Juniper (New Mexico)	Cow-Calf	10	Heavy Moderate	60 40	Decrease Increase	Highest Lowest	Pieper et. al. 1991
Coniferous Forest (Colorado)	Yearling-Cattle	16	Heavy Moderate Light	58 33 16	Decrease No Change No Change	Highest Intermediate Lowest	Smith 1967
Coniferous Forest (Oregon)	Cow-Calf	12	Heavy Moderate Light	34 25 10	Most Decrease Intermediate Decrease Least Decrease	Highest Intermediate Lowest	Skovlin et al. 1976
Chaparral (Texas)	Cattle-Sheep-Goats	20	Heavy Moderate Light	Not Given	Decrease Large Increase Increase	Highest Lowest Lowest	Reardon and Merrill 1976
Southern Pine Forest (Louisiana)	Cow-Calf	10	Heavy Moderate Light	57 40 35	Decrease Decrease Increase	Not Evaluated	Pearson and Whitaker 1974
Southern Pine Forest (Georgia)	Yearling-Cattle	4	Heavy Moderate Light	65 44 30	Decrease Increase Increase	Not Evaluated	Halls et al. 1956

Table 1. Continued.

Range Type/ Location	Livestock Type	Number of Years	Grazing Systems	Forage Use Level	Change in Proportion of Palatable Plants	Relative Poison Plant Availability	Reference
				(%)			
Deserts							
Sonoran Desert	Cow-Calf	10	Yearlong	52	No Change	No	Martin and
(Arizona)			Rotation	48	No Change	Difference	Severson 1988
Grasslands							
Mid-grass Prairie	Cow-Calf	16	Yearlong	35	Increase	No	Kothmann et
(Texas)			Rotation	35	Increase	Difference	al. 1978
Tall-grass Prairie	Yearling-Cattle	16	Season-Long	52	Most Decrease	No Definite	Owensby et
(Kansas)			Rotation	45	Least Decrease	Difference	al. 1973
Tall-grass Prairie	Cow-Calf	6	Yearlong	43	No Change	No	Drawe 1988
(Texas)			Rotation	41	No Change	Difference	
Shortgrass Prairie	Yearling-Cattle	13	Season-Long	40	No Definite Change	Lowest	Manley et.
(Wyoming)			Rotation	40	Decrease	Highest	al. 1997
Tall-grass Prairie	Yearling-Cattle	5	Season-Long	Not	No Change	No	Gillen et
(Oklahoma)			Rotation	Given	No Change	Difference	al. 1998
Mid-grass Prairie	Yearling-Cattle	9	Season-Long	44	Increase	No	Smoliak 1960
(Alberta, Canada)			Rotation	46	Increase	Difference	
Bunchgrass	Cow-Calf	10	Season-Long	30	Most Increase	No	Skovlin et
(Oregon)			Rotation	27	Least Increase	Difference	al. 1976
Woodland							
Chaparral	Cattle-Sheep-	20	Yearlong	Not	Least Increase	Highest	Reardon and
(Texas)	Goats		Rotation	Given	Most Increase	Lowest	Merrill 1976
Pinyon-Juniper	Cow-Calf	10	Yearlong	40	No Definite Change	No Definite	Pieper et
(New Mexico)			Rotation	55	No Definite Change	Difference	al. 1991
Coniferous Forest	Cow-Calf	12	Season-Long	21	Most Decrease	No	Skovlin et
(Oregon)			Rotation	23	Least decrease	Difference	al. 1976

Evidence that heavy grazing increases poisonous plant availability is more limited than that for plants of low palatability. However, 7 of the 22 grazing studies reviewed in Table 1 showed poisonous plants were definitely more available under heavy grazing on a biomass basis than under moderate to light grazing. These studies supported the theory that heavy grazing causes vegetational composition shifts towards poisonous plants. Desert and woodland studies showed more tendency for poisonous plants to increase under heavy grazing than those from grasslands.

Two important reasons why 12 of the 22 studies reviewed showed no definite increase in poisonous plants under heavy grazing may have to do with the relatively short time frame of the studies and lack of severity in the heavy grazing treatment. Fusco et al. (1995), on Chihuahuan Desert grassland rangeland in New Mexico, found that poisonous plants totally dominated areas within 1,000 meters of permanent waters on rangelands with a 50 year history of heavy grazing. However, on rangelands with a 50 year history of conservative grazing, the zone of poisonous plant domination extended only 500 meters from water. Across the entire study areas, poisonous plant biomass levels were 57% higher on the long term heavy compared to conservative grazed range.

Grazing Systems

Generally, rotation and year-long or season-long grazing systems have shown little difference in their effects on proportions of decreaser and poisonous plants (Table 1). An exception is chaparral range type of south Texas where the Merrill 3-herd/4-pasture system has definitely favored decreaser plants and reduced poisonous plants (Reardon and Merrill 1976, Merrill and Schuster 1978, Taylor and Ralphs 1992). A modification of the Merrill 3-herd/4-pasture system may have reduced white loco (*Oxytropis sericea* Nutt.) availability on mountain range in Utah (Taylor and Ralphs 1992). The literature convincingly shows grazing intensity has far more impact on vegetation composition changes through time than system of grazing.

Poison Plant Availability and Livestock Food Habits

Research is restricted on how range condition and grazing management affect poisonous plant levels in livestock diets. One study from the Chihuahuan Desert of south-central New Mexico evaluated poisonous plant levels in cattle diets over a 3 year period on rangelands in late-seral and mid-seral ecological condition (Daniel et al. 1993). Both areas were stocked conservatively, but poisonous plant biomass levels were about 60% higher on the mid-seral compared to late-seral range. Across the 3 year study period poisonous plants comprised 14% and 10% of cattle diets by weight and late- and mid-seral ranges, respectively. Total poisonous plant consumption never exceeded 20% of the diet on either range. Over a 3 year period no death losses from poisonous plants (220 cattle/year) were observed on either range (Fusco et al. 1995). Results from this study indicated that poisonous plant consumption by livestock is more related to grazing intensity than rangeland condition.

Grazing Management and Livestock Losses to Poisonous Plants

Grazing Intensity

Several range researchers and managers through the years have noted that elevated livestock death losses from poisonous plants were associated with heavy grazing intensities (Smith 1899, Stoddart and Smith 1943, Shoop and McIlvain 1971, Merrill and Schuster 1978, Taylor and Ralphs 1992). Various grazing studies generally supported by actual research show this observation (Table 2). Based on the author's review, sheep and goat death losses from poisonous plants are more elevated by heavy grazing than those from cattle. Generally, grazing intensities must involve more than 50% use of palatable forage species for elevated poisonous plant losses to occur. The author has had opportunity to evaluate cattle death losses from poisonous plants on several rangelands in Oregon and New Mexico. On mountain rangeland (the Starkey Experimental Range) in northeastern Oregon 100 yearling cattle per year over a 3 year period for a 120 day grazing season (20 June to 20 October) have been observed by the author. These rangelands were generally in high ecological condition and conservatively stocked. Only 2 animals died from poisonous plants over the 3 year period (Holechek 1980).

In south-central New Mexico, over the past 11 years, cattle death losses on the Chihuahuan Desert Rangeland Research Center and several surrounding rangelands under the control of the Bureau of Land Management have been monitored by the author. On the Chihuahuan Desert Rangeland Research Center, death losses to poisonous plants have been no more than 1% per year (1,100 observations). This area is generally in high ecological condition and pastures are conservatively or moderately stocked. On surrounding rangelands in lower ecological condition low death losses (1–2%) have been observed when grazing intensities were conservative to moderate (Fusco et al. 1995). However, when grazing intensities reached heavy to severe levels (over 60% use of forage) death losses in the spring were elevated to 4–8%.

On 2 occasions the author investigated cases where cattle death losses from poisonous plants took 10 to 25% of the herd. In these situations, grazing intensity was so severe (over 70% use of forage) that livestock had little choice other than to consume unpalatable/poisonous plants or starve. Based on these experiences, along with a review of the literature, the author concludes that heavy to severe livestock grazing pressure is generally the cause of excessive death losses to poisonous plants.

Holechek et al. (1999, 2001) review several long term grazing studies that show calf and lamb crops are closely associated with grazing intensity. Calf crops under heavy, moderate, and light grazing averaged 72%, 79%, and 82%, respectively, across all studies (Holechek et al. 1999). Lamb crops averaged 78%, 82%, and 87% across heavy, moderate, and light grazing intensities. Part of the depressed calf and lamb crops under the heavily grazed treatment in several of these studies was probably due to poisonous plant consumption. However, separation of poisonous plant from nutritional influences has not been done.

Grazing Systems

Livestock death losses under continuous and rotation grazing systems have shown little to no difference with 1 exception (Table 2). On chaparral rangeland in south-central Texas the Merrill 3-herd/4-pasture system has reduced livestock (cattle-sheep-goats) death losses compared to continuous grazing (Merrill and Schuster 1978, Taylor and Ralphs 1992). Lower poisonous plant availability (Table 1) appears to explain why livestock death losses have been almost nil under the Merrill system (Reardon and Merrill 1976).

Application of the Merrill 3-herd/4-pasture system on mountain range in Utah reduced the number of sick calves from poisoning by white locoweed (*Oxytropis sericea* Nutt) from 20 to 3% compared to rest-rest rotation grazing (Taylor and Ralphs 1992). Under rest-rotation grazing, the entire herd was concentrated into 1 pasture to force even use of all forage, including locoweed. In the Merrill 3-herd/4-pasture system, the grazing pressure was distributed over 3 pastures, and cattle were not forced to eat locoweed. A shortened grazing season also contributed to reduction in losses by removing all the animals before intoxication became serious or irreversible.

Table 2. Summary of studies evaluating influence of grazing intensities and grazing systems on livestock death losses from poisonous plants.

		Grazing Intensities			
Range Type/ Location	Livestock Type	Number of Years	Forage Use Level (%)	Death Loss (%)	Reference
Deserts					
Salt Desert	Ewe-Lamb	13	Heavy - 60	8.1	Hutchings and
(Utah)			Moderate - 35	3.1	Stewart 1953
Chihuahuan	Cow-Calf	20	Heavy - 50	3.5	Holechek 1992
Desert (New)			Conservative - 35	1.0	
(Mexico)					
Grasslands					
Shortgrass	Yearling-Steer	13	Heavy - 54	1.43	Klipple and
(Colorado)			Moderate - 37	0.33	Costello 1960
			Light - 21	0.14	
Annual	Ewe - Lamb	5	Heavy - 63	9 ewes	Rosiere and
Grassland			Moderate - 49	13 ewes	Torell 1996
(California)			Light - 44	6 ewes	
Bunchgrass	Cow-Calf	12	Heavy - 53	< 2	Skovlin et
(Oregon)			Moderate - 35	< 2	al. 1976
			Light - 20	< 2	
Mixed Prairie	Cow-Calf	6	Heavy - 50	2.6 cows	Heitschmidt
(Texas)			Moderate - 40	2.6 cows	et al. 1990
			Heavy - 50	8.3 calve	
			Moderate - 40	8.3 calves	
			Heavy - 50	No	Heitschmidt
			Moderate - 40	Difference	et al. 1982
Mixed Prairie	Cow-Calf	10	Heavy - 51	<2 Highest	Houston and
			Moderate - 38	<2 Lowest	
			Light - 20	<2 Lowest	1966
Woodward					
Pinyon-Juniper	Cow-Calf	10	Heavy - 55	< 2	Holechek
(New Mexico)			Moderate - 40	< 2	1994
Coniferous	Cow-Calf	12	Moderate - 34	< 2	Skovlin et
Forest			Heavy - 28	< 2	al. 1976
(Oregon)			Light - 17	< 2	
Chaparral	Cattle-Sheep-	21	Heavy	6.3 Bitterweed	Merrill and
	Goats		Moderate	3.3 Bitterweed	Schuster
			Light	0.7 Bitterweed	1978
	Goats	21	Heavy	4.0 Sachuista	Taylor and
			Moderate	3.3 Sachuista	Ralphs 1992
			Light	1.7 Sachuista	
	Goats	21	Heavy	3.1 Oak	Taylor and
			Moderate	2.6 Oak	Ralphs 1992
			Light	0.4 Oak	

Table 2 continued on page 275

Table 2. Continued.

			Grazing Systems			
Range Type/ Location	Livestock Type	Number of Years	Grazing System	Forage Use Level (%)	Death Loss (%)	Reference
Deserts						
Chihuahuan Desert (New Mexico)	Cow-Calf	20	Yearlong	30	< 2	Beck and McNeely 1993
			Rotation	30	< 2	
Grasslands						
Mixed Prairie (Texas)	Cow-Calf	6	Yearlong	40	2.6 cows	Heitschmidt et al. 1990
			Rotation	40-50	2.6 cows	
			Yearlong	40	8.3 calves	
			Rotation	40-50	8.3 calves	
Bunchgrass (Oregon)	Cow-Calf	12	Season-long	30	< 2	Skovlin et al. 1976
			Rotation	27	< 2	
Bunchgrass	Yearling Cattle (Oregon)	3	Season-long	30-35	< 1	Holechek et al. 1981
			Rotation	30-35	< 1	
Woodland						
Coniferous Forest (Oregon)	Yearling Cattle	3	Season-long	30-35	< 1	Holechek et al. 1981
			Rotation	30-35	< 1	
Coniferous Forest (Oregon)	Cow-Calf	12	Season-long	21	< 2	Skovlin et al. 1976
			Rotation	23	< 2	
Coniferous Forest (Oregon)	Yearling Cattle	5	Season-long	30-35	0	Holechek et al. 1987
			Rotation	30-40	0	
Pinyon-Juniper	Cow-Calf	10	Yearlong	40	< 2	Holechek 1994
			Rotation	50	< 2	
Chaparral (Texas)	Cattle-Sheep-Goats	21	Yearlong	Not Given	Lowest Under Merrill Grazing System	Merrill and Schuster 1978, Taylor and Ralphs 1992
			Rotation			

Multi-Species Grazing

Multi-species grazing involving cattle-sheep and goats has reduced livestock death losses from poisonous plants on chaparral ranges in south-central Texas (Merrill and Schuster 1978, Taylor and Ralphs 1992). Sheep death losses to bitterweed (*Hymenoxys odorata* D.C.) were greatest on pastures stocked with sheep only and least with a combination of multi-species grazing (cattle-sheep-goats), moderate stocking, and Merrill 3-herd/4-pasture grazing. Goat losses to sacahuista (*Nolina texana* wats.) were reduced by multi-species grazing. However, goat losses due to oak (*Quercus* spp.) consumption were little affected by stocking rate, multi-species grazing, or grazing system. Taylor and Ralphs (1992) concluded that grazing management alone will not eliminate livestock death losses caused by consumption of poisonous plants. However, livestock losses can be reduced through proper grazing management.

Special Poisonous Plant Problems

Certain poisonous plants have caused inordinate problems to livestock producers because of their widespread distribution and/or palatability to livestock under certain conditions. Considerable research has been directed towards management of livestock and rangelands to minimize losses from these plants. A more detailed discussion is presented by other papers in this symposium. Readers are also referred to Kingbury (1964), James and Johnson (1976), Keeler et al. (1978), James et al. (1988), Taylor and Ralphs (1992), and James et al. (1992) for overviews of specific management strategies to deal with various poisonous plants.

Summary and Conclusions

In this review of livestock poisonous plant losses and grazing management, 3 issues were addressed in some detail. These include the influence of grazing management on poisonous plant availability, poisonous plant consumption, and livestock death losses from poisonous plants. Long term studies were quite consistent in showing heavy grazing intensities increased proportions of unpalatable plants on most rangelands. This same relationship also occurred for poisonous plants but fewer studies confirmed it. Generally, poisonous plant levels on rangelands showed few differences among continuous and rotation grazing systems. However, there was evidence the Merrill 3 herd/4 pasture system in South Texas lowered poisonous plant levels compared to continuous grazing. Research regarding poisonous plant levels in livestock diets under different ecological condition levels and grazing management strategies is somewhat restricted. Available studies indicate poisonous plant consumption is much more related to grazing intensity than rangeland ecological condition. Actual death losses from poisonous plants were strongly related to grazing intensity and, to a much lesser extent, grazing system. The Merrill 3 herd/4 pasture system has lowered cattle, sheep, and goat death losses from poisonous plants in south Texas compared to continuous grazing. Carefully timed grazing can be used to minimize cattle losses from larkspur and locoweed. Aversive conditioning and herbicidal control of dense stands can be effective in reducing livestock losses to these plants. Proper stocking and careful timing of grazing are critical management practices in minimizing livestock losses from poisonous plants. In conclusion most livestock losses from poisonous plants do result from "poor" range management.

Literature Cited

Beck, R. F. and R. P. McNeely. 1993. Twenty-five year summary of year-long and seasonal grazing on the College Ranch. Livestock Research Briefs and Cattle Growers Short Course. New Mexico State University, Las Cruces, N.M.

Bentley, J. R. and M. W. Talbot. 1951. Efficient use of annual plants on cattle ranges in the California foothills. U.S. Dept. Agr.. Circ. 870.

Burzlaff, D. F. and L. Harris. 1969. Yearling steer gains and vegetation changes of western Nebraska rangeland under three rates of stocking. Nebr. Agr. Exp. Sta. Bull. 505.

Colville, F. J. 1898. Forest growth and sheep grazing in the Cascade Mountains of Oregon. U.S. Dept. Agr. For. Div. Bull. 15.

Cronin, E. H., P. Ogden, J. A. Young, and W. Laycock. 1978. The ecological niches of poisonous plants in range communities. J. Range Manage. 31:328–334.

Daniel, A., J. L. Holechek, R. Valdez, A. Tembo, L. Saiwana, M. Fusco, and M. Cardenas. 1993. Range condition influences on Chihuahuan Desert cattle and jackrabbit diets. J. Range Manage. 46:296–301.

Drawe, D. L. 1988. Effects of three grazing treatments on vegetation, cattle production, and wildlife on the Welder Wildlife Foundation Refuge, 1974–1982. Welder Wildl. Found. Contrib. B-8, Sinton, Tex.

Dyksterhuis, E.J. 1949. Condition and Management of Rangeland based on quantitative ecology. J. Range Manage. 2:104–115.

Ellison, L. 1960. Influence of grazing on plant succession of rangeland. Bot. Rev. 26:1–78.

Fusco, M., J. Holechek, A. Tembo, H. Daniel, and M. Cardenas. 1995. Grazing influences on watering point vegetation in the Chihuahuan Desert. J. Range Manage. 48:32–38.

Gay, C. W. and D. D. Dwyer. 1967. Poisonous range plants. New Mexico State Univ. Coop. Ext. Serv. Circ. 391.

Gillen, R. L., F. T. McCollum III, K. W. Tate, and M. E. Hodges. 1998. Tallgrass prairie response to grazing system and stocking rate. J. Range Manage. 51:139–146.

Hart, R. H. and M. M. Ashby. 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. J. Range Manage. 51:392–398.

Halls, L. K., O. M. Hale, and B. L. Southwell. 1956. Grazing capacity of wiregrass-pine ranges of Georgia. Georgia Agr. Exp. Sta. Tech. Bull. N.S. 2.

Heady, H. F and R. D. Child. 1994. Rangeland ecology and management. Westview Press, San Francisco, Calif.

Heitschmidt, R. K., M. M. Kothmann, and W. J. Rawlins. 1982. Cow-calf response to stocking rates, grazing systems, and winter supplementation at the Texas Experimental Ranch. J. Range Manage. 35:204–210.

Heitschmidt, R. K., J. R. Conner, S. K. Canon, W. E. Pinchak, J. W. Walker, and S. L. Dowhower.1990. Cow/calf production and economic returns from yearlong continuous deferred rotation and rotational grazing treatments. J. Agr. Prod. 3:92–99.

Herbel, C. H. and K. L. Anderson. 1959. Response of true prairie vegetation on major Flint Hills range sites to grazing treatment. Ecol. Monogr. 29:171–198.

Holechek, J. L. 1980. The effects of vegetation type and grazing system on the performance, diet, and intake of yearling cattle. Ph.D. Thesis. Oregon State Univ., Corvallis, Ore.

Holechek, J. L. 1992. Financial aspects of cattle production in the Chihuahuan Desert. Rangelands 14:145–149.

Holechek, J. L. 1994. Financial returns from different grazing management systems in New Mexico. Rangelands 16:237–240.

Holechek, J. L, T. J. Berry, and M. Vavra. 1987. Grazing system influences on cattle diet and performance on mountain range. J. Range Manage. 40:55–60.

Holechek, J. L., C. H. Herbel, and R. D. Pieper. 2001. Range management: principles and practices. 4th Ed. Upper Saddle River, N.J.

Holechek, J. L., M. Vavra, and J. Skovlin. 1981. Diet quality and performance of cattle on forest and grassland range. J. Anim. Sci. 53:291–299.

Holechek, J. L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: What we've learned. Rangelands 21(2):12–16.

Holechek, J. L., A. Tembo, A. Daniel, M. Fusco, and M. Cardenas. 1994. Long term grazing influences on Chihuahuan Desert rangeland. Southw. Nat. 39:342–349.

Houston, W. R. and R. R. Woodward. 1966. Effects of stocking rates on range vegetation and beef cattle production in the northern Great Plains. U. S. Dept. Agr. Tech. Bull. 1357.

Hutchings, S.S. and G. Stewart. 1953. Increasing forage yields and sheep production on intermountain winter ranges. U.S. Dept. Agr. Cic. 925.

James, L. F. 1978. Overview of poisonous plant problems in the United States. p. 3–5. *In:* Richard F. Keeler, Kent R. Van Kampen, and Lynn F. James (ed.) Effects of poisonous plants on livestock.

James, L. F. and A. E. Johnson. 1976. Some major plant toxicities in the western United States. J. Range Manage. 29:356–363.

James. L. F., M. H. Ralphs, and D. B. Nielsen (eds.). 1988. The ecology and economic impact of poisonous plants on livestock production. Westview press, Boulder, Colo.

James, L. F., D. B. Nielsen, and K. E. Panter. 1992. Impact of poisonous plants on the livestock industry. J. Range Manage. 45:3–8.

Johnson, L. A., L. A. Albee, R. O. Smith, and A. Moxon. 1951. Cows, calves, and grass. South Dakota Agr. Exp. Sta. Bull. 412.

Keeler, R. F., K. R. Van Kampen, and L. F. James (Eds.). 1978. Effects of poisonous plants on livestock. Academic Press, Inc., New York.

Kingsbury, J. 1964. Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, N.J.

Klipple, G. E. and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on shortgrass ranges of the central Great Plains. U.S. Dept. Agr. Tech. Bull. 1216.

Kothmanm, M. M., J. Waldrip, and G. W. Mathis. 1978. Rangeland vegetation of the Texas Rolling Plains: response to grazing management and weather. Proc. Internat.. Rangeland. Congr. 1:607–610.

Lang, R. L., O. K. Barnes, and F. Rauzi. 1956. Shortgrass range-grazing effects on vegetation and on sheep gains. Wyoming Agr. Exp. Sta. Bull. 343.

Launchbaugh, J. L. 1967. Vegetation relationships associated with intensity of summer grazing on a clay upland range site in the Kansas 20-24 inch precipitation zone. Kansas Agr. Exp. Sta. Tech. Bull. 154.

Laycock, W. A. 1978. Coevolution of poisonous plants and large herbivores on rangelands. J. Range Manage. 31:335–343.

Lang, R. L., O. K. Barnes, and F. Rauzi. 1956. Shortgrass range-grazing effects on vegetation and on sheep gains. Wyoming Agr. Exp. Sta. Bull. 343.

Manley, W. A., R. H. Hart, M. A. Smith, J. W. Waggoner Jr., and J. T. Manley. 1997. Vegetation, cattle, and economic responses to grazing strategies and pressure. J. Range Manage. 50:638–646.

Martin, S. C. and K. E. Severson. 1988. Vegetation response to the Santa Rita grazing system. J. Range Manage. 41:291–296.

Merrill, L. B. and J. L. Schuster. 1978. Grazing management practices affect livestock losses from poisonous plants. J. Range Manage. 31:351–354.

Molyneaux, R. J. and M. Ralphs. 1992. Plant toxins and palatability to herbivores. J. Range Manage. 45:13–18.

Nelson, A. 1898. The red desert of Wyoming and its forage resources. U.S. Dep. Agr. Div. Agrost.Bull. 13.

Nielsen, Darwin B. and Lynn F. James. 1991. Poisonous plants - Proc. 3rd Internat. Symp., Iowa State Univ. Press. Ames, Iowa.

Owensby, C. E., E. F. Smith, and K. L. Anderson. 1973. Deferred rotation grazing with steers in the Kansas Flint Hills. J. Range Manage. 26:393–395.

Pearson, H. A. and L. B. Whitaker. 1974. Forage and cattle responses to different grazing intensities on southern pine range. 27:444–446.

Pieper, R. D., E. E. Parker, G. B. Donart, and J. D. Wright. 1991. Cattle and vegetational response to four-pasture and continuous grazing systems. New Mexico Agr. Exp. Sta. Bull. 576.

Reardon, P. O. and L. B. Merrill. 1976. Vegetative response under various grazing management systems in the Edward Plateau of Texas. J. Range Manage. 29:195–198.

Rosiere, R. E. and D. T. Torell. 1996. Performance of sheep grazing California annual range. Sheep and Goat Res. J. 12:49–58.

Shoop, M. C. and E. H. McIlvain. 1971. Why some cattlemen overgraze and some don't . J. Range Manage. 24:252–257.

Sims, P. L., B. E. Dahl, and A. H. Denham. 1976. Vegetation and livestock response at three grazing intensities on sandhill rangeland in eastern Colorado. Colorado State Univ. Exp. Sta. Tech. Bull. 130.

Skovlin, J. M, R. W. Harris, G. S. Strickler, and G. A. Garrison. 1976. Effects of cattle grazing methods on ponderosa pine-bunchgrass range in the Pacific northwest. U.S. Dept. Agr. Tech. Bgull. 1531.

Smith, D. R. 1967. Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado. U.S. Dept. Agr. For. Serv. Tech. Bull. 1371.

Smith, J. G. 1895. Forage conditions of the prairie region. In: U.S. Department of Agriculture Yearbook. U.S. Gov.Printing Office, Washington, DC.

Smith, J. G. 1899. Grazing problems in the southwest and how to meet them. U.S. Dept. Agr. Div. Agrost. Bull. 16:1-47.

Smoliak, S. 1960. Effects of deferred-rotation and continuous grazing on yearling steer gains and shortgrass prairie vegetation of southeastern Alberta. J. Range Manage. 13:239–243.

Smoliak, S. 1974. Range vegetation and sheep production at three stocking rates on *Stipa-Bouteloua* prairie. J. Range Manage. 27:23–26.

Stoddart, L. A. and A. D. Smith. 1943. Range management. McGraw-Hill Book Company, N.Y.

Taylor, C. A. Jr. and M. H. Ralphs. 1992. Reducing livestock losses from poisonous plants through grazing management. J. Range Manage. 45:9–12.

Torell, L. A., J. M. Hawkes, and T. D. Stromei. 1998. Range livestock cost and return estimates from New Mexico, 1999. New Mexico State Univ. Agr. Exp. Sta. Res. Rept. 726.

USDA. 1968. 22 plants poisonous to livestock in the western states. USDA Agr. Info. Bull. 327.

Vallentine, J. F. 1990. Grazing management. Academic Press Inc., New York, N.Y.

Wooton, E. O. 1915. Factors affecting range management in New Mexico. U.S. Dept. Agr. Bull. 211.

J. Range Manage.
55: 277-284 May 2002

Snakeweed: Poisonous properties, livestock losses, and management considerations

KIRK C. McDANIEL AND TIMOTHY T. ROSS

Authors are Professors, Dept. of Animal and Range Sciences, New Mexico State Univ., Las Cruces, N.M. 88003.

Abstract

Snakeweeds (broom, *Gutierrezia sarothrae* (Pursh) Britt & Rusby); and threadleaf, *G. microcephala* (DC.) Gray) fall into that class of poisonous weeds that seldom cause direct livestock losses because they are highly unpalatable and animals rarely consume large quantities of plant material. However, when snakeweed becomes dominant on rangeland and retards growth of desirable forage, then indirectly it becomes a serious hazard to animal health. Confined and rangeland feeding trials conducted at New Mexico State University with cattle and sheep have failed to elicit reproductive failure with elevated snakeweed dosages. Snakeweed was shown to impair certain reproductive functions such as pituitary responsiveness to luteinizing hormone, and caused mild hepato-renal toxicity. Under rangeland conditions, livestock grazing in areas dominated by snakeweed reportedly have more serious problems, such as abortion. A commonality between confined feeding trials and rangeland grazing trials is that in the presence of snakeweed, animals typically display symptoms associated with a low-plane of nutrition such as lack of gain, emaciation, and occasional death. To reduce snakeweed dominance and improve range condition, management interventions such as herbicide or fire control may be necessary. Complicating the decision regarding snakeweed control is the uncertainty about treatment life and whether this relatively short-lived perennial weed might be eliminated by natural causes. Knowing the snakeweed population pattern in a given area greatly enhances management decisions.

Key Words: Poisonous plant, range weed, livestock grazing, broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt & Rusby), threadleaf snakeweed (*Gutierrezia microcephala* (DC.) Gray)

Resumen

"Snakeweeds" (broom, *Gutierrezia sarothrae* (Pursh) Britt & Rusby) y "Threadleaf" (*G. microcephala* (DC.) Gray) caen dentro de la categoría de las malezas tóxicas que raramente causan perdidas directas de ganado porque ellas no le gustan al ganado y raramente los animales consumen grandes cantidades de material vegetal de estas plantas. Sin embargo, cuando el "Snakeweed" llega a ser dominante en el pastizal y retarda el crecimiento de especies deseables, entonces se convierte en un serio peligro para la salud animal. Estudios de alimentación en confinamiento y en pastizal realizados en la Universidad Estatal de Nuevo Mexico con ovinos y bovinos han fallado en lograr un fracaso reproductivo con dosis elevadas de "Snakeweed". "Snakeweed" mostró deteriorar ciertas funciones reproductivas tales como la respuesta de la pituitaria a la hormona luteinizante y causo una toxicidad hepato-renal ligera. Bajo condiciones de pastizal, el ganado apacentando en áreas dominadas por "Snakeweed" tiene problemas mucho mas serios como abortos. Algo común entre los ensayos en confinamiento y los de apacentamiento en pastizales es que en la presencia de "Snakeweed" los animales típicamente muestran síntomas asociados con un plano nutricional bajo, tal como la falta de ganancia de peso, demacración y muerte ocasional. Para reducir la dominancia del "Snakeweed" y mejorar la condición del pastizal, es necesario realizar practicas de manejo tal como el uso de herbicidas o fuego para controlar esta planta. Algo que complica la decisión respecto al control del "Snakeweed" es la incertidumbre acerca de la duración del tratamiento y si esta especie perenne de vida relativamente corta pudiera ser eliminada por causas naturales. Conociendo el patrón de la población de "Snakeweed" de una área dada mejora grandemente las decisiones de manejo.

Broom (*Gutierrezia sarothrae* (Pursh) Britt & Rusby) and threadleaf (*G. microcephala* (DC.) Gray) snakeweed are short-lived perennial shrubs within the Asteraceae family. Because they are similar in appearance and often occupy the same ecological niches, they are commonly referred together in the literature as simply, snakeweed (Sterling et al. 1999). Both species are indigenous to North America with broom snakeweed distributed from Mexico to southern Canada, while threadleaf snakeweed is found mainly in the Chihuahuan and Sonoran deserts of Mexico and the southwestern United States.

Snakeweeds contain a rich mixture of alkaloids, flavonoids, saponins, terpenes, and other compounds that are often causal agents in various plants that poison rangeland livestock. These substances also render snakeweed highly unpalatable so that when given a choice animals usually will not eat the foliage. Bite into a snakeweed leaf and you'll quickly appreciate from the harsh burning taste why other common names, such as fireweed and turpentine weed are so appropriate. Snakeweeds are rarely eaten by any large wild or domestic animal (Smith et al. 1991) and with the exception of a few specialist foliage feeding insects, such as the red-kneed grasshopper (*Hesperotettix viridis* [Thomas]) (Thompson et al. 1995, Foster et al. 1981, Richman

This paper was supported by the New Mexico Agr. Exp. Sta., Las Cruces, NM 88003 and was funded in part by a special grant for Broom Snakeweed Research.

Author to whom correspondence should be addressed. Dept. of Animal and Range Sciences, New Mexico State University, Las Cruces, NM 88003. Phone: (505) 646-1191; Fax: (505) 646-5441; E-mail: kmcdanie@nmsu.edu.

Manuscript accepted 2 Sept. 01.

and Thompson 1995) snakeweeds are rarely damaged by grazing.

Pieper (1989) reviewed literature reporting snakeweed in herbivore diets and found it usually absent but occasionally as much as 3 to10% of grazed diets in cattle, horses, sheep, goats, mule deer, jack rabbits, and pronghorn antelope. When snakeweed is grazed by livestock it is most likely because it is the predominant green plant among other dormant or scarce species. Cattle, sheep, and horses are reportedly killed by ingesting 10 to 20% of an animals body weight with snakeweed (Kingsbury 1964), but problems with reproduction and abortion are more commonly reported (Dollahite and Anthony 1957, Smith and Flores-Rodriguez 1989).

While snakeweed poisoning problems can not be discounted, the literature suggests that it is the plants competitive nature that causes major economic damage to livestock producers. Under dense snakeweed stands losses from diminished forage and livestock production usually far outweighs it's toxic properties. In this paper we discuss some recent findings from research pertaining to snakeweed toxicology and management. We have placed special emphasis on research we have been involved in at New Mexico State University[1].

Toxicity Problems

Saponins have been identified as the primary toxic substance in snakeweed, but the plant also contains numerous other compounds (essential oils, mono- and sesquiterpenes, flavonals, tannins, alkaloids, etc.) that contribute to their toxicity. Kingsburg (1964) summarized the poisoning symptoms reported by various investigators (Mathews 1936, Dollahite and Anthony 1957, Dollahite and Allen 1959) and concluded in acute cases death occurs, but the major threat from snakeweed consumption is abortion. Other toxic effects include premature calves and decreased feed intake and body weight gains. Losses caused by abortion and birth related abnormalities in cattle, sheep, and goats from snakeweed are poorly documented and sporadic (Norris and Valentine 1957, Martinez et al. 1993).

Livestock displaying symptoms from snakeweed poisoning under rangeland conditions are likely to have a decreased nutrient status and body condition accelerated by malnutrition. Healthy grazing animals are not likely to eat the plant unless other forage is extremely scarce (Mathews 1936). Thus intuitively, rangelands with poor forage conditions (or range condition) are areas of concern but can be remedied in the short term with nutrient supplementation (Strickland et al. 1998) and in the long term by increasing forage availability.

Toxicity Studies at New Mexico State University (NMSU) from 1980 to 2000

Several studies have confirmed snakeweed toxicity under confined feeding conditions but, to our knowledge, no research has been able to demonstrate snakeweed poisoning under actual rangeland grazing experiments. Beck et al. (1999) grazed mature cows in various experiments on rangelands dominated by snakeweed on the Chihuahuan Desert Rangeland Research Center near Las Cruces, N.M. from 1992 to 1998 and never witnessed animals eating the plant. Similarly, grazing trials with goats in the same area from 1989 to 1993 reported little use of snakeweed except when other herbage was grazed out (Beck et al. 1996). According to Beck et al. (1996), heavy goat stocking for 5 summer seasons resulted in no grazing damage to snakeweed because the animals removed so little plant material. Cox (2000) examined cattle grazing paddocks with varying snakeweed densities on four New Mexico ranches and after conducting microhistological evaluations reported snakeweed present in only 1 of 337 fecal samples analyzed. Cox also followed individual animals placed in 1 ha sized paddocks with very high snakeweed densities (between 33 to 70% vegetation composition) and through bite count observations noted that snakeweed was usually not grazed but that certain animals ingested between 0.4 to 6% of their diet. Cox did not observe any visible toxicity symptoms from animals that ate the plant.

Most NMSU investigations studying snakeweed poisoning effects on animals have relied on findings from confined feeding trials (Table 1). Experiments usually have included field harvested snakeweed that is dried and ground in the lab and then added in graded dosages with hay, alfalfa, corn or soybean meal to produce isocaloric and isonitrogenous diets. Smith et al. (1991) examined the response of rats to increasing levels of snakeweed in the diet ranging from 0 to 25%. These authors found that pregnancy rates decreased when dietary snakeweed exceeded 12.5 %. They also reported that reproductive functions were impaired before evidence of liver or kidney damage. In the Smith et al. (1991) study, they found that after 35 days of snakeweed feeding that rats exhibited evidence of liver and biliary toxicosis indicated by elevated alkaline phosphates, gamma-glutamyltranspeptidase, and alanine aminotransferase. When pregnant rats were fed snakeweed at levels above10% in the diet, embryonic mortality and early fetal death was noted. Also, blood urea nitrogen and creatinine concentrations were elevated suggesting some damage to the kidneys. In the aforementioned experiments by Smith et al. (1991), snakeweed was harvested by hand clipping the new growth portion (5 to 10 cm) of the plant during pre-bloom.

Oetting et al. (1990) fed snakeweed to ewes at levels ranging from 0 to 25% of diets. With alfalfa hay as the base feed mixed with 25% snakeweed, ewes easily consumed the diet. Ewes fed 12.5 and 25% snakeweed with alfalfa hay experienced longer estrous cycles and higher serum progesterone concentrations than ewes fed less snakeweed. When the base feed included blue grama hay mixed with snakeweed, the ewes were unwilling to eat diets containing more than 10% snakeweed. Ewes that ate the blue grama hay base diet with 10% snakeweed experienced mild liver and kidney toxicosis and had significantly lower estrual activity than animals fed 0% snakeweed diets.

Working with cannulated sheep, Edrington et al. (1991) compared diets with 0, 50 or 100% fresh snakeweed placed directly in the rumen. Blood samples taken on these animals showed that the 50 and 100% snakeweed diets elevated levels of gamma-glutamyltranspeptidase, aspartate amino-transferase, and alkaline phosphates, and that unconjugated bilirubin increased in the serum. These symptoms indicate that hepato-toxicity was occurring with the ewes fed snakeweed. Also, rumen function was affected as indicated by a shift from high acetate to more propionate production in the rumen. These data agreed with a similar study reported by Hall et al. (1991).

Williams et al. (1993) conducted an experiment using 56 beef heifers fed either

[1]This paper was compiled in part, for the symposium: Do most livestock losses from poisonous plants result from 'poor' management? This symposium was held in conjunction with the Society for Range Management meeting in Boise, Ida. 13–18 Feb. 2000.

Table 1. Feeding studies investigating snakeweed toxicosis with various herbivores from 1986 to the present at New Mexico State University.

Species	Diet and Purpose	Findings	Authors
Rats	0, 12.5, 25% SW[1] Ovulation and embryonation	SW ingestion impaired fertility and reproduction in female rats. Higher embryonic death Lower ovulation Fewer offspring/litter	Smith et al. 1991
Rats	0, 5, 10, 15% SW Embryonic and fetal mortality	Body wt. declined (+17, +16, +1, -15 gm). Embryos/female declined (8.0, 7.3, 6.6, 6.3)	Edrington et al. 1991
Rats	0, 10% SW Protection from embryotoxins	Subcutaneous administration of cooking oils lowered embryo death.	Chambers et al. 1993 Smith et al. 1994
Rabbits	0, 5, 10% SW Nutritional and reproductive responses	Body wt. declined (-7.6, -10.6, -16.8%). Blood serum was altered. Delayed births	Miller et al. 1993
Ewes	0, 12.5, 25% SW Estral activity 0, 10% SW	Trial 1 Estrous cycle increased (17.0, 17.4, 17.8 d). Serum triglycerides decreased (21.8, 14.0, 10.8 mg/d) Trial 2 Control ewes had normal estral activity (7 of 7 ewes). 10% SW ewes had lower estrus (4 of 7 ewes).	Oetting et al. 1990
Ewes	0, 12.5, 25% SW Reproduction in Late gestation	Blood serum was altered Reproduction was not different.	Martinez et al. 1993
Ewes	0, 25% SW Endocrine function and pregnancy	Blood serum altered Body wt. was not different Pregnancy rates not different	Berndt et al. 1995
Ewes	0 and 20% SW Effects on liver and reproduction Reproduction was not effected.	Lutienizing hormone levels increased but sorbitol dehydrogenase hormone was not effected	Padilla et al. 2001
Heifers	0, 7.5, 15% SW Beef heifer performance	Total BW gain was less (62.4, 55.2, 51.6 kg). Conception rates and body condition scores the same. Direct bilirubin was elevated. Serum creatine kinase activity increased. Elevated serum AST. Higher triglicerides. Elevated creatinine. Decrease blood urea nitrogen. No overt toxicosis evident. Breeding and conception rates the same.	Williams et al. 1993
Heifers	0, 5, 30% SW	Birth rate and heifer gain the same. No toxic symptoms. Reproduction not different.	Martinez et al. 1993
Cows	Effect of dietary supplementation on SW toxicosis Fed hay, corn, or protein supplement	Protein supplementation improves animal tolerance to snakeweed	Strickland et al. 1998

[1]SW = Snakeweed

alfalfa hay (controls) or diets mixed with alfalfa plus 7.5 and 15% snakeweed. Forage intake was restricted to 7.7 kg daily. Entire snakeweed plants had earlier been mechanically harvested, air dried, chopped and mixed with the alfalfa. Heifers received their respective diets for 98 days. After 42 days of feeding, heifers were estrually synchronized and artificially inseminated after which bulls were placed with the heifers and rotated through pens daily. Heifers receiving the snakeweed diet gained less weight than the controls throughout the trial, however, conception rates and body condition scores were not different. Serum chemistries indicated a mild hepato-toxicosis. In a similar study, Martinez et al. (1993) assigned groups of 24 pregnant heifers (240 days pregnant) to 0, 15 or 30% whole plant snakeweed and chopped alfalfa hay diets. No abortions were recorded for any treatment suggesting that heifers can tolerate 15 to 30% snakeweed when fed a base diet of alfalfa. Martinez et al. (1993) conducted another study with ewes in late gestation feeding either alfalfa or a 25% snakeweed-alfalfa based diet. As with the heifers, no abortions were noted in the ewes and lamb birth weights were unaffected. It is important to note that both Williams et al. (1993) and Martinez et al. (1993) fed whole plant snakeweed rather than fresh or new growth clippings. Oetting et al. (1990) and Edrington et al. (1991) indicated that fresh leaf material is likely to be more toxic than whole plant snakeweed samples.

Berndt et al. (1995) conducted experiments to determine if new-growth snakeweed placed directly into ruminally cannulated ewes would alter the sensitivity of the pituitary gland to gonadotropin-releasing hormones (GnRH). In their first experiment, 8 ewes received no snakeweed or 25% snakeweed as a portion of a blue grama grass hay diet. After 35 days on the diets, ewes were administered 10 μg of GnRH and blood was collected at 15 minute intervals for 5 hours. After blood sampling, ewes were joined with fertile rams. The luteinizing hormone response to GnRH was significantly higher in ewes receiving 25% snakeweed compared to animals eating only blue grama hay. Treatments continued for 68 days after which ewes were euthanized and pregnancy status was determined by examination of uterine tissue. Pregnancy rates were unaffected by snakeweed ingestion. In a second experiment by Berndt et al (1995) alfalfa hay was used instead of blue grama as the base diet. Ewes were fed below NRC (1985) requirements similar to the first experiment. After 29 days on 0 or 25% snakeweed diets, a GnRH challenge was conducted. Unlike the first experiment, no differences were found for luteinizing hormone response. The authors indicated that the nutritive quality differences between blue grama and alfalfa hay base feed diets was probably most responsible for the differences in pituitary response to GnRH shown in these 2 experiments.

Strickland et al. (1998) conducted experiments to determine if dietary supplementation could lower snakeweed toxicity effects on beef cows in poor body condition. Dietary treatments were no snakeweed and 10% snakeweed mixed with 628 g cracked corn and 800 g of a 42% crude protein supplement provided daily. Dry matter intake was limited to 1.3% of body weight. Bromosulphothalein (BSP) clearance tests were conducted to determine the liver's ability to catalyze phase II biotransformations. Snakeweed consumption did not influence the elimination of BSP but the exchange rate from the blood to other tissues was accelerated. Supplementation with corn or protein increased the clearance rate of BSP. This suggests that if the nutrient status in an animal is improved, then there may be a greater tolerance to toxicants metabolized by phase II biotransformations. In unpublished data from this experiment, serum progesterone and estrogen concentrations did not differ among the 0 and 10% snakeweed diets or supplementation types. Also, ovarian follicular development was not affected by snakeweed or supplements.

Subsequently, 2 additional trials have been conducted at NMSU to determine the effects of snakeweed on biotransformation mechanism in sheep. Padilla et al. (2001) compared pair-fed wethers having diets containing 0% or 20% snakeweed on a dry matter basis. Caffiene and BSP clearance were measured to evaluate the ewes ability to eliminate xenobiotics. Caffiene clearance was not different between treatments but wethers consuming snakeweed exhibited reduced ($P < 0.05$) BSP clearance. In a second experiment, Padilla et al. assigned 10 ewes to either a 0% or 20% snakeweed diet and animals were again pair-fed to equalize intake. Blood samples were collected to measure luteinizing hormone (LH) and sorbitol dehydrogenase (SDH) which is a liver specific enzyme. Animals fed the snakeweed diet had higher baseline concentrations of LH but SDH concentrations were not different from the control diets. The authors suggested that the elevated LH in ewes consuming snakeweed was due to a high lipid content in the plant. Ewes were exposed to fertile rams and pregnancy rates in these experiments were similar for both diets.

Current research at NMSU is evaluating different extractions of snakeweed to identify specific toxicants. Also, experiments are being conducted to determine the relationship between liver damage and reproductive problems. A major question that remains unanswered related to snakeweed toxicity is a precise definition of its poisonous principal. Without this knowledge it is difficult to determine how snakeweed ingestion influences mechanisms of action within the animal (Strickland et al. 1998).

Snakeweed Impact on Animal and Forage Loss

Direct animal health problems from snakeweed consumption, such as abortion and death, were recognized as an important range management concern in the 1920's and 1930's (Mathews 1936, Smith et al. 1991). How widespread the problem is today is not known but some estimates are available. Based on a survey of county agents in west Texas, snakeweed poisoning causes 1% annual death loss in cattle and a 2.9% annual abortion rate (Torell et al. 1988 from McGinty and Welch 1987). Sheep and goat death losses were an estimated 0.7% and 0.4%, respectively, whereas abortion losses were 1.3% and 0.7%, respectively. As is the case with many poisonous plants, however, general estimates of loss are often not very meaningful because it is specific damage to a particular animal, herd or ranch operation that is most important. Thus most researchers agree that snakeweed related losses, such as abortion and birth-related abnormalities in cattle, sheep and goats are sporadic and vary widely by location, season, climate, soil, and range conditions (Norris and Valentine 1957, Martinez et al. 1993, Williams et al. 1993).

Indirect animal health problems resulting from emaciation, malnutrition, and lack of gain on rangeland densely infested with snakeweed is a greater economic burden to livestock producers than snakeweed poisoning (Torell et al. 1988). Grass production can be decreased by 90% or more in extremely dense snakeweed stands (McDaniel et al. 1982). Lack of suitable forage in the presence of snakeweed necessitates livestock producers to either provide a supplement, drastically reduce stocking rates, and/or remove the weed. Whatever alternative is chosen, the cost to producers is high. Economic losses from snakeweed varies depending on beef prices and production cost, but on the 10 million ha of rangeland in the western United States infested with snakeweed, losses are substantial (McDaniel and Torell 1987).

Snakeweed/Grass Interaction

The snakeweed-overstory and grass-understory biomass relationship has been expressed using sigmoidal growth and negative exponential equations (McDaniel et al. 1993). The downward sloping convex shape of an exponential equation implies that grass production is retarded with even a minor snakeweed presence, thus for management purposes control strategies that maximize snakeweed removal are likely to be most economically efficient (Tanaka and Workman 1988). The sigmoid shape (Fig. 1) implies that a minor amount of snakeweed does not affect grass biomass but that once a threshold is reached then grass biomass is drastically reduced, i.e. in a manner similar to that estimated by a negative exponential equation.

Having an appreciation of the snakeweed-overstory and grass-understory relationship has practical management implications when trying to decide whether to use prescribed fire or a herbicide to control snakeweed (Fig. 1). For example, in areas with a moderate to dense amount of snakeweed (areas with >300 kg/ha snakeweed), burning is usually impractical because fine fuels are often insufficient in quantity and uniformity to carry a fire (McDaniel et al. 1997). Rangelands with high amounts of snakeweed are generally better managed with an aerial herbicide application than fire. Where light amounts of snakeweed and sufficient grass occur (< 300 kg/ha snakeweed and > 500 kg/ha of grass), then prescribed fire is often a better management choice than herbicide control because it is less costly. An expectation after employing either control method is that a favorable grass response will offset treatment cost (Torell et al. 1988).

Rangelands dominated by snakeweed are often perceived as being in poor range condition because grass growth languishes beneath dense canopies. However, caution must be exercised to distinguish between what might be poor forage condition as opposed to poor ecological (range) condition. Rangelands with dense snakeweed may or may not be in poor range condition, but they are nearly always in poor forage condition. To further illustrate the importance of understanding the overstory-understory relationship, Figure 2 shows a 20 year comparison of snakeweed and grass biomass taken from undisturbed research plots near Vaughn and Roswell, New Mexico. A portion of this data, and the manner in which it was collected has been described in part elsewhere (McDaniel 1989, McDaniel and Duncan 1987). At these locations, data were acquired from replicated untreated plots (0.1 ha in size) placed in pastures that had a high initial density of snakeweed. Blue grama was the principal associated grass. Over the 20-year study period landownership did not change and, in general, the ranchers employed consistent grazing management practices through time. Figure 2 indicates that during years when snakeweed was highly dominant, such as in the early 1980's, grass growth was highly suppressed. Only after snakeweed naturally declined at these locations did grass yield increase. Typically, grass yield increases 4 to 6 fold after a dense snakeweed stand dies-out or when the weed is removed by herbicide spraying (McDaniel et al. 1982, McDaniel and Duncan 1987).

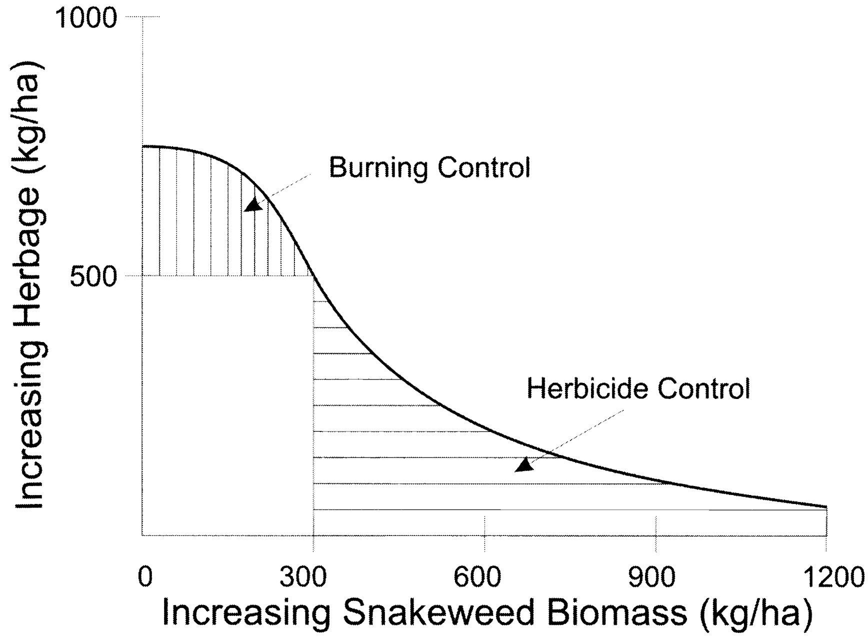


Fig. 1. Sigmoid curve illustrating the snakeweed-overstory and grass-understory relationship and areas where burning or herbicide control become most practical.

How Snakeweeds Longevity Effects Management Decisions

Snakeweed populations have been described in the literature as cyclic through time (Jameson 1970). That is, propagation occurs under favorable environmental conditions and plants survive until conditions become unfavorable, then they die. The term cyclic implies a regular and repeated life history pattern that is expected to occur over many years. In actuality, the number of snakeweed plants and length of time they might survive in a given area is neither repeatable or predictable thus the term "cyclic" must be used in a restrictive sense when describing snakeweed populations. A 100-year record set from permanent quadrats placed on the Joronada Experimental Range in southern New Mexico indicated that the average life expectancy for snakeweed was about 4 years, but that some individual plants lived longer than 15 years (Dittberner 1971). There was no indication from the Joronada data set that the snakeweed population was predictably cyclic over time.

Environmental events that influence snakeweed seed production (Wood et al. 1997), trigger germination (Kruse 1979, Mayeux and Leotta 1981, Mayeux 1983), and affect survival (McDaniel 1989) are becoming better understood. Close study of seedling establishment suggests that the optimal environmental conditions necessary for propagation occur only once or twice a decade in the southwestern United States. Snakeweed seedlings have been noted after above-average winter precipitation in the Chihuahuan Desert of southern New Mexico (Barnett 1996, Beck et al. 1999), and with above-average spring precipitation on blue grama rangeland in central New Mexico (McDaniel et al. 2000). Die-offs from weather usually result from summer drought but insects and old age are also responsible for natural plant losses (Pieper and Mc Daniel 1989).

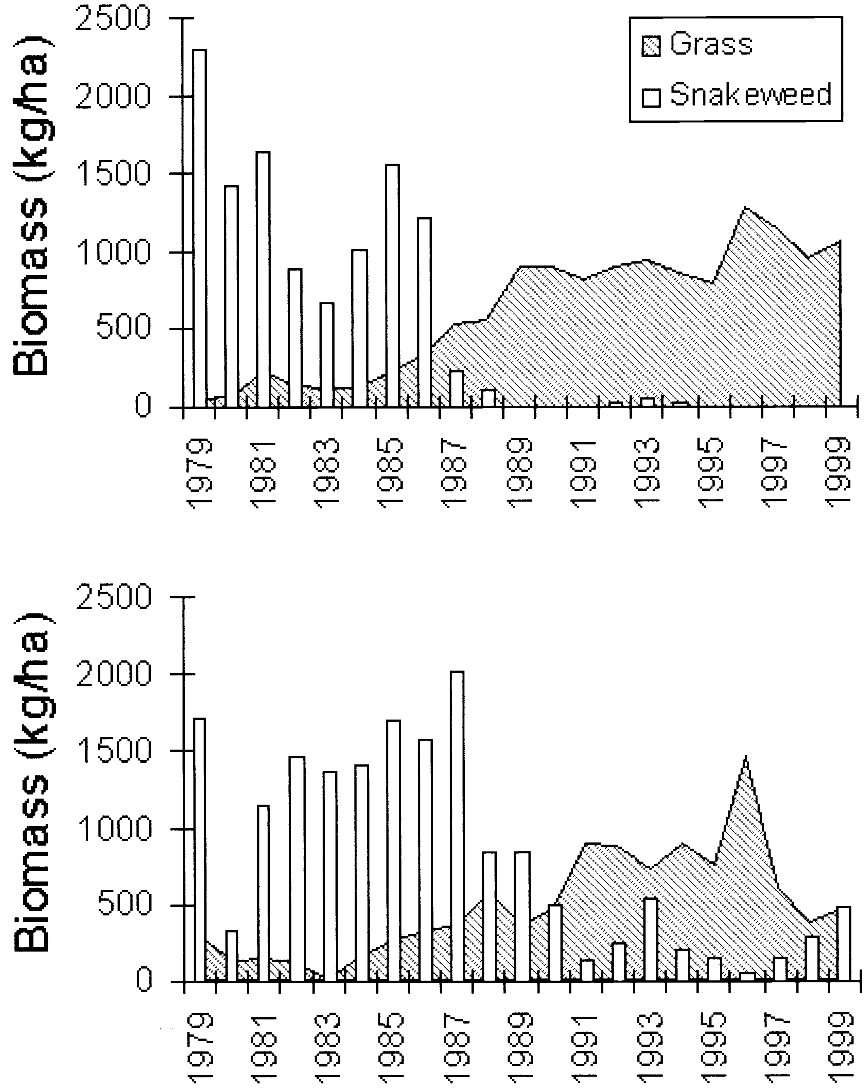


Fig. 2. Snakeweed biomass (bars) and grass biomass (shaded area) on native rangeland near Roswell (top) and Vaughn (bottom), New Mexico 1979 to 1999.

Because some describe snakeweed as a short-lived perennial (Lane 1985, Solbrig 1960, 1964), it seems logical to assume that fecundity and mortality rates may be predictable across a regional population. However, the snakeweed cyclic pattern is rarely identical from 1 ecological site to another (Mc Daniel 1989). Consider again Figure 2 giving the 20 year snakeweed biomass pattern near Vaughn and Roswell, New Mexico. These sites are within a 50 mile radius of each other and the snakeweed pattern at each shares certain similarities but also differences. In 1980, the region experienced severe summer drought and there was a significant die-off of mature snakeweed plants at Vaughn, but plants survived at Roswell. In 1981, spring rainfall was twice the regional average and a substantial crop of snakeweed seedlings (from 120 to 330 seedlings/m^{-2}) were produced at both locations. This was the only year over the 20 year record that a high number of seedlings were found at these locations and these propagules make up the generation of snakeweed that still persist at Vaughn today. Most snakeweed at Roswell were eliminated by root borers (*Crossidius puchellum*) in 1987–88 and the area has remained nearly snakeweed free since this time. The inconsistencies in how snakeweed persisted at these locations suggest that snakeweed populations on different ecological sites are affected by various external factors that can result in different local life history patterns. This brings into question the difficulty and perhaps value of trying to predict snakeweed's cyclic pattern across broad regional areas.

Snakeweed Management

The decision as what to do when snakeweed is a dominant plant involves basically 2 choices. One choice is to leave it alone and to manage around the plant. The hope is that drought, insects, or old age will cause it to die-out and that snakeweed propagation will not soon follow. The second choice is to intervene, using herbicide, fire or mechanical control to eliminate the plant. Consider Figure 2 again to illustrate how either choice can result in an economic hardship to a ranching operation. At Roswell the decision not to control snakeweed in the early 1980s meant the owner had to endure grass growth that was highly suppressed under a generation of snakeweed that lasted for 8 years (1981 to 1988). Fortunately, at this location, when mature snakeweed plants died new seedlings did not follow and this allowed grasses to recover over the next 11 years (1989 to 1999). If the Roswell owner had decided to control snakeweed shortly after plants established in 1981, then the treatment would probably have been economically beneficial. However, if the owner had waited and not controlled snakeweed until just before it naturally died (i.e. 1986-87), then little benefit would have been derived in terms of increased forage. According to Torell et al. 1988, an area where snakeweed is controlled by herbicide spraying must remain snakeweed free for a minimum of 4 years to be economically effective. In contrast, at Vaughn, snakeweed has persisted from 1981 to the present, thus the owner has experienced forage suppression for 20 years. If the Vaughn owner had decided to control snakeweed shortly after the new snakeweed generation established in 1981 then the benefits from eliminating the weed would have been long lasting. This timing is verified from herbicide control experiments conducted annually at the Vaughn location from 1979 to 1987 (Table 2; McDaniel 1987). In these experiments, the herbicide picloram was applied and usually provided 95% or better snakeweed control as determined from evaluations made 12 months after treatment. Sprays applied in 1979 and 1980 killed mature snakeweed but these treatments were short-lived because of the 1981 germination event that

Table 2. Snakeweed control 12 months after spraying with picloram[1], and subsequent evaluations made in 1988 and 1999 near Vaughn, N.M.

Year Sprayed	1st yr after treatment	1988	1999
	---- % Snakeweed Control-----		
1979	98	25	0
1980	95	3	0
1981[2]	--	--	--
1982	83	83	75
1983	100	100	100
1984	99	99	99
1985	99	99	100
1986	100	99	100
1987	100	100	100
1988	100	100	100

[1]Picloram applied at 0.56 kg/ha in 1979, 1980, and 1982; applied at 0.28 kg/ha in 1983 to 1988.
[2]No treatments made in 1981.

resulted in the treated areas to appear similar to nonsprayed rangeland within a few years of treatment. However, areas sprayed at the Vaughn location in 1982 or later have remained essentially snakeweed free for the next 18 years.

Eliminating snakeweed by herbicide or fire control can result in an increase in rangeland carrying capacity and can also reduce livestock losses caused by poisoning and malnourishment. McDaniel and Duncan (1987) reported that with 90% or greater snakeweed control with a herbicide, the carrying capacity at Vaughn changed from 1 AU/62 ha to 1 AU/20 ha, and at Roswell the change was from 1 AU/88 ha to 1 AU/7 ha. With commercial aerial application cost of $22 per ha to spray picloram at a 0.28 kg/ha rate, the buyer needs at least 4 years of benefit to justify the expense (Torell et al. 1988). Cost related to prescribed fire depends on the size of the area to be burned and available labor and logistical support. Typically, areas to be burned must be deferred at least 2 growing seasons: one season to build up adequate fine-fuel loads, and a second season for grass recovery (McDaniel et al. 1997). Combined, chemical control may be viewed as a reclamation tool to reduce high densities of snakeweed, whereas burning control is a tool for maintaining non-economic populations of snakeweed (Sterling et al. 1999).

Literature Cited

Beck, R. F., R. P. McNeely, and S. J. Muir. 1996. Effects of goats and drought on snakeweed. Abstract in 49th Ann. Meeting of Soc. for Range Mangement pp. 7. Feb. 10–15, 1996.

Beck, R. F., M. Nsinamwa, R. Santos, and R. D. Pieper. 1999. Dynamics of *Gutierrezia sarothrae* with drought and grazing. *In:* Eldridge and Freudenberger. pp. 502–504. Proc. of the VI Internat.. Range Congress, Vol. 1, Townsville, Australia.

Berndt, M. Y., T. T. Ross, and D. E. Hawkins. 1995. The effects of snakeweed (*Gutierrezia microcephala* and *G. sarothrae*) on endocrine function and establishment of pregnancy in ewes. *In:* Proc. West. Sect. Amer. Soc. Anim. Sci. 46:69–72.

Barnett, B. L. 1996. Influence of winter precipitation on broom snakeweed establishment in the Chihuahuan Desert. M.S. Thesis. New Mexico State Univ., Las Cruces, N.M.

Cox, S. H. 2000. Snakeweed (*Gutierrezia* spp.) consumption by grazing beef cattle. M. S. Thesis. New Mexico State University, Las Cruces, N.M.

Chambers, S.W., G.S. Smith, M. S. Stavanja, E. C. Staley, J. P. Thilstead, and D. M. Hallford. 1993. Safflower oil protects rats from embryotoxins of ingested snakeweed foliage. Proc. West. Sec. Amer. Soc. of Anim. Sci. 44:

Dittberner, P. L. 1971. A demographic study of some semi-desert grassland plants. M. S. Thesis, New Mexico State University, Las Cruces, N.M.

Dollahite, J. W. and T. J. Allen. 1959. Feeding perennial broomweed to cattle, swine, sheep, goats, rabbits, guinea pig, and chickens. Texas Agr. Exp. Sta. PR-2105. College Station, Tex.

Dollahite, J. W. and W. V. Anthony. 1957. Poisoning of cattle with *Gutierrezia microcephala*, a perennial broomweed. J. Amer. Vet. Med. Assoc. 130:525–30.

Edrington, G. S. Smith, M. D. Sanford, J. Medrano, T. T. Ross, and J. C. Thilsted. 1991. Ingested snakeweed foliage related to embryonic and fetal mortality of albino rats. *In:* Proc. West. Sec., Amer. Soc. Anim. Sci. 42:12-14.

Foster, D. E., D. N. Meckert, and C. J. DeLoach. 1981. Insects associated with broom snakeweed and threadleaf snakeweed in west Texas and eastern New Mexico. J. Range Manage. 34:446-454.

Hall, L.E., M.L. Galyean, and T.T. Ross. 1991. Effect of increasing level of snakeweed on digestibility of alfalfa and grass hay in vitro. Proc., West. Sec., Amer. Soc. Anim. Sci. 42:292.

Jameson, D. A. 1970. Value of broom snakeweed as a range condition indicator. J. Range Manage. 23:302–304.

Kingsbury, J. M. 1964. Poisonous plants of the United States and Canada. Prentice-hall, Inc. Englewood Cliffs, New Jersey, pp. 406–408.

Kruse, W. H. 1979. Temperature and moisture stress affect germination of *Gutierrezia sarothrae*. J. Range Manage. 23:143–45.

Lane, M. A. 1985. Taxonomy of *Gutierrezia* (Composiate: Astereae) in North America. Syst. Bot. 10:7-28.

Martinez, J. H., T. T. Ross, K. A. Becker, J. L. Williams, D. Campos, and G. S. Smith. 1993. Snakeweed toxicosis in late gestation ewes and heifers. *In:* Sterling, T. M. and D. C. Thompson (eds.).pp. 48–49. Snakeweed Research: Updates and Highlights. New Mexico Agric. Exp. Stn. Res. Report #674.

Mathews, F. P. 1936. The toxicity of broomweed (*Gutierrezia microcephala*) for sheep, cattle, and goats. J. Amer. Vet. Med. Assoc. 88:56–61.

Mayeux, H. S., Jr. 1983. Effects of soil texture and seed placement on the emergence of four subshrubs. Weed Sci. 31:380–84.

Mayeux, H. S. and L. Leotta. 1981. Germination of broom snakeweed and threadleaf snakeweed. Weed Sci. 29:530–534.

McDaniel, K. C. 1989. Use of herbicides in snakeweed management.*In:* Snakeweed: Problems and Perspectives. E. W. Huddleston and R. D. Pieper (eds.). pp. 85–99. New Mexico Agr. Exp. Sta. Bull. 751.

McDaniel, K. C. and K. W. Duncan. 1987. Broom snakeweed (*Gutierrezia sarothrae*) control with picloram and metsulfuron. Weed Sci. 35:837-41.

McDaniel, K. C. and L. A. Torell. 1987. Ecology and management of broom snakeweed. *In:* Integrated pest management on rangeland, a shortgrass prairie perspective. J. L. Capinera (ed.). Westview Press. Boulder, Colo., 101–15.

McDaniel, K. C., D. B. Carroll, and C. R. Hart. (2000). Broom snakeweed establishment on blue grama grasslands after fire and herbicide treatments. J. Range Manage 53:239–245.

McDaniel, K. C., C. Hart, and D. B. Carroll. 1997. Broom snakeweed control with fire on New Mexico blue grama rangeland. J. Range Manage. 50:652–59.

McDaniel, K. C., R. D. Pieper, and G. B. Donart. 1982. Grass response following thinning of broom snakeweed. J. Range Manage. 35:142–45.

McDaniel, K. C., L. A. Torell, and J. W. Bain. 1993. Overstory-understory relationships for broom snakeweed-blue grama grasslands. J. Range Manage. 46:506–11.

McGinty, A. and T. G. Welch. 1987. Perennial broomweed and Texas ranching. Rangelands 9:246–249.

Miller, R. J., G. S. Smith, and R. L. Byford. 1993. Nutritional, toxicological, and reproductive responses in female domestic rabbits fed snakeweed foliage. *In:* Proc. West. Sect. Amer. Soc. Anim. Sci. 44:122–125.

Norris, J. J. and K. A. Valentine. 1957. Principal livestock-poisoning plants. New Mexico A&M College, Agr. Extension Serv. Cir. 274.

NRC. 1985. Nutrient requirements of sheep (6th edition). National Academy Press, Washington D.C.

Oetting, B. C., T. T. Ross, K. Walraven, P. Kloppenburg, G. S. Smith, and D. M. Hallford. 1990. Effects of ingested snakeweed herbage on actual activity, blood progesterone, and serum clinical profiler of fine-wool ewes. *In:* Proc. West. Sect. Amer. Soc. Anim. Sci. 41:23–26.

Padilla, D. J., T. T. Ross, J. P. Strickland, D. M. Hallford, M. W. Salisbury, and J. L. Bollinger. 2001. Effects of snakeweed (*Gutierrezia* spp.) ingestion on reproduction and liver function in sheep. Proc., West. Sec., Amer. Soc. Anim. Sci. 52:45–49.

Pieper, R. D. 1989. Broom snakewood content of herbivore diets. *In:* Snakeweed: Problems and Perspectives. E. W. Huddleston and R. D. Pieper (eds.). pp. 203–10.New Mexico Agr. Exp. Sta. Bull. 751.

Pieper, R. D. and K. C. McDaniel. 1989. Ecology and management of broom snakeweed. *In:* Snakeweed: Problems and Perspectives. E. W. Huddleston and R. D. Pieper (eds.). New Mexico Agr. Exp. Sta. Bull. 751, 1–12.

Richman, D. B. and D. C. Thompson. 1995. Insect associations with woody snakeweeds in New Mexico, Texas, and Arizona. *In:* Papers from the Fourth Symposium on Resources of the Chihuahuan Desert Region. Chihuahuan Desert Res. Inst., Alpine, Tex..

Smith, G.S. and G.I. Flores-Rodriguez. 1989. Toxicity of snakeweeds. *In:* Huddleston and Pieper. pp. 211–219. Snakeweed: Problems and Perspectives. NMSU Agr. Exp. Bull. 751.

Smith, G. S., T. T. Ross, G. S. Flores-Rodriguez, B. C. Oetting, and T. S. Edrington. 1991. Toxicology of snakeweeds, *Gutierrezia microcephala* and *G. sarothrae*. *In:* James, Evans, Ralphs, and Child. pp. 236–246. Noxious Range Weeds. Westview Press, Boulder, Colo..

Smith, G. S., T. T. Ross, D. M. Hallford, J. P. Thisted, E. C. Stales, J. A. Greenberg, and R. J. Miller. 1994. Toxicology of snakeweeds (*Gutierrezia sarothrae* and *G. microcephala*). Proc. West. Sec. Anim. Soc. of Anim. Sci. 45:98–102.

Solbrig, O. T. 1960. Cytotazonomic and evolutionary studies in the North American species of *Gutierrezia* (Composiate). Controb. Gray herb. 188:1–61.

Solbrig, O. T. 1964. Intraspecific variation in the *Gutierrezia sarothrae* complex (Compositate-Asteraceae). Contrib. Gray Herb. 193:67–115.

Sterling, T. M.., D. C. Thompson, and K. C. McDaniel. 1999. Snakeweeds. In: Biology and Management of Noxious Rangeland Weeds. R. L. Sheley and J. K. Petroff (eds). Oregon State University Press, Corvallis, Ore.

Strickland, J. R., L. F. Gulimo-Klein, T. T. Ross, S. Slate, M. K. Petersen, T. May, and J. B. Taylor. 1998. Effects of nutrient supplementation in beef cows of poor body condition fed snakeweed (*Gutierrezia* spp.). Vet. and Hum. Tox. 40:278–284.

Tanaka, J. A. and J. P. Workman. 1988. Economic optimum big sagebrush control for increasing crested wheatgrass production. J. Range Manage. 41:172–178.

Thompson, D. C., K. C. McDaniel, L. A. Torell, and D. B. Richman. 1995. Damage potential of *Hesperotettix viridis* (Orthoptera Accidental) on a rangeweed, *Gutierrezia sarothrae*. Environ. Ento. 24:1315–1321.

Torell, L.A., H. W. Gordon, K. C. McDaniel, and A. McGinty. 1988. Economic impact of perennial snakeweed infestations. *In:* The ecology and economic impact of poisonous plants on livestock production. James, L. F., M. H. Ralphs, and D. B. Nielson (eds.) pp., 57-69. Westview Press. Boulder, Colo.

Williams, J. L., D. Campos, T. T. Ross, G. S. Smith, J. M. Martinez, and K. A. Becker. 1993. Heifer reproduction is not impaired by snakeweed consumption. *In:* Sterling, T. M. and D. C. Thompson (eds.). Snakeweed Research: Updates and Highlights. New Mexico Agr. Exp. Sta. Res. Report 674: 46–47.

Wood, B. L., K. C. McDaniel, and D. Clason. 1997. Broom snakeweed (*Gutierrezia sarothrae*) dispersal, viability, and germination. Weed Sci. 45:77–84.

J. Range Manage.
55: 285-290 May 2002

Ecological relationships between poisonous plants and rangeland condition: A Review

MICHAEL H. RALPHS

Author is Rangeland Scientist, USDA/ARS Poisonous Plant Lab, Logan Utah 84341.

Abstract

In the past, excessive numbers of livestock on western U.S. rangelands, reoccurring droughts, and lack of management resulted in retrogression of plant communities. Poisonous plants and other less palatable species increased with declining range condition and livestock were forced to eat these poisonous species because of a shortage of desirable forage, resulting in large, catastrophic losses. The level of management on most western rangelands has improved during the last 60 years, resulting in marked improvement in range condition; yet losses to poisonous plants still occur, though not as large and catastrophic as in the past. Some poisonous species are major components of the pristine, pre-European plant communities [tall larkspur (*Delphinium barbeyi* Huth), *Veratrum californicum* Durand, water hemlock (*Cicuta douglasii* (DC.)Coult. & Rose), bracken fern (*Pteridium aquilinum* (L.) Kuhn), chokecherry (*Prunus virginiana* L.), Ponderosa pine (*Pinus ponderosa* Lawson), and various oak species (*Quercus* spp.)]. Although populations of many poisonous seral increaser species have declined with better management, they are still components of plant communities and fluctuate with changing precipitation patterns [locoweed (*Astragalus* and *Oxytropis* spp.), lupine (*Lupinus* spp.), death camas (*Zigadenus* spp.), snakeweed (*Gutierrezia* spp.), threadleaf groundsel (*Senecio longolobis* Benth.), low larkspur (*Delphinium nuttallianum* Pritz.), timber milkvetch (*Astragalus miser* Dougl. ex Hook.), redstem peavine (*A. emoryanus* (Rydb.) Cory), western bitterweed (*Hymenoxys odor*ata D.C.), orange sneezeweed (*Helenium hoopesii* Gray), twin leaf senna (*Cassia roemeriana* Schelle), and white snakeroot (*Eupatorium rugosum* Houtt)]. Many of the alien invader species are poisonous: [*Halogeton glomeratus* (Bieb.) C.A. Mey, St. Johnswort (*Hypericum perforatum* L.), poison hemlock (*Conium maculatum* L.), tansy ragwort (*Senecio jacobaea* L.), hounds tongue (*Cynoglossum officinale* L.), leafy spurge (*Euphorbia esula* L.), yellow star thistle (*Centaurea solstitialis* L.) and other knapweeds (*Centaurea* spp.)]. Poisoning occurs when livestock consume these plants because they are either relatively more palatable than the associated forage, or from management mistakes of running short of desirable forage.

Key Words: Poisonous plants, rangeland condition, larkspur, *Delphinium* spp., locoweed, *Astragalus* spp., *Oxytropis* spp., lupine, *Lupinus* spp., death camas, *Zigadenus* spp.

Resumen

En el pasado, el número excesivo de ganado en los pastizales del oeste de los Estados Unidos, las sequías recurrentes y la falta de manejo resultaron en la retrogresión de las comunidades vegetales. Las plantas tóxicas y otras especies menos gustadas se incrementaron declinando la condición del pastizal y el ganado fue forzado a comer estas especies tóxicas debido a la escases de forraje deseable, resultando en perdidas grandes y catastróficas. Durante los últimos 60 años, el nivel de manejo de la mayoría de los pastizales del oeste ha mejorado resultando en una marcada mejoría de la condición del pastizal; pero las perdidas por plantas tóxicas todavía ocurren, aunque no son tan grandes ni catastróficas como en el pasado. Algunas especies tóxicas son componentes principales de las comunidades vegetales prístinas preeuropeas ["Tall larkspur" (*Delphinium barbeyi* Huth), *Veratrum californicum* Durand, "Water hemlock" (*Cicuta douglasii* (DC.)Coult.. & Rose), "Bracken fern" (*Pteridium aquilinum* (L.) Kuhn), "Chokecherry" (*Prunus virginiana* L.), "Ponderosa pine" (*Pinus ponderosa* Lawson) y varias especies de encino (*Quercus* spp.)]. Aunque las poblaciones de muchas de estas especies tóxicas incresoras han disminuido con un mejor manejo, ellas todavía son componentes de las comunidades vegetales y fluctúan con los patrones cambiantes de precipitación ["Locoweed" (*Astragalus* and *Oxytropis* spp.), "Lupine" (*Lupinus* spp.), "Death camas" (*Zigadenus* spp.), "Snakeweed" (*Gutierrezia* spp.), "Threadleaf groundsel" (*Senecio longolobis* Benth.), "Low larkspur" (*Delphinium nuttallianum* Pritz.), "Timber milkvetch" (*Astragalus miser* Dougl. ex Hook.), "Redstem peavine" (*A. emoryanus* (Rydb.) Cory), "Western bitterweed" (*Hymenoxys odorata* D.C.), "Orange sneezeweed" (*Helenium hoopesii* Gray), "Twin leaf senna" (*Cassia roemeriana* Schelle) y "White snakeroot" (*Eupatorium rugosum* Houtt)]. Muchas de las especies invasoras extranjeras son tóxicas: [*Halogeton glomeratus* (Bieb.) C.A. Mey, "St. Johnswort" (*Hypericum perforatum* L.)," Poison hemlock" (*Conium maculatum* L.), "Tansy ragwort" (*Senecio jacobaea* L.), "Hounds tongue" (*Cynoglossum officinale* L.), "Leafy spurge" (*Euphorbia esula* L.), "Yellow star thistle" (*Centaurea solstitialis* L.) y otras "Knapweeds" (*Centaurea* spp.)]. El envenenamiento ocurre cuando el ganado consume estas plantas porque ellas son de una gustocidad relativamente mayor que el forraje asociado o por errores de manejo durante escases de forraje deseable.

Poisoning Related to Overgrazing in the Past

Two factors contributed to the high incidence of poisonous plant problems on western U.S. rangelands: abundance of toxic plants, both in number of species and density of plants; and overgrazing. Western rangelands are extremely variable in topogra-

Manuscript 27 May 00.

Table 1. Poisonous plants found in physiographic regions and plant communities.

	Great Plains and Prairies	
Tall-grass prairie	Short/Mid-grass prairie	Oak/mesquite savanna
White snakeroot Riddells groundsel	Plains larkspur Locoweed Threadleaf groundsel Broom snakeweed Redstem peavine	Bitterweed Twin leaf senna Oak
	Southwest Deserts	
Sonoran Desert	Desert grasslands	Mohave Desert
Garboncillo Mescal bean Red-stem peavine Wooly paperflower	Sacahuista Rayless goldenrod Broom snakeweed	Desert baileya Milkweed Coyotillo
	Mountains	
Mountain brush	Mt. big sagebrush	Aspen / conifer
Orange sneezeweed Chokecherry Oak	Death camas Low larkspur Lupine	Tall larkspur Timber milkvetch False hellebore Ponderosa pine
	Colorado Plateau / Great Basin	
Salt desert shrub	Sagebrush steppe	Juniper / Pinyon
Halogeton Greasewood Horsebrush	Death camas Anderson larkspur Water hemlock	Locoweed Lupine Pingue

phy, soils, and climate, resulting in very diverse plant communities. Many of the plant species contain toxins, and if eaten in sufficient quantity, would poison animals. Kingsbury (1964) described over 1,000 poisonous plants, found mostly in the western US and Canada.

Livestock poisoning became a significant problem as settlers moved west and their livestock encountered a vast array of poisonous plants (Table 1). The plains and prairies were fully stocked by the 1880's, and the mountains and deserts by the turn of the century. The number of livestock on western rangelands exceeded the biological carrying capacity and management was generally lacking. Retrogression of the plant communities following misuse and reoccurring drought contributed to livestock poisoning. Poisonous and other less palatable species increased as the more desirable forage plants were heavily grazed and died out, and animals were forced, through shortage of other forage, to eat the poisonous species.

The problem was sufficiently severe that it became a national concern. The USDA Bureau of Plant Industry commissioned a team of scientists to study the problem beginning with V.K. Chestnut in 1894 and C.D. Marsh in 1905. Marsh (1913) published a short bulletin *Stock poisoning Due to Scarcity of Food* in which he listed the conditions where livestock were poisoned by major plants of that day:

1. The loco habit is usually acquired during a season of short feed, when the locoweeds (*Astragalus* and *Oxytropis* spp.) are the most attractive form of vegetation.
2. Larkspur *(Delphinium* spp.) poisoning is most likely to occur either during the season of short feed, or on overgrazed areas; in either case the larkspur is the most conspicuous form of vegetation to attract the animals and is eaten in lieu of anything better.
3. The roots of water hemlock (*Cicuta douglasii* (DC.)Coult.. & Rose) are picked up when there is little else to eat and with disastrous results.
4. Successive bands of sheep are driven over the same trail until everything suitable for food disappears, and then there follow cases of poisoning from wild cherry [chokecherry (*Prunus virginiana* L.)]. On some trails there is an almost continuous hedge of wild cherry, and the leaves are eaten as high as the sheep can reach.
5. Sheep are sometimes bedded in the same place for several successive days. Under such circumstances everything near the bed ground is eaten, and if there are any poisonous plants some of the sheep are pretty sure to get them.

Large catastrophic livestock losses occurred because there were too many livestock on the ranges, management was almost nil, and knowledge of poisonous plants was meager.

Rangelands today are in the best condition that they have been in for the last 100 years (Box and Malechek 1987), due to improved and intensified range and livestock management. Knowledge of poisonous plants, their toxins and conditions of poisoning has increased. Thus, the incidence of large, catastrophic losses has declined. The following is a chronological list of statements taken from the poisonous plant literature and prominent range management text books illustrating the evolution of the relationship between range condition and livestock poisoning:

Marsh (1913)—"Stock seldom eat poisonous plants by choice, but only when induced or compelled by the scarcity of other food or on overgrazed ranges."

Stoddart and Smith (1943)—"Poisonous plants cause great loss on western ranges. Losses are increasing in spite of increased knowledge concerning poisonous plants and treatment of poisoned animals."

Stoddart et al. (1949) "Poisoning is natures' sign of a sick range."

Stoddart and Smith (1955)— "Losses have decreased measurably because stockmen have learned to recognize poisonous species and have learned to avoid them or to minimize damage from them."

Stoddart et al. (1975)— "Poisonous plants are normal components of range ecosystems. Most losses can be avoided by good management; others occur with such irregularity due to unpredictable conditions that they constitute an ever-present hazard."

Vallentine (1990)— "Prolonged droughts and overgrazing sometimes force livestock to eat harmful amounts of poisonous plants. On good condition ranges, poisonous plants are subjected to intense competition from vigorous, high producing forage plants, and there is a great variety of plant species available for selective grazing."

Schuster (1978) stated that good range management is the surest and most economical means of reducing livestock loss to poisonous plants. Desirable forage

Table 2. Plant/animal/environment interactions of poisoning

Plant	Animal	Environmental
Ecology	Species and class	Plant population cycle
Habitat	Physiological condition	Toxin level
Abundance	Hunger	Animal behavior
Toxin	Preference	Relative palatability

species are encouraged, while undesirable and poisonous species are suppressed, and animals are provided abundant nutritious forage.

Plant/Animal/Environment Interactions of Poisoning

In spite of the improved range conditions, losses to poisonous plants continue to occur, although not at the catastrophic levels of the past. Dwyer (1978) stated "We are long past the time we can pass off poisonous plants as a symptom of an overgrazed range." Dwyer called attention to the need for research on plant/animal interactions of poisoning (Table 2). I would add to that, the environmental factors that influence both plants and animals. We need to consider individual plant species, their toxin and concentration within the plant; the plants' ecological status (Table 3), the soils and sites they occupy, their population cycles, and other factors that influence their relative abundance.

The animal factors depend first on whether the animal eats the toxic plant. Many plants are highly toxic, but seldom eaten [i.e. water hemlock, (*Cicuta douglasii* (DC.)Coult.. & Rose) narrow leaved milkweeds (*Asclepias* spp), jimson weed (*Datura stramonium* L.)]. If the animal eats the plant, poisoning depends on the toxin level in the plant, and the rate of consumption. The rate of consumption depends on the plants relative palatability and its abundance in the plant community. Palatability of any plant is relative to what other forage is available. Some poisonous plants are relatively more palatable than the associated vegetation, i.e. larkspur (*Delphinium* spp.) and locoweeds (*Astragalus* spp.), whereas the lack of better alternatives and hunger may drive animals to consume other poisonous plants. Some situations may cause animals to graze non-selectively, such as releasing hungry animals into areas of poisonous plants, or introducing non-native animals to areas of unfamiliar poisonous plants.

Environmental factors affect both plants and animals. Population cycles occur for many poisonous plants, with die-offs occurring during drought and population explosions during wet periods. Weather stress (drought, temperature, frost) can increase toxin concentration in many plants. Specific weather events can also affect grazing behavior, causing animals to increase consumption of specific poisonous plants. All of these factors interact to determine whether an animal is poisoned.

Ecological Status of Important Poisonous Plants

Larkspurs

Larkspurs kill more cattle on mountain and foothill rangelands than any other plant or disease. Early losses ranged from 3–5% of cattle grazing on larkspur infested rangelands, with over 5500 cattle deaths reported annually (Aldous 1917). We estimated over 1,000 cattle die annually from larkspur in the Intermountain Forest Service Region (Nielsen and Ralphs 1988). Losses of similar magnitude occur in the Rocky Mountain and Northern Forest Service Regions, and additional losses occur on private rangelands. Larkspurs contain norditerpenoid alkaloids, which cause muscular paralysis and rapid death from respiratory failure. Sheep are more resistant to larkspur alkaloids than are cattle (Olsen 1978).

The tall larkspur complex is comprised of 4 species: tall larkspur (*D. barbeyi* Huth.) in southcentral Wyoming, Colorado and southern Utah; duncecap larkspur (*D. occidentale* Wats.) in north and western Wyoming, Montana, Idaho, northern Utah and Nevada; Sierra larkspur (*D. glaucum* Wats.) in California and Oregon and northward to Alaska; and waxy larkspur (*D. glaucescens* Rydb) in southwest Montana and central Idaho. These species differ in toxicity (Ralphs et al. 1997), but inhabit similar ecological sites.

Ellison (1954) conducted one of the most comprehensive ecological studies of the subalpine vegetation of the Wasatch Plateau in central Utah. Tall larkspur occurred in 2 plant communities. It was a principal component of the mixed upland herb association in its climax stage, comprising 2–5% of total cover, ranging up to 50% in some areas. Tall larkspur was also one of the most conspicuous species of the tall forb community on snow drift sites and at the edge of wet meadows and along streams. Abusive grazing from 1880 to 1905 practically destroyed the original herbaceous vegetation, resulting in accelerated erosion and destructive flooding in the valleys below. Tall larkspur was one of the most tenacious forbs in the original complex, persisting on elevated hummocks held together by its extensive root system. Forest Service management and reduction in livestock from 1910 to 1950 arrested the deterioration, which allowed secondary succession to proceed. Range surveys in 1912, 1936, and 1946 documented improvement in vegetation composition. Ellison compared ungrazed relic areas to ranges grazed by either sheep or cattle. Tall larkspur declined on sheep range, indicating that sheep grazing reduced its density. Thus on sheep ranges, it acts as a decreaser species. On ranges grazed by cattle, its density did not change. It is doubtful that further reduction in live-

Table 3. Ecological status of important poisonous plants.

Pristine species Pre-European	Seral Increaser species	Alien Invader species
Tall larkspur	Locoweed	Halogeton
Western false hellebore	Lupine	St. Johns wort
Water hemlock	Death camas	Poison hemlock
Bracken fern	Snakeweed	Tansy ragwort
Chokecherry	Threadleaf groundsel	Houndstongue
Ponderosa pine	Low larkspur	African rue
Oak spp.	Timber milkvetch	Leafy spurge
	Bitterweed	Yellow star thistle
	Twin leaf senna	Knapweeds
	White snakeroot	
	Orange sneezeweed	

stock grazing, or removal of grazing would decrease larkspur populations.

Sierra larkspur is described as an increaser species in the transition from the fescue prairie to forest in western Canada (Looman 1984). Overgrazing of range and open forests in this area led to an increase in its density, and significant cattle poisoning. With continued heavy grazing, it can be grazed out of the fescue grasslands. In the northern boreal forests and in the tops of the Sierra and Cascade mountains, it occurs along stream banks and willow thickets as a minor component of the climax community.

The low larkspur species form a complex group which introgress into each other. *D. menziesii* DC. was first to be implicated with poisoning of sheep in Montana (Wilcox 1897). *D. bicolor* Nutt. of the northwest was studied thoroughly in early toxicity studies (Chesnut and Wilcox 1901). *D. nelsonii* Greene occurs throughout Utah and Colorado. Presently, *D. nuttalanium* Pritz. which extends northward into Canada, now encompass all of these species, except for *D. bicolor*. All of these species or varieties are considered increaser plants; increasing in density as grazing pressure increases and range condition deteriorates. Thus, improvement in range condition is likely to reduce their density.

The low larkspurs grow early in the spring, flower in May and June, then senesce. They are toxic throughout their growing period but only cause poisoning problems when they grow in dense patches. Normally, they are scattered, but in cool wet springs when grasses are slow to develop, they increase, or are more apparent, thus causing poisoning. Since they dry up in early summer, the management recommendation is to wait until low larkspur matures and other forages are abundant before turning cattle in (Pfister and Gardner 1999).

Plains larkspur (*D. geyerii* Greene) causes most of the poisoning problems in Wyoming and eastern Colorado (Alley and Lee 1970). It is favored by cool, wet springs, when most poisoning occurs before grasses start rapid growth. Anderson larkspur (*D. andersonii* Gray) generally grows as isolated plants on foothill ranges throughout the Intermountain region. It only causes problems when it grows in dense patches on overgrazed ranges where little other forage is available (Fleming et al. 1923).

Locoweeds

Marsh(1909) stated, "The so-called 'locoweed disease' has been a source of most serious complaint for many years, especially from stockmen on the Great Plains east of the Rocky Mountains. While the losses have varied in severity, they have reached such a magnitude as to make the matter of national concern." Marsh surveyed the government files and existing literature and found that locoweed poisoning was often confused with starvation. Marsh's early opinion was "An abundance of good feed would greatly reduce and perhaps eliminate the problem."

White locoweed, or white pointloco (*Oxytropis sericea* Nutt. ex Torr. & Gray), is the most wide-spread locoweed species, ranging on the eastern foothills of the Rocky mountains from Canada to New Mexico, and on mountain tops in the Colorado Plateau and Great Basin. Payne (1957) conducted a study of its' ecology and life history and concluded that white locoweed was found on dry sites, such as rocky ridges and gravely plains. His research found the overriding soil factor influencing the presence of white locoweed was the presence of coarse rock fragments. Soils with greater than 15% of coarse fragments by volume, or very shallow soils with fractured rock beneath favored white locoweed. Soil texture was not definitive, since all soils where it occurred were varieties of loam. He concluded that the coarse rocks allowed for deep percolation of water, which can be accessed by the deep tap root of white locoweed, thus allowing it to survive in droughty sites. Ralphs and Cronin (1987) also found that white locoweed preferred shallow rocky soils in north western Utah, where it exhibits a stress tolerant survival strategy.

Payne's (1957) second objective was to determine the influence of grazing on the abundance of white locoweed. He described 8 fence line contrasts encompassing the same soils, but differing range condition. Basal density index of white locoweed increased as range condition deteriorated from excellent to good condition, but decreased when condition further declined from good to fair. He concluded that white locoweed was a typical increaser species, and was positively correlated with other increaser grasses and forbs, such as prairie junegrass, western wheatgrass, blue grama, needleleaf sedge, fringed sagewort, and phlox.

In germination trials, Payne (1957) reported white locoweed had a higher germination rate on bare soils. He reasoned that bare soils would provide greater scarification from soil particles for the hard seed coat, and that higher soil temperatures would enhance germination. He concluded that range deterioration caused by heavy grazing is a factor in the increase of white locoweed populations.

Weather also influences locoweed populations. Although white locoweed appears to be more persistent and longer-lived than *Astragalus* locoweeds, its populations still cycle. Marsh (1909) observed the white locoweed was particularly abundant in wet years, but nearly disappeared in dry seasons. We found that white locoweed populations in northeast New Mexico and north central Colorado died out in the respective droughts in 1996 and 1997 (Ralphs, unpublished data).

Many of the semi-desert *Astragalus* locoweeds experience extreme population cycles and exhibit opportunistic survival strategies that are independent of grazing pressures. They germinate following autumn rains, remain green over winter, flower in spring, and may continue to grow for 1 or 2 years until the next drought occurs, and the population dies back (Welsh 1989). Barnes (1913) related that the spring of 1888 was a particularly bad loco (probably *A. lentiginosus* Dougl.) season in northern Arizona, and that thousands of locoed horses and cattle died. The previous winter was unusually wet, followed by heavy rains in the early spring. Population outbreaks of *A. lentiginosus* var. *wahweapensis* Welsh occurred every 6 to 8 years in the Henry Mountain area of southeast Utah (Ralphs and Bagley 1988) and were strongly correlated with above-average fall and spring precipitation. Population outbreaks of *A. pubentissimus* T. & G. occurred in eastern Utah in 1918, 1957, 1965 (James et al. 1968), and in 1996 (Ralphs, unpublished data), causing catastrophic livestock loss, yet the plants were practically nonexistent in other years. Standing crop of woolly locoweed (*A. mollissimus* Torr.) averaged 190 kg/ha in a grazing trial at Gladstone NM in 1991 (Ralphs et al. 1993), but totally died out 2 years later.

In summary, most locoweeds are increaser species; increasing as range condition declines. Therefore, improving range condition should reduce their density, though will probably not eliminate the problem. Populations of both *Oxytropis* and *Astragalus* locoweeds cycle with weather. They tend to increase during wet years, and die out during drought.

Milkvetch Species Containing Nitrotoxins

About half of the *Astragalus* species in North America contain nitrotoxins. Unlike the locoweeds, nitrotoxins cause acute poisoning in the form of respiratory failure, and more long-term weakness in the hind legs from demylenization of the spinal cord.

Timber milkvetch (*A. miser* Dougl. ex Hook) is an important poisonous plant of the upper rough fescue grasslands and lower montain areas of British Columbia and Alberta Canada. It also occurs in open areas of woodlands and within the mountain big sagebrush communities southward throughout the Rocky Mountains. MacDonald (1952) stated that overgrazing was undoubtedly the greatest single factor contributing to timber milkvetch poisoning. It is unpalatable when adequate forage is available, but upon depletion of desirable forage, stock will consume large quantities. Later grazing studies verified that cattle avoided eating timber milkvetch when adequate grass was available, but consumed increasing quantities as grass became scarce (Quinton et al. 1989). However in timbered areas, milkvetch was relatively more palatable than pinegrass (Majak et al. 1996). Timber milkvetch poisoning remains a significant poisoning problem in southern Canada even though range conditions have improved.

Red-stem peavine (*A. emoryanus* (Rybd.) Cory) is a winter annual on shortgrass prairies of southern New Mexico and west Texas. In dry years, plants are small and scattered. When precipitation is timely and abundant, seeds germinate and plants grow profusely, often forming a veritable carpet on large areas of rangeland. A population outbreak occurred in the winter of 1974 and spring of 1975 in the region surrounding Roswell New Mexico. Cattle mortality averaged 2–3%, and morbidity averaged 15–20% (Williams et al.1979)

Lupine

Lupines (*Lupinus* spp.) are among the most conspicuous of the flowering plants on foothill and mountain rangelands, with over 100 species in the western US and Canada. Because of hybridization, their taxonomy is difficult. There are 2 toxic syndromes caused by Lupines. Quinolizidine alkaloids cause acute respiratory failure, primarily in sheep. The following species have been responsible for the majority of sheep losses: *L. leucophyllus* Dougl. ex Lindl., *L. leucopsis* Agardh., *L. argenteus* Pursh, *L. sericeus* Pursh (Marsh and Clawson 1916). Many other species contain varying levels of quinolizidine alkaloids and have caused poisoning experimentally, or on isolated occasions. Most of the species that cause sheep poisoning are increaser species. They occur in the native plant communities, but increase with disturbance. In the past, the most widespread disturbance was overgrazing. Areas around watering holes, salt licks, bed grounds, and trail driveways often had dense concentrations of lupine. Lupine species also increase rapidly following fire. The combinations of dense concentrations of lupine and hungry animals that graze indiscriminately set up the conditions of poisoning. Kingsbury (1964) stated, "Almost all cases of loss occur under circumstances which cause the animals to consume large quantities of podded lupine over a brief period of time. These include driving hungry animals quickly through areas heavy with lupine, so that they have little chance to be selective in their grazing; unloading or bedding down hungry animals where lupine is the major vegetation; and trailing animals where snow has covered the grasses, leaving lupines as the only green vegetation available."

The second lupine syndrome is crooked calf disease (Shupe et al. 1967). This occurs when a pregnant cow consumes Lupine species between the 40 to 70th days of gestation. The teratogen stops uterine motility during this period, causing permanent curvature of the spine and limbs in the position the fetus is lying. The teratogenic alkaloid anagyrine has been found in *L. sulphureus, L. sericeus, L. caudatus Kell., L. laxiflorus* Dougl., *L. latifolius* Agardh, and teratogenic piperdine alkaloids have been found in *L. formosus* and *L. arbustus* Dougl. ex Lindl.. The teratogenic alkaloids are generally higher during flowering. Keeler et al. (1977) recommended that pregnant cows should not be given access to lupine during their 40 to 70 day of gestation, especially when the teratogen level was high during flowering or in the seed pod stage.

Good range management and corresponding improved range condition has reduced dense patches of lupine, and the knowledge of the stressful conditions that cause sheep to graze it have greatly reduced the incidence of acute poisoning in sheep. Scattered incidents of crooked calf disease occur infrequently when the management recommendations of Keeler are ignored.

Death Camas

Marsh and Clawson (1922) stated that "Of all the poisonous plants which cause losses to the sheepmen of the western stock ranges, death camas (*Zigadenus* spp.) without a doubt, is the most troublesome." There are over 15 species of death camas distributed throughout the western states, and in many areas grow in great abundance. They contain sterodial glycoalkaloids which cause salavation, nausea and respiratory failuare. Death camas is one of the first plants to begin growth in the spring. Its early growth combined with early turnout of livestock resulted in poisoning. The range management principle to wait until range readiness when grass and other forage was available, greatly reduced poisoning problems.

Although a significant problem in the past, few cases of poisoning occur today. Dense concentrations are seldom found. Most commonly, individual plants are scattered among sagebrush and other vegetation. Furthermore, it is an apparent plant, and sheepmen know to avoid areas where it grows, especially if their sheep are hungry.

Conclusion

Western U.S. rangelands are inherently susceptible to poisonous plant problems because of the wide variety of plants containing toxic compounds. Overgrazing intensified poisoning problems by causing the desirable forage species to decline, allowing less palatable and poisonous species to increase, thereby compelling livestock to consume poisonous plants with resulting catastrophic losses. This has been a hard lesson to learn. Some ranchers are still struggling with the problem. Schuster's (1978) solution still applies, "Good range management is the surest and most economical means of reducing livestock loss to poisonous plants."

However, poisoning still occurs, even on good condition rangelands. Some poisonous plants are part of the pristine or climax plant community and will be abundant on better condition rangelands. If these species are palatable, like tall larkspur, extensive management strategies must be developed to avoid the conditions where cattle are likely to eat them (Pfister et al. 1997, 1993). Abundance of other toxic plants will vary with the climate (locoweeds, milkvetch, low larkspur, lupine, snakeweed). It is necessary to recognize the weather conditions and climatic factors that favor their increase and make other grazing arrangements. In these cases, short-term herbicide control or aversion conditioning may get a rancher through the critical periods.

Literature Cited

Aldous, A.E. 1917. Eradicating tall larkspur on cattle ranges in the national forests. USDA Farmers Bull. 826.

Alley, H.P. and G. Lee. 1970. What can be done about controling larkspur on western rangelands. Down to Earth 26:31–32.

Barnes, W.C. 1913. Western grazing grounds and forest ranges. The Breeder's Gazette, Chicago. 390 pp.

Box, T.W. and J.C. Malechek. 1987. Grazing on the American rangelands. Proc. West. Sec. Anim. Sci. 38:107–115.

Chesnut, V.K. and E.V. Wilcox. 1901. The sotck-poisoning plants of Montana. USDA Bot. Bull. 26.

Dwyer, D.D. 1978. Impact of poisonous plants on western U.S. grazing systems and livestock operations. pp. 13–21, *In:* R.F. Keeler, K.R. VanKampen, and L.F. James (eds), Effects of Poisonous Plants on Livestock. Academic Press. N.Y.

Ellison, L. 1954. Subalpine vegetation of the Wasatch plateau, Utah. Ecol. Mono. 24:80-184.

Fleming, C.E., M.R. Miller, and L.R. Vawter. 1923. The low larkspur (*Delp-hinium andersoni*). Univ. Nev. Agr. Exp. Sta. Bull. 105.

Looman, J. 1984. The biological flora of Canada: 5. *Delphinium glaucum* Watson, tall larkspur. Canada Field-Nauural. 98:345–361.

James, L.F., K.L. Bennett, K.G. Parker, R.F. Keeler, W. Binns, and B. Lindsay. 1968. Loco plant poisoning in sheep. J. Range Manage. 21:360–365.

Keeler, R.F., L.F. James, J.L. Shupe, and K.R. VanKampen. 1977. Lupine-induced crooked calf disease and a management method to reduce incidence. J. Range Manage. 30:97–102.

Kingsbury, J.M. 1964. Poisonous plants of the United States and Canada. Prentice Hall, Englewood Cliffs, N.J.

Marsh, C.D. 1909. The locoweed disease of the plains. USDA Anim. Ind. Bull. 112.

Marsh, C.D. 1913. Stock poisoning due to scarcity of food. USDA Farm. Bull. 536.

Marsh, C.D. and A.B. Clawson. 1916. Lupines as poisonous plants. USDA Bull.405.

Marsh, C.D. and A.B. Clawson. 1922. The stock poisoning death camas. USDA Farm. Bull. 1273.

MacDonald, M.A. 1952. Timber milkvetch poisoning on British Columbia ranges. J. Range Manage. 5:16–21.

Majak, W., L. Stroesser, J.H. Hall, D.A. Quinton, and H. E. Douwes. 1996. Seasonal grazing of Columbia milkvetch by cattle on rangelands in British Columbia. J. Range Manage. 49:223–227.

Nielsen, D.B. and M.H. Ralphs 1988. Larkspur: economic considerations. pp. 119-129 *In:* L.F. James, M.H. Ralphs and D.B. Nielsen (eds), The Ecology and Economic Impact of Poisonous Plants on Livestock Production. Westview Press. Boulder Colo.

Olsen, J.D. 1978. Tall larkspur poisoning in cattle and sheep. J. Amer. Vet. Med. Assoc. 173:762-765.

Payne, G.F. 1957. Ecology and life history of the poisonous plant, white locoweed (*Oxytropis sericea* Nutt.). Ph.D Diss. Texas A&M Univ., College Station, Tex.

Pfister, J.A. and D.R. Gardner. 1999. Consumption of low larkspur (Delphinium nuttallianum) by cattle. J. Range Manage. 52:378–383.

Pfister, J.A., D.R. Gardner and K.W. Price. 1997. Grazing risk on tall larkspur-infested ranges. Rangelands 19:12–15.

Pfister, J.A., M.H. Ralphs, G.D. Manners, K.E. Panter, L.F. James, B.L. Stegelmeier, and D.R. Gardner. 1993. Tall larkspur poisoning in cattle: current research and recommendations. Rangelands 15:157–160.

Quinton, D.A., W. Majak, and J.W. Hall. 1989. The effect of cattle grazing on the growth and miserotoxin content of Columbia milkvetch. J. Range Manage. 42:368–371.

Ralphs, M.H. and V.L. Bagley. 1988. Population cycles of Wahweap milkvetch on the Henry Mountains and seed reserve in the soil. Great Basin Natur. 48:541–547.

Ralphs, M.H. and E.H. Cronin. 1987. Locoweed seed in soil: density, longevity, germination and viability. Weed Sci. 35:792–795.

Ralphs, M.H., D.Graham, R.J. Molyneux, and L.F. James. 1993. Seasonal grazing of locoweeds by cattle in northeastern New Mexico. J. Range Manage. 46:416–420.

Ralphs, M.H., G.D. Manners, J.A. Pfister, D.R. Gardner, and L.F. James. 1997. Toxic alkaloid concentration in tall larkspur species in the western U.S. J. Range Manage. 50:497–502.

Schuster, J.L. 1978. Poisonous plant management problems and control measures on U.S. rangelands. pp. 23–34, *In*: R.F. Keeler, K.R. VanKampen, and L.F. James (eds), Effects of Poisonous Plants on Livestock. Academic Press. N.Y.

Shupe, J.L., W. Binns, L.F. James, R.F. Keeler. 1967. Llupine a cause of crooked calf disease. J. Amer. Vet. Med. Assoc. 151:198–203.

Stoddart, L.A. and A.D. Smith. 1943. Range Management 1st Ed. McGraw-Hill, N.Y.

Stoddart, L.A. and A.D. Smith. 1955. Range Management 2nd Ed. McGraw-Hill, N.Y.

Stoddard, L.A., A.H. Holmgren, and C.W. Cook. 1949. Important poisonous plants of Utah. Utah Agr. Exp. Sta. Special Report 2.

Stoddart, L.A., A.D. Smith and T.W. Box. 1975. Range Management 3rd Ed. McGraw-Hill, N.Y.

Valentine, J.F. 1990. Grazing Management. Academic Press, N.Y.

Welsh, S.L. 1989. *Astragalus L.* and *Oxytropis* DC.: definitions, distributions, and ecological parameters. pp. 3–13, *In:* L.F. James, A.D. Elbein, R.J. Molyneux, C.D. Warren (eds.), Swainsonine and Related Glycosidase Inhibitors. Iowa State Univ. Press. Ames Iowa..

Wilcox, E.V. 1897. Larkspur poisoning of sheep. Mont. Agr. Exp. Sta. Bull. 22.

Williams, M.C., L.F. James and B.O. Bond. 1979. Emory milkvetch (*Astragalus emoryanus*) poisoning in chicks, sheep and cattle. Amer. J. Vet. Res. 40:403-406.

J. Range Manage.
55: 291-300 May 2002

Risk management to reduce livestock losses from toxic plants

JAMES A. PFISTER, FRED D. PROVENZA, KIP E. PANTER, BRYAN L. STEGELMEIER, AND KAREN L. LAUNCHBAUGH

Pfister, Panter, and Stegelmeier are Rangeland Scientist, Research Animal Scientist, and Veterinary Pathologist, respectively, with the USDA-ARS Poisonous Plant Research Laboratory, Logan, Utah 84341. Provenza is Professor, Rangeland Resources Department, Utah State University, Logan, Utah 84322. Launchbaugh is Assistant Professor, Department of Rangeland Resources, University of Idaho, Moscow, Idaho 83844. Pfister's email: jpfister@cc.usu.edu

Abstract

Risk of livestock losses to poisonous plants can be reduced on many ranges through prudent management based on application of existing knowledge. Poisonous plants can be categorized using both acceptability to livestock and a plant's toxic potential. Acceptability encompasses forage qualities such as taste and chemistry (i.e., nutrient and toxin concentrations) and postingestive feedback from an animal's daily and long-term (e.g., body condition) nutritional and toxicological state. Toxic potential reflects aspects of plant chemistry, including seasonal or other changes in concentration or functionality of the toxin(s), and type of toxicity (i.e., acute or chronic). Persistent livestock losses to poisonous plants may indicate that ranges are over-grazed or improperly managed. Aggressive management schemes that employ high stocking rates and grazing intensities may yield greater returns, but may also increase risk if poisonous plants are present. Plants may be ranked according to toxicity and acceptability. Six interrelated categories of plants are discussed: 1) always toxic and acceptable to livestock; 2) always toxic and not acceptable; 3) always toxic and acceptable at certain times; 4) toxic only at certain times and acceptable to livestock; 5) toxic at certain times and unacceptable; and 6) toxic at certain times and acceptable at certain times. Each category involves differing risk and uncertainty. Within this management matrix, strategies for dealing with specific poisonous plants can be customized depending on how much and when the plant is eaten by livestock, and when the plant is most toxic.

Key Words: grazing management, diet selection, poisonous plants

Resumen

El riego de perdidas de ganado por plantas tóxicas puede ser reducido en muchos pastizales a través de un manejo prudente basado en la aplicación del conocimiento existente. Las plantas tóxicas pueden ser categorizadas usando la aceptabilidad por el ganado y un potencial tóxico de la planta. La aceptabilidad incluye las cualidades del forraje tales como sabor y química (nutrientes y concentraciones de toxinas) y la retroalimentación postingestiva del estado nutricional y toxicológico diario y de largo plazo (condición corporal) del animal. El potencial tóxico refleja aspectos de la química de la planta, incluyendo cambios estacionales o de otra naturaleza en la concentración o funcionalidad de la toxina(s) y el tipo de toxicidad (aguda o crónica). Perdidas persistentes de ganado por plantas toxicas pueden indicar que los pastizales están sobreutilizados o manejados impropiamente. Los esquemas agresivos de manejo que emplean cargas animal e intensidades de apacentamiento altas pueden en rendir grandes retornos, pero pueden también incrementar el riesgo si las plantas toxicas están presentes. Las plantas pueden ser clasificadas de acuerdo a la toxicidad y aceptabilidad. Se discuten 6 categorías interrealcionadas de plantas: 1) siempre tóxica y aceptable por el ganado; 2) siempre tóxica y no aceptable ; 3) siempre tóxica y aceptable en ciertas ocasiones; 4) tóxica solo en ciertas ocasiones y aceptada por el ganado; 5) tóxica en ciertas ocasiones y no aceptable y 6) tóxica en ciertas ocasiones y aceptable en ciertas ocasiones. Cada categoría involucra diferente riesgo e incertidumbre. Dentro de esta matriz de manejo, las estrategias para tratar con plantas tóxicas especificas pueden ser personalizadas dependiendo de que tanto y cuando la planta es comida por el ganado y cuando la planta es más tóxica.

"Nature has established patterns originating in the return of events, but only for the most part" (von Leibniz 1703). How closely humans pay attention to the patterns generated by past events, and use that information to understand risk and make rational decisions, often determines success or failure at many of life's junctures, including grazing livestock on ranges with toxic plants. Interestingly, the earliest form of gambling used a type of dice known as an "astragalus" (Bernstein 1996). Rather than a genus of toxic plant, this astragalus was the squarish, virtually indestructible, talus or ankle bone taken from sheep. Games of chance and grazing ranges infested with toxic plants are activities rife with elements of risk and need for thoughtful decision-making. Risk is derived from the Latin *risicare* meaning 'to dare.' Grazing livestock on ranges with poisonous plants should not entail excessive risk, providing managers take the best available information, combine it with personal experience, and make rational choices.

Can all losses to poisonous plants be avoided? Probably not. In spite of advancements such as analyses for toxic compounds,

Invited paper presented at a symposium "Do most livestock losses to poisonous plants result from 'poor' range management?" held in Boise, Ida., February 16, 2000.

Manuscript accepted 25 May 01.

knowledge of consumption patterns, and predictive quantitative models lighting the way, the data for decision-making come from an imperfect or "only for the most part" past. Creatures, plants, and the environment are dynamic and continually interacting, thus, decision-making will never be perfect. Nonetheless, knowledge improves the odds in gambling and grazing. Therefore, research-based decision-making can reduce risks and losses. The objective of this paper is to review management insights and options that may reduce the likelihood of livestock consuming lethal or debilitating amounts of poisonous plants.

A Management Matrix

Poisonous plants can be simultaneously categorized using both **acceptability** to livestock and **toxic potential** (Merrill and Schuster 1978, Fig. 1). We use the term "acceptability" as an expression integrating palatability and preference to avoid the misleading connotations associated with the latter terms (Provenza et al. 1998). Acceptability in this paper encompasses forage qualities such as taste and nutrient or toxin concentrations and postingestive feedback. Postingestive feedback results from an animal's short-term (e.g., within-day energy status) and long-term (e.g., body condition) nutritional (Provenza 1995) and toxicological states (Kingsbury 1978). These forage qualities and feedback therefore directly and indirectly influence forage intake (Provenza et al. 1992, Provenza 1995). Acceptability within the foraging milieu is influenced greatly by an animal's past experiences such as social and environmental interactions (Provenza et al. 1992, 1993). Toxic potential reflects primarily aspects of plant chemistry, including seasonal or other changes in concentration or functionality of the toxin(s), and the type of induced toxicity (e.g., acute or chronic). As we view it, a plant's toxic potential does not involve postingestive feedback or impacts on diet selection.

Management Factors That Influence Risk

Acceptability of toxic plants

Various stressors affect the selection of toxic plants by livestock. When naive animals are introduced into unfamiliar pastures they often ingest more toxic plants than experienced animals on the same ranges (Schuster 1978, Krueger and Sharp 1978). Naive animals first introduced into large pastures usually display increased exploratory behavior and reduced ability to prehend forage (Arnold and Maller 1977) and may simultaneously broaden diet selection thresholds so that normally avoided toxic plants are then eaten (Strydom and Joubert 1983, Kellerman 1987, Fredrickson et al. 2000). Animals are also more likely to eat familiar, toxic plants in unfamiliar settings (Burritt and Provenza 1997). Further, animals under stress may not only ingest more toxic plants, but they may be less able to degrade or tolerate toxins because stress effects various body systems (Freeland and Janzen 1974, Foley et al. 1995, Illius and Jessop 1995). Naive animals initially exposed to some toxic plants may be more vulnerable because of reduced detoxification abilities either from a lack of adapted rumen microbes (Duncan et al. 2000) or a lack of inducible enzyme systems (Galtier 1999). In contrast, experienced animals, including insects, may consume plants containing toxins to which they are partially or completely adapted (Harborne 1988). For example, kangaroos (*Macropus* spp.) tolerate plants containing the highly toxic fluoracetate, yet given a choice between *Gastrolobium* species with high and low concentrations of fluoracetate, kangaroos feed primarily on the plant with lower amounts (Mead et al. 1985).

The acceptability of toxic plants may also be affected by daily levels of energy or nutrient intake. Ruminant livestock react very quickly to short-term nutrient stress and alter diet selection to compensate (Villalba and Provenza 1999a, 1999b). Typical short-term nutrient stress may be triggered by day-to-day excesses or deficits of protein or energy (Cooper et al. 1993, Kyriazakis and Oldham 1993, Villalba and Provenza 2000, Cosgrove and Niezen 2000). Ruminants select for foods higher in protein or energy when eating

	Generally Acceptable to Livestock	**Generally Unacceptable to Livestock**	**Acceptable only at Certain Times**
Always Toxic	*Astragalus* spp. *Oxytropis* spp.	*Hymenoxys odorata* *Senecio* spp. *Asclepias* spp. *Pteridium aquilinum* *Nicotiana* spp. *Hypericum perforatum*	*Halogeton glomeratus* *Pinus ponderosa* *Veratrum* spp. *Solanum* spp. *Zigadenus* spp.
Toxic Only at Certain Times	*Quercus* spp. *Lupinus* spp. *Prunus virginianus* *Cicuta* spp.	*Tetradymia* spp.	*Delphinium* spp. *Conium maculatum*

Fig. 1. A management matrix or framework to simultaneously categorize toxic plants according to both acceptability to livestock and the toxic potential of the plant.

meals low in these nutrients (Villalba and Provenza 1999a, 1999b) or when parasite loads cause metabolic protein deficiency (Cosgrove and Niezen 2000).

Providing supplemental protein or energy may raise the threshold at which animals are intoxicated (Illius and Jessop 1995), allowing animals to ingest more of such toxins as terpenes (Villalba et al. 2000a) and tannins (Villalba et al. 2000b). Supplements may also aid in detoxification once a toxin is ingested. Polyethelene glycol (PEG) binds irreversibly to tannin compounds, and has been successfully added to both feed and water to improve intake of tannin-containing shrubs in the U.S. and in Israel (Priolo et al. 2000, Titus et al. 2000). Activated charcoal adsorbs some plant toxins and allows livestock to increase intake of toxic bitterweed (Poage et al. 2000) and terpene-laden sagebrush (Villalba et al. 2000a).

Long-term nutrient stress or low body condition may also impact diet selection (Tayler 1959). Animals in poor body condition may expand diet selection to include poorly acceptable poisonous plants (Noble et al. 1994, Hancock et al. 1996, Pascual et al. 1999). Conversely, animals in good body condition may restrict intake of poor quality (Foot 1972) or toxic plants.

Either short- or long-term nutrient stress may have other implications for diet selection. First, animals under nutritional stress may be less able to detoxify plant toxins (Illius and Jessop 1995, 1996) and may suffer relatively greater harm from the metabolic effects of the toxin (Freeland and Janzen 1974, Foley et al.1999). Conversely, animals in good body condition that eat toxic plants may have enhanced abilities to tolerate or detoxify some toxins, and may suffer fewer negative postingestive consequences when they consume poisonous plants. Much of the detoxification that occurs in the liver, for example, is inducible, and depends partially on nutrients or metabolites to enhance or facilitate degradation (Illius and Jessop 1995). Detoxification requires additional nutrients to allow body systems to alter toxins and maintain acid-base equilibrium (Illius and Jessop 1995, Jessop and Illius 1997, Foley et al. 1999). For example, low protein diets decrease the amount and activity of detoxification activity in the liver (e.g., cytochrome P450 enzyme system, McLean and McLean 1969).

Poorly nourished animals on some ranges may be stressed by shortages of energy and protein, and be in poor body condition. These animals may experience hunger to such an extent that they increase intake of toxic plants in spite of potentiated negative feedback (Provenza 1995). In this case, one would expect substantial increases in dead or impaired animals (Meyer and Karasov 1991). Some of the catastrophic livestock losses (e.g., Chesnut and Wilcox 1901) that occurred in the late 1800's and early 1900's may be attributed to this type of situation. Interestingly, if animals survive a toxic insult, they may later eat less of the toxic plant because of the potentiated gastrointestinal feedback.

Persistent livestock losses to poisonous plants may indicate that ranges are either degraded or seasonally over-utilized (Merrill and Schuster 1978, Holechek 2002, Ralphs 2002). Even temporary excess utilization may induce livestock losses as grazing animals consume otherwise poorly acceptable poisonous plants (Schuster 1978). Many toxic plants are not highly preferred when other desirable forages are available (Taylor and Ralphs 1992). Even if animals eat small amounts of many poisonous plants, they will suffer few ill effects if other nontoxic forage makes up the majority of their diet because of low amounts of a toxin, and the influence of nutrients as discussed above. Management-intensive grazing systems also generally increase the likelihood of poisonous plant losses when management errors foster short-term over-utilization and/or hungry livestock (Merrill and Schuster 1978). Aggressive management schemes that employ higher stocking rates and grazing intensities may yield greater returns, but also increase risks of poisoning if toxic plants are present; toxic plants may also proliferate under intensive grazing schemes (Holechek 2002).

Why do animals return to eat a plant that has been aversive in the past? Generalist herbivores, including range livestock, have a natural propensity to sample plants in their environment (Westoby 1974). When ingestion of a toxic plant in small amounts causes no or few negative effects, animals are likely to increase consumption of the plant. In addition, many toxic plants contain substantial nutritional value (larkspur: Pfister et al. 1989, locoweed: Ralphs and Molyneux 1989) and provide positive digestive feedback. Both locoweed (*Astragalus lentiginosus* Doug. ex Hook.) and plains larkspur (*Delphinium geyeri* Greene) contain more than 20% crude protein early in the spring (Pfister unpublished observations). Eating some of a toxic plant provides needed nutrients with little toxicity, but increased consumption results in heightened adverse effects because of the dose-response characteristic of many toxins. Partial avoidance or "partial preference" (Day et al. 1998) for a toxic forage would likely result in a grazing animal eating variable but increasing quantities of the forage, until negative feedback from toxins, or excess of nutrients (Provenza 1996) became sufficiently strong to temporarily drive the animal "off" the feed (e.g., larkspur; Pfister et al. 1997a). Each time a toxic forage is eaten without negative consequences, the aversion is weakened and will eventually vanish without additional negative feedback (Lane et al. 1990, Ralphs and Stegelmeier 1998). Aversions are generally dose-dependent, and stronger aversions are formed to compounds that create intense illness (duToit et al. 1991, Ralphs and Cheney 1993, Launchbaugh and Provenza 1994).

Concentration of plant toxins

Management of toxic plants is usually easier and more successful when the toxin is known, and management schemes can be devised to take advantage of seasonal patterns and reduced toxicity (e.g., larkspur: Pfister et al. 1994, Gardner and Pfister 2000). Toxicity of plants is usually related to a specific compound, and in the case of reproductive effects, animals are poisoned at specific physiological stages when they eat plants such as lupine (*Lupinus* spp.) or veratrum (*Veratrum* spp.; Panter et al. 1992, Panter et al. 2002). Pfister et al. (1988, 1997b) identified a toxic window when most deaths from tall larkspur (*Delphinium barbeyi* Huth.) occur, and also determined that an early grazing period is relatively risk-free even though larkspur alkaloid concentrations are high. Cattle typically eat little or no tall larkspur before larkspur elongates flowering racemes, providing a 4 to 6 week low-risk period for grazing. Many producers, however, put cattle into larkspur-infested pastures when the plant is flowering and the risk is higher, even though consumption by cattle usually increases during the flower stage of growth (Pfister et al. 1988). Conversely, late in the grazing season, the risk of grazing tall larkspur-infested ranges is also relatively low; even though cattle eat large quantities of larkspur during the pod stage, once the pods dry out, the alkaloid concentration is low (Gardner and Pfister 2000).

Does the concentration of a particular toxin alter the likelihood that livestock will graze the plant? Many plant toxins, such as alkaloids, are reported to taste bitter (Bate-Smith 1972), whereas tannin-rich plants are typically astringent (Harborne 1988). There are apparently large differences in the taste responses of livestock species to bitter and astringent solutions (Arnold and Hill 1972). Goats appear to be less sensitive to bitter than are sheep, and cattle are least sensitive, whereas cattle are most sensitive and sheep the least sensitive to astringent solutions (Arnold and Hill 1972). These conclusions must be viewed with caution because taste thresholds and postingestive feedback were confounded. Garcia and Hankins (1975) argued that animals inherently avoid most alkaloids because a bitter taste is often linked with toxicity. Some forage plants such as reed canarygrass (Phalaris arundinaceae L.) and certain lupines are unpalatable because of high alkaloid concentrations (Ralphs and Olsen 1987). Nonetheless, Robinson (1979), Glendinning (1994), and Nolte et al. (1994) concluded that alkaloids are not universally repellent to herbivores. Additionally, Molyneux and Ralphs (1992) suggest that some toxic alkaloids are not bitter tasting to livestock.

Pfister et al. (1996a) found that high concentrations of toxic alkaloids in tall larkspurs have essentially no impact on how much tall larkspur is eaten by cattle in the short-term, and that postingestive feedback, not flavor, regulates larkspur intake (Pfister et al. 1990). Cattle that consume high concentrations of tall larkspur alkaloids experience negative postingestive feedback from the nutritious larkspur plants (Pfister et al. 1990), leading to a cyclic pattern of intake with 1 to 2 days of high consumption followed by several days of low or no larkspur intake (Pfister et al. 1997a). Sheep are relatively resistant to poisoning from larkspur alkaloids, and in contrast to cattle, sheep intake of larkspur is negatively affected by higher alkaloid concentrations (Pfister et al. 1996a).

Toxic plants within a management matrix

Always toxic and generally acceptable to livestock

Locoweeds (*Astragalus* and *Oxytropis* spp.) are widespread on rangelands in the western U.S. They contain the toxic indolizidine alkaloid swainsonine. Abundant winter and spring moisture causes rapid growth of locoweed before cool season grasses have initiated growth. Locoweeds are difficult to manage because 1) they are readily eaten by livestock once consumption begins (Ralphs et al. 1993), 2) swainsonine is found in both green and dry material (Ralphs and Molyneux 1989), 3) very low concentrations of swainsonine are toxic if ingested continuously over several weeks (Pfister et al. 1996b), and 4) cattle often select locoweeds in preference to dry dormant forages (Ralphs et al. 1997). Two recently determined characteristics of locoweed have potential to provide management options not recognized in the past. First, swainsonine is quickly excreted from animals once they stop ingesting locoweeds (Stegelmeier et al. 1995a); and second, swainsonine has a "threshold" effect in that once sufficient toxin is consumed, all susceptible enzymes within cells are inhibited, so ingesting more swainsonine does not lead to greater damage or enzyme inhibition (Stegelmeier et al. 1995b). Taken together, these characteristics of swainsonine indicate that it may be possible to formulate "on-off" or cyclic grazing systems such that livestock are grazed for 10-14 days on locoweed-infested ranges, then allowed at least 14 days for detoxification (Stegelmeier, unpublished data). Ingestion of even a small amount of locoweed leads to tissue damage (Van Kampen and James 1970), particularly in the central nervous system where rapid injury may be expected (McFarlane et al. 2000). Lesions may be subtle, however, and resolve quickly once animals are removed from locoweed (Huxtable et al. 1982, Pfister et al. 1996b, Stegelmeier unpublished data). An "on-off" grazing scheme may allow animals to eat some locoweed without hitting an irreversible toxic threshold and thereby avoid permanent tissue damage (Stegelmeier, unpublished observations).

Simple changes in grazing management may provide remarkable benefits with locoweed. Producers in northern Utah graze cattle each summer on high elevation ranges in the Raft River Mountains. For many years, the producers used a rest rotation grazing system, wherein 3 pastures were grazed in sequence, and 1 pasture was rested each summer. Range condition improved over a 10-year period (Ralphs et al. 1984), yet annual losses to locoweed (*Oxytropis sericea* Nutt. in T. & G.) exceeded 20%. Based on observations that most consumption of locoweed occurred after flowering during August, the grazing season was reduced from 71 to 47 days, cattle numbers were increased, and the grazing method was altered to a Merrill 3-herd, 4 pasture system (Ralphs et al. 1984). Changing the grazing system reduced animal density and resulted in less locoweed eaten. As a result, yearly losses declined to about 3%. These simple changes altered diet selection and dramatically reduced losses, as cattle were no longer forced to eat locoweed.

Always toxic and generally not acceptable to livestock

Consumption of toxic plants in this category is usually linked to a management-driven crises such as lack of forage from drought and overgrazing. Periodic droughts occur frequently in much of western North America, and astute livestock producers maintain a forage reserve. The lack of forage contributes significantly to consumption of plants in this category, as these plants are not likely to be eaten to excess unless animals are forced to consume them (Merrill and Schuster 1978). With proper management, losses should be few because of the low acceptability of species such as senecios (*Senecio* spp.), bitterweed (*Hymenoxys odorata* DC.), and milkweeds (*Asclepias* spp.). Losses from species in this category may be linked to consumption of dried toxic material in hay (Baker et al. 1989).

Most of the losses to *Senecio* spp. occur from 3 species: *S. jacobaea* L., *S. longilobis* Benth., and *S. riddellii* T. & G. (Kingsbury 1964). These plants contain pyrrolizidine alkaloids (PA), sometimes in large quantities (e.g., 18% of dry weight, Molyneux and Johnson 1984). Ingestion of even small quantities of PAs causes liver damage that is cumulative over many months (Stegelmeier 1999). Because *Senecio* spp. are generally not acceptable to livestock, cattle and horse losses usually occur from chronic intoxication when they eat small quantities over several weeks when other forage is lacking (Sharrow et al. 1988). Sheep and goats are relatively resistant to senecio poisoning (Stegelmeier 1999). Affected animals may show only mild depression and poor performance until they show clinical signs; once clinical signs are apparent animals rarely recover (Johnson et al. 1985). Losses to *Senecio* spp. can be minimized through proper range management and careful planning for periodic drought (Sharrow et al. 1988) and ensuring that hay is free from senecio.

Milkweeds (*Asclepias* spp.) are perennial forbs that generally are not acceptable to livestock unless other forage is scarce or it is eaten in hay. The principal toxic species in the western U.S. are *A. subverticillata* (Gray) Vail, *A. eriocarpa* Benth., *A. fascicularis* Decne. in DC, and *A. labriformis* Jones. The latter plant contains cardiac glycosides (cardenolides), potent toxins that disrupt heart function. Preventive management entails maintaining rangelands in good condition, and ensuring that hungry livestock do not have access to the plant.

Always toxic and acceptable only at certain times to livestock

Halogeton glomeratus (Bieb) C.A. Mey. is an annual forb that invaded desert rangelands in the western U.S. Halogeton is responsible for large losses of sheep, particularly during the 1940's and 1950's (Young et al. 1999). Halogeton contains sodium and potassium oxalates, which if ingested in high enough amounts cause acute hypocalcemia and impairment of cellular enzymes leading to death. Halogeton is acceptable to cattle and sheep, particularly when sheep are hungry and not thirsty. Acceptability of halogeton also increases when animals are salt deprived (Young et al. 1999). At times, halogeton may be an important forage source for adapted sheep grazing desert rangelands (James and Cronin 1974). Sheep gradually introduced to oxalate-containing plants over several days can be adapted to high oxalate-containing plants with low risk (James and Cronin 1974). Overgrazing of rangelands can lead to plant community disturbance and increased populations of halogeton, resulting in fewer alternative forages and greater likelihood of poisoning. Excessive stocking rates can also increase halogeton losses, as sheep have fewer alternative forage sources (James and Cronin 1974). Virtually all the large losses of sheep to halogeton poisoning can be attributed to poor management (Young et al. 1999).

Ponderosa pine (*Pinus ponderosa* Law.) occurs throughout western North America. Pregnant cattle that ingest pine needles or bark during mid- to late-gestation are at risk of aborting their calves (James et al. 1989). The toxic in pine needles and bark is a diterpene resin acid, isocupressic acid (Gardner et al. 1999). The toxin presumably restricts blood flow to the fetus, leading to fetal stress and abortion (or early birth). Consumption of pine needles by cattle is greatest during cold winter temperatures coinciding with reduced amounts of available forage, either from snow cover or previous grazing (Pfister and Adams 1993, Pfister et al. 1998). Although this implies that cattle eat pine needles from hunger, our observations indicate that this is not the case. We have observed cattle leave winter feeding grounds with hay remaining to forage in stands of pine trees (Pfister, personal observations). Field and pen studies at our laboratory suggest that most cattle acquire a preference for pine needles, even if they initially refuse to eat fresh green needles (Pfister, Villalba, and Provenza, unpublished data). There are several management options that reduce the risk of abortions. First, because cattle are more susceptible to abortions as gestation advances, a prudent management option is to limit cattle exposure to pine trees once cattle have entered the third trimester of gestation (Short et al. 1992). If that is not possible, our observations suggest that risk is reduced by ensuring that the pasture has adequate forage not covered by snow (Pfister, personal observations). If snow cover is too deep, supplementation can substitute for some forage, and be timed to disrupt daily grazing patterns (Adams et al. 1986) to reduce cattle grazing in areas with pine trees (Pfister, personal observations). Because cattle learn to like pine needles, producers with serious losses should also consider changing calving dates from spring to fall, thereby moving late-gestation to summer when cattle are less likely to eat pine needles (Uresk and Paintner 1985). Another option is to delay winter calving into late spring (e.g., May or June). Cattle eat few pine needles as air temperatures warm, snow cover disappears, and cool season grasses begin growth during March and April (Pfister, unpublished observations).

Steroidal veratrum-type alkaloids are found in species of *Veratrum* (false hellebore) and *Zigadenus* (death camas). Ingestion of false hellebore by pregnant sheep on gestation day 14 results in "monkey-faced" or cyclopian lambs with potentially severe craniofacial defects (Binns et al. 1962). Sheep are primarily affected because of their propensity to eat false hellebore (Keeler 1983). Cattle rarely eat the plant, and no special management is needed to reduce consumption. Sheep management to avoid losses to false hellebore is relatively simple (Panter et al. 2002). First, because the window of fetotoxicity is relatively narrow between 14 to 33 days gestation, pregnant animals should not be allowed access to veratrum-infested pastures for about 1 month after the rams are removed (Keeler 1983, Panter et al. 1992). This is not difficult to accomplish because false hellebore is limited in distribution to moist mountain habitats, is easy to identify, and grows in dense patches.

Death camas (*Zygadenus* spp.) is one of the first plants to grow during spring on foothill rangelands, and animals may graze the plant if other forage is lacking. Death camas toxicity is characterized by excessive salivation, frothing around the mouth, nausea and sometimes vomition (Kingsbury 1964, Panter et al. 1987). If the dose is sufficient, muscular weakness is followed by ataxia, recumbency, and death from heart failure. Generally, recognizing the presence of death camas and understanding the acutely toxic nature of the plant will aid in avoiding problems. Losses occur sporadically on foothill ranges. Panter et al. (1987) identified 3 contributing circumstances that contributed to a loss of over 250 sheep in 1 band. First, hungry ewes with lambs were driven through death camas-infested pasture. Second, sheep were bedded near death camas, so the plant was readily available for grazing. Third, the herder stressed the sheep by rapidly driving them from the area, thus increasing the death loss (Panter et al. 1987).

Toxic only at certain times, and generally acceptable to livestock

Lupines (*Lupinus* spp.) are both toxic and teratogenic (i.e., causing birth defects) to livestock (Panter and James 1995). Some lupines contain quinolizidine alkaloids that cause acute respiratory failure in sheep (Kingsbury 1964). Lupine toxicity is seen clinically as a neurologic disease that progresses from depression and lethargy to muscular weakness, collapse, respiratory failure and death (Panter et al. 1999). Birth defects are apparently caused by the effects of 2 different, but related, alkaloids, anagyrine and ammodendrine (Keeler 1978, Panter et al. 1992, Panter et al. 2002). For unknown reasons, cattle are uniquely sensitive to the effects of anagyrine, and ingestion of alkaloid-rich lupines (*Lupinus laxiflorus* Douglas ex

Lindl., *L. caudatus* Kellogg, and *L. sericea* Pursh) causes the condition "crooked calf disease" in cattle (Shupe et al. 1967, Keeler 1989, Panter et al. 1994). Losses of livestock can largely be prevented by understanding 2 interrelated aspects of lupine poisoning. First, the highest concentrations of toxic alkaloids occur in immature lupine plants and seed pods. Anagyrine concentrations are highest (> 5 mg/g) in early growth, and decline to less than 0.5 mg/g after seed shatter, except that concentrations increase in seeds as lupine matures (Keeler 1976). Second, pregnant cattle are susceptible to the teratogenic effects of alkaloids during a window from days 40 to 70 of gestation, occasionally extending to 100 days (Shupe et al. 1967, Panter et al. 1997). Birth defects in cattle can be prevented by using breeding or grazing programs that avoid placing pregnant cattle in lupine-dominated pastures in the first trimester of gestation (Keeler et al. 1977, Panter et al. 1992, Panter et al. 2002). Alternatively, risk can be reduced by allowing only short-term access to lupines by pregnant cattle in some form of rotational grazing (Panter et al. 1999).

Acute toxicity problems from lupine are less common now, but large sheep losses occurred frequently 100 years ago (Chesnut and Wilcox 1901). Deaths occur when livestock, usually sheep, ingest a large amount of seed pods in a short time period (James et al. 1968). This can be prevented by using lupine-free hay and avoiding lupine-dominated ranges when alternative forage is scarce.

Water hemlocks (*Cicuta* spp.) are the most acutely toxic plants in North America; the toxin is a long-chain alcohol named cicutoxin. The large tuber is most toxic, and above ground parts are less toxic. Toxicity of tubers decreases with maturation, and dry stems and leaves are relatively non-toxic (Panter et al. 1988). Green seeds may be toxic (Panter, personal observations), although dry seeds are not toxic to hamsters (Panter, unpublished data). During the spring, the immature plant and tubers are generally well accepted by livestock, particularly cattle, as water hemlock begins growth before other plants (Panter et al. 1988). Affected animals show increased respiration, excessive salivation, nervousness, and tremors progressing to siezures and death (Panter et al. 1996). Most losses to water hemlock can be avoided if livestock producers identify and destroy water hemlock plants along streams, ditches or in swamps. Because tubers are easily exposed in moist soil, and are less toxic when mature, keeping livestock away from the plant during spring when the soil is wet and soft prevents most poisonings.

Oak brush (*Quercus* spp.) includes numerous species in western North America. The primary toxic species are *Q. gambelii* Nutt., *Q. havardii* Rydb., *Q. undulata* Torr., and *Q. turbinella* Greene, but many other species may cause problems at specific times (Basden and Dalvi 1987). The toxins are thought to be polyphenolic tannins (Panciera 1978). Clinical signs include anorexia, rumen atony and constipation, followed by gastroenteritis and diarrhea. Pathological lesions usually involve acute kidney failure (Panciera 1978). Chronic consumption of excessive oak brush can lead to kidney and liver disease; producers in west Texas label such animals "shinneried" because they have become poisoned on shinnery oak (*Q. havardii*). Immature leaves, buds, and recently fallen acorns are typically more toxic and more acceptable to livestock than are mature leaves and dry acorns (Panciera 1978). Cattle can consume large amounts (50% of their diet) of oak brush without serious effects (Dollahite et al. 1966), thus management can be directed toward keeping oak consumption below toxic levels. This is accomplished by ensuring that livestock have adequate amounts of alternative forages during spring when immature leaves are available, and during autumn when acorns fall. When livestock consume large amounts of oak brush, supplementation with calcium hydroxide (10%, Dollahite et al. 1966) or polyethylene glycol (Titus et al. 2000) can help prevent toxicosis.

Toxic only at certain times and generally unacceptable to livestock

Plants that are toxic only at certain times and are generally unacceptable to livestock are relatively easy to manage with proper grazing practices. Snakeweeds (*Gutierrizia* spp.) are widespread low-growing shrubs with a reputation for causing abortions and unthriftiness in cattle (James et al. 1999). The toxin is suspected to be a diterpene acid (Gardner et al. 1999). Snakeweeds are not usually acceptable to cattle unless lack of forage due to drought, overgrazing, or snow cover forces consumption. Management of snakeweed lies primarily in promoting abundance of alternative forage, including residual forage saved for periodic drought.

Horsebrush (*Tetradymia* spp.) is a shrub that begins growth early in spring. Sheep often eat horsebrush when stressed from storms or hunger during movement from winter to summer range (Johnson 1978). *Tetradymia canescens* DC. is reported to be less toxic, but more acceptable to sheep than *T. glabrata* T. & G. (Johnson 1978). The toxin is suspected to be the sesquiterpene, tetradymol (Jennings et al. 1978). Horsebrush causes liver damage with or without secondary photosensitization, and photosensitized animals may subsequently develop a swollen head (Johnson 1978). Toxicity from horsebrush is potentiated by prior consumption of black sagebrush (*Artemisia nova* A. Nels, Johnson 1978), but the mechanism is not known. It is possible that other sagebrush species also potentiate horsebrush toxicity. Losses can largely be avoided by making certain that sheep have adequate feed and do not eat sagebrush before grazing horsebrush-dominated range (Johnson 1978).

Toxic only at certain times and acceptable only at certain times

Poison hemlock (*Conium maculatum* L.) is well accepted by livestock, and may even be addictive (Kingsbury 1964, Panter and Keeler 1989). Piperidine alkaloids in poison hemlock stimulate the central nervous system and cause frequent urination and defecation, dilated pupils, increased heart rate, muscular weakness and trembling and ataxia. This initial stage is followed by depression with further muscular weakness, collapse, and death due to respiratory paralysis (Panter et al. 1988). The alkaloids are also potent teratogens that induce skeletal malformations that are indistinguishable from those caused by lupines (Keeler 1978, Panter et al. 1988).

Poison hemlock contains 5 major alkaloids, of which the most toxic alkaloid is γ-coniceine, (Panter and Keeler 1989). The concentrations and distribution of different alkaloids in poison hemlock are affected by many factors, including environmental changes and plant maturity (Cromwell 1956, Leete and Olson 1972). Drought stress increases total alkaloid concentrations (Fairbairn and Challen 1959). Immature poison hemlock often has a high concentration of γ-coniceine, which may then be converted predominately into coniine during active growth. During flowering, concentrations of γ-coniceine also shift to coniine (Cromwell 1956). Thus, coniine is the major alkaloid in mature plants and seed, whereas γ-coniceine dominates the alkaloid mix in early spring growth and fall regrowth.

The γ-coniceine is about 8 times more toxic than coniine (Bowman and Sanghvi 1963, Panter et al. 1998), and this difference has important management implications. The most critical time of the year to avoid poison hemlock is spring because the plant often appears before other forage has emerged. Green seed pods may be eaten in mid-to-late summer (Panter and Keeler 1989). Poison hemlock also may regrow in fall after seed shatter. Ingestion during fall may cause fetotoxicity in pregnant cattle if they are in the first trimester (days 30–75, Panter et al. 1988). Even though toxicity decreases upon drying, sufficient toxin may be retained to poison livestock (Galey et al. 1992). Thus, if poison hemlock has invaded hay fields, the contaminated hay can poison livestock. Cattle appear to be particularly susceptible because of their acceptance of the plant and their sensitivity to the teratogenic alkaloids (Panter et al. 2002).

Conclusions

There is no question that 'poor' range management contributes to livestock losses from poisonous plants and greatly increases risk of losses. Overgrazing will surely increase the risk of losses to some toxic plants. Notwithstanding, plant-animal interactions are very complex, and as Dwyer (1978) pointed out "we are long past the time when we can pass off poisonous plants as a symptom of an overgrazed range." If the mere presence of toxic plants is not an indication of an overgrazed range, what can we conclude about livestock losses in general on rangelands? Our intuition, and Holechek's (2002) data, suggest that many livestock losses are a direct result of 'poor' management, or management errors. Differences in management may be subtle and difficult to verify, particularly if losses are not catastrophic. Is using an inappropriate grazing system 'poor' management? Is it 'poor' management if livestock producers fail to learn what poisonous plants are present on a range, and then lose animals to poisoning? And, is failure to apply existing knowledge another example of 'poor' management? As Pogo said "we have met the enemy and they are us." Nonetheless, some poisonous plants are acceptable to livestock under many differing circumstances (e.g., locoweeds, larkspurs, lupine), and even very careful managers will have losses to these types of plants. Prudent and judicious management can, however, reduce the risk of such losses, and even allow some poisonous plants to be used as nutritious forages at select times.

Research-based recommendations on poisonous plants have reduced livestock losses to many poisonous plants. Perhaps most noticeable of these reduced losses is in teratology, with marked reductions in losses from such plants as veratrum, lupine, and locoweeds (James 1999). Even so, a new and less experienced generation of livestock producer occasionally forgets the lessons of the past with attendant large losses (Chesnut and Wilcox 1901). In 1997 in Adams County, Washington, more than 4000 calves, or 30% of the population, were born with lupine-induced birth defects (Panter et al. 1999), in part because some livestock producers forgot the harsh lessons learned by an earlier generation. This scenario might be replayed with other toxic plants as experienced range managers and livestock producers are replaced by less-experienced personnel, and as ranches are subdivided or managed by proxy from afar.

New research into potential preventive measures may provide livestock producers with additional tools. Development of vaccines with immunogenic activity against plant toxins in some specific instances may allow animals to eat more of a toxic plant with fewer deaths or production problems (Edgar et al. 1998). Techniques to screen and cull livestock that are susceptible to a specific plant toxin may be practical in the future. Further, genetic heritability may allow producers to breed livestock that are less susceptible to various toxicoses (Launchbaugh et al. 1999, Snowder et al. 2001). For example, the heritability of pulmonary hypertension (high altitude disease) is 78% in yearling bulls, and high altitude disease has decreased substantially because livestock producers determine pulmonary arterial pressure (PAP) in bulls (Will et al. 1975, Schimmel and Brinks 1982). Risk may also be decreased as livestock producers modify diet selection through food aversion learning or other means (Ralphs et al. 2001). Diet selection is a complex issue, but as we understand in greater depth about when and why animals eat specific poisonous plants, management alternatives will emerge that reduce risk. Further, dietary selection is influenced to some extent by inherited characteristics (Launchbaugh et al. 2000), and it may be possible to alter selection for some toxic plants through breeding programs.

The essence of risk management is to use information from the past to avoid similar losses in the future. The past, however, provides only imperfect knowledge. In our view, the risk of livestock losses to toxic plants will likely continue to diminish as knowledge and understanding increase, but risk will never vanish entirely.

Literature Cited

Adams, D.C., T.C. Nelsen, W.L. Reynolds, and B.W. Knapp. 1986. Winter grazing activity and forage intake of range cows in the Northern Great Plains. J. Anim. Sci. 62 :1240–1246..

Arnold, G.W. and J.L. Hill. 1972. Chemical factors affecting selection of food plants by ruminants, p. 71–101. *In:* J.B. Harborne (ed.) Phytochem. Ecol.. Academic Press, London.

Arnold, G.W. and R.W. Maller. 1977. Effects of nutritional experience in early and adult life on the performance and dietary habits of sheep. Appl. Anim. Behav. Sci. 3:5–26.

Baker, D.C., R.A. Smart, M.H. Ralphs, and R.J. Molyneux. 1989. Hound's-tongue (*Cynoglossum officinale*) poisoning in a calf. J. Amer. Vet. Med. Assoc. 194:929–930.

Basden, K.W. and R.R. Dalvi. 1987. Determination of total phenolics in acorns from different species of oak trees in conjunction with acorn poisoning in cattle. Vet. Hum. Tox. 29:305–306.

Bate-Smith, E.C. 1972. Attractants and repellants in higher animals. p. 45–56. *In:* J.B. Harborne (ed.). Phytochemical ecology. Academic Press, N.Y.

Bernstein, P.L. 1996. Against the Gods: the remarkable story of risk. John Wiley and Sons, Inc., N.Y.

Binns, W., L.F. James, J.L. Schupe, and E.J. Thacker. 1962. Cyclopian-type malformation in lambs. Arch. Environ. Health 5:106–108.

Bowman, W.C., and I.S. Sanghvi. 1963. Pharmacological actions of hemlock (*Conium maculatum*) alkaloids. J. Pharm. Pharmacol. 15:1–25.

Burritt, E.A. and F.D. Provenza. 1997. Effect of an unfamiliar location on the consumption of novel and familiar foods by sheep. Appl. Anim. Behav. Sci. 54:317–325.

Chesnut, V.K. and E.V. Wilcox. 1901. The stock-poisoning plants of Montana. USDA Bull. 26. Washington, D.C.

Cooper, S.D.B., I. Kyriazakis, D.H. Anderson, and J.D. Oldham. 1993. The effect of physiological state (late pregnancy) on the diet selection of ewes. Anim. Prod. 56:469A.

Cosgrove, G.P. and J.H. Niezen. 2000. Intake and selection for white clover by grazing lambs in response to gastrointestinal parasitism. Appl. Anim. Behav. Sci. 66:71–85.

Cromwell, B.T. 1956. The separation, microestimation and distribution of the alkaloids of hemlock (*Conium maculatum*). Biochem. J. 64:259–266.

Day, J.E.L., I. Kyriazakis, and P.J. Rogers. 1998. Food choice and intake: towards a unifying framework of learning and feeding motivation. Nutr. Res. Rev. 11:25–43.

Dollahite, J.W., G.T. Housholder, and B.J. Camp. 1966. Effect of calcium hydroxide on the toxicity of post oak (*Quercus stellata*) in calves. J. Amer. Vet. Med. Assoc. 148:908–912.

Duncan, A.J., P. Fructos, and S.A. Young. 2000. The effect of rumen adaptation to oxalic acid on selection of oxalic-acid-rich plants by goats. Brit. J. Nutr. 83:59–65.

du Toit, J.T., F.D. Provenza, and A. Nastis. 1991. Conditioned taste aversions: how sick must a ruminant get before it learns about toxicity in foods. Appl. Anim. Behav. Sci. 30:35–40.

Dwyer, D.D. 1978. Impact of poisonous plants on western U.S. grazing systems and livestock operations. p. 13–21. *In:* Keeler, R.J., K.R. Van Kampen, and L.F. James (eds.). Effects of poisonous plants on livestock. Academic Press, N.Y.

Edgar, J.A., K.A. Than, A.L. Payne, N. Anderton, J. Baell, Y.Cao, P.A. Cockrum, A. Michalewicz, P.L. Stewart, and J.G. Allen. 1998. Towards a commercial vaccine against lupinosis. p. 196–200. *In:* T. Garland and A.C. Barr (eds.). Toxic plants and other natural toxicants. CAB International, Wallingford, Oxon, UK

Fairbairn, J.W. and S.B. Challen. 1959. The alkaloids of hemlock (*Conium maculatum*): distribution in relation to the development of the fruit. Biochem. J. 72:556–561.

Foley, T.D.A., S. McLean, and S.J. Cork. 1995. Consequences of biotransformation of plant secondary metabolites on acid-base metabolism in mammals- a final common pathway? J. Chem. Ecol. 21:721–743.

Foley, W.J., G.R. Iason, and C. McArthur. 1999. Role of plant secondary metabolites in the nutritional ecology of mammalian herbivores- how far have we come in 25 years? p. 130–209. *In:* H.G. Jung and G.C. Fahey, Jr. (eds.). Nutritional Ecology of Herbivores. Amer. Soc. Anim. Sci., Il.

Foot, J.Z. 1972. A note on the effect of body condition on the voluntary intake of dried grass wafers by Scottish Blackface ewes. Anim. Prod. 14:131–134.

Fredrickson, E.L., R.E. Estell, K.M. Havstad, W.L. Shupe, and L.W. Murray. 2000. The effect of feeding ewe lambs a 15% tarbush (*Flourensia cernua* DC) pellet pre- and post-weaning on the subsequent diet selection of tarbush. J. Arid Environ. 44:123–131.

Freeland, W.J. and D.H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Nat. 108:269–289.

Galey, F.D., D.M. Holstege, and E.G. Fisher. 1992. Toxicosis in dairy cattle exposed to poison hemlock (*Conium maculatum*) in hay: isolation of Conium alkaloids in plants, hay, and urine. J. Vet. Diagn. Invest. 4:60–64.

Galtier, P. 1999. Biotransformation and fate of mycotoxins. J. Toxic. Toxin Rev. 18:295–312.

Garcia, J. and W.G. Hankins. 1975. The evolution of bitter and the acquisition of toxiphobia. p. 39–45. *In:* D.A. Denton and J.P. Coghlan (eds.), Olfaction and Taste, Vol. 5. Academic Press, N.Y.

Gardner, D.R. and J.A. Pfister. 2000. Late season toxic alkaloid concentrations in tall larkspur (*Delphinium* spp.) J. Range Manage. 53:331–336.

Gardner D.R., K.E. Panter, and L.F. James. 1999. Pine needle abortion in cattle: metabolism of isocupressic acid. J. Agr. Food Chem. 47:2891–2897.

Gardner, D.R., L.F. James, K.E. Panter, J.A. Pfister, M.H. Ralphs, and B.L. Stegelmeier. 1999. Ponderosa pine and broom snakeweed: poisonous plants that affect livestock. J. Nat. Toxins 8:27–34.

Glendinning, J.I. 1994. Is the bitter rejection response always adaptive? Physiol. Behav. 56:1217–1227.

Hancock, R.D., A.J. Coe, and F.C. de Albite Silva. 1996. Perinatal mortality in lambs in southern Brazil. Trop. Anim. Health Prod. 28:266–272.

Harborne, J.B. 1988. Introduction to ecological biochemistry. 3rd Ed. Academic Press, Inc., San Diego, Calif.

Holechek, J. 2002. Do most livestock losses to poisonous plants result from poor range management? J. Range Manage. in press

Huxtable, C.R., P.R. Dorling, and S.U. Walkley. 1982. Onset and regression of neuroaxonal lesions in sheep with mannosidosis induced experimentally with swainsonine. Acta Neuropathol. 58:27–33.

Illius, A.W., and N.S. Jessop. 1995. Modeling metabolic costs of allelochemical ingestion by foraging herbivores. J. Chem. Ecol. 21:693–719.

Illius, A.W., and N.S. Jessop. 1996. Metabolic constraints on voluntary intake in ruminants. J. Anim. Sci. 74:3052–3062.

James, L.F. 1999. Teratological research at the USDA-ARS Poisonous Plant Research Laboratory. J. Nat. Toxins 8:63–80.

James, L.F. and E.H. Cronin. 1974. Management practices to minimize death losses of sheep grazing halogeton-infested range. J. Range Manage. 27:424–426.

James, L.F., W. Binns, and J.L. Shupe. 1968. Blood changes in cattle and sheep fed lupine. Amer. J. Vet. Res. 29:557–560.

James, L.F., K.E. Panter, B.L. Stegelmeier, D.R. Gardner, and J.A. Pfister. 1999. Principal poisonous plants of the western United States. p. 271–275. *In:* Current Veterinary Therapy 4: Food Animal Practice. Howard, J.L., and R.A. Smith (eds.). W.B. Saunders Co., Philadelphia, Penn.

James, L.F., R.E. Short, K.E. Panter, R.J. Molyneux, L.D. Stuart, and R.A. Bellows. 1989. Pine needle abortion in cattle: a review and report of 1973–1984 research. Cornell Vet. 79:39–52.

Jennings, P.W., S.K. Reeder, J.C. Hurley, J.E. Robbins, S.K Holian, A. Holian, P. Lee, J.A.S. Pribanic, and M. Hull. 1978. Toxic constituents and hepatotoxicity of the plant Tetradymia glabrata (*Asteraceae*). p. 217–228. *In:* Keeler, R.F., K.R. Van Kampen, and L.F. James (eds.). Effects of poisonous plants on livestock. Academic Press, N.Y.

Jessop, N.S. and A.W. Illius. 1997. Modeling animal responses to plant toxicants, p. 243–253. *In:* J.P.F. D'Mello (ed.) Handbook of Plant and Fungal Toxicants. CRC Press, Boca Raton, Fla.

Johnson, A.E. 1978. Tetradymia toxicity- a new look at an old problem. p. 209–216 *In:* Keeler, R.F., K.R. Van Kampen, and L.F. James (eds.). Effects of poisonous plants on livestock. Academic Press, N.Y.

Johnson A.E., R.J. Molyneux, and L.D. Stuart. 1985. Toxicity of Riddell's groundsel (*Senecio riddellii*) to cattle. Amer. J. Vet. Res. 46:577–582.

Keeler, R.F. 1976. Lupin alkaloids from teratogenic and nonteratogenic lupins: III. Identification of anagyrine as the probable teratogen by feeding trials. J. Tox. Environ. Health 1:887–898.

Keeler, R.F. 1978. Reducing incidence of plant-caused congenital deformities in livestock by grazing management. J. Range Manage. 31:355–360.

Keeler, R.F. 1983. Naturally occurring teratogens from plants. p. 161–199. *In:* R.F. Keeler and A. T. Tu (eds.), Handbook of Natural Toxins. Marcel Dekker, Inc., N.Y.

Keeler, R.F. 1989. Quinolizidine alkaloids in range and grain lupins. p. 133–167. *In:* P.R. Cheeke (ed.), Toxicants of Plant Origin. Vol. 1, Alkaloids. CRC Press, Boca Raton, Fla.

Keeler, R.F., L.F. James, J.L. Schupe, and K.R. Van Kampen. 1977. Lupine-induced crooked calf disease and a management method to reduce incidence. J. Range Manage. 30:97–102.

Kellerman, T.S. 1987. Activated charcoal as prophylaxis against sensciosis. p. 70. *In:* Biennial Rep. Vet. Inst., Onderstepoort, So. Africa.

Kingsbury, J.M. 1964. Poisonous plants of the United States and Canada. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Kingsbury, J.M. 1978. Ecology of poisoning, p. 81--91. *In:* R.F. Keeler, K.R. Van Kampen, and L.F. James (eds.), Effects of poisonous plants on livestock. Academic Press, N.Y.

Krueger, W.C. and L. A. Sharp. 1978. Management approaches to reduce livestock losses from poisonous plants on rangelands. J. Range Manage. 31:347–350.

Kyriazakis, I. and J.D. Oldham. 1993. Diet selection in sheep: the ability of growing lambs to select a diet that meets their crude protein (N x 6.25) requirements. Br. J. Nutr. 69:617–629.

Lane, M.A., M.H. Ralphs, J.D. Olsen, F.D. Provenza, and J.A. Pfister. 1990. Conditioned taste aversion: potential for reducing cattle loss to tall larkspur. J. Range Manage. 43:127–131.

Launchbaugh, K.L., and F.D. Provenza. 1994. The effect of flavor concentration and toxin dose on the formation and generalization of flavor aversions in lambs. J. Anim. Sci. 72:10–13.

Launchbaugh, K.L., F.D. Provenza, and J.A. Pfister. 2002. Herbivore response to anti-quality factors in forages. J. Range Manage. In press.

Launchbaugh, K.L., J.W. Walker, and C.A. Taylor. 1999. Foraging behavior: experience or inheritance. p. 28–35. *In:* K.L. Launchbaugh, K.D. Sanders, and J.C. Mosley. (eds.). Grazing behavior of livestock and wildlife. Idaho For. Wildl. and Range Exp. Sta. Bull. No. 70, Moscow, Ida.

Leete, E. and J.O. Olson. 1972. Biosynthesis and metabolism of the hemlock alkaloids. J. Am. Chem. Soc. 94:5472–5477.

McFarlane, I., K.C. Breen, L. DiGiamberardino, and K.L. Moya. 2000. Inhibition of N-glycan processing alters axonal transport of synaptic glycoproteins in vivo. Neurochem. 11:1543–1547.

McLean, A.E.M. and E.K. McLean. 1969. Diet and toxicity. Brit. Med. Bull. 25:278–284.

Mead, R.J., A.J. Oliver, D.R.King, and P.H. Hubach. 1985. The co-evolutionary role of fluoracetate in plant-animal interactions in Australia. Oikos 44:55–60.

Merrill, L.B. and J.L. Schuster. 1978. Grazing management practices affect livestock losses from poisonous plants. J. Range Manage. 31:351–354.

Meyer, M.W. and W.H. Karasov. 1991. Chemical aspects of herbivory in arid and semiarid habitats. p. 167–187. *In:* Palo, T.R., and C.T. Robbins (eds.). Plant defenses against mammalian herbivory. CRC Press, Boca Raton, Fla.

Molyneux, R.J. and A.E. Johnson. 1984. Extraordinary levels of production of pyrrolizidine alkaloids in *Senecio riddellii*. J. Nat. Prod. 47:1030–1032.

Molyneux, R.J. and M.H. Ralphs. 1992. Plant toxins and palatability to herbivores. J. Range Manage. 45:13–18.

Noble, J.W., J.D.B. Crossley, B.D. Hill, R.J. Pierce, R.A. McKenzie, M.. Debritz, and A.A. Morley. 1994. Pyrrolizidine alkaloidosis of cattle associated with *Senecio lautus*. Aust. Vet. J. 71:196–200.

Nolte, D.A., J.R. Mason, and S.L. Lewis. 1994. Tolerance of bitter compounds by an herbivore, *Cavia porcellus*. J. Chem. Ecol. 20:303–308.

Panciera, R.J. 1978. Oak poisoning in cattle. p. 499–506. *In:* Keeler, R.J., K.R. Van Kampen, and L.F. James (eds.). Effects of poisonous plants on livestock. Academic Press, N.Y.

Panter, K.E. and L.F. James. 1995. Alkaloid toxicants and teratogens of plant origin. p. 145–154. *In:* D.L. Gustine and H.E. Flores (eds.), Phytochemicals and Health. Amer. Soc. Plant Physiol. Ser., Vol. 15. Rockville, Md.

Panter, K.E. and R.F. Keeler. 1989. Piperidine alkaloids of poison hemlock (*Conium maculatum*). p. 109–132. *In:* P.R. Cheeke (ed.), Toxicants of Plant Origin. Vol. 1, Alkaloids. CRC Press, Boca Raton, Fla.

Panter, K.E., D.C. Baker, and P.O. Kechele. 1996. Water hemlock (*Cicuta douglasii*) toxicoses in sheep: pathologic description and prevention of lesions and death. J. Vet. Diagn. Invest. 8:474–480.

Panter, K.E., D.R. Gardner, and R.J. Molyneux. 1994. Comparison of toxic and teratogenic effects of *Lupinus formosus*, *L. arbustus,* and *L. caudatus* in goats. J. Nat. Toxins 3:83–93.

Panter, K.E., L.F. James, and D.R. Gardner. 1999. Lupines, poison-hemlock and *Nicotiana* spp: toxicity and teratogenicity in livestock. J. Nat. Toxins 8:117–134.

Panter, K.E., R.F. Keeler, and D.C. Baker. 1988. Toxicoses in livestock from the hemlocks (*Conium* and *Cicuta* spp.). J. Anim. Sci. 66:2407–2413.

Panter, K.E., R.F. Keeler, L.F. James, and T.D. Bunch. 1992. Impact of plant toxins on fetal and neonatal development: a review. J. Range Manage. 45:52–62.

Panter, K.E., M.H. Ralphs, R.A. Smart, and B. Duelke. 1987. Death camas poisoning in sheep: a case report. Vet. Hum. Toxicol. 29:45–48.

Panter, K.E., D.R. Gardner, R.E. Shea, R.J. Molyneux, and L.F. James. 1998. Toxic and teratogenic piperidine alkaloids from *Lupinus, Conium,* and *Nicotiana* species. p. 345–350. *In:* T. Garland and A.C. Barr (eds.), Toxic Plants and Other Natural Toxicants. CAB Intern., Oxon, U.K.

Panter, K.E., D.R. Gardner, C.C. Gay, L.F. James, R. Mills, J.M. Gay, and T.J. Baldwin. 1997. Observations of *Lupinus sulphureus*-induced "crooked calf disease". J. Range Manage. 50:587–592.

Panter, K.E., L.F. James, D.R. Gardner, M.H. Ralphs, J.A. Pfister, B.L. Stegelmeier, and S.T. Lee. 2002. Influence of management strategies on reproductive losses to poisonous plants. J. Range Manage. In press.

Pascual, J.A., S.L. Fryday, and A.D.M. Hart. 1999. Effects of food restriction on food avoidance and risk of acute poisoning of captive feral pidgeons from fonofos-treated seeds. Arch. Env. Cont. Toxicol. 37:115–124.

Pfister, J.A. and D.C. Adams. 1993. Factors influencing pine needle consumption by grazing cattle during winter. J. Range Manage. 46: 386–390.

Pfister, J.A., K.E. Panter, and D.R. Gardner. 1998. Pine needle consumption by cattle during winter in western South Dakota. J. Range Manage. 51:551–556.

Pfister, J.A., F.D. Provenza, and G.D. Manners. 1990. Ingestion of tall larkspur by cattle: separating effects of flavor from postingestive consequences. J. Chem. Ecol. 16:1697–1705.

Pfister, J.A., G.D. Manners, D.R. Gardner, and M.H. Ralphs. 1994. Toxic alkaloid levels in tall larkspur (*Dephinium barbeyi*) in western Colorado. J. Range Manage. 47:355–358.

Pfister, J.A., D.C. Adams, M..J. Arambel, J.D. Olsen, and L.F. James. 1989. Sublethal levels of toxic larkspur: effects on intake and rumen dynamics in cattle. Nutr. Rep. Intern.40:629–636.

Pfister, J.A., G.D. Manners, D.R. Gardner, K.W. Price, and M.H. Ralphs. 1996a. Influence of alkaloid concentration on acceptability of tall larkspur (*Delphinium* spp.) to cattle and sheep. J. Chem. Ecol. 22:1147–1168.

Pfister, J.A., G.D. Manners, M.H. Ralphs, Z.X. Hong, and M.A. Lane. 1988. Effects of phenology, site and rumen fill on tall larkspur consumption by cattle. J. Range Manage. 41:509–514.

Pfister, J.A., F.D. Provenza, G.D. Manners, D.R. Gardner, and M.H. Ralphs. 1997a. Tall larkspur ingestion: can cattle regulate intake below toxic levels? J. Chem. Ecol. 23:759–777.

Pfister, J.A., B.L. Stegelmeier, C.D. Cheney, L.F. James, and R.J. Molyneux. 1996b. Operant analysis of chronic locoweed intoxication in sheep. J. Anim. Sci. 74:2622–2632.

Pfister, J.A., M.H. Ralphs, G.D. Manners, D.R. Gardner, K.W. Price, and L.F. James. 1997b. Early season grazing of tall larkspur- (*Delphinium* spp.) infested rangelands. J. Range Manage. 50: 391–398.

Poage, G.W.III, C.B. Scott, M.G. Bisson, and F.S. Hartmann. 2000. Activated charcoal attenuates bitterweed (*Hymenoxys odorata*) toxicosis in sheep. J. Range Manage. 53:73–78.

Priolo, A. , G.C. Waghorn, M. Lanza, L. Biondi, and P. Pennisi. 2000. Polyethylene glycol as a means for reducing the impact of condensed tannins in carob pulp: effects on lamb growth, preformance, and meat quality. J. Anim. Sci. 78:810–816.

Provenza, F.D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range Manage. 48:2–17.

Provenza, F.D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. J. Anim. Sci. 74:2010–2020.

Provenza, F.D., J.J. Lynch, and J.V. Nolan. 1993. The relative importance of mother and toxicosis affects the acquisition of food aversions in sheep. J. Chem. Ecol. 19:313–323.

Provenza, F.D., J.A. Pfister, and C.D. Cheney. 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. J. Range Manage. 45:36–45.

Provenza, F.D., J.J. Villalba, C.D. Cheney, and S.J. Werner. 1998. Self-organization of foraging behaviour: From simplicity to complexity without goals. Nutr. Res. Rev. 11:199–222.

Ralphs, M.H. 2002. Ecological relationships between poisonous plants and rangeland condition. J. Range Manage. in press.

Ralphs, M.H. and C.D. Cheney. 1993. Influence of cattle age, lithium chloride dose level, and food type in the retention of food aversions. J. Anim. Sci. 71:373–379.

Ralphs, M.H. and R.J. Molyneux. 1989. Livestock grazing locoweed and the influence of swainsonine on locoweed palatability and habituation. p. 39–49. *In:* James, L.F., A.D. Elbein, R.J. Molyneux, and C.D. Warren. (eds.), Swainsonine and related glycosidase inhibitors. Iowa State Univ. Press, Ames, Iowa

Ralphs, M.H. and J.D. Olsen. 1987. Alkaloids and palatability of poisonous plants. p. 78–83. In: USDA Forest Serv. Tech. Rep.

Ralphs, M.H. and B.L. Stegelmeier. 1998. Ability of apomorphine and lithium chloride to create food aversions in cattle. 56:129–137.

Ralphs, M.H., D. Graham, M.L. Galyean, and L.F. James. 1997. Research observation: Influence of overwintering feed regimen on consumption of locoweed by steers. J. Range Manage. 50:250–252.

Ralphs, M.H., D. Graham, R.J. Molyneux, and L.F. James. 1993. Seasonal grazing of locoweeds by cattle in northeastern New Mexico. J. Range Manage. 46:416–420.

Ralphs, M.H., L.F. James, D.B. Nielsen, and K.E. Panter. 1984. Management practices reduce cattle loss to locoweed on high mountain range. Rangelands 6(4):175–177.

Ralphs, M.H., F.D. Provenza, J.A. Pfister, D. Graham, G.C. Duff, and G. Greathouse. 2001. Conditioned food aversion: from theory to practice. Rangelands 23:14–18.

Robinson, T. 1979. The evolutionary ecology of alkaloids. p. 413–448. *In:* G.A. Rosenthal and D.H. Janzen. (eds.), Herbivores: Their Interaction with Secondary Plant Metabolites. Academic Press, N.Y.

Schimmel, J.G. and J.S. Brinks. 1982. Relationships of pulmonary arterial blood pressures and postweaning traits in yearling beef bulls. Amer. Soc. Anim. Sci. West. Sec. Proc. 33:203–205.

Schuster, J.L. 1978. Poisonous plant management problems and control measures on U.S. rangelands. p. 23–34. *In:* Keeler, R.F., K.R. Van Kampen, and L.F. James (eds.). Effects of poisonous plants on livestock. Academic Press, N.Y.

Sharrow, S.H., D.N. Ueckert, and A.E. Johnson. 1988. Ecology and toxicology of Senecio species with special reference to Senecio jacobaea, and Senecio longilobus. pp. 181–196. *In:* L.F. James, M.H. Ralphs, and D.B. Nielsen (eds.). The ecology and economic impact of poisonous plants on livestock production. Westview Press, Boulder, Colo.

Short, R.E., L.F. James, K.E. Panter, R.B. Staigmiller, R.A. Bellows, J. Malcolm, and S.P. Ford. 1992. Effects of feeding ponderosa pine needles during pregnancy: comparative studies with bison, cattle, goats, and sheep. J. Anim. Sci. 70:3498–3504.

Shupe, J.L., W. Binns, L.F. James, and R.F. Keeler. 1967. Lupine, a cause of crooked calf disease. J. Amer. Vet. Med. Assoc. 151:198–203.

Snowder, G.D., J.W. Walker, K.L. Launchbaugh, and L.D. Van Vleck. 2001. Genetic and phenotypic parameters for dietary selection of mountain big sagebrush (*Artemisia tridentata* Nutt. spp. *vaseyana* (Rydb.) Beetle) in Rambouillet sheep. J. Anim. Sci. 79:486–492

Stegelmeier, B.L. 1999. Pyrrolizidine alkaloid toxicosis. p. 281–282. *In:* Current Veterinary Therapy 4: Food Animal Practice. Howard, J.L., and R.A. Smith (eds.). W.B. Saunders Co., Philadelphia, Penn.

Stegelmeier, B.L., L.F. James, K.E. Panter, and R.J. Molyneux. 1995a. Serum swainsonine concentration and α-mannosidase activity in cattle and sheep ingesting *Oxytropis sericea* and *Astragalus lentiginosus* (locoweeds). Amer. J. Vet. Res. 56:149–154.

Stegelmeier, B.L., L.F. James, K.E. Panter, and R.J. Molyneux. 1995b. Tissue and serum swainsonine concentrations in sheep ingesting *Astragalus lentinginosus* (locoweed). Vet. Hum. Toxicol. 37:336–339.

Strydom, J.A. and J.P.J. Joubert. 1983. The effect of pre-dosing *Homeria pallida* Bak. to cattle to prevent poisoning. J. So. Afr. Vet. Assoc. 54:210–203.

Tayler, J.C. 1959. A relationship between weight of internal fat, "fill" and the herbage intake of grazing cattle. Nature 184:2021–2022.

Taylor, C.A. and M.H. Ralphs. 1992. Reducing livestock losses from poisonous plants through grazing management. J. Range Manage. 45:9–12.

Titus, C.H., F. D. Provenza, A. Perevolotsky, and N. Silanikove. 2000. Preferences for foods varying in macronutrients and tannins by lambs supplemented with polyethylene glycol. J. Anim. Sci. 78:1443–1449.

Uresk, D.W. and W.W. Paintner. 1985. Cattle diets in a ponderosa pine forest in the northern Black Hills. J. Range Manage. 38:440–442.

Van Kampen, K.R. and L.F. James. 1970. Sequential development of the lesions in locoweed poisoning. Clin. Toxicol. 5:575–580.

Villalba, J.J. and F.D. Provenza. 1999a. Effects of food structure and nutritional quality and animal nutritional state on intake behaviour and food preferences of sheep. Appl. Anim. Behav. Sci. 63:145–163.

Villalba, J.J. and F.D. Provenza. 1999b. Nutrient-specific preferences by lambs conditioned with intraruminal infusions of starch, casein, and water. J. Anim. Sci. 77:378–387.

Villalba, J.J. and F.D. Provenza. 2000. Postingestive feedback from starch influences the ingestive behavior of sheep consuming wheat straw. Appl. Anim. Behav. Sci. 66:49–63.

Villalba, J.J., F.D. Provenza, and R.E. Banner. 2000a. Influence of macronutrients and medicines on use of toxin-containing foods by sheep and goats. I. Responses to sagebrush. J. Anim. Sci. (In press)

Villalba, J.J., F.D. Provenza, and R.E. Banner. 2000b. Influence of macronutrients and medicines on use of toxin-containing foods by sheep and goats. II. Responses to quebracho tannin. J. Anim. Sci. (In press).

von Leibniz, G.W. 1703. New essays on human understanding. Cambridge Texts in the History of Philosophy, Cambridge University Press, Cambridge, U.K.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Nat. 108:290–304.

Will, D.H., J.L. Hicks, C.S. Card, and A.F. Alexander. 1975. Inherited susceptibility of cattle to high-altitude pulmonary hypertension. J. Appl. Physiol. 38:491–494.

Young, J.A., P.C. Martinelli, R.E. Eckert, Jr., and R.A. Evans. 1999. Halogeton: a history of the mid-20th century range conservation in the intermountain area. USDA Agr. Res. Serv. Misc. Pub. 1553, Washington, D.C.

J. Range Manage.
55:301-308 May 2002

Reproductive losses to poisonous plants: Influence of management strategies

KIP E. PANTER, LYNN F. JAMES, DALE R. GARDNER, MICHAEL H. RALPHS, JAMES A. PFISTER, BRYAN L. STEGELMEIER, AND STEPHEN T. LEE

Authors are Research Scientists, USDA, Agricultural Research Service, Poisonous Plant Research Laboratory, Logan, Utah, 84341.

Abstract

Poisonous plants that impair normal reproductive functions in livestock include *Veratrum californicum* Durand, lupines, ponderosa pine (*Pinus ponderosa* Dougl.), broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. & Rusby), locoweeds(*Astragalus* and *Oxytropis* spp.), selenium-containing forages, phytoestrogenic plants, endophyte-infected grasses and others. In this review we focus on lupines, locoweeds and ponderosa pine needles to demonstrate the broad and diverse effects that poisonous plants have on reproduction. Certain lupines (*Lupinus* spp.) contain quinolizidine and piperidine alkaloids that are fetotoxic and when grazed by pregnant cattle during specific stages of gestation induce skeletal birth defects and cleft palate, "crooked calf disease". Poison-hemlock (*Conium maculatum*) and some *Nicotiana* spp. contain similar alkaloids and induce identical birth defects in cattle, pigs, goats and sheep when ingested at certain stages of gestation. Locoweeds (species of the *Astragalus* and *Oxytropis* genera containing the indolizidine alkaloid swainsonine) interfere with most processes of reproduction when grazed for prolonged periods of time. Animals can recover normal reproductive function if withdrawn from locoweed grazing before severe poisoning occurs. While most animals may recover reproductive function, permanent neurological deficits may preclude normal reproductive behavior. Ponderosa and lodgepole pine needles (*Pinus* spp.) cause abortion in cattle when grazed during the last trimester of gestation. The specific chemical constituents responsible for the abortions belong to a class of compounds called labdane resin acids, including isocupressic acid (ICA), succinyl ICA, and acetyl ICA. Basic management recommendations to reduce reproductive losses to poisonous plants include: (1) keep good records; (2) know what poisonous plants grow on ranges and understand their effects; (3) develop a management plan to provide for alternate grazing in poisonous plant-free pastures during critical times; (4) provide for balanced nutrition, including protein, energy, minerals and vitamins; (5) maintain a good herd health program; (6) integrate an herbicide treatment program to reduce poisonous plant populations or to maintain clean pastures for alternate grazing; and, (7) manage the range for maximum forage production.

Key Words: Poisonous plants, lupine, locoweed, ponderosa pine, reproduction, management

Resumen

Las plantas tóxicas que deterioran las funciones reproductivas normales del ganado incluyen a las siguientes especies: *Veratrum californicum* Durand, "Lupines", "Ponderosa pine" (*Pinus ponderosa* Dougl.), "Broom snakeweed" (*Gutierrezia sarothrae* (Pursh) Britt. & Rusby), "Locoweeds"(*Astragalus* and *Oxytropis* spp.), forrajes que contienen selenio, plantas fitoestrogénicas, zacates infectados con hongos endófitos y otros. En esta revisión nos enfocamos en los "Lupinus", "Locoweeds"y hojas de "Ponderosa pine"para demostrar la amplitud y diversidad de efectos que las plantas tóxicas tienen en la reproducción. Ciertos "Lupines" (*Lupinus* spp.) contienen alcaloides quinolizidina y piperidina que son tóxicos para el feto, y cuando son apacentados por vacas preñadas durante etapas especificas de la gestación inducen a defectos esqueléticos al nacimiento y platosquisis, "enfermedad del becerro encorvado". "Poison-hemlock" (*Conium maculatum*) y algunas especies de *Nicotiana* spp. contienen alcaloides similares y cuando son ingeridos en ciertas etapas de la gestación inducen a defectos al nacimiento idénticos en bovinos, cerdos, caprinos y ovinos. Cuando los "Locoweeds" (especies de los géneros Astragalus and Oxytropis genera que contienen el alcaloide indolizidina swainsonina) son apacentados por largos periodos de tiempo interfieren con la mayoría de los procesos reproductivos. Los animales pueden recobrar sus funciones reproductivas normales si son retirados del "Locoweed" antes de que ocurra una intoxicación severa. Mientras que la mayoría de los animales puede recobrar su función reproductiva, déficit neurológicos permanentes pueden imposibilitar el comportamiento reproductivo normal. Las hojas de "Ponderosa" y "Lodgepole pine" (*Pinus* spp.) causan aborto en los bovinos cuando las apacientan durante el último trimestre de la gestación. Los constituyentes químicos específicos responsables de los abortos pertenecen a una clase de compuestos llamados ácidos resina labdano, incluyendo el acido isocupresico (ICA), ICA sucinil y ICA acetil. Las recomendaciones básicas de manejo para reducir las perdidas reproductivas por plantas tóxicas incluyen: (1) mantener buenos registros; (2) saber que plantas tóxicas crecen en los pastizales y entender sus efectos; (3) desarrollar un plan de manejo para proveer un apacentamiento alternativo en potreros libres de plantas tóxicas durante las épocas criticas; (4) suministrar una nutrición balanceada, incluyendo proteína, energía, minerales y vitaminas; (5) mantener un buen programa de salud del hato; (6) integrar un programa de tratamiento con herbicidas para reducir las poblaciones de plantas tóxicas o para mantener potreros limpios para apacentamiento alterno y (7) manejar el pastizal para obtener la máxima producción de forraje.

Manuscript accepted 26 May 2001.

Lupinus spp.

Lupinus spp. (lupines) contain quinolizidine and piperidine alkaloids that are toxic and teratogenic. Lupines have caused large losses to the sheep and cattle industries in the past and they continue to cause significant losses to the cattle industry in the western U.S. Recent calf losses from congenital birth defects have been reported in Oregon, Idaho, California, Nevada, Montana and Washington from 1992–1997 (personal communications). In 1992, 56% of the calves from a single herd of cows either died or were destroyed because of skeletal malformations and/or cleft palate (Panter et al. 1997). In the spring of 1997 over 4000 calves (> 35% of the calf crop) in Adams County, Washington were destroyed due to lupine-induced crooked calf disease (Dr. Clive Gay, unpublished data, 1997).

The clinical signs of acute poisoning begin with nervousness, depression, grinding of the teeth, frothing of the mouth, relaxation of the nictitating membrane of the eyes, frequent urination and defecation, and lethargy. These signs progress to muscular weakness and fasciculations, ataxia, collapse, sternal recumbency leading to lateral recumbency, respiratory failure, and death. Signs may appear as early as 1 hour after ingestion and progressively get worse over the course of 24–48 hours, even if further ingestion does not occur. Generally, if death does not occur within this time frame, the animal recovers completely if undisturbed (Panter et al. 1994).

More than 150 quinolizidine alkaloids have been structurally identified from genera of the Fabaceae family, including *Lupinus, Laburnum, Cytisus, Thermopsis* and *Sophora* (Kinghorn and Balandrin 1984). Eighteen western U.S. lupine species have been shown to contain the teratogen anagyrine (Fig. 1) with 14 of these containing teratogenic levels (Davis and Stout 1986). Two species, *L. formosus* E. Green and *L. arbustus* Lindley, contain teratogenic levels of the piperidine alkaloid ammodendrine (Fig., 1; Panter et al. 1998). Lupine alkaloids are produced by leaf chloroplasts and are translocated via the phloem and stored in epidermal cells and in seeds (Wink et al. 1995).

Piperidine and quinolizidine alkaloid content and profile vary between lupine species and in individual plants depending on environmental conditions, season of the year and stage of plant growth (Wink and Carey 1994). Alkaloid content (per gram of plant) may be highest during early growth stages, decreasing through the flower stage and concentrating in the maturing seeds. Seed pods are grazed by sheep and were responsible for large losses in the early 1900's (Chestnut and Wilcox 1901). The seed pod stage is a time when pregnant cattle may graze lupines resulting in deformed calf losses (Panter et al. 1997). Teratogenic effects depend on the amount of plant ingested and the concentration of teratogenic alkaloids in the plant. For example if a lupine species contained 2% total alkaloid and 25% of that was anagyrine, research suggests that the cow would need to consume between 2 and 4 gm dry weight of plant material per kg body weight per day over a period of many days (at least 8-10) to cause birth defects (Gardner and Panter 1993). Seed pods usually contain higher levels of the toxins and are often more palatable than other plant parts.

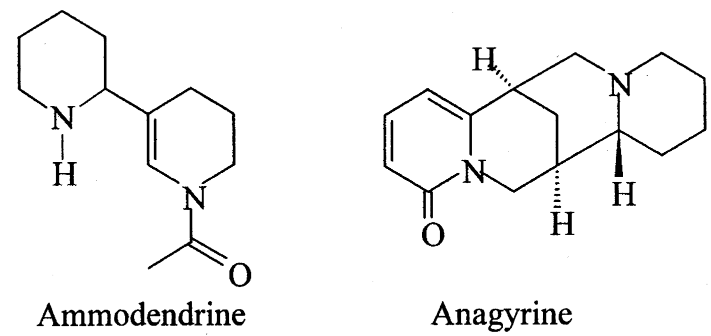


Fig. 1. Two teratogenic alkaloids from *Lupinus* spp. that cause crooked calf disease and cleft palate. Ammodendrine is a piperidine alkaloid and anagyrine is a quinolizidine alkaloid.

Influences of site and elevation on alkaloid content have been described (Carey and Wink 1994). Total alkaloid content decreases as elevation increases and was shown to be 6 times higher in plants at 2,700 m vs plants collected at 3,500 m. This phenomenon persisted even when seedlings from the highest and lowest elevations were grown under identical green house conditions, suggesting evolutionary genetic differences. For many lupines, the time and degree of seeding varies from year to year. Many lupines possess high nutrient qualities and would be considered good range forage if the toxic/teratogenic alkaloids were not present. In some circumstances, lupine is considered good range forage and may be grazed relatively safely. Most deaths have occurred under conditions in which animals consume large amounts of pods or toxic plants in a brief period. This has been reported in sheep, but reports of death losses in cattle are rare. Most losses happen when livestock are driven through an area of heavy lupine growth, unloaded into such an area, trailed through an area where the grass is covered by snow but the lupine is not, or when animals are forced to eat the plants due to over-grazing. Recently, 10 yearling stocker calves died after grazing *Lupinus argenteus* containing predominantly the piperidine alkaloids ammodendrine and N-methyl ammodendrine (Fig. 1; Panter et al. 2001). Poisonings generally occur in the late summer and fall when seed pods are present and lupine remains green after other forage has matured or dried.

Teratogenicity

Those lupine species containing the teratogenic alkaloid anagyrine present significant risks to cattle producers when pregnant cows are allowed to graze on infested pastures during susceptible stages of gestation. The defects are characterized as one or more of the following: arthrogryposis (contracture and malalignment defects of the limbs), scoliosis (spinal column twisting), torticollis (deformed neck), kyphosis (spinal depression) and cleft palate (Panter et al. 1990). While the bone and joint development appears to be normal, the defects are believed to be contracture-type defects resulting from abnormal tendon, muscle and ligament tension induced by a lack of fetal movement during susceptible periods of gestation (Panter et al. 1990).

Susceptible Periods of Gestation

The susceptible periods of gestation have been defined in cattle. The severity and type of the malformations also depend on the alkaloid dosage ingested, the stage of pregnancy when the plants are eaten, and the length of time ingestion takes place. The most critical gestational period for exposure in cattle is 40-70 days, with susceptible periods extending to 100 days (Shupe et al. 1968a, 1968b; Panter et al. 1997). The cleft palate-induction period in cattle was recently defined within gestation days 40–50 (Panter et al. 1998).

Livestock Species Differences

The syndrome known as crooked calf disease associated with lupine ingestion was first reported in the late 1950's and included various skeletal contracture-type birth defects and occasionally cleft palate (Palotay 1959, Wagnon 1960, Binns and James 1961, Shupe et al. 1967a, 1967b). Epidemiologic evidence and chemical comparison of teratogenic and non-teratogenic lupines has determined that the quinolizidine alkaloid anagyrine is the teratogen (Keeler 1973, 1976). A second teratogen, ammodendrine, was found in *Lupinus formosus* and induced similar types of skeletal birth defects (Keeler and Panter 1989). Further research determined that the anagyrine-containing lupines only caused birth defects in cattle and did not affect sheep or goats. No breed predilection or genetic susceptibility to the lupine-induced condition has been determined in cattle. The piperidine-containing lupine *L. formosus* (i.e., no anagyrine) caused birth defects in experimentally treated cattle and goats (Keeler and Panter 1989, Panter et al. 1994). Other piperidine alkaloids and piperidine-containing plants also cause contracture-type birth defects and cleft palate in cattle, sheep, pigs and goats (Panter et al. 1999a, 2000). These studies led to speculation about possible metabolism or absorption differences between cattle and small ruminants. Keeler and Panter (1989) hypothesized that cattle might metabolize the quinolizidine alkaloid anagyrine to a complex piperidine, meeting the structural characteristics determined for the simple teratogenic piperidine alkaloids in poison-hemlock (Keeler and Balls 1978). This was supported by feeding trials with other piperidine alkaloid-containing plants, extracts, and pure compounds. Even though comparative studies supported the hypothesis that the cow may convert the quinolizidine alkaloid anagyrine to a complex piperidine by ruminal metabolism, recent evidence reporting the absorption and elimination patterns of many of the quinolizidine alkaloids, including anagyrine, in cattle, sheep, and goats does not support this theory (Gardner and Panter 1993).

Mechanism of Action

The proposed mechanism of action for lupine-induced malformations and cleft palate in cattle has been elucidated using a goat model. Panter et al. (1990) hypothesized that the mechanism involves a chemically-induced reduction in fetal movement much as one would expect with a sedative, neuromuscular blocking agent, or anesthetic. This proposed mechanism of action was supported by experiments using radio ultrasound where a direct relationship was recorded between reduced fetal activity and severity of contracture-type skeletal defects and cleft palate in sheep and goats. Further research suggests that this inhibition of fetal movement must be over a protracted period of time during specific stages of gestation.

Ultrasonographic studies (Panter et al. 1991) demonstrated that strong fetal movement occurs in the untreated goat at about day 35 of gestation, with extension-type movements of the fetal head and neck. Under the influence of certain teratogenic alkaloids through days 35–41 of gestation, fetuses remained tightly flexed with their chin on the sternum and there were no extension-type movements. Subsequently, the newborn goats from affected does had cleft palates but no other birth defects. Panter and Keeler (1992) suggested that these cleft palates were caused by an alkaloid-induced mechanical interference by the tongue between palate shelves during programmed palate closure times (day 38 in goats; between days 40 to 50 in cows).

In addition to lupines, poison-hemlock and certain *Nicotiana* spp. contain piperidine and quinolizidine alkaloids that are structurally similar to those expected to be toxic and teratogenic. Other potentially teratogenic genera include: *Genista, Prosopis, Lobelia, Cytisus, Sophora, Pinus, Punica, Duboisia, Sedum, Withania, Carica, Hydrangea, Dichroa, Cassia, Ammondendron, Liparia, Colidium* (Keeler and Crowe 1985). Many plant species or varieties from these genera may be included in animal and human diets, but toxicity and teratogenicity are dependent on dose, rate of ingestion, and alkaloid level and composition in the plant.

Prevention and Treatment

Prevention of poisoning and birth defects induced by *Lupinus* can be accomplished by using a combination of management techniques including: 1) identification of lupine species and alkaloid profiles; 2) coordinating grazing times to avoid the most toxic stages of plant growth such as early growth and the seed pod stage; 3) altering breeding times, either advancing, delaying or changing from spring to fall calving; 4) reducing lupine plant density through herbicide treatment; 5) managing grazing to maximize grass coverage; 6) intermittent grazing, allowing short duration grazing of lupine pastures with frequent rotation when cows are first observed grazing lupine plants; and 7) diversify livestock programs to include stockers or sheep grazing on heavily infested pastures. These recommendations have been available for many years and some have been used successfully to reduce losses from lupine (Keeler et al. 1977). Further discussion of these recommendations follow:

1) Identification of toxic lupine species is a key element in managing livestock to avoid losses. Keeler (1976) identified anagyrine as the teratogenic quinolizidine alkaloid in lupine species. Those species with a known history of teratogenic risk include *L. sericeus* Pursh., *L. caudatus* Kellogg, *L. leucophyllus* Douglas ex. Hooker, *L. latifolius J. Agardh, L. sulphureus,* Douglas ex. Lindley, *L. polyphyllus Lindley, L. argenteus* Pursh. *L. formosus* E. Greene, *L. arbustus* Lindley. Wink et al. 1995, identified 14 lupine species containing teratogenic levels of anagyrine. Therefore, identification of lupine species found in pastures and subsequent quantitative analysis to identify chemical composition will determine risk.

2) Chemical analysis of lupines indicate the alkaloid concentration in the vegetative material. Generally, alkaloids are highest in the early growth and seed pod stage (Keeler 1973). The alkaloids are translocated and concentrated in the seeds (Wink and Carey 1994). Thus, avoiding grazing during the early growth stage or seed pod stage of plant growth will minimize risk. This is especially true for the seed pod stage as cattle and sheep are reported to graze seed pods (Chestnut and Wilcox 1901, Keeler et al. 1977, Panter et al. 1997). Proximate analysis of seed pods demonstrated that lupine seeds are a good source of protein (Panter et al. 2001). Cattle and sheep are less likely to graze early growth lupines if there is adequate good quality grass.

3) Research has determined that the susceptible period of gestation for induction of "crooked calf disease" is 40 to 70 days

extending to day 100 in extreme cases (Shupe et al. 1968b; Panter et al. 1997). Therefore, preventing exposure of pregnant cattle to lupines, especially, in the seed pod stage, during the susceptible stages of pregnancy will prevent losses. This can be accomplished by changing breeding schedules the most extreme of which would be changing from a spring calving program to a fall calving program. This has been used in some cases in the northwest where lupine-induced crooked calf disease has been a serious problem.

4) Lupines often grow in localized areas within a pasture. Therefore, herbicide control may be accomplished and economical by spraying limited areas of land where lupine populations are most dense. This method of treatment would reduce numbers of lupine plants and may increase forage production. Control of poisonous plants will allow greater flexibility in management by increasing length of time of grazing, pasture productivity and increase stocking rate. All of these parameters factor into the economic benefit of herbicide use. Effective herbicides include 2,4-D with or without dicamba at 1.2:0.6 kg ai/ha (combination) or 2.2 kg ai/ha (2,4-D alone), or triclopyr at 0.6-1.68 kg ai/ha. Bud to early bloom is the most effective plant growth stage for control (Ralphs et al. 1991). Once control of lupine has been accomplished, management for maximum forage production will help prevent further infestations.

5) Grazing programs and pasture management to maximize grass production is an important method in preventing lupine and other poisonous plant problems. This is especially true during drought years as lupine is a deep rooted legume and often increases in density after drought years.

6) Research has determined that the mechanism of action of lupine induced crooked calf disease is an alkaloid-induced reduction in fetal movement over a protracted period during susceptible stages of gestation. By interrupting this mechanism and removing the pregnant animal from the lupine source for brief periods (3–5 days), normal fetal movement would be restored and malformations could be avoided. Recent research would suggest this intermittent period to be 5–7 days and would depend on close observation of cattle to determine when they start grazing lupine plants. This would require intense management and a relatively clean pasture where cattle could be moved during this intermittent period.

7) Lupine poisoning in sheep was extensive in the early 1900's and large losses were reported, however most of these losses occurred when lupine hay containing many seed pods were fed or sheep were grazed on concentrated patches of lupine (Chestnut and Wilcox 1901). Sheep are more resistant to the toxic effects of lupine than are cattle and malformations are infrequent and not associated with anagyrine. Therefore, sheep could be used as an alternate livestock specie for lupine grazing or potentially sheep could be grazed ahead of cattle to reduce lupine seed pod availability. Also, few reports of overt toxicoses in cattle are reported. Clearly, the malformation issue is the largest economic risk from lupine to cattle producers. Using stockers could potentially utilize lupine infested ranges more efficiently thus avoiding the "crooked calf disease" issue. A combination of grazing stockers on lupine infested pastures and cow-calf pairs on the cleaner pastures could potentially enhance utilization of ranges. By using a combination of these management tools, most losses can be avoided and ranges utilized more efficiently.

When malformed calves are born, decisions must be made as to the disposition of these calves. Severity of malformations often determine the outcome at the time of birth. Calves with severe arthrogryposis, scoliosis, cleft palate etc. should be euthanized soon after birth as they will not be economical to keep and often cannot survive more than a few days. Calves with contractures of the front legs in which they can lock the knee joint will usually straighten up and as long as they can travel with their mother and nurse, will grow relatively normally and can be considered economical to keep.

Locoweeds

Locoweeds, species of *Oxytropis* and *Astragalus* that contain the α-mannosidase inhibitor swainsonine (Fig. 2), reduce reproductive performance in multiple ways when livestock graze these plants for extended periods of time. Most aspects of reproduction are affected, including mating behavior and libido in males, behavioral estrus and conception in females, fetal growth and development and neonatal/maternal behavior. While extensive research has characterized and described histological changes in most organ systems (Van Kampen and James 1970), detailed studies describing the magnitude of physiological problems and mechanisms of action are very limited and therefore further research is needed.

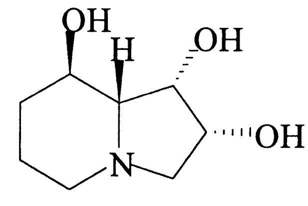


Fig. 2. Swainsonine, the indolizidine alkaloid toxin in locoweeds.

Once animals begin to graze locoweed, measurable increases in serum swainsonine cause an immediate decline in serum α-mannosidase activity. Alpha-mannosidase is an important enzyme in cellular glycoprotein processing, and many reproductive hormones and receptors are glycoproteins. While these measurable changes are diagnostic during the grazing of locoweeds, the rapid clearance of swainsonine from serum ($t_{1/2}$≈.20 hrs) and accompanying recovery of α-mannosidase activity ($t_{1/2}$≈.65 hours) limits serum analysis of these parameters as a reliable test for locoweed exposure if animals have not ingested locoweed in the previous several days (Stegelmeier et al. 1995a, 1995b). Currently, diagnosis of locoweed poisoning relies on history of locoweed ingestion, behavioral changes, loss of condition and, in terminal cases, histological evidence of neurovisceral vacuolation. Histological lesions induced by locoweed ingestion and experimental feeding of purified swainsonine (James et al. 1991, Stegelmeier et al. 1995a, 1995b) have been compared and found to be the same. Lesions appear to develop in a threshold-like fashion since the severity of lesions does not increase at higher locoweed doses (Stegelmeier et al. 1995a, 1995b). Animal tissues that accumulate high swainsonine concentrations (such as liver and kidney) develop lesions more rapidly, and at lower dosages of locoweed, than do other organ systems (such as blood and muscle). Even though α-mannosidase activity recovers quickly, tissue repair and return to normal organ function occur more slowly (Stegelmeier et al. 1999). We would expect this to be true also for the reproductive system.

Effects on Female Reproduction

Locoweeds affect almost every aspect of reproduction in the female, such as estrus behavior, estrous cycle length, ovarian function, conception, embryonic and fetal viability, and maternal/infant bonding (Pfister et al. 1993, Panter et al. 1999b, 1999c).

Locoweed fed to cattle and sheep at various times and dosages temporarily altered ovarian function, increased estrous cycle length, altered breeding behavior and reduced conception rates. Recent feeding trials with locoweeds (*A. mollissimus*, Torr., *A. lentiginosus* Douglas and *O. sericea* Nutt. ex. Torr. and Gray) in cycling ewes demonstrated that after 20 days of locoweed feeding at 10–15% of their diet, estrus was delayed and shortened, conception rates decreased and the number of viable embryos collected from superovulated ewes was reduced (Panter, K. E., unpublished data).

While only a few abnormal morula-stage embryos were collected from ewes fed locoweed for 30 days (Panter, K.E., unpublished data), recent in vitro data demonstrated that swainsonine added to culture media at different concentrations (up to 6.4 μg/ml) did not directly interfere with oocyte maturation (IVM), in vitro fertilization (IVF), or embryo growth and development (Wang et al. 1999). Pregnancy rates were not different from controls when swainsonine-cultured bovine embryos were transferred to recipient cows. This research suggests that the effects of locoweed on early embryo viability and development may not be from primary effects of swainsonine but rather secondary pathways, and result from the effects of locoweed (swainsonine) on maternal aspects of reproduction such as the pituitary/hypothalamic axis where glycoprotein gonadotropins are produced and released.

Mature cycling cows fed *Oxytropis sericea* at 20% of their diet for 30 days showed moderate signs of toxicity. The estrous cycle length increased during locoweed feeding and conception was decreased (Panter et al. 1999c). After feeding stopped, normal estrous cycle length returned relatively soon and cows bred normally, although conception was delayed in some cows (repeat breeders) for up to 3 estrous cycles. In another study cycling heifers fed *O. sericea* equivalent to 3 dosages of swainsonine (0.25, 0.75, and 2.25 mg/kg/day) showed ovarian dysfunction in a dose-dependent pattern (Panter, unpublished data). Heifers receiving the highest dose for 45 days had enlarged ovaries by day 20 of locoweed feeding. Observation of these ovaries by ultrasound suggested that both the luteal phase (observation of corpus luteum) and follicular phase (observation of a follicular cyst) were prolonged and persisted throughout the feeding period (Panter, unpublished data). Within 30 days after locoweed feeding had stopped, ovaries appeared normal via ultrasound, and 15 days later when heifers were necropsied the ovaries were similar in appearance to those of controls.

While gross and microscopic lesions in the dam may resolve quickly after locoweed ingestion ceases, effects on the fetus may be prolonged and severe enough to result in abortion, small and weak offspring at birth, or reduced maternal/infant bonding and impaired nursing ability of the neonate (Panter et al. 1987, Pfister et al. 1993). Locoweed ingestion by pregnant ewes during gestation days 100–130 disrupted normal maternal infant bonding compared to control ewe-lamb pairs (Pfister et al. 1993). Lambs from mothers ingesting locoweed failed to suckle within 2 hours after birth, were slower to stand, and were less vigorous than control lambs. Thus, maternal ingestion of locoweed disrupted the learning ability of their neonatal lambs. Swainsonine is also excreted in the milk and can result in further intoxication of nursing offspring or exacerbate intoxication when offspring begin to graze locoweeds and continue to nurse their locoweed-grazing mothers (James and Hartley 1977, Ralphs et al. 1994). In northern Colorado, Knight and Greathouse (1996) reported that locoweed-intoxicated weanling calves required 64 more days in the feedlot than normal calves to reach slaughter weight and condition. This same group of calves also demonstrated immunological deficiencies and the incidence of respiratory and other diseases and mortality was higher than normal.

Effects on Male Reproduction

The effects of locoweed ingestion are also detrimental to male reproductive function. Panter et al. (1989) reported transient degenerative changes in the seminiferous, epididymal, and vas deferens epithelia after feeding locoweed to yearling rams for 70 days. Clinically, there were changes in behavior, reduced libido, and loss of body condition. There were no gross changes in testicular circumference or tissue appearance but, histologically, there was foamy, cytoplasmic vacuolation in the epithelium of the seminiferous tubules, epididymis and vas deferens and reduced spermatozoa production. Semen contained significantly more abnormal spermatozoa, including retained perinuclear cytoplasmic droplets, detached tails, bent tails and marked decreases in motility. These changes in spermatozoa were transient and by 70 days after locoweed feeding stopped, the rams appeared clinically normal. More recent studies using 2-year-old rams further confirmed these results. Long-term neurological deficits did not reverse, and in some rams intensified, which precluded using these animals for breeding. After withholding locoweed for 60 days, semen parameters appeared normal, but the neurological deficits including proprioceptive defects, tremors and aberrant behavior did not reverse but rather intensified. Over half (5/7) of the treated rams lost weight and became emaciated. All treated rams were euthanized and necropsied (Wang et al. 1998, Panter, unpublished data); histological evaluation of tissues has not been completed.

Ortiz et al. (1997) reported several delayed effects after feeding *Oxytropis sericea* to breeding age ram lambs for 35 days. Subsequently, 35 days after locoweed feeding had stopped, they found reduced sperm motility and decreased scrotal circumference in all treated rams. There was also reduced testosterone responses to a gonadotrophin releasing hormone (GnRH) challenge, suggesting that locoweed affected testicular function. The delayed effect was expected as the normal cycle of spermatogenesis in sheep is about 60 to 70 days. Panter et al. (1989) demonstrated that increased spermatozoa abnormalities peaked after continuous feeding of locoweed for 70 days.

Prevention and Recommendations

While research and field observations have demonstrated that locoweed affects almost every aspect of reproduction in livestock, several questions still need to be answered. How much locoweed can livestock eat, and over what time period, before reproduction declines? What functions are affected first? How long does it take for reproductive function to return to normal once locoweed ingestion stops? When are reproductive effects irreversible? What are the modes of action?

When does neurological dysfunction preclude use of animals for reproduction? Many of these questions are being studied at this time which will provide information that will aid management decisions to improve reproductive performance and allow better utilization of locoweed-infested ranges.

Recent research demonstrated that effects of locoweed on livestock are almost immediate. After one day of experimental feeding of locoweed to cows and sheep, blood serum α-mannosidase activity dropped significantly concomitant to an almost immediate rise in serum swainsonine (Stegelmeier et al. 1995b). Therefore, there is no 100% safe period of grazing locoweed. However, this is not to say that a certain amount of locoweed grazing cannot be tolerated by animals, but decisions must be made based on the livestock programs and sound research-based decisions as to how much locoweed can be grazed before production decreases.

At present, it is recommended that breeding males should not be exposed to locoweeds within 90 days of the breeding season; pregnant animals should be removed from locoweed infested pastures as soon as locoweed ingestion begins; loco-free pastures should be maintained with herbicides as a place to move animals when they start to graze locoweeds; and, breeding females should not be allowed to graze locoweeds for extended periods of time generally more than 2–3 weeks.

Ponderosa Pine and Related Species

Ponderosa pine needles (PN) induce abortion in cattle when eaten during the last trimester of gestation (James et al. 1989, 1994). A labdane resin acid, isocupressic acid (ICA), was identified as the abortifacient compound (Gardner et al. 1994; Fig. 3). Further studies identified 2 other labdane resin acids, succinyl ICA and acetyl ICA, both of which are hydrolyzed in the rumen to ICA (Gardner et al. 1996, 1997). Rumen and liver metabolites have recently been identified but abortifacient activity of the major metabolites have yet to be characterized (Gardner et al. 1999). Pine needles were not abortifacient in goats and sheep nor was ICA abortifacient in goats when administered orally or iv (Gardner, D. R., unpublished data).

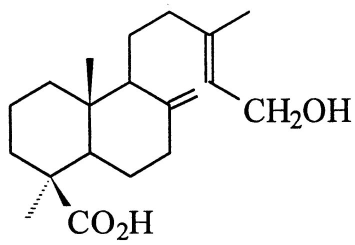


Fig. 3. Isocupressic acid, the labdane resin acid in Ponderosa pine needles responsible for abortions in cattle.

Twenty-three other tree and shrub species found throughout the western and southern states were analyzed for ICA (Gardner et al. 1998, Gardner and James, 1999). Significant levels (>0.5% dry weight of the needles) were detected in *Pinus jefferyi* Grev. and Balf.(Jeffrey pine), *P. contorta* Dougl. (lodgepole pine), *Juniperus scopulorum* Sarg. (Rocky Mountain juniper) and *J. communis* L. (common juniper) and from *Cupressus macrocarpa* Hartw. (Monterey cypress) from New Zealand and Australia. Abortions were induced when lodgepole pine and common juniper containing 0.7% and 2.5% ICA, respectively, were experimentally fed to pregnant cows, inducing abortions in 9 and 3.5 days, respectively (Gardner et al. 1998). This research confirmed field reports of lodgepole pine needle abortion in British Columbia, Canada (France, B., personal communication, 1997). Monterey cypress is known to cause abortions in cattle in New Zealand and Southern Australia and contained ICA levels of 0.89% to 1.24%. The level of ICA in ponderosa pine needles is generally in the range of 0.5% and 1.7% (Gardner et al. 1994, Gardner and James 1999).

Occasional toxicoses from pine needles have been reported in field cases but are rare and have only occurred in pregnant cattle. No toxicity other than abortion in cattle has been demonstrated from ICA or ICA derivatives. However, the abietane-type resin acids in ponderosa pine needles (concentrated in new growth pine tips) were shown to be toxic but not abortifacient at high doses when administered orally to cattle, goats, and hamsters. Pathological evaluations of intoxicated animals included nephrosis, edema of the central nervous system, myonecrosis, and gastroenteritis (Stegelmeier et al. 1996). While abietane-type resin acids may contribute to the occasional toxicoses reported in the field, they do not contribute to the abortions. Most cow losses in the field are associated with difficult parturition or post abortion toxemia due to retained fetal membranes.

Cattle readily graze ponderosa pine needles, especially during the winter months in the western U.S. Pine needle consumption increases during cold weather, with increased snow depth, and when other forage is reduced or unavailable (Pfister and Adams 1993). Cattle are easily averted to green PN using an emetic (lithium chloride) paired with PN consumption, but aversions extinguish if cattle ingest dry needles intermingled with dormant grasses. Further research is underway to determine if cows can be successfully averted from green and dry needles simultaneously.

Recommendations and Prevention

Currently, recommendations to remove pregnant cattle in the last trimester of pregnancy from ponderosa pine-infested pastures or fencing around pine trees are the only preventive measures to ensure no losses from grazing pine needles.

When calves are born premature, some things can be done to improve the chances of calf and cow survival. Calves over 255 days gestation are likely to survive if given colostrum and kept warm and dry. The earlier the calves are born the less likely they are to survive. Cows will have retained fetal membranes and agalactia. Cows will come to their milk in a few days if the calf is encouraged to nurse, however the calf should be supplemented until that time. Generally, the placenta will be expelled in 10 to 15 days post partum if untreated. Oxytocin injection will aid in milk let down and also facilitate loss of the retained placenta. Cows should be monitored daily and if temperature is elevated appropriate antibiotic therapy should be administered. The local veterinarian should be consulted for appropriate treatment of the retained placenta.

Conclusion

In this brief review we have discussed the effects of 3 classes of poisonous plants and their toxins that affect reproductive performance in livestock. While the effects described vary depending on the plant species or livestock species involved, the fact remains that natural toxins from poisonous plants have powerful and often detrimental effects on biological systems and especially reproductive function. These effects on reproduction may be subtle, like those described for locoweeds, before overt toxicosis becomes evident; they may be obvious and dramatic, as described in pine needle abortion in cattle; or the observed effects may be delayed yet dramatic as is the case when offspring are born with severe skeletal defects or cleft palate many months after the poisonous plant was ingested. These effects can be significant and cause large economic losses to livestock producers. Poisonous plant research provides new information and tools to better manage livestock grazing systems thus reducing losses and enhancing product quality. Additional spin-off benefits from research on poisonous plants include the development of animal models for human disease, new techniques and technologies such as antibody-based diagnostic tools (ELISA's) and treatments (vaccines), the discovery of novel compounds and improved management strategies that will enhance animal and human health.

Literature Cited

Binns, W. and L.F. James. 1961. A congenital deformity in calves, similar to "crooked calf disease," has been experimentally produced by feeding heifers lupine and lead. Proc. Western Sec. Amer. Soc. Anim. Prod. 12, LXVI, 1-3.

Carey, D.B. and M. Wink. 1994. Elevational variation of quinolizidine alkaloid contents in a lupine (*Lupinus argenteus*) of the Rocky Mountains. J. Chem. Ecol. 20:849–857.

Chesnut, V.K. and E.V. Wilcox. 1901. The stock-poisoning plants of Montana: A preliminary report. U.S. Dept. of Agr. Bull. No. 26. pp. 100–110. Washington D.C.

Davis, A.M. and D.M. Stout. 1986. Anagyrine in western American lupines. J. Range Manage. 39:29–30.

Gardner, D.R. and L.F. James. 1999. Pine needle abortion in cattle: Analysis of isocupressic acid in North American Gymnosperms. Phytochem. Anal. 10:1–5.

Gardner, D.R. and K.E. Panter. 1993. Comparison of blood plasma alkaloid levels in cattle, sheep and goats fed *Lupinus caudatus*. J. Nat.. Toxins 2:1–11.

Gardner, D.R., K.E. Panter and L.F. James. 1999. Pine needle abortion in cattle: Metabolism of isocupressic acid. J. Agr. Food Chem. 47:2891–2897.

Gardner, D.R., K.E. Panter, L.F. James and B.L. Stegelmeier. 1998. Abortifacient effects of lodgepole pine (*Pinus contorta*) and common juniper (*Juniperus communis*) on cattle. Vet. Human Toxicol. 40:260–263.

Gardner, D.R., R.J. Molyneux, L.F. James, K.E. Panter and B.L. Stegelmeier. 1994. Ponderosa pine needle-induced abortion in beef cattle: Identification of isocupressic acid as the principal active compound. J. Agr. Food Chem. 42:756–761.

Gardner, D.R., K.E. Panter, R.J. Molyneux, L.F. James and B.L. Stegelmeier. 1996. Abortifacient activity in beef cattle of acetyl- and succinyl- isocupressic acid from ponderosa pine. J. Agr. Food. Chem. 44:3257–3261.

Gardner, D.R., K.E. Panter, R.J. Molyneux, L.F. James, B.L. Stegelmeier and J.A. Pfister. 1997. Isocupressic acid and related diterpene acids from *Pinus ponderosa* as abortifacient compounds in cattle. J. Nat. Toxins 6:1–10.

James, L.F. and W.J. Hartley. 1977. Effects of milk from animals fed locoweed in kittens, calves, and lambs. Amer. J. Vet. Res. 38:1263–1265.

James, L.F., K.E. Panter, H.P. Broquist and W.J. Hartley. 1991. Swainsonine-induced high mountain disease in calves. Vet. Human Toxicol. 33:217–219.

James, L.F., R.J. Molyneux, K.E. Panter, D.R. Gardner and B.L. Stegelmeier. 1994. Effect of feeding Ponderosa pine needle extracts and their residues to pregnant cattle. Cornell Vet. 84:33–39.

James, L.F., R.E. Short, K.E. Panter, R.J. Molyneux, L.D. Stuart and R.A. Bellows. 1989. Pine needle abortion in cattle: A review and report of 1973-1984 research. Cornell Vet. 79:39-52.

Keeler, R.F. 1973. Lupine alkaloids from teratogenic and nonteratogenic lupins. II. Identification of the major alkaloids by tandem gas chromatography-mass spectrometry in plants producing crooked calf disease. Teratology 7:31–35.

Keeler, R.F. 1976. Lupin alkaloids from teratogenic and nonteratogenic lupins. III. Identification of anagyrine as the probable teratogen by feeding trials. J. Toxicol. Environ. Health 1:887–889.

Keeler, R.F. and L.D. Balls. 1978. Teratogenic effects in cattle of *Conium maculatum* and Conium alkaloids and analogs. Clin. Toxicol. 12:49–64.

Keeler, R.F. and M.W. Crowe. 1985. Anabasine, a teratogen from the *Nicotiana* genus, pp. 324-333. In: A.A. Seawright, M.P. Hegarty, L.F. James and R.F. Keeler (eds.), Plant Toxicology, Queensland Poisonous Plant Committee, Yeerongpilly.

Keeler, R.F. and K.E. Panter. 1989. Piperidine alkaloid composition and relation to crooked calf disease-inducing potential of *Lupinus formosus*. Teratology 40:423–432.

Keeler, R.F., L.F. James, J.L. Shupe and K.R. Van Kampen. 1977. Lupine-induced crooked calf disease and a management method to reduce incidence. J. Range Manage. 30:97–102.

Kinghorn, A.D. and M.F. Balandrin. 1984. pp. 105–148. *In:* S.W. Pelletier (ed). Alkaloids: Chemical and Biological Perspectives, John Wiley and Sons, N.Y.

Knight, A.P. and G. Greathouse. 1996. Locoweed in northern Colorado: Its effects on beef calves, p. 30. *In:* Locoweed and Broom Snakeweed Research Update. Agr. Exp. Sta., Coop. Exten. Service, College of Agr. and Home Econ., New Mexico State University.

Ortiz, A.R., D.M. Hallford, M.L. Galyean, F.A. Schneider and R.T. Kridli. 1997. Effects of locoweed (*Oxytropis sericea*) on growth, reproduction, and serum hormone profiles in young rams. J. Anim. Sci. 75:3229–3234.

Palotay, J.L. 1959. "Crooked calves". Western Vet. 6:16–20.

Panter, K.E. and R.F. Keeler. 1992. Induction of cleft palate in goats by *Nicotiana glauca* during a narrow gestational period and the relation to reduction in fetal movement. J. Nat. Toxins 1:25–32.

Panter, K.E., D.R. Gardner and R.J. Molyneux. 1994. Comparison of toxic and teratogenic effects of *Lupinus formosus, L. arbustus* and *L. caudatus* in goats. J. Nat. Toxins 3:83–93.

Panter, K.E., D.R. Gardner and R.J. Molyneux. 1998. Teratogenic and fetotoxic effects of two piperidine alkaloid-containing lupines (*L. formosus* and *L. arbustus*) in cows. J. Nat. Toxins 7:131–140.

Panter, K.E., L.F. James and D.R. Gardner. 1999a. Lupines, poison-hemlock and *Nicotiana* spp: Toxicity and teratogenicity in livestock. J. Nat. Toxins 8:117–134.

Panter, K.E., L.F. James and W.J. Hartley. 1989. Transient testicular degeneration in rams fed locoweed (*Astragalus lentiginosus*). Vet. Human Toxicol. 31:42–46.

Panter, K.E., T.L. Wierenga and T.D. Bunch. 1991. Ultrasonographic studies on the fetotoxic effects of poisonous plants on livestock, pp. 589–610. *In:* R.F. Keeler and A.T. Tu, (eds.) Handbook of Natural Toxins: Volume 6, Toxicology of plant and fungal compounds. Marcel Dekker, Inc, N.Y.

Panter, K.E., T.D. Bunch, L.F. James and D.V. Sisson. 1987. Ultrasonographic imaging to monitor fetal and placental developments in ewes fed locoweed (*Astragalus lentiginosus*). Amer. J. Vet. Res. 48:686–690.

Panter, K.E., H.F. Mayland, D.R. Gardner and G. Shewmaker. 2001. Death losses in beef cattle after grazing *Lupinus argenteus* (silvery lupine). Vet. Human Toxicol. 43(5):279-282.

Panter, K.E., T.D. Bunch, R.F. Keeler, D.V. Sisson and R.J. Callan. 1990. Multiple congenital contractures (MCC) and cleft palate induced in goats by ingestion of piperidine alkaloid-containing plants: Reduction in fetal movement as the probable cause. Clin. Toxicol. 28:69–83.

Panter, K.E., D.R. Gardner, L.F. James, B.L. Stegelmeier and R.J. Molyneux. 2000. Natural toxins from poisonous plant affecting reproductive function in livestock, pp.154–172. *In:* A.T. Tu and W. Gaffield (eds.), Natural and Selected Synthetic Toxins: Biological Implications. ACS Symp. Series 745. Amer. Chem. Soc., Washington, D.C.

Panter, K.E., L.F. James, B.L. Stegelmeier, M.H. Ralphs and J.A. Pfister. 1999b. Locoweeds: Effects on reproduction in livestock. J. Nat. Toxins 8:53–62.

Panter, K.E., M.H. Ralphs, L.F. James, B.L. Stegelmeier and R.J. Molyneux. 1999c. Effects of locoweed (*Oxytropis sericea*) on reproduction in cows with a history of locoweed consumption. Vet. Human Toxicol. 41:282–286.

Panter, K.E., D.R. Gardner, C.C. Gay, L.F. James, R. Mills, J.M. Gay and T.J. Baldwin. 1997. Observations of *Lupinus sulphureus*-induced "crooked calf disease". J. Range Manage. 50:587–592.

Pfister, J.A. and D.C. Adams. 1993. Factors influencing consumption of ponderosa pine needles by grazing cattle during winter. J. Range Manage. 46:394–398.

Pfister, J.A., J.B. Astorga, K.E. Panter and R.J. Molyneux. 1993. Maternal locoweed exposure in utero and as a neonate does not disrupt taste aversion learning in lambs. Appl. Anim. Behav. Sci. 36:159–167.

Ralphs, M.H., T.D. Whitson and D.N. Ueckert. 1991. Herbicide control of poisonous plants. Rangelands 13:73–77.

Ralphs, M.H., D. Graham, L.F. James and K.E. Panter. 1994. Locoweed effects on a calf crop. Rangelands 16:35–37.

Shupe, J.L., L.F. James and W. Binns. 1967b. Observations on crooked calf disease. J. Amer. Vet. Med. Assoc. 151:191–197.

Shupe, J.L., W. Binns L.F. James and R.F. Keeler. 1967a. Lupine, a cause of crooked calf disease. J. Amer. Vet. Med. Assoc. 151:198–203.

Shupe, J.L., W. Binns, L.F. James and R.F. Keeler. 1968b. A congenital deformity in calves induced by the maternal consumption of lupin. Aust. J. Agr. Res. 19:335–340.

Shupe, J.L., L.F. James, W. Binns and R.F. Keeler. 1968a. Cleft palate in cattle. The Cleft Palate J. 1:346–354.

Stegelmeier, B.L., L.F. James, K.E. Panter and R.J. Molyneux. 1995b. Serum swainsonine concentration and α-mannosidase activity in cattle and sheep ingesting *Oxytropis sericea* and *Astragalus lentiginosus* (locoweeds). Amer. J. Vet. Res. 56:149–154.

Stegelmeier, B.L., R.J. Molyneux, A.D. Elbein and L.F. James. 1995a. The comparative pathology of locoweed, swainsonine, and castanospermine in rats. Vet. Pathol. 32:289–298.

Stegelmeier, B.L., D.R. Gardner, L.F. James, K.E. Panter and R.J. Molyneux. 1996. The toxic and abortifacient effects of Ponderosa pine. Vet. Pathol. 33:22–28.

Stegelmeier, B.L., L.F. James, K.E. Panter, M.H. Ralphs, D.R. Gardner, R.J. Molyneux and J.A. Pfister. 1999. The pathogenesis and toxicokinetics of locoweed (*Astragalus* and *Oxytropis* spp.). J. Nat. Toxins 8:35-45.

Van Kampen, K.R. and L.F. James. 1970. Pathology of locoweed (*Astragalus lentiginosus*) poisoning in sheep, Sequential development of cytoplasmic vacuolation in tissues. Pathol. Vet. 7:503–508.

Wagnon, K.A. 1960. Lupine poisoning as a possible factor in congenital deformities in cattle. J. Range Manage. 13:89–91.

Wang, S., G.R. Holyoak, K.E. Panter, G. Liu, R.C. Evans and T.D. Bunch. 1998. Resazurin reduction assay for ram sperm metabolic activity measured by spectrophotometry. Proc. Soc. Exp. Biol. Med. 217:197–202.

Wang, S., K.E. Panter, G.R. Holyoak, R.J. Molyneux, G. Lin, R.C. Evans and T.D. Bunch. 1999. Development and viability of bovine preplacentation embryos treated with swainsonine in vitro. Animal Reprod. Sci. 56:19–29.

Wink, M. and D.B. Carey. 1994. Variability of quinolizidine alkaloid profiles of *Lupinus argenteus* (Fabaceae) from North America. Biochem. Syst. Ecol. 22:663–669.

Wink, M., C. Meibner and L. Witte. 1995. Patterns of quinolizidine alkaloids in 56 species of the genus *Lupinus*. Phytochemistry 38:139–153.

J. Range Manage.
55:309-311 May 2002

Halogeton grazing management: historical perspective

JAMES A. YOUNG

The author is Range Scientist, USDA, Agricultural Research Service, 920 Valley Road, Reno, Nev. 89512.

Abstract

Halogeton [*Halogeton glomeratus* (Bieb.) C. A. Mey], is a fleshy, annual, herbaceous species that was accidentally introduced into the western U. S. during the 20th century. Because it is highly poisonous to sheep (*Ovis aries*), this rather diminutive herb became the center of attention for biological research on Intermountain rangelands during the 1950s. Grazing management for halogeton involves procedures to prevent accidental poisoning of the grazing animals, and management to encourage the density and vigor of competing perennial vegetation to biologically suppress halogeton. Halogeton became most abundant in salt desert rangelands and the lower elevation portions of the sagebrush (*Artemisia*)/bunchgrass zone. In the sagebrush zone the introduced perennial crested wheatgrass [*Agropyron desertorum* (Fisher) Schultes] was widely planted to both suppress halogeton and to provide alternative forage for livestock. In the salt deserts, the management of native chenopod shrubs was the key to suppressing halogeton. The key species in salt deserts was the highly preferred semi-woody species winterfat [*Krascheninnikova lanata* (Pursh) A. D. J. Meeuse & Smit]. In many parts of the Intermountain region, halogeton has declined in importance because of the reduced importance of the range sheep industry and improved range condition. In the south central Great Basin, halogeton is still considered a serious problem.

Key Words: Salt deserts, poisonous plant, plant ecology

Searching in 1934 for plants for the USDA, Forest Service herbarium, Ben Stahmann and S. S. Hutchings first collected halogeton [*Halogeton glomeratus* (Bieb.) C. A. Mey] southeast of Wells, Nev. (Young et al. 1999). It took a considerable period of time for the new collection to be identified. When it was finally identified as Halogeton there was virtually nothing in the scientific literature concerning the characteristics of the species. It took much longer to arrive at a species name for the plant. The first choice was *H. sativa* (L.) C. A. Mey, which would place the origin of the introduction in North Africa or Spain. Eventually, it was decided by international experts in taxonomy of the Chenopodiaceae that *H. glomeratus* was the correct taxon. The distribution of the species was roughly indicated as Middle Asia east of the Caspian Sea.

Manuscript accepted 30 May 01.

Resumen

El "Halogeton" [*Halogeton glomeratus* (Bieb.) C. A. Mey], es una especie herbácea anual carnosa que fue introducida accidentalmente al oeste de los Estados Unidos durante el siglo 20. Debido a que es altamente tóxica para los ovinos (*Ovis aries*), en la década de los años 50 esta diminutiva hierba vino a ser el centro de atención de la investigación biológica de los pastizales Intermontanos. El manejo del apacentamiento para "Halogeton" involucra procedimientos para prevenir el envenenamiento accidental de los animales en apacentamiento y el manejo para promover la densidad y vigor de la vegetación perenne competitiva para suprimir biologicamente el "Halogeton". El "Halogeton" vino a ser mas abundante en los pastizales desérticos salados y en las porciones de baja elevación de la zona de "Sagebrush" (*Artemisia*)/pastizal amacollado. En la zona del "Sagebrush"el zacate perenne introducido "Crested wheatgrass" [*Agropyron desertorum* (Fisher) Schultes] fue ampliamente plantado para suprimir el "Halogeton" y proveer una alternativa forrajera para el ganado. En los desiertos salados, el manejo de los arbustos nativos Chenopodiaceos fue la calve para suprimir el "Halogeton". La especie calve en los desiertos salados fue la especie semi-leñosa altamente preferida "Winterfat" [*Krascheninnikova lanata* (Pursh) A. D. J. Meeuse & Smit]. En muchas partes de la región intermontana el "Halogeton" ha disminuido en importancia debido a la reducida importancia de la industria ovina en pastizales y el mejoramiento de la condición de los pastizales. En la Gran Cuenca sur central el "Halogeton" `todavía es considerado un serio problema.

First Reported Toxicity

By chance, the first reported poisoning of sheep by halogeton occurred near Wells, Nev. (Young et al. 1999). Nick Goicoa lost 160 head from a band of sheep in November 1942. C. H. Kennedy of the Nevada Department of Agriculture made a postmortem and found the stomach filled with leaves he thought were mountain mahogany (*Cercocarpus ledifolius* Nutt.). Kennedy sent the stomach material to C. E. Fleming, Chair of the Department of Range Management at the University of Nevada. Fleming compared the recovered material with herbarium specimens and correctly identified the plant as halogeton.

Fleming sent his assistant Fred Harris, to Wells to investigate the apparent halogeton poisoning (Young et al. 1999). With the help of local sheep herders, Harris was able to identify several other fairly large scale losses that previously occurred in halogeton patches, but were not connected with the invasive weed. L. M. Burge of the Nevada Department of Agriculture launched a survey of the area infested around Wells and was amazed to discover the exotic species occurred over much of northern Nevada.

M. R. Miller (1943), an agricultural chemist at the University of Nevada, published in Science that dried sample of halogeton herbage contained total oxalates equivalent to 19% (later determined as high as 20%) anhydrous oxalic acid. The poisonous agent of halogeton had been identified. Professor Miller initially used a gold pan to recover the oxalate crystals.

Eco-physiology of Halogeton

The range sheep industry became very alarmed about the potential danger from the newly recognized poisonous plant. After World War II, research was initiated on many aspects of the ecology and toxicity of halogeton. When it was discovered that halogeton infestations existed in California, Utah, Idaho, and Wyoming, the research became regional in nature. National publicity about what was termed the "killer" weed brought USDA, Agricultural Research Service (ARS) into the fight against halogeton (Young 1988). Initially, many of the ARS scientists working on halogeton were transferred from Forest Service Experiment Stations.

The autecology of halogeton was enumerated as an annual species that was highly adapted, but not restricted to salt affected soils. Individual plants were capable of tremendous seed production. It became apparent that halogeton was not a highly competitive species, but essentially populations exploded in the ecological void left by repeated disturbance such as livestock trails, un-surfaced roads that were periodically graded, trampled areas near watering points or corrals and most significantly in rangeland areas denuded by excessive grazing (Young et al. 1999). Halogeton had a competitive advantage in that leachate from its herbage concentrated salts on the soil surface (Kinsinger and Eckert 1961). In time, the salt concentrations prohibited the establishment of plants other than halogeton.

Lack of understanding the nature of the dimorphic seeds produced by halogeton and their inherent germination ecology was to interact with subsequent management strategies. Early in the autecological studies of halogeton it was noted that both black and brown seeds were produced by the same plant (Tisdale and Zappettini 1953). The black seeds proved to be highly germinable. The seed consisted of a tightly coiled embryo with a minimal covering. Germination started almost as soon as the seeds were moistened. The brown seeds had very low or no germinations (Cronin 1973). Many people made the assumption that the brown seeds were obviously immature and therefore not viable. This led to the assumption that all halogeton seeds would germinate in a given year with no persistent seedbank. Therefore, if a given crop of halogeton was entirely prevented from setting seed the plant could be eradicated. M. C. Williams (1960) determined that brown seeds were produced first by halogeton plants and shorter day lengths induced black seed formation. A long term, regional study of the longevity of buried black and brown halogeton seeds confirmed the brown seeds (brown because of retained bracts) remained viable and germinable in the soil for almost 10 years (Robocker et al. 1969). Halogeton seeds had both simulations and continuous germination strategies.

Halogeton Control Measures

The initial approach to halogeton infestations was to attempt to eradicate the poisonous pest (Young et al. 1999). It was soon determined that infestations were much too extensive to make eradication feasible. The Nevada Department of Agriculture, under the direction of L. M. Burge, launched an extensive halogeton control program using weed oil and the relatively new herbicide 2,4-D [(2,4-dichlorophenoxy) acetic acid]. Both herbicides were very effective in killing halogeton, but unless the weed was replaced with a desirable perennial plant, halogeton reappeared the next year. Re-infestation came from the large seedbanks of brown seeds.

Halogeton Biological Suppression

In 1933, a wildfire burned several hundred acres of degraded sagebrush range east of Wells, Nev. (Young et al. 1999). J. H. Robertson was conducting research on range revegetation for the Intermountain Forest and Range Experiment Station of the Forest Service. Robertson borrowed an old drill and towed it around the burn with his pickup, seeding representative soil types to crested wheatgrass [*Agropyron desertorum* (Fisher) Schultes]. Halogeton invaded the burned area. Robertson took range managers and ranchers on tours of his meandering seeding showing how the perennial grass suppressed halogeton.

The Bureau of Land Management (BLM), USDI, launched a massive program of halogeton suppression through seeding crested wheatgrass. Seedings ranged in area from small patches to a single seeding of 15,000 acres (6,000 ha) (Mathews 1986). This program was encouraged by Marion Clawson when he was the Director of the BLM. He correctly saw halogeton as the symptom of the true problem which was a vastly overgrazed range resource. Crested wheatgrass seeding enlarged the forage base. The technology necessary to make perennial grass seedings successful came from a dynamic group of talented researchers that included A. C. Hull, Jr., Jerry Klump, A. P. Plummer, and J. H. Robertson (Young and MacKenzie 1985).

Unfortunately, crested wheatgrass is not adapted to salt affected soils. Attempts to seed halogeton infested sites on the margins of the salt deserts resulted in failure (Young et al. 1999). The lack of adapted plant material for revegetation in the salt deserts was a major stumbling point in the entire halogeton program.

Winterfat

The native plant species that was closely tied to negative aspects of halogeton invasion was winterfat [*Krascheninnikovia lanata* (Pursh) A.D.J. Meeuse & Smit]. In an environment where most shrubs are not highly preferred by domestic livestock, winterfat was a significant exception. It has been suggested that winterfat is the plant that made domestic livestock possible in the Great Basin (Young and Sparks 1985).

Winterfat is a key forage species in salt desert communities. The browse of this semi-woody species is highly preferred by domestic livestock during the winter months. Winterfat is a component species of many plant communities in the salt deserts (Billings 1945). It is best known for the extensive, near mono-specific plant communities it forms on certain soils in the deserts (Gates et al. 1956). These expanses of nearly pure winterfat constituted excellent winter ranges.

Winterfat communities historically were not subject to stand renewal by wildfires because of a lack of herbaceous vegetation to carry fires. The relatively dense monocultures were subject to natural catastrophic stand renewal caused by outbreaks of native insects (Young et al. 1999). In the Great Basin, winterfat often is found growing under near truly arid conditions where the annual depth of wetting in the soil profile may be less than 25 cm. Winterfat is often growing in a very fragile environmental setting. The classic management formula for winterfat winter ranges is to remove livestock in the early spring while there is still sufficient soil moisture available to allow for growth and replenishment of carbohydrate reserves for fall flowering.

Unfortunately, many winterfat communities were excessively grazed and once halogeton was introduced it rapidly colonized any openings in winterfat communities (Eckert 1954). This remains a very serious problem in the central Great Basin. It is further complicated by the exotic annual cheatgrass (*Bromus tectorum* L.) replacing halogeton on some of the winterfat sites.

Management of Grazing Animals

Much of what is known about managing livestock to prevent halogeton poisoning has been developed by the Poisonous Plant Research Unit of USDA, ARS, located at Logan, Utah. Lynn F. James, the research leader for the Poisonous Plant Laboratory, and his associates have contributed much of the literature concerning halogeton intoxication of herbivores and livestock management strategies (Young et al. 1999). James and Cronin (1974) offered the following management points to minimize range sheep losses from halogeton poisoning: 1) avoid over grazing that creates habitat for halogeton, 2) develop grazing management programs that result in improving range condition, 3) reduce grazing pressure during droughts, 4) avoid late spring grazing that injures native perennials, 5) supply adequate water, 6) observe the sheep and know what they are grazing, 7) allow time for rumen microorganisms to adapt to oxalates, 8) introduce animals to halogeton-infested areas gradually, 9) do not unload animals from trucks into halogeton patches unless there is supplemental feed and water, 10) never allow hungry animals to graze in large, dense patches of halogeton, and 11) do not trail thirsty animals into watering places surrounded by halogeton without food supplement. The continued use by the Great Basin range sheep industry of non-resident herders, often from countries with vastly differing environments, has contributed to the occurrence of halogeton poisoning (Ralphs and Sharp 1988). Adequate training of such herders is often hampered by language barriers.

Present Status of Halogeton

The range of halogeton continues to expand (Young et al. 1999). It is now found east of the Missouri River and in Canada on the northern Great Plains (see Young et al. 1999 for maps of the progression of halogeton spread over time). In the Great Basin, halogeton has largely declined in importance except for the previously mentioned continued colonization of winterfat stands. The range sheep industry has greatly declined. This decline in sheep numbers, coupled with greatly improved grazing management, has resulted in improved range condition in many salt desert winter ranges.

Halogeton has faced increased competition from more vigorous native vegetation and from competing exotic annuals. Barbwire Russian thistle (*Salsola paulsenii* Litv.) has invaded much of the Great Basin and it overlaps in ecological requirements with halogeton to a greater extent than Russian thistle (*S. targus* L.) (Young and Evans 1979). The invasion of the upper portions of the salt desert ranges by cheatgrass has also contributed to the decline in the distribution and abundance of halogeton (Young and Tipton 1990).

The general decline in the range sheep industry in the Great Basin can not be blamed only on halogeton poisoning. Labor cost, predation and economic factors also contributed to the reduction in sheep, but for individual operators who suffered large death losses, halogeton poisoning was very significant.

Literature Cited

Billings, W. D. 1945. The plant associations of the Carson desert region, western Nevada. Bulter Univer. Botany Studies 7:89–123.

Cronin, E. H. 1973. Pregermination treatment of black seed of halogeton. Weed Sci. 21:125–127.

Eckert, R. E., Jr. 1954. A study of competition between whitesage and halogeton in Nevada, J. Range Manage. 7:223–225.

Gates, D., L. A. Stoddart, and C. W. Cook. 1956. Soil as a factor influencing plant distribution on the salt deserts of Utah. Ecol. Monogr. 26:155–175.

James, L. F. and E. H. Cronin. 1974. Management practices to minimize death losses of sheep grazing halogeton infested ranges. J. Range Manage. 27:424–426.

Kinsinger. F. E. and R. E. Eckert, Jr. 1961. Emergence and growth of annual and perennial grasses and forbs in soils altered by halogeton leachate. J. Range Manage. 14:194-197.

Mathews, W. L. 1986. Early use of crested wheatgrass seeding in halogeton control. pp 27–28. *In:* K. L. Johnson (ed.) Crested Wheatgrass Symposium. Utah State Univ., Logan, Utah.

Miller, M. R. 1943. *Halogeton glomeratus,* poisonous to sheep. Sci. 97:227–229.

Ralphs, M. H. and L. A. Sharp. 1988. Management to reduce livestock loss from poisonous plants. pp. 391–407 *In:* L. F. James, M. H. Ralphs, and D. B. Nielson (eds.) The Ecology and Economic Impacts of Poisonous Plants on Livestock Production. Westview Press, Boulder, Colo.

Robocker, W. C., M. C. Williams, R. A. Evans, and P. J. Torell. 1969. Effect of age, burial, and region on germination and viability of halogeton seeds. Weed Sci. 17:63–65.

Tisdale, E. W. and G. Zappettini. 1953. Halogeton studies on Idaho ranges. J. Range Manage. 6:225–236.

Williams, M. C. 1960. Biochemical analyses, germination, and production of black and brown seed of *Halogeton glomeratus*. Weeds 8:452–461.

Young, J. A. 1988. The public response to the catastrophic spread of Russian thistle (1880) and halogeton (1945). Agr. History 62:122–130.

Young, J. A. and R. A. Evans. 1979. Barbwire Russian thistle seed germination. J. Range Manage. 32:390–394.

Young, J. A. and D. McKenzie. 1982. Rangeland drill. Rangelands 4:108–113.

Young, J. A. and B. A. Sparks. 1985. Cattle in the cold desert. Utah State Univer. Press, Logan, Utah

Young, J. A. and Tipton, F. 1990. Invasion of cheatgrass into arid environments of the Lahontan Basin. pp 37–41 *In:* McArthur, E. D., Romney, E. V., Smith, S. D., and Tueller, P. T. (eds.) USDA, Forest Service, Gen. Tech. Report INT-276, Ogden, Utah.

Young, J. A., P. C. Martinelli, R. E. Eckert, Jr., and R. A. Evans. 1999. Halogeton. Misc. Publ. 1553. Agr. Res. Serv., USDA, Washington, D. C.

Book Reviews

Natural Resources Management Practices: A Primer. By Peter F. Ffolliott, Luis A. Bojorquez-Tapia, and Mariano Hernandez-Narvaez. 2001. Iowa State University Press, Ames, Iowa. 237 p. US $52.95 hardbound. ISBN 0-8138-2541-5.

Effective management of natural resources requires comprehensive approaches to solving problems. Natural resource managers must consider whole ecosystems in making decisions, because the consequences of not doing so could be serious. The authors of *Natural Resources Management Practices: A Primer* state that the purpose of this book is to "introduce natural resource management practices that are used to achieve societal goals and objectives to students enrolled in college curricula focusing on natural resources management, conservation ecology, and environmental sciences." They present a comprehensive approach to how we should manage our natural resources, emphasizing sustainability, "guiding and organizing the use of natural resources on the land to provide desired goods and services without harming soil and water resources, or detrimentally affecting the environment."

In 14 chapters, this book emphasizes the relationship of multiple-use management to ecosystem-based management. The authors utilize a wide range of resource literature in attempting to form a clear and concise approach to manage our natural resources. The approach can be perceived as a summary of various other more in-depth works in natural resource sciences, which could be difficult for the beginner to understand.

The subjects of this book include all the aspects of natural resources including the management and practices involved with watershed and water, rangelands, timber, agroforestry, wildlife, fisheries, outdoor recreation, wilderness, fire and pests, soil conservation, rehabilitation of disturbed lands, integrated pest management, and research. The discussions of these topics often include how different nations or projects are dealing with solving the issues of concern related to the particular subject; for example, the chapter on watershed and water management practices examines different water harvesting systems used by the United States, Western Australia, and Israel.

Five appendices are included. The appendices are: *English to metric conversions, plot studies, statistical methods, computer simulation models, and geographic information systems.* The contents of the appendices are well written and help the reader understand natural resources and how they are applied. These appendices are helpful largely due to their versatility and potential interdisciplinary use, in both science and business applications.

Natural Resource Management Practices: A Primer succeeds partially in the authors' attempt to cover such a broad amount of subject matter. In only 237 pages it may down play the complexity of natural resources management and may be inadequate in the presentation of some subjects. One example of this inadequacy is in the authors' description of grazing systems in which only one diagram is provided to demonstrate a four-block balanced rotational system, and no diagrams are provided to describe the other grazing systems mentioned. The use of various diagrams in this instance, and in others, would greatly have aided the understanding of most individuals reading this book as part of an introductory course. There is also little explanation of animal-units and little mention of how to calculate the varying animal demands for forage and water.

The chapter on fire and pest management, however, is effective in describing to the reader the Fire-Danger Rating System indices of the USDA Forest Service, how it is used, and control practices for both fire and pests. One problem with this chapter is the lack of clear statement of the importance of fire in maintaining ecosystems where it was part of its natural ecology. Techniques of prescribed burning and suppression techniques are covered in good detail.

Natural Resources Management Practices: A Primer was written as a textbook for students in biological sciences who are interested in natural resources management. It was meant to be a general reference for professionals involved in managing natural resources, and to private individuals who deal with those professionals. Because of its broad approach to the subject, this book is well suited to be used by newcomers who are beginning a course of study in natural resources, and as a light introduction for people working with professionals. It may be too elementary to be of great use as a field guide for professionals in natural resource fields. The greatest value of this book is its inclusion of fairly recent developments in natural resources and its related fields such as computer mapping, geographic information systems, and integrated pest management. Its discussion of the uses of these developments in management is its greatest strength.—*Chase W. Metzger,* Washington State University, Pullman, Washington.

Grassland Resource Assessment for Pastoral Systems By Peter S. Harris. 2000. FAO. Rome. 150 p. ISBN 92-5-10437-2.

Grassland Resources Assessment for Pastoral Systems is a detailed guideline of the assessment process. Each aspect of assessment, analysis, modeling and presentation is covered clearly and comprehensively. Harris deals well with "those involved in the design and execution of pastoral projects and others dealing with traditional, extensive livestock production," balancing the them effectively. The book is organized into 7 chapters which progress through the assessment process for grassland systems. This progression ultimately leads to the practical inclusion of computer modeling, particularly the use of Resource Assessment for Pastoral Systems (RAPS), demonstrating its effectiveness and usefulness in the case studies.

An introduction to grasslands, their locations worldwide, past and present pressures, and the changes that have affected them are presented in Chapter 1. Grasslands are defined clearly and this definition is maintained throughout. Consideration of as many variables as possible is particularly emphasized, as assessment should incorporate unique circumstances and interpretations.

In Chapter 2, Harris examines various models and management systems used in pastoral systems. Grazing resource management and development are discussed involving grassland condition, grassland dynamics and implications for sustainable development. Box 3 (Pg. 11) provides a useful illustration of different strategies for matching forage supply and livestock forage requirements. Harris uses a number of examples and strategies for irregular forage supplies and other extreme situations such as drought.

Chapter 3 presents a detailed description of the information required for grassland and livestock resource assessment. This chapter includes sources of information, socio-economic conditions, government policies, and services and infrastructure that need to be considered. Chapter 3 also provides a guideline to giving general descriptions of the development or project areas and the identification and classification of land units and forage resources.

Assessors are made aware that the information obtained can override the technical opportunities available. Some livestock statistics, some other uses of grazing lands, and issues of data quality are also provided. Harris notes both incorrect uses of data such as "single year data sets," and generalization of yield data, consequences they may have, and ways to avoid them. He highlights the importance of local knowledge and identifying development options in the scope of socio-economic limits.

Chapter 4 details development assessment and grazing management options. An initial description of the impacts that have occurred, and are still occurring, on grassland condition and the environment are initially outlined. Forage/livestock relationships are interpreted, using both dry matter (DM) and metabolisable energy (ME). Reference is made to the shortcomings in the use of both DM and ME. Harris discusses livestock carry capacity and patterns. He emphasizes the non-equilibrium nature of grassland systems and its importance in the interpretation of results gathered. A discussion of development potential assessment follows. Chapter 4 concludes with an explanation of design and implementation of environmentally sustainable management systems. Harris makes is clear that there can be both successes and failures due to both human error and unpredictable natural catastrophes.

The essence of the book lies in Chapter 5. Harris uses the techniques previously outlined in the description of a model grassland and livestock resources for development planning. This description includes the criteria that needs to be met in order for Resources Assessment for Pastoral Systems (RAPS) to be a practical tool. As Harris suggests, few models are available that are specific for grasslands and forage production systems. The traditional use of DM balance is considered inaccurate by the author, and the causes of this inaccuracy are briefly outlined. The chapter concludes with a guide to using RAPS to represent a current pastoral system.

In Chapter 6 Harris presents practical applications and outputs of the model in case studies from China, Sudan, Ethiopia and Bhutan. Maps, figures and graphs illustrate the usefulness and clarity of the model and its outputs. These case studies highlight the need to adapt to different circumstances, and to the "heterogeneity of pastoral environments."

Chapter 7 is a neat summary of the book, tying together previous discussions. Harris again discusses the importance of using this book as a basis of assessment, and the need to assess each situation uniquely. A summary of each of the case studies follows, examining the different situations and how RAPS was adapted for them.

Harris covers a wide scope of techniques available to obtain the most useful and unbiased assessment. The assessment process is thorough and informative. A strong aspect of the book is the author's ability to discuss the advantages and disadvantages from the point-of-view of both an assessor and operator. The overall focus of the book is the implementation of computer models, particularly RAPS, into grassland assessment. Harris gives a detailed description of the model and supports it with case studies from around the globe.

The book places particular emphasis on the importance of encompassing political, economic, social and environmental issues. This approach is slowly gaining recognition. The assessment of a grassland system and implementation of a project is a complex process involving a large number of variables. Ultimately the book should be a useful reference and will provide valuable support to technical assist projects for which the Food and Agriculture Organization of the United Nations (FAO) is known.—*Tamara Boland*, University of New England, Armidale, NSW, Australia.

Forests Under Fire. By Christopher J. Huggard and Arthur R. Gomez. 2001. The University of Arizona Press, Tucson. 307 p. US$40.00 cloth. ISBN 0-8165-1775-4.

Forests Under Fire provides an excellent description of how management practices such as timber harvesting, rangeland grazing and outdoor recreation are responsible for the dramatic transformations of our Southwestern forests. The authors explain the unnatural conversions of vegetative surroundings, and examine the threats the new transitions have imposed on wildlife. According to the authors, these adverse ecosystem shifts can be attributed to humans, and to the application of scientific management practices. *Forests Under Fire* examines the history of scientific land management, blames mismanagement for historical disasters, and bring attention to a desire for change. The book contains 9 chapters and 31 illustrations, through which the authors attempted to identify the shifts and changes in national forest management.

Chapter 1, *Industry and Indian Self-Determination: Northern Arizona's Apache Lumbering Empire, 1870-1970,* by Arthur R. Gomez, and Chapter 2, *A Social History of McPhee: Colorado's Largest Lumber Town,* by Duane A. Smith focus on the small private timber industry. These chapters look at management from the perspective of different ethnic groups. They also introduce the concept of "cross-agency competition" between the U.S. Bureau of Indian Affairs and the U.S. Forest Service, and reveal 2 conflicting aspects of forest management: conservation and exploitation.

Chapter 3, *The Vallecitos Federal Sustained-Yield Unit: The (All Too) Human Dimensions of Forest Management in Northern New Mexico, 1945-1998*, by Suzanne S. Forrest, and Chapter 4, *Grazing the Southwest Borderlands: The Peloncillo-Animas District of the Coronado National Forest in Arizona and New Mexico, 1906-1996*, by Diana Hadley look at the 2 major Southwest industries of logging and grazing, respectively. In Chapter 3 Suzanne Forrest looks at the trends of logging practices after World War II and discusses the concept of sustained yield. Diana Hadley, in Chapter 4, recalls the history of grazing and the movement of grazing practices from a destructive era, to a conservation era, to an era of ecosystem strategies. Most range managers believe that this "new ecosystem strategies era" will lead to some of the best scientific management. This era has the best chance to prevent landscape fragmentation, protect habitat, benefit wildlife, and restore and sustain rangelands.

Chapter 5, *America's First Wilderness Area: Aldo Leopold, the Forest Service, and the Gila of New Mexico, 1924-1987* by Christopher J. Huggard shows how the book *A Sand County Almanac* by Aldo Leopold inadvertently led to poor scientific management. Huggard stresses that although *A Sand County Almanac* was a very popular book and brought a "theoretical basis for modern environmentalism," some of Leopold's ideas have contributed to mismanagement. In his essay Huggard argues that while bringing concern for wilderness preservation, Leopold's forest management strategies, which included predator extermination and fire suppression, misguided management immensely, especially in the Gila Wilderness Area. This chapter also discusses the Wilderness Act of 1964 and how it was conceived as a plan to reverse the damage done by Leopold's ethic.

Chapter 6, *Where There's Smoke: Wildfire Policy and Suppression in the American Southwest* by John Herron describes how aesthetics have held the highest value in forests for many people, and how fire suppression became a concept which nearly everyone seemed to support. Herron also tells how Smokey Bear becomes a well-known symbol and describes his influence in persuading the public to believe that fire suppression is a sound management practice. Forest managers have gradually realized how dangerous this idea is, as serious outbreaks of hot, large fires have occurred in recent years throughout the Southwest, bringing devastating consequences. In some cases, fire suppression plans have eventually been revised. Herron claims that it is "too late," and discusses the millions of acres and hundreds of homes that have been destroyed because of the philosophy of fire suppression.

Chapter 7, *Struggle in an Endangered Empire: The Search for Total Ecosystem Management in the Forests of Southern Utah, 1976-1999* by Thomas G. Alexander discusses how foresters are moving from a functionalist approach to "holistic ecosystem management," and describes how "entire ecosystems should be managed as whole organisms."

Chapter 8, *Biopolitics: A Case Study of Political Influence on Forest Management Decisions, Coronado National Forest, Arizona, 1980's – 1990's* by Paul W. Hirt exposes the struggles and difficulties that national forest managers face when balancing demands of environmentalists, politicians, and timber harvesters, and the public. Hirt also discusses the battle of "squirrels versus scopes," how it is still not over, and how it keeps drawing in more individuals and organizations as the battle continues. Hirt expresses his concern, stating that "Political considerations often exercise a controlling influence over biological decisions," which has the potential to lead to devastating consequences.

Chapter 9, *Epilogue: Seeing the Forest Not for the Trees: The Future of Southwestern Forests* by Hal K. Rothman brings attention to the idea that forests are shifting from the "extractive to recreational use," and explains the influence tourists can have on the uses and management treatments of our forests. He also stresses the need for forest managers to be aware of this new-found power of tourists and recreational users. Rothman concludes by saying that he believes forest managers and ecosystem management trends are headed in the right direction, and that he foresees a positive future.

Forests Under Fire starts in the past and explains the steps that have affected our forests and their management. It brings attention to "who calls the shots" on public lands by addressing controversies and policies that have been adopted along the way. In these essays, the authors examine how practices such as overcutting, overgrazing, predator extermination, fire suppression, or intense recreational uses have contributed to the damages done to Southwestern ecosystems. Although this book focuses on the Southwestern United States, many of the ideas described by the authors could be applied to forests anywhere.—*Daralyn D. Spies*, Washington State University, Pullman, Washington.

March *JRM* Erratums

The correct title to the article by Catherine Erichsen-Arychuk, Edward W. Bork, and Arthur W. Bailey starting on page 164 is:

"Northern dry mixed prairie responses to summer wildfire and drought"

The correct title to the article by James A. Young, Charlie D. Clements, and Robert R. Blank starting on page 194 is:

" Herbicide residues and perennial grass establishment on perennial pepperweed sites"

Journal of Range Management
Manuscript Submission and Copyright Release Form

This form must be completed and submitted with the manuscript. If the manuscript is not accepted for publication, this affidavit shall have no legal effect and may be considered null and void.

Please Print

1. Manuscript Title:

____

____

2. Name and Address of Correspond Author:

Name______________________ Address______________________

______________________ Telephone ( ) ______________________

E-Mail______________________ Fax # ( ) ______________________

3. Membership

I (we) affirm that at least one of the authors is a current member of the Society for Range Management.

Yes __________ No __________

Name of Member: ______________________

4. Assurance of Content:
I (we) have read this manuscript and I (we) affirm that the content of this manuscript or a major portion thereof has not been published in a refereed journal, and it is not being submitted for publication elsewhere.

5. Section Preference:

- ❑ Plant Physiology
- ❑ Animal Ecology
- ❑ Plant Ecology
- ❑ Plant-Animal Interactions
- ❑ Grazing Management
- ❑ Animal Physiology
- ❑ Improvements
- ❑ Reclamation
- ❑ Soils
- ❑ Hydrology
- ❑ Economics
- ❑ Measurement/Sampling

6. Publication Costs:
The current charge for publication is $80 per printed page in the *Journal* for members for the first 3 printed pages. Page 4 and beyond is $100/page. For nonmembers the charge is $100/page. Reprints may be ordered. The following agency or individual will be responsible for publication costs:

Name ____

Address ____

7. Copyright Release:

Copyright laws make it necessary for the Society to obtain a release from authors from all material published. To this end, we ask you to grant us all rights, for your article.

Whereas the Society is undertaking to publish the *Journal of Range Management*, of which the undersigned is the author of one or more parts, the author grants and assigns exclusively to the Society for its use any and all rights of whatsoever kind or nature now or hereafter protected by the copyright laws (common or statutory) of the United States and all foreign countries in all languages in and to above-named article, including all subsidiary rights. The Society, in turn, grants to the author(s) the rights or republication in any book of when he or she is author or editor, subject only to giving proper credit in the book to the original *Journal* publication of the article by the Society. Each author agrees that the material furnished for the *Journal* has been be published elsewhere. The corresponding author will be given an opportunity to read and correct the edited manuscript as page proofs, but if the author(s) fails to return page proofs to the production editor of the *Journal* within the time specified by the editor, production and publication may proceed with the author's approval of the edited manuscript.

The author(s) will receive no monetary return from the Society for the use of material contained in the manuscript.

I (we) agree to the foregoing terms:

Author (print or type) ______________________ Date ______________________

Signature ______________________ Citizen of (country ______________________

Author (print or type) ______________________ Date ______________________

Signature ______________________ Citizen of (country ______________________

Author (print or type) ______________________ Date ______________________

Signature ______________________ Citizen of (country ______________________

Author (print or type) ______________________ Date ______________________

Signature ______________________ Citizen of (country ______________________

I (we) agree to the foregoing terms except item 7. I (we) am unable to sign a copyright release for reasons stated below:

____

____

Send this form and 4 copies of the manuscript on line-number paper to:

Editor
Journal of Range Management
7820 Stag Hollow Road
Loveland, Colorado 80538

INSTRUCTIONS FOR AUTHORS (from revised *Handbook and Style Manual*)

Eligibility

The *Journal of Range Management* is a publication for reporting and documenting results of original research and selected invitational papers. Previously published papers are unacceptable and will not be considered for publication. Exceptions to this criterion are research results that were originally published as department research summaries, field station reports, abstracts of presentations, and other obscure and nontechnical handout publications. Manuscripts submitted to the *JRM* are the property of the *Journal* until published or released back to the author(s). Manuscripts may not be submitted elsewhere while they are being considered for this journal. Papers not accepted for publication are automatically released to the authors.

Kinds of Manuscripts

Journal Articles report original findings in Plant Physiology, Animal Nutrition, Ecology, Economics, Hydrology, Wildlife Habitat, Methodology, Taxonomy, Grazing Management, Soils, Land Reclamation (reseeding), and Range Improvement (fire, mechanical chemical). *Technical Notes* are short articles (usually less than 2 printed pages) reporting unique apparatus and experimental techniques. By invitation of the Editorial Board, a *Review* or *Synthesis Paper* may be printed in the journal. *Viewpoint* articles or *Research Observations* discussing opinion or philosophical concepts regarding topical material or observational data are acceptable. Such articles are identified by the word *viewpoint* or *observations* in the title.

Manuscript Submission

Contributions are addressed to the **Editor, Gary Frasier, *Journal of Range Management,* 7820 Stag Hollow Road, Loveland, Colorado 80538**. Manuscripts are to be prepared according to the instructions in the *Journal's Handbook* and *Style Manual*. If the manuscript is to be one of a series, the Editor must be notified. Four copies of the complete manuscript, typed on paper with numbered line spaces are required. Authors may retain original tables and figures until the paper is accepted, and send good quality photocopies for the review process. Receipt of all manuscripts is acknowledged at once, and authors are informed about subsequent steps of review, approval or release, and publication.

Manuscripts that do not follow the directives and style in *Journal* handbook will be returned to the authors before being reviewed. A manuscript number and submission date will be assigned when the paper is received in the appropriate format.

Manuscript Review

Manuscripts are forwarded to an Associate Editor, who usually obtains 2 or more additional reviews. Reviewers remain anonymous. These reviewers have the major responsibility for critical evaluation to determine whether or not a manuscript meets scientific and literary standards. Where reviewers disagree, the Associate Editor, at his discretion, may obtain additional reviews before accepting or rejecting a manuscript. The Associate Editor may also elect to return to the author those manuscripts that require revision to meet format criteria before the *Journal* review.

The Associate Editor sends approved manuscripts, with recommendations for publication, to the Editor, who notifies the author of a projected publication date. Manuscripts found inappropriate for the *JRM* are released to the author by the Associate Editor. Manuscripts returned to an author for revision are *returned to the Associate Editor for final acceptability of the revision*. Revisions not returned within 6 months, are considered terminated. Authors who consider that their manuscript has received an unsatisfactory review may file an appeal with the Editor. The Editor then may select another Associate Editor to review the appeal. The Associate Editor reviewing the appeal will be provided with copies of an correspondence relating to the original review of the manuscript. If the appeal is sustained, a new review of the manuscript may be implemented at the discretion of the Editor.

Authors should feel free to contact the Associate Editor assigned to their manuscript at any stage of the review process: to find out where the paper is in the process; to ask questions about reviewer comments; to ask for clarification or options if a paper has been rejected.

Page Proofs

Page proofs are provided to give the author a final opportunity to make corrections of errors caused by editing and production. Authors will be charged when extensive revision is required because of author changes, even if page charges are not assessed for the article. One author per paper will receive page proofs. These are to be returned to the **Production Editor, 3059A Hwy 92, Hotchkiss, Colorado 81419-9548**, within 48 hours after being received. If a problem arises that makes this impossible, authors or their designates are asked to contact the Production Editor immediately, or production and publication may proceed without the author's approval of his edited manuscript.

Page Charges and Reprint Orders

Authors are expected to pay current page charges. Since most research is funded for publication, it will be assumed that the authors are able to pay page charges unless they indicate otherwise in writing, when submitting a manuscript. When funds are unavailable to an author, no page charges will be assessed. Only the Editor will have knowledge of fund status of page charges; the Associate Editors and reviewers will accept or reject a manuscript on content only.

An order form for reprints is sent to one author with the page proofs. Information as to price and procedure are provided at that time. The minimum order is 100; no reprints are provided free of charge.

Basic Writing Style

Every paper should be written accurately, clearly, and concisely. It should lead the reader from a clear statement of purpose through materials and methods, results, and to discussion. The data should be reported in coherent sequence, with a sufficient number of tables, drawings, and photographs to clarify the text and to reduce the amount of discussion. Tables, graphs, and narrative should not duplicate each other.

Authors should have manuscripts thoroughly reviewed by colleagues in their own institution and elsewhere before submitting them. Peer review before submission insures that publications will present significant new information or interpretation of previous data and will speed *JRM* review process.

Particular attention should be given to literature cited: names of authors, date of publication, abbreviations or names of journals, titles, volumes, and page numbers.

It is not the task of Associate Editors or *Journal* reviewers to edit poorly prepared papers or to correct readily detectable errors. Papers not properly prepared will be returned to the author.