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Phosphorus supplementation of range cows in the Northern Great Plains

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Abstract

Low phosphorus (P) levels in Northern Great Plains rangeland forage combined with limited data on the P requirements of range cows (*Bos taurus*), precipitated 2 studies conducted to compare the performance of P supplemented and no P supplemented (control) beef cows. Phosphorus supplementation levels ranged from 4 to 8 g day^{-1} depending on estimated P needs at different times of the year. The 2 groups of cows previously had been involved in replacement heifer growing studies, with P treatments established 462 and 402 days, respectively, before initiation of these studies. Winter feed consisted of mixed hay, primarily smooth bromegrass (*Bromus inermis* Leyss.), with corn silage (*Zea mays* L.) fed only in 1982 and 1983 from calving to the time cows were turned on summer pasture. Summer pastures contained primarily western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve], needleandthread (*Stipa comata* Trin. and Rupr.), green needlegrass (*S. viridula* Trin.), blue grama [*Bouteloua Gracilis* (H.B.K.) Griffiths] and upland sedges (*Carex* spp.). The P status of cows used in these studies appeared to be estimated more reliably by forage P than by serum or fecal P. According to P levels in hay and pasture, the diets of control cows were below recommended P levels for about 9 months of the year. However, weight change differences between P supplemented and control cows during the first lactation and gestation periods were gradually lost by the end of the studies. Conception rates of control cows were slightly lower ($P<0.08$) in the first but not the second study. There were no differences in average calving date or calf birth weights, but P supplementation did increase ($P<0.01$) calf weaning weights. Cow weight changes, calf weaning weight differences, forage and serum P data, and in the first study conception rate differences indicate that Northern Great Plains forages are marginal to deficient in P for optimal production of beef cows. The most consistent benefit from P supplementation was an increase in calf weaning weights. Data also indicate that energy supplementation for 30 days after calving may increase conception rates.

Key Words: forage phosphorus, extrusa, energy supplement, native range, fecal minerals.

Forages grown on Northern Great Plains rangelands are often low in phosphorus (P) (Sarvis 1941) compared to NRC (1984) recommendations. However, Karn (1992) reported that range cows offered ad libitum access to P in a mixture with salt showed no benefit from the practice over 3 grazing seasons, probably due to low and variable P intakes. In subsequent research with growing heifers, Karn (1995) obtained P intake levels of 4–6 g day^{-1} using ground oats and dried molasses to stimulate consumption. However, heifer weight gains were not consistently affected; in 1984 P supplementation of Hereford-Simmental heifers increased weight gains, but in 1981 weight gains of Hereford and Hereford-Angus crossbred heifers were not affected. In other research, Call et al. (1978) reported no response to P supplementation of grazing cattle in Utah and Judkins et al. (1985) reported that supplementation of grazing cows in New Mexico was beneficial only during a drought. Read and Engels (1986a) reported that P suplementation at one location in South Africa dramatically improved cow and calf weight gains and reproductive performance, while reducing mortality, but at another location only weaning weights were improved. Fishwick et al. (1977) reported that 12 g P daily was inadequate for beef cows, but in a subsequent study this group reported that 10–12 g P daily was adequate to maintain normal blood P concentration, voluntary intake and digestibility (Bass et al. 1981).

Blood P is often used to estimate P status, but Read and Engels (1986b) indicated that unless plasma P was below 20 mg liter^{-1} it was insensitive to changes in dietary P. Diet P itself, is difficult to determine for grazing animals because extrusa samples are affected by salivary P (Langlands 1966), and it is difficult to clip samples as selectively as animals graze (Langlands 1974). Thus, Holechek et al. (1985) used fecal P to predict dietary P levels in range cattle. In short-term feeding trials, Sanson et al. (1990) reported an r^2 of 0.78 between P intake and fecal P, but cautioned that the usefulness of this relationship may be limited by differences in the availability of dietary P.

Phosphorus supplementation is recommended for grazing cattle in the Northern Great Plains, but documented benefits are lacking. Thus, the objectives of this research were to determine the effect of P supplementation on the performance of range cows and to compare diet, serum, and fecal P as methods of determining the P status of grazing cattle.

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Materials and Methods

Phosphorus supplementation studies with young beef cows, just before their first parturition, were initiated on 19 February 1982 and 1 March 1985 and continued until 4 November 1983 and 26 October 1987, respectively. Fifty-three Hereford and Hereford-Angus crossbred cows were used in the first study and 55 Hereford-Simmental cows were used in the second study. Twenty-six cows in the first study and 28 in the second were assigned to receive supplemental P and 27 cows in each group were maintained as controls and received no supplemental P. These cows had previously been used in replacement heifer growing studies (Karn 1995) and were continued on the same P treatments. Thus P supplemented cows in the current studies had already been receiving 4–6 g P day^{-1} for 462 and 402 days, respectively when these studies were initiated. Average initial cow weights were 407 kg in the first study and 470 kg in the second study.

Supplementation

Cows were supplemented by treatment group and fed in a bunk. Monosodium phosphate was used as the supplemental P source and ground oats and dried molasses were used as a carrier to aid mineral consumption. Supplements for P supplemented and control cows, and the periods they were used are shown in Table 1. Control cows received only the carrier used with the P supplement. In 1982, before calving, both treatment groups were maintained together, except when supplemented, but after calving they were maintained in separate groups until they were turned on summer pasture. During the summer of 1982, and for all subsequent time periods in both studies, cows were maintained together at all times except when they were corralled, separated by treatment group, and supplemented. Cows had previously been trained to go into 2 separate pens at feeding; training was facilitated by using either a mild electric shock as a negative reinforcement or supplement as a positive reinforcement (Karn and Lorenz 1984). This separation procedure facilitated relatively rapid supplementation, resulting in minimum disturbance to normal cow grazing patterns, even when calves were at side. Generally, cows were penned only 45–60 minutes for feeding. Supplements were fed on Monday, Wednesday, and Friday from 19 February to 31 May 1982; for the remainder of the 1982 study and for all of the 1985 study, cows were fed only on Monday and Friday when they received 4 and 3-day portions of supplement, respectively.

Table 1. Supplements and the periods they were fed to phosphorus (P) supplemented and no P supplemented (control) range cows during studies beginning in 1982 and 1985 and ending in 1983 and 1987[1].

Period	P	P		Control	
		Ground oats	Dried molasses	Ground oats	Dried molasses
		---- (g day^{-1}) ----		-- (g day^{-1}) --	
			1982		
19 Feb. 1982–12 Mar. 1982	6	28.5	28.5	28.5	28.5
12 Mar. 1982–15 Nov. 1982	8	57.0	28.5	57.0	28.5
15 Nov. 1982–11 Mar. 1983	4	28.5	28.5	28.5	28.5
11 Mar. 1983– 4 Nov. 1983	8	57.0	28.5	57.0	28.5
			1985		
1 Mar. 1985–15 Mar. 1985	6	28.5	28.5	28.5	28.5
15 Mar. 1985–12 Nov. 1985	8	57.0	28.5	57.0	28.5
12 Nov. 1985–17 Mar. 1986	4	28.5	28.5	28.5	28.5
17 Mar. 1986– 7 Nov. 1986	8	57.0	28.5	57.0	28.5
7 Nov. 1986–16 Mar. 1987	4	28.5	28.5	28.5	28.5
16 Mar. 1987–26 Oct. 1987	8	57.0	28.5	57.0	28.5

[1] Supplement amounts are daily averages for supplements fed at 2, 3 or 4 day intervals.

In 1986 and 1987 in addition to their normal treatment supplements, every other cow to calve on both the P supplemented and control treatments, respectively, received supplemental oats fed Monday through Friday at the rate of 1.8 kg day^{-1} from the day after calving until 27 May in 1986 and 29 May in 1987. Supplemental oats were fed for an average of 30 days in 1986 and 32 days in 1987. The oats contained 125 g kg^{-1} crude protein and 3.5 g kg^{-1} P. Cows were bunk fed supplemental oats in the same pens where they were normally supplemented. Cows not receiving supplemental oats received only their previously described supplements (Table 1).

Management and Sampling

During the winter, mixed hay which was primarily smooth bromegrass (*Bromus inermis* Leyss.) was fed free choice. Cows received corn silage (*Zea mays* L.) at about 8 kg day^{-1} for approximately 90 days after calving in 1982 and 1983 only. From the time cows began to calve in April until they were turned on summer pasture, for all years except 1983, they were maintained in small calving pastures with access to harvested feeds and some grass. In 1983 cows were confined to a drylot during this period and fed only harvested feeds. Vitamin A was provided during the winter, at the rate of 20,000 IU per day, via a vitamin A, D, and E premix fed with treatment supplements.

During the summer, cows were rotated between adjoining 92 and 99 ha native pastures containing primarily western wheatgrass [*Pascopyrum smithii* (Rydb.), A. Löve], needleandthread (*Stipa comata* Trin. and Rupr.), green needlegrass (*S. viridula* Trin.), blue grama [*Bouteloua gracilis* (H.B.K.) Griffiths], and upland sedges (*Carex* spp.). These pastures have been described in more detail by Karn (1992). Trace mineralized salt containing 96-98.5% salt, 0.35% zinc, 0.34% iron, 0.20% manganese, 0.033% copper, 0.007% iodine, and 0.005% cobalt (Akzo Salt, Inc., Clarks Summit, Penn.) was available at all times.

Hereford and Hereford-Angus crossbred cows used in the first study were mated to Tarentaise bulls in 1982 and 1983, while Hereford-Simmental crossbred cows used in the second study were mated to Angus bulls in 1985 and to Simmental bulls in 1986 and 1987. Two bulls were used each year over a 60-day breeding season. Pregnancy was determined by rectal palpation following weaning in 1983 and 1987.

Cows were weighed following an overnight stand without feed or water at the beginning and end of each study, at monthly intervals during each summer grazing season and just before each calving period. Summer grazing seasons were from 2 June to 10 November 1982, 23 May to 4 November 1983, 3 June to 6 November 1985, 2 June to 30 October 1986, and 1 June to 26 October 1987. Calves were weighed at birth, at monthly intervals during the summer and when they were weaned at the end of the summer grazing season. Calves were allowed to remain with their mothers until just before being weighed.

Milk production was estimated over 24 hours by the weigh-suckle-weigh technique described by Neville (1962) using a morning and evening nursing cycle on 22 August and 6 October 1983, 16 July 1985, and 31 July 1986. In 1987 one nursing cycle following a 13 hour separation period on 8 October was used to estimate 24 hour milk production (Williams et al. 1979). Milk samples were collected for mineral analysis by hand milking on 4 November 1983. This was facilitated by injecting 2 ml of oxytocin into the tail vein just before milking.

Blood samples were collected from the jugular vein of each cow on 10 June and 5 November 1982; 23 May and 28 October 1983; 31 May and 25 October 1985; 31 March, 11 June and 23 October 1986; and 6 March, 1 June and 26 October 1987. Serum was removed from samples by centrifugation, frozen and stored for approximately 6 months before analysis.

Extrusa samples were collected from pastures every 2 weeks during each grazing season with 3 mature esophageally fistulated steers. Steers were allowed to graze until collection bags were full, which usually occurred within 30 minutes. Fistulated steers were penned off feed over night before each sampling date; this procedure did not appear to affect grazing selectivity. Individual steer collections were mixed, subsampled, frozen, and freeze dried for nitrogen (N) and in vitro digestible organic matter (IVDOM) analyses. Extrusa subsamples for mineral analyses were squeezed to remove saliva (Hoehne et al. 1967) and dried in a forced air oven at 50°C.

Fecal samples were obtained in 1986 and 1987 from 2 randomly determined subgroups of cows within each of the P supplemented and control groups. At least 6 cows within each subgroup were sampled at each collection period and an attempt was made to sample the same cows each time. Collections were made on alternate weeks, the day after extrusa forage samples were taken. Samples were obtained immediately after defecation and composited over cows within each subgroup, providing 2 fecal samples for the P supplemented group and 2 samples for the control group. Samples were frozen and freeze dried. Winter feed, extrusa, and fecal samples were ground to pass a 1 mm screen before being analyzed.

Chemical and Statistical Analyses

Phosphorus and N in extrusa, hay, and corn silage and P in serum, milk, and feces were determined with a Technicon Autoanalyzer (Technicon Industrial Systems, Tarrytown, N. Y. 10591). Atomic absorption was used to determine Ca, Mg, and K in extrusa and fecal samples, Ca and Mg in serum and milk and Ca in hay and corn silage. In vitro digestible organic matter was determined by the procedure of Moore and Mott (1974).

Cow weights, calf birth dates, and milk production were analyzed according to a completely randomized design. Fecal data were analyzed as a randomized complete block and treatment was tested with the treatment × date interaction term. Conception rate data were analyzed for each study separately and over both studies using chi-square analysis. Calf weaning weights were analyzed by GLM covariance procedures (SAS 1985), by year and over all 5 years, using birth date to correct for differences in calf age and least squares means to adjust for unequal animal numbers. When calf weaning weight data for the 2 studies were combined the following model was used: treatment, study, treatment × study, calves (treatment × study), calf sex, treatment × calf sex, year (study), and treatment × year(study). The treatment × study term was not significant, therefore it was eliminated from the model. The treatment and study terms were tested using calves (treatment × study) as the error term. It was assumed there was no method of supplementation interaction, therefore animals were considered as experimental units. Serum data were analyzed by covariance, using element levels determined when treatments were first established with these animals in replacement heifer studies (Karn 1995), in order to correct for initial element differences among animals. Treatment differences were considered significant at the 5% probability level unless otherwise indicated.

Results and Discussion

Hay fed during calving and lactation periods in the winter of 1982 had the highest P level of any hay used during these studies (Table 2). Corn silage fed after calving in the first study also had a relatively high level of P, compared to the range of 2.2 to 2.7 g kg^{-1} recommended by the NRC (1984) for cows with average and superior milk production, respectively. Hays used in 1985, 1986 and 1987 had P levels that were well below the NRC (1984) recommendation (2.1 g kg^{-1}) for dry pregnant cows during the last third of gestation.

Table 2. Mean (± SD) phosphorus (P), calcium (Ca), crude protein (CP), and in vitro digestible organic matter (IVDOM) of hay and corn silage fed to P supplemented and control cows in studies beginning in 1982 and 1985.

Feed	Year	P	Ca	CP	IVDOM
	-------- (g kg^{-1} dry matter) ---------				(g kg^{-1})
			1982		
Hay	1982	1.89±0.56	5.10±1.56	—	—
Corn Silage	1982	2.28±0.15	2.31±0.29	—	—
Hay	1983	1.16±0.24	4.44±1.27	—	—
Corn Silage	1983	2.11±0.16	4.45±0.51	—	—
			1985		
Hay	1985	1.25±0.24	7.11±1.70	104±27	688±39
Hay	1986	1.19±0.36	7.43±3.04	104±38	582±24
Hay	1987	1.42±0.32	11.40±4.08	108±27	549±38

Extrusa P levels, averaged over years by month for the first study (1982-1983), were adequate (NRC 1984) for lactating cows, based on percent P in the extrusa, only in June. However during other summer months, especially in 1983, it is possible that even with low forage P levels (Table 3) cows could have consumed more P than expected through increased forage consumption. Extrusa P data for the second study (1985–1987) suggest that average monthly P levels may have been slightly higher than in the first study, but for much of the time based on percent P in the extrusa, levels were still marginal to deficient for lactating cows. Magnesium levels in the extrusa were below 2.0 g kg^{-1}, which is the level suggested by Underwood (1966) as necessary to prevent grass tetany, for all monthly averages except July 1982-1983. However, there were no instances of grass tetany. Mean extrusa crude protein levels were marginal to deficient for lactating beef cows (NRC 1984) during September and October, of both studies and extrusa K levels were marginal (NRC 1984) during September and October of the first study. Although extrusa samples were squeezed to remove saliva as suggested by Hoehne et al. (1967), samples may still have contained higher P levels than unmasticated forage (Langlands 1966). This suggests that dietary P levels for control cows may have been even lower than indicated by data in Table 3. Although there may be problems using extrusa samples for mineral analysis, they are more readily accepted than hand clipped samples as a means of sampling pastures for chemical analysis.

Table 3. Mean (± SD) monthly chemical composition data from extrusa samples of native pastures grazed by phosphorus (P) supplemented and control cows in 1982-83 and 1985-87[1,2]

Month	P	Ca	Mg	K	Crude Protein	IVDOM[3]
	(g kg^{-1} dry matter)					(g kg^{-1})
			1982-83			
Jun.	2.18 ± 0.35	6.78 ± 2.4	1.78 ± 0.51	12 ± 1.0	132 ± 17	696 ± 53
Jul.	1.96 ± 0.41	6.24 ± 1.7	2.07 ± 0.22	11 ± 2.0	107 ± 16	637 ± 64
Aug.	1.75 ± 0.12	5.40 ± 1.3	1.37 ± 0.24	7 ± 0.3	99 ± 15	610 ± 47
Sep.	1.54 ± 0.18	4.54 ± 1.2	1.35 ± 0.01	6 ± 0.2	67 ± 5	602 ± 39
Oct.	1.32 ± 0.33	3.06 ± 0.8	0.89 ± 0.08	4 ± 0.6	56 ± 1	580 ± 37
Season mean	1.77 ± 0.40	5.32 ± 1.9	1.49 ± 0.47	8 ± 3.0	94 ± 30	628 ± 60
			1985-87			
Jun.	2.20 ± 0.32	5.29 ± 2.3	1.65 ± 0.50	27 ± 13.6	100 ± 16	703 ± 54
Jul.	2.14 ± 0.25	6.03 ± 2.1	1.86 ± 0.37	24 ± 11.4	90 ± 16	668 ± 78
Aug.	2.15 ± 0.40	5.62 ± 1.4	1.57 ± 0.34	21 ± 12.7	91 ± 24	638 ± 59
Sep.	1.87 ± 0.12	4.57 ± 1.2	1.42 ± 0.26	18 ± 10.0	81 ± 19	624 ± 60
Oct.	1.71 ± 0.28	3.51 ± 0.4	1.00 ± 0.24	14 ± 8.6	74 ± 15	615 ± 56
Season mean	2.02 ± 0.33	5.05 ± 1.8	1.52 ± 0.45	21 ± 11.6	88 ± 19	652 ± 67

[1] Monthly means are averages of 3 or 4 collection dates for 1982-83 and 6-7 collection dates for 1985-87.
[2] Means over months are averages of 10 dates for Mg and K and 19 dates for other data in 1982-83 and 32 dates for all data in 1985-87.
[3] IVDOM=in vitro digestible organic matter.

Fecal P levels averaged over the grazing season were higher ($P<0.05$) for P supplemented cows in 1986 (Table 4), and differences between treatments were consistent at all sampling dates (Fig. 1). Season-long differences in fecal P levels between P supplemented and control cows also occurred in 1987, and they were consistent among sampling dates (Fig. 2) but differences were less than in 1986 (Table 4). Read and Engels (1986b) reported that fecal P differences between P supplemented and unsupplemented cows decreased when feed intake and consequently fecal output declined for unsupplemented cows. In the current study, P supplemented and control cows were gaining weight at approximately the same rate, therefore P supplemented cows may have been absorbing and utilizing more P in 1987 than in 1986, thus less P was eliminated in the feces. Early in the season in both 1986 and 1987 fecal P was much higher than forage (extrusa) P, but by October fecal P from control cows was only slightly higher than forage P (Fig. 1 and 2). There was an r^2 of 0.64 between fecal P from control cows and forage (extrusa) P in 1986 but in 1987 the r^2 was only 0.28. In 1986 fecal Ca levels were higher and fecal K levels were lower, and in 1987 fecal Mg levels were lower for P supplemented cows, but fecal N levels were not affected by supplemental P in either year (Table 4).

Serum P was higher for control than P supplemented cows in June of 1982, but P supplemented cows had higher serum P in November of 1982 ($P<0.08$) and May and October of 1983 (Table 5). Normal serum P levels according to Underwood (1981) range between 40-60 mg liter^{-1}. Read and Engels (1986b) reported that plasma P levels below 20 mg liter^{-1} were useful in identifying P deficiency, but at higher levels, plasma P seemed to be of little use in distinguishing between P adequate and P deficient animals. The lowest average serum P levels (38 and 33 mg

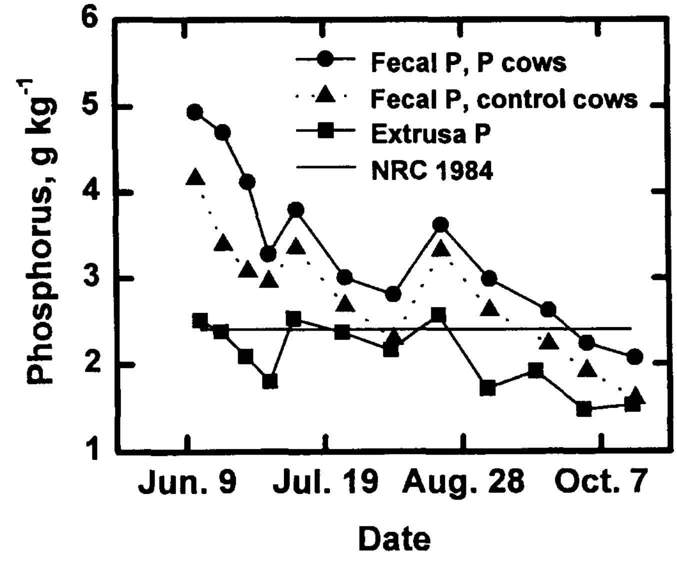

Fig. 1. Phosphorus (P) levels in pasture (extrusa) samples compared to fecal P from P supplemented and no P supplemented (control) range cows in 1986.

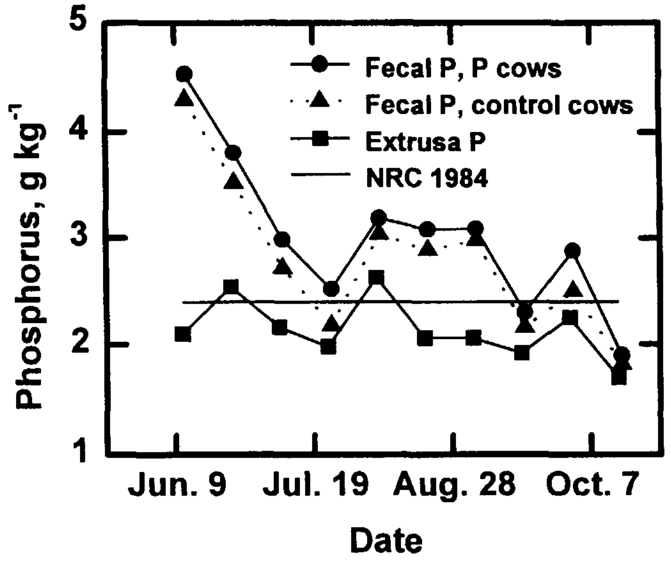

Fig. 2. Phosphorus (P) levels in pasture (extrusa) samples compared to fecal P from P supplemented and no P supplemented (control) range cows in 1987.

Table 4. Phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), and nitrogen (N) in fecal samples collected from P supplemented and no P supplemented (control) range cows during the summers of 1986 and 1987[1].

Treatment	1986 P	1986 Ca	1986 Mg	1986 K	1986 N	1987 P	1987 Ca	1987 Mg	1987 K	1987 N
	(g kg^{-1} dry matter)					(g kg^{-1} dry matter)				
P	3.20*	14.4*	5.13	5.66*	17.4	3.03*	12.0	3.96*	6.37	18.4
Control	2.68*	13.4*	4.77	6.20*	17.6	2.81*	13.2	4.12*	6.32	18.7
SE[2]	.002	.007	.004	.002	.004	.001	.012	.001	.004	.003

[1] Treatment means are averages of 2 replications and 11 dates in 1986 and 2 replicates and 10 dates in 1987.

[2] SE = Standard error of the mean = $\frac{\sqrt{EMS}}{N}$, where EMS = error mean square used to test treatments, and N = the number of observations/mean.

* Within a year and mineral, treatments differ (P<0.05).

liter^{-1}) for control cows in these studies were in October 1983 and March 1986, respectively. Low serum P in 1983 was likely due to low forage P for about 3 months and the demands of lactation; in 1986 low serum P was likely the result of 7 months on a low P diet. The lowest serum P level for P supplemented cows was 44 mg liter^{-1} in June of 1982.

Serum P in the second study was higher for P supplemented cows in October 1985, March 1986 and October of 1986 (P<0.08). Serum Ca was higher for control cows in November 1982, May 1983, and October of 1985 (Table 5). Similar increases in plasma Ca for unsupplemented compared to P supplemented cows was reported by Read and Engels (1986b), but the effect was more prevalent in late lactation. Underwood (1966) indicated that this inverse relationship between plasma P and Ca was the result of mobilization of these elements from bone to supply needed P, with the corresponding Ca remaining as excess in the plasma. Serum Mg levels above 20.0 mg liter^{-1} are considered normal for grazing cows by the Committee on Mineral nutrition (1973). All cows in both studies, except P supplemented cows (19.0 mg liter^{-1}) in May of 1983 had serum Mg levels above 20.0 mg liter^{-1} (Table 5).

Milk samples collected in October 1983 were similar in P, Ca, and Mg levels for control and P supplemented cows and averaged 1042, 1375, and 128 mg liter^{-1} on a whole milk basis, respectively. Milk levels of Ca, P, and Mg were within normal limits (Committee on Mineral Nutrition 1973, Kemp 1971). Read and Engels (1986a) reported that milk composition was only slightly affected in cows with a severe P deficiency.

Milk production for 24 hours (±SE), estimated on 22 August and 6 October 1983, 16 July 1985, 31 July 1986 and 8 October 1987 by the weigh-suckle-weigh technique was 5.3 ± 0.06 vs 4.7± 0.06, 3.4 ± 0.07 vs 2.6 ± 0.08, 7.4 ± 0.04 vs 7.0 ± 0.05, 9.5 ± 0.06 vs 8.4 ± 0.07 and 8.3 ± 0.08 vs 7.5 ± 0.08 kg for P supplemented and control cows, respectively. Although milk production for P supplemented cows was numerically greater at each sampling period, differences were only significant (P<0.05) for the 31 July 1986 date.

Cow weights at the beginning of these studies were 406 and 407 kg, and 473 and 466 kg for P supplemented and control cows used in the first and second studies, respectively. Weight gain or loss comparisons between P supplemented and control cows in Table 6 were always made with cows that had similar calving and lactation histories. Cows that lost calves or failed to breed were not included in weight comparisons during that breeding and lactation cycle, because their weight gains were always much higher than those of lactating cows. During the 1982 calving and nursing period P supplemented cows lost more weight (P<0.05) than control cows (Table 6), but during the following winter gestation period, P supplemented cows gained more weight (P<0.05) than control cows. Cow weight changes were not different during the

Table 5. Serum phosphorus (P) ± SE, calcium (Ca) ± SE, and magnesium (Mg) ± SE for P supplemented and no P supplemented (control) range cows for studies beginning in 1982 and 1985 and ending in 1983 and 1987[1, 2,3].

Date	P: P	P: Ca	P: Mg	Control: P	Control: Ca	Control: Mg
	(mg liter^{-1})			(mg liter^{-1})		
1982						
Jun. '82	44 ± 1.6*	92 ± 1.5	—	53 ± 1.6*	93 ± 1.5	—
Nov. '82	45 ± 1.8[4]	95 ± 0.8*	—	41 ± 1.7[4]	101 ± 0.7*	—
May '83	76 ± 2.3*	90 ± 0.9*	19 ± 0.1*	57 ± 2.4*	96 ± 1.0*	21 ± 0.1*
Oct.. '83	51 ± 1.8*	102 ± 1.1	22 ± 0.2	38 ± 1.8*	105 ± 1.2	22 ± 0.1
1985						
May '85	54 ± 1.4	101 ± 0.7	20 ± 0.4	55 ± 1.5	102 ± 0.8	21 ± 0.4
Oct.. '85	61 ± 1.8*	103 ± 0.6*	20 ± 0.3	46 ± 1.9*	107 ± 0.6*	20 ± 0.3
Mar. '86	47 ± 0.9*	107 ± 0.9	22 ± 0.3	33 ± 0.9*	107 ± 0.9	21 ± 0.4
Jun. '86	53 ± 2.6	97 ± 1.0	25 ± 0.4	55 ± 2.8	98 ± 1.1	24 ± 0.4
Oct.. '86	48 ± 1.2[4]	99 ± 0.7	22 ± 0.3	45 ± 1.3[4]	99 ± 0.7	23 ± 0.3
Mar. '87	46 ± 1.4	93 ± 1.3	23 ± 0.4	48 ± 1.5	94 ± 1.4	23 ± 0.4
Jun. '87	53 ± 1.8	100 ± 1.4	24 ± 0.4	56 ± 1.9	96 ± 1.4	24 ± 0.4
Oct.. '87	48 ± 2.0	90 ± 2.4	22 ± 0.6	47 ± 2.0	92 ± 2.5	22 ± 0.7

[1] All means except serum Mg for May and October 1983 are least squares adjusted.

[2] Summer data are for lactating cows only.

[3] SE = Least squares mean standard error from SAS GLM.

[4] Treatments within a date and mineral are different (P<0.08).

*Treatments within a date and mineral are different (P<0.05).

Table 6. Weight changes (±SE) for phosphorus (P) supplemented and no P supplemented (control) cows during calving and nursing, and gestation periods for studies beginning in 1982 and 1985 and ending in 1983 and 1987[1,2]

Period	Beginning Date	Length	P No. cows[3]	P Gain	Control No. cows[3]	Control Gain
		(days)		(kg)		(kg)
				1982		
Calving & Nursing '82	2-19-82	259	23	-31.8 ± 0.9*	22	-8.8 ± 1.0*
Gestation '83	11-05-82	117	22	52.0 ± 0.7*	21	34.9 ± 0.8*
Calving & Nursing '83	3-03-83	246	23	25.5 ± 0.8	21	22.6 ± 0.8
Cumulative Gain	2-19-82	622	23	52.6 ± 1.6	21	65.1 ± 1.8
				1985		
Calving & Nursing '85	3-01-85	250	27	8.3 ± 0.6[4]	23	0.3 ± 0.7[4]
Gestation '86	11-06-85	124	27	43.9 ± 0.5*	25	21.4 ± 0.5*
Calving & Nursing '86	3-11-86	226	25	36.7 ± 0.8[4]	23	47.8 ± 0.9[4]
Gestation '87	10-23-86	151	23	15.4 ± 0.7	22	8.2 ± 0.7
Calving & Nursing '87	3-24-87	216	23	31.8 ± 0.9	21	39.1 ± 1.0
Cumulative Gain	3-01-85	967	23	137.7 ± 1.1	21	137.5 ± 1.2

[1] SE = Standard error of the mean = $\sqrt{\frac{EMS}{N}}$, where EMS = error mean square used to test treatments, and N = the number of observations/mean.

[2] Initial cow weights were 406 and 407 kg in 1982 and 473 and 466 kg in 1985 for P supplemented and control cows, respectively.

[3] One cow on each treatment died in the first study and 2 control and 1 P supplemented cows died in the second study. Two P supplemented and 5 control cows in the first study and 3 cows on each treatment in the second study were eliminated because they were open or lost calves. Retained dry cows were not included in calving and nursing or in the following gestation period data, but they were included in the next cycle if they were lactating.

[4] Treatments differed (P<0.08).

* Treatments differed (P<0.05).

calving and nursing period of 1983, and cumulative weight gains for the study were not significantly different. In the second study, P supplemented cows gained slightly more weight than control cows (P<0.08) during their first calving and lactation period and during the subsequent winter gestation period (P<0.05). However, during the 1986 calving and lactation period control cows gained more (P<0.08) weight than P supplemented cows, which agrees with results for the 1982 calving and lactation period when control cows lost less weight than P supplemented cows (Table 6). Weight gains for the remainder of the second study and cumulative weight gains for the full study were not significantly different between treatments.

Conception rates of P supplemented cows, analyzed over the 2 years of the first study, were higher (P<0.08) than rates of control cows (100 vs 93.6%) (Table 7). However, there were no conception rate differences between P supplemented and control cows in the second study, or when both studies were analyzed together. Feeding 1.8 kg oats, 5 days per week, post calving in 1986 and 1987 did have a positive effect on conception rate, resulting in a conception rate of 100% across P supplemented and control treatment cows for the 2 years combined, compared to an 88% conception rate for cows not receiving supplemental oats post calving. Oats were fed after calving to determine if milk production and calf weight gains were limited more by energy than P during this period. The apparent positive effect on conception rate was unexpected. Feeding oats after calving did not affect cow weights or calf weaning weights and there were no interactions between oats and P for any performance trait measured. Fishwick et al. (1977) reported that a long period of P inadequacy did not affect the subsequent reproductive performance of cows grazing on green grass at the time of breeding, and Call et al. (1978) reported that reproduction in Hereford cows was not adversely affected by

Table 7. Conception rates for phosphorus (P) supplemented and no P supplemented (control) range cows for studies beginning in 1982 and 1985 and ending in 1983 and 1987.

Calving year	Post calving treatment	P No. exposed	P No. bred	P Conception	Control No. exposed	Control No. bred	Control Conception
				- - - (%) - - -			- - - (%) - - -
				1982			
1982	—	24	24	100.0	26	25	96.2
1983[1]	—	23	23	100.0	21	19	90.5
1982-83		47	47	100.0[2]	47	44	93.6[2]
				1985			
1985	—	28	27	96.4	26	25	96.2
1986	Oats	13	13	100.0	11	11	100.0
1986	—	13	11	84.6	13	11	84.6
1987[1]	Oats	12	12	100.0	10	10	100.0
1987[1]	—	12	11	91.7	12	11	91.7
1985-87		78	74	94.9	72	68	94.4
1982-87		125	121	96.8	119	112	94.1

[1] Data were based on palpation results in the fall.

[2] Treatment means for 1982-83 were different (P<0.08).

Table 8. Mean birth date (±SE), birth weight (±SE) and least squares adjusted weaning weights (±SE) of calves from phosphorus (P) supplemented and no P supplemented (control) cows for studies beginning in 1982 and 1985 and ending in 1983 and 1987[1,4].

		P			Control				
Year	No. calves	Birth date	Birth wt	Adj. Wean wt.[3]	No. calves	Birth date	Birth wt.	Adj. Wean wt.[3]	Wean wt. difference
		(DOY[2])	(kg)	(kg)		(DOY[2])	(kg)	(kg)	(kg)
1982									
1982	26	97.0 ± 0.5	28.5 ± 0.1	171.9 ± 3.5[5]	24	97.5 ± 0.5	28.6 ± 0.2	162.2 ± 3.5[5]	9.7
1983	24	97.9 ± 0.5	34.5 ± 0.1	216.0 ± 3.8	25	97.1 ± 0.4	35.0 ± 0.1	210.9 ± 4.1	5.1
1985									
1985	28	101.8 ± 0.4	32.9 ± 0.1	236.8 ± 3.3	26	100.7 ± 0.4	33.1 ± 0.2	234.4 ± 3.6	2.4
1986	27	105.7 ± 0.3	37.6 ± 0.2	258.0 ± 3.1[5]	25	103.5 ± 0.4	36.8 ± 0.2	248.3 ± 3.2[5]	9.7
1987	23	105.0 ± 0.6	37.8 ± 0.2	271.4 ± 3.5[5]	22	108.6 ± 0.6	36.8 ± 0.2	259.5 ± 4.1[5]	11.9
1982-87	128	101.5 ± 0.1	34.2 ± 0.1	223.8 ± 2.0**	122	101.3 ± 0.1	34.1 ± 0.1	215.9 ± 2.3**	7.9

[1] Calf numbers are for birth date data, calf numbers for birth weight and adjusted weaning weights may vary due to death loss.
[2] DOY=Day of Year
[3] Weaning weights were analyzed using birth date as a covariant to adjust for differences in calf age and least squares to adjust for unequal numbers.
[4] SE=Standard error
[5] Adjusted weaning weights were different ($P<0.06$).
**Adjusted weaning weights over all 5 years were different ($P<0.01$).

a diet containing only 1.4 g kg^{-1} P. Read and Engels (1986a) however, reported markedly different reproductive results from 2 locations in South Africa; P supplementation of cows at 1 location had no effect on reproduction, but at a second location P supplementation resulted in a 50% improvement in conception rate. Improved reproduction in P supplemented cows at the second location was likely due to a substantial increase in feed intake.

Mean birth dates (day of year) of calves were not different between P supplemented and control cows in either study (Table 8). It had been anticipated that P supplemented cows might return to estrus and rebreed earlier than control cows. Calf birth weights were also unaffected by P supplementation (Table 8) which agrees with Fishwick et al. (1977). However, birth weights were increased by P supplementation at one location in South Africa where feed intakes had been severely depressed, but not at another location where feed intakes were normal (Read and Engels 1986a). Calf weaning weights adjusted by birth date in a covariance analysis and adjusted for unequal calf numbers using least squares procedures were higher ($P<0.06$) for P supplemented cows in 1982, 1986, and 1987 (Table 8). Treatment differences between unadjusted weaning weights were as great or greater than differences between adjusted weaning weights each year. Over the 5 calf crops of these 2 studies, adjusted weaning weights of calves from P supplemented cows were 7.9 kg heavier ($P<0.1$) than calves from control cows. These results are supported by the tendency of P supplemented cows to produce more milk and are in agreement with Fishwick et al. (1977) and Read and Engels (1986a).

In the studies reported here extrusa forage P was probably the best indicator of the cows' dietary P status. Serum P has been reported in other studies to be an unreliable indicator of an animal's P status, but at times in these studies, usually in the fall, lower serum P levels in control cows seemed to reflect forage P levels. The relationship between dietary and fecal P needs more study before fecal P can be considered a useful indicator of P intake.

Forage P levels encountered in these studies were below NRC (1984) recommendations much of the year, however differences in cow weight changes early in the studies were gradually lost by the end of the studies. The effect of consuming forages with low P levels during fall and winter months may have been offset by consumption of forages with relatively high P levels during early summer. Nevertheless P supplementation resulted in an apparent increase in conception rates in the first study and significantly heavier calf weaning weights 3 out of 5 years. Thus, P supplementation of range cows in the Northern Great Plains appears to be beneficial, and based on forage P levels the most useful time to supplement appears to be during the late summer and fall period. The most consistent benefit of P supplementation was heavier calf weaning weights. The data also suggest that conception rates may be improved by providing an energy supplement for 30 days after calving.

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Recovery of leafy spurge seed from sheep

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Abstract

Sheep are often used to graze North American rangelands infested with leafy spurge (*Euphorbia esula* L.), a long-lived perennial forb from Eurasia. Our objective was to determine if sheep grazing infested rangelands disperse leafy spurge seed by transport in their fleece or by depositing seeds in their feces. Twenty-four yearling Targhee ewes grazed a 2.4 ha native bunchgrass range site infested with leafy spurge from late-May through mid-August of 1993 and 1994. Six of the 24 ewes were shorn in October 1993. To recover leafy spurge seeds from those fleeces, we used a standard method to test wool for vegetable matter. On average, 38 seeds were recovered per fleece. During these summers, 6 small groups (n = 4 sheep per group) each grazed 3 separate paddocks. We estimated the density of leafy spurge seed before the groups were moved into 1 of 3 paddocks. After the sheep were moved into a paddock (day 0), we collected fresh feces from each group on or about day 4, 10, and 14. Feces were then washed over sieves to recover leafy spurge seeds. All seeds were tested for germinability and viability. The number of viable seeds excreted daily per ewe was estimated. In 1993, 1,796 ± 405 (S.E.) leafy spurge seeds m^{-2} were produced in the field, whereas in 1994, 399 ± 63 (S.E.) leafy spurge seeds m^{-2} were produced. The summer of 1994 was much drier than the summer of 1993. We estimated that 41 to 144 leafy spurge seeds were excreted daily per animal in mid-July 1993. Viability of seeds in the feces averaged 5%, whereas viability of seeds collected from seed stalks was 42%. We estimated that the ewes excreted from 2 to 41 leafy spurge seeds daily at the peak in mid-July 1994. Viability of seeds excreted during 1994 averaged 24%, whereas viability of seeds collected from seed stalks was 68%. Sheep can pick up leafy spurge seed in their fleece, and will consume and pass viable seed. However, viability of seed recovered from feces was highly variable and almost always lower than seed collected in the field. Despite reduced seed numbers and viability, sheep have the potential to spread leafy spurge and should be managed accordingly.

Key Words: weeds, feces, fleece, seed dispersal.

Leafy spurge (*Euphorbia esula* L.) is a perennial Eurasian forb that was first discovered in North America in 1827 (Selleck et al. 1962). This plant is considered noxious and currently infests over 1.1 million ha in the Northern Great Plains of the United States and Prairie Provinces of Canada (Lacey et al. 1985). Chemical control of leafy spurge is not cost-effective for most native rangelands (Lym and Messersmith 1987). Biological control with insects shows some promise, especially if it is integrated with herbicides (Lym 1994). This plant has had a major impact on the economy of North Dakota (Thompson et al. 1990).

Sheep and goats will graze leafy spurge and can be used to control infestations (Lacey et al. 1985). However, when sheep graze leafy spurge during the mature seed stage, seeds may become embedded in their fleece when seeds dehisce from capsules (Bakke 1936). Sheep also may pick up seed from the soil surface on bedgrounds. In the past, numerous plant species were introduced to Europe via sheep fleeces (Ridley 1930). Also, sheep on Utah rangelands pick up and presumably disperse capitula of squarrose knapweed [(*Centaurea virgata* Lam. var. *squarrosa* (Willd.) Boiss]; Roche and Roche 1992).

Sheep consuming leafy spurge seeds may also disperse viable seeds in their feces (Harmon and Keim 1934, Lehrer and Tisdale 1956, Özer 1979, Thill et al. 1986, Simao Neto et al. 1987, Dastgheib 1989). Viability of seed recovered from feces may be enhanced or reduced compared with seed that has not passed through sheep (Harmon and Keim 1934, Lacey et al. 1992, Wallander et al. 1995). Germinability of seeds recovered from feces generally decreases as residence time in the gastrointestinal tract of sheep increases (Özer 1979, Lacey et al. 1992, Wallander et al. 1995).

Before capsules of leafy spurge dehisce, sheep grazing infested rangeland consume seeds in capsules that may protect seed from mastication, rumination, and other digestive processes (Wallander and Olson, unpublished data). In 1 study, sheep were dosed with a known amount of mature leafy spurge seed (Lacey et al. 1992); only 18% of the seeds was recovered in their feces within 9 days. Viability of those seeds was reduced compared with unfed seed. Our objective was to determine if sheep grazing leafy spurge-infested rangeland can disperse leafy spurge seed by picking up seeds in their fleece, or by ingesting and passing viable seed in their feces.

Materials and Methods

Our study site was located in Gallatin County in southwestern Montana (111°33' W 45°40' N) at 1,480 meters above sea level

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on northeast facing bluffs above the Madison River. Soils are classified as loamy skeletal mixed Aridic Calciborolls (USDA 1995). The rangeland cover type is Idahoe fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith; Shiflet 1994). Leafy spurge cover varied from 0 to 70% on the site. Seeds of leafy spurge are roundish oval, obovate in outline and circular in cross-section, 2.0–2.5 mm long, 1.3 to 1.5 mm wide (Bakke 1936, Delorit 1970). Depending on seed color, 100 leafy spurge seeds weigh from 182 to 302 mg (Wicks and Dercheid 1953).

At our study site, a 2.4 ha pasture was divided into 3 similar sized blocks. Each block was further divided into 2 lanes. One lane of each block was for a group of yearlings (n = 4) that had been exposed to leafy spurge as lambs (experienced), the other was for a group of yearlings (n = 4) that had not been exposed to leafy spurge as lambs (naive). All yearlings were Targhee ewes, averaging 55 kg. Their staple length at the beginning of summer was approximately 2.5 cm with a fiber diameter of 22–23 microns. Each lane was divided into 3 paddocks. These yearlings were rotated twice through these paddocks infested with leafy spurge from late May until mid-August in 1993 and 1994. From mid-August until early October 1993, a subset of yearlings were kept in a small, tame pasture that did not contain any leafy spurge before they were sheared for the fleece study.

Seed in Fleece

In October 1993, 6 of 12 naive sheep were shorn and these raw fleeces (grease) were weighed. Each fleece was tested for vegetable matter using standard methods (ASTM 1993). In this test, wool was compressed in a cylinder and 3 subsamples of 50 cores (1.3 cm diameter) were removed from each fleece. Subsamples were weighed and digested in concentrated sodium hydroxide which dissolves wool fiber proteins. The remaining vegetable matter includes intact leafy spurge seed. Average number of leafy spurge seed recovered from the subsamples was multiplied by grease fleece weights to estimate the number of seeds per fleece.

Seed in Feces

As leafy spurge seed began to mature, seed densities were estimated immediately before sheep were moved into the next paddock. To determine seed densities, we walked diagonal linear transects across each paddock. A 0.25 m^2 frame was placed on the soil surface every 15 paces and then all leafy spurge material within the frame that contained seed was clipped. Twenty frames within each paddock were clipped. Each sample was bagged separately and air-dried. Seeds were categorized as immature capsules (less than 1/2 full size), mature capsules (full size), immature seed (yellow or yellow band), or mature seed (reddish brown up to gray and mottled; Wicks and Dercheid 1964), and then counted.

While the ewes were grazing a particular paddock, we collected 5 fresh fecal samples at least twice in each paddock, and often 3 times. Fecal samples were usually collected immediately after the ewe defecated. Seeds and capsules were readily visible in the field. Each fresh fecal sample was carefully inspected in the field, and cleaned if necessary, for capsules or seeds originating from the soil surface. Thus, we eliminated potential contamination by seed from sources other than seed ingested by the ewes. Sampling dates usually coincided with day 4, 10, and 14 after sheep entered a paddock. We repeated this sampling 3 times in 1993 and 1994.

Each fecal sample collected in 1993 was air dried, weighed, and then washed over sieves to recover leafy spurge seed. Dry weight of fecal samples ranged from 4 to 100 g. In 1994, the entire fecal sample was weighed fresh, then a subsample was air dried and weighed to estimate moisture content. The remaining sample was washed while moist over sieves to recover leafy spurge seeds. Wet weight of manure samples collected in 1994 ranged from 6 to 249 g. Moisture content ranged from 10 to 50%.

Number of seeds per gram of feces recovered from the field was estimated and expressed on an air-dried basis. The number of seeds excreted daily per animal was estimated by multiplying seeds per gram feces by 400 g. Mature, pregnant ewes grazing winter range defecate approximately 400 g dry matter daily (Soder 1993). Although pregnancy increases forage intake and fecal output, especially in the last trimester, forage intake and fecal output are lower on winter range (Soder 1993). Even though our yearlings were grazing summer range where forage intake and fecal output would be high, they were not pregnant and they were smaller than mature ewes. Based on these counteracting factors, we believe that 400 g is an appropriate estimate of fecal output. Polypay wethers (51 kg) have considerably higher fecal output (653 to 1,001 g dry matter per day), although these results were from confined animals consuming alfalfa pellets ad libitum (Hatfield et al. 1991).

Fecal samples were washed through 2 sieves to recover leafy spurge seed. A #10 sieve (2 mm opening) was placed on top of a #16 sieve (1 mm opening). Fecal samples were placed on the top sieve, rinsed with running water, and rubbed lightly to break up the sample. The #10 sieve retained full-sized capsules whereas the #16 sieve retained whole seeds and pieces of leafy spurge capsules. Fine organic material washed through both sieves. Dry fecal samples collected in 1993 were soaked in cold water for 4 hours before washing. Material retained by both sieves was collected, wrapped in paper towels, and dried at 37°C for 24 hours. After drying, samples were placed in cold storage until they could be examined for seeds. The accuracy of this procedure was tested by spiking each of 5 fecal samples with 30 mature seeds. All 30 seeds were recovered from each sample.

Percent germination of mature seed recovered from feces and collected from seed stalks was tested. Depending on the number of seeds recovered from each fecal sample, 1 to 20 seeds were placed on moist blotter paper in individual petri plates (n = 5 plates per fecal sample). For seed collected from seedstalks, we placed 20 seeds on each of the 5 petri plates. Seeds were treated with 10% (volume) chlorine bleach solution for 10 minutes and rinsed 3 times with deionized water. These plates were placed in diffuse light in a greenhouse set at 21°C daytime (14 hours) and 13°C nighttime (10 hours) temperatures. Deionized water was added as needed. After 21 days, these plates were moist stratified at 4°C for 30 days in the dark. Following stratification, plates were returned to the greenhouse to test germination for 21 days. Germinated seedlings with radicles greater than 10 mm and open cotyledons were removed every 3–4 days. Seed that did not germinate was tested for viability using tetrazolium (Grabe 1970).

Statistical Analyses

Average leafy spurge seed production (m^{-2}) in each lane was estimated for 3 sampling dates in 1993 and 1994, coinciding with when the sheep were moved into a new paddock and the beginning of a fecal collection period. The number of seed excreted daily per animal was estimated for 7 fecal sampling dates in 1993 and 1994. Least-square means of seed production and the number of seed excreted daily per animal were dependent variables in separate models. Collection period, block, and treatment (naive or experienced) were main effects with number of mature leafy spurge seed m^{-2} in the field as a covariate (PROC GLM; SAS 1988). Collection dates were tested within collection periods. In a second model, percent viability was the dependent variable, and collection period, block, treatment, and class (seed recovered from feces or collected from field) were main effects. Percent viability data were transformed (arcsine squareroot) to prevent the dependence of the variance on the mean, which is inherent with data that have binomial distributions (Sokal and Rohlf 1995). We present nontransformed data in figures. Viable seed excreted daily per animal was derived by multiplying the estimated number of seed excreted daily per animal by percent viability of seed recovered from the feces that day.

Results

Seed in Fleece

On average, 38.7 leafy spurge seeds were found in each fleece (Table 1), although 3 fleeces did not contain any leafy spurge seed. Fleece weights were about 50% of normal because the ewes were shorn in October, 6 months earlier than normal.

Seed in Feces

In late June 1993, 1,796 ± 405 (S.E.) leafy spurge seeds m^{-2} were produced in the field combining numbers of seeds in the different categories (Fig. 1a). Most of these seeds were in immature capsules. The proportion of mature seed collected from seedstalks increased as the summer progressed, although total number of seed decreased through the summer (P = 0.005). In 1994, 399 ± 63 (S.E.) leafy spurge seeds m^{-2} were produced on 8 July (Fig. 1b). Most of the seeds were mature at this time. Total number of seed decreased through the summer (P = 0.005). Besides sampling later, 1994 was considerably drier than 1993 and thus the plants may have been more advanced phenologically.

Table 1. Estimated number of leafy spurge seeds recovered from 6 fleeces in October 1993.

Sheep number	Fleece wt.	Seeds in fleece
	(kg)	(No.)
1	2.7	0
2	2.6	129
3	2.7	0
4	2.7	29
5	3.1	0
6	2.4	74

mean = 38.7 ± 21.6 s.e.

At the peak, 144 leafy spurge seeds were excreted daily per animal on 17 July 1993 (Fig. 2a). More seeds were excreted during this third week of July than in the other periods (period effect, P = 0.05). The number of seeds excreted daily per animal was lower in 1994 than in 1993. It peaked at about 40 seeds on 11 July 1994 (period effect, P = 0.76, Fig. 2b). In 1994, the number of seeds excreted was lowest on the first sampling date shortly after they had been moved from the previous paddock, and highest 3–4 days later (collection date within period effect, P = 0.02).

In 1993, viability of seed recovered from fecal samples increased after mid-July (period effect, P = 0.001), yet it was always lower than seed collected from seedstalks (P = 0.0007; Fig. 3a). In 1994, viability of seed recovered from fecal samples was lower than seed collected from seedstalks (P = 0.0002), but there was no trend through the summer (period effect, P = 0.26; Fig. 3b). Overall, viability of seed recovered from feces was lower in 1993 than in 1994. Viable seed excreted daily per animal ranged between 0 and 17 in 1993 and 0 and 10 in 1994 (Fig. 4a, b).

Discussion

Sheep grazing leafy spurge infested rangeland collected seed in their fleece. However, we believe that the crimped nature of wool would result in seed readily adhering to wool fibers and becoming embedded. Unless the seed drops before it has a chance to

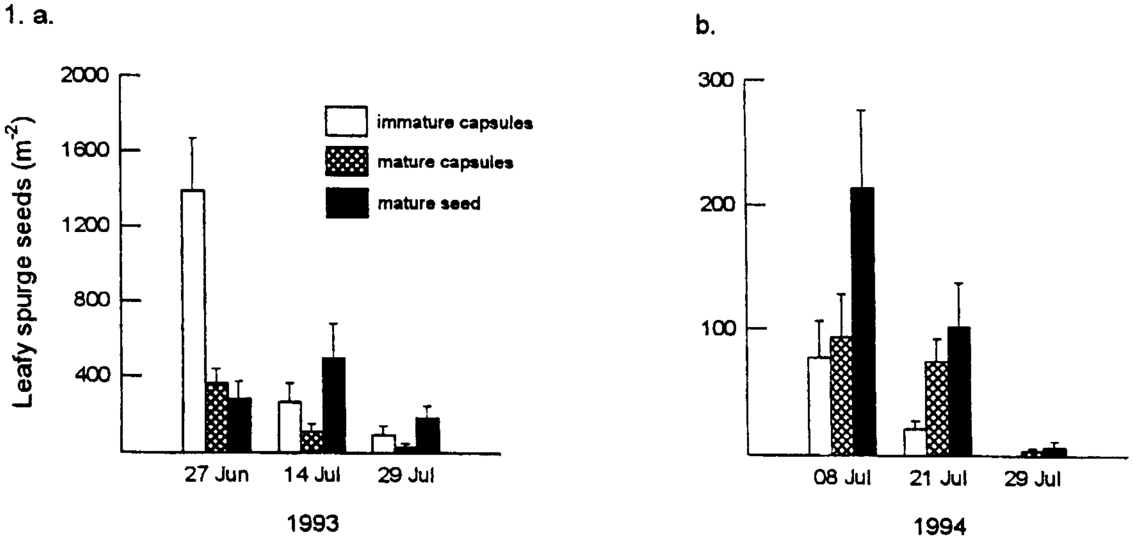

Fig. 1. Number of leafy spurge seed contained in immature capsules, mature capsules, and present as mature seed in a. 1993 and b. 1994. Sampling dates were immediately before sheep entered a new paddock. Note different scales on the y-axis for 1993 and 1994. Error bars represent ± 1 S.E.

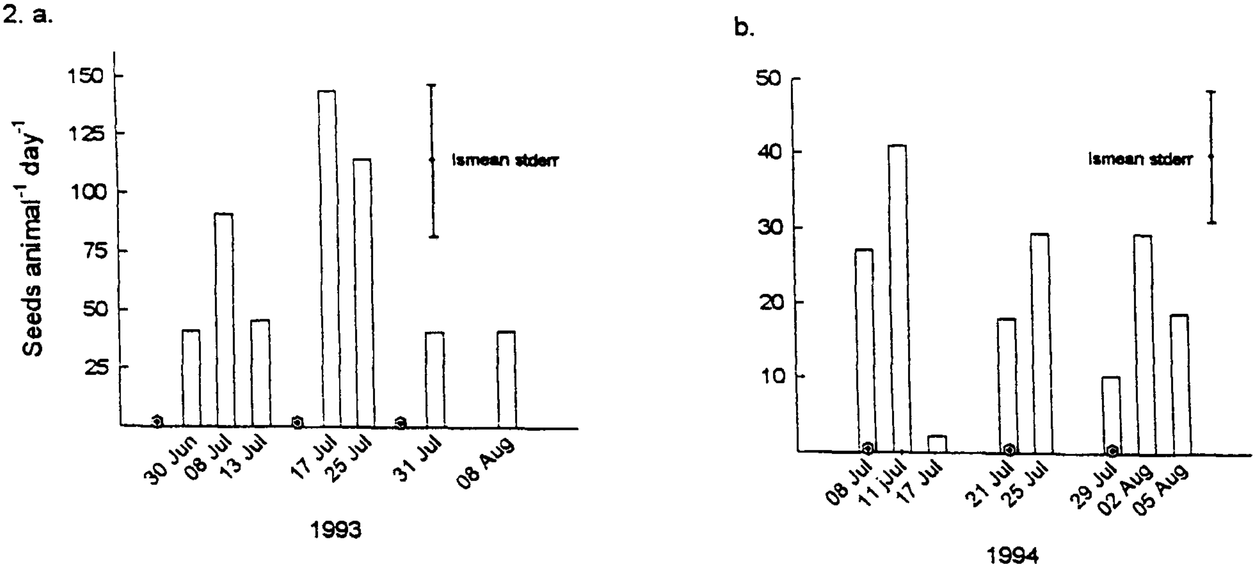

Fig. 2. Estimated number of leafy spurge seed excreted in feces of sheep in a. 1993 and b. 1994. Symbols indicate when sheep entered a new paddock. Note different scales on the y-axis for 1993 and 1994. Error bar represents ± 1 S.E. of least square mean.

become embedded, it is unlikely that seed would be dispersed later. More likely, the seed would fall out during shearing or processing (Ridley 1930).

Seed in capsules collected from seedstalks did not germinate. When opened for the tetrazolium test, most of these seeds were empty or contained a small embryo compared with mature seed. At this early stage of seed development, sheep ingesting leafy spurge capsules have a very low potential to spread viable seed. Wicks and Dersheid (1964) found that leafy spurge seed less than 13 days old does not germinate.

More seed was excreted by ewes in 1993 than in 1994. Presumably, this is related to the greater seed production in 1993, which reflects the abnormally high precipitation during spring and summer. Surprisingly, the proportion of viable seed produced was lower in 1993 than in 1994, indicating that seed quantity and quality can be inversely related. In 1993, the seeds may not have matured fully. Besides abnormally high precipitation, temperatures were cool during the summer of 1993 and seed could have developed more slowly. On the other hand, the differences could simply reflect the differences in how fecal samples were processed. They were dried in 1993, then seed was recovered several months later by rewetting the samples. In 1994, seeds were recovered from fresh, moist feces.

The amount of seed excreted in the feces of naive and experienced sheep was similar. This indicates that these groups of sheep were consuming similar quantities of seeds. In a 3 year (1992–1994) study on grazing behavior of these same sheep, both groups spent similar amounts of time grazing leafy spurge, and

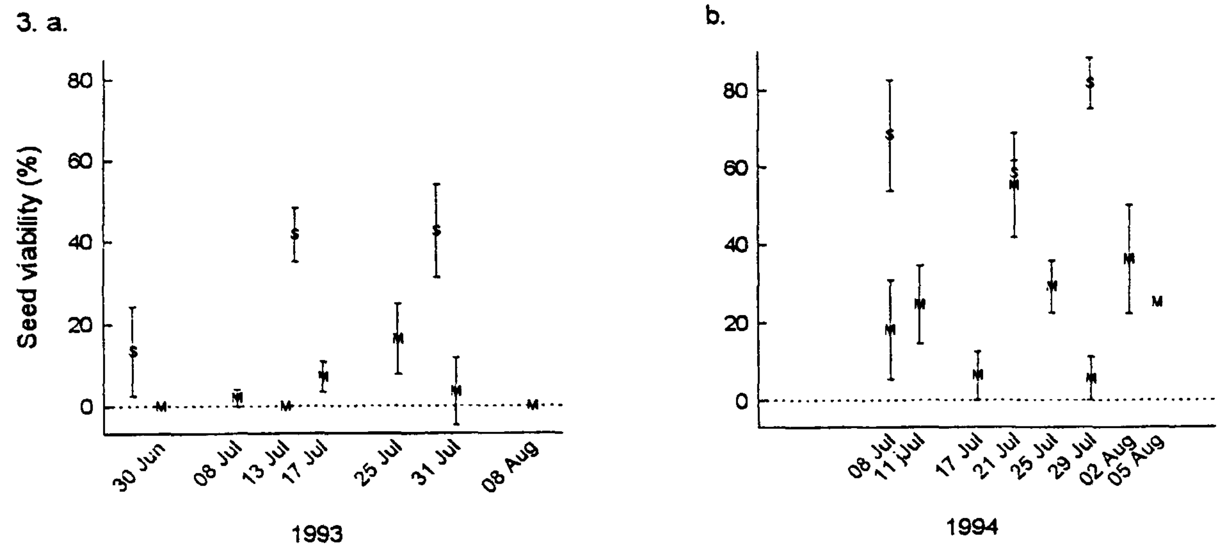

Fig. 3. Viability (%) of leafy spurge seed excreted in feces (M), and seed collected to determine densities at the site (S) in a. 1993 and b. 1994. Error bars represent ± 1 S.E.

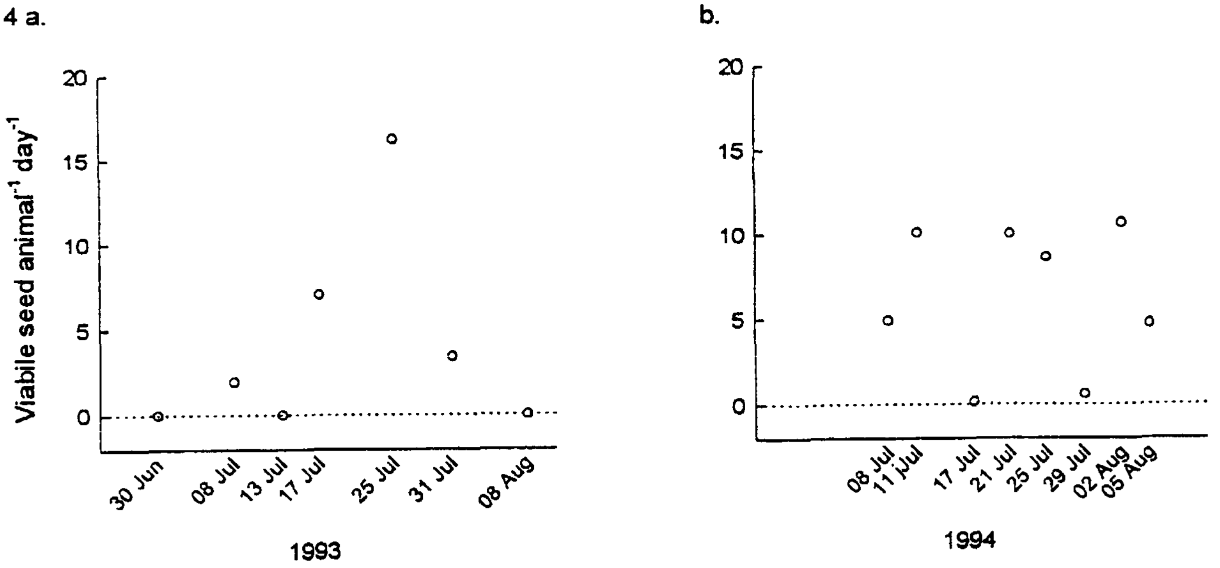

Fig. 4. Estimated number of viable leafy spurge seeds excreted daily per animal in a. 1993 and b. 1994.a

had similar biting rates of this species in mid- and late summer (Olson et al., 1996). The estimated number of seeds excreted peaked at 144 in 1993 and 40 in 1994. In another field study, about 120 seeds of another forb, *Echium plantaginaum* L., were excreted daily per sheep; germination of this seed was reduced by digestion (Piggin 1978). Based on a controlled dosing study, germination of leafy spurge seed is also reduced by passing through sheep and goats (Lacey et al. 1992).

In early July 1993 and the summer of 1994, seed excreted in feces was low on the first collection date within a period, increased on the second collection date, and then was low again on the final collection date. On the first collection date, the low number could reflect that the sheep had just left a paddock in which they had removed most of the seedheads shortly after they entered that paddock. On the second collection date, high numbers of excreted seed could reflect high consumption as they entered that fresh paddock. Most seeds of leafy spurge pass through sheep within 3–4 days (Lacey et al. 1992). On the third collection date, the low number could reflect that many of the available seeds had been consumed earlier, and had already passed through the digestive tract.

During both summers, seed that passed through sheep was less viable than seed collected in the field. Passing through the gastrointestinal tract of sheep, seed is constantly exposed to a warm, moist environment including microbial and enzymatic digestion. Apparently, one or more of these factors reduces viability of leafy spurge seed. Lacey et al. (1992) found that leafy spurge seed that was pulse-dosed to sheep was not viable after 4 days residence in the gastrointestinal tract. Whereas sheep digestion reduces viability, some leafy spurge seed in feces collected in our field study was viable. For a plant considered noxious such as leafy spurge, this would be undesirable if sheep are moved from infested to noninfested areas during seed set. Even with this potential for spreading viable leafy spurge seed via feces, these seeds may not germinate readily from feces in the field. In a study that did not include leafy spurge, germination from feces was very low during a 2 year period (Karl et al. 1994).

Conclusion

Sheep grazing leafy spurge infested rangeland pick up seed in their fleece. We did not trace the path of this embedded seed, however it is unlikely that this seed will fall out on site. On the other hand, seeds that are consumed and passed through the digestive tract may enhance the dispersal of leafy spurge. Land managers using sheep to graze leafy spurge are advised to graze leafy spurge so that it does not flower, or if it does set seed, to not move sheep from infested to noninfested areas unless the animals are confined for at least 5 days (Lacey et al. 1992).

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Range or meadow regrowth and weaning effects on 2-year-old cows

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Abstract

Eighty 2-year-old spring calving primiparous cows were assigned to 2 weaning and 2 grazing treatments (20 cows/treatment) from 7 September to 7 November in 1991, 1992, and 1993. Grazing treatments were native sandhills range or subirrigated meadow regrowth. Weaning treatments were weaning on 7 September or 7 November. Calves weaned on 7 September grazed subirrigated meadow regrowth after weaning. Crude protein of diets from esophagelly fistulated cows averaged 7.6% on range and 12.3% on subirrigated meadow on an organic matter (OM) basis. In vitro organic matter digestibility was 55.1% on range and 61.1% on subirrigated meadow. No year X grazing treatment or weaning X grazing treatment interactions were detected ($P>0.10$) for any traits measured. Forage organic matter consumed by cows differed between years: 7.7 kg day^{-1} in 1991 and 10.5 kg day^{-1} in 1992; but was similar ($P>0.10$) for all grazing and weaning treatments. Cows grazing meadow gained more body weight and body condition than cows grazing range. Dry cows gained more weight and body condition ($P<0.01$) than lactating cows. Lactating cows grazing meadow maintained body weight and body condition, while lactating cows grazing range lost body weight and body condition. Calves nursing cows on meadow gained 28.8 kg more ($P<0.01$) than calves nursing cows on range and 34.4 kg more than weaned calves grazing meadow. Body weight gains of weaned calves grazing meadow and calves nursing cows on range were similar ($P>0.10$). We concluded that dry cows and cows that grazed subirrigated meadow regrowth during September and October increased body condition score over lactating cows and cows grazing range, respectively. Calf body weight gains were greatest for nursing calves on subirrigated meadow, but grazing weaned calves on subirrigated meadow was an effective alternative for calf growth to calves nursing cows on range.

Key Words: subirrigated meadow, intake, digestibility, body condition, beef cattle

Body condition of cows at calving affects pregnancy rate and breeding date (Richards et al. 1986). Body condition score of spring calving cows wintered on range is influenced by fall body condition (Adams et al. 1987). Adams et al. (1993) found that cows suckling calves on Montana range lost body condition during August and September. They attributed the loss in body condition to inadequate consumption of crude protein. On a dry basis, diets of cattle grazing Sandhills range during August to October contain 6 to 8% crude protein (Rittenhouse et al. 1970). Hollingsworth et al. (1995) reported 11.2% crude protein on an OM basis in diets of cows grazing grass regrowth on subirrigated meadow during October. Meadow regrowth would be a higher quality forage for cattle than range in the fall.

Cow body condition during the fall can be maintained or increased by weaning the calf earlier or providing the cows with supplements (Short et al. 1994). Reducing the cows' nutrient requirements by weaning their calves or by providing them with higher quality forage to meet the nutrient demands might allow the cow to enter winter grazing in higher body condition. Our objectives were to determine if September weaning or grazing subirrigated meadows would improve body condition score of spring-calving primiparous beef cows during September and October over lactating cows on native range and to determine nutrient intakes by dry and lactating cows grazing native range or subirrigated meadow regrowth.

Resúmen

Ochenta y dos vacas primerizas de dos años de edad fueron utilizadas en dos tratamientos de destete y dos tratamientos de pastoreo (20 vacas/tratamiento), del 7 de Septiembre al 7 de Noviembre durante tres años (1991, 1992 y 1993). Los tratamientos de pastoreo fueron: a) Pastizal nativo y b) Humedales subirrigados. Por su parte los tratamientos de destete fueron: 1) Destete en Septiembre y 2) Destete en Noviembre. Muestras esofágious de la dieta (con vacas fistuladas), promediaron 7.6% de proteina cruda en el tratamiento a) y 12.3% en el tratamiento b). Los valores de digestibilidad in vitro de la dieta, fueron 55.1% y 61.1%, para los tratamientos a) y b), respectivamente. No se detectaron interacciones entre tratamientos. El consumo diario de materia organica difirió entre años: 7.7 kg/d en 1991 y 10.5 kg/d en 1992, más fue similar ($P>0.10$) en todos los tratamientos. Las vacas en los humedales ganaron significativamente ($P<0.01$) más peso (28.8kg) mientras que las vacas en pastizal nativo perdieron peso y condicción. No hubo diferencias ($P>0.10$) en los pesos al destete de los tratamientos de pastoreo, más los becerros del destete de Noviembre fueron 34.4kg. Más pesados que los destetados en Septiembre.

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Materials and Methods

The study was conducted on native range and subirrigated meadow at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory near Whitman, Neb. Eighty 2-year-old crossbred (1/4 Hereford, 1/4 Angus, 1/4 Simmental, and 1/4 Gelbvieh) primiparous beef cows and their calves were assigned to 2 weaning and 2 grazing treatments from 7 September to 7 November in 1991, 1992, and 1993. Grazing treatments were native sandhills range or subirrigated meadow regrowth after July haying. Weaning treatments were weaning on 7 September or on 7 November. Calves weaned on 7 September grazed subirrigated meadow regrowth after weaning in 1992 and 1993.

The range site (82 ha) was classified as sands and was in excellent condition. The dominant grass species were: little bluestem [*Andropogon scoparius* (Michx.) Nash], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], sand bluestem (*Andropogon hallii* Hack.), switchgrass (*Panicum virgatum* L.), sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths]. Common forbs and shrubs include western ragweed (*Ambrosia psilostachya* Dc.) and leadplant [*Amorpha canescens* (Nutt.) Pursh].

The subirrigated meadow soils were classified as Gannett-Loup fine sandy loam (course-loamy mixed mesic Typic Haplaquoll). Dominant vegetation on the 45 ha subirrigated meadows site was smooth bromegrass (*Bromus inermis* Leyss.), redtop (*Agrostis stolonifera* L.), timothy (*Phleum pratense* L.), slender wheatgrass [*Elymus trachycaulum* (Link) Gould ex shinn.], quackgrass [*Elytrigia repens* (L.) Nevski.], Kentucky bluegrass (*Poa pratensis* L.), prairie cordgrass (*Spartina pectinata* Link), and several species of sedges (*Carex* spp.), and rushes (*Juncus* spp.). Less abundant grass species were big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans*), and switchgrass. Forbs were a minor vegetation component.

Individual cows and calves were weighed and cows scored for body condition after 16 hours without feed or water on 7 September and 7 November. Body condition scores were based on a palpated determination of fleshing over the ribs and thoracic vertebrae. Body condition was scored from 1 (thinnest) to 9 (fattest) according to the system described by Richards et al. (1986).

Fecal output by 40 cows (10 cows/treatment) was determined on 7 through 12 October 1991 and 14 through 19 October 1992. Each cow on the intake trial was orally dosed with an intraruminal continuous chromium-releasing device[1] 5 days before a 5-day fecal collection period. Three to five hundred g of feces were obtained from the rectum of each cow daily at about 0800.

Twelve esophageally-fistulated cows (6 cows/grazing treatment, avg. body weight = 500 kg) were used to obtain diet samples from range and meadow during 1991 and 1992. Diets were collected 9 October 1991 and 15 October 1992. Cows were fitted with screen-bottom collection bags and forage samples were collected during a 30- to 45-min. grazing period.

Eight steers in 1991 and 7 steers in 1992 (avg. body weight = 400 kg) were assigned to each of the range and meadow grazing treatments. Steers were fitted with fecal collection bags for total collection and dosed with the same intraruminal continuous Cr releasing device as the cows to obtain a correction factor for fecal output (Adams et al. 1991, Hollingsworth et al. 1995). Feces contained in collection bags were weighed, mixed subsampled (150 to 300 g), and emptied twice daily at 0800 hours and again at 1800, during the 5-day collection period.

All fecal and extrusa samples were stored frozen until chemical analyses were performed. Extrusa and fecal samples were free-dried and ground to pass a 1-mm screen in a Wiley mill. Dry matter, organic matter (OM), and crude protein (CP) of extrusa and feces were determined by standard methods (AOAC 1990), neutral-detergent-fiber (NDF) was determined according to Van Soest et al. (1991), and acid-detergent-fiber (ADF) by the method of Van Soest (1963). In vitro organic matter digestibility (IVOMD) of esophageal extrusa was determined by the modified procedures of Tilley and Terry (1963) with the addition of 1 g urea to the inoculum/buffer mixture (Weiss 1994). Fecal samples were analyzed for chromium concentration by atomic absorption spectrophotometry using an air plus acetylene flame (Williams et al. 1962). Forage organic matter intake was calculated by dividing fecal organic matter by the organic matter indigestibility of esophageal extrusa.

Year and year X pasture were considered random effects. Data were analyzed using mixed model methods of SAS (1990). Because no year X pasture interactions were detected ($P>0.10$), data were pooled across years. Treatments were arranged as the main plot and weaning treatments as the sub-plot. Treatments were separated using non-orthogonal contrasts. Contrasts were: 1) range vs subirrigated meadow, 2) September vs November weaning, 3) September vs November weaning on subirrigated meadow, and 4) September vs November weaning on range. All differences mentioned in this paper are significant at the $P<0.01$ probability level unless otherwise noted.

Results and Discussion

During 1991 and 1992, CP concentration and IVOMD were higher, and ADF and NDF concentrations were lower in fistula forage samples from subirrigated meadow than from range (Table 1). Forage organic matter intake (Table 2) was similar ($P>0.10$) for all grazing and weaning treatments; pasture X weaning and pasture X year interactions were not significant ($P>0.10$).

Cow body weights and body condition scores differed ($P<0.05$) between range and meadow and between September and

Table 1. Crude protein (CP), neutral-detergent-fiber (NDF), and acid-detergent-fiber (ADF) concentrations and in vitro organic matter digestibility (IVOMD) of diets collected from esophageally-fistulated cows grazing on native range or subirrigated meadow.

	Treatments[1]		
Item	Range	Meadow	SE[3]
CP, % of OM[2]	7.6**	12.3	0.6
ADF, % of OM	47.8**	42.9	0.8
NDF, % of OM	79.6**	64.9	1.0
IVOMD, % of OM	55.1**	61.1	0.01

[1] The year X forage type interaction was not significant $P>0.10$ for all nutrient items.
[2] OM = Organic matter.
[3] SE = Standard error of mean.
**Range and meadow were different $P<0.01$.

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[1] Captec Chrome manufactured by Captec Pty. Ltd., Australia, distributed internationally by Nufarm Limited, Manu Street, P.O. Box 22-407, Otahunu, Auckland 6, New Zealand.

Table 2. Organic matter (OM) intake, body weight, body weight gain, body condition score, and body condition score gain of dry (D) and lactating (L) cows grazing range (R) or subirrigated meadow (M) regrowth from September to November.

	Treatments				Contrasts			
	R		M					
Item	D[1]	L	D	L	R vs M	D vs L	R+D vs R+L	M+D vs M+L
Intake kg/day	9.1	9.0	8.9	9.4	NS[2]	NS	NS	NS
Intake, kg/100 kg body wt.	2.0	2.1	2.0	2.2	NS	NS	NS	NS
	---------- Cow body weight ----------							
Final body wt., kg.	460.0	434.9	475.6	463.3	*	**	**	**
Body wt. gain, kg.	41.9	-12.9	93.8	61.7	*	**	**	**
	---------- Cow body condition ----------							
Final score	5.3	4.9	5.9	5.2	*	**	**	**
Body condition score gain	0.0	-0.4	0.6	0.0	*	**	**	**

[1]D calves weaned 7 September; L, calves weaned 7 November.
[2]NS, Contrast was not significant P>0.10.
*, Contrast was significant P<0.05.
**, Contrast was significant P<0.01.

November weaning (Table 2). Cows grazing subirrigated meadow regrowth gained more body weight and were heavier at the end of the trial than cows grazing on range (P<0.05). Dry cows gained more body weight and were heavier at the end of the trial than lactating cows. Year X grazing treatment and grazing treatment X weaning treatment interactions were not significant.

Lactating cows grazing range had lower body weights and condition scores than dry cows grazing range. Dry cows grazing subirrigated meadow gained more body condition scores and body weight (P<0.05) than lactating cows grazing subirrigated meadow. Loss of body weight and body condition scores of lactating cows on range have been reported during the late summer-early fall (Adams et al. 1989, Adams et al. 1993).

Importance of weaning and/or forage effects on a production system would be affected by amount of milk produced, growth as with 2-year old cows, late summer body condition score, and available feed resources for the winter. Cows with higher levels of milk production have greater nutrient requirements (NRC 1984) and are more likely to lose body weight and body condition during the late summer-early fall (Adams et al. 1993). If cows are thin in late summer, weaning in September or grazing subirrigated meadow would likely be beneficial. On ranches where cows graze low quality range or consume low quality forage during winter, benefits of weaning and/or grazing meadow could be important. Thin cows grazing range during winter will likely be thin at spring calving (Adams et al. 1987). During winter thinner cows have a greater energy requirement than fatter cows (Thompson et al. 1983) which could make it more difficult for thinner cows to consume enough forage to meet energy requirements. Increases in cow body condition score duirng winter are not expected (Villalobos 1993) with or without appropriate supplements. Even with supplements, loss of body condition was reported for cows grazing sandhills winter range (Sanson et al. 1990).

Table 3. Body weight and body weight gains of nursing calves grazing range or subirrigated meadow and weaned calves grazing subirrigated meadow from September to November.

Item	Nursing[1]		Weaned
	Range	Meadow	Meadow
Finals body wt., kg.	232.4[b]	264.9[a]	230.6[b]
Body wt. gain, kg.	29.7[b]	64.7[a]	33.6[b]

[1]Unweaned, calves weaned on 7 November: weaned, calves weaned on 7 September.
[ab]Least squares means in same row with different letters differ P<0.01.

Harsh winter weather would also affect the importance of body condition score. During harsh weather cows consume less range forage and digestibility is reduced (Kartchner 1980, Adams et al. 1986). Maintenance requirements of the cow are also increased during cold (NRC 1984), making it difficult for cows to consume enough forage to meet energy requirements.

Body condition score is more closely related to reproduction than is body weight in beef cattle (Dziuk and Bellows 1983). Cows in low body condition (i.e., score < 4) at calving may breed later or fewer will breed during a controlled breeding season than cows in higher body condition (i.e., score > 5), especially if body condition is declining between calving and the beginning of the breeding season (Richards et al. 1986).

Body weight of calves at the beginning of the trial was similar for all treatments each year (data not shown). Body weights of calves on 7 November and body weight gains over the trial of calves nursing cows on subirrigated meadow were greater than calves nursing cows on range or weaned calves grazing on subirrigated meadow (Table 3). Body weight on 7 November of calves weaned in September was similar to that of suckling calves grazing range.

The increased gains of calves nursing cows on meadow regrowth over calves nursing cows on range is partially explained by the difference in chemical composition of diets between range and meadow forage, especially crude protein. The protein content of the forages would have affected the quality of the calf diets and possibly the amount of milk produced by the cow and consumed by the calf. The improved body weight gain of nursing calves on meadow over weaned calves on meadow is best explained by more rumen escape protein provided by the milk to the intestines. Milk protein escapes ruminal digestion via the esophageal groove (Ruckebusch 1988). Hollingsworth-Jenkins (1994) found that, in calves grazing vegetative range, escape protein was limiting before energy or rumen degradable protein.

Conclusion

For production systems where cows are wintered on low quality forages, maintenance, or increased body condition during the summer or fall could be a benefit. Gain in body condition score during winter would not be expected.

We concluded that weaning in September or grazing subirrigated meadow regrowth during September and October maintain or increase body condition and body weight over cows suckling a calf or grazing range, respectively. Where there is not enough subirrigated meadow regrowth or a comparable high quality forage to support both cows and calves, weaning and grazing the calf on meadow or comparable forage and grazing a dry cow on range offers potential to maintain calf gains while maintaining or improving body condition of the cow.

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Effects of ruminant digestion on germination of Lehmann love-grass seed

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Abstract

Lehmann lovegrass (*Eragrostis lehmanniana* Nees) seed (germination 96%, dormant 0%) was used in 4 experiments to study the potential of sheep as a dispersal agent. Five, 4-year-old, ruminally cannulated wethers were used to examine effects of ruminant digestion on seed recovery and germination. All wethers were ruminally evacuated, and rumens were cleansed and reinoculated with strained ruminal fluid. After a 21-day adaptation to pelleted alfalfa, 4 experiments were conducted. Experiment 1 was designed to test viability of Lehmann lovegrass seeds exposed to ruminal and postruminal digestion. Lehmann lovegrass seed (10 g) was dosed intra-ruminally via ruminal fistula, and total fecal collections made. Of the viable seed ruminally dosed, 37% germinated within 21 days after recovery. Also, 98 to 100% of the seed that germinated was recovered within 72 hours of dosing. Experiment 2 was designed to test the influence of ruminal microbial digestion on seed degradation and viability, using in sacco nylon bag techniques. *In sacco* dry matter disappearance increased linearly from 5.5% at 3 hours of incubation to 16% at 120 hours. Germination of seed was not greatly affected until after 72 hours of ruminal incubation. Experiment 3 was designed to examine the effect of mastication on viability of Lehmann lovegrass seeds. Seeds were mixed with seed-free Lehmann lovegrass straw in a proportion of 1 to 10 (seed to straw) and 10 g fed to each wether. Boli were recovered manually via ruminal fistula. Thirty five percent of the seed fed entered the rumen without damage due to mastication. Experiment 4 compared *in vitro* techniques and *in sacco* techniques used to estimate the effect of digestion on seed viability. *In vitro* incubation techniques yielded similar results as *in sacco* techniques. We conclude that ruminants are potential disseminating agents of Lehmann lovegrass seed.

Resúmen

Semillas de pasto Africano (*Eragrostis lehmanniana*) con una germinación de 96%, fueron utilizadas en 4 experimentos para estudiar el potencial de los ovinos como agentes dispersantes de semilla. Se utilizaron 5 carneros con fistula ruminal para examinar los efectos de la digestion ruminal sobre la recuperación y germinación de la semilla. Después de un periodo de adaptación de 21 dias, se iniciaron los experimentos: *Experimento 1.-* Se dosificaron 10 g de semilla intraruminalmente, colectando todas las heces fecales. A las 72 horas se recupero el 90% de la semilla y a los 21 dias, germino el 37% de esta. *Experimento 2.-* Utilizando bolsas de nylon *in sacco*, se probo la influencia de la digestión ruminal sobre la degradación y viabilidad de la semilla. La desaparición de la materia seca se incremento linearmente de 5.5% a 3 horas de incubacion, a 16% a las 120 horas. La germinación de la semilla no fue afectada hasta después de 72 horas de incubacion ruminal. *Experimento 3.-* Se busca examinar el efecto de la masticación sobre la viabilidad de las semillas. Las semillas fueron mezcladas con paja en una proporción 1 a 10. El bolo ruminal fue recuperado manualmente a través de la fistula ruminal y el 35% de la semilla no fue dañado por la masticación. *Experimento 4.-* Se comparo la digestibilidad *in vitro* con la digestibilidad in sacco en términos de la viabilidad de la semilla, más no fueron detectadas diferencias. Con estos experimentos, se concluye que los rumiantes son agentes diseminadores potenciales de semillas de past Africano.

Key Words: *Eragrostis lehmanniana*, seed dispersal, digestion, mastication, sheep.

In 1932, several South African grasses were imported to the southwestern United States to reclaim land damaged by a combination of overuse and drought (Cox et al. 1988). Among these grasses, Lehmann lovegrass (*Eragrostis lehmanniana* Nees) establishes easily, and flourishes in areas too harsh for many revegetation species. Within 8 years of introduction, this species was used in revegetation projects throughout southwest Texas, southern New Mexico and southern Arizona. Although this species lessens soil erosion and provides good early season forage, it is also a highly competitive plant that is less palatable than native species (Ruyle and Cox 1985). Replacement of more palatable and nutritious native grass species has resulted in pure stands of Lehmann lovegrass (Anable et al. 1992). The area of expansion now exceeds the area of introduction (Cox and Ruyle 1986). Furthermore, expansion of Lehmann lovegrass may escalate due to development and release of cold hardy hybrids (Holzworth 1980).

Currently, expansion of Lehmann lovegrass is attributed to caryopsis (hereafter referred to as seed) dispersal by wind and surface water movement. Anable et al. (1992) examined the

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spread of Lehmann lovegrass into livestock exclosures and concluded that livestock are not necessary for seed dispersal. Yet, ruminants apparently act as dispersal agents of some grasses (Janzen 1984) and livestock may be involved in Lehmann lovegrass expansion. The objectives of our research were to 1) examine the influence of mastication and ruminal total tract digestion by sheep on passage rate, recovery and germination of Lehmann lovegrass seed and 2) compare in vitro and in sacco techniques to evaluate effects of ruminant digestion on seed germination.

Materials and Methods

Lehmann lovegrass seed purchased for these experiments was stated by the vendor to contain 99.41% pure seed with a germination of 40% plus 45% dormant seed (Lot No. 14117, Granite Seed Company, Lehi, Utah). A sample of the seed was submitted to New Mexico Department of Agriculture State Seed Laboratory, Las Cruces, N.M. to verify species and purity, plus germination and dormancy percentages. Germination and dormancy estimates obtained from the State Seed Laboratory were then used to verify our estimates of germination and dormancy percentages. For experiments requiring estimates of germinable seed (seed germinating within 21 days under standard conditions), 100 seeds were placed on 9 cm no. 615 qualitative filter paper[1] in 10 X 1.5 cm Petri dishes containing seed germination paper[2]. After wetting the seeds with a 0.2% KNO_3 solution containing captan, labeled Petri dishes were then placed in sandwich bags, sealed and incubated in a growth chamber with a 16 hour dark period at 20°C followed by 8 hours light at 30°C. Seedlings were counted and removed every 7 days until 21 days when both seedlings and unsprouted seed were counted. When indicated, presence of viable dormant seed was estimated using a topographical tetrazolium test (2, 3, 5-triphenyl tetrazolium; AOSA 1970). To determine the number of seeds per gram of air equilibrated dry weight, 23, one gram samples were manually counted. From these counts we determined that 13,309 seeds (±169) weigh 1 g.

Five, 4-year-old, ruminally cannulated Polypay X Rambouillet wethers were housed in individual pens (1.5 X 6 m) with free access to fresh water. Salt supplements were not offered during the study. Before initiation of the study, ruminal contents were evacuated manually and the rumen was cleansed until water removed from the rumen was clear and without particulate matter to remove seeds from other plant species. An aliquot (300 ml) of ruminal fluid was strained through 8 layers of cheesecloth and reintroduced into the rumen as a source of inoculum. During the next 21 days, all wethers were fed 2 equal proportions of prebloom pelleted alfalfa at 0800 and 1600 hours to provide 35 g dry matter • kg body weight^{-1} • day^{-1}. Alfalfa was pelleted into 95 mm pellets after being ground to pass a 32 mm sieve. Alfalfa pellets were sampled weekly, composited, and submitted for wet lab analysis (DHIA Forage Testing Laboratory, Ithaca, N.Y.). Results of these analyses are listed in Table 1. After the 21 day adaption period, wethers were used in the following 4 experiments.

Table 1. Compositional analysis of alfalfa pellets

Component	
Dry matter, %	91.5
	Dry matter basis
Crude protein, %	18.9
Acid detergent fiber, %	26.1
Neutral detergent fiber, %	33.1
Calcium, %	1.82
Phosphorus, %	0.21
Magnesium, %	0.4
Sodium, %	0.158
Iron, ppm	286
Zinc, ppm	25
Manganese, ppm	46
Molybdenum, ppm	4.8

Experiment 1

This experiment examined germination of ruminally dosed Lehmann lovegrass subjected to both ruminal and postruminal digestion. The day prior to dosing Lehmann lovegrass seed, all wethers were fitted with total fecal collection bags. At 0700 hours the following day, fecal bags were emptied and 10 g (133,090 seeds) of air-dried Lehmann lovegrass seed was placed into the rumen, cranial to the dorsal pillar and ventral to the ruminal cardia. For 10 days fecal bags were emptied daily at 0700 hours and feces thoroughly mixed and weighed. Five, 10 g aliquots of feces (wet basis) were placed on 40 and 60 mesh standardized soil sieves and cool tap water was run over the feces until feces were completely dissociated and particle size appeared uniform. Residual remaining on the sieves was then placed in Petri dishes and percent germination was determined. Sieve sizes were selected based on a preliminary study in which known amounts of seeds were added to 10 g of seed-free feces and seed recovery was measured and calculated. Recovery using this method was 96% (SE = 2.4) for 20 replicates. Another aliquot of feces was obtained each day for dry matter (DM) and ash content (AOAC 1990).

Statistical analyses across days were performed using GLM procedures of SAS (1989). Data were arranged in a randomized complete block design with data blocked by wether and day used as treatment. Blocking by wether accounts for the correlation among days within wether. Log transformations (count +1) were made to normalize the data. In the case of a significant ($P < 0.05$) F-test, means were separated using Sheffe's mean separation procedures.

Experiment 2

This experiment estimated the influence of ruminal digestion on seed germination, and immediately followed Experiment 1. Preweighed nylon bags[3] (10 X 15 cm; 40 μm pore size) containing 1 g Lehmann lovegrass seed were incubated in duplicate with a blank, intraruminally for 0, 3, 6, 12, 24, 36, 48, 72, 96, and 120 hours in each of the 5 wethers. After removal, the bags were washed until water draining from the bag was clear. One hundred seeds were removed from each bag for germination tests, the

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[1] Ahlstrom FIltration, Mt. Holly Springs, Penn.

[2] Kimpak®, Seedburo Equipment Co., Chicago, Ill.

[3] Ankom, Fairport, N.Y.

remainder of the seeds were left in the nylon bags and dried at 45°C for 48 hours. Before calculating disappearance from the nylon bags, a correction factor (avg wt of 100 seeds) was added to the weight of the nylon bag contents. In sacco dry matter disappearance rate of seeds was calculated using a model described by Mertens and Loften (1980). Statistical analyses were performed as in Experiment 1, except that data were distributed normally, therefore log transformations were not performed.

Experiment 3

This experiment was designed to estimate degree of Lehmann lovegrass seed damage due to mastication. Seed-free, hand cut Lehmann lovegrass (length < 2.5 cm) was mixed with Lehmann lovegrass seed in a proportion of 10 to 1 (DM basis). Each ruminally-evacuated wether was fed 10 grams of the mixture. The resulting boli were manually recovered via the ruminal fistula as boli entered the ruminal cardia. Boli were composited by animal, free moisture allowed to drain, and damaged and undamaged seeds were manually separated using a dissecting microscope. Undamaged seeds were defined as seeds with intact seed coats and having typical seed size and shape. Once separated, damaged and undamaged seeds were then dried at 45°C for 48 hours, allowed to air equilibrate and weighed. Means and standard errors of the proportion of damaged seed and seed recovery are reported.

Experiment 4

This experiment was designed to examine use of in vitro 2-stage digestion techniques to estimate the effect of ovine digestion on germination of Lehmann lovegrass seed. For the most part, modifications of Tilley and Terry (1963) as described by Ocumpaugh and Swakon (1993) were used in this study. In brief, 100 seeds were placed in 50 ml centrifuge tubes containing 0.25 g of alfalfa pellets ground to pass a 1 mm screen. To this, 28 ml of McDougall's solution prewarmed to 39°C was added. Subsequently, 7 ml of rumen fluid was added, the tube flushed with CO_2, agitated and incubated in a water bath maintained at 39°C for 0, 24, 48, or 72 hours. Inoculum was obtained from each wether 4 hours post-feeding (1200) on the last day of Experiment 2 and composited. After incubation, each tube was centrifuged for 20 min. at 2,000 X g and liquid decanted from the tube. Next, 35 ml of acid-pepsin was added to each tube and incubated at 39°C for 7 hours. Seeds and remaining alfalfa were isolated and thoroughly rinsed by filtration. Seeds were then counted and germination determined. Four replicates were used per incubation time, and alfalfa laboratory standards, with blanks, were run simultaneously using 48 hour ruminal fluid - 48 hour acid pepsin incubation times to compare activity of ruminal inoculum with prior runs.

Results

The seed used in this study had a germination percentage of 96% and no dormant seed. Germination estimates did not differ when measured after a 14 day prechill at 5°C. Estimates obtained from the New Mexico Department of Agriculture State Seed Laboratory were similar (95% germination and 0% dormant without prechill, 94% germination and 1% dormant with prechill). However, our estimates differed from those provided by the supplier (40% germination, 45% dormant). This difference is probably due to a 6 month interval between the supplier's tests and ours, during which time an after-ripening effect may have occurred that altered dormancy (pers. comm., Mark Pater, NRCS, Tucson Plant Materials Center).

Experiment 1

The 24 hour period following ruminal dosing, 17,870 to 33,563 germinable seeds were excreted (mean = 21,873, SE = 6,622), accounting for 13 to 25% of the seed ruminally dosed. During the second day, 16,840 to 26,496 germinable seeds (mean = 21,135, SE = 4,292) were excreted while, 451 to 4,319 germinable seeds were excreted during day 3 (mean = 1,811, SE = 1,466). Within the first 3 days, 98 to 100% of all germinable seeds were excreted. On day 4, the number of germinable seeds ranged from 0 to 422 (mean = 186, SE = 184). No germinable seeds were detected on day 5, while 42 and 40 germinable seeds were found in the feces of wethers 18 and 223, respectively, on day 6. No germinable seeds were found in fecal collections on days 7 and 8. The last day germinable seeds were detected in the feces was day 9 when 40 germinable seeds were excreted by wether 280. Interestingly, no seeds were detected in the feces of this wether for the 5 days prior to day 9. Total seed recovery (number of germinable seeds detected in the feces per number of germinable seeds dosed) varied between 32 and 49% (mean = 37, SE = 7). Because of the difficulty of finding seeds in the feces that did not germinate within 21 days, and due to the low percentage of dormant seed dosed, we did not count dormant or non-viable seeds. Consequently, recovery data may be slightly conservative.

Experiment 2

Percent ruminal in sacco dry matter (DM) disappearance of Lehmann lovegrass seed is illustrated in Figure 1. The nonlinear model of Mertens and Loften (1980) did not provide a good fit of the data. However, using linear regression following the initial disappearance of 6.0% (SE = 1.4) within the first 3 hours, disappearance increased at a rate of 0.09% hour^{-1} $\hat{y}$ 0.0876x + 6.0909, $R^2 = 0.88$). At 72 hours, the time at which 98% of the seeds have exited the digestive tract, in sacco DM disappearance of seed was 13.4% (SE = 0.58). Because the population of seeds in nylon bags may change with incubation time, no adjustment was made for germinable seed (96%). Percent germination of ruminally incubated seed is illustrated in Figure 2. Germination declined from 92.3% (SE = 0.92) at 0 hour to 76.1% (SE = 5.93) at hour 9. Percent germination did not change substantially until hour 96 (mean = 29.6, SE = 14.85); after which, percent germination declined to 2.1% (SE = 3.40) at hour 120.

Experiment 3

Thirty-five percent of seed (SE = 6) fed did not appear to be damaged by mastication. Recovery of viable seeds fed in this experiment was 74% (SE = 13). Incomplete recovery represents a potential source of bias.

Experiment 4

Using in vitro techniques percent of seeds germinating was 95 (SE = 1.1), 89 (SE = 5.5), 56 (SE = 8.9), and 52 (SE = 13.6) for incubation times of 0, 24, 48, and 72 hours, respectively. Except for the loss of 4 seeds from 3 tubes incubated for 72 hours, and 2 seeds from 1 tube incubated for 48 hours, all seeds were recov-

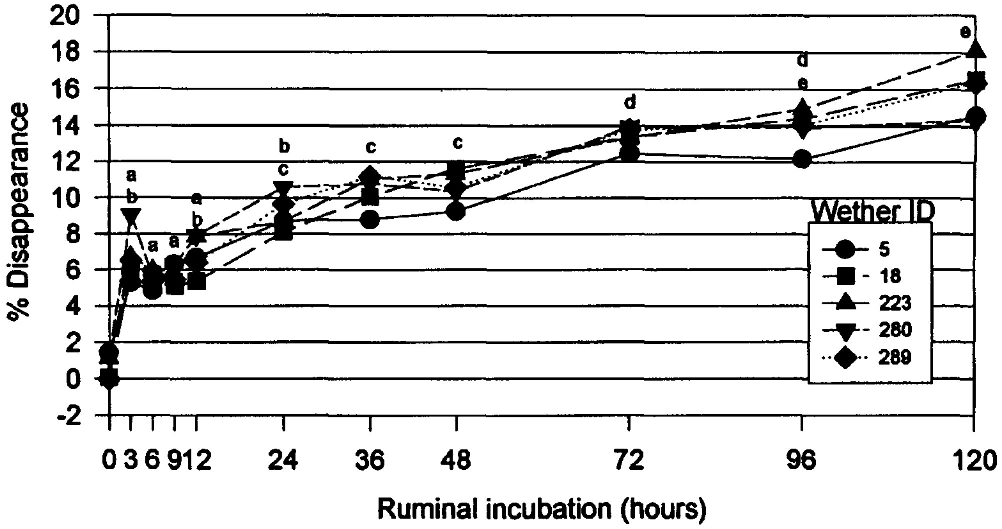

Fig. 1. In sacco dry matter disappearance of Lehmann lovegrass seed ruminally incubated in wethers. Hours with different letters differ, P < 0.05.

ered. Because of the large standard error associated with these estimates, we determined viability of seeds that did not germinate. Of the seeds incubated for 48 and 72 hours, 10 (SE = 7.1) and 28% (SE = 11.0), respectively, of the seeds were viable but did not germinate within 21 days.

Discussion

A large proportion of Lehmann lovegrass seeds consumed by sheep remain viable after excretion. If seeds deposited on the soil via sheep feces germinate and become established, then established plants will form new loci from which dispersal of seeds by other mechanisms will increase plant density and encroachment into adjacent areas (Moody and Mack 1988). Because Lehmann lovegrass is a prolific seed producer, the probability of a seed becoming established can be very low, yet the probability of a plant becoming established may be quite high. The distance from the parent plant that a seed is deposited will be determined by interactions of animal behavior, physiology, and environmental constraints influencing animal travel, digestion, and dunging patterns. Germination and establishment of the seed, once deposited on the soil, depends upon a complex set of seed physiology by environmental interactions.

Livestock must first select and consume seeds to effectively distribute seed via digestive processes. After flowering, sheep and beef cattle often graze the tops of reproductive culms by stripping seed from the culm. This behavior often occurs between grazing bouts, and during the cessation of morning and afternoon feeding bouts when grazing intensity, as determined by bite rate,

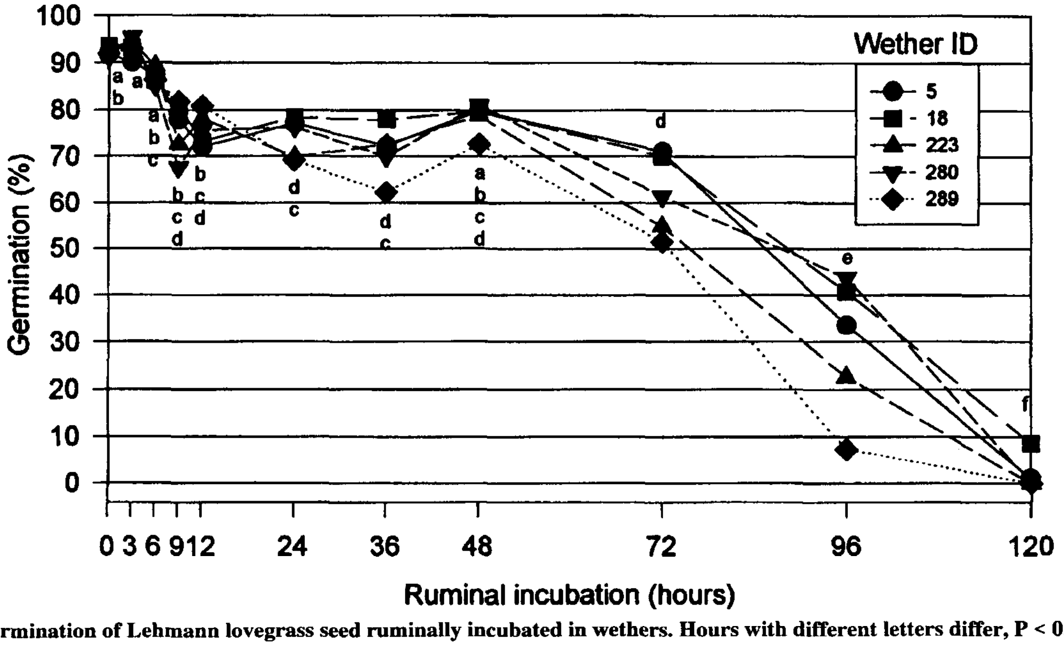

Fig. 2. Percent germination of Lehmann lovegrass seed ruminally incubated in wethers. Hours with different letters differ, P < 0.05.

is reduced. For example, Abu-Zanat (1989) observed that beef cows ate the top portions of Lehmann lovegrass to harvest the seed-heads and green herbage at the top of the plant; thus, avoiding residual vegetation in the lower portions of the plant. Given the more selective nature of sheep, sheep are more likely to exhibit this behavior. It is commonly accepted that Lehmann lovegrass is unpalatable during the growing season when growing in pastures with other perennial grasses (Bridges 1941, Ruyle and Cox 1985); yet, Reese (1980) showed percent use of Lehmann lovegrass during the summer months was greater than use of native perennial grasses (*Bouteloua eriopida*). This inconsistency suggests animal preference for Lehmann lovegrass does vary. Furthermore, production of Lehmann lovegrass seed under favorable conditions can approach 448 kg ha^{-1} (Anderson and Hafenrichter 1963), or six billion seeds ha^{-1}. Under these conditions, even occasional use of Lehmann lovegrass may lead to significant seed consumption.

Once selected, prehension and mastication of the seed and associated plant parts are the first processes that can damage the seed and its viability. Disarticulation of seed during prehension represents a reduction of potential seed intake. This aspect has not been examined but is likely to depend heavily upon plant phenology and mode of prehension. The proportion of seeds damaged by mastication is likely to be quite variable since ruminant chewing behavior during eating is erratic, lacking repetitive behavior (Beauchemin 1991). Factors affecting seed damage in our study likely include stress due to close human interaction (Le Neindre et al. 1993), stress due to confinement (Baldock and Sibley 1990, Lynch et al. 1992), and effects of ruminal distension on eating rate (Baumont et al. 1990). Because conditions imposed by the study probably altered eating rate and chewing behavior, the effect of chewing on seed damage under free-ranging conditions cannot be directly determined based upon these data. However, our data indicate that considerable Lehmann lovegrass seed can bypass the buccal cavity undamaged. Seed damage due to mastication by beef cattle is likely to be much less than damage by sheep. For example, processing of cereal grains, especially corn and sorghum, improves their digestibility for cattle considerably, yet processing is unnecessary when feeding grains to sheep (Hale 1973). Sheep do not require processing of feed grains because they chew their meals more thoroughly than cattle (Owens and Goetsch 1988).

Within a given diet, seed size, density and shape are primary determinants of the time a seed is exposed to ruminal digestion and rumination (Kaske and Engelhardt 1990, Sutherland 1988). Research examining these attributes on ruminal particulate dynamics is largely restricted to forage leaf and stem fractions, with few studies comparing a range of particle densities representative of seeds commonly encountered by the grazing animal. The seed of Lehmann lovegrass is spheroidal to cylindrical measuring 0.6 × 0.4 mm (Sumrall et al. 1991). When dry, seed density is 3.0 g ml^{-1} and approaches 2.6 g ml^{-1} when hydrated (Unpublished data. Fredrickson et al.). Density of forage particles in the rumen range from less than 1 g m^{-1} (Van Soest 1975) to 1.4 g ml^{-1} (Hooper and Welch 1985). Based upon studies examining ruminal passage of forage particles, Lehmann lovegrass seed should have a short residence time in the mast (Sutherland 1988, Katoh et al. 1988), and a high probability of exiting the rumen via the reticulo-omasal orifice (Kaske and Engelhardt 1990) without being impeded from exiting the rumen by the omasum (Poppi et al. 1980). The short residence time in the rumen lessens the probability of seed damage by rumination and ruminal digestive processes. Size and density attributes of Lehmann lovegrass seeds also suggest rapid movement through the postruminal intestinal tract. This view is supported by studies examining postruminal passage rates in steers (Siciliano-Jones and Murphy 1986).

Simao Neto et al. (1987) studied seed passage of signal grass (*Brachchiaria decumbens*; 1.1 g ml^{-1}, 2 mm × 4.7 mm) and carpet grass (*Axonopus affinis*; 1.6 g ml^{-1}) through the digestive tract of livestock. Recovery of undamaged seeds fed to sheep was 0.7 and 6.6% for signal and carpet grass, respectively, while recovery of seed fed to cattle was 22 and 37%, respectively. Mean retention time in the digestive tract did not differ between livestock species, with mean retention times of approximately 60 and 55 hours for signal and carpet grass, respectively. Simao Neto et al. (1987) also suggest that sheep provide a considerably more conservative estimate of the influence of ruminant digestion on seed viability. From data in Experiment 1 and 3 (combined effect of mastication plus ruminal and intestinal digestion), we estimated total recovery of germinable seed to be approximately 13.1% (SE = 3.9). Also, 48% (SE = 6) of the germinable seed was recovered within 24 hours, suggesting mean retention time approached 24 hours. Size, density, and shape of Lehmann lovegrass seed may explain, at least in part, the reduced mean retention time and greater recovery of viable seed than observed by Simao Neto et al. (1987). Other aspects of animal physiology and diet also should be considered. For example, Jones and Simao Neto (1987) determined that although the proportion of seed in the diet did not affect seed recovery, quality of the diet did. Ten percent of the seed was recovered when sheep were fed a low quality diet, and 28% was recovered when fed medium or high quality diets. This agrees with reports that digestive passage rates increase with diet quality (Galyean and Owens 1991) and recovery of viable seeds are greater when resident time in the digestive tract is least (Ocumpaugh et al. 1995).

Based upon in sacco data obtained in Experiment 3, it appears that Lehmann lovegrass seed is resistant to ruminal digestion with 16% disappearance at 120 hours. In contrast, in sacco dry matter disappearance for a low quality mature forage is 39% (5.9% crude protein, King et al. 1995), and 29% for disappearance of whole corn incubated in sheep on a roughage diet (Flachowsky et al. 1992). This indicates that whole seeds from graminoids are resistant to ruminal digestion and that Lehmann lovegrass seed is more resistant than corn. Ruminal incubation does affect 21 day germination, but this effect is minimal until 72 hours. At 120 hours of incubation, few seeds germinated. That seeds incubated in vitro for 48 and 72 hours had a greater percent of dormant seeds than seeds not incubated indicates a shift toward increased dormancy with longer in vitro incubation periods which may have important consequences affecting seedbed ecology and establishment of Lehmann lovegrass.

In vitro techniques described by Ocumpaugh and Swakon (1993) appear to be a good indicator of the effects of ruminal digestion on seed viability if dormant (seeds not germinating but viable) and germinable seeds are considered for both the 48 and 72 hour incubation times. Because of obvious bias due to partial seed recovery and difficulty recovering nongerminable seed from feces, a comparison between in vitro and in situ total tract influences on germination was not made. However, gastric digestion may influence seed physiology and may affect interpretation of digestion effects on seed viability. A combination of ruminal in sacco and postruminal mobile nylon bag techniques (Vanhatalo and Ketoja 1995) may provide a better test of the accuracy of in vitro techniques to predict the effect of total tract digestion on seed germination.

Because it is not known if Lehmann lovegrass seeds will germinate and establish in arid environments after passing through the digestive tract of sheep, we cannot conclude that sheep contribute to the expansion of Lehmann lovegrass populations. Lehmann lovegrass seeds are excreted in a nutrient-rich environment. Furthermore, Lehmann lovegrass seeds germinate better with light exposure and large temperature fluctuations (Roundy et al. 1992), although temperature fluctuations may be greater for seeds in feces the amount of light affecting the seeds will be reduced. This may maintain dormancy and cause a sustained release of viable seed that will be exposed to a variety of conditions, including conditions favorable for Lehmann lovegrass establishment or continued dispersal via phase II mechanisms described by Chambers and MacMahon (1994). Seeds from other grasses remain viable after being buried in feces for periods greater than 30 months (Wicklow and Zak 1983).

Conclusions

The rapid expansion of Lehmann lovegrass from seeded areas into adjoining native rangelands is thought to be due to seed dispersal by wind and water. The possible influence of ruminants and other seed predators on the expansion of Lehmann lovegrass in North America has received little attention. This study confirms Lehmann lovegrass seeds can pass through the ruminant digestive tract and remain viable. If seeds germinate and establish in dung, or after decay of dung, then ruminants must be considered as a factor that facilitates the spread of Lehmann lovegrass. In this case, knowledge of gastrointestinal passage rates and effects of digestion on seed viability will be helpful in developing management strategies that seek to reduce the rate of lovegrass spread.

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Comparing techniques for determining steer diets in northern Chihuahuan Desert

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Abstract

Diets determined by bite count and microhistological analysis of esophageal extrusa and feces were compared for steers grazing on grass-shrublands in the northern Chihuahuan Desert. The study was conducted on the Chihuahuan Desert Rangeland Research Center near Las Cruces, New Mexico. The purpose was to determine the similarity of 3 dietary techniques on arid, heterogeneous rangeland. It was proposed that the number of bites of each species eaten was directly proportional to the weight eaten as determined by the 2 microhistological techniques. Samples of diets were collected in 4 seasons from 2 steers grazing in a continuous yearlong pasture and in seasonlong rotation pastures.

The 3 dietary techniques did not give similar (P<0.10) estimates of the diets eaten by the steers. Mean similarity indices were highest (77%) comparing diets from analysis of esophageal and fecal material. Lowest mean similarity indices (57%) were from comparing diets from bite count and fecal analysis. Much of the discrepancy between techniques was because of different size plants being eaten and heterogeneity of plant distribution. An importance ranking of dietary species using the 3 techniques showed that the top 3 species comprised over 68% of the total diets. Any of the 3 techniques can be used to determine the common species in the diets which may be all that is necessary for some management and analysis needs.

Resúmen

Los métodos del conteo del bocados y del análisis microhistologico de nuestras esofágicas y de heces, fueron comparados en novillos pastoreando en una comunidad de pastos y arbustivas en el norte del Desierto Chihuahuense. El estudio se llevo a cabo en el Centro de Investigaciones sobre Pastizales del Desierto Chihuahuense, cerca de Las Cruces, New Mexico, utilizando novillos y colectando muestras durante leas 4 estaciones del año. Se propuso que el numero de bocados de cada especie consumida era directamente proporcional al peso consumido.

Los resultados de los métodos fueron estadisticamente diferentes (P<0.10). Los indices de similaridad fueron mayores (77%), cuando se comparó la dieta en muestras esofágicas con las de heces fecales. Los indices de similaridad fueron menores (57%) cuando se comparo el conteo de bocados con el análisis microhistologico de heces. Mucha de la discrepancia de los datos obtenidos entre tratamientos, fue debida al diferente tamaño de las plantas consumidas y a la hetergenidad de la vegetación. Los 3 métodos mostraron que 3 especies constituyeron el 88% del total de la dieta, sugiriendo que cualesquiera de los métodos puede ser util para este tipo de estudios.

Key Words: bite count, microhistological diet analysis, desert grassland.

One of the basic problems confronting the range scientist is an accurate assessment of the nutritive value and botanical composition of the grazing animal's diet. Knowledge of foods used by herbivores is basic to the management of their populations and environments (Galt et al. 1969, Ward 1970).

Techniques and the variations used for determining diets are discussed in Holechek et al. (1984). Three techniques commonly used are direct animal observations and analysis of either fecal materials or esophageal fistula extrusa. There are several studies where technique comparisons have been made, but only limited information is available on dietary comparisons of the 3 aforementioned techniques, particularly in an arid environment, such as the northern Chihuahuan Desert.

The primary hypothesis tested in this study was that there are no differences in the estimates of the various species compositions in the diets among the 3 techniques. Direct observation (bite count or feeding time) is easy and simple and requires no equipment or surgery, but difficulty may arise in identification of plant species or situations where an animal may eat more than 1 species in a bite (Holechek et al. 1984). A problem with bite count method (Reppert 1960) is getting an estimate of weight consumed for each species. Regelin et al. (1974) simulated deer diets by hand plucking and found negligible differences between percentages of bites for a species and the percentage weight for the same species calculated by hand plucking. Getting actual weights for bites as proposed by Free et al. (1971) is difficult because of heterogeneity of the rangelands and the need for esophageal fistulated animals. Another potential source of error is developing an exchange ratio between bites of small plants and large plants as suggested by Sanders et al. (1980). Therefore, because of the difficulty in obtaining bite weights, number of bites of each species was assumed in this study to be directly pro-

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portional to weight intake of each species as proposed by Regelin et al. (1974).

The other 2 techniques studied also have problems. Both require extensive training in the use of microscopes, identification of plant fragments and careful preparation of microscopic slides (Holechek and Gross, 1982). Using esphogeal fistulated animals involves extra care of the animals. Vavra et al. (1978) and Coates et al. (1987) point out that diets from esophageal extrusa represent only a small portion of the total diet that animals select and eat from a pasture.

Diets determined from feces better represent the diets being selected from the whole pasture over a longer time period (Holechek et al. 1984). It also allows the estimation of diets without disturbing the animals. Problems associated with using fecal material to estimate diets are the different digestion rates of plant species, difficulty of identification due to greater degradation of cell wall material, and determining the age of fecal material sampled.

Holechek et al. (1984) ranked 13 dietary techniques by accuracy, precision, cost, and time. Microhistological analysis of feces and microhistological analyses of esophageal extrusa were ranked 2 and 4, respectively, while bite count with tame animals was ranked 7th. Vavra et al. (1978) mentioned that the esophageal method is often considered the standard. However, they also point out that analysis of fecal material to determine diets may be more important and practical when working with wildlife or where it is difficult to handle fistulated animals.

Study Area

This study was conducted on the New Mexico State University Chihuahuan Desert Rangeland Research Center located 38 km north of Las Cruces, N.M. Pastures in 2 grazing strategies were sampled, continuous yearlong grazing, and rotationally grazed pastures. The pastures varied in size from 500 ha to 1,250 ha. Each grazing strategy had a cow herd. Each of the 3 rotational pastures were grazed for an entire season at approximately the same time each year. Elevation of the study pastures varies from 1,330 to 1,348 m. Climate of the area is arid, typified by very low relative humidity. Daily temperature fluctuations of 22°C are not uncommon. Average maximum temperature varies from a high of 36°C in June to a low of 13°C in January. The average wind velocity is 3.2 km per hour with highest wind movement occurring in April and May. Average annual precipitation is 23 cm (1930 to 1988) of which 52% falls during the growing season of July through September. Annual rainfall was near 30% above average in 1987 and 1988, preceding and during this study.

The general area is classified as semidesert grassland, composed primarily of herbaceous species with light to dense stands of shrubs scattered throughout the area. Vegetation is similar across all study pastures, but species differ in abundance in each part of the pastures. Major grass species are black grama (*Bouteloua eriopoda* [Torr.] Torr.), mesa dropseed (*Sporobolus flexuosus* [Thurb] Rydb.), three-awns (*Aristida* spp.) and fluffgrass (*Erioneuron puchellum* [H.B.K.] Tateoka). Many forb species are common on the pastures. Primary shrubs include mesquite (*Prosopis glandulosa* Torr.), snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby), soaptree yucca (*Yucca elata* Engelm.), longleaf ephedra (*Ephedra trifurca* Torr.) and fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.). Surface soil layers vary from loamy fine sands to sandy loams, with depths to caliche varying from 10 to 100 cm (Beck 1978). Soils have almost no humus or organic matter and there is little change in texture between surface soil and subsoil.

Materials and Methods

Diet Sampling

Two yearling crossbred steers (Brangus X Hereford) weighing about 225 kg were esophageally fistulated. The steers were put on the study pastures 10 days before collecting samples in each season. After dietary samples were collected, steers were removed from the pastures and placed in drylot until the next sampling period.

Samples were collected for 6 days in each of the following months: May, August, and December 1988 and March 1989. Collections were made for 3 consecutive days from the rotation pasture where cows were grazing and for 3 consecutive days from the continuous yearlong pasture where another herd of cows were grazing. Steers were allowed from 1 to 5 days to adapt to the next pasture before sampling was again initiated. The sampling scheme involved taking esophageal samples and counting bites each collection day. Fecal samples were always collected 24 hours later. Procedures for collecting fistula samples involved penning the animals in late afternoon until initiation of collection the following morning at 0700 hours. Overnight fasting helps prevent regurgitation of rumen contents when sampling the following morning, but may cause the animals to be less selective (Holechek et al. 1984). However, as reported by Coates et al. (1987) and observed in this study, the steers did not appear to be less selective or eat faster compared to observations at other times. Before grazing, the stainless steel cannulas were removed from each steer and canvas bags with screen bottoms were placed on each animal for collecting samples. Steers were driven to an area near where the cows were grazing and allowed to graze for 30 minutes. Collection bags were then removed and the cannulae replaced. The bite count procedure consisted of a person following each steer, counting and recording each bite the steer ate during the 30 minutes of esophageal sampling. The observer stayed close to the steer, generally less than 3 m, in order to recognize plants being eaten.

After esophageal and bite count sampling was completed each morning, steers were released to graze freely until being penned that evening. Samples of the esophageal extrusion from each steer were immediately placed on ice for transportation to the laboratory where it was dried, stored and ground for later botanical analysis. Fresh fecal samples were collected from each steer as soon as they were observed defecating early in the morning (days 2 thru 7) before they started to graze. Fecal samples were treated the same as the esophageal samples.

Botanical Analyses

Microscopic slide preparation and analysis were the same for esophageal fistula and fecal material. Five slides were prepared from each fecal and esophageal fistula sample. Sample material was soaked in sodium hydroxide and mounted using techniques described by Holechek (1982). The slides were dried at room temperature for 3 to 4 weeks before analysis. Slides of reference plant species collected from the study area were prepared in the same manner as those for the fecal and fistula material. These reference slides were used to aid in correctly identifying the plant fragments contained in the esophageal fistula and fecal material. The observer practiced on slides prepared with known mixtures of plants from the study site as described by Holechek and Gross (1982). Twenty fields were systematically observed at 125x magnification for a total of 100 fields/sample. Plant fragments were identified by epidermal characteristics and recorded as frequencies. Relative frequency of each species in the diet of each steer for each day was calculated and this was converted to relative density (Fracker and Brischle 1944) to obtain an estimate of the weight of each plant species in the diet.

Number of bites of each plant species was divided by total number of bites of all species and a percentage that each species comprised of the diet was obtained. Number of bites were considered proportional to the intake weight of a species as suggested by Regelin et al. (1974), and were not adjusted for bite size as suggested by Free et al. (1971).

Herbage Available

Herbage available (kg/ha) was measured in the same locations where steers grazed during collection periods. Ten 0.5 × 1.0 m quadrats were clipped each day along a transect where the steers grazed each day. A total of 60 quadrats were clipped for each collection period. Current year's growth was clipped at ground level and separated from old growth. Samples were air dried and the weight of each species recorded.

Weight of mesquite leaves, longleaf ephedra green stems and soaptree yucca green leaves was determined by dimension analysis (Ludwig et al. 1975). Shrub weight available per unit area was determined by multiplying density of shrubs times average volume times average weight per volume. Density of shrubs was determined from thirty, 50 × 4 m transects in each pasture in the areas where the steers grazed. The volume of each shrub occurring in the transects was determined by measuring the height and the long and short diameters. Mesquite volume was determined using the upper half prolate spheroid formula and the volume for the other shrubs was determined using a formula for a cylinder (Ludwig et al. 1975).

Data Analyses

Diet techniques were compared for major species and groups of species. Diets were compared in a mixed model factorial experiment in a completely randomized block design. Steer-day was the experimental unit. Observations within a season and grazing strategy were pooled across days for a total of 48 records. The main effects, steer (considered block), grazing strategy and season were tested using the steer × grazing strategy × season interaction as the testing term. Diet techniques and associated interactions were tested using the residual error term with 16 degrees of freedom. The loss of degrees of freedom by pooling across days within a season and grazing strategy allowed the sources of variation to be tested with more precise error terms (SAS 1985) in a general linear model. Least square means were used to calculate all probability values testing the hypothesis that the diets estimated by each technique were similar. Significant differences were noted where $P<0.10$.

Diets determined by each technique were also compared with each other for each sampling period using Kulczynski's similarity index (Oosting 1956): $2\ w/a+b \times 100$, where $W =$ is the total sum of the lowest of each pair of percentages common to the diets determined by 2 techniques; a and b represent the sum of all percentages found, respectively, in the a and b diets. The index may vary from 0% (no similarity) to 100% which indicates diets are identical.

For similarity indices mean and standard errors were calculated by season and grazing strategy. Individual species were also ranked as to their abundance in the mean diet determined by each technique across seasons and grazing strategies (Vavra et al. 1978). This importance value allows the comparison of which species were the overall important constituents in the diets.

Results and Discussion

The 3-way interaction, dietary technique × grazing strategy × season was significant for 5 of the 8 common species and plant groups tested (Table 1). In each sampling period steers were hazed early in the morning to where the resident cows were grazing. The cows, being familiar with the pastures grazed on certain vegetation types in the different seasons. Therefore, the steers had differing amounts available of the common forage plants between pastures and among seasons. The differences in availability of forage plants (Table 2) were reflected in the diets selected. The higher amount of available forage in December was because the cows were grazing more in the grassland areas and because late summer and early fall rains caused an increase in forb growth.

Differences within a dietary technique between grazing strategies (Table 1) reflects the variation in the amount available of a particular species between locations where the resident cow herds were grazing in their respective pastures. For example, in May, black grama comprised 3% of the bite count diet on the yearlong pasture (5 kg/ha available) and 13% of the diet on the seasonal pastures (118 kg/ha available, Table 2).

The 3 dietary techniques did not give similar estimates of the diets eaten by the steers. The method suggested by Regelin et al. (1974) of bites being equal and directly proportional to the weight of each species being consumed was not supported by this study. The handplucks they collected from forage species to simulate deer's diets needed to be fairly uniform. Because of mouth size and style of eating, deer generally eat smaller and more uniform bites compared to steers. Steers can eat large amounts of forage rather indiscriminately, often eating more than 1 species and several plant parts in a bite. However, steers can also take small bites. For example, the amount of three-awns in the bite count diets was greater than the amounts determined by the other 2 techniques for 3 of the 4 sampling periods (Table 1). These differences are probably because the steers tended to take many small bites from around the base of the three-awns where there were more green leaves rather than a few large bites from the top where more seedheads and dead plant material were present. This same pattern can be seen in the May and March sampling period for the other-forbs category. In these seasons there were many forbs of small stature, and though many bites were recorded, they comprised little of the diet weight determined by the analysis of esophageal and fecal material. For croton an opposite pattern was found; the number of bites generally underestimated the amount of weight being consumed as compared to the other 2 techniques. This was because of crotons' larger stature and upright growth form which allowed the steers to often eat an entire plant in 1 bite.

Table 1. Comparison of steer diets in 1988–1989 (% relative weight averaged across 3 sampling days) using 3 techniques: bite count, microhistological examination of esophageal extrusa and microhistological examination of feces in 2 grazing strategies in the northern Chihuahuan Desert.

		Month and grazing strategy							
		May 1988		August 1988		December 1988		March 1989	
Species	Technique	Yearlong	Rotation	Yearlong	Rotation	Yearlong	Rotation	Yearlong	Rotation
		(%)							
Aristida spp.	Bite[1]	14^{a}	13^{a}	T	T	12^{a}	14^{a}	21^{a}	15^{a}
	Esoph.	6^{b}	5^{b}	1	1	3^{b}	1^{b}	7^{b}	1^{b}
	Fecal	1^{b}	3^{b}	1	1	1^{b}	1^{b}	4^{b}	1^{b}
Bouteloua eriopoda[2]	Bite	3^{y}	13^{x}	10	4	44^{ax}	2^{y}	24^{by}	43^{bx}
	Esoph.	8	15	10	7	27^{bx}	3^{y}	27^{aby}	71^{ax}
	Fecal	8	12	11	3	8^{c}	T	36^{ay}	79^{ax}
Sporobolus spp.[2]	Bite	67^{bx}	38^{y}	62	58^{b}	9^{cy}	49^{bx}	22^{b}	12
	Esoph.	81^{ax}	35^{y}	63	54^{b}	42^{by}	80^{ax}	54^{ax}	12^{y}
	Fecal	79^{ax}	39^{y}	69	74^{a}	61^{ay}	84^{ax}	53^{ax}	15^{y}
Other grasses	Bite	3	0	5^{ab}	1	3	3	9^{a}	9^{a}
	Esoph.	T	T	5^{ax}	T^{y}	2	T	8^{ax}	T^{by}
	Fecal	0	0	2^{b}	T	2	T	3^{b}	T^{b}
Croton potsii	Bite	0^{b}	1^{c}	1^{b}	5^{b}	17^{x}	0^{y}	5^{ax}	0^{y}
	Esoph.	T^{by}	7^{bx}	3^{by}	17^{ax}	17^{x}	3^{y}	T^{b}	T
	Fecal	10^{ay}	24^{ax}	8^{ay}	15^{ax}	19^{x}	3^{y}	1^{ab}	T
Psilostrophe tagentina[2]	Bite	T^{y}	20^{bx}	2^{y}	25^{ax}	1	0	11^{a}	12^{a}
	Esoph.	0^{y}	28^{ax}	1^{y}	19^{ax}	1	0	2^{b}	1^{b}
	Fecal	0^{y}	9^{cx}	0	0^{b}	0	0	0^{b}	7^{b}
Other forbs[2]	Bite	11^{a}	14	20^{ax}	5^{y}	12^{ay}	23^{ax}	7^{a}	7^{a}
	Esoph.	3^{by}	10^{x}	16^{ax}	2^{y}	7^{aby}	13^{bx}	1^{by}	10^{ax}
	Fecal	1^{by}	13^{x}	9b	6	5^{by}	12^{bx}	1^{b}	1^{b}
Shrubs[2]	Bite	3	1	T	1	1y	10^{ax}	1	2
	Esoph.	T	T	1	T	1	1^{b}	1	5
	Fecal	T	1	1	1	3	1^{b}	2	3

[1] Superscripts a,b,c indicate differences ($P < 0.10$) between diet techniques for a species within grazing strategy and month, superscripts x,y indicate diet differences ($P < 0.10$) for a species between grazing strategies within month.

[2] Species or group of species had significant ($P < 0.10$) dietary technique X grazing strategy X season interaction.

Another difficulty with the bite count method was that of identifying individual species of plants in all growth stages at distances up to 3 m. Theurer et al. (1976) and Bjugstad et al. (1970) reported that problems with the bite count method included plant species identification and determination of the quantity of a plant consumed. Some differences found when comparing bite count to the other techniques were probably due to individual observers over or underestimating the number of bites.

The bite count procedures does not require the use of esophageal fistulated animals but does require relatively gentle animals. Forbes and Beattie (1987) showed that biting rate was slower for fistulated animals than non-fistulated animals. More

Table 2. Availability (kg/ha) of herbage in 4 seasons (1988-1989) in yearlong and rotationally grazed pastures in the northern Chihuahuan Desert. Numbers are mean and mean standard error of 3 transects of 10 clipped plots each, n = 3.

	Month and grazing strategy							
	May 1988		August 1988		December 1988		March 1989	
	Yearlong	Rotation	Yearlong	Rotation	Yearlong	Rotation	Yearlong	Rotation
Species	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
	(kg/ha)							
Aristida spp.	134 ± 15	69 ± 35	57 ± 16	16 ± 14	115 ± 34	41 ± 27	21 ± 9	36 ± 19
Bouteloua eriopoda	5 ± 5	118 ± 22	77 ± 32	0 ± 0	184 ± 157	1 ± 1	18 ± 13	160 ± 81
Sporobolus spp.	70 ± 28	31 ± 21	98 ± 56	66 ± 24	156 ± 42	144 ± 15	43 ± 14	48 ± 17
Other grasses	28 ± 21	1 ± 1	1 ± 1	2 ± 1	33 ± 6	8 ± 6	14 ± 5	6 ± 5
Croton potsii	1 ± 1	1 ± 1	10 ± 5	57 ± 17	30 ± 11	0 ± 0	1 ± 1	0 ± 0
Psilostrophae tagetina	0 ± 0	4 ± 3	0 ± 0	62 ± 7	1 ± 1	0 ± 0	5 ± 5	12 ± 2
Other forbs	7 ± 2	12 ± 2	18 ± 6	26 ± 5	57 ± 33	28 ± 12	5 ± 2	9 ± 4
Ephedra spp.[1]	21 ± 4	0 ± 0	5 ± 3	1 ± 1	3 ± 1	2 ± 1	3 ± 2	3 ± 2
Gutierrezia spp.[1]	67 ± 24	137 ± 64	132 ± 17	69 ± 22	131 ± 31	178 ± 73	79 ± 19	71 ± 36
Prosopis glandulosa	13 ± 3	5 ± 2	5 ± 1	13 ± 4	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Yucca elata	39 ± 7	90 ± 22	63 ± 38	53 ± 14	63 ± 17	38 ± 7	0 ± 0	120 ± 18
Total	385	468	466	365	773	440	189	465

[1] Green leaves on *Prosopis*; green stems on *Ephedra* spp.

Table 3. Kulczynski similarity indices (%) comparing dietary techniques for steers grazing on continuously and rotationally grazed pastures in 4 seasons, 1988-1989.

	Month and grazing strategy[1]									
	May 1988		Aug. 1988		Dec. 1988		Mar. 1989		Mean	
Dietary techniques	Yearlong x̄ ± SE	Rot.. x̄ ± SE	Yearlong x̄ ± SE	Rot.. x̄ ± SE	Yearlong x̄ ± SE	Rot.. x̄ ± SE	Yearlong x̄ ± SE	Rot.. x̄ ± SE	Yearlong x̄ ± SE	Rot.. x̄ ± SE
	(%)									
Bite count vs. esophageal analysis	80 ± 52	69 ± 5	77 ± 3	82 ± 5	62 ± 5	61 ± 8	55 ± 7	53 ± 11	69 ± 3	66 ± 4
Bite count vs. fecal analysis	69 ± 5	56 ± 6	75 ± 5	66 ± 2	37 ± 6	57 ± 7	50 ± 8	46 ± 11	58 ± 4	56 ± 4
Esophageal analysis vs. fecal analysis	84 ± 3	67 ± 5	75 ± 4	68 ± 3	67 ± 7	91 ± 2	84 ± 3	75 ± 8	78 ± 3	75 ± 3

[1] Yearlong = Continuous grazing; Rot. = Rotational grazing.
[2] Numbers are mean and mean standard error, n = 6.

research is needed to evaluate the similarity of diets and bite rate between fistulated and non-fistulated animals.

The amount of time between when fecal samples and samples for the other 2 techniques were collected may not have allowed enough time for passage of food stuff. Voth and Black (1973) pointed out that a major limitation of fecal analysis is inaccuracy in assessment of actual diets when they include a high component of forbs, shrubs or both. Vavra et al. (1978), found differences between diets estimated from esophagal extrusa and fecal samples collected 24 hours later. Simao Neto et al. (1987), in studying the passage rate of seeds through ruminants, recovered the greatest amount of seed between 48 and 72 hours after ingestion. In this study, since samples for each steer were averaged across days, the mean time between fecal collection, and other dietary samples for comparison purposes was 40 hours. This length of time may have been too great for some forbs and plant parts that digest readily and it may have been too short of time for plants with low digestibility (Sanders et al. 1980, McInnis et al. 1983).

Esophageal fistula slides compared well with the reference slides, but fecal material which was partially digested was difficult to compare with undigested samples on the reference slides. Holechek and Valdez (1985) reported observers found more difficulty in identifying fragments in fecal material than undigested fragments from esophageal samples. In other instances plant fragments were present in feces, but were so transparent that cellular structure was not easily discernible. This observation was also noted by Ward (1970) and Sanders et al. (1980). Slater and Jones (1971) reported that some species may become unidentifiable in feces.

Another reason for differences among techniques was apparently because of the different lengths of the sampling periods. Ingesta collected from the esophagus was an actual portion of the diet for only a short time period (30 minutes) in a small area. Therefore, direct comparisons between what a steer grazed for 24 hours (fecal sample) and what a steer grazed for only 30 minutes (esophageal and bite count samples) may not be a valid comparison.

Mean similarity indices between dietary techniques varied among seasons and between grazing strategies (Table 3). Generally the highest similarities were between the diets estimated by esophageal and fecal analysis (67% to 91%) while the lowest similarities were between bite count and fecal analysis (37% to 75%). The low similarities indicate the problems already discussed and that no single technique will give an adequate estimation of dietary composition or intake under all situations. Vavra et al. (1978), discussed the idea that it may not always be necessary for many management and research activities to have an exact estimate of amount of intake for each plant species. Rather they suggest ranking species by an "importance value" based on amount a species makes up of the diet. Ranking the species in the diets determined by the 3 techniques in this study shows little difference in the top 3 ranks among techniques (Table 4). The top 3 ranks of plants contribute nearly 68% to the diets averaged across the 4 seasons. The less common species are not as consistently ranked because they were not as evenly distributed across the study pastures as were the top ranked species.

Any of the 3 dietary techniques provides similar information regarding the importance of major plant species in grazing animals in the northern Chihuahuan Desert. However, the 3 techniques do not give the same estimate of weight intake for a plant species. To improve the estimate of intake for large ruminants using the bite count technique it is necessary to modify the bite count techniques as suggested by Reppert (1960) or Free et al. (1971). However, as Mohammad et al. (1995) suggests, fecal analysis may be the most appropriate for most situations. The technique a person chooses to use should depend on resources available, how the data will be used, and the expertise of the observers.

Table 4. Importance rank of forage components based on abundance in diets of steers determined by 3 techniques averaged across sampling date and grazing strategy.

	Dietary technique		
Importance rank	Bite count	Esophageal analysis	Fecal analysis
1	*Sporbolus*	*Sporobolus*	*Sporbolus*
2	*Bouteloua*	*Bouteloua*	*Bouteloua*
3	Other forbs	Other forbs	Croton
4	*Aristida*	*Psilostrophe*	Other forbs
5	*Psilostrophe*	*Croton*	*Aristida*
6	Other grass	*Aristida*	Shrub
7	*Croton*	Other grass	Other grass
8	Shrub	Shrub	*Psilostrophe*

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Comparison of techniques for determining the nutritional carrying capacity for white-tailed deer

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Abstract

Estimates of carrying capacity for herbivores are useful for determining the relative value of different ranges. We compared 6 estimates of nutritional carrying capacity for white-tailed deer (*Odocoileus virginianus* L.): digestible energy consumed by tame deer, and 5 methods using forage supplies of dry matter, digestible energy, digestible nitrogen, dry matter*digestible energy, and dry matter*digestible nitrogen in two 1-ha enclosures of different shrub plant communities in southern Texas. For the north enclosure, carrying capacity estimates (90% CI) were 3.65 (CI = 3.61–3.69), 4.5 (CI = 3.7–5.3), 9.4 (CI = 7.3–11.5), 15.2 (CI = 11.6–18.8), 3.5 (CI = 2.7–4.3), and 3.5 (CI = 2.7–4.3) deer ha^{-1} 58 days^{-1} for the digestible energy tame deer, dry matter, digestible energy, digestible nitrogen, dry matter*digestible energy, and dry matter*digestible nitrogen techniques, respectively. Corresponding estimates for the south enclosure were 2.6 (CI = 2.5–2.7), 3.5 (CI = 3.2–3.9), 6.8 (CI = 6.0–7.6), 10.1 (CI = 8.8–11.3), 2.1 (CI = 1.8–2.6), and 2.8 (CI = 2.4–3.1). Some methods for estimating carrying capacity provided different absolute estimates, but all produced similar relative estimates between enclosures. Similar relative results between enclosures suggests any of the methods can be used to determine the relative nutritional quality of plant communities. However, the dry matter-based technique was less expensive than the other techniques; therefore, there is no need to use more costly techniques for determining the relative stocking rates for white-tailed deer, unless forage quality differs greatly among plant communities.

Key Words: carrying capacity, digestible energy, digestible nitrogen, *Odocoileus virginianus* L., southern Texas.

Estimates of nutritional carrying capacity are useful for comparing the ability of different ranges to support wildlife populations (Moen 1973, Robbins 1973, Bobeck 1977, Wallmo et al. 1977, Mautz 1978, Hobbs et al. 1982, Potvin and Huot 1982, Hobbs and Swift 1985). Traditional methods for estimating nutritional carrying capacity have been derived by dividing the range supply of dry matter, digestible energy, and digestible nitrogen by the product of an animal's daily requirements and the time period of interest, such as dormant season length (Wallmo et al. 1977, Hobbs et al. 1982, Potvin and Huot 1982). Hobbs and Swift (1985) developed an integrated approach for estimating carrying capacity using both forage quantity and quality. These techniques have been useful for comparing the relative productivity of plant communities and understanding the relationship between ungulates and environmental conditions (Wallmo et al. 1977, Hobbs et al. 1982, Potvin and Huot 1982, Hobbs and Swift 1985).

Estimating digestible energy consumed by tame deer is an alternative technique for determining nutritional carrying capacity (Clark 1977, Cowan and Clark 1981, Potts and Cowan 1983). Ullrey et al. (1969, 1970) first documented the relationship between digestible energy intake and rate of weight change of tame white-tailed deer. Clark (1977) used this relationship to estimate the nutritional carrying capacity for small enclosures using the rate of weight change, estimated digestible energy intake, number of trial days, energy requirements, and size of area. However, the tame-deer technique has not been critically evaluated, nor have the results been compared to traditional techniques.

We evaluated the use of digestible energy consumed by tame deer and traditional forage-based methods to estimate the nutritional carrying capacity of shrub communities for white-tailed deer. We defined nutritional carrying capacity as the maximum number of animals that can forage on a given plant community without weight loss for a given period of time. We compared the absolute and relative estimates of carrying capacity using the tame-deer technique to those based on traditional methods involving range supplies of dry matter, digestible energy, digestible nitrogen, dry matter*digestible energy, and dry matter*digestible nitrogen. We also compared the cost of each technique.

Study Area

We conducted the study on two 1-ha enclosures on the San Vicente Ranch, Hidalgo County, Tex. Cover in the north enclosure consisted of 2 plant communities: 27% in intervening 15-m-wide strips of shrubs and 73% in 122-m-wide roller-chopped areas. Shrubs were composed primarily of lime pricklyash (*Zanthoxylum fagara* Sarg.) with smaller percentages of brasil

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(*Condalia hookeri* M.C. Johnst.), honey mesquite (*Prosopis glandulosa* Torr.), and spiny hackberry (*Celtis pallida* Torr.). In the roller-chopped area, forbs and grasses were the main forage categories. Common forbs were onion (*Allium* sp.), partridge pea senna (*Cassia fasciculata* Buckl.), croton (*Croton* spp.), and gaillardia (*Gaillardia* sp.). Threeawn (*Aristida* spp.), buffle sandbur (*Cenchrus ciliaris* L.), and coast sandbur (*C. incertus* M.A. Curtis) were the common grasses. The south enclosure consisted of a grass and shrub savannah community that was not manipulated by humans. Brasil and lime pricklyash were the primary shrubs in the south enclosure.

Weather is typical of semiarid areas. Summer temperatures are consistently >32°C. Annual precipitation at San Manuel, Tex. (8 km east of the study area), averages 680 mm (J. Chapa, unpubl. data, Natl. Oceanic and Atmos. Adm., San Manuel, 1987). Temperatures and precipitation were normal for the area during the study.

Methods

We determined carrying capacity during summer. In southern Texas, summers and winters can be stressful for deer because of lack of precipitation. Drought periods result in large weight loss of deer (Long et al. 1965, Fowler et al. 1967, Wheaton and Brown 1983) and sometimes large population losses (Teer 1984).

Digestible Energy Consumed by Tame Deer

In July 1987, we constructed two 1-ha electric fence enclosures on the ranch. We selected a 1-ha enclosure to ensure sufficient vegetation for ≥30-day trials. At least this duration of trial is needed so deer lose weight slowly and steadily (e.g., 10 g $kg^{-0.75}$ day^{-1}) (Potts and Cowan 1983) because deer on 0 or near 0 intake have a wide variation of weight loss among individuals (Hershberger 1984).

On 24 July we randomly placed four 2.5–4.5-year-old tame does in each enclosure. All does used in the study produced fawns from 15 June to 7 July 1987. We removed fawns from their mothers 2 days after birth. From weaning to the start of the trial, we fed deer a commercial pelleted feed containing 16% protein and 3.3 kcal g^{-1} of digestible energy. Deer also foraged on forbs, grasses, and brush for 60 days prior to the trial, which acclimated them to natural forage.

Prior to initial and final weighings, we withheld food from the deer for 24 hours to standardize rumen fill (Potts and Cowan 1983). Although the rumen requires 2–4 days to completely empty, Potts and Cowan found this amount of time stresses the deer before trials.

We weighed deer with a portable platform scale at the beginning and end of each trial and once each week (Potts and Cowan 1983). We used the initial and final weights to determine their rate of weight change and the intermediate weights to assess weekly condition. We fed deer a small portion of pelleted feed to get them to voluntarily enter a crate mounted on the scale. This was the only supplemental feed they received during the trial. We subtracted the digestible energy supplied by the supplemental feed (approx. 3.3 kcal g^{-1}) from the final results. We terminated trials when (1) visual condition of deer had declined significantly and (2) visual inspection of the enclosure showed little available forage.

We used the regression equation, $Y = 0.0844X - 13.4$ ($R^2 = 0.96$, MSE = 2.58) to predict digestible energy intake for deer based on their rate of weight change (Clark, unpubl. data, Pennsylvania State Univ.). Y is the rate of weight change per deer in g $kg^{-0.75}$ day^{-1} and X is the digestible energy consumed $kg^{-0.75}$ $deer^{-1}$ day^{-1}. Clark conducted feeding trials using 19 adult does, and trials took place during the winter. Clark fed deer on different levels of maintenance digestible energy and determined their rates of weight loss. This equation predicted that the maintenance level of digestible energy was 159 kcal $kg^{-0.75}$ day^{-1}, which was consistent with other published values (Ullrey et al. 1969, 1970). We assumed that the regression equation developed by Clark (unpubl. data, Pennsylvania State Univ.) using penned does in winter in Pennsylvania accurately predicted the digestible energy consumed by deer in this study in summer. Summer is a period of weight loss for deer in Texas, and winter is a period of weight loss in Pennsylvania.

We also assumed the feeding behavior of tame and wild deer was similar (McMahan 1964, Watts 1964, Healy 1967, Wallmo and Neff 1970, Olson-Rutz and Urness 1987). In addition, for calculating estimates of carrying capacity, we assumed deer consumed a maintenance diet and lost no weight.

Knowledge of the precision of estimates of carrying capacity using the tame-deer technique is important. McCall (1988) determined the precision of the tame-deer technique using 3 adjacent 0.4-ha enclosures. Carrying capacity estimates for the 3 enclosures were 6.0 (90% CI = 5.9-6.1) deer ha^{-1} 72 $days^{-1}$, 5.4 (CI = 5.2-5.7), and 5.3 (CI = 5.1-5.4), respectively. Differences in carrying capacity estimates among enclosures were probably because of differences in usable forage. At the start of the trial, there was 730 kg ha^{-1} of forage in enclosure 1, 590 in enclosure 2, and 450 in enclosure 3. Six-hundred sixty kg ha^{-1} of forage was consumed from enclosure 1, 550 from enclosure 2, and 630 from enclosure 3, which included production of forage during the trial.

Forage Dry Matter, Digestible Energy, Digestible Nitrogen, Dry Matter*Digestible Energy, and Dry Matter*Digestible Nitrogen

We estimated carrying capacity by dividing the total range supply of dry matter, digestible energy, and digestible nitrogen by the product of a deer's daily dry matter, digestible energy, and digestible nitrogen requirement and the trial days. In addition, we estimated carrying capacity by integrating dry matter and digestible energy, and dry matter and digestible nitrogen (Hobbs and Swift 1985). Quantifying range supplies of each nutrient required an assessment of usable amounts of principal deer foods. We determined principal deer foods by (1) recording bite-count data from the tame deer in the enclosures (Whelan et al. 1971) and (2) microhistological analysis of rumen contents of 8 wild deer collected during September on the ranch (Gray et al. 1980). Principal deer foods were those that made up ≥5% of deer diets during the trial. We determined usable forage by the difference between the biomass of principal browse, forbs, and grasses at the beginning (27 July) and end of the trial (22–24 September).

Before the trial, we determined biomass of forage using a double-sampling technique because it was non-destructive to the vegetation in the enclosures (Scanlon and Sharik 1986). In each enclosure we randomly selected twenty 0.25-m^2 plots. On each plot we made ocular estimates of cover to a height of 180 cm above ground, against a 50-x 50-cm screen. Outside the enclosures, we estimated cover on 60 additional plots (n = 30 north, n = 30 south) from 27 July to 5 August 1987. We clipped all of the outside plots and developed regression equations for each major plant type (forb, grass, brasil, honey mesquite, lime pricklyash, spiny hackberry) to estimate the biomass of available forage on unclipped plots within the enclosures. We oven dried forage from all plots by plant type at 40°C for 2 weeks and weighed to the nearest 0.1 g. At the end of the trial, we clipped thirty 0.25-m^2 plots from each plant community (2 north enclosure, 1 south enclosure) within each enclosure to determine the biomass of forage remaining. To calculate total dry matter of usable forage in each enclosure, we summed mean values for principal forages.

We collected three 50-g samples of principal forbs, grasses, and the 4 shrub species from 5 to 7 August 1987, for analysis of digestible energy and digestible nitrogen. We dried samples at 40°C for 2 weeks and analyzed for dry matter, ash, in vitro digestibility of organic matter (IVDOM) (Tilley and Terry 1963), and nitrogen content (Assoc. Off. Anal. Chem. 1970). We determined IVDOM using rumen inoculum from a fistulated Jersey cow fed alfalfa (*Medicago sativa*) hay. We calculated digestible energy for IVDOM using the formula of Bryant et al. (1981) modified for use with IVDOM.

Assumptions are inherent in the forage-based techniques. For the digestible nitrogen-based estimate, researchers may not select forage samples as high in nitrogen as those selected by ungulates (Swift 1948, Wier and Torrell 1959, Longhurst et al. 1968). Researchers are also uncertain how animals mix the various forages in their diet to balance their requirements (Hobbs and Swift 1985). Furthermore, it is assumed that ungulates select forages with the highest energy and nitrogen content, but secondary plant compounds of forage also may influence diet selection and digestibility (Bryant and Kuropat 1980). Additionally, energy and nitrogen requirements derived from penned animals may not be accurate for wild ungulates. Finally, weather may change the supply of available forage daily making forage quantity and quality difficult to assess (Potvin and Huot 1982, McCall 1988).

Data Analysis

We used Cowan and Clark's (1981) technique and equations to estimate nutritional carrying capacity for the enclosures using digestible energy consumed by tame deer. We calculated the digestible energy consumed per deer during the trial by multiplying the digestible energy consumed per day per deer by the number of trial days and the deer's metabolic weight ($kg^{0.75}$). We determined the total digestible energy consumed by all deer in the enclosure by summing the digestible energy consumed per deer. We then calculated estimates of carrying capacity for each enclosure by dividing the total digestible energy consumed by the deer in the enclosure by the product of the deer's daily digestible energy requirement (159 kcal $kg^{-0.75}$ day^{-1}) and the trial length (58 days). We reported carrying capacity as deer per ha per trial days.

We calculated estimates of carrying capacity using dry matter by dividing the total range supply of dry matter by the product of the deer's daily intake of dry matter (mean intake of dry matter from the 2 enclosures) and the trial length. We calculated the mean daily intake per enclosure by dividing the total dry matter of useable forage per enclosure by the product of the number of deer per enclosure and the trial length. Carrying capacity estimates using digestible energy were calculated by dividing the total range supply of digestible energy by the product of the deer's daily digestible energy requirement (159 kcal $kg^{-0.75}$ day^{-1}), the mean metabolic weight of deer per enclosure, and the trial length. We calculated total range supply of digestible energy as the sum of the products of usable dry matter of forage values and their digestible energy content.

We determined digestible nitrogen-based estimates of carrying capacity by dividing total forage supply of nitrogen by the product of each deer's daily requirement (0.77 g N $kg^{-0.75}$ day^{-1}) (Holter et al. 1979), the mean metabolic weight of a deer per enclosure, and trial length (58 days). Total plant community supply of nitrogen was calculated by summing the products of usable forage dry matter values for each category or species and their nitrogen values. True digestible nitrogen was estimated by multiplying the total N supply by 0.90 (Robbins 1973:Table 26).

We followed Hobbs and Swift's (1985) methods for estimating carrying capacity based on combining dry matter and digestible energy, and dry matter and digestible nitrogen of forage. We assumed a diet quality level for maintenance of digestible energy of 159 kcal $kg^{-0.75}$ day^{-1}, and of digestible nitrogen of 1.3 g N 100 g^{-1} dry matter. We did not separate plant parts of the same plant species for determining nutritional quality.

We calculated approximate 90% confidence intervals for estimates of carrying capacity using bootstrap approximations (Sprent 1989). We drew 1,000 subsamples from each nutritional parameter of forage with replacement. We used subsamples to calculate 1,000 iterations of the carrying capacity equations. For the tame-deer technique, variance associated with the estimated intake of digestible energy and the variance related to weekly weights of deer were used to develop confidence intervals. We did not include the variance in weight loss among deer within the same enclosure because these weights were not independent from each other due to dominance hierarchy that was observed among deer (McCall 1988). For the dry matter, digestible energy, digestible nitrogen, dry matter*digestible energy, and dry matter*digestible nitrogen-based techniques, variances associated with the mean estimate of dry matter for each forage type were included. Approximate confidence intervals were determined by excluding the extreme $1/2N\propto$ values from the ranked carrying capacity iterations (Sprent 1989). One thousand iterations were calculated to achieve sufficient sample size for testing (Efron and Tibshirani 1993).

Cost of Techniques

We compared the cost (labor and materials) of each technique for estimating carrying capacity. We assumed a minimum wage of \$4.90 $hour^{-1}$ for labor costs. We did not include the expense of raising the deer and housing them while the trials were not in progress in our cost comparison because deer could be used for other projects during this time.

Results

Estimated carrying capacity ranged from 3.5–15.2 deer ha^{-1} 58 $days^{-1}$ in the north enclosure and 2.1–10.1 deer ha^{-1} 58 $days^{-1}$ in the south enclosure (Table 1). Estimates using digestible energy of tame deer, dry matter*digestible energy, and dry matter*digestible nitrogen did not differ within an enclosure. Estimates using forage digestible energy and digestible nitrogen differed from each other and all of the other techniques. The

Table 1. Comparison of nutritional carrying capacity estimates (deer ha^{-1} 58 days^{-1}) using digestible energy (DE) consumed by tame deer, and forage dry matter (DM), DE, digestible nitrogen (DN), DM*DE, and DM*DN for the north and south 1-ha enclosures on the San Vicente Ranch, Hidalgo County, Tex., 24 July to 19 September 1987.

	North		South	
Technique	Estimate	CI[1]	Estimate	CI
	(Deer ha^{-1} 58 days^{-1})			
DE tame deer	3.65Aa[2]	3.61–3.69	2.6Ab	2.5–2.7
DM forage	4.5Ba	3.7–5.3	3.5Ba	3.2–3.9
DE forage	9.4Ca	7.3–11.5	6.8Ca	6.0–7.6
DN forage	15.2Da	11.6–18.8	10.1Db	8.8–11.3
DM*DE forage	3.5ABa	2.7–4.3	2.1Ab	1.8–2.6
DM*N forage	3.5ABa	2.7–4.3	2.8Aa	2.4–3.1

[1] CI = Confidence Interval.

[2] Means within the same column sharing the same upper case letter do not differ (P<0.10); means within a row with the same lower case letter do not differ (P<0.10).

average daily dry matter intake for the 2 enclosures was 2.06 kg deer^{-1} day^{-1}. The tame-deer trial lasted 58 days, from 24 July to 19 September 1987.

Estimates of total digestible energy consumed by deer using the tame-deer technique in the north enclosure (560,960 kcal) was greater than in the south enclosure (404,630 kcal) (Table 2). Estimates of usable dry matter, digestible energy, and digestible nitrogen were higher for the north (540 kg dry matter ha^{-1}, 1,447,410 kcal digestible energy ha^{-1}, 11.3 kg digestible nitrogen ha^{-1}) than the south enclosure (420 kg dry matter ha^{-1}, 1,042,290 kcal digestible energy ha^{-1}, 7.5 kg digestible nitrogen ha^{-1}). Consequently, all estimates of carrying capacity were higher for the north than south enclosure. Estimates (digestible energy from tame deer, dry matter forage, digestible energy forage, digestible nitrogen of forage, dry matter*digestible energy, dry matter*digestible nitrogen) were 1.4, 1.3, 1.4, 1.5, 1.6, and 1.3 times greater, respectively, for the north than the south enclosure; however, only digestible energy of tame deer, digestible nitrogen, and dry matter*digestible energy differed statistically (P<0.10).

Estimates of carrying capacity using the tame-deer technique ($2,820 enclosure^{-1}) were 8 times more costly than using the dry matter-based technique (80 plots at $4.38 plot^{-1} = $350), 7 times more costly than using digestible energy from forage (80 plots at $5.00 plot^{-1} = $400), and 6 times more costly than the digestible nitrogen-based technique (80 plots at $5.63 plot^{-1} = $450). There were no additional costs for running the dry matter*digestible energy and dry matter*digestible nitrogen-based techniques than for treating the nutrients separately. Thirty-four percent of the cost for the tame-deer technique was for labor and 66% for materials. Fencing accounted for 70% of the materials costs; however, fencing could be amortized over several trials. Enclosures required 20.6 days enclosure^{-1} to construct and 4.4 days enclosure^{-1} to remove (1 day = 8 hours).

Discussion

Although some of the absolute estimates of nutritional carrying capacity differed, each technique provided a similar index to the relative carrying capacity of the north versus the south enclosure (carrying capacity north/carrying capacity south = 1.3–1.6). Greater forage supplies of dry matter, digestible energy, and digestible nitrogen on the north resulted in the higher estimates of carrying capacity relative to the south.

For the north enclosure, estimates of carrying capacity using dry matter, dry matter*digestible energy, and dry matter*digestible nitrogen of forage were the same because digestible energy and digestible nitrogen concentrations of all forages were greater than or equal to the critical dietary levels. Estimates using dry matter and dry matter*digestible nitrogen were also the same for the south enclosure as digestible nitrogen concentrations also exceeded critical levels. However, the digestible energy value of 1 forage species in the south enclosure resulted in only 50% of it being usable before digestible energy for all forages fell below critical levels. Thus, not all the forage was nutritionally useful to deer (Hobbs and Swift 1985) in the south enclosure, resulting in a carrying capacity estimate for dry matter*digestible energy that was lower than for dry matter.

Confidence intervals for estimates of carrying capacity using dry matter, digestible energy, digestible nitrogen, dry matter*digestible energy, and dry matter*digestible nitrogen of forage, were higher than those from the tame-deer technique because of the high variance associated with the double-sampling technique used to estimate usable forage. Traditional estimates of carrying capacity using digestible energy and digestible nitrogen normally involve clipping a sample of plots (Hobbs et al. 1982), which would probably result in lower confidence intervals.

Despite its assumptions, the tame-deer technique appears to be a valid method for estimating relative carrying capacity as it produced similar results to those of the forage-based estimates. The

Table 2. Nutritional carrying capacity data and calculations using estimated digestible energy (DE) consumed by tame deer from the north (N) and south (S) 1-ha enclosures on the San Vicente Ranch, Hidalgo County, Tex., from 24 July to 19 September 1987.

Enc.[1],	Deer #	Weight		Avg. MWT[2]	Wt. Change	Mean Wt. Change	Y[3]	X[4]	Total DE Intake	Supp. Feed[5]	Net DE Intake[6]	Total DE Enc.[7]
		Begin	End									
		(kg)		(kg)		(g day^{-1})			(kcal)			
N	1	45.4	44.2	17.3	-1.1	-19.6	-1.1	145.4	146,000	2,300	143,710	
	2	47.0	43.8	17.5	-3.2	-54.7	-3.1	121.7	123,330	2,850	120,480	560,960
	3	44.7	44.7	17.3	0.0	0.0	0.0	158.8	159,140	980	158,160	
	4	44.2	42.9	17.0	-1.4	-23.5	-1.4	142.4	139,970	1,360	138,610	
S	5	39.7	36.5	15.3	-3.2	-54.7	-3.6	116.5	103,600	2,130	101,470	
	6	41.3	37.9	15.8	-3.4	-58.7	-3.7	114.7	104,990	1,020	103,970	404,630
	7	43.1	41.3	16.6	-1.8	-31.3	-1.9	136.4	130,930	0	130,930	
	8	40.6	34.7	15.2	-5.9	101.7	-6.7	79.5	79,090	1,830	68,260	

[1] Enc. = Enclosure.

[2] Avg. MWT = Average metabolic weight during trial (kg$^{0.75}$).

[3] Y = Mean weight change day^{-1} MWT^{-1}.

[4] X = Predicted intake (kcal MWT^{-1}).

[5] Supp. Feed = Supplemental feed.

[6] Net DE Intake = Total DE intake - supplemental feed.

[7] Tot. DE Enc.$^{-1}$ = Total DE per enclosure.

tame-deer technique has advantages and disadvantages relative to Hobbs and Swift's (1985) technique. As in Hobbs and Swift's technique, the tame-deer method integrates diet quality and food quantity, which facilitates decisions on stocking densities of herbivores. The advantage of the tame-deer technique is that it relates forage consumed to weight change of animals. Thus, there is no need to predict how deer mix forages containing different concentrations of digestible energy in their diet to balance energy needs, nor is it necessary to know how digestible energy is distributed within the available forage. In addition, it is not necessary to assume deer select higher quality forage items in preference to lower quality ones. A disadvantage of the tame-deer method is that it assumes regression equations from penned deer reflect the digestible energy consumed by animals in enclosures. The primary disadvantage of the tame-deer method is that it is costly (\$2,800 1-ha enclosure^{-1}) to construct a large number of enclosures to sufficiently sample variable plant communities. Forage-based estimates of carrying capacity are less expensive, which enable managers to increase sample sizes, thus better account for the variability within and among plant communities. However, many physiological and behavioral characteristics of free-ranging deer make it difficult to estimate the exact number of animals that can be supported on a range.

To improve the precision of estimates of carrying capacity using the tame-deer technique, specific criteria should be used to decide when to terminate trials. We ended trials when visual condition of deer deteriorated significantly and visual inspection of the enclosure indicated little available forage. However, we suggest ending trials when the average weight of deer drops by 15.0%, or some other specific amount, which provides more objective criteria for stopping trials. The accuracy of estimates may be improved by developing a regression equation to predict digestible energy consumed from rate of weight loss using penned does from the region of the country and the season of the year in question.

Because all the assumptions inherent in each carrying capacity technique are unlikely to be met, absolute measures of carrying capacity are questionable. Therefore, we believe the value of carrying capacity estimates lies in relative comparisons of sites. Although some methods for estimating carrying capacity provided different absolute results in our study, all produced similar relative estimates between enclosures. Therefore, we believe any of the methods can be used to determine the relative nutritional quality of different plant communities. However, we recommend using supplies of forage dry matter to estimate carrying capacity as it was the least expensive technique for sampling variable plant communities and provided similar relative results to the other techniques. Hobbs and Swift's (1985) technique may be more useful than the other forage-based techniques for estimating the relative stocking rates of deer where forage quality differs greatly among areas, such as between burned and unburned areas. However, in our study forage quality was greater than minimum requirements for all forage species, except one, making calculation of the Hobbs and Swift technique unnecessary. Future studies should estimate carrying capacity using all of the forage-based techniques used in this study. If these results indicate that digestible energy, digestible nitrogen, dry matter*digestible energy, and dry matter*digestible nitrogen estimates of carrying capacity are relatively similar to dry matter estimates, then dry matter alone should be used.

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Effect of weed seed rate and grass defoliation level on diffuse knapweed

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Abstract

Diffuse knapweed (*Centaurea diffusa* Lam.), an invasive weed, has reduced forage production and biodiversity, and increased soil erosion on over a million hectares of rangeland in the western United States. This study evaluated the effects of a single grass defoliation on establishment of diffuse knapweed seeded at 2 rates into a bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith)/needle-and-thread (*Stipa comata* Trin. & Rupr.) community and a crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) community. Six defoliation levels (0, 20, 40, 60, 80, 100%) and 2 seeding rates (3,000, 6,000 diffuse knapweed seeds) were applied to 1 m^2 plots in a randomized-complete-block design (n=4). Diffuse knapweed was seeded in the fall of 1992, and grasses were defoliated on 28 April 1993. The number of flowering culms and weed seedlings were counted in September 1993. Densities of diffuse knapweed seedlings, juveniles, and adults, as well as plant standing crop, were determined in May 1994. Seed rate had minimal effect on diffuse knapweed density. By May 1994, densities of diffuse knapweed were about 20 and 30 plants m^{-2} on undefoliated bluebunch wheatgrass and crested wheatgrass plots, respectively, indicating that defoliation is not required for this noxious weed to become established. Higher levels of grass defoliation (>60%), especially of bluebunch wheatgrass, enhanced diffuse knapweed establishment, indicating that moderate (≤60%) defoliation would not necessarily accelerate invasion by diffuse knapweed.

Key Words: *Centaurea diffusa*, bluebunch wheatgrass, crested wheatgrass, defoliation, rangeland weeds.

Diffuse knapweed (*Centaurea diffusa* Lam.), a deep taprooted biennial, was introduced to North America from Eurasia around 1900 (Roché and Roché 1988). Between 1950 and 1975, it spread from 9 to 28 counties in the Pacific Northwest (Roché and Talbott 1986). Diffuse knapweed has been found in at least 102 counties and occupies about 1.2 million hectares in the western United States (Lacey 1989). Diffuse knapweed has the potential to invade over 4.8 million hectares of range and forest land in Washington by the year 2007 (Roché 1994).

Centaurea spp. (knapweed) invasion has reduced biodiversity and forage for wildlife and livestock, and deteriorated soil and water resources (Watson and Renney 1974, Myers and Berube 1983, Tyser and Key 1988, Lacey et al. 1989). Diffuse knapweed invades pristine, ungrazed native plant communities (Lacey et al. 1990), as well as grazed communities (Roché 1994).

In grazed communities, invasions may be enhanced by selective and excessive grazing of desirable forage species (Lacey et al. 1990). Dense stands of diffuse knapweed may also reflect a greater resistance to defoliation, or altered competitive interactions between diffuse knapweed and perennial grasses, or both (Briske 1990).

Timing, intensity, and frequency of defoliation affect the competitive interaction between weeds and perennial grasses, and thus the ability of a perennial grass to withstand weed invasion (Maschinski and Whitham 1989, Briske 1990). An appropriate combination of timing, intensity, and frequency of grazing management should allow desirable species to remain competitive. On seasonally-grazed rangelands free of weeds, moderate defoliation and alternating grazing seasons maintains desirable species and constitutes proper grazing management. Because much of the emphasis in weed research in the past has been on control (Zimdahl 1994), little is known about the effects of grazing management on weed establishment.

The objective of this study was to determine the effects of the level of a single grass defoliation and 2 seeding rates of diffuse knapweed on its establishment. A bluebunch wheatgrass dominated plant community was used because it is widely distributed, an important native forage species, and susceptible to diffuse knapweed invasion. The crested wheatgrass pasture was selected because this introduced species has been seeded throughout the west, and it is often used to revegetate diffuse knapweed dominated rangeland (Hubbard 1975).

Materials and Methods

Study Sites

The study was conducted from 1992 to 1994 on 2 sites. Both sites were within the bluebunch wheatgrass (*Pseudoroegeneria spicata* (Pursh) Scribn. & Smith)/needle-and-thread (*Stipa comata* Trin. & Rupr.) habitat type of eastern Washington (Daubenmire 1970). The sites were about 7 and 9 km northwest of Plymouth, Wash., respectively. Given their proximity to one another, climatic effects were assumed to be similar. This habitat

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type is susceptible to invasion by diffuse knapweed (Roché 1994). At Site 1, co-dominant species were bluebunch wheatgrass and needle-and-thread. The understory was primarily Sandberg's bluegrass (*Poa sandbergii* Vasey), with few forbs present. This site had not been grazed for over 20 years. Site 2 was a seeded monoculture of 'Fairway' crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.). The stand was established in 1982, and since then has not been grazed or disturbed by humans. Diffuse knapweed was absent from both sites.

The soil type at both sites was a well-drained, Warden very fine sandy loam (coarse, silty, mixed, mesic, Xerollic Camborthids) with zero slope, that had an effective rooting zone exceeding 90 cm. Elevations at Site 1 and Site 2 were 450 and 720 m, respectively. Temperature extremes for the sites range from 50 to -34°C with an average frost-free season of about 145 days. The 59 year average annual precipitation is about 225 mm.

Temperature and precipitation were monitored daily at a weather station 1 km from each site within the same habitat type (Table 1). Precipitation for the first year (August 1992–July 1993) of the study was 374 mm with most of the precipitation falling in November (99 mm) and April (77 mm). In the second year (August 1993–July 1994), precipitation was 171 mm with May receiving the highest moisture.

Table 1. Environmental conditions near both study sites. Environmental conditions were monitored daily.

Month	Total precipitation	Total wind run	Temperature max.	min.	ave.
	(mm)	(Km/day)		(°C)	
Aug. 1992	0	57.5	31.7	12.8	21.7
Sep.	18	75.1	24.4	7.8	16.1
Oct.	25	52.9	18.9	5.0	11.7
Nov.	99	54.2	8.9	1.1	5.0
Dec.	48	86.2	3.3	- 3.3	0.0
Jan. 1993	16	48.5	- 1.1	- 7.8	- 4.4
Feb.	17	71.2	2.8	- 4.4	- 1.1
Mar.	37	70.3	10.6	0.6	5.6
Apr.	77	93.2	17.2	3.9	10.6
May	21	94.7	25.6	10.0	17.8
Jun.	8	77.2	25.6	10.0	17.8
Jul.	8	60.5	26.1	10.6	18.3
Aug.	3	49.6	29.4	11.1	20.0
Sep.	1	38.8	27.8	7.2	16.7
Oct.	3	32.1	20.6	3.9	11.7
Nov.	12	42.1	6.7	- 5.6	0.6
Dec.	23	49.5	4.4	- 0.5	2.2
Jan. 1994	22	41.8	8.3	0.0	3.9
Feb.	20	68.0	6.7	- 2.8	1.7
Mar.	4	83.5	16.1	0.5	8.3
Apr.	10	101.9	20.0	5.6	12.8
May	51	77.2	23.9	8.9	16.7
Jun.	14	80.0	26.7	9.4	18.3
Jul.	8	49.7	33.9	13.3	23.3

Experimental Design

Twelve treatments (2 diffuse knapweed seeding rates, 6 defoliation levels) were applied to 1 m^2 plots in a randomized-complete-block design (n=4 at each site). Plots were located and clipped to an 8 cm stubble height in mid-August 1992. Diffuse knapweed seeds collected during the summer of 1992 from areas near both sites were broadcast-seeded on the plots. Lots of 500 (3,000 seeds per plot) or 1,000 (6,000 seeds per plot) diffuse knapweed seeds were broadcast biweekly beginning 1 September and ending 15 November 1992 to mimic natural seed rain. These rates are within the typical range of seeds produced by a single knapweed plant in this area (unpublished data, Sheley and Larson).

On 28 April 1993, grasses in each plot were hand-clipped to defoliation levels of 0, 20, 40, 60, 80, or 100%. Grasses were in the boot stage, and are often grazed at this time in eastern Washington rangelands. Defoliation levels were calibrated by clipping nearby grasses and comparing their weights with total grass weights. Although diffuse knapweed seedlings were not clipped at this time, they were counted to determine seedling densities.

Established diffuse knapweed plants were recounted on 15 and 16 September 1993, and each rosette was measured in 2 directions, perpendicular to one another, to provide an indicator of the foliar cover of each plant. Diffuse knapweed densities were counted at this time. In addition, we counted the number of flowering culms on each grass plant.

On 28 May 1994, the above-ground biomass of all grasses was harvested from each plot. In addition densities of seedling (3–4 leaves), juvenile (5–8 leaves), and adult (greater than 8 leaves) diffuse knapweed plants were determined. Diffuse knapweed plants were harvested on 1 July 1994, dried at 60°C until weights were constant and then weighed.

Data Analysis

Data were first analyzed with multiple linear regression (least squares) models using defoliation level and seeding rate as independent variables. Scatterplots of the residual versus the standardized predicted values indicated that most of the data did not fit a linear model. Therefore, all data were analyzed with least square means ANOVA. Means were compared using LSDs of $P \leq 0.05$.

Each site was analyzed separately. Year was not included in the model because data represented sequential sampling of plots treated in 1993, and followed through time. In 1993, data were collected nondestructively and only seedling densities were determined, while 1994 data included diffuse knapweed densities by age class and plant weights. All block interactions were nonsignificant ($P \geq 0.05$) and were pooled into the residual error term. Only reduced models were examined. Arithmetic means and standard errors are presented in figures.

Results

Defoliation reduced the number of flowering culms produced by the grasses at both sites by September 1993 (Fig. 1a,b). Bluebunch wheatgrass and needle-and-thread plants that were not defoliated had the highest number of flowering culms. Plants defoliated by 20% had more flowering culms than those defoliated by 40, 60, and 100%, but were not different from those defoliated 80% because of high variability. Crested wheatgrass plants defoliated at the 80 and 100% had fewer flowering culms than plants with less defoliation (Fig. 1b).

On the bluebunch wheatgrass site, plants defoliated 80 and 100% in April 1993 weighed less 1 year later than those defoliated less than 40% (Fig. 1c). Weights of grasses defoliated by 40, 60, and 80% were similar. Plants defoliated by 0 and 20% weighed the most, but were similar to those defoliated at 40%. One year after defoliation, crested wheatgrass biomass production was similar regardless of defoliation level (Fig. 1d).

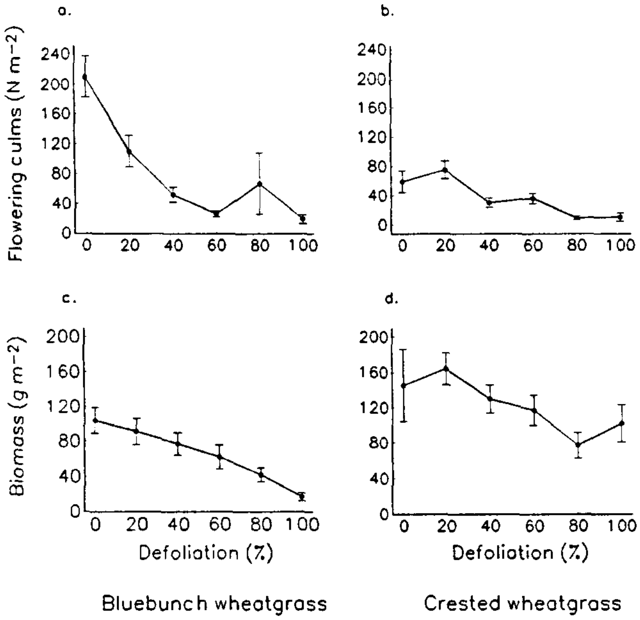

Fig. 1. Response of bluebunch wheatgrass and crested wheatgrass flowering culms 5 months after defoliation and biomass 1 year after defoliation. Error bars represent ± 1 SE.

Before defoliation in April 1993, diffuse knapweed seedling densities on plots that had been seeded with 3,000 and 6,000 seeds the previous fall were similar (bluebunch wheatgrass, P=0.56; crested wheatgrass, P=0.67). Densities averaged 239 plants m^{-2} at the bluebunch wheatgrass site and 330 plants m^{-2} at the crested wheatgrass site. Grasses had not been defoliated at this time. By September 1993, there was still no effect of seeding rate on diffuse knapweed density across all defoliation treatments (bluebunch wheatgrass, P=0.22; crested wheatgrass, P=0.65).

At the bluebunch wheatgrass site, diffuse knapweed seedling densities were affected by level of defoliation by September 1993 (Fig. 2a). Where grasses were defoliated 100%, diffuse knapweed density averaged 33 plants m^{-2}. Diffuse knapweed densities in plots with grasses defoliated at the other levels were similar, ranging from 8 to 16 plants m^{-2}. On the crested wheatgrass site, diffuse knapweed densities were similar regardless of defoliation level (P=0.23; Fig. 2b).

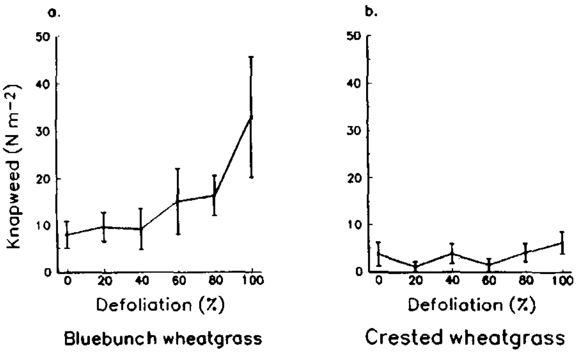

Fig. 2. Diffuse knapweed seedling densities 5 months after grass defoliation. Error bars represent ± 1 SE.

By late May 1994, the higher seeding rate (6,000 seeds vs. 3,000 seeds m^{-2}) resulted in more seedlings (18.2 vs. 11.3) and more total (29.2 vs. 22.8) diffuse knapweed plants on the crested wheatgrass site; however, seeding rate had not affected diffuse knapweed seedling densities on the bluebunch wheatgrass site (P=0.18; Fig. 3a, c).

By late May 1994, adult and total diffuse knapweed densities on the bluebunch wheatgrass site had been affected by the different defoliation levels in 1993 (Fig. 3c,d). Plots with grasses defoliated by 80 and 100% had more adult diffuse knapweed plants than where grasses were defoliated 0 and 20%. Total diffuse knapweed densities were similar where grasses were defoliated 0 to 60%. Adult diffuse knapweed densities on the crested wheatgrass site were affected by defoliation (Fig. 3g). Diffuse knapweed densities were similar where grasses had been defoliated 0 to 60%, but higher where defoliated by 100%. Adult diffuse knapweed densities at 100% defoliation were similar to those defoliated by 80%. Density of seedling and juvenile diffuse knapweed plants were unaffected by defoliation at this time (Fig. 3a,b,e,f).

At the end of the study, diffuse knapweed plants weighed more where grasses were defoliated at the 100% level than where they were defoliated from 0 to 60% on the bluebunch wheatgrass site (Fig. 4a). On the crested wheatgrass site, diffuse knapweed weighed more where grasses were defoliated by 100% than where defoliated from 0 to 80% (Fig. 4b). Foliar cover of diffuse knapweed was not affected by grass defoliation at either site (bluebunch wheatgrass P=0.56; crested wheatgrass P=0.62).

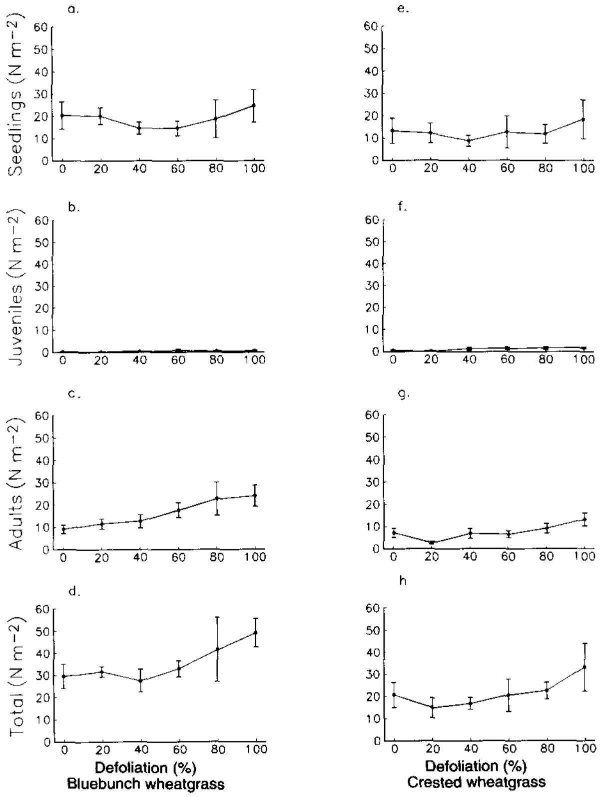

Fig. 3. Response of diffuse knapweed seedling, juvenile, adult, and total densities to defoliation after 1 year. Error bars represent ± 1 SE.

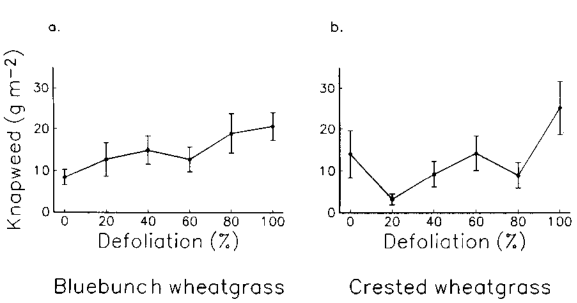

Fig. 4. Diffuse knapweed biomass 15 months after grass defoliation. Error bars represent ± 1 SE.

Discussion

The invasion of semi-arid grasslands by alien weeds is often regulated by seed availability and disturbance, such as grazing (Milchunas et al. 1992). Seeding rate seldom had an effect on the establishment of diffuse knapweed in this study. In comparing 11 different sites over 4 years, Schirman (1981) concluded that only 0.1% of the seeds produced must establish to maintain the population. In the first year of our study, the number of available safe sites probably limited diffuse knapweed seedling establishment (Harper 1977). In the second year, the higher seeding rate resulted in higher diffuse knapweed seedling densities on the crested wheatgrass site, which may reflect the greater residual seedbank at the higher seeding rate. *Centaurea* seeds can remain dormant but viable in the soil for up to 10 years (Callihan et al. 1993, Davis et al. 1993).

In this study, crested wheatgrass recovered regardless of the level of defoliation. Crested wheatgrass is widely recognized as a grazing-tolerant species because of its ability to regrow after defoliation (Cook et al. 1958, Caldwell et al. 1981). Cook et al. (1958) found that the number of flowering culms 1 year after defoliation was similar whether crested wheatgrass plants were clipped to a 2.5 or a 7.5 cm stubble; however, this similar response occurred only on plots that received supplemental water. On a dry site, such as in this study, we would expect defoliation to have a greater effect.

Number of bluebunch wheatgrass flowering culms 5 months after defoliation and weights 1 year after defoliation were reduced by increasing levels of defoliation. In our study, the plants were defoliated when they were in the boot stage, when they are least tolerant to defoliation (Blaisdell and Pechanec 1949, Mueggler 1972, Caldwell et al. 1981).

Diffuse knapweed successfully established on both the bluebunch wheatgrass and crested wheatgrass sites without grass defoliation. Our data support Lacey et al.'s (1990) observation that diffuse knapweed rapidly invades pristine bluebunch wheatgrass-dominated plant communities even without grazing. In their study, diffuse knapweed became established after a hail storm, which may have provided disturbance to allow seeds to germinate and survive. Tyser and Key (1989) reported that spotted knapweed (*Centaurea maculosa* Lam.) invades pristine rough fescue/Idaho fescue grasslands in Glacier National Park. They attributed some of this invasion to small scale disturbances such as badger mounds, ground squirrel activity, and elk wallows. In our study, diffuse knapweed established with and without defoliation. Although a vigorous stand of crested wheatgrass prevented diffuse knapweed invasion on a dry site (about 200 mm ppt.) in British Columbia, diffuse knapweed invaded another crested wheatgrass stand in a higher precipitation area (about 300 mm ppt.; Berube and Myers 1982). They attributed this difference to crested wheatgrass's ability to reduce soil moisture early in the growing season hindering seedling establishment of other species. In wetter areas, this reduction in soil moisture would not be as pronounced, allowing other species, such as diffuse knapweed, to become established. We speculate that the high amount of spring (April, May) precipitation during our study favored knapweed seedling establishment.

Grass defoliation rarely affected diffuse knapweed seedling densities. The shallow-rooted weed seedlings may have avoided competition with the established perennial grasses, similar to conditions that encourage the establishment of cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.; Sheley and Larson 1994). Once the deep taproot of diffuse knapweed reaches the zone occupied by perennial grass roots, selective defoliation of the grasses would alter the competitive relationship between diffuse knapweed and the grasses. Defoliation often reduces root growth of grasses (Crider 1955, Richards 1984), but has less effect on forbs (Olson and Wallander 1997). This would reduce the competitiveness of the grass relative to the weed, encouraging the establishment and growth of diffuse knapweed.

Defoliation greater than 60% was usually needed to increase diffuse knapweed densities or weights. In a greenhouse study, Kennett et al. (1992) found that root crown and foliage growth of spotted knapweed were limited by competition from bluebunch wheatgrass. In our study, grasses defoliated at low to moderate levels recovered fully, similar to those in nondefoliated plots, and minimized diffuse knapweed establishment and growth.

Diffuse knapweed invades grazed and ungrazed sites. Although this clipping study indicated that moderate defoliation does not accelerate invasion, disturbances associated with grazing, such as trampling and exposed mineral soil, were not examined. Future research should focus on developing grazing strategies aimed at reducing the rate of spread of diffuse knapweed.

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Influence of Japanese brome on western wheatgrass yield

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Abstract

Japanese brome (*Bromus japonicus* Thunb.) has invaded many northern mixed-prairie plant communities. Understanding interactions of population dynamics of this and associated species is critical for proper management of communities infested with this annual. Objectives of this study were to determine the effect of Japanese brome removal on aboveground forage production and daily plant water relations of western wheatgrass [*Pascopyrum smithii* Rydb. (Love)] and Japanese brome in a western wheatgrass dominated northern mixed grass prairie community. During early spring of 1991, a wet year, and 1992, a dry year, 2 treatments, undisturbed and complete (total) removal of Japanese brome seedlings, were applied by hand at silty clay loam and clay field sites in circular, 1-m^2 quadrats. Vegetation in additional quadrats was left undisturbed or Japanese brome was removed to assess plant water relations at each site in 1992. Total standing crop was reduced 500 kg ha^{-1} with removal of Japanese brome, while standing crop of western wheatgrass was increased 220 kg ha^{-2} with Japanese brome removal. Increased standing crop of western wheatgrass appeared to result from increased tiller density of 153 tillers m^{-2} rather than increased weight per tiller. Western wheatgrass water relations were essentially unaffected by Japanese brome removal in 1992. Removal of Japanese brome from Northern Great Plains plant communities may increase production of associated perennial grasses, but managers should also expect a short-term decrease in total standing crop.

Key Words: *Bromus japonicus, pascopyrum smithii,* Northern Great Plains

Invasion of Japanese brome (*Bromus japonicus* Thunb.), an introduced weedy graminoid, into numerous mixed-prairie communities in the Northern Great Plains (Haferkamp et al. 1993, Whisenant 1990) may reduce forage production of perennial grasses and performance of grazers. Through competition for water and nutrients, annual bromes may reduce forage production of associated perennials, such as western wheatgrass [*Pascopyrum smithii* Rydb. (Love)], through reduction in number (i.e. density) and/or size of tillers. For example, Rummell (1946) found competition from downy brome (*Bromus tectorum* L.) reduced plant height, number of tillers, foliage weight, as well as root weight and length of western wheatgrass transplants.

Annual bromes have been shown to compete with seedlings of perennial seeded grasses (Buman et al. 1988; Drawe and Palmblad 1977; Harris 1967, 1977; Reichenberger and Pyke 1990; Young and Evans 1973), and perennial plants the second year after seeding (Andersen et al. 1990, Romo and Eddleman 1987). Several researchers have shown increases in forage yields of western wheatgrass when ranges were treated with burning (Gartner et al. 1986, 1978, Whisenant 1990) and herbicides (Currie et al. 1987) to reduce Japanese brome. Lewis et al. (1975) hypothesized that reductions of western wheatgrass forage yields in ungrazed and lightly grazed pastures at Cottonwood, S. Dak. in 1963 may have been due to lack of spring precipitation coupled with competition from Japanese brome.

Studies are lacking, however, that quantify the effect of removing Japanese brome seedlings without the effects of burning, herbicides, or grazing, treatments that can affect both perennial and annual grasses. Our study was designed to determine the effect of hand removing Japanese brome seedlings on annual aboveground forage production and daily water relations of western wheatgrass in a western wheatgrass dominated northern mixed grass prairie community without the influence of herbicides, burning, or grazing.

Materials and Methods

Study Sites

Research was conducted on the Fort Keogh Livestock and Range Research Laboratory (46°22'N 105°5'W) near Miles City, Mont. Regional topography ranges from rolling hills to broken badlands with small intersecting ephemeral streams flowing into large rivers located in broad, nearly level valleys. Indigenous vegetation on the 22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Kuchler 1964). Annual precipitation averages 338 mm, with about 60% received from April through September (NOAA 1982-90). Daily temperatures range from >38°C during summer to <–40°C during winter. The average frost-free growing season is 150 days.

Two study sites were located about 7 km apart. Topography of both sites ranged from gently sloping (< 2%) to level. Soils at the

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silty clay loam site were largely Kobar silty clay loams (fine, montmorillonitic, Borollic Camborthid). Soils at the clay site were primarily a composite of Absher heavy clays (fine, montmorillonitic, Borollic Natrargids) and Gerdrum clay pans (Borollic Natrargids). Vegetation at both sites was dominated by western wheatgrass, blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths], Sandberg's bluegrass (*Poa secunda* Presl.), sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], and Japanese brome. Yellow sweet clover (*Melilotus officinalis* [L.] Lam.) was also present on the silty clay loam site in 1991.

Japanese brome seedlings were abundant by March of both years. In 1991, inflorescences emerged in May, seeds ripened in mid-June, and most plants were senesced by early July. Phenological development was similar in 1992; plants advanced from the 2 to 3-leaf stage to hard dough during the period from 15 April to 22 June. However, plants senesced slightly earlier (late June) in 1992 because of dry conditions. Western wheatgrass tillers began emerging in March and April both years. Tillers remained in the 4 to 6-leaf stage throughout the growing season, few produced inflorescences either year, and height of tillers at harvest averaged 37 cm in 1991 and 27 cm in 1992.

Experimental Design and Methods

Investigations were conducted at 2 sites in 2 years. Each study site encompassed about 0.1 ha and was chosen in spring based on ocular estimates of residual standing crop of Japanese brome and western wheatgrass. These standing crops were our best guides for potential species composition during the current growing season. Ten blocks were located within each site and year, each within a uniform stand of Japanese brome and western wheatgrass. Two circular, 1-m^2 quadrats were marked within each block, and treatments (1) undisturbed or (2) total Japanese brome seedling removal randomly assigned to quadrats. Emerging seedlings were removed by hand several times from mid April to early June in both 1991 and 1992.

Table 1. Degrees of freedom (df), mean squares (MS), and significance levels for AOV models used to statistically analyze standing crops and western wheatgrass tiller density and weight per tiller for 2 years, 2 sites, and 2 treatments.

		Standing crops				Western wheatgrass	
	df	Japanese brome	Total	Total minus brome	Western wheatgrass	Tiller density	Weight/ tiller
Model		MS	MS	MS	MS	MS	MS
Year (Y)	1	32,854	2,578,051**	2,028,845**	291,949*	1,849,536**	32.44**
Site (S)	1	830,607**[1]	2,680,438**	526,825*	575	433,946*	6.78**
Y * S	1	230,824*	3,100	180,424	1,242,611**	118,272	0.41
Error a	36	37,281	85,733	86,011	57,519	32,044	0.24
Treatment (R)	1	11,802,932**	5,391,581**	1,240,020**	971,876**	470,018**	0.03
Y * R	1	12,873	6,401	1,119	100,991	188,568**	0.09
S * R	1	751,401**	810,192**	1,107	6,394	53,045	0.16
Y * S * R	1	191,258**	3,672	141,928	14,301	19,096	0.03
Error b	36	36,899	76,745	43,686	39,062	19,397	0.22

[1] Levels of significance *$P \leq 0.05$ **$P \leq 0.01$.

Standing crop and density measurements were made after Japanese brome matured in early July 1991 and late June 1992. Herbage was clipped to ground level in a circular, 0.25-m^2 quadrat located at the center of each circular, 1-m^2 treatment quadrat, oven-dried for 48 hours at 60°C, and weighed. Density of western wheatgrass tillers was determined by counting within the same quadrat.

To assist in interpretation of standing crop data, 5 additional treatment blocks were installed at both sites in 1992 to assess plant water relations. Western wheatgrass tillers growing in the undisturbed and total-removal treatments and Japanese brome plants growing in the undisturbed treatment were monitored on 7 May, 8 June, and 22 June 1992 at the silty clay loam site and on 14 May, 10 June, and 24 June 1992 at the clay site. Xylem pressure potentials were determined at about 0430, 0830, 1230, 1630, and 2030 hours on the youngest fully-expanded leaf using standard pressure chamber techniques (Scholander et al. 1965). Stomatal conductance was measured on western wheatgrass tillers growing in the undisturbed and total removal plots at about 0930, 1330, and 1730 hours on the same days as xylem pressure potentials were determined. Conductance measurements on a given day were made on the youngest, fully-expanded leaf. Leaf area within the chamber was determined with a LI-COR[1] LI-3000 portable area meter after measurements were completed. A LI-COR[1] LI-1600 steady state porometer, equipped with a cylindrical cuvette was used to measure stomatal conductance, ambient air temperature, and relative humidity. Photosynthetically active radiation was measured with a LI-COR[1] LI-190S-1 quantum sensor. Soil water content was determined gravemetrically for the 0 to 30, 30 to 60, and 60 to 90-cm depths in undisturbed areas at both sites.

Height of 1 premarked western wheatgrass tiller, located near the center of all 30 treatment quadrats, was measured on 6 dates in 1992 between 15 April and 22 June. Heights were measured from the soil surface to the tip of the longest extended leaf.

Statistical Analyses

Analyses of variance were used to test the effect of years, sites, and removal treatments on all standing crop components and western wheatgrass tiller weights and densities (Table 1). Effects of years, sites, and their interaction were tested with the residual variation between blocks within year-site combinations (error a); effects of brome removal and interaction of removal treatments with year and site were tested with residual intra-block variation (error b). Regression analysis was used to examine the effect of Japanese brome standing crop on western wheatgrass standing crop and tiller density.

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[1] Mention of a trademark of proprietary product does not constitute a guarantee or warranty of the product by USDA-ARS and does not imply approval to the exclusion of other products that may also be available.

Table 2. **Degrees of freedom (df), mean squares (MS), and significance levels for tiller height, xylem pressure potential, and stomatal conductance of western wheatgrass for 2 sites and 2 treatments for 1992; and xylem pressure potentials of western wheatgrass and Japanese brome on undisturbed quadrats at both sites in 1992.**

Height			Xylem pressure potential				Stomatal conductance			Xylem pressure potential			
					SCL[2]	C		SCL	C			SCL	C
Model	df	MS	Model	df	MS	MS	df	MS	MS	Model	df	MS	MS
Site (S)	1	351*[1]	Treatment (R)	1	12	58	1	12,513	36,066	Species (Sp)	1	1	79
Error a	28	93	Error a	4	53	182	4	14,885	8,194	Error a	8	22	161
Treatment (R)	1	2,843**	Date (D)	2	1,045**	19,723**	2	1,422,610**	845,454**	Date (D)	2	3,384**	27,775**
S * R	1	135	R * D	2	73*	53	2	12,400	10,310	Sp * D	2	380**	893**
Error b	28	59	Error b	16	18	142	16	18,632	9,492	Error b	16	23	92
Date (D)	6	1,191**	Time (T)	4	2,029**	973**	2	304,039**	85,313**	Time (T)	4	1,234**	789**
S * D	6	94**	R * T	4	11	20	2	19,827*	3,139	Sp * T	4	132**	215*
R * D	6	48**	D * T	8	292**	663**	4	73,966**	24,584**	D * T	8	117**	381**
S * R * D	6	5	R * D * T	8	7	44	4	5,840	6,167	Sp * D * T	8	80**	199*
Error c	337	7	Error c	96	19	76	46	6,263	3,652	Error c	96	17	78

[1] Significant differences *P≤0.05 **P≤0.01.

[2] Sites silty clay loam (SCL) and clay (C).

Analysis of variance was used to test effects of site, treatment, and date on western wheatgrass tiller height (Table 2). Effect of site was tested with the pseudo-replicate block within-site mean square (error a); effects of treatment and site by treatment interaction were tested with the block within site by treatment interaction mean square (error b); and effects of date and interactions of date with site and treatments were tested with residual inter-date mean square (error c).

Split-split-plot analyses of variance (Table 2) were used to test effects of removal treatment, date, and time on xylem pressure potential and stomatal conductance of western wheatgrass at each site separately. While a common experimental protocol was implemented at each site, sampling dates were not common to both sites and, hence, data from each site were analyzed separately. Effects of removal treatments were tested with block by treatment interaction mean square (error a); effects of date and treatment by date interaction were tested with residual inter-date mean square (error b); and effects of time and interactions of time with

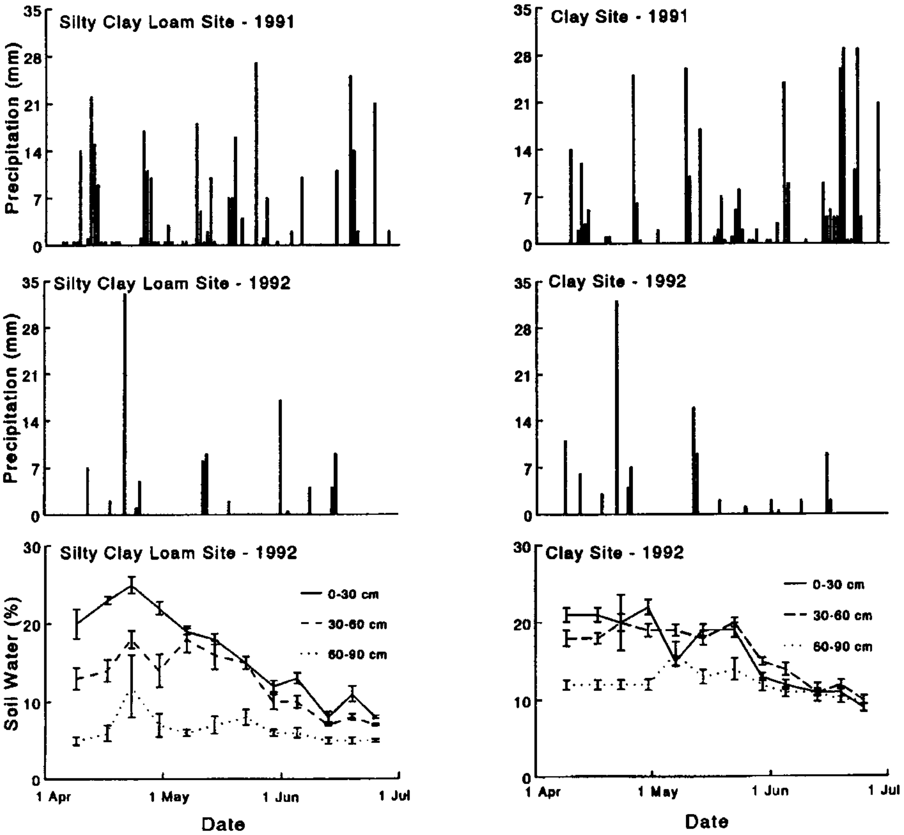

Fig. 1. **Precipitation at the silty clay loam and clay sites during 1991 and 1992, and soil water content (means ± standard errors) for both sites collected from undisturbed treatments in 1992. Because of failure of the automated weather station located at the clay site, precipitation data were supplemented with records from the Frank Wiley Airfield (NOAA 1991- 92) located about 11 km from the plots.**

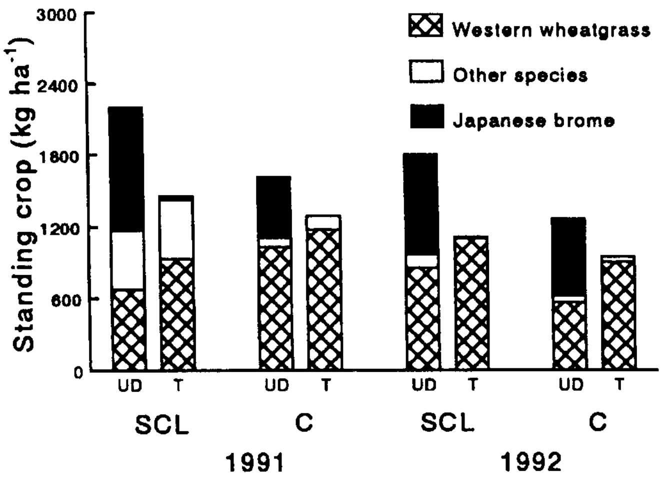

Fig. 2. Standing crops for Japanese brome, other vegetation, and western wheatgrass growing in undisturbed (UD) and total removal (T) plots on the silty clay loam (SCL) and clay (C) sites in 1991 and 1992.

treatments and dates were tested with residual intra-date mean square (error c). Analysis of variance was used to test the effects of plant species, date and time on xylem pressure potentials of western wheatgrass and Japanese brome in undisturbed plots (Table 2). Effect of species was tested with the pseudo-replicate block within species mean square (error a); effects of date and species by date interaction was tested with residual inter-date mean square (error b); and effect of time and interactions of time with species and date were tested with residual intra-date mean square (error c). In all analyses, means were separated by Fisher's Least Significant Difference procedure.

Results and Discussion

Differences between years in precipitation patterns and differences between sites in soil texture, and thus soil water dynamics, resulted in 4 different environments (Fig. 1). Precipitation in April, May, and June totaled 333 mm in 1991 and 101 mm in 1992 compared to the long-term 164-mm average (NOAA 1991-1992). Temporary dynamics of soil water in the 0 to 30-cm and 30 to 60-cm depths but not the 60 to 90-cm depths of the soil profile were closely influenced by precipitation events in 1992. The rate and degree of seasonal decline in soil water was slightly greater at the silty clay loam than the clay site (Fig. 1). However, even at equal soil water contents, fine-textured particles (e.g. clay and silt), will exert greater forces of retention on water than larger particles (e.g. sand) because of their greater surface area per unit mass.

With removal of Japanese brome seedlings, standing crop of total vegetation was reduced, but total standing crop minus Japanese brome and western wheatgrass standing crop were increased (Table 3 and Fig. 2). These changes did not appear to be affected by variation in associated species or variations in growing season precipitation. Western wheatgrass tiller density increased with brome removal, but weight per tiller was unaffected by brome removal (Table 3). Rummell (1946) also reported competition from downy brome reduced the number of shoots produced by western wheatgrass rhizomes. Significant linear relationships were found when data for both western wheatgrass standing crop and tiller density were regressed against Japanese brome standing crop.

Standing crop (g 0.25 m^{-2}): $Y = 25.52 - 0.28\,X$ $r^2 = 0.20$ $P<0.01$

Tiller density (Number 0.25 m^{-2}): $Y = 163.71 - 2.19\,X$ $r^2 = 0.16$ $P<0.01$

The year effect detected on community dynamics was likely caused by variation in amount and distribution of rainfall, whereas the site effect may have simply been due to different soil textures (Tables 1 and 3). Standing crops were generally greater in

Table 3. Significant responses of a western wheatgrass dominated plant community to total removal of Japanese brome seedlings during 1991 and 1992 on a silty clay loam (SCL) and clay (C) site.

Species	Year			Site				Total	
Characteristic	91		92	SCL		C	Undisturbed	removal	LSD$^{0.05}$
Total standing crop (kg ha^{-1})	1,638a		1,279b						133
					SCL		2,002a	1,282c	178
					C		1,435b	1,117c	
Standing crop minus	1,226a		908b						133
Japanese brome (kg ha^{-1})				1,148a		985b			133
							942b	1,192a	95
Western wheatgrass									
Standing crop (kg ha^{-1})		91		846b		1,100a			154
		92		974b		730c			
							803b	1,023a	90
Tiller density (No. m^{-2})		91					389c	445c	89
		92					596b	846a	
				495b		642a			81
Weight/tiller (g)	0.25a		0.12b						0.02
				0.22a		0.16b			0.02
Japanese brome									
Standing crop (kg ha^{-1})		91			SCL		1,110a	25d	174
					C		508c	6d	
		92			SCL		839b	<1d	
					C		647c	<1d	

Means in rows or columns for each characteristic followed by the same letter are not significantly different at P≥0.05.

1991 than 1992 and greater on the silty clay loam than the clay site. One exception was that western wheatgrass standing crop was greatest on the clay site in 1991 and the silty clay loam site in 1992. Tiller density was consistently greater in 1992 than 1991 and greater on the clay than the silty clay loam site. In contrast, weight per tiller was greater in 1991 than 1992 and greater on the silty clay loam than the clay site. Greater fall precipitation was likely the cause for greater tiller density in 1992 than in 1991. Rainfall totaled 118 mm in September, October, and November 1991 compared to 24 mm in fall 1990. We have observed new western wheatgrass tillers emerging during falls with above average precipitation. Tiller weight, however, would have benefited more from the 333 mm rainfall that occurred in April, May, and June 1991 compared to 155 mm rainfall during the same period in 1992.

The reduction in total forage standing crop following early season removal of Japanese brome seedlings is in agreement with findings of others where burning (Gartner et al. 1978, 1986) and herbicides (Hewlett et al. 1981) were the methods of brome removal. After applying atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine], Hewlett et al. (1981) speculated that reduction in total forage production may have resulted from the adverse effect of atrazine on perennials. Herbicide, however, was not a factor interfering with production of perennial grasses in our study.

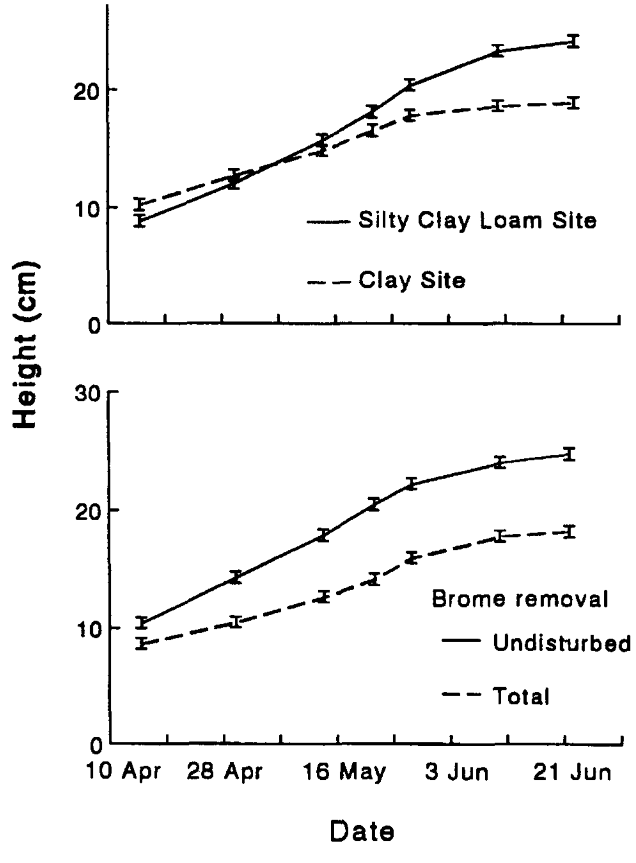

Fig. 3. Means ± standard errors for heights of western wheatgrass tillers (significant site by date and treatment by date interactions) during 1992.

Forage production of perennial grasses and forbs did not increase adequately to compensate for loss of standing crop resulting from Japanese brome removal. This may have been a short-term phenomena. Eissenstat and Caldwell (1989) report that root growth into soil gaps allows plants to occupy a greater soil volume and soil microsites richer in resources. However, greater resource acquisition due to increased root volume (added resources) may not be immediately apparent. We do not know the extent of western wheatgrass rhizome and root growth into soil gaps where Japanese brome had been removed. Mueller (1941) reported that new rhizomes of western wheatgrass form concurrently with the shoots, provided there are adequate resources (e.g. carbohydrates, water, etc.) for growth.

Height of western wheatgrass tillers during 1992 was most affected by date and treatment, but some inconsistency in response resulted in significant site by date and treatment by date interactions (Table 2 and Fig. 3). Western wheatgrass tillers were shorter on the silty clay loam than clay site through late April and taller on this site thereafter. Maximum tiller height was similar in April for both removal treatments, but soon diverged with taller tillers occurring in undisturbed quadrats than with total removal (Fig. 3).

Reduction in maximum tiller height of western wheatgrass with removal of Japanese brome seedlings might have resulted from increased light or a phytochrome response to increased red light reaching western wheatgrass tillers. Casal et al. (1987) found both leaves and stems of annual ryegrass (*Lolium multiflorum* Lam.), smut grass [*Sporobolus indicus* (L.) R.Br.], and dallisgrass (*Paspalum dilatatum* Poir.) grew longer at higher far red:red ratios. Several authors have also reported amount of far red relative to red light increases within plant canopies in proportion to amount of green leaf material present (Casal and Smith 1989, Kasperbauer 1971, Kasperbauer and Karlen 1986).

Xylem pressure potentials and stomatal conductance for western wheatgrass were essentially unaffected by removal of Japanese brome seedlings (Table 2). One exception was the May collection on the silty clay loam site. Xylem pressure potential averaged –1.64 MPa in the undisturbed quadrats and -1.94 MPa in those where brome was removed. Allen (1982), however, reported stomatal resistances for western wheatgrass correlated well with decreases in biomass when western wheatgrass plants were grown with Russian thistle (*Salsola kali* L. var *tenuifolia*) in a greenhouse experiment.

Our study was not designed to determine if presence of Japanese brome decreased soil water content. Melgoza et al. (1990), however, found that downy brome reduced water resources around established plants of needle-and-thread (*Stipa comata* Trin. and Rupr.) and little rabbitbrush [*Chrysothamnus viscidiflorus* (Hook.) Nutt.]. Reduction in soil water resulted in more negative pressure potentials in the native species growing with downy brome than without. Potential increases in soil water that may have been realized through brome removal in our study could have been utilized through increased evaporation from the soil surface of the disturbed plots and/or increased growth and transpiration by western wheatgrass and other species.

Plant water stress increased as the growing season advanced and occurred earlier on the clay than the silty clay loam site (Fig. 4 and Table 2). By 10 June on the clay site, the midday xylem pressure potentials of western wheatgrass were only slightly more negative or equal to predawn pressure potentials. This phenomena occurs in western wheatgrass when leaves begin to roll and

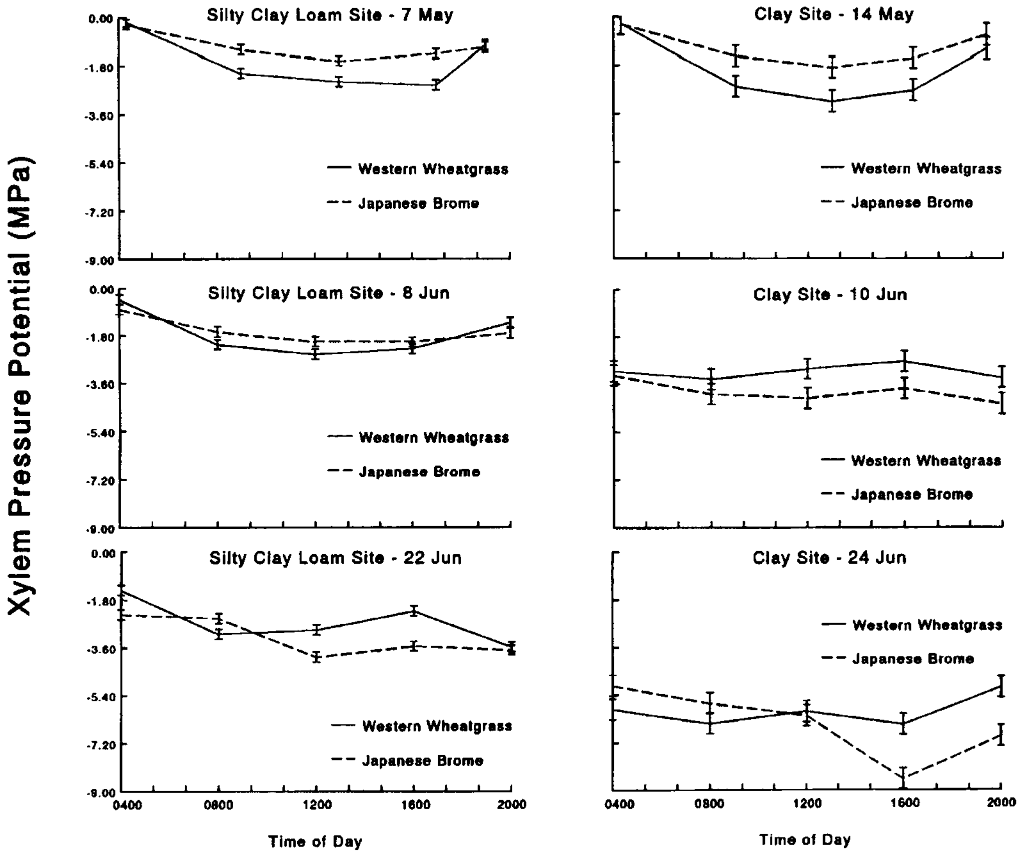

Fig. 4. Mean ± standard errors for xylem pressure potentials of western wheatgrass and Japanese brome leaves (significant time-of-day by species interactions) from undisturbed plots for both the silty clay loam and clay sites in 1992. Data were analyzed by site.

leaf tips begin to senesce. A similar response was reported for Sandberg's bluegrass by Link et al. (1990). Generally, xylem pressure potentials of western wheatgrass were more negative than those of Japanese brome from 0800 to 1600 hours early in the growing season. However, when plant water stress increased, as noted by onset of the cyclic pattern, xylem pressure potentials of Japanese brome were most negative. This shift reflects advancing senescence of Japanese brome. Stomatal conductance of western wheatgrass followed a pattern similar to xylem pressure potentials, declining as the growing season advanced and declining more rapidly on the clay than the silty clay loam site (data not shown).

Conclusions and Management Implications

Standing crop of western wheatgrass was increased 200 kg ha^{-1} with removal of Japanese brome, although the impact was not detected in plant water relations measured during the dry year 1992. The increase in forage appeared to result from an increase in tiller density and not an increase in weight per tiller. Tiller density was increased with an increase in fall precipitation, as well as removal of Japanese brome, which could have increased availability of spring soil moisture. Tiller weight increased with an increase in growing-season precipitation. The increase in western wheatgrass standing crop and reduction of total standing crop occurred regardless of variations in associated plant species or variation in growing-season precipitation. Increasing the clay content of soil and advancing plant phenology appeared to have a greater effect on western wheatgrass plant water relations than removal of Japanese brome.

Although removal of Japanese brome from Northern Great Plains rangelands will increase production of associated perennial grasses, it will also produce at least a short-term reduction in total forage production. Implementation of grazing management tactics and variation in environmental conditions will probably also influence this relationship.

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Preparing sagebrush seed for market: Effects of debearder processing

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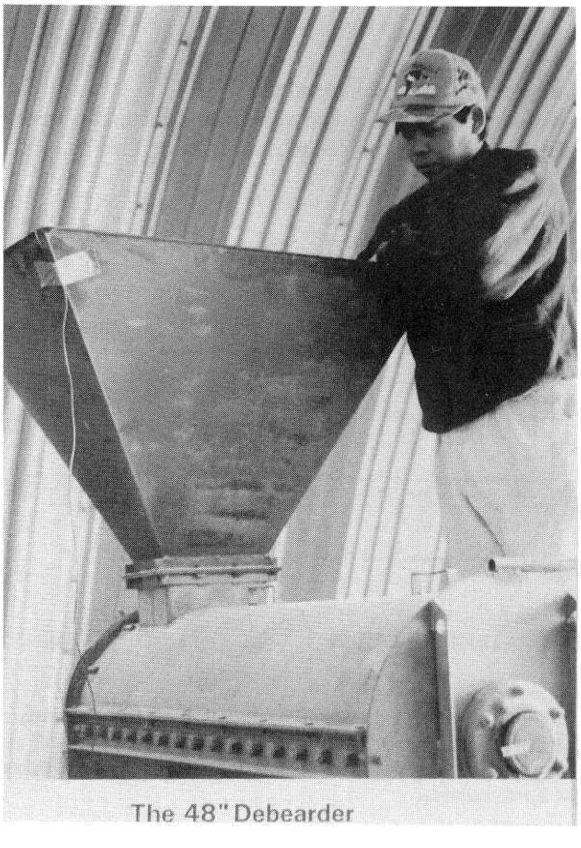
Abstract

Debearders are machines originally developed to remove grain from bearded (awned) seed heads of small grains. They are now used in many types of seed cleaning, including preparing sagebrush seed for market. Some people have suggested that debearders may decrease sagebrush seed quality. We tested this hypothesis by using a debearder to process seeds of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) and measuring subsequent seed quality. Seed stalks were cut from 2 Wyoming locations, stored in an unheated warehouse, and then processed with a debearder for 2, 4, 6, 8, or 10 min. Seed germination and seedling vigor were tested at 2-month intervals up to 16.5 months after processing. Temperature and relative humidity inside the debearder increased linearly from 14.0 to 22.4°C and from 59.0 to 81.2% during the 10-min. processing time. However, the moisture content of seed materials did not change during this period. The number of undamaged seeds per gram of material did not change with processing and was similar between collections. Stem length decreased with processing duration while percent of seed with pericarp removed increased. Germination percentage, time to 50% germination (T_{50}) and seedling vigor were similar among treatments in both collections. Germination percentage increased in the first 4.5 months after processing and then remained at that level up to 16.5 months. Germination rate decreased (T_{50} increased), but seedling vigor did not change with storage time. We recommend that seed dealers continue to use properly adjusted debearders to process sagebrush seed.

Key Words: *Artemisia tridentata* ssp. *wyomingensis*, germination rate, seedling vigor, seed damage, pericarp, afterripening.

Sagebrush (*Artemisia* L.) is commonly recommended for revegetation of disturbed lands within its range. However, sagebrush seedings have often failed. These failures have been attributed to several factors, including a need for better quality seed (Medin and Ferguson 1972, Welch 1995). Yet, little has been done to guide seed dealers in preparing native seeds for commerce. As noted by Young and Young (1992), most methods of harvesting sagebrush seed produce a mass of trashy material composed of seed stalks and flower parts with the small seeds buried in the mixture. Commercial seed dealers process this mixture with debearders to rub seeds from harvested seed heads and floral parts. Debearders have rotating and fixed tines enclosed in a cylinder and set at an angle so that seed materials are vigorously rubbed while being moved through the cylinder. Processing time is regulated by a weighted discharge gate. The speed of rotating tines and the clearance between rotating and fixed tines can also be adjusted (Young and Young 1986).

Questions by seed dealers on the proper use of debearders for sagebrush seed prompted us to investigate the effect of debearder processing on seed quality. We wished to learn how processing



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influenced quality characteristics of sagebrush seed including physical damage of seeds, seed germination, germination rate and seedling vigor.

Materials and Methods

Seed Sources and Handling

Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) seed materials were obtained from a commercial supplier and represent sources being used in Wyoming and adjacent states. One harvest site was located in Lincoln County, Wyo., at 2,044 m elevation (collection 1) and the other near Casper, Wyo., at 1,624 m (collection 2). Seedheads were cut and placed in large woven polypropylene bags during late October, 1993. Harvested materials were stored in an unheated warehouse for approximately 4.5 months before processing. Post-harvest handling, including seed processing, followed common commercial practice. Seed weight (d.w., mean±SE) was 0.22±0.01 and 0.23±0.01 mg with moisture content (%d.w., mean±SE) of 12.1±0.3 and 11.4±0.5% for collections 1 and 2, respectively.

Equipment

Seed materials were processed with a 1.2-m (48-in.) Simon-Day debearder, instrumented with 2 copper-constantan thermocouples, 1 inside and 1 outside, as illustrated in Fig. 1. Processing temperatures were recorded at 1-min. intervals using a CR7 Campbell Scientific data logger. The clearance between stationary and rotating tines was 2 cm, tines were set at 103°, and the debearder was operated at 400 RPM. The relative humidity (RH) inside the debearder and inside bags of seed material was measured with a Vaisala HMI-36 sensor system and data processor. Warehouse air temperatures during the test ranged from 4 to 14°C.

Experimental Design and Procedure

Four bags (approximate 5 kg/bag) of seed materials were fed into the debearder with the outlet door closed. Two samples of about 20 grams each were collected from the rear of the cylinder through the outlet door after 2, 4, 6, 8, and 10 min, and RH was measured at the same intervals. Approximately 5 min. were required to obtain samples and to measure RH at each interval. The order of processing for collection and replication was randomized. Between each run (replications or collections) the debearder was cleaned and allowed to cool to a starting temperature of approximately 14°C (measured outside the debearder, thermocouple 2). The experimental design was a randomized complete block for seed collection with 4 replications and 5 repeated measurements over time. Relative humidity was measured at the same intervals. Data collected from the 20 g-samples included the number of undamaged seeds per gram seed materials and the number of seeds without pericarp. The length of 10 stems with a diameter between 0.5 to 1.0 mm was measured to determine the severity of seed processing. The moisture content of seed materials in each treatment was determined on a dry weight basis after 24 hours of drying in an oven at 80°C.

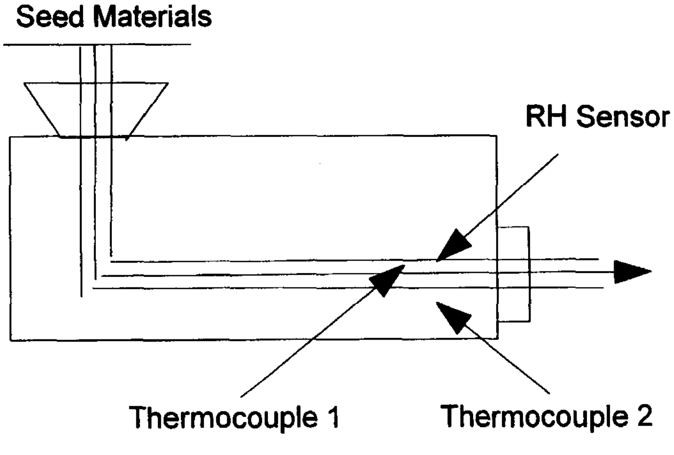

Fig. 1. Debearder schematic showing location of temperature and RH sensors during processing of Wyoming big sagebrush seed. Thermocouple 1 was attached inside the debearder and thermocouple 2 was outside.

We also conducted a test designed to determine how hot the seed material could get. We gradually added an additional 4 bags of seed materials from collection 1 (total of 8 bags) to the machine while keeping the outlet door closed. Samples were collected after an additional 10 min. of processing.

Seed Germination Test and Data Analysis

Germination percentage, germination rate and seedling vigor of samples from each treatment were tested at 0.5, 2.5, 4.5, 6.5, 8.5, 10.5, 12.5, 14.5, and 16.5 months after processing. A completely randomized design with 4 replicates was used for seed quality tests. Twenty seeds from each collection were placed on 1 mm-thick germination paper on slant boards (Booth and Griffith 1994). Seeds were imbibed at 5°C for 4 days, then incubated at 20°C for 14 days under 12 hours light in an incubator. Germination was counted every day and seeds were considered germinated if the radicle was ≥1 mm long. Germination rate (T_{50}) was determined by the time to reach 50% of the total germination measured after 14 days. Seedling axial length was obtained at the end of the germination test using a digitizing tablet (Booth and Griffith 1994), and was used as an index of seedling vigor. The number of undamaged seeds per gram, percent seeds with pericarp removed, stem length, germination percentage, germination rate and seedling vigor were analyzed with ANOVA and regression (Snedecor and Cochran 1980).

Results

The relative humidity inside bags of stored pre-processing seed materials was higher for collection 2 than 1, averaging 49.6 versus 45.6% at 14°C. Temperatures inside the debearder increased linearly with processing time from 13.7°C at the beginning to 22.6°C after 10 min. for collection 1 and from 12.8 to 22.3°C for collection 2 (Fig. 2). Relative humidity also increased linearly with processing time up to 81.3 and 83.1% after 10 min. for collections 1 and 2. The moisture content of seed materials did not change with processing time, but it was higher in collection 1 than 2, averaging 13.6 and 13.2%.

Stem length decreased linearly with increasing processing time from 1.6 cm after 2 min. to 1.0 cm after 10 min. and was similar among the 2 collections (Fig. 3). The percent of seeds without pericarp increased linearly with processing time from 22.7 to

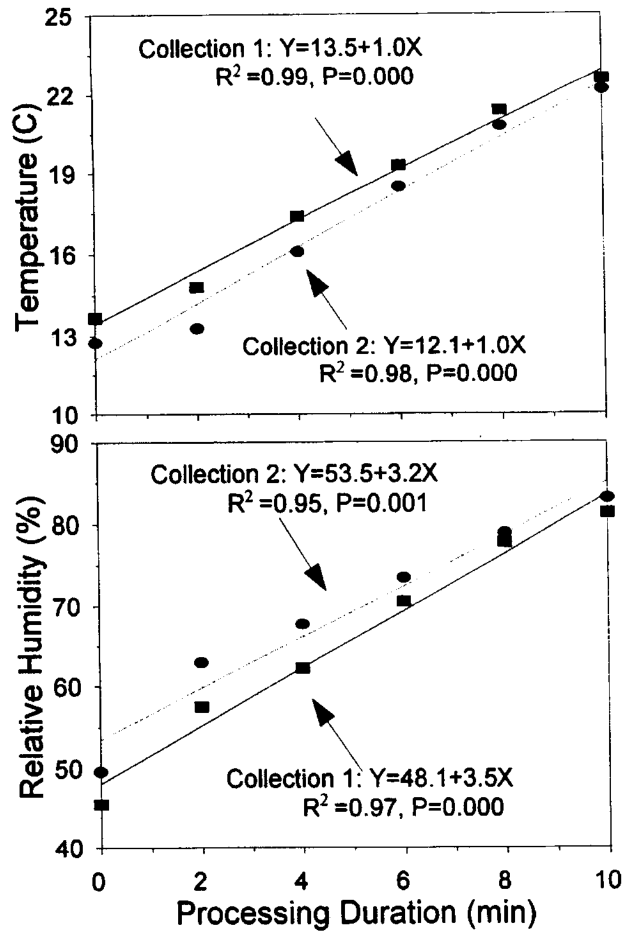

Fig. 2. Changes in temperature and relative humidity inside the debearder while processing Wyoming big sagebrush seeds.

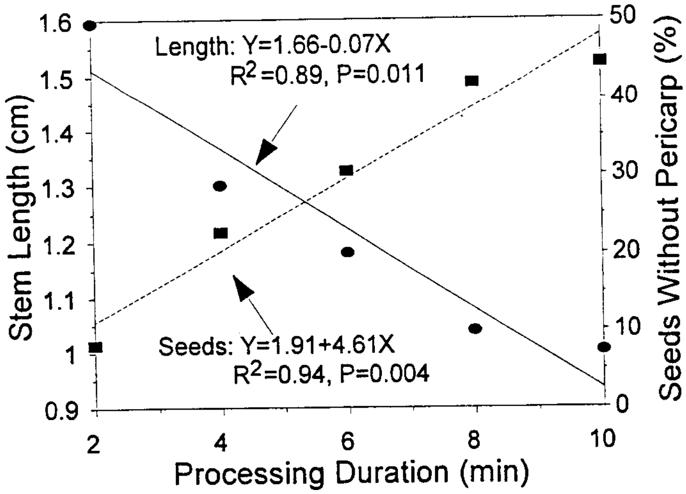

Fig. 3. Stem length and percent of Wyoming big sagebrush seed without pericarp after processing with a debearder. Data of the 2 collections were pooled.

44.5%, and was similar between collections. The number of undamaged seeds per gram did not change with the processing time and was similar between collections, with a mean of 351±12/g.

Total germination, germination rate and axial length were similar among treatments in both collections (Table 1). This was true also for seeds stored at room temperature up to 16.5 months after processing. Therefore, data were pooled and means are shown in Fig. 4. Total germination was higher in collection 2 than collection 1 after 0.5, 2.5, 6.5, 8.5, and 14.5 months, but was similar between collections at other times. Germination increased with storage time up to 4.5 months and was maintained at a relatively high level, but decreased after 16.5 months. Germination rate and seedling vigor were similar among seed collections and data were pooled. T_{50} increased linearly with storage time (Fig. 4). Seedling vigor did not change significantly during 16.5 months of storage.

By overloading the machine and holding the outlet door closed for 20 min. we were able to generate a maximum temperature inside the debearder of 25°C. Percent of seeds with pericarp removed increased to 62.4% while the number of undamaged seeds did not change, averaging 347±17/g (data not shown). Germination percentage, germination rate and seedling vigor were not affected by this treatment.

Discussion

Operating time in the debearder does subject seeds to increasingly severe treatment. This is evident by the negative relationship between processing time and stem length and the positive relationship between processing time and percent of seeds with pericarp removed (Fig. 3). We attribute the lack of difference in number of undamaged seeds per gram to the small seed size.

Table 1. Seed quality of Wyoming big sagebrush after debearder processing.

	Time in debearder (min.)						
	2	4	6	8	10	mean±SE	F-test (P)
Germination (%)							
Collection 1	54.2	48.8	55.0	57.5	53.3	53.8±2.5	0.85[1]
Collection 2	67.5	60.0	63.8	65.0	66.3	64.5±2.8	0.85
Germination rate (T_{50})							
Collection 1	3.0	2.0	2.5	2.8	2.5	2.6±0.2	0.11
Collection 2	2.8	2.8	2.8	2.3	1.8	2.5±0.1	0.11
Seedling axil length (mm)							
Collection 1	24.7	25.8	24.0	28.1	25.8	25.7±0.8	0.55
Collection 2	26.2	25.8	25.0	26.1	24.8	25..6±0.6	0.55

[1] Data were pooled among collections.

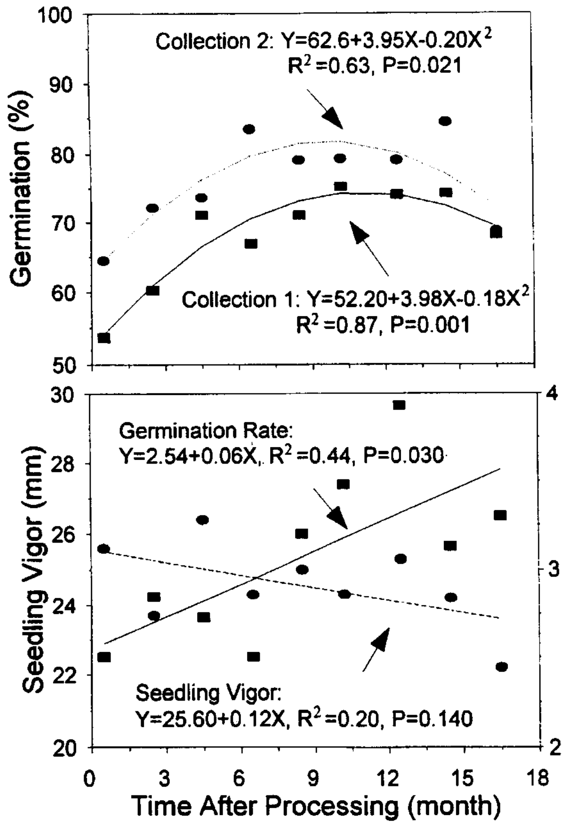

Fig. 4. Changes in seed germination, germination rate and seedling vigor of Wyoming big sagebrush during storage at room temperature after processing with a debearder. Data of the 2 collections were pooled together for germination rate and seedling vigor.

Total germination, germination rate and seedling vigor did not change with processing time, implying that processing time up to 10 min. or longer might not be as critical as anticipated. Welch (1995) also reported that increasing processing time increased the number of seeds without pericarp. He also found no loss of seed viability when Wyoming big sagebrush seed was processed with a properly adjusted debearder.

The temperature and relative humidity inside the debearder during seed processing increased with processing duration. As air temperature increases, the water holding capacity of the air also increases. Therefore, the RH (the pressure of water vapor in the air divided by the equilibrium vapor pressure) decreases unless water vapor is added. The increasing RH inside the debearder indicates water was being driven out of seed materials. The water loss during processing, however, was not enough to allow us to detect a change in the moisture content of seed materials after processing. Even after an additional 10 min. of processing, seed damage, germination, germination rate, and seedling vigor did not change. Pericarp removal did not influence seed quality in this study.

We noted an increase in germination percentage over the first 4.5 months processed seeds were stored at room temperature. This implies either an afterripening requirement [time for embryo maturation (page 377, Young and Young 1992)] or the release of dormancy induced during warehouse storage before seed processing. Because seed quality was not influenced by seed processing, the different storage conditions before and after processing may account for this change. Given the indeterminate nature of most wildland seed production, we suggest that afterripening was responsible for the germination increase. Afterripening may be delayed by the cool and humid pre-processing storage of bagged seedheads, but occur in the relatively dry conditions of the laboratory. This is the first evidence of a possible afterripening requirement in sagebrush. During seed storage after processing, germination rate declined, which confirms the observation by seed dealers (R. Dunne, pers. comm.). However, the rate of vigor loss was not significant in our study, possibly due to the difference between commercial and laboratory storage conditions.

In summary, when seeds of Wyoming big sagebrush were processed through a debearder following standard commercial procedures, germination and seedling vigor were not affected by processing duration and seed damage was not increased by increasing processing time. Total germination, germination rate and seedling vigor changed with time after seed processing (during seed storage). We recommend that seed dealers continue to use properly adjusted debearders to process sagebrush seed.

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Nitrogen and biomass dynamics following brush control in the cross timbers

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Abstract

Converting marginal hardwood forest to grassland has the potential of increasing economic output with livestock grazing. Nitrogen (N) management during conversion needs to be evaluated to minimize possible adverse effects on the environment. This study was conducted to determine temporal changes in quantities of N and biomass within ecosystem compartments after herbicide application in a mature post oak (*Quercus stellata* Wangenh.)-blackjack oak (*Quercus marilandica* Muenchh.) forest. The 4 treatments evaluated included; 1) no brush kill with no grass overseeding, 2) brush kill with no grass overseeding, 3) brush kill with cool-season grass overseeding, 'K-31' tall fescue (*Festuca arundinacea* Schreb.), and 4) brush kill with warm-season grass overseeding, 'Plains' Old World bluestem [*Bothriochloa ischaemum* var. *ischaemum* (L.) Keng.]. Excellent brush kill was accomplished with 2.2 kg a.i. ha^{-1} tebuthiuron (*N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N'*-dimethylurea) applied in spring 1993. Total N was measured during a 21-month period (June 1993 to February 1995), in 15- × 25-m plots, within 8 compartments; soil (0 to 60 cm), roots (0 to 60 cm), litter, top growth of herbaceous plants, woody plants <2.5 cm in diameter, and leaves, branches, and boles from trees >2.5 cm in diameter. Stored N in tall fescue forage was 6 to 7 times greater than in Old World bluestem or native vegetation by June 1994 and was 2 times greater in October 1994 and February 1995. Above-ground biomass of tall fescue and Old World bluestem was not different in October 1994 or February 1995, but both were greater than native vegetation. Litter biomass and total N in litter decreased, especially in the tall fescue overseeding treatment. Total N in the soil for all treatments averaged 5,100 kg ha^{-1} and fluctuations were not detectable among treatments. Total N changes in other compartments were not observable or were minimal. Brush kill and overseeding with grass had little influence on total N stored within the ecosystem for 21 months after treatment. N was redistributed to the herbaceous biomass compartment and away from the litter compartment after herbicide application, regardless of the overseeding treatment applied.

Key Words: post oak-blackjack oak, nitrogen cycling, nutrient budget, tebuthiuron.

Resúmen

El transformar un bosque marginal a pastizal inducido posee el potencial de incrementar el rendimiento económico por medio del apacentamiento de ganado. El comportamiento del nitrógeno (N) durante dicha transformación necesita ser evaluado para minimizar los posibles efectos adversos. El presente estudio fue llevado a cabo para determinar cambios temporales en la cantidad de N y biomasa dentro del ecosistema, después de la aplicación de herbicida (Tebuthiuron) en un bosque de *Quercus marilandica*. Los 4 tratamientos evaluados incluyeron: 1) Testigo (sin hericida ni siembra), 2). Herbicida sin siembra de pastos, 3) Herbicida más siembra de festuca K-31 (*Festuca arundinacea*), y 4). Herbicida más siembra se pastos de tallo azul (*Bothriochloa ischaemum*). Se logró una mortandad excelente con la aplicación de 2.2 kilogramos de i.a/ha de tebuthiuron aplicado en la primavera de 1993. El N total fue medido durante un periodo de 21 meses (Junio 1993 a Febrero de 1995) en lotes de 15 × 25 m, dentro de 8 compartimientos: suelo (0 a 60 cm.), raices (0 a 60 cm.), mantillo orgánico, crecimiento aereo de plantas herbaceas, plantas leñosas de más de 2.5 cm. de diametro y en hojas, ramas y copas de arboles menores de 2.5 cm. de diametro. El N almacenado en la siembra de festuca alta fue de 6 a 7 veces mayor que en el de pasto tallo azul o en la vegetacion nativa (testigo) en Junio de 1994 y fue 2 veces mayor en Octubre de 1994 y Febrero de 1995. La biomasa aerea de festuca alta y de pasto tallo azul no fue diferente en Octubre de 1994 ni en Febrero de 1995, pero ambos fue superior a la de la vegetacion nativa. La biomasa del mantillo orgánico y el total de N en el mantillo, disminuyeron especialmente en el tratamiento de siembra con festuca alta. El total de N en el suelo para todos los tratamientos promedio 5,100 kg/ha. y no se detectaron fluctuaciones entre tratamientos. Los cambios totales de N en otros compartimientos fueron minimos o no observables. La mortandad de arbustivas y la siembra con pastos tuvieron poca influencia sobre el N total almacenado dentro del ecosistema durante 21 meses despues del tratamiento. El N fue redistribuido al compartimiento de la biomasa herbacea despues de la aplicacion del herbicida, sin importar el tratamiento de siembra de pastos.

Oklahoma, Texas, and Kansas contain more than 4 million hectares of the cross timbers vegetation type (SCS 1981, Engle 1994). Much of this land has little economic value other than recreational use. Livestock production on these areas is marginal since lack of proper management (i.e., prescribed fire) in the past has reduced thousands of hectares to unmerchantable hardwoods

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(Byrd et al. 1984). Herbicide treatments can improve use and production from this land (Elwell and Cox 1950, Elwell 1968, Elwell et al. 1970, Scifres et al. 1981, McCollum et al. 1987, Scifres et al. 1987, Smith et al. 1987, Smith 1988, Engle et al. 1991, Stritzke et al. 1991), but such severe disturbances may also have negative environmental impacts.

The fate of N within the ecosystem after disturbance is an environmental concern that has been studied in a variety of forests and shrublands (Likens et al. 1970, Hibbert et al. 1974, Knight et al. 1983, Lloyd-Reilley et al. 1984). When disturbances such as clear-cutting and herbicide treatment occur in forests, large amounts of organic matter can be mineralized resulting in an abundance of available N (Vitousek 1981). Significant N losses through leaching and runoff are typical when plant uptake is temporarily reduced well below the available source of nutrients (Vitousek and Melillo 1979). Negative environmental consequences of N loss may include a decline in site fertility and productivity.

At the Cross Timbers Experimental Range near Stillwater, Okla., Stritzke et al. (1991) evaluated the response of overstory woody species and Engle et al. (1991) determined the response of understory herbaceous vegetation during secondary autogenic succession after application of herbicides and fire. In the closed overstory of these mature post oak-blackjack oak forests, herbaceous plants were sparse and understory herbage production did not peak until 2 years after herbicide treatment (Engle et al. 1991). A lag time resulted between expected N release and available vegetation for N uptake. Herbage production peaked at 4,800 kg ha^{-1}, but by 10 years post treatment, total herbaceous production had dropped to as much as half of the maximum (Unpublished data, Engle et al., Bernardo et al. 1992). Similar herbage production response has been noticed in other studies (Davis 1967, Klimo and Kulhavy 1994). It is possible that loss of N from the ecosystem was partially responsible for the reduced level of production, although no research has been done to date on the fate of nitrogen in the cross timbers following brush control. If indeed N is lost after brush control, it is also possible that capturing the mineralized N in herbaceous material will result in a more sustainable forage production system. The objective of this study was to determine effects of brush kill and grass establishment by overseeding on the temporal variation in N storage within ecosystem compartments of the cross timbers.

Materials and Methods

Study Area

This study was conducted on the Oklahoma State University Research Range, located approximately 11 km southwest of Stillwater, Okla. The vegetation of the area is dominated by post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Muenchh.). The site is an upland forest on a sandy savannah range site. We established study plots on nearly level topography of Stephenville sandy loam soils (fine-loamy, siliceous, thermic Ultic Haplustalfs). Soils in the series have an average depth of 60 cm, are well drained, and are moderately permeable. Annual precipitation in the area averages 830 mm, falling mostly from April to October. Mean annual temperature is 15.5 °C, with the mean in January of 2.3°C, and the mean in July of 27.6°C (Myers 1982).

Treatments and Design

Sixteen plots, (15 × 25 m), with 4 replications of 4 treatments were arranged in a completely randomized design. The 4 treatments evaluated included; 1) no brush kill with no grass overseeding (untreated control), 2) brush kill with no grass overseeding, 3) brush kill with cool-season grass overseeding, and 4) brush kill with warm-season grass overseeding. The brush kill with no grass overseeding treatment, which revegetated by secondary autogenic succession, consisted of mostly annual forbs. The overseeded cool-season grass was 'K-31' tall fescue (*Festuca arundinacea* Schreb.). 'Plains' Old World bluestem [*Bothriochloa ischaemum* var. *ischaemum* (L.) Keng.] was the warm-season grass overseeded. Brush kill was achieved with tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N'*-dimethylurea), which was applied to 8 of the plots in March 1993 and to 4 of the plots in May 1993, at a rate of 2.2 kg a.i. ha^{-1}. The tebuthiuron effect on overstory oaks resulted in excellent control with results similar to those reported by Stritzke et al. (1991). To prepare a seedbed, leaf litter in the 12 herbicide-treated plots was removed by burning on 30 September 1993. Eight plots were immediately overseeded (4 with tall fescue at 15 kg PLS ha^{-1} and 4 with Old World bluestem at 6 kg PLS ha^{-1}) and 4 were left unseeded. The remaining 4 served as controls and were not treated with herbicide, burned, or overseeded. Tall fescue emerged in the Fall of 1993 and established 100% ground cover by April 1994. Old World bluestem emerged in the Spring of 1994 and established 100% ground cover by August 1994.

Field Sampling

Plots were randomly subdivided into 6 sections to match 6 sampling dates over a 21-month period (June 1993 through February 1995). All compartments were randomly sampled in a different section at each date to avoid disturbance before sample collection. Sampling dates corresponded to either expected pulses of plant N uptake or mineralized N in the soil. We sampled in June 1993 to measure base N levels before tebuthiuron treatment was effective. November 1993 sampling coincided with expected maximum accumulation of mineralized N in biomass of original vegetation because growth of both cool-season and warm-season vegetation is insignificant by then. We sampled in January 1994 to correspond with maximum accumulation of mineralized N in the soil, because mineralization by this time is minimal, tall fescue would not be actively growing, and Old World bluestem would not yet have germinated. The June 1994 sampling represented reduced N uptake and near maximum accumulation of mineralized N by tall fescue, corresponding to time of seed production and reduced growth in tall fescue. The October 1994 sampling, after the first killing frost, represented maximum accumulation of mineralized N by Old World bluestem.

Finally, sampling in February 1995, we expected maximum mineralized N in the soil before uptake by tall fescue and Old World bluestem began in the second growing season. Biomass and N concentrations were determined in samples from 5 compartments: soil, roots, litter, herbaceous plants, and woody plants with a diameter at breast height (dbh) of <2.5 cm. We collected samples for N concentrations in 3 additional compartments: leaves, branches, and boles from trees with a dbh >2.5 cm. Biomass in compartments of trees with a dbh >2.5 cm was estimated from values of Johnson and Risser (1974).

Soils were sampled and composited from 5 random locations per plot. Samples were taken with a 2.5-cm diameter corer at 4 depth increments (0 to 15, 15 to 30, 30 to 45, and 45 to 60 cm). Root biomass was sampled in 3 root cores per plot by driving a 6.5 cm diameter corer into the ground and extracting cores in the same depth increments as soil. Litter samples were collected to mineral soil within three 0.25-m^2 circular quadrats per plot. Herbaceous material and woody (<2.5 cm dbh) material were sampled within three 1.0-m^2 circular quadrats per plot. Twenty tree leaves per plot were collected randomly on those dates when leaves were alive and present in the canopy. Ten branches (<1.25 cm in diameter) per plot were randomly collected, excluding current years growth. Two bole samples per plot were randomly collected with a 5.15-mm increment borer.

Laboratory Procedures

Soil samples were dried at 90°C in a forced air drying oven and ground in a hammer mill to pass a 2.0-mm mesh screen. Biomass samples were dried at 65°C. Litter, herbaceous, and woody samples were weighed, composited, and subsampled by quartering before grinding. Roots were separated from root core samples by washing the composited samples with water through 20-mesh and 32-mesh screens simultaneously to recover root fragments. All biomass samples were ground in Wiley and Udy mills consecutively to pass 4.0-mm and 0.5-mm mesh screens, respectively. Both soil and biomass samples were analyzed in the LECO N analyzer, model FP 428, by dry combustion for total N as described by Bremner and Mulvaney (1982). Total compartment N was calculated as the product of the compartment N concentration and mass. Total N value for the ecosystem in each treatment over time was calculated as the sum of all N in all compartments. Soil total N values by depth were adjusted for differences in bulk density by using the average weight of 60 core samples per 15-cm soil depth increment taken from the study area in February 1995. Nitrogen values were converted to kg ha^{-1}. We present total soil N for the beginning June 1993 sampling date and the ending February 1995 sampling dates because laboratory analysis was done on these samples initially. No treatment differences were detected, so we did not analyze the samples from other dates.

Statistical Analysis

Statistical analysis was performed with a split-plot-in-time arrangement of treatments in an analysis of variance. Treatments were main units and dates were subunits. Differences between treatments were detected with the following single-degree-of-freedom contrasts: no brush kill vs. brush kill, brush kill with overseeding vs. brush kill with no overseeding, and brush kill with cool-season grass overseeding vs. brush kill with warm-season grass overseeding. A 2-tailed t-test was used to compare means in all compartments and contrasts except for the herbaceous compartment. We expected an increase in total N in the herbaceous material in June 1994, so a 1-tailed t-test was used to compare treatment means for this date. However, we had no basis for anticipating whether tall fescue or Old World bluestem would have accumulated greater total N in October 1994 or February 1995, so we used a 2-tailed t-test to contrast the overseeding treatments at those dates.

Results and Discussion

Below-ground Nitrogen and Biomass

Total soil N (0 to 60 cm) in June 1993 was about 5,000 kg ha^{-1} (Table 1). Johnson and Risser (1974) reported 9,591 kg ha^{-1} total soil N to an average soil depth of 300 cm in a similar post oak-blackjack oak area. Our values appear high but are likely more accurate for the 0- to 60-cm soil layer than those of Johnson and Risser because we measured total N in 4 succeeding soil layers. Johnson and Risser estimated total N for lower soil depths based on total N in the 0- to 15- and 30- to 45-cm soil layers only. Soil organic matter and total N decrease with soil depth and would be difficult to estimate at 300 cm from samples at 30 cm. Sears et al. (1986) reported total soil N values ranging from 1,346 to 2,153 kg ha^{-1} (0 to 60 cm) in the sand shinnery oak (*Quercus havardii* Rydb.) community of West Texas, which are half those we reported. The primary soil in the sand shinnery oak community of West Texas is a fine sand 40 to 70 cm deep. Less organic matter and total N would be expected in the sandy, more arid soils of West Texas.

No differences were detected in total soil N among treatments at the June 1993 or February 1995 sampling (Table 1). Either the 21-month sampling period was too brief for changes in total soil N to be detected in response to woody material decomposition, or total N was not affected by brush kill. Differences might have been detected in the top 5 cm of soil if sampling depth increments had been smaller. Soil NO_3-N, however, in all the brush kill plots compared to the untreated plots rose from <3 kg ha^{-1} to >60 kg ha^{-1} (Gay et al. 1996), but at maximum levels this represented only about 1.0% of the total N in the soil.

Table 1. Total N in soil by treatment and depth in a post oak-blackjack oak community in the cross timbers of north central Oklahoma following herbicide application.

	June 1993				February 1995			
Depth (cm)	Control[1]	No seed	Fescue	OWB	Control	No seed	Fescue	OWB
	(kg ha^{-1})							
0 to 15	1,920[2]	1,980	1,710	1,810	1,860	1,810	1,710	1,400
15 to 30	590	990	870	700	930	1,010	1,060	850
30 to 45	930	1,220	1,230	1,170	1,310	1,390	1,350	1,220
45 to 60	1,000	1,090	990	870	1,350	1,400	1,380	1,160
0 to 60	4,430	5,280	4,800	4,540	5,450	5,610	5,510	4,620

[1] Treatments are: control = no brush kill with no overseeding, no seed = brush kill with no overseeding, fescue = brush kill with tall fescue overseeding, OWB = brush kill with Old World bluestem overseeding.

[2] No differences P> 0.05.

Table 2. Total N and biomass in roots (<2.5 cm diameter) by date and treatment in a post oak-blackjack oak community in the cross timbers of north central Oklahoma following herbicide application.

Soil depth and treatment[1]	Jun 1993		Nov 1993		Jan 1994		Jun 1994		Oct 1994		Feb 1995	
	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass
(0 to 15 cm)	(kg ha^{-1})											
Control	31	4,000	55	6,110	37	3,890	22	3,260	44	7,060	22	2,450
No seed	42	5,480	34	3,960	31	4,470	27	3,970	32	4,320	24	2,600
Fescue	50	6,530	26	3,030	34	4,410	39	4,790	42	5,020	46	4,370
OWB	31	4,470	40	4,763	28	3,460	22	2,890	24	2,810	25	3,270
Contrasts[2]												
Control vs brush kill	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
No seed vs seed	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Fescue vs OWB	- - -	- - -	- - -	- - -	- - -	- - -	†	†	*	†	†	- - -
(15 to 60 cm)[3]												
Control	49	9,400	85	13,680	89	14,550	64	12,860	71	13,270	97	17,630
No seed	67	10,670	109	15,970	77	12,070	59	8,960	47	7,800	53	8,690
Fescue	118	18,470	66	10,740	83	13,790	80	13,930	71	10,840	63	11,000
OWB	74	13,540	102	15,010	71	11,200	47	7,520	59	9,680	73	12,890

[1] Treatments are: control = no brush kill with no overseeding, no seed = brush kill with no overseeding, fescue = brush kill with tall fescue overseeding, OWB = brush kill with Old World bluestem overseeding.

[2] †, *, Significant at the 0.10, and 0.05 probability levels, respectively. Dashed line represents no difference in contrast.

[3] No significant treatment F-tests for the lower depth increments. These data represent a sum of the lower 3, 15-cm depth increments.

Root biomass differed ($P \leq 0.10$) between tall fescue overseeding and Old World bluestem overseeding in June and October of 1994 in the 0- to 15-cm soil layer (Table 2). The smaller root quantity in plots overseeded with Old World bluestem could help explain the lack of N uptake in that treatment (Gay et al. 1996). Total N stored in root biomass was also lower in the Old World bluestem plots. Our estimate of 18,000 kg ha^{-1} in root (<2.5 cm) biomass to a depth of 60 cm and 115 kg N ha^{-1} in roots in June 1993 averaged over all treatments appears lower than the 30,000 kg ha^{-1} root biomass (0 to 60 cm) and 169 kg N ha^{-1} for a similar area reported by Johnson and Risser (1974).

Above-ground Nitrogen and Biomass

Total N within the litter compartment was reduced after brush kill by June 1994 (Table 3), but burning in late September 1993 apparently had little influence on litter biomass or total N because no difference was detected in the control vs. brush kill contrast in November 1993. Lab analysis of leaf litter collected before burning suggested an average of 8,900 kg biomass ha^{-1} and 177 kg N ha^{-1} could have been lost in burning the brush kill plots, assuming all of the N was volatilized from the leaf litter consumed by fire. This agrees with Van Lear and Kapeluck (1989) who estimated losses of N ranging from 130 to 170 kg ha^{-1} in a burned, mixed pine-hardwood forest. Our burning was done on 30 September 1994 and post-burn litter was not collected until November 1994. The lack of detectable differences could have occurred because leaf fall had not completely occurred in September and leaf fall after that date disguised any burning effects. We may have also overestimated the amount of leaf litter that was actually consumed by fire. The differences in total litter N found in June 1994 were still observed in October 1994 and February 1995 in the brush kill plots, which were burned, compared to the no brush kill plots. By February 1995, the tall fescue overseeding plots had less litter biomass and less total litter N than plots overseeded with Old World bluestem. The difference may have begun in April 94 when a more mesic micro-climate at the soil surface was created by the overseeded tall fescue, allowing litter decomposition to begin sooner than in the Old World bluestem plots. Ground cover establishment for tall fescue was April 1994 whereas for Old World bluestem it was August 1994.

Herbaceous biomass increased after brush kill both with and without overseeding (Table 4). Both the tall fescue and Old World bluestem overseeding treatments produced >3,000 kg ha^{-1} above-ground biomass the first growing season compared to 1,800 kg ha^{-1} in the brush kill with no overseeding. However, there was a difference in total N stored in tall fescue and total N

Table 3. Total N and biomass in litter by date and treatment in a post oak-blackjack oak community in the cross timbers of north central Oklahoma following herbicide application.

Treatment[1]	Jun 1993		Nov 1993		Jan 1994		Jun 1994		Oct 1994		Feb 1995	
	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass
	(kg ha^{-1})											
Control	292	23,500	111	15,900	221	18,000	335	24,900	253	18,100	230	19,600
No seed	371	27,400	137	14,700	223	16,500	266	18,900	150	10,200	155	13,400
Fescue	336	24,700	78	17,300	219	15,600	162	12,100	122	8,170	82	5,810
OWB	337	25,800	154	14,800	278	20,100	229	15,700	150	10,900	171	14,300
Contrasts[2]:												
Control vs brush kill	- - -	- - -	- - -	- - -	- - -	- - -	*	**	**	*	*	**
No seed vs seed	- - -	- - -	- - -	- - -	- - -	- - -	- - -	†	- - -	- - -	- - -	- - -
Fescue vs OWB	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	†	†

[1] Treatments are: control = no brush kill with no overseeding, no seed = brush kill with no overseeding, fescue = brush kill with tall fescue overseeding, OWB = brush kill with Old World bluestem overseeding.

[2] †, *, **, significant at the 0.10, 0.05, and 0.01 probability levels respectively. Dashed line represents no significant difference in contrast.

Table 4. Total N and biomass in above-ground herbaceous plant material by date and treatment in a post oak-blackjack oak community in the cross timbers of north central Oklahoma following herbicide application.

Soil depth and treatment[1]	Jun 1993		Nov 1993		Jan 1994		Jun 1994		Oct 1994		Feb 1995	
	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass
	-(kg ha^{-1})-											
Control	0.1	10	0.1	10	0.2	20	0.4	30	0.2	20	0.0	0
No seed	0.1	10	0.0	0	0.0	0	7.4	240	26.5	1,790	7.7	640
Fescue	0.0	0	0.0	0	0.0	0	40.6	1,760	66.3	3,480	41.8	2,600
OWB	0.1	10	0.0	0	0.0	0	6.3	210	34.3	3,100	21.9	2,380
Contrasts[2]:												
Control vs brush kill	---	---	---	---	---	---	***	***	***	***	***	***
No seed vs seed	---	---	---	---	---	---	---	---	*	---	**	*
Fescue vs OWB	---	---	---	---	---	---	***	*	*	---	---	---

[1] Treatments are: control = no brush kill with no overseeding, no seed = brush kill with no overseeding, fescue = brush kill with tall fescue overseeding, OWB = brush kill with Old World bluestem overseeding.

[2] *, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels respectively. Dashed line represents no significant difference in contrast.

stored in Old World bluestem. Whereas untreated plots contained almost no N in herbaceous biomass, plots with tall fescue overseeding sequestered over 60 kg N ha^{-1} in above-ground biomass by October 1994, compared to 34 kg N ha^{-1} in plots overseeded with Old World bluestem. Unseeded brush-kill plots, which revegetated through secondary autogenic succession, stored about half the N in above-ground biomass as the tall fescue-overseeded plots and about the same as Old World bluestem-overseeded plots. Growth stage when harvested may partially explain the lower concentrations of N observed in Old World bluestem than in tall fescue. It is also known that 1 characteristic of plants with the C_4-photosynthetic pathway (i.e. Old World bluestem) is a more efficient use of N (Waller and Lewis 1979). This does not explain, however, why Old World bluestem did not produce more biomass than tall fescue if the N present was more efficiently utilized by Old World bluestem. One likely explanation is that during Old World bluestem seedling establishment in May and June of 1994, precipitation was half of the long term mean for the area (118 mm vs. 225 mm) (Table 5). Soil water within the seedling root zone was limiting plant growth and N uptake. When rainfall amounts returned to normal, there was insufficient time in the growing season for substantial growth of Old World bluestem.

Table 5. Precipitation summary during experiment and long-term precipitation average at the Oklahoma Agriculture Experiment Station, Stillwater Agronomy Research Station, Stillwater, Okla.

	Year			
Month	1993	1994	1995	1893-1994
	(mm)			
January	57	1	26	29
February	63	54	3	35
March	61	94	119	60
April	211	120	112	86
May	241	72		127
June	87	46		102
July	65	86		74
August	78	91		75
September	119	71		95
October	17	49		73
November	43	134		53
December	27	18		36
Total	1069	836		843

Small (<2.5 cm dbh) woody plants were a minor biomass component (Table 6) and had little influence on ecosystem total N after brush kill. Biomass and total N in the brush kill treatments were less than in control treatments, but total N was <0.1% of the N in the entire system and less than 0.4% of the N in above-ground and below-ground biomass combined.

We have observed that branches of large trees (>2.5 cm dbh) do not begin to fall until 2 years post-herbicide treatment, and tree boles remain standing for 3 to 10 years after treatment. Decomposition is slow because the biomass is suspended and remains relatively dry. Indeed, neither N concentrations in branches or boles changed over the 21-month period (Table 7). Total N stored in these compartments, obtained by using Johnson and Risser (1974) tree biomass data, did not change either. Biomass reported by Johnson and Risser (1974) was 109,500 kg ha^{-1} for tree boles, 64,563 kg ha^{-1} for branches, and 4,759 kg ha^{-1} for leaves. While biomass of boles and branches did not change over the 21-month period, leaf biomass was reduced the second growing season after herbicide treatment and tree mortality. Minimal leaf production in the 1994 growing season resulted in 110 kg N ha^{-1} that was not taken up by tree roots.

Summary and Conclusions

Brush kill and overseeding with grass had little influence on total N stored within the ecosystem for 21 months after treatment. Although soil NO_3-N increased following brush kill (Gay et al. in press), total N within the soil remained unchanged. Total N in roots did not change except in the 0- to 15-cm soil layer. Herbaceous above-ground biomass and total N increased regardless of the treatment applied. Total N and biomass decreased within the litter compartment in all the brush-kill treatments. The most evident changes in N distribution occurred in the brush kill followed by overseeding with tall fescue.

A range of values from beginning and ending sampling dates in this post oak-blackjack forest indicate that of the total N stored within the ecosystem, 77 to 88% is stored in the soil, 2 to 3% in small (<2.5 cm) roots, 1 to 6% in litter, 0 to 1% in herbaceous material, and 8 to 15% in all woody biomass. Total ecosystem N

Table 6. Total N and biomass in small (<2.5 cm dbh) woody plants by date and treatment in a post oak-blackjack oak community in the cross timbers of north central Oklahoma following herbicide application.

Treatment[1]	Jun 1993		Nov 1993		Jan 1994		Jun 1994		Oct 1994		Feb 1995	
	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass	Total N	Biomass
	(kg ha^{-1})											
Control	4.0	348	0.3	26	0.7	79	4.4	424	2.4	304	3.0	420
No seed	2.4	218	0.4	57	0.7	74	1.3	65	0.4	66	0.3	46
Fescue	1.9	95	0.4	32	0.4	45	0.4	27	0.5	44	0.3	26
OWB	0.8	45	0.9	94	0.0	2	0.2	10	0.0	2	0.0	3
Contrasts[2]:												
Control vs brush kill	---	---	---	---	---	---	***	**	**	**	***	*
No seed vs seed	---	---	---	---	---	---	---	---	---	---	---	---
Fescue vs OWB	---	---	---	---	---	---	---	---	---	---	---	---

[1] Treatments are: control = no brush kill with no overseeding, no seed = brush kill with no overseeding, fescue = brush kill with tall fescue overseeding, OWB = brush kill with Old World bluestem overseeding.

[2] *, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels respectively. Dashed line represents no significant difference in contrast.

ranges from 5,500 to 6,600 kg ha^{-1}, of which 770 to 940 kg ha^{-1} is stored in above-ground biomass excluding forest floor N. This estimate of N in above-ground biomass is similar to the 902 kg ha^{-1} reported by Johnson and Risser (1974). Others, summarized by Khanna and Ulrich (1991), have reported much lower values of 139 kg N ha^{-1} in an oak-hickory (*Quercus-Carya*) forest in Missouri and 470 kg N ha^{-1} in an oak-hickory forest in Tennessee, with a near equivalent value of 995 kg N ha^{-1} in an oak-hickory forest in North Carolina. These results indicate the post oak-blackjack oak forest of the cross timbers is a nitrogen-rich ecosystem, in a productive temperate climate, with the potential for redistribution of N to enhance utilization from these marginal forests by grazing and browsing animals. Longer-term studies are needed because decomposition of woody biomass, which was the second largest N pool in this ecosystem, would ultimately influence redistribution or loss of N.

Table 7. N concentration by compartment and date for each treatment (n=4) in a post oak-blackjack oak community in the cross timbers of north central Oklahoma following herbicide application.

Compartment and treatment[1]	Sampling Date					
	Jun 93	Nov 93	Jan 94	Jun 94	Oct 94	Feb 95
	(% N)					
Leaves						
Control	1.94[2]	---[3]	---	2.14	1.45	---
No seed	2.32	---	---	---	---	---
Fescue	2.35	---	---	---	---	---
OWB	2.60	---	---	---	---	---
Branches						
Control	0.65	\	0.73	0.42	0.51	0.51
No seed	0.68	\	0.69	0.48	0.55	0.53
Fescue	0.68	\	0.74	0.51	0.59	0.49
OWB	0.74	\	0.76	0.53	0.49	0.58
Boles						
Control	0.25	0.26	0.24	0.18	0.19	0.18
No seed	0.24	0.24	0.24	0.19	0.18	0.21
Fescue	0.26	0.23	0.23	0.17	0.18	0.19
OWB	0.26	0.22	0.24	0.19	0.17	0.18

[1] Treatments are: control = no brush kill with no overseeding, no seed = brush kill with no overseeding, fescue = brush kill with tall fescue overseeding, OWB = brush kill with Old World bluestem overseeding.

[2] No differences P>0.05.

[3] Dashed line indicates live leaves were not available in the canopy for sampling. Backslash indicates missing samples.

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Actinorhizal plants in rangelands of the western United States

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Abstract

Actinorhizal plants are a diverse group of trees and shrubs that have the ability to form a dinitrogen-fixing symbiosis with *Frankia* bacteria. Actinorhizal plants are found throughout the world and are a significant component of rangelands in the western United States. Many actinorhizal species play important ecological roles in the habitats where they occur. Actinorhizal shrubs such as bitterbrush (*Purshia tridentata* [Pursh DC.]), mountain mahogany (*Cercocarpus* spp), and *Ceanothus* spp. are among the most important wildlife browse species in the western U.S. Other actinorhizal taxa such as alders (*Alnus*) and dryads (*Dryas*) play important roles in soil development and community succession following disturbance. Despite their importance, the biology of these plants in rangeland ecosystems is poorly understood. Particularly lacking is understanding of the dinitrogen-fixing ability of these plants and how symbioses with *Frankia* bacteria affects the ecology of these plants in western U.S. rangelands. Difficulty in isolating and culturing *Frankia* bacteria and in measuring inputs of fixed N from actinorhizal plants has contributed to slow progress in this field. In spite of these shortcomings, the actinorhizal plants of western U.S. rangelands represent a valuable resource for expanded utilization. This review is a summary of current knowledge of actinorhizal range plants and their *Frankia* symbionts. It is intended to provide a scientific basis for the study and utilization of this symbiosis for those involved in rangeland research and management.

Key Words: *Frankia*, symbiosis, reclamation, dinitrogen fixation, browse.

Resúmen

Las plantas actinorizoides son un grupo diverso de arboles y arbustos que poseen la habilidad de formar una simbiosis fijadora de nitrógeno con bacterias del genero *Frankia*. Las plantas actinorizoides se encuentran por todo el mundo y comprenden un componente significativo de los pastizales del Oeste de los Estados Unidos. Muchas especies actinorizoides juegan un papel ecológico importante en los habitats en donde se encuentran. Los arbustos actinorizoides como *Purshia tridentata*, *Cercocarpus* spp. y *Ceanothus* spp., se encuentran entre las especies mas importantes para ramoneo por la fauna silvestre en el Oeste de los Estados Unidos. Otras especies actinorizoides, tales como *Alnus* y *Dryas*, juegan papeles importantes en el desarrollo del suelo y en la sucesión después de un disturbio. A pesar de su importancia, la biologia de estas plantas en los ecosistemas de pastizales naturales en poco comprendida, desconociéndose la habilidad que tienen estas plantas de fijar nitrógeno y como las simbiosis con bacterias del genero *Frankia*, afectan la ecologia de estas plantas en los pastizales del Oeste de los Estados Unidos. La dificultad en aislar y cultivar la bacteria *Frankia* y en medir los flujos del nitrógeno fijado por medio de las plantas actinoriziodes, ha contribuido al lento progreso en este campo de estudio. A pesar de estas carencias, las plantas actinorizoides de los pastizales de los Estados Unidos representan un valioso recurso. Esta revisión es un resumen del actual conocimiento sobre las plantas actinorizoides de los pastizales y sus simbiontes. Esta revisión tiene como intención el proveer una base cientifica para el estudio y utilización de estas simbiosis y el manejo de pastizales con dichas especies.

Actinorhizal plants are a group of taxonomically diverse species capable of forming a symbiosis with N_2-fixing soil actinomycetes of the genus *Frankia*. The term "actinorhizal" is formed from the roots "actino" for the *Frankia* actinomycete and "rhiza" for the plant roots bearing the symbiosis (Baker and Schwintzer 1990). This symbiosis should not be confused with the more well-known symbioses between plants and non-N_2-fixing mycorrhizal fungi or between legumes and N_2-fixing *Rhizobia* bacteria. *Frankia* are filamentous, branching, and primarily saprophytic bacteria of the order Actinomycete. *Frankia* can live both symbiotically in root nodules and saprophytically in soil. Plants from 8 families and 25 genera are known to form a symbiosis with *Frankia* (Benson 1988, Dawson 1992). All actinorhizal plants are woody, with the exception of 2 subshrubs in the genus *Datisca* that have herbaceous shoots arising from woody perennial rootstocks. There are over 100 actinorhizal species native to the United States, and several introduced species are now widely naturalized and regarded as noxious weeds (e.g. Russian-olive [*Elaeagnus angustifolia* L.], autumn-olive [*Elaeagnus umbellata* Thunb.], Australian pine or she-oak [*Casuarina equisetifolia* Forst. & Forst.]). Most actinorhizal species are capable of growing in N-free culture and of fixing ecologically significant amounts of N in perennial woody root nodules (Fig. 1). This ability allows them to flourish in soils where low levels of available N may preclude the growth of other species.

Actinorhizal plants are found throughout the world from the tropics to the arctic. The vast majority of actinorhizal species, however, are native to temperate regions, where they fill the eco-

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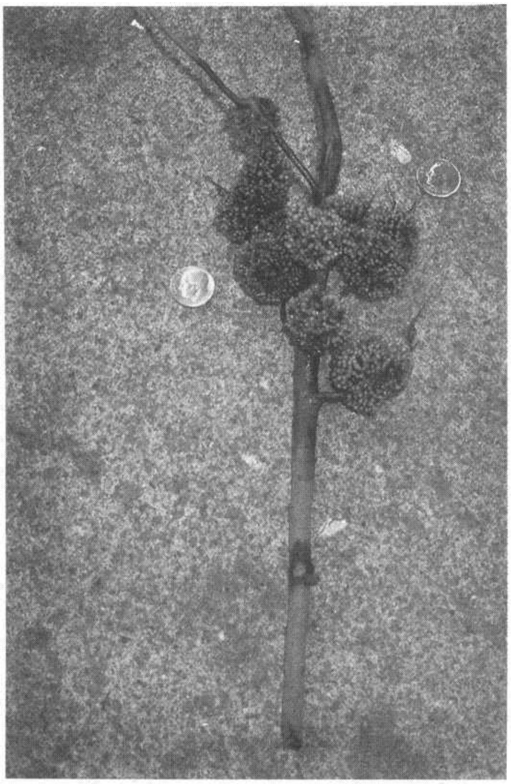

Fig. 1. A root segment from an actinorhizal *Alnus rubra* Bong. tree showing numerous perennial, woody root nodules that contain N_2-fixing *Frankia* bacteria. The coins in the photo are approximately 18 mm in diameter.

logical role occupied by woody legumes in tropical and subtropical regions. There are approximately 80 actinorhizal plant species native to western U.S. rangelands. These species represent approximately one third of the World's known actinorhizal plants, and 6 of the 8 known actinorhizal plant families (Table 1). The western U.S. is a center of diversity for actinorhizal plant genera in the family Rosaceae, and the genus *Ceanothus* (family Rhamnaceae) which is composed of over 40 species. Actinorhizal plants in the western U.S. are ecologically diverse, occurring in alpine, tundra, forest, shrubland, grassland, desert, and riparian habitats.

Common actinorhizal species of western rangelands include bitterbrush (*Purshia tridentata* [Pursh] DC.), mountain mahogany (*Cercocarpus* spp.) (Fig. 2), cliffrose (*Cowania mexicana* [Torr.]), alders (*Alnus* spp.) (Fig. 2), buffaloberry (*Shepherdia* spp.) (Fig. 2), silverberry (*Elaeagnus commutata* Berbh.), Russian-olive (*Elaeagnus angustifolia*), and numerous species of Ceanothus (*Ceanothus* spp.) (Fig. 2). A single species in the genus *Rubus* (family Rosaceae) has been reported to be actinorhizal (Becking 1979), however, this observation has never been confirmed despite numerous surveys by several research teams (J.O. Dawson personal communication) *Rubus* is, thus, not currently accepted as an actinorhizal genera (Stowers 1985). The genus *Dryas* (family Rosaceae) is considered to be actinorhizal but it is interesting to note that alpine populations in the lower 48 states, and central and southern Europe, have never been reported to be nodulated. Most actinorhizal plants in the western U.S. are woody shrubs, therefore, they are most often found in mountain and desert shrublands, chaparral, or open-canopy forests. Bitterbrush and mountain mahogany in the western U.S. form some of the most extensive stands of actinorhizal plants in the world, with bitterbrush alone occupying some 136 million ha in 11 states (Hormay 1943, Findley 1994).

There is little published research on actinorhizal rangeland shrub species despite the ecological importance of the actinorhizal symbiosis in the western U.S. (reviewed by Klemmedson 1979). The purpose of this review is to summarize the current state of knowledge regarding actinorhizal shrubs and their *Frankia* symbionts. It is intended to provide a scientific basis for the utilization and study of this symbiosis for those involved in rangeland research and management. For a more complete introduction to the biology of *Frankia* and actinorhizal plants, readers are referred to Schwintzer and Tjepkema (1990).

Ecological Importance of Actinorhizal Plants

Actinorhizal plants and their *Frankia* symbionts play an important role in the successional development of plant communities (Crocker and Major 1955, Lawrence et al. 1967, Conrad et al. 1985, Hibbs and Cromack 1990, Thilenius 1990). The ability to fix atmospheric N_2 allows actinorhizal plants to colonize sites where lack of available soil N may limit establishment and growth of other plants. Once established on a site, actinorhizal plants can fix N_2 and add N to the soil in the form of leaf litter and dead root tissue. Actinorhizal plants, therefore, build up soil organic matter and create a more favorable habitat for other plants (Crocker and Major 1955, Lawrence et al. 1967, Olff et al. 1993, Chapin et al. 1994) and soil organisms (Aplet 1990). Examples of important early successional actinorhizal plants in the western U.S. include sweetgale (*Myrica gale* L.) and sitka alder (*Alnus viridis sinuata* Regel.) in coastal wetlands of Alaska (Thilenius 1990), numerous species of *Ceanothus* in chaparral, forest, and mountain shrublands (Hickey and Leege 1970, Leege 1979, Conrad et al. 1985), the genus *Alnus* in the Pacific Northwest (Hibbs and Cromack 1990), and species of *Dryas* in arctic and alpine habitats in Alaska (Crocker and Major 1955, Lawrence et al. 1967). Alders and dryads were common colonizers of glacial till following the retreat of continental glaciation in the northern hemisphere (Ritchie 1987).

Other actinorhizal genera such as *Purshia*, *Shepherdia*, and *Ceanothus*, that are usually early successional shrubs, can occasionally persist as mid or later seral components of shrublands or open-canopied forests (Conrad et al. 1985, Dawson 1990). The ecological significance of the actinorhizal symbiosis in later seral communities is not as well-documented as in primary seres and is a topic deserving further study.

Most actinorhizal plants also possess a symbiotic relationship with mycorrhizae (Williams 1979, Rose and Youngberg 1981, Ba et al. 1987, Berliner and Torrey 1989). There is evidence that bitterbrush, mountain mahogany, and Australian she-oak (*Casuarina equisetifolia* L.), have the ability to simultaneously form a 3-way association with *Frankia*, vesicular-arbuscular mycorrhizae, and ectomycorrhizae (Williams 1979, Ba et al. 1987). The presence of mycorrhizae can lead to increased nodulation by *Frankia* (Fraga-Beddiar and Le Tacon 1990), and an increased phosphorus uptake from the mycorrhizal association may result in higher rates of N_2-fixation relative to non-mycorrhizal plants (Rose and Youngberg 1981). The presence of mycorrhizal associations may also facilitate direct transfer of N from

Table 1. Actinorhizal plant taxa of rangelands in the western United States (number of subspecies).

Family	Genus	native species	exotic species
Betulaceae	*Alnus*	*incana* (2) *maritima, oblongifolia, rhombifolia, rubra, serrulata, viridis* (2)	*cordata, glutinosa*
Casuarinaceae	*Casuarina*		*cunninghamiana, equisetifolia, stricta*
Datiscaceae	*Datisca*	*glomerata*	
Elaeagnaceae	*Elaeagnus*	*commutata*	*angustifolia, pungens, umbellata*
	Shepherdia	*argentea, canadensis, rotundifolia*	
Myricaceae	*Myrica*	*californica, cerifera, gale, hartwegii, heterophylla, pusilla*	
Rhamnaceae	*Aldolphia*	*californica*	
	Ceanothus	*americanus, arboreus, connivens, cordulatus, crassifolius, cuneatus* (4), *cyaneus, dentatus, diversifolius, fendleri, ferrisae, foliosus* (3), *fresnesis, gloriosus* (4), *greggii* (3), *griseus, hearstiorum, herbaceous, impressus, incanus, integerrimus, jepsonii* (2), *lemmonii, leucodermis, maritimus, martinii, masonii, megacarpus* (2), *oliganthus* (2), *ophiochilus, palmeri, papillosus* (2), *parryi, parvifolius, pinetorum, prostratus* (3), *purpureus* (2), *roderickii, sanguineus, serpyllifolius, spinosus, thyrisiflorus, tomentosus, velutinus* (2), *verrucosus*	
Rosaceae	*Cercocarpus*	*intricatus* (2), *ledifolius* (3), *montanus* (7), *traskiae*	
	Chamaebatia	*australis, foliosa*	
	Cowania	*ericaefolia, mexicana, subintegra*	
	Dryas	*drummondii, integrifolia* (4), *octopetala* (5)	
	Purshia	*glandulosa, tridentata*	

Adapted from: Vines 1960, Hitchcock and Cronquist 1973, Stephens 1973, Barbour and Major 1988, Dawson 1992, and USDA 1995.

actinorhizal to associated plant species via shared fungal mycelia (Arnebrant et al. 1993).

The amount of fixed-N_2 added to ecosystems by actinorhizal plants varies considerably (Table 2). Rates of N accretion for slow-growing actinorhizal shrubs in the arid rangelands of the western U.S. do not approach those measured for alders (*Alnus* spp.) and snowbrush (*Ceanothus velutinus* Dougl.) in the more mesic forests of the Pacific Northwest (Table 2). However, this does not mean that the seemingly low rates of N accretion observed for plants such as bitterbrush and mountain mahogany are not ecologically significant. The actual percentage of the total ecosystem N pool resulting from N_2-fixation by actinorhizal plants may be similar in mesic and arid systems.

Nitrogen content in the litter of some actinorhizal plants is elevated due to a lack of N retranslocation from senescing leaves. Most deciduous plants will typically translocate one half or more of their foliar N prior to leaf abscission (Chapin and Kedrowski 1983, Côté and Dawson 1986). Several actinorhizal taxa, that have been examined, translocate a much smaller fraction (11 to 24%) of their foliar N prior to abscission (Dawson and Funk 1981, Côté and Dawson 1986, Llinares et al. 1992, Killingbeck 1993).

There is relatively little direct information regarding the production and release of fixed N by actinorhizal shrubs in western U.S. rangelands. Tiedemann and Furniss (1985) found a 6-fold increase in soil total N beneath canopies of curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) relative to intershrub areas, compared to a 3-fold increase over intershrub areas for non-actinorhizal shrubs. Lepper and Fleschner (1977) found 4 times as much N under mixed stands of limber pine (*Pinus flexilis* James) and mountain mahogany than under adjacent limber pine stands lacking the actinorhizal shrub.

The lack of information regarding N inputs to western U.S. rangelands by actinorhizal plants can be attributed to the difficulty of making such measures. Typical methods for measuring N production and release from actinorhizal plants include acetylene

Table 2. Some estimates of nitrogen accretion by various actinorhizal plants.

Species	Location	Habitat	(kg N ha^{-1} yr^{-1})	Methods	Reference
Alnus rubra	numerous	Pure stands	100-200	various	Binkley et al. 1994
A. rubra	numerous	Mixed forest stands	50-100	various	Binkley et al. 1994
Shepherdia canadensis	British Columbia	Clearcut	1	acetylene reduction	Hendrickson and Burgess 1989
Ceanothus greggii	California	Shrubland	0.1	acetylene reduction	Kummerow et al. 1978
C. sanguineus	British Columbia	Clearcut	24-50	N accretion	Binkley and Husted 1983
C. velutinus	Oregon	Burn /clearcut	70-108	N accretion	Youngberg and Wollum 1976
C. velutinus	Oregon	Clearcuts	101	acetylene reduction	McNabb and Cromack 1983
C. velutinus	Oregon	Clearcuts	95-100	N accretion	Binkley et al. 1982
C. velutinus	Oregon	Clearcuts	0-20	N accretion	Zavitkovski and Newton 1968
Cercocarpus ledifolius	California	Open forest	7	acetylene reduction	Lepper and Fleschner 1977
Purshia tridentata	Oregon	Open forest	<1	acetylene reduction	Dalton and Zobel 1977

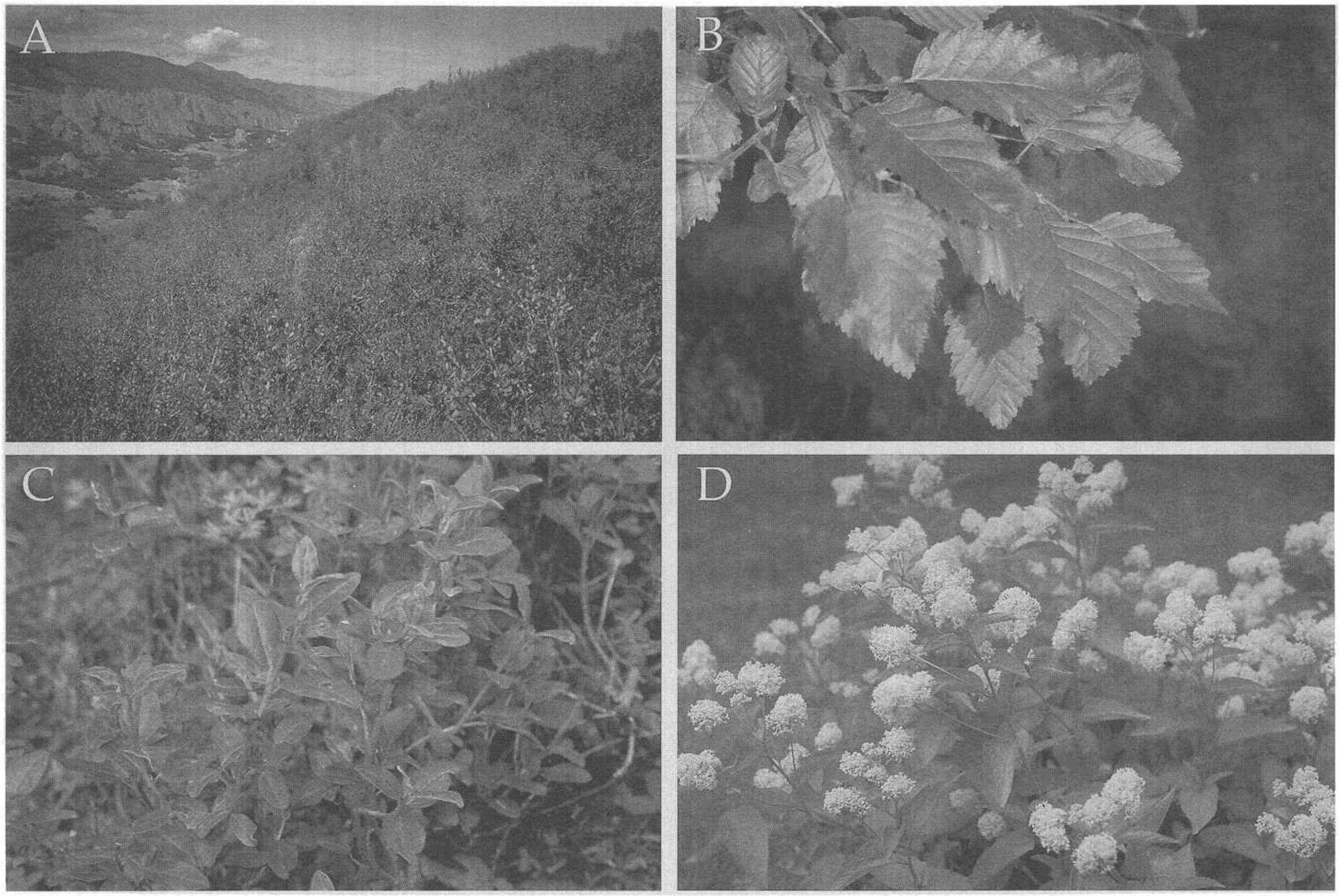

Fig. 2. Some actinorhizal plants characteristic of western U.S. rangelands: A) A stand of mountain mahogany (*Cercocarpus montanus* Raf.) shrubs in the Front Range of Colorado, B) Thinleaf alder (*Alnus incana tenuifolia* Nutt.) along a mountain stream in New Mexico, C) Russet buffaloberry (*Shepherdia canadensis* Nutt.) growing beneath an open pine forest in Wyoming, D) New Jersey tea (*Ceanothus americanus* L.) from a prairie in Kansas.

reduction, natural isotope (^{15}N) techniques, and N accretion studies (Table 2). For a detailed description of these and other methods see Silvester (1983) or Winship and Tjepkema (1990). There is a great deal of uncertainty in estimating community or ecosystem level inputs of fixed-N using these methods. These uncertainties are especially difficult to address in arid and semiarid systems where the relatively low rates of N_2-fixation require greater sensitivity of measurement.

The role of facilitation often attributed to actinorhizal plants during primary succession (Lawrence et al. 1967, Blundon et al. 1993, Chapin et al. 1994) may have as much to do with the addition of organic matter to soils as the direct effects of N inputs. Crocker and Major (1955) demonstrated that within 50 years of glacial retreat at Glacier Bay, Alaska, thickets of actinorhizal alders had built an organic surface horizon 6–7 cm deep amounting to 5-6 kg m^{-2} of organic matter. Actinorhizal species of *Ceanothus* and *Purshia*, which commonly colonize burned areas in western U.S. rangelands (Martin 1983, Conrad et al. 1985), may also provide inputs of soil organic matter. The ecological importance of N_2-fixation in these situations may simply be that it enables actinorhizal plants to colonize the site, allowing for their subsequent role in soil organic matter development.

Many actinorhizal plants provide nutritious forage for herbivores because of low foliar C:N ratios, high protein content, and high N content of dormant tissue (Table 3). Many actinorhizal species have evolved under high levels of herbivory, and for some, growth may be stimulated by browsing (Urness and Jensen 1983, Bilbrough and Richards 1989). Rapid growth of actinorhizal plants following herbivory may be due to the relative availability of fixed-N_2 from their *Frankia* symbionts. This type of response is common in plants provided with high nutrient levels (Maschinski and Whitham 1989).

In western U.S. rangelands, most actinorhizal shrubs are important browse species for big game. Austin and Urness (1983) found the summer diet of mule deer (*Odocoileus hemionus*) in Utah consisted of 8% bitterbrush in May and increased steadily to 92% by September. Woodis (1989) found that over a 2-year period Nevada mule deer's diets consisted of 51% bitterbrush. Rominger et al. (1988) found 74 to 92% of the summer diet of bighorn sheep (*Ovis canadensis*) in the Front Range of Colorado consisted of actinorhizal mountain mahogany leaves. In Idaho, 25 to 85% of the annual production of actinorhizal redstem ceanothus (*Ceanothus sanguineus* Pursh.) and 68 to 80% of snowbrush were utilized by elk (*Cervus elaphus*) (McCulloch 1955).

Many actinorhizal shrubs are also browsed by livestock (Van Dersal 1938, Hormay 1943, Young and Payne 1948, Furbush 1962, Thilenius and Hungerford 1967, Hickey and Leege 1970, Phillips 1970, Leckenby et al. 1982, Shaw and Monsen 1986).

Table 3. Nutritional value of some actinorhizal browse species.

Shrub	Location	plant part	CP[a]	NDF[b]	ADF[c]	ADL[d]	IVDDM[e]	Reference
			%	%	%	%	%	
Ceanothus cordulatus	California	Leaves	13.6	27.2	15.2	7.9	33.6	Kie 1986
C. greggii	Arizona	Stems +& leaves	10.0		30.0		55.0	Urness et al. 1977
C. integerrimus	California	Leaves	17.5	31.5	17.2	8.1	58.8	Kie 1986
Cercocarpus ledifolius	Utah	Stems + leaves					53.5	Urness et al. 1977
C. ledifolius	Nevada	Stems + leaves	12.0				65.3	Woodis 1989
C. montanus	Colorado	Stems (dormant)	6.4				29.7	Kufeld et al. 1985
C. montanus	New Mexico	Leaves	12.8	42.6	28.4	15.7		Nunez-Hernandez et al. 1991
C. montanus	Utah	Stems					28.5	Urness et al. 1977
C. montanus	Colorado	Stems + leaves	6.6 - 16.3					Dietz et al. 1962
C. montanus	Colorado	Stems + leaves (dormant)	7.9		47.9	23.2	36.6	Gibbs 1978
C. spp.	Colorado	Stems + leaves	18.1					Cook et al. 1977
Cowania mexicana	Utah	Stems (dormant)	8.8				37.6	Welch et al. 1983
Purshia glandulosa	California	Stems (dormant)	9.3				37.0	Welch et al. 1983
P. tridentata	Nevada	Stems + leaves	15.2				63.6	Woodis 1989
P. tridentata	Colorado	Stems + leaves	19.4					Cook et al. 1977
P. tridentata	Colorado	Stems + leaves	7.4 - 13.9					Dietz et al. 1962
P. tridentata	Colorado	Stems + leaves (dormant)	7.4		50.7	27.4	37.3	Gibbs 1978
P. tridentata	Colorado	Stems (dormant)	5.9				24.1	Welch et al. 1983
P. tridentata	Idaho	Stems (dormant)	6.9				28.3	Welch et al. 1983
P. tridentata	California	Stems (dormant)	7.9				30.6	Welch et al. 1983
P. tridentata	Utah	Stems + leaves					30.0	Urness et al. 1977

[a]CP = Crude protein, [b]NDF = Neutral detergent fiber, [c]ADF = Acid detergent fiber, [d]ADL = Acid detergent lignin,[e]IVDDM = In vitro digestible dry matter

Carefully managed livestock grazing may be a valuable tool for stimulating browse production of some actinorhizal shrubs (Garrison 1953, Tueller and Tower 1979, Leckenby et al. 1982, Urness and Jensen 1983, Bilbrough and Richards 1989, Woodis 1989). Hormay (1943) suggests that bitterbrush becomes unpalatable to livestock if it is not grazed moderately each year. Heavy grazing by livestock followed by a rest period may be a useful tool for encouraging regeneration of bitterbrush stands (Phillips 1970). Although grazing can be beneficial for increasing browse production of actinorhizal shrubs, the long-term survival of individual shrubs can be reduced by heavy browsing (McConnell and Smith 1977), especially during the summer (Young and Payne 1948). Frequent light grazing may be detrimental to actinorhizal shrubs in areas where they are a small component of the plant community, as livestock may preferentially browse them (Hormay 1943).

Many small mammals and birds use actinorhizal plants for food and shelter (McAtee 1936, Van Dersal 1938, Evans et al. 1983, Knopf and Olson 1984, Vander Wall 1994). Inputs of N and organic matter to soils by actinorhizal plants may stimulate soil biological activity (Aplet 1990), which in turn may benefit higher trophic groups. Dawson (1990) suggests that riparian alder trees might be an important source of N to planktonic organisms at the beginning of food chains in cold infertile streams and montane lakes supporting important trout fisheries. Many actinorhizal species have rich nectaries that attract insects (Hayes 1976, Ferris and Brown 1981) and many ornamental species of *Ceanothus* can be cultivated in order to attract nectar-feeding butterflies.

Biology of Frankia

Frankia is a slow-growing filamentous actinomycete that produces 3 cell types: hyphae, vesicles, and spores. Hyphae are vegetative cells that are usually branched and less than 1 μm in diameter. The hyphae differentiate to form vesicles and sporangia. Vesicles are terminal swellings on hyphae and are the sites of N_2-fixation. *Frankia* hyphae often produce sporangia which are structures containing numerous spores. The spores are resting structures and probably play an important role in the dormancy and survival of *Frankia* under adverse conditions (Sussman and Halvorson 1966, Burleigh and Torrey 1990, Burleigh and Dawson 1995). Sporangia can be produced in actinorhizal nodules and in vitro in most *Frankia* strains, depending on cultural conditions. Sporulation of *Frankia* in vitro appears to be controlled by temperature, carbon (C) source, and osmotic stress (Tisa et al. 1983, Burleigh and Dawson 1991). Sporulation coincides with the seasonal senescence of vesicles in infected cells of actinorhizal nodules (Becking et al. 1964, Becking 1970, VandenBosch and Torrey 1985). In arid regions sporulation may be triggered by soil drying (Burleigh and Dawson 1991).

Research on *Frankia* has been hampered due to the difficulty of isolating and culturing *Frankia* from root nodules. Despite numerous efforts, it was not until 1978 that *Frankia* was successfully isolated and cultured by Callaham et al. (1978). As a result of these difficulties, a reliable set of criteria for classifying *Frankia* taxa has not yet been established in the scientific community. Pure cultures of *Frankia* isolates are often classified based on their host affinities as first defined by Baker (1987), and they are usually given identifying codes based on the plant species from which they were isolated (Lechevalier 1983). Lalonde et al. (1988) proposed the assignment of some *Frankia* strains to 2 species, *Frankia alni* and *Frankia elaeagni*, based on genotypic and phenotypic differences (Lalonde et al., 1988). This classification, however, was not widely accepted by *Frankia* researchers. Recent studies based on DNA relatedness have identified 8 (Nazaret et al. 1991), 9 (Fernandez et al. 1989, Akimov and Dobritsa 1992), and 4 (Normand et al. 1996) genomic groups of *Frankia*.

About half of the genera, but only a small fraction of actinorhizal species, have had pure cultures of *Frankia* isolated from their root nodules. Most cultures are from the genera *Alnus*, *Casuarina*, *Myrica*, and *Elaeagnus* (Lechevalier 1986), and many of these cultures have been isolated from actinorhizal plants growing outside their native range. There is a possibility, therefore, that *Frankia* cultures may have been identified with host plants that are not of the actinorhizal taxa with which these strains evolved naturally. There are numerous genera of actinorhizal plants from which isolates of symbiotic *Frankia* have not been obtained, and many *Frankia* cultures that have been obtained are not capable of reinfecting the host plants from which they were isolated (Lechevalier 1986). Notably missing from culture collections are isolates from Rosaceous and Rhamnaceous actinorhizal shrubs of the western U.S. Until culture collections become more representative of the true diversity of actinorhizal species, it is unlikely that an acceptable taxonomic classification of *Frankia* will be possible. Current efforts by Philippe Normand in Lyon, France to combine PCR techniques in conjunction with 16S ribosomal RNA sequences derived from *Frankia* in intact nodules have enabled some taxonomic relationships to be established among isolated and nonisolated *Frankia* (Normand et al. 1996).

Frankia bacteria are usually found in soils beneath nodulated host plants (Van Dijk 1979, Oremus 1980, Dawson and Klemp 1987, Smolander and Sundman 1987, Arveby and Huss-Danell 1988, Smolander 1990), probably due to the release of *Frankia* from decaying root nodules (Van Dijk 1984). There are numerous reports of *Frankia* in soils lacking actinorhizal host plants (Rodriguez-Barrueco 1968, Bermudez de Castro et al. 1976, Van Dijk 1984, Huss-Danell and Frej 1986, Dawson and Klemp 1987, Zitzer et al. 1991, Paschke and Dawson 1992a, 1992b, Paschke et al. 1994), which indicates that *Frankia* is not an obligate symbiont. *Frankia* can apparently be spread in the environment via the activity of some bird species (Paschke and Dawson 1993, Burleigh and Dawson 1995) and other biological vectors (Paschke 1993).

Most actinorhizal plants are usually found to be nodulated in their native habitats. Root nodules can account for a notable portion of belowground biomass in some systems. For instance, McNabb and Kromack (1983) reported 750 kg ha^{-1} of nodule biomass for snowbrush growing in western Oregon. There are actinorhizal plant genera, however, that seem to be sparsely nodulated. The most notable of these are bitterbrush and cliffrose that are native to the arid western U.S. (Dalton and Zobel 1977, Nelson 1983, Righetti et al. 1983) and certain species of she-oak (*Casuarina* spp. and *Allocasuarina* spp.) which are native to the arid interior of Australia (Lawrie 1982). Low levels of nodulation in these plants may be due to the low density of infective *Frankia* in the arid surface soils where these plants grow (Lawrie 1982, Righetti and Munns 1982). Lack of moisture (Righetti et al. 1986, Dawson et al. 1989), or other factors may limit the growth of free-living saprophytic *Frankia* in arid regions.

The presence of nodules on host plants is a good indication that *Frankia* is present in the soil. There is no simple test for determining presence or absence of *Frankia* in soil that is devoid of host plants. One method to test for *Frankia* is to grow actinorhizal plants in the test soil and check for nodulation. Quantitative estimates of *Frankia*-propagule abundance can be made by inoculating host plants with a series of soil dilutions and measuring the relationship between soil quantity and the number of nodules formed (Van Dijk 1984, Paschke 1993). Such tests need to be conducted under aseptic and N-limiting conditions. Another approach is the use of molecular probes to detect *Frankia* DNA and RNA in situ. Molecular methods have been used to study *Frankia* ecology in soils (e.g. Hahn et al. 1990b, Myrold and Huss-Danell 1994), but the cost and difficulty of interpreting results may limit widespread use by researchers.

Methodology for Working with Actinorhizal Plants

Methods for propagating actinorhizal species of western rangelands have been developed for most major taxa (Table 4) while many minor species still await cultivation. Ease of propagation varies considerably within this diverse group of species.

Nursery stock of actinorhizal species often lack root nodules (Danielson and Visser 1990). Seedlings of actinorhizal plants have been experimentally inoculated with *Frankia* and mycorrhizal fungi prior to planting in order to increase nodulation and mycorrhizal infection (Benoit and Berry 1990, Torrey 1992). This can greatly increase the survivability of planted seedlings. It may also be beneficial, in some cases, to inoculate existing stands of actinorhizal plants with *Frankia*, although, this has never been attempted on a large scale. As techniques for mass-culturing of *Frankia* are refined and cultures become more readily available, this might become a possible management tool for stimulating the vigor of actinorhizal shrub stands.

Actinorhizal plants within the families Betulaceae, Myricaceae, and Elaeagnaceae can be readily nodulated by *Frankia* cultures or nodules from species within the same family (Torrey 1990). A lack of pure cultures of *Frankia* from other actinorhizal taxa native to western U.S. rangelands, and a lack of knowledge of host-specificity, precludes specific recommendations for optimum plant-*Frankia* combinations. Most *Frankia* cultures that are currently available do not effectively nodulate actinorhizal plants in the Rosaceae (Kohls et al. 1994) and Rhamnaceae (Torrey 1990) families. Crushed nodules of these plants offer a viable alternative to pure cultures. Kohls et al. (1994) were able to nodulate several Rosaceous shrubs using crushed nodules of yellow dryad (*Dryas drummondii* Richards) collected in Alaska.

Common to *Frankia*—host plant associations is the development of nodules that do not fix N_2 (VandenBosch and Torrey 1983, Hahn et al. 1988, Hahn et al. 1990a). These nodules and the *Frankia* strains that inhabit them are referred to as "ineffective". Ineffective nodules that use carbohydrates from the host plant might actually be pathogenic and demonstrate the fine line between a pathogen and a symbiont. The occurrence of ineffective strains of *Frankia* and the potential for competitive interactions between ineffective and effective *Frankia* beneath stands of European black alder (*Alnus glutinosa* (L.) Gaertn.) has been

Table 4. A brief guide to the cultivation of common actinorhizal plant species of western U.S. rangelands.

Taxa	Scarification	Stratification[a]	Germination temperature	Notes	In vitro Reference[b]	References[b]
Alnus incana tenuifolia		0 to 90 days	20 to 30 °C	Will root from cuttings treated with hormone	5	7, 13
A. rubra		0	15 to 25	12 hr in aerated $H_2$0 improves germination	5, 7	1, 7, 14
A. viridis crispa		60 to 90	20 to 25		5	1, 7, 14
A. viridis sinuata					5	14
Elaeagnus angustifolia		0 to 90	20 to 25	12 hr in aerated $H_2$0 improves germination	6	1, 7, 14
E. commutata		0 to 90	20 to 25	H_2O soluble inhibitor in seed coat	4	1, 7
Shepherdia argentea		60 to 90	20 to 25			1, 7, 14
S. canadensis	30 min conc. H_2SO_4	0 to 90	20 to 25	Cuttings root with some difficulty		1, 7, 9, 14, 15
Myrica cerifera.		30 to 90		Will root from cuttings treated with hormone		7, 14
M. gale		30 to 90	20 to 25	Root cuttings will produce shoots, light required for germination		1, 7, 11, 14
Ceanothus americanus	30 min H_2O at 57°C or 5 min at 100°C	0 to 90		Preventative fungicide needed, cuttings root well		1, 7, 14
C. cordulatus	H_2O at 70°C until cool	0		Preventative fungicide needed		1, 14
C. cuneatus	H_2O at 70°C until cool	90		Preventative fungicide needed		1, 14
C. diversifolius	H_2O at 70°C until cool	60 to 90		Preventative fungicide needed		1, 14
C. fendleri	H_2O at 85°C until cool			Preventative fungicide needed	8	1, 9
C. integerrimus	H_2O at 85°C until cool	60 to 90		Preventative fungicide needed		1, 14
C. prostratus	30 sec H_2O at 100°C	90 to 115		Preventative fungicide needed		1, 14
C. sanguineus	H_2O at 88°C until cool	0 to 115		Preventative fungicide needed		1, 14
C. velutinus	H_2O at 85°C until cool	30 to 90		Preventative fungicide needed		1, 9, 14
Cercocarpus ledifolius.		0 to 90	3 to 20	Pretreat seeds 15 min in 30% H_2O_2		1, 2, 14
C. montanus	5 min conc. H_2SO_4	0 to 90	3 to 20			1, 14
Cowania mexicana		15 to 30	25 day / 10 night			1, 3, 14
Dryas drummondii		0 to 120	5 to 15	Pretreat seeds 15 min in 30% H_2O_2		12
Purshia tridentata		0 to 90	3 to 20	Pretreat seeds 15 min in 30% H_2O_2		1, 3, 10, 14

[a] Cold stratification is usually done in moist sand at 3°C.

[b] References: [1] USDA For. Serv. 1974, [2] Young et al. 1978, [3] Young and Evans 1981, [4] Fung 1984, [5] Tremblay and Lalonde 1984, [6] Bertrand and Lalonde 1985, [7] Dirr and Heuser 1987, [8] Borland 1989, [9] Krishnan 1989, [10] Meyer and Monsen 1989, [11] Schwintzer and Ostrofsky 1989, [12] Benoit and Berry 1990, [13] Java and Everett 1992, [14] Young and Young 1992.

reported by Van Dijk and Sluimer-Stolk (1990). These observations illustrate the danger of introducing *Frankia* that is not well characterized into western U.S. rangelands without prior considerations of effectivity and competition with native *Frankia* strains.

At this time, there is no commercially available *Frankia* inoculum for actinorhizal plants. Several university and government laboratories maintain collections of *Frankia* cultures for research. For now, nurseries and land managers must rely on field-collected soil or nodules for establishing actinorhizal symbioses. A reliable source of soil or nodules for inoculum is from beneath nodulated actinorhizal plants near the planting site. Methods for inoculating actinorhizal plants with *Frankia* can be found in Périnet et al. (1985), Benoit and Berry (1990) and Molina et al. (1994).

Future Recommendations

The study of the actinorhizal symbiosis is in its infancy. Despite the abundance of actinorhizal plants in western U.S. rangelands, this region and its actinorhizal flora are greatly underrepresented in the actinorhizal literature. Many questions need to be addressed. These include: 1) to what extent do actinorhizal shrubs contribute to the N economy of rangelands? 2) with what types of *Frankia* do actinorhizal shrubs in the Rosaceae and Rhamnaceae families form a symbiosis? 3) what factors limit nodulation and N_2-fixation in actinorhizal rangeland vegetation? 4) can browse productivity be enhanced by large-scale inoculation of rangelands with *Frankia*? Other areas that need to be addressed are the isolation and culture of *Frankia* strains from the Rosaceae and Rhamnaceae families, methods for the large-scale production of actinorhizal seedlings and their appropriate *Frankia* and mycorrhizae symbionts, and the possible transfer of the actinorhizal symbiosis to non-actinorhizal taxa.

Because of their importance in natural ecosystems, actinorhizal plants are slowly gaining recognition as valuable trees and shrubs for diverse uses by humans. Throughout the world, actinorhizal plants are used for reclamation of disturbed soils, windbreaks and soil stabilization, interplanting with food and wood crops, commercial products, and to provide food and cover for wildlife and livestock (Dawson 1986, Bulloch 1987, Baker and Schwintzer 1990, Diem and Dommergues 1990, Wheeler and Miller 1990, Dawson 1992). The actinorhizal species of rangelands in the western U.S. have the potential for similar utility (Table 5). Many of the actinorhizal shrubs in the Rhamnaceae and Rosaceae families are adapted to survive on harsh sites, which makes them ideally suited for reclamation. Species of *Elaeagnus*, *Shepherdia*, and *Alnus* have the potential to add large amounts of fixed N and C to soils and they should be given more consideration as soil-improvement tools. The development of sterile cultivars of the weedy exotics Russian- and autumn-olive would allow for their expanded use and would be a major achievement for the reclamation industry.

The Rosaceous actinorhizal plants of the western U.S. perhaps hold great promise for progress in actinorhizal research. It is within this family that numerous non-actinorhizal genera coexist.

Table 5. Actinorhizal plant species characteristic of western U.S. rangelands and their possible uses.

Taxa	Range	Habitat	Uses
Alnus rubra	Pacific N.W., N. Idaho	Streambanks, moist slopes and floodplains	Lumber, soil stabilization, soil improvement
A. viridis sinuata	Coastal Alaska to Cascades	Moist rocky streambanks and slopes, open woodlands	Soil stabilization, reclamation
Elaeagnus commutata	N. Rockies to Minnesota	Dry rocky slopes, rocky stream beds	Wildlife, reclamation, ornammental
Shepherdia canadensis	W. Cascades to Rockies	Open forests, dry rocky slopes	Reclamation, wildlife
S. argentea	California to Upper Midwest	Streambanks, alkaline soils, low meadows	Ornamental, wildlife
Myrica spp.	Coastal regions	Streambanks, lakeshores, moist slopes and floodplains, coastal bogs	Soil stabilization, wildlife, reclamation
Ceanothus cordulatus	S. Oregon to Baja California	Open forests, disturbed sites	Browse
C. cuneatus	California to Oregon	Chaparral, open dry forests	Browse
C. diversifolius	California	Forest understory	Soil stabilization
C. gloriosus	Coastal California	Coastal bluffs	Ornamental, soil stabilization
C. griseus	California	Open slopes, bluffs	Ornamental
C. integerrimus	Oregon to S. Rockies	Chaparral, open forests, riparian forests	Browse
C. prostratus	Sierra Nevada to S. Cascades	Dry disturbed sites, open forests	Soil stabilization, ornamental
C. sanguineus	Cascades to N. Rockies	Mountain shrublands, forest clearings	Browse, reclamation
C. velutinus	Cascades, Sierra Nevada, Rockies	Forest understories and clearings, disturbed sites	Reclamation, browse, ornamental
Cercocarpus spp.	Western U.S.	Dry slopes and ridges, canyon bottoms, chaparral foothills	Browse, reclamation, soil stabilization, ornamental
Cowania spp.	Great Basin to W. Texas	Dry shallow soils	Browse, ornamental
Dryas drummondii [a]	Alaska to S. Rockies	Tundra, alpine and polar rocky terraces	Reclamation
Purshia tridentata	W. Cascades to Rockies	Chaparral, dry slopes, open dry forests	Browse, reclamation, soil stabilization

[a] Nodulation status uncertain in alpine habitats of lower 48 states.

Many of these non-actinorhizal genera are closely related to actinorhizal species, which suggests the possibility of future genetic manipulation. Non-nodulating Apache plume (*Fallugia paradoxa* [D. Don] Endl.), for example, can be grafted onto the nodulated root stock of cliffrose (Kyle et al. 1986). The genetic transfer of nodulating ability has been attempted in non-actinorhizal birch (*Betula* spp.) trees (a close relative of alders) (Séguin and Lalonde 1990). If successful, genetic transfer of nodulating ability to species of the Rosaceae (e.g. strawberry, cherry, apple, and raspberry), could represent a significant use of gene transfer technology. Before these goals are pursued however, the more immediate task of understanding the basic biology of this symbiosis in rangeland systems is at hand.

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Seedling dynamics of *Festuca* spp. in a grassland of Patagonia, Argentina, as affected by competition, microsites, and grazing

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Abstract

The effects of competition, grazing, and microsites on seedling dynamics of *Festuca* spp. were investigated in a semiarid steppe of Patagonia, Argentina. In an exclosure and an adjacent grazed area, the level of root competition for seedlings was controlled through root exclusion tubes (0.1 m diameter, 0.4 m long) installed adjacent to 7 similarly-sized *Festuca pallescens* plants and in the interspace between *F. pallescens* plants. Seedling dynamics at the phenological stages of a) recently emerged and up to 4 leaves and b) 5 leaves and up to 1 tiller were followed inside the tube area (no competition) and in paired circles (competition) for approximately 3 growing seasons. Peak density of *Festuca* spp. seedlings occurred in fall and early spring, when water content in the first 0 to 5 cm of the soil was above 8%. Seedling densities of *Festuca* spp. at the 2 phenological stages were significantly reduced by grazing. At the phenological stage of 1 to 4 leaves, seedlings were not affected by root competition, although their densities were significantly higher for seedlings adjacent to *F. pallescens* plants than in the interspace between plants. This was due to higher soil water content in these areas throughout the season in the 0 to 5 cm of the soil. Seedling densities at the phenological stage of 5 leaves and up to 1 tiller were significantly higher when there was no competition from neighboring grass plants as compared to seedlings exposed to competition. In regard to microsite differences, seedling density was significantly greater in the interspaces than adjacent to mature plants. These results suggest that although higher seedling densities can be obtained by excluding the area from grazing, intraspecific competition for soil water during the summer drought period can act as a barrier for further *Festuca* spp. seedling establishment.

Resúmen

Los efectos de la competencia, pastoreo y micrositios en la dinámica del establecimiento de plantúlas de *Festuca* spp. en una estepa semiarida de la Patagonia en Argentina. Utilizando una área excluida del pastoreo, se controló el nivel de competencia radical de las plantúlas utilizando tubos de 40 cm. de largo y 10 cm. de diámetro, instalados junto a 7 plantas de similar tamaño de *Festuca pallescens.* Se observó la dinámica de las plantúlas en los estados fenologicos de: a) Recien emergidas y hasta con 4 hojas y b) De 5 hojas hasta un tallo floral, durante 3 épocas de crecimiento. La densidad máxima de plantúlas ocurrió en el otoño y al inicio de la primavera, cuando el contenido de humedad en los primeros 5 cm. del perfil de suelo, estaba arriba de un 8%. La densidad de plantúlas fue reducida significativamente por el pastoreo. En el estado de 4 hojas, las plantulas no se vieron afectadas por la competencia radicular. Las densidades de plantúlas en el estado de 5 hojas-un tallo, fueron significativamente mayores cuando no habia competencia de plantas adyacventes. En cuando a micrositios, se detectaron un mayor numero de plantúlas en los interespacios de planta y planta, que en las áreas adyacentes a plantas maduras. Estos resultados suguieren, que aunque es posible lograr altas densidades de plantúlas excluyendo el área del pastoreo, la competencia por aqua durante el verano (sequia), puede actuar como una barrera para el establecimiento de plantúlas de *Festuca* spp.

Key Words: *Festuca pallescens*, grassland steppe, soil water, Argentina.

In arid and semiarid ecosystems, water is important not only in controlling plant productivity (Noy-Meir 1973, Lauenroth 1979, Defossé et al. 1990, Lauenroth and Sala 1992), but also in determining the pulse of seed germination (Mack and Pyke 1984). In these ecosystems, the successful establishment of a seedling and survival to an adult plant is determined by a series of factors, of which the availability of soil water during critical periods is one of the most important (Reichenberger and Pyke 1990). In water-limited environments, competition for soil water between grass seedlings and established vegetation can be particularly significant (Robberecht et al. 1983). The grass steppe rangelands of western Patagonia, Argentina, are characterized by their low vegetation cover, high winds, and erratic precipitation. These rangelands, which have been subjected to continuous grazing by sheep since the beginning of the century, exhibit several typical signs of deterioration. The increased size of bare soil patches, the decreased vegetation cover, and the lack of re-establishment of native perennial plants are among the most important indicators of rangeland deterioration in western Patagonia (Soriano 1983, Ares et al. 1990).

The Sub-Andean District of the Patagonian Phytogeographic Province (Soriano 1956, Cabrera 1976) is one of the most important grazing areas of Patagonia in regard to productivity and for-

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age value (Defossé et al. 1990). In this district, the most important forage grass is *F. pallescens* (St. Yves) Parodi, a perennial cool season grass that reproduces strictly from seed (Soriano 1960, Bertiller 1992). In many areas of this floristic district, overgrazing has reduced the cover of *F. pallescens* and species diversity, and increased bare soil patches colonized by annuals and perennials of low forage value instead of by *F. pallescens* seedlings (Ares et al. 1990). Although protection from grazing and wind has been shown to increase seedling emergence and survival of *F. pallescens* as compared to grazed and wind exposed areas, only a few individuals become established as plants in these patches. The lack of *F. pallescens* seedling establishment in these bare soil patches (or microsites in the interspace between tussocks), where other annuals and perennials succeed, suggests that differences in root phenology and water demand during critical periods might favor establishment of invaders at the expense of *F. pallescens* seedlings.

Root phenology has been shown to be an important factor in the degree of competition among seedlings of different species (Harris 1967, 1977, Harris and Wilson 1970). Among individuals of the same species, competition may be more intense, because of similarities in their growth form, seasonal timing of growth, and resource requirements (Yeaton and Cody 1976, Turkington et al. 1979). The effect of competition for soil water and its effects on seedling establishment of *F. pallescens* in the grassland steppe in Patagonia is not well understood. This study addresses one of the possible causes that prevents re-establishment of *F. pallescens* in one of the most important grassland areas of Argentine Patagonia. The objectives of this study were, therefore, to determine: (1) the effects of competition and microsites on seedling densities of *Festuca* spp. at the phenological stages of a) recently emerged and up to 4 leaves, and b) 5 leaves and up to 1 tiller in grazed and ungrazed areas of a *Festuca* grassland, (2) the dynamics of soil water in the 0 to 5 and 5 to 20 cm soil depth as affected by microsites and grazing, and (3) how the dynamics of soil water in different soil profiles affect seedling densities at these 2 phenological stages.

Materials and Methods

Study Site

This study was conducted in the southwestern part of the Chubut province of Argentina at the Media Luna Ranch (45° 36′ S, 71° 25′ W, 700 m above mean sea level), in an area representative of the Sub-Andean Floristic District of the Patagonian Phytogeographic Province (Soriano 1956, Cabrera 1976). The site is a grass steppe dominated by *F. pallescens*, which comprised about 50% of the vegetation cover (Defossé et al. 1990, Bertiller 1992). Soils are uniformly coarse textured and well drained. They accumulate organic matter in the surface and down to 0.3 m. A detailed description of the soils of this area has been given in Beeskow et al. (1987). The climate of this area is cold and wet in winter and warm and dry in summer. The growing season extends from September to April and seed dispersal occurs from mid- to late-summer (Bertiller et al. 1991). Average precipitation is 374 mm per year, 67% of which falls in winter and early spring in the form of either rain or snow. Mean annual temperature is 4.5°C, with mean minimum in July (–3.7°C) and mean maximum in January (11.7°C). Freezing temperatures can occur at any time during the year, and strong westerly winds blow with high intensity all year around, and especially during spring and summer. The study site was located in an allotment of 700 ha in an area representative of this grassland. An exclosure was built in 1983 to carry out different long-term ecological studies. The grazed area outside the exclosure has been grazed from May to December at a stocking rate of about 1.5 sheep per ha for at least the past 25 years.

Competition, Microsites, and Grazing Experiment

In the exclosure and in the adjacent grazed area, 7 similarly-sized *F. pallescens* plants were selected on the basis of basal area and height measurements. Two root exclusion tubes of 0.1 m of diameter and 0.4 m long, similar to those described in Cook and Ratcliff (1984), were inserted in the soil on the leeward side of each chosen plant in the winter season prior to the start of the experiment. The length of the tubes was based on the root biomass distribution of *F. pallescens* in the soil profile. While roots of this species may reach depths of up to 1 m into the soil profile, 95% of the roots are concentrated in the upper 0 to 40 cm, with the highest concentration (80%) in the 5 to 20 cm soil depth (Merino 1983). One tube was placed at the outer edge of a *F. pallescens* plant (adjacent microsite). The second tube was placed 0.4 m from the center of the plant, in the interspace between 2 *F. pallescens* plants (interspace microsite). A ring of 0.1 m diameter, paired to each tube, was used as a control. Seedlings in these rings would be exposed to competition. At the beginning of the study, all aerial vegetation inside the tubes and in the control paired rings was cleared with minimal disturbance of the soil seed bank.

In the early spring following the installation of the root exclusion tubes, 15 seeds of *F. pallescens* were sown both inside the tubes and in the paired rings, and covered with a thin layer of soil of approximately 1 mm thick. From a previous study in that area, we found that after seed dispersal, seeds of *F. pallescens* were homogeneously distributed in the soil, and that there was little or no seed transport during fall and winter (Bertiller and Coronato 1994). These characteristics of seed dispersal and distribution were important and allowed us to begin the experiment with statistically similar quantities of seeds in both leeward and central microsites in regard to both the sown seeds and seeds stored in the seed bank.

The dynamics of seedlings at 2 phenological stages were followed inside the tubes and in the paired circles for about 3 growing seasons. Because *F. pallescens* grows in association with *F. pyrogea* in the study area, and it is difficult to differentiate these species at the seedling stage, they were censused together as *Festuca* spp. However, the contribution of *F. pyrogea* to the aboveground biomass of this grassland is negligible as compared to *F. pallescens* (Defossé et al. 1990). Seedlings of *Festuca* spp. were classified then in 2 groups: (1) recently emerged and up to 4 leaves, and (2) 5 leaves and up to 1 tiller. This classification was based on a previous study in the area (Defossé and Bertiller, unpublished), in which we found that after the phenological stage of 4 leaves, seedlings of *F. pallescens* start to rapidly elongate their root system into deeper soil horizons, and may likely start to compete with adult plants for available soil water. At every sampling date, water content in the 0 to 5, and 5 to 20 cm soil depth was determined gravimetrically from 12 replicates taken in adjacent and interspace microsites in both the exclosure and the grazed area.

To determine the significance of the effects of competition of established vegetation, grazing, and microsite location on (1) densities of *Festuca* spp. seedlings having up to 4 leaves, and (2) densities of seedlings of *Festuca* spp. having from 5 leaves and up to 1 tiller, analyses of variance (SPSS for Windows, Norusis 1993) based on the square-root-transformed seedling density data were used. Analysis of variance was also used to determine significant differences in soil water content in the 0 to 5, and 5 to 20 cm soil depth as affected by sampling dates, microsites, and grazing. Unless stated otherwise, the level of significance used throughout this study was determined at the probability level of $p < 0.01$.

Results

Influence of Soil Water

As in many other arid and semiarid ecosystems, the availability of water in the first 0 to 5 cm of the soil was the determinant factor in the success of seedling emergence in the *Festuca* steppe. The dynamics of soil water in the first 0 to 5 cm of the soil showed high water availability during late fall and winter, with a steady decline from spring to summer. Water content in the 0 to 5-cm soil depth was not significantly different in the exclosure from the grazed area (Table 1 and Fig. 1, top), but it was significantly higher in adjacent microsites as compared to interspace microsites during the different sampling dates. These differences were more noticeable during late fall, winter, and early spring (Table 1 and Fig. 1, top). In the 5 to 20 cm soil depth, soil water was less affected by the seasonal variation, and showed significantly higher soil water availability during the summer drought as compared to the 0 to 5 cm of the soil (Fig. 1, bottom). Soil water content was not significantly different in the 5 to 20 cm of the soil in either the exclosure as compared to grazing treatment or in adjacent as compared to interspace microsites (Table 1 and Fig. 1, bottom).

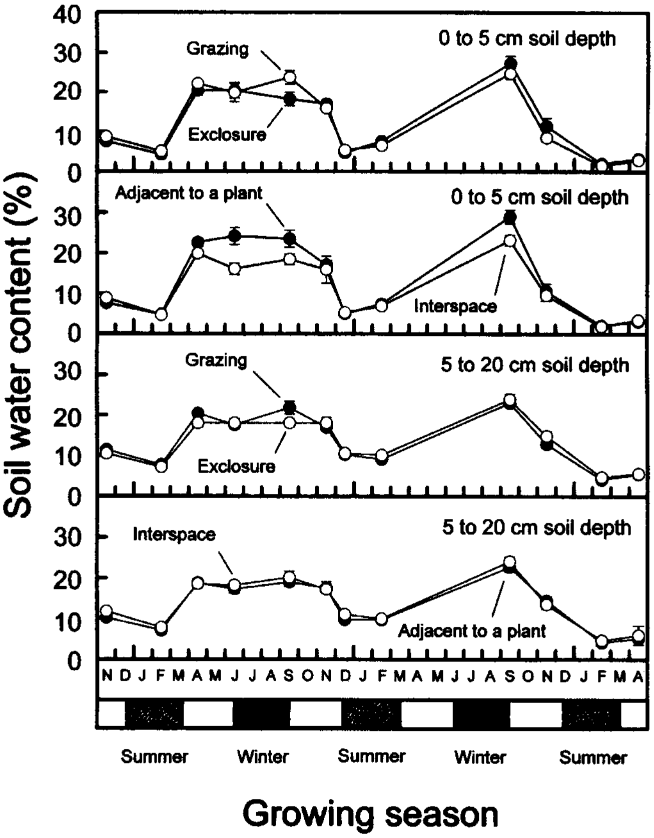

Fig. 1. Dynamics of water in the 0 to 5 and 5 to 20 cm of the soil profile during 3 successive growing seasons in a steppe of Patagonia, Argentina, as affected by grazing and microsites. Each point represents the mean ±1 standard error of the mean.

Table 1. Three-way analysis of variance for the effects of grazing, microsites, and sampling dates on the dynamics of water in the 0 to 5, and in the 5 to 20 cm of the soil in the Media Luna Ranch in Patagonia, Argentina. All values in the table have been rounded to 2 decimal places.

Source of Variation	Sum of Squares	d. f.	Mean Square	F	Significance of F
Soil depth: 0 to 5 cm					
Main effects	**18694.16**	**13**	**1438.01**	**99.99**	**0.00****
Sampling date	18429.67	11	1675.42	116.50	0.00**
Grazing	0.47	1	0.47	0.03	0.85^{ns}
Microsite	264.01	1	264.01	18.35	0.00**
Two-way interactions	**888.09**	**23**	**38.61**	**2.68**	**0.00****
Sampling date-Grazing	326.33	11	29.66	2.06	0.02**
Sampling date—Microsite	560.28	11	50.93	3.54	0.00**
Grazing-Microsite	1.48	1	1.48	0.10	0.74^{ns}
Three-way interactions	**34.14**	**11**	**3.04**	**0.21**	**0.99^{ns}**
Sampling date-Grazing-Microsite	34.14	11	3.04	0.21	0.99^{ns}
Soil depth: 5 to 20 cm					
Main effects	**41399.03**	**13**	**3184.54**	**210.69**	**0.00****
Sampling date	41362.15	11	3760.19	248.78	0.00**
Grazing	8.44	1	8.44	0.56	0.45^{ns}
Microsite	26.80	1	26.80	1.77	0.18^{ns}
Two-way interactions	**844.68**	**23**	**36.72**	**2.43**	**0.00****
Sampling date-Grazing	602.17	11	54.74	3.62	0.59^{ns}
Sampling date-Microsite	238.04	11	21.64	1.43	0.00**
Grazing-Microsite	4.33	1	4.33	0.28	0.15^{ns}
Three-way interactions	**47.34**	**11**	**4.30**	**0.28**	**0.99^{ns}**
Sampling date-Grazing-Microsites	47.34	11	4.30	0.28	0.99^{ns}

Significance: ** $p < 0.01$; *$p < 0.05$; n.s. not significantly different.

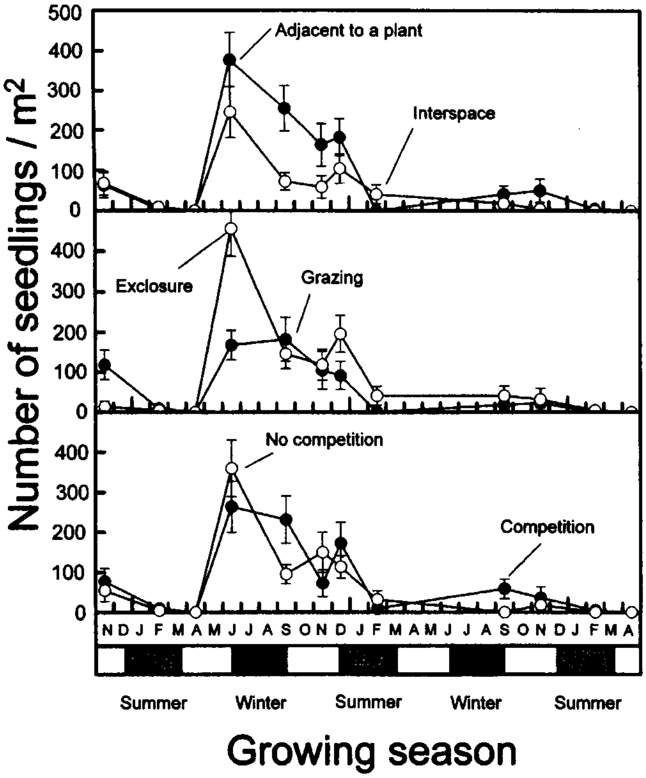

Fig. 2. Dynamics of seedlings recently emerged and up to 4 leaves as affected by microsites (top), grazing (center), and competition (bottom) during 3 successive growing seasons in a steppe of Patagonia, Argentina. Each point represents the mean ±1 standard error of the mean.

High soil water availability coincided with the highest densities of seedlings of *Festuca* spp. up to 4 leaves for the different treatments in spring and late fall over the 3 growing seasons considered (Fig. 2). Seeds were sown in September (spring) when water started to steadily diminish in the first 0 to 5 cm of the soil. By November, only a portion of these seeds had emerged. Peak densities for this category occurred by the following fall, when the first 0 to 5 cm of the soil were replenished with water. After that peak, high densities of seedlings with up to 4 leaves occurred when soil water content was above 8% in the 0 to 5 cm of the soil. Densities of seedlings with 5 leaves and up to 1 tiller, by contrast, did not show any particular pattern, and after the second sampling date, they ranged in the different treatments from about 20 to 60 seedlings per m^2 for the entire study period (Fig. 3).

Effects of Microsites

Similar densities of seedlings up to 4 leaves were observed in adjacent and interspace microsites during the first 3 sampling dates. For the remainder of the study period, except for the sampling done in February of the second growing season, significantly greater seedling densities were found in the microsites adjacent to adult *F. pallescens* plants as compared to microsites in the interspace between plants (Table 2 and Fig. 2, top). Except for the sampling done in November and February of the second growing season, seedlings having 5 leaves and up to 1 tiller had significantly greater density in interspace microsites as compared to adjacent microsites (Table 3 and Fig. 3, top).

Effects of Grazing

Seedling densities of all categories were similarly affected by the grazing treatment. Although the grazed area initially showed significantly higher densities of seedlings up to 4 leaves, this effect was short lived. For the majority of the study period, significantly higher densities of seedlings up to 4 leaves were found in the exclosure as compared to the grazing area (Table 2 and Fig. 2, center). For seedlings with 5 leaves and up to 1 tiller, grazed areas showed significantly higher densities for the second and third sampling dates after sown. However, this coincided with the normal rest period in the area. When grazing resumed in this area the next season, significantly higher seedling densities were found in the exclosure as compared to the grazed area for the rest of the study period (Table 3 and Fig. 3, center).

Table 2. Four-way analysis of variance for the effects of competition, grazing, microsites, and sampling dates on emergence and survival of seedlings up to 4 leaves of *Festuca* spp. in a grassland of Patagonia, Argentina. All values in the table have been rounded to 2 decimal places.

Source of Variation	Sum of Squares	d. f.	Mean Square	F	Significance of F
Main effects	**98.33**	**14**	**7.02**	**20.06**	**0.00****
Sampling date	91.29	11	8.30	23.70	0.00**
Grazing	2.13	1	2.07	6.21	0.01**
Microsite	4.04	1	4.65	13.15	0.00**
Competition	0.25	1	0.25	0.73	0.39^{ns}
Two-way interactions	**40.15**	**36**	**1.11**	**3.20**	**0.00****
Sampling date-Grazing	19.77	11	1.79	5.14	0.00**
Sampling date—Microsite	10.38	11	0.94	2.69	0.00**
Sampling date-Competition	5.92	11	0.53	1.53	0.11^{ns}
Grazing-Microsite	3.80	1	3.80	10.85	0.00**
Grazing-Competition	0.09	1	0.09	0.26	0.60^{ns}
Microsite-Competition	0.17	1	0.17	0.49	0.48^{ns}
Three-way interactions	**28.88**	**34**	**0.67**	**1.92**	**0.00****
Sampling date-Grazing-Microsite	6.76	11	0.61	1.75	0.04 *
Sampling date-Grazing-Competition	8.99	11	0.81	2.32	0.00**
Sampling date-Microsite-Competition	7.07	11	0.64	1.83	0.04 *
Grazing-Microsite-Competition	0.04	1	0.04	0.14	0.71^{ns}

Significance: ** $p < 0.01$; * $p < 0.05$; n.s. not significantly different.

Effects of Competition

Competition affected seedling densities at the 2 phenological stages differently. Also, of the factors examined in this study, belowground competition was the single most important factor for seedling survival of older seedlings (see Fig. 3). Densities of young seedlings, i.e., those with up to 4 leaves, were not significantly different for plants not exposed to competition (inside root exclusion tubes) or exposed to competition (outside exclusion tubes) (Table 2 and Fig. 2, bottom). In contrast, older seedlings, i.e., those with 5 leaves and up to 1 tiller, were significantly affected by belowground competition. Densities of these older seedlings was significantly lower in response to competition as compared to seedlings that were not exposed to competition (Table 3 and Fig. 3, bottom).

Discussion

In water-limited environments, the availability of water near the soil surface appears to be a key factor for seedling emergence and survival (Wilson and Briske 1978, Mack and Pyke 1984). As found in the Patagonian grassland steppe studied, seedling emergence was most affected by soil water in the top 5 cm of the soil. In addition to the importance of soil water near the surface, the proximity of a seedling to an adult plant, e.g., on adjacent microsites, appeared to be an important factor. These adjacent microsites had higher soil water content near the surface than the microsites in the interspace between tussocks, and thus provided a more suitable microenvironment for seedlings in the younger age group. However, as seedlings developed a more extensive root system and used water deeper in the soil profile, their densities decreased on adjacent microsites relative to interspace microsites. Higher survival of older seedlings in the interspace microsite was also observed by Soriano and Sala (1986). Although water content was similar between adjacent and interspace microsites at the greater soil depths, the higher densities of older seedlings found in interspace microsites was due to lower competition for soil water in those microsites; interspace microsites had lower root concentrations than microsites adjacent to adult plants (Soriano et al. 1987).

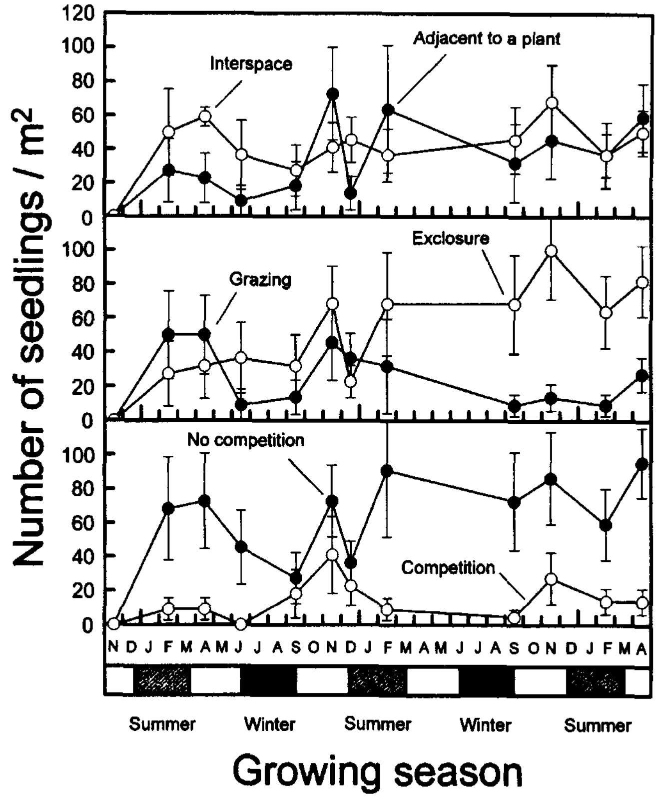

Fig. 3. Dynamics of seedlings with 5 leaves and up to 1 tiller during 3 successive growing seasons as affected by microsites (top), grazing (center), and competition (bottom) in a grassland of Patagonia, Argentina. Each point represents the mean ±1 standard error of the mean.

Competition for soil water was also a significant factor in the grassland steppe, especially for older seedlings. Densities of younger seedlings, i.e., those with up to 4 leaves, were not affect-

Table 3. Four-way analysis of variance for the effects of competition, grazing, microsites, and sampling dates on survival of seedlings of *Festuca* spp. having 5 leaves and up to one tiller in a grassland of Patagonia, Argentina. All values in the table have been rounded to 2 decimal places.

Source of Variation	Sum of Squares	d. f.	Mean Square	F	Significance of F
Main effects	**21.31**	**14**	**1.52**	**7.24**	**0.00****
Sampling date	6.57	11	0.59	2.84	0.00**
Grazing	3.36	1	3.32	15.79	0.00**
Microsite	1.06	1	1.06	5.06	0.02**
Competition	10.34	1	10.34	49.14	0.00**
Two-way interactions	**15.12**	**36**	**0.42**	**1.99**	**0.00****
Sampling date-Grazing	5.63	11	0.51	2.43	0.00**
Sampling date—Microsite	1.43	11	0.13	0.61	0.81^{ns}
Sampling date-Competition	3.24	11	0.29	1.40	0.16^{ns}
Grazing-Microsite	1.23	1	1.23	5.85	0.01**
Grazing-Competition	2.84	1	2.84	13.50	0.00**
Microsite-Competition	0.74	1	0.74	3.52	0.06^{ns}
Three-way interactions	**6.61**	**34**	**0.19**	**0.92**	**0.59^{ns}**
Sampling date-Grazing-Microsite	0.94	11	0.08	0.40	0.95^{ns}
Sampling date-Grazing-Competition	2.33	11	0.21	1.00	0.43^{ns}
Sampling date-Microsite-Competition	1.61	11	0.14	0.69	0.74^{ns}
Grazing-Microsite-Competition	1.72	1	1.72	8.17	0.00**

Significance: ** $p < 0.01$; * $p < 0.05$; n.s. not significantly different.

ed by belowground competition. These younger seedlings, which had shallow root systems, relied mostly on the availability of water in the 0 to 5 cm soil layer, and were unaffected by root competition with adult plants. Older seedlings, i.e., those with 5 leaves and up to 1 tiller, in contrast, were severely affected by root competition from adult *F. pallescens* plants. In a study carried out in a different area of the same grassland as the present study, Abadie (1967) found that after several years of grazing exclusion, *F. pallescens* bunchgrasses increase in size, yet little or no seedling establishment of *F. pallescens* occurred. This also suggests that competition between older seedlings and adult *F. pallescens* might be significant. Intraspecific competition may be more detrimental for survival of older seedlings than interspecific competition, since seedlings and adult plants share similar root and shoot phenology and similar water demands (Yeaton and Cody 1976, Robberecht et al. 1983). Differences in root phenology among species have been shown to be an important factor in seedling establishment of different species in semiarid ecosystems (Harris 1967, 1977, Harris and Wilson 1970, Reichenberger and Pyke 1990). In the Patagonian grassland steppe, the failure of *Festuca* spp. seedling establishment may be due, in part, to competition for soil water during critical periods with adult *Festuca* plants. The increased prevalence of adventive and other native annuals and perennials in the Patagonian grassland steppe may be related in part to differences in root phenology and water demands between these adventive species and seedlings of *Festuca* spp.

Grazing also appeared to be a significant factor in this grassland steppe, as evidenced by the consistently higher seedling densities of both categories found in areas protected from grazing. Since soil water availability for the entire soil profile, the number of seeds in the germinable seed bank (Bertiller 1992, Bertiller and Coronato 1994), and the number of seeds sown were similar in the exclosure and the grazed area at the beginning of this study, the significant reductions found in seedling densities at the 2 phenological stages studied between protected and grazed areas were due to the effects of grazing and trampling. The detrimental effects of grazing were more severe on microsites in the interspaces than on microsites adjacent to adult plants, and indicated that sheep tended to step between tussocks instead of on or adjacent to tussocks. This is consistent with Balph and Malecheck (1985), who found higher trampling incidence on tussock interspaces than on tussocks in a semiarid *Agropyron* grassland. Grazing has been suggested to either promote (Savory and Parsons 1980, Savory 1983, Gibson et al. 1987, Oesterheld and Sala 1990) or to reduce (Mack and Pyke 1984, Salihi and Norton 1987) seedling establishment. These apparent contradictory findings may be due to variations in the grazing treatment, and thus the specific effects of grazing appears to be highly related to the season of grazing, the kind of grassland grazed, and the stocking rate used. In the Patagonian grassland steppe, the season of grazing and the stocking rate used has been shown to be detrimental for *Festuca* spp. seedling establishment.

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Reminder!

The *Trailboss News* will be mailed separately starting in January 1997 and not as a supplement with the *Journal* or *Rangelands*. This will enable the *TBN* staff to publish more current information to the SRM membership. If you have information or position announcements to be published in the *Trailboss News* please have it to the Denver office by the 1st of the month. Due to publication scheduling information after the first may not be published. For further information contact the Patty Rich or Marlene Richards at 303-355-7070.

J. Range Manage.
50:80–84

Development and vigor of diploid and tetraploid Russian wildrye seedlings

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Abstract

Poor seedling vigor limits the use of Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] for complementary pasture. Tetraploid ($2n=4x=28$) plants of Russian wildrye have greater seedling vigor in greenhouse studies when compared to plants with the normal diploid chromosome complement ($2n=2x=14$). Objectives of this research were (i) to compare seedling emergence and development of diploid and tetraploid Russian wildrye in solid-seeded, single-row field plots and (ii) to document early seedling development and morphology in a controlled environment chamber. Seed mass averaged 2.70 mg seed^{-1} for diploids and 4.66 mg seed^{-1} for tetraploids. Initial seedling emergence averaged approximately 33% greater for tetraploids than diploids for both early and late field planting dates. Tiller number averaged only slightly, and generally not significantly, greater for diploids than tetraploids (maximum difference of 0.3 tillers plant^{-1}) in solid-seeded rows in the field. Seedling height was consistently greater for tetraploids than diploids, a result of greater leaf length. Larger leaf size did not result in fewer leaves or in slower leaf development for tetraploids. Seedling emergence from a 63 mm depth in a controlled environment chamber averaged 46% for tetraploids and 10% for diploids at a 16/13°C diurnal temperature regime and 11 and 6%, respectively, for tetraploids and diploids at a 23/18°C temperature regime. Coleoptile length averaged 61 mm for tetraploids and 49 mm for diploids at the 16/13°C temperature regime and 42 and 43 mm for tetraploids and diploids, respectively, at the 23/18°C temperature regime. Tetraploid Russian wildrye provides a unique germplasm pool from which additional improvement in seedling vigor can be accomplished beyond the limits that are possible from continued selection in diploid germplasm.

Key Words: *Psathyrostachys juncea*, seedling emergence, coleoptile length, seedling tillers, Haun score.

Resúmen

El débil vigor de establecimiento de sus plantulas limita el uso del centeno silvestre ruso (*Psathyrostachys juncea*), para su utilización en praderas complementarias. Las plantas tetraploides ($2n=4x=28$) del centeno silvestre ruso poseen un mayor vigor en el establecimientos de las plantulas en estudios de invernadero al ser comparadas con plantas con el complemento normal diploide de cromosomas ($2n+2x=14$). Los objetivos de esta investigación fueron: 1) el comparar la emergencia de las plantulas y el desarrollo de centeno silvestre ruso diploide y tretaploide en una siembra en surcos. 2) el documentar el desarrollo de las plantúlas y su morfologia en una cámara de ambiente controlado. La masa de la semilla promedio que de 2.70 mg para las variedades diploides y 4.66 mg para las tetraploides. La emergencia de las plantulas inciales promedió, aproximadamente un 33% más para las tretaploides que para las diploides, tanto para fechas de siembra tempranas, como tardias. El numero de tallos promedio fue solo ligeramente mayor para los diploides más no significativo, que para los tetraploides (diferencia máxima de 0.3 tallos por planta). La altura de las plantulas fue consistentemente mayor para los tetraploides que para las diploides, como resultado de una mayor longitud de hoja. El mayor tamaño de hoja no resulto en menos hojas o en un desarrollo lento de la hoja para los trataploides. La emergencia de las plantulas de una profundidad de 63 mm en una cámara de ambiente controlado, promedio 46% para los tretaploides y 10% para los diploides en un régimen de temperatura diurna de 16/13°C y 11 y 6% respectivamente para tretaploides y diploides en un régimen de temperaturas de 23/28°C. La longitud del coleoptilo promedio 61 mm para los tretaploides y 49 mm. para los diploides en el regimen de temperatura 16/13°C y 42 y 43 mm. para los tetraploides y diploides, respectivamente, en el régimen de temperatura de 23/18°C. El centeno silvestre ruso tretaploide suministra un conglomerado (pool) de germoplasma único, mediante el cual se puede obtener un mejoramiento adicional del vigor de las plantulas, más alla de los limites posibles de la selección continuada de germoplasma diploide.

Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] is an introduced, cool-season, bunchgrass with broad adaptation to semiarid regions of North America (Rogler and Schaaf 1963, Smoliak and Johnston 1980). Russian wildrye produces an abundance of basal leaves that maintain relatively high levels of digestibility and protein with advancing maturity (Knipfel and Heinrichs 1978). The species provides valuable pasture that is often used to complement native rangeland during the late- summer and fall when nutritive quality of most forages is relatively low.

Poor vigor during establishment is a major factor limiting more widespread use of Russian wildrye (Lawrence 1963). Genetic gain from selection for improved seedling vigor has been accomplished and is evident in diploid cultivars such as 'Swift' (Lawrence 1979), 'Bozoisky-Select' (Asay et al. 1985), and 'Mankota' (Berdahl et al. 1992). Seedling vigor was greater for

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tetraploid than diploid Russian wildrye in greenhouse studies (Lawrence et al. 1990; Berdahl and Barker 1991; Jefferson 1993). An induced tetraploid cultivar of Russian wildrye with improved seedling vigor, 'Tetracan', has been licensed for sale in Canada (Lawrence et al. 1990).

Critical comparisons of seedling emergence and seedling development between diploid and tetraploid Russian wildrye have not been reported in field environments that are similar to those encountered by commercial producers. Also, seedling morphology and development at early stages determine the genetic potential for initial seedling emergence, and these parameters have not been defined for Russian wildrye in rigidly controlled environments. Objectives of this study were: (i) to compare seedling emergence and development of diploid and tetraploid Russian wildrye in solid-seeded plots in field studies, and (ii) to document early seedling development and morphology of diploid and tetraploid Russian wildrye in a controlled environment chamber.

Materials and Methods

Plant Materials

Three diploid entries, 'Vinall', 'Mankota', and Mandan R1831, and the 3 tetraploid entries, Mandan R4X28-23, Mandan R4X29-11, and Mandan R4X37-25, were included in this study. Even though a relatively small sample of germplasm was involved, none of the entries had parent clones in common. Vinall was developed by USDA-ARS at Mandan, N.D. and released in 1960 (Hein 1960). Mankota, also developed by USDA-ARS at Mandan, has improved seedling vigor and forage yield compared with Vinall and was released cooperatively by USDA-ARS, USDA-NRCS, and the North Dakota Agricultural Experiment Station in 1991 (Berdahl et al. 1992). Mandan R1831 is an experimental strain selected primarily for high seedling vigor and seed yield. The tetraploid strains were developed at Mandan using a nitrous oxide technique to double the chromosome number of diploid parents that were previously selected for high seedling vigor and overall plant vigor (Berdahl and Barker 1991). The tetraploid entries all had regular meiosis (Berdahl and Barker 1991). All seed was harvested from field plots near Mandan in 1988 and stored in a deep freeze at –20°C. Germination percentage, measured according to procedures of the Association of Official Seed Analysts (1981), and seed mass are recorded in Table 1.

Table 1. Germination percentage and seed mass of 3 diploid and 3 tetraploid Russian wildrye entries harvested in 1988 near Mandan, N.D.

Ploidy level	Entry	Germination[2]	Seed mass
		- - (%) - -	(mg seed^{-1})
Diploid	Vinall	96.8 a[1]	2.58 d
	Mankota	94.0 ab	3.03 c
	Mandan R1831	97.5 a	2.48 d
Tetraploid	Mandan R4X28-23	87.5 c	4.45 b
	Mandan R4X29-11	95.0 ab	4.73 ab
	Mandan R4X37-25	95.0 ab	4.80 a

[1] Means followed by the same letter are not significantly different (P≤0.05) based on a Waller-Duncan K-ratio T test.

[2] Final germination counts were based on 4 replicates of 100 seeds germinated 14 days between 2 blotters in petri dishes maintained at 20/30°C, 16/8 hour photoperiod, according to procedures of the Association of Official Seed Analysts (1981).

Field Study

A site near Mandan, N.D. (46° 55'N, 100°55'W) at an altitude of 500 m with a Parshall fine sandy loam soil (coarse-loamy, mixed Pachic Haploborolls) was chosen for the field study. The site had been fallowed the previous year and was cultivated, harrowed, and hand-raked prior to planting. Planting dates were 25 April and 24 May 1991 and 4 May and 10 June 1992, which provided a relatively early and a relatively late planting date within each year for the northern Great Plains region. The 6 entries, 3 diploid and 3 tetraploid, were replicated 6 times in a randomized-complete-block design. Each of the 4 plantings was randomized separately. Each plot consisted of a single row 2 m long with a 0.5 m spacing between plots. Planting depth was controlled by pressing a 2.5 × 2.5 cm × 2.0 m marker into the soil to create a 2.5 cm furrow for each row. Each plot was hand-planted with 100 seeds spaced ≈ 2.0 cm apart. Planted furrows were carefully covered with soil. A person with a mass of 80 kg packed each row by placing a piece of wooden plywood (2.0 m × 45 cm × 1.25 cm thick) over the row and walking on the plywood. The study received only natural precipitation and no fertilizer. Rainfall for 60 days immediately following each planting date was adequate and well-distributed, totaling 97 mm for the 25 April 1991, 126 mm for 24 May 1991, 139 mm for 4 May 1992, and 182 mm for the 10 June 1992 plantings.

Seedling emergence was measured at 2- or 3-day intervals on an entire plot and data were adjusted according to percentage pure live seed. Tiller number, Haun score, and seedling height were measured at 7-day intervals on a subsample of 5 randomly selected seedlings per plot. The primary tiller of each of the 5 seedlings in each subsample was marked with a chicken leg-band and used for repeated measurements of Haun score (Haun 1973) and plant height. All seedlings remained vegetative during the growing season immediately after planting; thus, Haun score described seedling development stages numerically according to number of leaves present. Seedling height was measured as distance from ground level to the tip of the last fully expanded leaf, extended vertically.

Growth Chamber Study

Seedling emergence and coleoptile length were measured on the same 3 diploid and 3 tetraploid entries in a growth chamber study. Two planting depths, 25 and 63 mm, and 2 diurnal temperature regimes, 23/18°C and 16/13°C, with a 14/10-hour photoperiod were investigated. Light radiation at soil level was 900 μ mol m^{-2}s^{-1}. An experimental unit for each of the 6 entries consisted of 10 seeds planted in a PVC cylinder measuring 5.2 cm inside diameter by 20 cm high. Soil was a Parshall fine sandy loam (coarse-loamy, mixed Pachic Haploborolls) packed in each cylinder to a bulk density of 1.4 g cm^{-3} with a field capacity of 24% soil water by volume. Each cylinder was watered to field capacity after planting with a 50% Hoagland's solution containing 0.1 g N liter^{-1}. Cylinders were brought to field capacity with tap water the second day. Thereafter, cylinders were watered to maintain 50% available water (17% soil water by volume) and brought to field capacity with 50% Hoagland's solution once weekly.

Soil was washed from developing seedlings 17 days after planting for the 23/18°C temperature regime and 19 days after planting for the 16/13°C regime. Coleoptile length was measured as total distance of the coleoptile tip above the seed, regardless of whether the coleoptile had emerged from the soil surface.

Statistical Analysis

Separate ANOVA's were first run on each of the 4 field plantings. Means and variances were similar within the early and within the late planting dates for the 2 years. Separate ANOVA's for the early and late dates were combined over years. Entries and years were considered as random effects in the statistical model that included replicates/years, entries, years, entries × years, and entries × replicates/years as sources of variation. Entry × year interaction effects were tested for significance using the expected mean square for entry × replicate/year as the error term. Entry effects were tested using entry × year as the error term, and differences among ploidy levels were tested using a single degree of freedom comparison. Each successive measurement for specific seedling traits over the growing season was treated as a separate variable. Differences in Haun scores between early and late planting dates were tested for significance using a t-test of unpaired observations.

The 2 ploidy levels, 2 planting depths, and 2 temperature regimes in the growth chamber study were analyzed as a completely randomized design arranged in a 2 × 2 × 2 factorial with 3 replicates. The 3 diploid and 3 tetraploid entries were treated as subsamples/ploidy level. Ploidy level, planting depth, and temperature regime were all considered to have fixed effects in the ANOVA, and all main effects and interaction effects were tested using the expected mean square for replicates/ploidy level × planting depth × temperature regime as the error term. Since most of the interaction effects for seedling emergence and coleoptile length were significant, simple effects of ploidy level were examined within each level of planting depth and temperature regime. Differences in seedling emergence between temperature regimes were tested for significance for diploids and tetraploids using a t-test of unpaired observations.

Results and Discussion

Seedling Emergence

Stebbins (1971) reported that increased cell size associated with higher ploidy levels resulted in improved seedling vigor in many diploid species. Lawrence et al. (1990) and Berdahl and Barker (1991) attributed improved seedling emergence of tetraploid over diploid Russian wildrye in greenhouse studies primarily to greater seed mass for tetraploid germplasm. Seed mass in this study averaged 2.70 mg seed^{-1} for diploids and 4.66 mg seed^{-1} for tetraploids (Table 1), a 72% increase in seed mass for tetraploid over diploid entries. Entry × year-and ploidy level × year-interaction effects for seedling emergence in this field study were low and were not significant for any of the seedling counts within early and late planting dates. Patterns of seedling establishment were different for the 2 planting dates. Initially, seedling emergence was greater ($P<0.01$) for tetraploids than diploids in both the early (Table 2) and late (Table 3) plantings. In early plantings, tetraploids averaged more ($P<0.01$) live seedlings than diploids on all observation dates over a 34-day period. Emergence occurred more rapidly in late plantings, and seedling counts were similar for diploids and tetraploids during a 14 to 26-day period after planting. Stand density of established seedlings was excellent for both diploids and tetraploids for the 2 planting dates in both years of this study.

Diploid and tetraploid seedlings emerged differently from a deep planting (63 mm) in the 2 controlled temperature regimes (Table 4). When the diurnal temperature regime was decreased from 23/18°C to 16/13°C (14/10 hours light/dark), seedling emergence did not increase significantly for diploids and increased dramatically from 11.1 to 45.7% ($P\leq 0.01$) for tetraploids. Coleoptile length measured from the 63 mm planting depth also increased when temperature was reduced, and the relative increase was much greater for tetraploids than diploids. Time from planting to emergence for tetraploids at the 63 mm depth averaged 7.5 days for the 23/18°C temperature regime and 15.2 days for the 16/13°C temperatures. Increased coleoptile length at lower temperatures was the most logical reason for improved emergence of tetraploids from deep planting. Tetraploids likely have a greater potential coleoptile length than diploids because of the greater seed mass and increased cell size in tetraploid plants. McElgunn and Lawrence (1970) reported that emergence of diploid Russian wildrye seedlings was severely impeded beyond a 45-mm planting depth, and they attributed this failure to emerge to inadequate elongation of the coleoptile. Although an emerging

Table 2. Means for seedling traits of 3 diploid and 3 tetraploid Russian wildrye entries averaged over early field plantings made 25 April 1991 and 4 May 1992 near Mandan, N.D.

		Days after planting					
Ploidy level	Trait	18	20	22	25	27	34
		(number)					
Diploid	Seedlings per 2.0 lineal m of row (100 possible)	27.1	40.9	52.1	55.6	56.3	53.5
Tetraploid		37.4	53.3	63.3	66.0	65.6	63.5
		**	**	**	**	**	**
		Days after planting (1991/1992)					
		41/43	48/50	55/57	63/66	76/78	
		(tillers per plant)					
Diploid	Tiller number	2.4	2.9	3.9	6.8	7.8	
Tetraploid		2.2	2.7	3.8	6.5	7.5	
		**	*	NS	NS	NS	
Diploid	Haun score	4.6	5.3	6.0	7.2	9.2	
Tetraploid		4.6	5.4	6.0	7.2	9.1	
		NS	NS	NS	NS	NS	
		(cm)					
Diploid	Seedling height	10.3	12.9	14.8	18.5	23.9	
Tetraploid		11.7	14.7	17.1	20.9	26.5	
		**	**	**	**	**	

*, **Differences significant at $P\leq 0.05$ and $P\leq 0.01$, respectively. NS = Not significant.

Table 3. Means for seedling traits of 3 diploid and 3 tetraploid Russian wildrye entries averaged over late field plantings made 24 May 1991 and 10 June 1992 near Mandan, N.D.

		Days after planting					
Ploidy level	Trait	12	14	17	19	21	26
		(number)					
Diploid	Seedlings per 2.0 lineal m	26.7	63.6	66.7	66.5	64.1	61.6
Tetraploid	of row (100 possible)	34.3	66.3	68.3	67.4	65.6	63.1
		**	NS	NS	NS	NS	NS
		Days after planting (1991/1992)					
		40/43	47/50	54/57	61/64	68/66	
		(tillers per plant)					
Diploid	Tiller number	2.5	3.5	5.8	7.6	8.7	
Tetraploid		2.5	3.4	5.7	7.4	8.5	
		NS	NS	NS	NS	*	
Diploid	Haun score	4.9	5.8	6.7	7.3	7.9	
Tetraploid		4.8	5.8	6.7	7.3	7.8	
		NS	NS	NS	NS	NS	
		(cm)					
Diploid	Seedling height	12.5	14.0	15.4	16.5	17.1	
Tetraploid		13.9	15.4	17.0	18.1	18.7	
		**	**	**	**	**	

*, **Differences significant at P≤0.05 and P≤0.01, respectively. NS = Not significant.

seedling is primarily dependent on the rigid coleoptile for penetration through soil, the first true seedling leaf also is capable of limited penetration. The coleoptile did not penetrate to the soil surface for many tetraploid seedlings at the 63-mm planting depth (data not presented). In some instances, seedling emergence was dependent on coleoptile development plus elongation and soil penetration by the first true seedling leaf. Mesocotyls of the diploid or tetraploid seedlings were not elongated at the 63-mm planting depth, in contrast to a report by Rogler (1954) that a small percentage of crested wheatgrass [*Agropyron desertorum* (Fischer ex Link) Schultes] seedlings developed an elongated mesocotyl when seeded deeply.

Although caution must be used in extending results from controlled environment studies to the field, the potential for tetraploids to emerge from deeper plantings than diploids in a controlled environment has important implications. Deeper planting depths would place seeds and, subsequently, seedling crowns at deeper depths where extremes in soil water and temperature would be reduced. Also, improved coleoptile growth and seedling emergence for Russian wildrye at lower temperatures suggests that, aside from soil water availability, establishment potential may be improved by early spring planting when average temperatures are lower. Relationships between seedling development and temperature in Russian wildrye require further investigation.

Tiller Development

Tiller number tended to be only slightly higher for diploid than tetraploid seedlings in competitive sward conditions in the field (Tables 2 and 3). Jefferson (1993) found that seedlings of the tetraploid Russian wildrye cultivar Tetracan had significantly fewer (P<0.01) and larger (P<0.01) tillers than the diploid cultivars Swift and 'Mayak' in a greenhouse study. The relative magnitude of the difference between diploids and tetraploids in tiller number was much greater in the greenhouse study (Jefferson 1993) than in our field study. The greenhouse environment may have allowed fuller potential expression of tiller number than solid-seeded rows in the field where interplant competition was high. We have observed that mature tetraploid plants generally produce fewer tillers with a greater culm diameter than diploids in space-plant field nurseries. The potential for high tillering capacity may be important in a bunchgrass such as Russian wildrye in situations when plant density in field plantings is less than optimum. Thus, high tillering capacity may be an important selection criterion in improving tetraploid Russian wildrye through plant breeding.

Haun Scores

Frank et al. (1985) reported a linear relationship between rate of phyllochron development (addition of new leaves) and accumulation of heat units (growing degree-days) in 4 cool-season forage grass species. Temperatures were higher after the late than the early planting dates. Eight weeks after planting, Haun scores (a measure of leaf number) averaged 6.7 for the late and 6.0 for the early planting dates, a significant difference (P<0.01) (Tables 2 and 3). No differences in Haun scores were found between diploid and tetraploid seedlings at either planting date. Similar rates of leaf development for diploid and tetraploid seedlings, even though tetraploids had larger leaves, suggest that reproductive tillers of diploid and tetraploid Russian wildrye may also develop at similar rates.

Table 4. Seedling emergence percentage and coleoptile length of 3 diploid and 3 tetraploid Russian wildrye entries grown under 2 temperature regimes at 2 planting depths in a growth chamber.

		Temperature and light regime			
		23/18°C, 14/10 hours		16/13°C, 14/10 hours	
		Planting depth		Planting depth	
Ploidy level	Trait	25 mm	63 mm	25 mm	63 mm
		(%)			
Diploid	Emergence	85.3	5.7	76.6	10.0
Tetraploid		85.3	11.1	87.7	45.7
		NS	**	*	**
		(mm)			
Diploid	Coleoptile length	29	43	31	49
Tetraploid		30	42	31	61
		NS	NS	NS	**

*, **Differences between ploidy levels significant at P≤0.05 and P≤0.01, respectively. NS = Not significant.

Plant Height

Although the magnitude of the differences was not great, tetraploid seedlings were consistently taller than diploids (P<0.01) at all measurement dates for both the early and late plantings (Tables 2 and 3). Seedling height reflects leaf length, which would be expected to be greater in tetraploids due to increased size of plant cells. Large leaves provide a visual impression that tetraploid seedlings are much more vigorous than diploids. Large leaf size may be important in assimilating total carbon and in providing competition for weeds. Seedling counts began to decline approximately 4 weeks after planting for the early planting date and 3 weeks after the late planting date (Tables 2 and 3), probably due primarily to high interplant competition. The rate of decline in live seedlings was relatively low and similar for diploids and tetraploids.

Conclusions

Jefferson (1993) pointed out that diploid Russian wildrye cultivars selected for improved seedling vigor are still inferior to crested wheatgrass (*Agropyron* spp.) in stand establishment capability. Consequently, the majority of producers in semiarid regions of the Canadian Prairies continue to use crested wheatgrass for reseeding marginal cropland to grass, even though established Russian wildrye pastures often produce greater animal gains. Increased size of plant cells, organs, and tissues in tetraploid compared to diploid Russian wildrye results in important changes in plant morphology. Tetraploids provide a new, unique germplasm pool for Russian wildrye and provide an opportunity to make substantial improvements in seedling vigor. Seed mass of tetraploid entries averaged 72% greater than diploid entries in this study. Coleoptile length and seedling emergence were much greater for tetraploids than diploids at a 63-mm planting depth in a controlled environment chamber. Initial seedling emergence was more rapid for tetraploids than diploids in field studies with a planting depth of about 25 mm. Seedling height was consistently greater for tetraploids, a result of increased leaf length. Larger leaf size did not result in reduced leaf number or slower development of leaves. Diploid seedlings may have the potential to develop more tillers than tetraploids, but diploids averaged only slightly more tillers, usually not significant, than tetraploids in solid-seeded rows in field studies.

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Determination of animal behavior-environment relationships by Correspondence Analysis

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Abstract

The paper describes an analytical procedure to preliminarily investigate large scale animal-environment interactions. The method is based on Correspondence Analysis applied over a contingency table in which the columns are percentage categories of animal activities and the rows, states of environmental variables. Each cell entry in the table represents the number of times a row and a column have been recorded together. This means that investigation of animal-environment interactions does not require defining specific sampling stations, or subdividing the study area into environmental units; i.e. the method can be used in studies in which sampling consisted of following the animals and noting their activities and characteristics of the environment. The graphical display resulting from the analysis shows the main patterns of association between animal activities and environment, and its numerical output allows one to identify the variables that have played a major role in the display. Taking into account these variables and their associated animal activities, the method allows one to define archetypal habitat models for each animal activity. Correspondence Analysis of animal activities by environmental variable matrices may give insights about animal's perception of the environment. The use of the method is illustrated by analyzing habitat preferences of free-ranging cattle during 2 different seasons on an estate in Spain. Results indicate the validity of the method as a first global analysis of the relative importance of environmental variables for the distribution of the animal activities in the landscape.

Key Words: habitat preferences, multivariate analysis, dehesa, cattle, Mediterranean grasslands.

The analytical approach adopted when investigating animal habitat preferences largely depends on the degree of previous knowledge of such preferences. If animal-habitat relationships are well known and the objective is to test specific hypotheses, numerical procedures such as Generalized Linear Modeling can be used (McNaughton 1985). Whereas if the aim is to generate hypotheses, the variables measured can be too numerous to allow an effective use of these techniques. In this case, it can be difficult to gain an overall view of the relationships between habitat factors and animal activities and distribution from numerous separate analyses (Ter Braak 1986, Montaña and Greig-Smith 1990). Alternatively, this can be achieved by using multivariate techniques. For instance, data on the frequency of a number of animal activities at a series of sites can be analyzed by techniques of multidimensional scaling (e.g. Principal Components Analysis, Canonical Correspondence Analysis).

Ordination analyses have been widely used on data in which the sampling sites are considered as analytical entities (they are treated as variables). However, in studies aimed at determining what factors are conditioning the use the animals make of their territory, specific sampling sites may not have been considered (Coppock et al. 1986). For example, if the sampling consisted of following nomadic ungulates and noting characteristics of their feeding behavior (foraging velocity, biting rate, bite size) and of the vegetation they feed on (composition, height, plant density, phenological status). Is it possible to use multivariate analyses in cases like this? In this paper we show that relationships between environment and animal behavior can be easily highlighted by using Correspondence Analysis without considering sampling sites as part of the data. The basic idea is to apply this analysis to contingency tables in which animal activities and environmental factors are incorporated as multistate qualitative variables. This method produces a general descriptive overview of the environmental factors associated with each type of behavior, and provides information about the importance of each factor in conditioning animal activities. Moreover, by taking into account the more relevant environmental variables and the activities to which they are associated, it allows one to easily define archetypal habitat models for different sets of animal activities. The method works equally well with ordinal and cardinal qualitative variables, so it may be used as a complement to analyses with a more limited capacity of dealing with qualitative data such as regression (Ben-Shahar and Skinner 1988).

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Materials and Methods

Study Area

We illustrate the use of the method by analyzing data on cattle behavior and habitat factors gathered on a private estate, in the Madrid province, Spain. This estate is part of the "Parque Natural de la Cuenca Alta del Rio Manzanares", a protected area which preserves a large remnant of one of the most characteristic and ecologically valuable agroecosystems of central and southwest Spain: the *dehesa*, an open savanna-like holm oak (*Quercus rotundifolia* Lam.) woodland. This agroecosystem is characterized by the combination of most of the components of the natural Mediterranean forest, including tree and shrub species and wild fauna, with livestock raising, pastures, forestry practices and some rotating crops (Joffre et al. 1988). A considerable amount of ecological research has been conducted on the estate, including analyses of the spatial and temporal dynamics of pasture community succession (Pineda et al. 1981a, 1981b; Casado et al. 1985, Gómez-Sal et al. 1986, Espigares and Peco 1993), studies on the temporal behavioral patterns of cattle (De Miguel et al. 1991) and on their role in the transfer of matter throughout the ecosystem (Gómez-Sal et al. 1992).

The estate covers 3,000 ha, and its elevation ranges from 610 to 720 m. The climate is Continental-Mediterranean with most of the annual rainfall of 600 mm occurring in winter. The yearly mean temperature is 13°C, with extremes of –7°C and 37°C for January (coldest month) and August (warmest month) respectively. The area has undulating topography covered by granitic sediments (Fig. 1). Many parts of the estate are ploughed periodically to eliminate thickets and encourage pasture growth. This leads to a diversified landscape in which different successional stages (from pastures to cleared and dense woodlands) occur in close proximity. The wooded vegetation consists of woodlands and scattered trees, mainly holm oak in the intermediate and more elevated zones. Scattered ash trees (*Fraxinus angustifolia* Vahl.) occur in lowlands. Pastures are dominated by therophytes, and scrub vegetation consists mainly of holm oak in shrub form, together with *Cistus ladanifer* L., *Santolina rosmarinifolia* L., *Thymus zigys* L., *Daphne gnidium* L. and *Phillyrea agustifolia* L. High temperatures and drought in summer, and intense cold in winter lead to a sharp decrease in pasture production during these seasons. Consequently, cattle are supplied with additional fodder at these times.

Sampling

About 400 free-ranging cattle graze on the estate. Starting in early May, the behavior of cattle was surveyed in 35 sampling days distributed through 1 and a half years. The observation days were distributed weekly, although during some winter and early summer periods they occurred once a fortnight. The sampling was interrupted during 2 months in the first summer when the cattle were moved to a nearby estate. On sample days, both the behavior of cattle and environmental factors were recorded at 10 min. intervals from sunrise to sunset. To avoid influencing their behavior, the animals were followed on foot and observed from hidden positions, at least 100 m away. Before the first observation, an animal was chosen at random to serve as a guide during the rest of the day. Every 10 min., the size of the herd surrounding this animal was noted, and an area of observation of cattle activities and environmental factors was defined. This area was within a radius of ≈ 50 m around the guide animal. A maximum of 10 animals were taken into account in each observation. This consisted of recording the number of animals involved in 10 basic activities (Hafez and Schein 1969, Low et al. 1981a, 1981b), namely grazing, browsing, fodder ingestion, standing rumination, lying rumination, standing resting, lying resting, traveling, occasional displacement, and other occasional activities (e.g. defecating, urinating, cleaning). In addition, in each area of observation the aerial percentage cover of all tree and shrub species was visually estimated. Wind intensity (4 subjective categories), air temperature 1.5 m above the ground in a shaded position, and general geomorphological and vegetational characteristics were also noted. For analytical purposes, quantitative variables were subdivided into a number of states (Table 1), which were determined by arbitrary evaluation of the width of the ecological gradients existing on the study area (Ben-Shahar and Skinner 1988). Data analyzed in this paper are based on a total of 2,662 observations of cattle behavior and environmental factors.

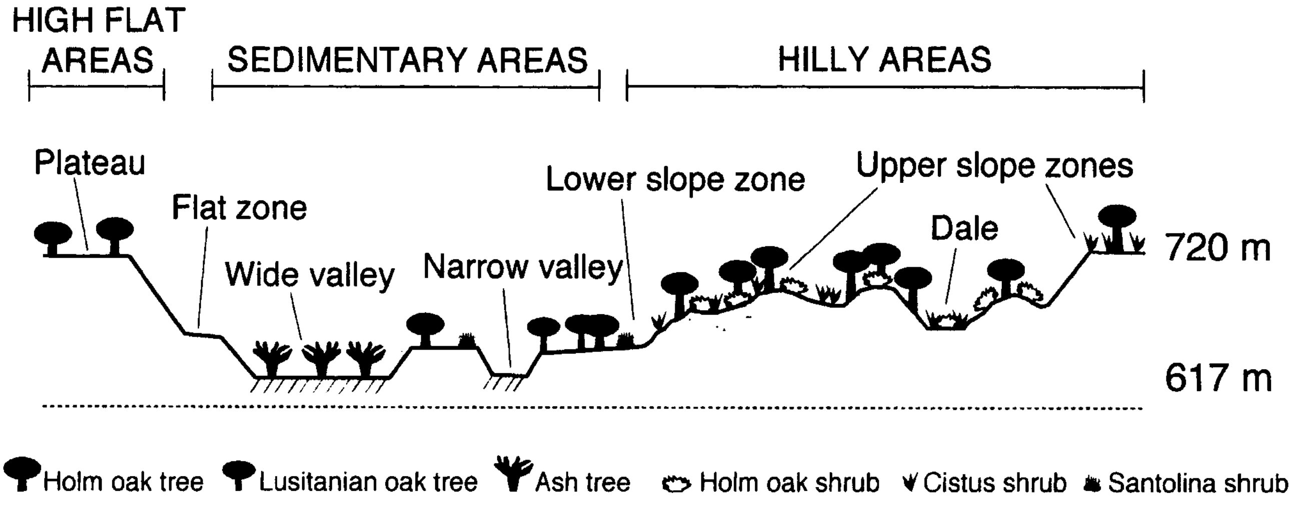

Fig. 1. Scheme of the range.

Data Analysis

Cattle behavior changed dramatically from season to season during the study (De Miguel et al. 1991). Accordingly, we analyzed the habitat preferences of cattle for groups of observation days which were typical for a season of the year. By using the taxonomic distance method (Engelman 1983), we classified the observation days according to the proportion of activity spent on the 10 basic types of behavior considered in the study. The dendrogram resulting from the analysis (not included) separated the days into 4 major groups (De Miguel 1989), namely spring, early summer, autumn-winter (hereafter called winter days), and an heterogeneous group including days with fodder supply. We illustrate the use of Correspondence Analysis for studying animal-habitat selection investigating the feeding behavior of the cattle in the winter and spring groups, each including 6 and 7 days, respectively. Within each day, the percentage of animals involved in each activity was calculated for each individual observation of cattle behavior. The calculation of percentage values involved all the activities sampled, although only 4 feeding activities, namely grazing, browsing, fodder ingestion and resting-ruminating, were considered for the ordination analyses.

Correspondence Analysis is a multivariate ordination technique commonly used in ecological studies, and several descriptions on its numerical properties are available in the literature (Greenacre 1984, Digby and Kempton 1987, Montaña and Greig-Smith 1990). This analysis displays rows and columns in a two-way contingency table as points in a multidimensional space. The contingency tables analyzed in the present study were created by expressing the states of the environmental variables (Table 1b) as the frequencies of occurrence of percentage classes of cattle feeding activities (Table 1a), with the rows being the states of the environmental variables and the columns, percentage classes of cattle activities. Specifically, each cell entry of each contingency table represented the number of times that a row and a column

Table 1. Variables used for Correspondence Analysis and their codes.

a) Behavioral variables

Parameter	% Categories	Codes	Parameter	% Categories	Codes
Grazing	0	G0	Fodder ingestion	0	F0
	1-10	G1		1-10	F1
	11-25	G2		11-25	F2
	26-50	G3		26-50	F3
	51-75	G4		51-75	F4
	76-100	G5		76-100	F5
Browsing	0	B0	Resting-ruminating	0	R0
	1-10	B1		1-10	R1
	11-25	B2		11-25	R2
	26-50	B3		26-50	R3
	51-75	B4		51-75	R4
	76-100	B5		76-100	R5

b) Environmental variables

Parameter	Categories	Codes	Parameter	Categories	Codes
Herd size	1-10	HD1	Temperature (°C)	-6-0	T1
(No. individuals)	11-25	HD2		1-5	T2
	26-75	HD3		6-10	T3
	76-200	HD4		11-15	T4
	>200	HD5		16-20	T5
Wind intensity	Negligible	WI0		21-25	T6
	Low	WI1		26-30	T7
	Medium	WI2		>30	T8
	Strong	WI3			
Holm oak tree (%)	1-20	TO1	Holm oak shrub (%)	1-20	SO1
	21-40	TO2		21-40	SO2
	41-60	TO3		41-60	SO3
Lusitanian oak (%)	1-20	TL1		61-80	SO4
	21-40	TL2	*Santolina* shrub (%)	1-20	SS1
Ash tree (%)	1-20	TA1		21-40	SS2
	21-40	TA2	*Cistus* shrub (%)	1-20	SC1
	41-60	TA3		21-40	SC2
				41-60	SC3
Geomorphology			Vegetation types		
Plateau		GM1	Grassland	VT1	
Upper zone with undulating relief		GM2	Open dehesa without scrub	VT2	
Upper zone of slope		GM3	Open dehesa with some scrub	VT3	
Middle zone of slope		GM4	Open dehesa with abundant scrub	VT4	
Flat zone in middle part of slope		GM5	Open woodland of Ash tree	VT5	
Flat zone in lower part of slope		GM6	Dense dehesa without scrub	VT6	
Lower zone of slope		GM7	Dense dehesa with scrub	VT7	
Dale without quaternary sediments		GM8	Dense woodland of Holm oak	VT8	
Narrow valley with sediments		GM9			
Wide valley with sediments		GM10			

were recorded together in a particular group of days. In the calculation process of the analysis, the points (i.e. rows and columns) are plotted in Euclidean space, and treated as vectors of relative frequencies or profiles. Thus, the positions of the points in the multivariate space do not depend on the total summation of their respective frequencies of occurrence, the so-called "masses" in the terminology of the Correspondence Analysis (Benzécri 1970). The points, however, are weighted differentially according to their respective masses for the definition of the ordination axes. Thus, although the directions of the principal multifactorial axes resulting from the analysis tend to reflect the directions of greatest dispersion of clouds of points, they are also conditioned by the masses assigned to the points (Greenacre and Vrba 1984). Two ordinations that can be jointly displayed result from the analysis, 1 for the columns (here percentage classes of animal activities) and 1 for the rows (states of environmental variables). The graphical output of the analysis reflects gradients of variation in the data. In general, the greater the distance between 2 behaviors along an axis, the greater the differences between the habitats on which they normally occur. The numerical output of the Correspondence Analysis provides information on the importance of the axes in explaining the total variability, as well as on the contribution of the axes to the inertia of the points in the multivariate space. The contribution values of the points to each axis are the basis for the interpretation of its ecological significance (Ben-Shahar and Skinner 1988). In our case, we considered relevant all the variables' states that exhibited absolute contribution greater than 2 at least for 1 axis (Greenacre 1984). In the case of cattle activities, we considered all their percentage classes in order to show trends in cattle habitat use.

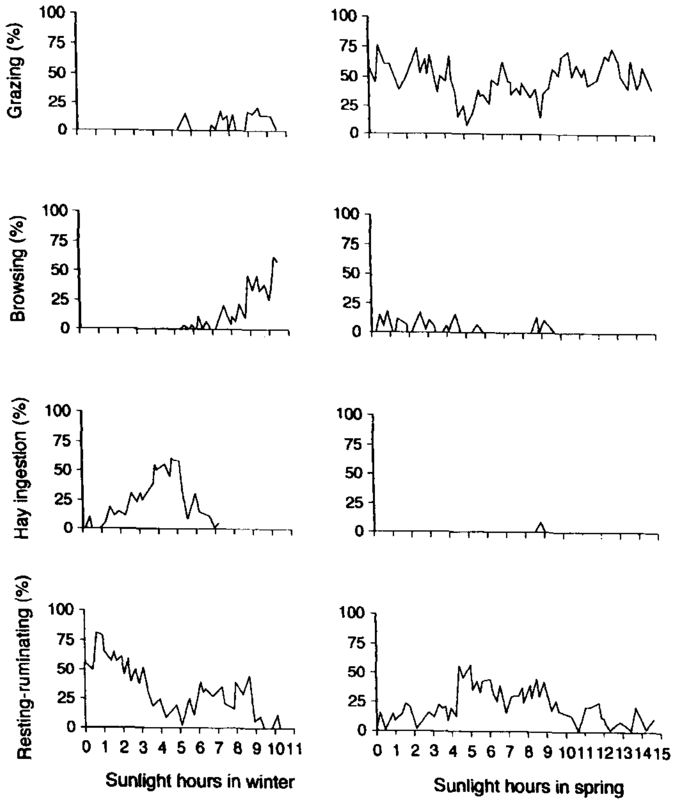

Fig. 2. Daily patterns of 4 cattle feeding activities in winter and spring seasons. For each group of days, curves were obtained by calculating the average percentage value of an activity at a particular time of the day. Calculations were performed using 10 min. intervals. Sunrise time is indicated by 0.

Results and Discussion

Interpreting the ordination results considered the daily patterns of variation in feeding activities of the cattle in winter and spring (Fig. 2). The ordination results were used to define archetypal habitats (Fig. 3b and 4b) for each feeding activity in each season. These archetypal habitats were built taking into account the variables' states adjacent to each behavioral category in each ordination plane.

Winter

The first 2 principal axes of the winter data ordination accounted for 38.4% + 18.3% = 56.7% of the total inertia. Axis 1 showed the main characteristics of cattle behavior in this season. It reflected a transition in terms of behavior and habitats occurred throughout the winter days, with the mornings being dominated by fodder ingestion and resting-ruminating, and the evenings by foraging activities. Thus, the negative end of axis 1 was characterized by various intensities of fodder ingestion and resting-ruminating, as well as by low intensity grazing (Fig. 3). Fodder ingestion and resting-ruminating were the most important activities in winter, as reflected by their percentages of daily occurrence (19% and 46%, respectively). The coincidence of various percentage classes of the fodder ingestion and resting-ruminating activities in the same part of the multivariate space (Fig. 3) indicates that they often occurred in the same sites though alternating in their intensities (see also Fig. 2). The manner in which fodder was distributed in the estate may account for these results. The fodder was delivered to the same place each morning for several days. Early in the morning, when the temperature was still very low (–6 to 5°C), the cattle began waiting for the fodder in this place, forming a large herd (ranging from 76 to >200 animals) as indicated by the negative end of axis 1. While waiting, the cattle remained resting and ruminating (Fig. 2), and eventually eating fodder from previous days, or grazing if there was pasture available. Once the fodder had been delivered, its ingestion became the most important activity for a period of 2 hours (Fig. 2). After this period, the animals remained in the same place resting and ruminating for 2–3 hours, and then began searching for additional food for the rest of the day (Fig. 2). The characteristics of the places in which fodder was supplied were reflected by negative end of axis 1 (Fig. 3). These were mainly open dehesa habitats without scrub, and open woodlands of ash tree, located on low plains and wide valleys, respectively.

The positive end of axis 1 was dominated by browsing and grazing activities (Fig. 3), which occupied only a small portion of the activity of the animals during day-time (9%). These activities occurred mainly in the evening (Fig. 2) and in small herds (1 to 25 individuals), though in different types of habitat as indicated by axis 2 of the ordination (Fig. 3). Further inspection of data showed that each winter evening was dominated by 1 of these 2 activities (i.e. they tended to be mutually exclusive in temporal terms). Browsing increased towards the positive end of axis 2. The lowest intensities of this activity were associated with habitats of open dehesa with abundant shrubs of the species *Cistus ladanifer* which is rarely consumed by cattle (personal observa-

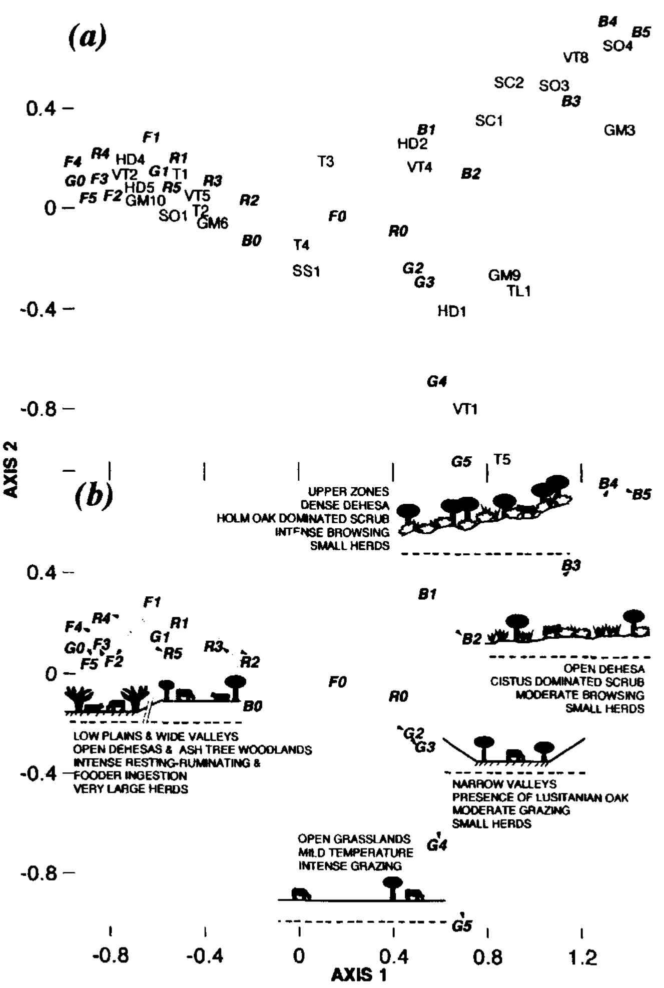

Fig. 3. Correspondence Analysis of the winter data (with scarce grass). Only environmental variables' states with relatively high absolute contribution to at least 1 axis (Table 2) are presented and were considered for interpretation. Codes are explained in Table 1. Geomorphological and vegetational representations are explained in Fig. 1. Figs. a and b are given separately to facilitate interpretation, but may be directly superimposed. a. Crude ordination result. Percentage classes of cattle feeding activities are in bold. b. The percentage classes corresponding to each cattle activity are connected by arrows, showing directional gradients (increase in values). Diagrams were drawn according to the positions of the states of the variables in the ordination result, and illustrate archetypal habitats for different types of cattle behavior.

tion). Intense browsing was related to more appropriate habitats for this activity. It took place on upper slope woodlands with abundant holm oak in shrub form, which is a highly suitable species for browsing. These results reflect the behavior displayed by cattle on winter evenings when traveling from the site in which fodder was supplied to brush areas (Gómez-Sal et al. 1992). During the course of these displacements the animals eventually spent some time browsing in open dehesa areas because it was necessary to pass through them to reach the upper slope woodlands. The low temperatures associated with the positive end of axis 2 of the ordination (Table 2) suggested that the concentration of animals in brush areas was linked to a searching for shelter against adverse weather.

In contrast to browsing, grazing increased towards the negative end of axis 2 (Fig. 3). Moderate grazing was associated with moderate temperatures and narrow valleys with presence of Lusitanian oak (*Quercus faginea* Lam.) trees which is indicative of deep fertile soils (De Miguel 1989). The pasture communities of such areas are typically dominated by perennial grass species (*Agrostis catellana* Boiss. & Reuter, and *Festuca ampla* Hackel) capable of maintaining relatively high productivity during winter. Intense grazing occurred in open grasslands and notably was associated with the mildest winter temperatures (T5: 16–20°C). In this way, the high absolute contribution of the variable T5 to axis 2 of the ordination (Table 2) indicates that temperature was an important factor in determining the kind of feeding activity exhibited by the cattle during winter.

Spring

Similar to the case of the winter data, the first 2 principal axes of the spring data ordination accounted for 38.7% + 18.4% = 57.1% of the total variance. Intense resting-ruminating activity, nonexistent to light grazing and herds of 26–200 animals occurred in the positive end of axis 1, where they were associated with relatively high temperatures, and open plateau grasslands on which wind speed is normally high. The cattle often rested and ruminated in these windy spots during the afternoon hours of the hottest spring days (Fig. 2) presumably to avoid being disturbed by biting flies (Senft et al. 1987) which are particularly active in this period of the day (Fig. 4). Another kind of habitat preferred by cattle to rest and ruminate is illustrated by the negative end of the axis 2. This part of the multivariate space was dominated by dense dehesa with some scrub, high percentage cover of holm and Lusitanian oak trees, and herds with more than 200 animals. These variables showed high absolute contribution to axis 2 (Table 3), and define a kind of habitat characterized by tree shadows in which the cattle can find shelter from the sun (Fig. 4). The high percentage cover of Lusitanian oak trees suggest that these were cool areas, suitable to rest and ruminate when temperature is high. The overall percentage of daily time devoted to resting and ruminating in spring was 25%.

Grazing and browsing increased towards the negative end of axis 2 (Fig. 4), indicating that these activities tend to occur in similar habitats in spring. Contrasting with what happened in winter, when the cattle spent only one tenth of the day foraging, the percentages of daily occurrence of grazing and browsing in spring were 50% and 1%, respectively. The fodder given to the cattle in winter may account for these differences. On the other hand, the large proportion of time devoted to grazing in spring suggests that browsing consisted of occasional events during grazing bouts (Fig. 3). The high availability of pasture in spring may explain these results, since it is likely that grazing alone could fulfill the food requirements of the animals in this season. According to the graphic display of the ordination (Fig. 4), intense grazing and occasional intense browsing events, were associated with dales and lower zones of slopes occupied by open dehesa woodlands with some scrub. In addition, the ordination also shows that moderate grazing and light browsing and resting-ruminating took place in open dehesa habitats at the upper zone of slopes. The concentration of grazing activity in lowlands may be explained by the potentially large herbage production of these areas, which is a consequence of the high water and nutrient availability of soils (Casado et al. 1985). In contrast with resting-ruminating, intense grazing activity occurred mainly in dispersed small herds, as indicated by the proximity of the variable HD1 (herd of 1–10 animals) to the percentage class of the grazing activity G5 in the multivariate space (Fig. 4).

Factors Influencing Cattle Feeding Behavior

The data indicate that food availability was of prime importance in determining activity patterns and habitat preferences of the cattle. For instance, this was reflected by the daily distribution of animal activities in winter which seemed to be strongly determined by the manner in which the fodder was supplied in the estate. Thus, whereas the occurrence of resting and ruminating was markedly associated with the places and time in which fodder was provided, grazing and browsing were virtually relegated to the evening time (Pratt et al. 1986, Putman et al. 1987). Moreover, when browsing dominated winter evenings, it occurred in areas exhibiting an abundance of the most favored shrub species of the cattle in the estate (holm oak in shrub form). Similarly, in spring, when herbage was available all over the estate, intense grazing was clearly associated with fertile lowlands having high production. At this time browsing visiting browsing areas was negligible. Accordingly, the feeding behavior of the cattle seems to conform with the behavior of optimal predators which tend to specialize on the most profitable prey (in this case vegetation type), even when food is abundant in the home range (Duncan 1983, Crawley 1983, Senft et al. 1987).

Pratt et al. (1986) also found that food was of prime importance in determining the habitat preferences and activity patterns of both cattle and ponies in the New Forest, England. However, they found that shelter was an important consideration at all times during winter, since in this season the animals restricted their foraging to communities providing cover. Similarly, Duncan (1983) reported that the behavior of a herd of horses in a Mediterranean wetland in France was primarily determined by food abundance, whereas weather and biting insects had some effects on horses' distribution, particularly for non-feeding activities. Environmental factors other than food also strongly condition the behavior of the study cattle. In spring, increased temperatures and/or activity of biting insects during midday were associated with an intensification of resting and ruminating activities, either in dense woodlands of holm and Lusitanian oaks or in windy places. Similarly, during winter evenings, weather conditions seemed to be particularly important in determining whether cattle grazed in exposed open areas or in grasslands of narrow valleys, or browsed in sheltered woodlands. These areas were associated with relatively low, moderate and high temperatures, respectively.

Our results suggest a consistent relationship between herd size and animal activity in the 2 seasons. Moderate and intense grazing and browsing activities were associated with herds of small size (from 1 to 25 individuals), while moderate and intense resting-ruminating activity was associated with large groups. This was the case even in spring when cattle behavior was not conditioned by fodder supply. These variations in the herd behavior could be associated with the distribution of the areas most appropriate for feeding or resting-ruminating. For example, if preferred feeding areas were numerous and too small to be exploited by large groups of animals, or only a few areas were suitable for resting-ruminating. The first possibility seems to be quite likely, bearing in mind that the spatial variation of vegetation types in the estate is large, and that the animals were apparently highly selective in terms of the areas they preferred for feeding. Under such circumstances, the distribution of the animals in small foraging herds may increase their efficiency in using available food resources, particularly when those resources are scarce. For example, foraging in small groups may reduce competition for food, and the likelihood of over-exploiting the best food-providing places or "wasting" the food available in other smaller areas (Crawley 1983, Pullian and Caraco 1984). Due to the high heterogeneity of the estate in terms of geomorphology and vegetation structure the second possibility seems to be less likely. A third alternative would be that cattle are highly social animals, with strong social cohesiveness and herding behavior (Pratt et al. 1986, Begon et al. 1990).

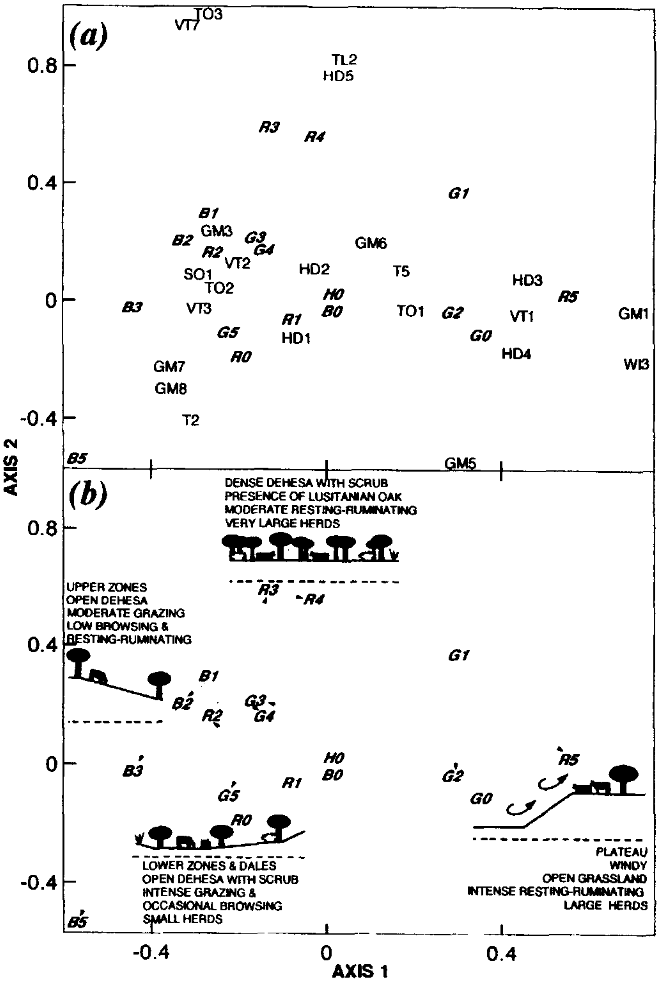

Fig. 4. Correspondence Analysis of the spring data (with pasture widely available). Conventions as in Fig. 3.

Correspondence Analysis of Animal Activities by Environmental Variable Matrices

Community ecology provides some examples in which Correspondence Analysis has been applied on contingency tables of species (either plants or animals) by states of environmental variables (Greenacre and Vrba 1984, Ben-Shahar and Skinner 1988, Rodríguez et al. 1995). Montaña and Greig-Smith (1990) compared this approach with the more classical one of considering sites as analytical entities for the analysis. This comparison was based on an artificial data set in which relationships among several hypothetical response and explanatory variables (which could represent hypothetical animal activities and environmental factors, respectively) at a series of sites were established by the authors. Correspondence Analysis of the matrix of response variables by states of explanatory variables only needed 2 axes to adequately reflect all the original relationships between the variables. Conversely, Correspondence Analysis applied to the matrix of response variables by sites needed 6 axes for the same purpose. (Note that in this latter case the relationships between response and explanatory variables were not derived from calculations of the analysis, but they were established a posteriori, taking into account the correlations of the sites' scores with the explanatory variables). This result is not surprising, since conceptually the 2 analyses had different goals: the first 1 looked for relationships between response and explanatory variables, whereas the second 1 searched primarily for trends of variation of the response variables at the sites. Nevertheless, the result is useful since it demonstrates the greater validity of the first approach when the objective is to identify relationships between animal activities and environmental factors.

In this paper, Correspondence Analysis has been applied over true contingency matrices created by expressing the states of environmental variables as frequencies of occurrence of different categories of animal activity. This means that the variable states and categories of cattle behavior with potentially greater weight in the analysis have been those exhibiting higher total frequencies of occurrence (i.e. those with greater mass value). In theory, the approximation followed here would attempt to detect those habitat characteristics which are most associated with the principal animal activities in the area under study. If, on the contrary, one wished to by-pass the particular characteristics of the study area and to obtain more general results, the weight of the rare variables could be increased in the analysis by some form of data standardization, for example assigning equal masses to all the variable states (Greenacre and Vrba 1984). In practice, such transformations are usually unnecessary (Digby and Kempton 1987), particularly when the analysis is applied over true contingency tables (Greenacre 1984). This is because Correspondence Analysis provides an intrinsic scaling of the data by row and columns averages (Digby and Kempton 1987), which results in rarer variables actually having greater weight in the analysis than if only their total frequencies of occurrence were taken into account (Hill 1973, Digby and Kempton 1987). An example of this is provided by the categories of cattle activity high grazing and no browsing (i.e. G5 and B0) in the winter ordination. Compared with the other behavioral categories, no browsing exhibited the highest mass in winter, whereas high grazing had only an intermediate value (masses = 0.212 and 0.024, respectively) (Table 2). In spite of this, both no browsing and high grazing had similar absolute contribution to the axis 1 of the ordination (absolute contribution = 6.02 and 6.51). Furthermore, whereas no browsing had only an intermediate absolute contribution to axis 2, high grazing exhibited the highest absolute contribution to this axis (absolute contribution = 5.13 and 46.42).

According to Greenacre and Vrba (1984), there are no generally accepted rules to enable an appropriate choice to be made in relation to the reweighting of the variables. However, these authors recommend that, whatever the decision, the worker should always calculate and carefully examine the unweighted masses of the variables, especially when interpretation proceeds

Table 2. Composition of the 2 principal axes of the Correspondence Analysis performed over the winter data. Name, name of the variable; Mass, mass of the variable (see Methods); Acon, absolute contribution of the axis to the inertia of the elements. Only environmental variable states with absolute contribution > 2 to at least 1 axis are presented. Variable codes defined in Table 1.

In terms of states of environmental variables				In terms of percentage classes of cattle activities			
Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶	Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶
VT1	14	331	1535	G0	206	150	744
VT2	22	395	46	G1	5	4	5
VT4	14	206	73	G2	5	74	38
VT5	22	204	1	G3	5	94	64
VT8	12	943	829	G4	4	78	349
TL1	8	361	111	G5	24	651	4642
SO1	39	320	3	B0	212	602	513
SO3	13	811	589	B1	1	14	14
SO4	3	215	212	B2	2	69	8
SS1	17	0	204	B3	6	371	223
SC1	8	281	210	B5	10	860	1054
SC2	16	677	740	B6	19	2180	1890
GM3	305	428	76	F0	191	480	20
GM6	50	201	92	F1	1	8	8
GM9	2	65	510	F2	2	46	3
GM10	17	200	9	F3	11	252	11
T1	13	201	14	F4	11	420	54
T2	24	203	10	F5	34	838	13
T3	77	3	228	R0	124	1378	186
T4	23	0	200	R1	16	174	125
T5	8	278	1596	R2	9	7	0
HD1	40	779	1213	R3	11	50	24
HD2	225	367	342	R4	3	76	12
HD4	11	251	29	R5	88	1124	80
HD5	58	1006	89				

† Multiplied by 1,000.
¶ Multiplied by 100.

Table 3. Composition of the 2 principal axes of the Correspondence Analysis performed over the spring data. Conventions as in Table 2. Variable codes defined in Table 1.

In terms of states of environmental variables				In terms of percentage classes of cattle activities			
Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶	Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶
VT1	53	1784	69	G0	70	2015	411
VT2	31	381	197	G1	5	100	389
VT3	26	424	2	G2	12	213	1
VT7	1	20	1164	G3	42	244	942
TO1	77	639	24	G4	38	162	615
TO2	47	634	46	G5	83	873	610
TO3	1	20	1164	B0	235	28	0
TL2	3	0	989	B1	2	30	93
SO1	28	449	109	B2	6	94	137
GM1	12	1438	5	B3	4	162	0
GM3	11	152	302	B5	3	200	439
GM5	2	29	218	F0	249	0	0
GM6	36	68	638	R0	136	1256	1384
GM7	9	223	212	R1	5	6	10
GM8	10	244	438	R2	18	226	274
WI3	6	690	123	R3	22	78	3955
T2	5	99	428	R4	5	1	735
T5	59	417	383	R5	64	4318	6
HD1	77	75	557				
HD2	54	12	311				
HD3	15	699	54				
HD4	5	232	82				
HD5	3	0	989				

† Multiplied by 1,000.
¶ Multiplied by 100.

to the less stable features of the data. By doing this, the author can always avoid giving too much attention to weak trends.

Applications of the Technique

Correspondence Analysis of animal activities by environmental variable matrices is a versatile method in numerical terms. It provides a non parametric description of the relationships between the variables under study, which can be either quantitative and qualitative (Table 1). Thus, the method can be used as a complement to analyses with a limited capacity of dealing with qualitative data such as regression (Ben-Shahar and Skinner 1988). In addition, whereas regression analyses are used to explain 1 response variable using several explanatory variables, Correspondence Analysis may analyze large numbers of both kinds of variables simultaneously. Hence, it can be useful for preliminary investigations of behavioral problems that can be conceptualized as multivariate. For example, it could be used to analyze plant species preferences of ungulates using chemical and morphological properties of the forage. (Note that whereas qualitative variables like plant species identity do not require any modification, quantitative variables such us forage fibber content or biting rate must be subdivided into categories before analysis).

The method may also provide clues about animals' perception of the environment. Most studies on animal behavior-environment relationships consist of identifying subunits within a study area (plant communities, habitat types, landscapes) and searching for differences between them in terms of animal behavior. The ideal way of defining such subunits is to use criteria that match animals' perception of the characteristics under study (Senft et al. 1987). However, since this is unknown, the environmental subunits are usually defined arbitrarily. Correspondence Analysis of animal activities by environmental variable matrices allows a different approach. With this technique there is still subjectivity in the selection of the variables to be considered in the study. However, due to the way that Correspondence Analysis operates, the importance that each environmental variable has in the result largely depends on its degree of association with animal behavior. Therefore, the definition of habitat types can be made taking into account relevant environmental variables (i.e. those with high loadings in the analysis) and the animal activities to which they appear associated in the graphical display. These habitat types would be archetypal models, since they were constructed using characteristics of the preferred places to perform each animal activity. From an applied stand point, these model habitats could be used as reference to both subdividing the study territory onto environmental units, and/or modifying existing habitats to meet the animals' requirements. For example, shrub removal practices are common in the dehesa grazing systems (Joffre et al. 1988) and are probably necessary in order to maintain economically viable levels of pasture production (Huntsinger and Bartolome 1992). However, our results suggest that it can be damaging for cattle to excessively diminish the shrub areas (Gómez-Sal 1992). In particular, since they were preferred over the open grasslands during the coldest winter evenings, probably because they offer both plants for browsing and shelter against low temperatures.

To conclude, Correspondence Analysis allows the determination of characteristics of the habitats in which each type of animal activity is usually performed. This method is appropriate for searching for broad relations between animal behavior and a number of aspects of the environment. Thus, it can be a useful tool for hypothesis generation about the habitat characteristics which may be important for a causal explanation of spatial variation of the animals' behavior.

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The economic impacts of increased grazing fees on Gila National Forest grazing permittees

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Abstract

The purpose of this research was to estimate the impacts of increased federal grazing fees on current holders of grazing permits on the Gila National Forest (GNF) in western New Mexico. A multi-period linear programming (LP) model was developed using 1992 national forest ranch budgets as baseline data. Discounted net returns (returns over variable costs) were maximized over a 60-year planning horizon under current fee regulations, and with alternative fees computed for various recent legislative and administrative grazing fee proposals. Small, medium, and large ranches were considered in the impact assessment. In addition to livestock income and expenses, off-ranch income, family living expenses, and debt obligations were directly considered in the analysis.

An estimated 7% of the current Gila National Forest grazing permit holders—those medium and large ranches with high debt—would be expected to go out of business even if the current grazing fee were continued. At a federal grazing fee of $3.96/AUM as proposed by Rangeland Reform '94, an additional 20% of GNF permittees would be expected to go out of business. These would be the small high-debt ranches and large ranches with intermediate levels of debt. A grazing fee of $8.70/AUM would be expected to cause all current GNF ranchers with debt to go out of business.

Average annual USFS grazing use by existing permit holders was estimated to decrease by about 120,000 AUMs when the grazing fee was increased to $3.96/AUM, but grazing fee receipts would increase by 31% with the higher fee, assuming no new permit holders or consolidations occurred. The largest grazing fee receipts were generated at the $3.96/AUM fee.

Key Words: public land policy, grazing fees, Rangeland Reform '94, linear programming.

Grazing fees and the use of public rangelands is a continuing controversy. A 1994 proposal called Rangeland Reform '94 created a forum for continued debate about the grazing use of western public rangelands. Under the Bureau of Land Management (BLM) and U.S. Forest Service (USFS) preferred management alternative, as outlined in Rangeland Reform '94 (USDI/USDA 1994a, pp. 2-8—2-18), public land grazing fees would double, grazing advisory boards would be replaced with multiple resource advisory boards, new range conservation standards would be imposed, rules and regulations would be enforced more strongly, subleasing of federal land would be penalized, and ownership of new range improvements would be vested to the federal government.

These reform proposals have been perceived to greatly alter the administration and use of western public lands. Most public land ranchers see implementation of Rangeland Reform '94 as the end of their livelihood and way of life. This has created renewed interest in state and/or private ownership of the public domain and elicited thousands of comments both for and against the reform proposal.

As a result of the debate and controversy about public land management, federal land agencies backed away from implementing new land use regulations and did not increase the grazing fee. Congressional legislation was introduced to address many of the proposals included in Rangeland Reform '94 but they also have not been adopted. The controversy continues and it is possible, if not anticipated, that some of the proposals, including a higher grazing fee, will eventually be implemented.

Rangeland Reform '94 has not been the only recent attempt to increase public land grazing fees; rather, it has been an annual event since grazing fee studies were completed in 1986 (USDA/USDI 1986). Various grazing fee formulas have been proposed, ranging from continuing the current Public Rangeland Improvement Act (PRIA) fee ($1.98/AUM in 1994) to the $8.70/AUM fee proposed by Congressmen Synar, Darden, and Atkins (Synar et al. 1991).

It is widely believed that small ranch operations would be impacted most by higher grazing fees and altered land use policies; special breaks have been proposed for small part-time ranchers using public lands (Nadler 1995). Cost and return estimates for small ranch operations continually show negative returns to ranch investment (when opportunity costs are included), and the perception is that these ranches are vulnerable to higher fees and more costly land use policies. Yet, when nonfarm income is considered it is not clear who would be most affected by altered land use policies. Operators of small ranches or other family members generally work off the ranch, and a major part of disposable family income comes from non-farm sources. Other factors including debt level and level of public land dependency would be expected to be equally important when evaluating ranch specific impacts of altered public land use policies.

Numerous studies were conducted which estimated the potential impacts of BLM policy changes proposed in Environmental Impact Statements (EISs) written in the 1970's and 1980's (Gee 1981, Olson and Jackson 1975, Peryam and Olson 1975, Torell et

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al. 1981, Wilson et al. 1985). These earlier studies generally found that the potential impact of increased grazing fees and altered land use policies depended largely on the level of federal land dependency and the equity position of the ranch owner. Changing the allowed season of use or stocking rate was found to have a much larger impact on net ranch returns and optimal production strategies than doubling the grazing fee (Torell et al. 1981).

Several recent studies have estimated the impact of higher grazing fees proposed under Rangeland Reform `94. Using a simulation model for ranches in Montana, Wyoming, Colorado, and New Mexico, Richardson et al. (1993) estimated the $4.28/AUM fee initially proposed by BLM and USFS in Rangeland Reform `94 (USDI/USDA 1993) would not force ranchers out of business over the next 6 years, though it would reduce income and net worth. Similarly, the BLM and USFS concluded in the Draft EIS for Rangeland Reform `94 that initiating the BLM/USFS proposed action alternative would be similar to continuing current management over the long term. Continued growth in employment and income in other sectors was projected to compensate for the relatively small employment and income reductions caused by decreases in reduced federal forage use (USDA/USDI 1994b, p. 33). The income loss was estimated to vary in direct proportion to the level of dependency on federal rangeland. This strong relationship between lost income and level of dependency was also evident in a budgeting assessment of Rangeland Reform '94 impacts to New Mexico ranchers (Torell et al. 1994).

The objective of this research was to estimate the ranch-level impacts of grazing fee increases proposed in Rangeland Reform `94 and in earlier fee legislation. These alternative fee proposals plus the current PRIA fee formula cover the range in value over which future grazing fees will most likely be established.

The impacts to ranchers currently using the Gila National Forest (GNF) in western New Mexico are considered. Ranchers in this area depend heavily on public land forage. USFS allotments are grazed yearlong and GNF ranchers depend on public land grazing for almost all yearlong grazing capacity.

Methods, Procedures, and Model Development

A multi-period linear programming (LP) model was developed that optimizes the net present value (NPV) of returns over variable costs for small, medium, and large ranches using the Gila National Forest (GNF). Ranch budgets prepared by Torell et al. (1993a,b,c) were used to define typical production rates, production practices, costs, and returns for cow/calf ranches using the GNF during the 1992 production year. Gross livestock receipts, return over variable costs, and the residual return to ranch investment were used as measures of ranch profitability under each grazing fee scenario. Optimal AUM use for the GNF was estimated under each fee rate, along with grazing fee receipts from current permit holders.

The Multi-Period Linear Programming Model

Linear programming is a mathematical procedure that maximizes or minimizes a linear objective function subject to a set of linear constraints that define resource use and limits. Ranch management applications typically define a linear profit function, and this function is maximized subject to linear constraints that define seasonal resource limits, forage use rates, production relationships and transfer rates between various production and sale activities.

Past studies using linear programming (LP) to evaluate altered land use policies have considered a single-year model; the objective of the model was to maximize returns over a single production period (e.g., Gee 1981, Olson and Jackson 1975, Peryam and Olson 1975, Torell et al. 1981, Wilson et al. 1985).

A limitation of the single-period LP model is that inter-year variation and dependence of variables like cash flows, debt repayment capacity, herd size, and forage production, among others, are not explicitly recognized or considered. In addition, average prices and costs are usually defined for a typical or average production year (Gee 1981, Torell et al. 1981, Wilson et al. 1985), but this averaging procedure may suggest production strategies that would not be optimal when inter-year linkages and dependencies are considered.

The LP model developed for this study is a multi-period profit-maximizing model that removes many of these limitations. Livestock production is considered to take place over T years. Similar to the single-period model formulation, there are alternative production and marketing activities that could potentially be used each year, but some of these activities now include the transfer of resources (e.g., cows, operating capital) between years. Production during any given year is limited by available resources that year and the transfer of resources from previous years.

The problem is to maximize the NPV of economic returns from livestock production over the T-year planning horizon. Mathematically, the problem can be stated as

$$\text{Maximize } Z = C_1X_1 + C_2X_2(1+r)^{-1} + \ldots + C_TX_T(1+r)^{1-T} \qquad (1)$$

subject to the restrictions:

$$\begin{array}{lll}
A_{11}X_1 & \{\le = \ge\}B_1 & (2) \\
A_{21}X_1 + A_{22}X_2 & \{\le = \ge\}B_2 & \\
\vdots \qquad \ddots & \vdots & \\
A_{k1}X_1 + A_{k2}X_2 + \ldots + A_{kk}X_k & \{\le = \ge\}B_k & \\
\qquad A_{(k+1)2}X_2 + A_{(k+1)3}X_3 + \ldots + A_{(k+1)(k+1)}X_{k+1} & \{\le = \ge\}B_{k+1} & \\
\qquad \ddots \qquad \ddots \qquad \vdots & & \\
A_{T(T-k)}X_{T-k} + \ldots + A_{TT}X_T & \{\le = \ge\}B_T &
\end{array}$$

With this multi-period formulation, the production activities and restrictions of the LP model are partitioned by year. Each X_t defines the production activities for year t. Similarly, C_t defines the per-unit prices and costs defined for year t, but this matrix is now multiplied by the discount factor given by $(1+r)^{1-t}$, where r is the discount rate used to discount future returns.

The diagonal matrices of the constraint set, as given by A_{tt}, define the within-year input-output coefficients, while those below and to the left of the diagonal refer to between-year coefficients. The between-year coefficients provide for the transfer of resources between years, and $A_{t(t-1)}$ will include most of these transfers. An example is the transfer of brood cows and cash balances from year t-1 to year t.

Other production activities may interact with activities in the more distant past and matrices $A_{t(t-2)}, A_{t(t-3)}, \ldots, A_{t(t-k)}$ are included to capture these interactions. An example would be intermediate borrowing with an anticipated payback (cash requirement) over the next k years.

The major activities in the model included forage harvesting, the raising and sale of livestock, and borrowing and repayment of debt. The major resource restrictions of the model included available forage and cash. In addition, equations were included to transfer forage, establish typical ratios between classes of livestock, transfer livestock raised to sale activities, and transfer brood stock and cash balances between years.

Three types of forage (USFS, state trust land, and deeded land) could potentially be harvested each year. Profit-maximizing resource use was considered with no minimum-use restrictions imposed. Forage requirements for various animal classes were defined using standard animal unit (AU) equivalency factors.

Equations defining animal class ratios included calf crop, minimum cow replacement rates, maximum number of cows to be replaced with raised heifer calves, and the number of horses. Animal classes that could be sold included cull animals, brood cows, weaned calves, and raised yearlings. Yearlings were transferred between the raise activity at t-1 and the sell activity at t. This is the first linkage between years.

A cow transfer equation was included as an accounting restriction. This equation limited the source of brood cows during year t to include those raised during period t-1 (less a death loss), replacements raised in period t-1 or cows purchased at time t. Three production options were available for cows transferred: they could be raised again at time t, they could be sold, or they could be culled, which reduced the number of cows available for further transfer. An initial endowment of brood cows was included during year 1 as defined in the representative Gila National Forest (GNF) ranch budgets. Optimal herd size during other years was determined within the model. Because each animal class raised at time t is expressed as a ratio to the number of brood cows, the cow transfer equation limits the production of all livestock classes.

Livestock sales revenue at time t can be used to meet production expenses at time t, to repay short- and intermediate-term debt obligations, or used to purchase brood animals. In addition, a residual amount must remain to provide for payment of family living expenses, fixed costs, and long-term debt obligations. Off-ranch income is included as an additional source of income.

If funds are limiting, and if profit maximizing, borrowing can be with either an intermediate or short-term payback. The equation structure allows short-term borrowing to purchase intermediate assets (brood stock) but not the use of intermediate borrowing to cover short-term expenses. Equations are included that force everything borrowed to be repaid.

Intermediate-term borrowing is repaid over 5 years, with cash balances reduced over this repayment period by the amount of the amortized principal and interest payment. Intermediate-term borrowing is not allowed in the last 5 years of the planning horizon to assure all debts are repaid. Further, additional long-term borrowing is not considered. The model assumes a long-term debt obligation is already in place and restrictions require the repayment of this loan over a 30-year period.

A borrowing limit was included to restrict the amount that could be borrowed at time t. For the initial runs with current grazing fees, this limit was set at 70% of the asset value defined for each representative ranch budget. It was assumed that increased grazing fees would eliminate the market value of grazing permits, thus, for those runs considering increased fees, the estimated market value of grazing permits was subtracted from the asset value.

The multi-period linear programming (LP) model maximizes discounted net returns over 60 years (T=60). For practical purposes this is equivalent to maximizing returns over an infinite planning horizon, because at a positive discount rate the NPV of returns beyond this point are nearly zero.

Fixed costs, family living expenses, and debt obligations were subtracted from the model objective function (optimal return over variable costs) to compute residual returns to owned ranch capital. Net present value was determined using a 7% discount rate. All costs and prices were assumed to remain constant at 1992 levels in real terms. The 7% discount rate reflects a 3-4% real rate of return plus a risk premium.

Table 1 defines the production and marketing activities included in the LP model, along with the objective function coefficient used for each activity. Table 2 further defines livestock prices that varied by year. A more complete description of the LP model is provided by Drummond (1993), including definition of the LP matrix tableau, specific equations and activities, a detailed summary of optimal solution values, and the computer code for the GAMS (General Algebraic Modeling System) programming model (Brooke et al. 1992) used in the analysis.

Defining the LP model for the Gila National Forest

General Model Parameters

Production parameters and the resource base for each ranch size are shown in Table 3 and a summary of costs and returns for the 1992 production year is given in Table 4. This summary includes each of the ranch sizes and 3 different initial debt loads assumed in the analysis. Income consisted of gross livestock sales and outside or off-ranch income, which was defined from New Mexico data compiled from a 1991 Western Livestock Producers Alliance funded survey (Fowler et al. 1994). This survey, conducted in 14 western states, compiled information about rancher revenue and expenditures in rural communities. It was found that small- and medium-size ranches generally have at least 1 person or full time equivalent (FTE) working off the ranch to supplement ranch income. Large-size ranches have an average of 0.75 FTE working off the ranch. It was then assumed that small and medium size ranches had 1.0 FTE in off-ranch income, and the large ranch had 0.75 FTE. An average wage rate of $9/hour for 2,000 hours per FTE was used to compute off-ranch income (New Mexico Economic Development Dept. 1992). The total assumed salary is similar to the $23,000 average off-ranch income reported by participants of a 1990 New Mexico finance survey (NMDA 1990).

Off-ranch income is crucial to the analysis. As shown in Table 4, if off-ranch income were not available for the 1992 production year, only the medium and large ranches with no debt would have positive net income after production expenses and debt obligations were considered. Only the medium and large representative ranches with little if any debt could remain in business without outside income.

Overhead expenses were divided into 3 categories: a family living allowance, fixed ranch expenses, and capital improvement. The family living allowance included items such as groceries, clothing, medical expenses, recreation, and others, as defined for New Mexico by the Western Livestock Producers Alliance cost survey. Fixed ranch expenses include telephone, electricity, heating, insurance, and property taxes, as defined by NMSU ranch budgets (Torell et al. 1993a,b,c). Capital improvement is a depreciation allowance for replacement of range improvements, equipment, and machinery. The level of herd replacement is optimally defined within the linear programming (LP) model and replacement heifers are either bought or saved from the herd for replacement and expansion.

Table 1. Costs, prices and activities used in the LP model.

		Cost (price) per unit		
Activity Description	Units	Small ($)	Medium ($)	Large ($)
Use of 1 acre of deeded land grazing during year t	Acre	0	0	0
Use of 1 acre of state land grazing during year t	Acre	-0.62	-0.62	-0.62
Use of 1 AUM of USFS grazing during year t	AUM	Variable with alternative fee evaluations		
Raise one brood cow at time t	Head	-112[1,2]	-116[1,2]	-137[1,2]
Raise replacement cow at time t	Head	-112[1]	-116[1]	-136[1]
Buy brood cow at time t	Head	Variable (see Table 2)		
Raise one bull at time t	Head	Cost included when raising brood cow		
Raise one horse at time t	Head	Cost included when raising brood cow		
Raise one steer calf at time t	Head	Cost included when raising brood cow		
Raise one steer calf at time t	Head	Cost included when raising brood cow		
Raise one steer yearling at time t	Head	-127	-124	-109
Raise one heifer yearling at time t	Head	-127	-124	-109
Sell one brood cow at time t	Head	Variable (see Table 2)		
Sell one cull cow at time t	Head	Variable (see Table 2)		
Sell one cull bull at time t	Head	Variable (see Table 2)		
Sell one steer calf at time t	Head	Variable (see Table 2)		
Sell one heifer calf at time t	Head	Variable (see Table 2)		
Sell one steer yearling at time t	Head	Variable (see Table 2)		
Sell one heifer yearling at time t	Head	Variable (see Table 2)		
Transfer returns from livestock sales in year t to year t+1	$	0	0	0
Transfers return from livestock sales in year t to purchase brood cows and replace capital assets	$	0	0	0
Borrow money to meet short-term cash uses in year t	$	0	0	0
Borrow money to purchase brood cow and replace capital assets	$	0	0	0
Repay at time t one dollar of short-term loan made one year prior	$	-0.12	-0.12	-0.12
Repay at time t one dollar of intermediate-term loan made k years prior	$	Variable[3]		

[1] Excludes grazing fees.

[2] Calculated using total variable cost from the appropriate 1992 NMSU ranch budgets minus grazing fees and divided by mature cows and replacements. The cost per cow will not be the same per cow cost reported by Torell et al. (1993 a,b,c) because the published budgets do not average costs over replacement heifers.

[3] The interest paid at time t on each dollar of intermediate loan made k years prior was calculated as the loan payment less the principal payment due on the loan.

No debt, a 20% debt/asset ratio and a 40% debt/asset ratio were defined to typify the range of debt obligations found on New Mexico ranches, using a 1990 New Mexico Department of Agriculture finance survey (NMDA 1990). This survey found that during 1990, 36% of New Mexico livestock producers reported no debt. Similarly, 52% reported debt/asset ratios between 0 and 39%, and 12% had a debt/asset ratio over 40%. To capture the economic profile of the highest debt group, the debt/asset ratio used in the analysis should have been more than 40%. However, initial budgeting and model analysis indicated negative returns and an infeasible solution for the LP model at debt levels at or above 40%. Net income was negative for the high debt group during 1992, even at the assumed 40% debt/asset ratio (Table 4). These individuals must either have above-average management and production, have off-ranch income or accumulated wealth greater than what was assumed in the modeling analysis, or produce at a lower cost than defined to be representative for Gila National Forest (GNF) ranches.

Prices received for livestock varied each year and were obtained from data compiled for the Clovis, New Mexico livestock auction as an average annual price. Beef prices for 1979 through 1992 were indexed to 1992 levels using the input cost index (ICI), an index constructed to track the cost of raising livestock on western public land ranches (USDA/USDI 1986). The 14-year beef price cycle shown in Table 2 was repeated systematically to define beef prices for the 60-year linear programming (LP) analysis. Production costs were not indexed because they have not been cyclic but rather exhibit a gradual annual increase similar to the rate of inflation.

Base Runs at the Current PRIA Grazing Fee

Base runs of the linear programming (LP) model were made using the $1.92/AUM grazing fee generated from the PRIA fee formula for the 1992 production year. This fee was used for each of the 60 years in the LP analysis. In reality, the PRIA fee formula is indexed to the Beef Cattle Price Index, Prices Paid Index, and Forage Value Index which results in a different fee each year.[1] The procedure used assumes the PRIA fee formula would maintain average fees at the constant 1992 rate of $1.92/AUM. Yet, evaluating the formula performance over the past 25 years indicates that PRIA-generated fees declined in real terms and fell further and further behind reported private land lease rates (USDA/USDI 1992). The assumption of constant real fees under PRIA gives a conservative estimate of value change when compared to other fee formulas.

Rangeland Reform '94

Under the preferred grazing fee policy proposed in Rangeland Reform '94 (USDI/USDA 1994, p. 2-36), grazing fees on BLM and USFS lands would be set by a new formula indexed by the

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[1] The range in grazing fees under PRIA has been from $2.41/AUM in 1980 to $1.35/AUM in 1985-87.

Table 2. Real (Constant 1992) beef prices ($/cwt) considered in the LP analysis.

Price Year	Year in the model	Calf		Yearling		Cull		Brood Cow	
		Steer	Heifer	Steer	Heifer	Cow	Bull	Sell	Buy
		($/CWT)	($/CWT)	($/CWT)	($/CWT)	($/CWT)	($/CWT)	($/CWT)	($/CWT)
1979	1,15,29,43,57	125.54	107.89	103.85	93.51	67.56	79.53	522	580
1980	2,16,30,44,58	87.92	82.15	77.76	74.68	54.21	63.08	602	669
1981	3,17,31,45,59	72.58	61.53	65.62	57.80	44.00	51.23	492	547
1982	4,18,32,46,60	70.00	59.61	65.39	57.43	42.18	47.30	460	511
1983	5,19,33,47	70.53	58.69	62.39	56.18	38.93	45.02	442	491
1984	6,20,34,48	71.50	58.85	63.63	55.90	39.87	45.31	418	464
1985	7,21,35,49	79.43	65.61	67.11	59.08	41.81	48.36	434	482
1986	8,22,36,50	80.71	66.61	66.69	58.87	41.77	47.43	440	489
1987	9,23,37,51	103.34	88.07	84.43	76.36	49.92	57.20	526	584
1988	10,24,38,52	109.01	93.65	87.68	79.79	50.88	60.42	584	649
1989	11,25,39,53	103.02	88.93	83.87	76.99	48.81	59.68	587	652
1990	12,26,40,54	105.31	94.16	88.19	83.09	54.92	65.79	589	654
1991	13,27,41,55	105.48	94.18	88.00	83.02	53.70	64.52	610	677
1992	14,28,42,56	96.46	85.86	81.72	76.82	50.57	60.58	630	700
Average		91.49	78.99	77.60	70.68	48.51	56.82	524	582

Sources: Market News Reports for the Clovis, N.M. livestock market. Brood cow sale and purchase prices were from selected NMSU livestock cost and return publications and extrapolated for some years when data were not available. The sale price of a brood cow was assumed to be 11% more than the purchase price to account for marketing and transportation costs. All prices have been adjusted to constant 1992 levels.

forage value index (FVI). The grazing fee would be phased in over 3 years, with the fee set at $2.75/AUM during the first year, $3.50/AUM the second, and with full implementation to the base value of $3.96/AUM during the third year. For the modeling analysis presented here, the phase-in fees were considered during the first 2 years, then the fee was assumed to remain constant in real terms at the $3.96/AUM base rate. Only 2 alterations were made relative to the base model: the grazing fee was increased, and the borrowing limit was decreased because it was assumed the market value of federal grazing permits would be eliminated when higher fees were implemented. This assumption is consistent with the findings of Torell and Kincaid (1996), who report a continued decline in public land grazing permit values because of the uncertainty about future grazing fees and public land policies. The average value of representative Gila National Forest (GNF) ranches was estimated using a ranch value model described by Torell and Kincaid (1996). The contributory value of federal grazing permits for small, medium and large GNF ranches were estimated to be $93,729 ($858/USFS AUY), $138,266 ($656/USFS AUY), and $193,879 ($415/USFS AUY), respectively. These estimated permit values were subtracted from the total asset values shown in Table 4 when considering grazing fees higher than $1.96/AUM.

Synar Grazing Fee Proposal.

Under the Synar grazing fee proposal (Synar et al. 1991), higher fees would have been phased in over 4 years with $4.35/AUM the first year, $5.80/AUM the second, $7.25/AUM the third, and $8.70/AUM or fair market value, whichever was higher, in year 4 and thereafter. The phase-in fees of the Synar proposal were considered for the first 4 years in the LP models with an assumed constant $8.70/AUM fee after that. The value of federal grazing permits were assumed to be eliminated, reducing ranch borrowing capacity.

Estimating Total Impacts to Current GNF Ranchers

A total of 366,094 AUMs were permitted for grazing use on the Gila National Forest (GNF) during 1992. These AUMs were allocated to 132 grazing permittees using 143 allotments (personal communication, Chuck Sundt, USFS-GNF range specialist, March 1993). National forest grazing records indicate approximately 15% of the AUMs are used by ranchers classified with small herd sizes (S <150 AUY) when categorized according to NMSU budgets. Similarly, 27% of the AUMs are permitted for

Table 3. Livestock production parameters, land acreage and forage sources for representative ranches using the GNF in 1992.

	Small	Medium	Large
Livestock production parameters and herd size			
Number of mature cows	86	230	517
Number of AUY	113	301	667
Cows per bull	13	13	13
Number of horses	4	10	14
Cow replacement rate (%)	14	14	14
Calf death loss (%)	4	4	4
Yearling death loss (%)	2	2	2
Cow death loss (%)	2	2	2
Bull death loss (%)	1	1	1
Calf crop (%)	76	76	76
Productive life of bulls	5	5	5
Sale weights			
Cull cows	910	910	910
Cull bull	1,475	1,475	1,475
Yearling heifers	740	740	740
Yearling steers	760	760	760
Heifer calves	410	410	410
Steer calves	460	460	460
Land acreages and forage sources			
Owned rangeland			
Acres	650	4,339	8,532
AUMs	98	651	1,440
% of total AUMs	7%	18%	18%
State Lease			
Acres	0	2,893	5,689
AUMs	0	434	960
% of total AUMs	0	12	12
U.S. Forest Service			
Acres	8,350	16,876	33,181
AUMs	1,253	2,531	5,599
% of total AUMs	93%	70%	70%

Table 4. Costs and returns for represetnative GNF ranches with alternative levels of current debt obligation, 1992.

	Small			Medium			Large		
	No Debt	20% Debt	40% Debt	No Debt	20% Debt	40% Debt	No Debt	20% Debt	40% Debt
Income/cost category									
Gross livestock sales[1]	$28,871	$28,871	$28,871	$78,315	$78,315	$78,315	$174,168	$174,168	$174,168
Variable costs	13,426	13,426	13,426	$37,797	$37,797	$37,797	$94,809	$94,809	$94,809
Fixed costs									
Family living allowance	6,933	6,933	6,933	8,901	8,901	8,901	12,805	12,805	12,805
Other fixed expenses	5,880	5,880	5,880	9,398	9,398	9,398	14,186	14,186	14,186
Capital improvement	5,816	5,816	5,816	14,370	14,370	14,370	22,551	22,551	22,551
Total costs	32,055	32,055	32,055	70,466	70,466	70,466	144,351	144,351	144,351
Annual loan payment	0	6,709	13,418	0	15,627	31,253	0	30,779	61,558
Total costs +									
Real estate loan payment	32,055	38,764	45,473	70,466	86,093	101,719	144,351	175,130	205,909
Net ranch income	–3,184	–9,893	–16,602	7,489	–7,778	–23,404	29,817	–962	–31,741
Off ranch income	18,000	18,000	18,000	18,000	18,000	18,000	13,500	13,500	13,500
Net income	14,816	8,107	1,398	25,849	10,222	–5,404	43,317	12,538	–18,241
Asset values									
Land, building and improvements	199,525	199,525	199,525	441,933	411,933	441,933	861,273	861,273	861,273
Machinery and equipment	31,100	31,100	31,100	66,550	66,550	66,550	85,550	85,550	85,550
Livestock	85,663	85,663	85,663	228,068	228,068	228,068	503,935	503,935	503,935
Total asset value	316,288	316,288	316,288	736,551	736,551	736,551	1,450,758	1,450,758	1,450,758
Current debt obligations									
Debt/asset ratio	0%	20%	40%	0%	20%	40%	0%	20%	40%
Debt obligation	0	63,258	126,515	0	147,310	294,620	0	290,152	580,303

[1] Costs and livestock sales are for the 1992 production year as defined by Torell et al. (1993a,b,c). Costs and returns during other years considered in the LP analysis varied with beef prices and optimal level of production.

use by medium-size ranches (150 AUY ≤ S ≤ 350 AUY), and 58% by large-size ranches (S > 350 AUY). Using these percentages, ranchers with small, medium, and large herd sizes are permitted to use 54,536 AUMs, 97,737 AUMs and 213,821 AUMs of USFS grazing on the GNF, respectively.

New Mexico State University (NMSU) ranch budgets were not defined from grazing use records for the GNF; thus, some discrepancy in average herd size, forage use, and level of forest dependency would be expected. It is important, however, that an impact assessment consider the correct number of federal AUMs when aggregating to the total. Thus, the number of ranchers considered in the analysis was not defined to be the actual number using the GNF. Rather, it was the equivalent number of ranchers based on USFS AUM use. This was calculated by dividing the total AUMs of permitted use on the GNF (by size category) by the average AUMs of USFS use defined for each NMSU ranch budget. Table 5 gives the 9 types of ranch models developed, and the multipliers used to aggregate from ranch-level impacts to total impacts for current GNF ranchers.

Results

Results are presented and discussed in the following order. First, optimal production for each ranch size with the 1992 PRIA fee of $1.92/AUM is defined for ranchers using the Gila National Forest (GNF), given the defined costs, prices, and model assumptions. Next, optimal production under alternative grazing fee proposals are evaluated and compared to the PRIA base run. Results are then aggregated to estimate total impacts to ranchers using the GNF and total grazing fee receipts to the USFS.

A detailed listing of optimal solution values for each of the 60 years considered in the analysis is not given because optimal forage use and livestock production strategies were similar between years. However, net ranch returns varied considerably between years depending on the definition of annual beef prices. Drummond (1993) provides a detailed listing of annual LP solution values.[2]

Optimal ProductionStrategies: Current PRIA Grazing Fees

Small Ranches

An optimal production strategy was found for each of the 3 assumed debt loads. Small ranches with no current debt and with a 20% debt/asset ratio would optimally borrow no additional funds. The ranch with a 40% debt/asset ratio would not have enough production and sales to cover expenses during years with low beef prices, such as years 5 through 8 (Table 2), and would borrow to meet cash shortfalls. It would take several years of continued borrowing to catch up. Once the long-term land loan was fully paid in year 30, additional funds would not be borrowed.

Forage was a limiting resource during all years. Deeded AUMs would always be used to capacity. Similarly, the maximum number of USFS AUMs were used in all years, except the first year when herd size was restricted and the last year when all cows would optimally be sold.

The optimal number of brood cows was relatively constant, ranging from a low of 81 head to a high of 88 head.[3] Optimal pro-

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[2] Drummond presents the results of a $4.28/AUM grazing fee as originally proposed by USDI/USDA (1993) versus the $3.96/AUM fee considered here. Annual returns were different but optional production strategies were the same.

Table 5. Number of ranches and USFS AUMs used to aggregate to total GNF ranch-level impacts for current permit holders.

		Debt/Asset Ratio				% of Total
Ranch Size		0%	20%	40%	Total	Ranches
Small	USFS AUMs	19,769	28,555	6,590	54,914	15
	No. ranches	23 (16)[1]	34 (23)	8 (5)	65 (44)	49(36)
Medium	USFS AUMs	35,584	51,399	11,861	98,845	27
	No. ranches	14 (14)	20 (20)	4 (5)	38 (39)	29(32)
Large	USFS AUMs	76,441	110, 414	25,480	212,335	58
	No. ranches	10(14)	15 (20)	4 (4)	29 (38)	22(31)
Total	USFS AUMs	131,693	191,166	41,235	366,094	100
	No. ranches	47 (44)	69 (63)	16 (14)	132 (121)	
	Percent of total (%)	36	52	12	100	

[1] The first number shown is the actual number of GNF ranches estimated to be in this category. The bracketed () number is the equivalent number of ranches of equal size to NMSU ranch budgets.

duction was as a cow/calf ranch, similar to the ranches currently found on the Gila National Forest (GNF). Retaining calves for sale as yearlings was not optimal during any of the production years.

Table 6 defines average annual net returns and the optimal NPV found for each ranch size and debt load. With no debt, the small ranch returned $215,642 in discounted net returns to operator labor, management, and owned capital.[4] Annual income over the 60-year planning period was estimated to average $15,195 for the no-debt ranch, $11,841 for the 20% debt/asset ratio ranch and $8,118 for the 40% debt/asset ratio ranch. Annual returns varied from about $6,300 to $25,000 depending on beef prices.

Medium Ranches.

An optimal linear programming (LP) solution was not possible for the high debt model because cash flow requirements could not be met for the medium size ranch. Annual net returns were estimated to average $26,665 for the no-debt model and $10,794 for the 20% debt model. They varied from about -$600 to +$54,000 for the no-debt ranch, and from -$21,000 to +$38,300 for the 20% debt ranch. Negative returns during some years were covered by either borrowing or inter-year fund transfers.

The no-debt ranch would not optimally borrow any money, and available forage would always limit production. The 20% debt/asset ranch borrowed approximately $14,000 of short-term capital in years 7 through 10 and again in years 20 through 23 because of the relatively low beef prices and resulting cash flow shortages during these years. The optimal number of brood cows ranged from 215 to 235 head, while forage use remained relatively constant over the planning period.

Large Ranches

Average annual returns were estimated to be $46,171 for the large no-debt ranch and $13,913 for the 20% debt/asset ranch (Table 6). Cash flow restrictions could not be met for the 40% debt/asset model (infeasible). Net annual returns varied from about +$1,000 to over +$220,000 for the no-debt ranch, and from -$65,000 to +$191,000 for the 20% debt ranch. The optimal number of brood cows ranged from 425 to 530 head.

Optimal Production Strategies: Rangeland Reform '94

Small Ranches.

The average $2.04/AUM fee increase proposed in Rangeland Reform '94 ($3.96/AUM–$1.92/AUM) would mean a $2,556 decrease in net annual small ranch returns if the strategy were to pay the higher fee on all available USFS AUMs. This was the optimal strategy during all years except the first and second years. Herd size was restricted during the first year and not adjusted to full capacity until year 3 with the higher fee. Optimal herd size and marketing strategies would remain unchanged between the 2 grazing fee situations once the fee was fully implemented.

With the grazing fee at $3.96/AUM, the small ranch with 20% debt would borrow about $1,000 in short-term funds during the 7th, 8th, 21st, and 22nd years. With a long-term debt payment due each year until the 30th year, funds would be limiting and production strategies would be altered slightly for this reason.

The small-size ranch with a 40% debt/asset ratio was infeasible at the $3.96/AUM grazing fee, as the model could not meet cash flow restrictions during selected years and repay all debt obligations. Thus, it is estimated that small-size Gila National Forest (GNF) ranchers with high debt (approximately 4% of the current GNF ranchers) would face cash flow shortages if fees were increased to $3.96/AUM (Table 8).

With a 40% debt/asset ratio and at the current fee, the small ranch made an average annual return over variable costs of $15,456 (Table 6). This was $12.34/USFS AUM, and this amount would be the average annual loss in net ranch income (NRI) from these high-debt small ranches going out of business.

Additional computer runs were made (not shown) to determine the maximum grazing fee at which small high-debt ranchers could still meet cash flow restrictions. This fee was estimated to be $3.15/AUM. At this fee, cash flow restrictions could be met by pushing to the maximum borrowing limit and rolling debt forward until the last year of the 60 year planning period when assets were sold. However, it is unlikely this strategy would be financed by even the most trusting banker.

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[3] It should be recognized that only a limited number of possible production options were considered to be feasible for GNF ranchers. Production options like purchase of yearling stockers, leasing forage, or investing funds elsewhere were not considered. Including more production options would be expected to cause greater variation in optimal cow herd size.

[4] This residual return does not follow the traditional definition because a family living allowance has already been subtracted. This allowance would be a partial payment for operator labor and management.

Table 6. Average net ranch returns for representative GNF ranchers at the 1992 PRIA fee of $1.92/AUM.

	Annual Average Amount	NPV No Debt	Annual Average Amount	NPV 20% Debt	Annual Average Amount	NPV 40% Debt
Small						
Optimal average returns over variable costs	$15,824	$225,091	$15,824	$225,074	$15,456	214,941
Off-ranch income	18,000	270,395	18,000	270,395	18,000	270,395
Family living expense	-6,933	-104,147	-6,933	-104,147	-6,933	-104,147
Fixed costs and capital replacement	-11,696	-175,696	-11,696	-175,696	-11,696	-175,696
Long-term debt payment[1]	0	0	-6,709	-89,080	-13,418	-178,160
60-year average	15,195		11,841		8,118	
NPV		215,642		126,545		27,332
Medium						
Optimal average returns over variable costs	$41,334	$586,551	$41,090	$578,694	Out of business	
Off-ranch income	18,000	270,395	18,000	270,395		
Family living expense	-8,901	-133,710	-8,901	-133,710		
Fixed costs and capital replacement	-23,768	-357,041	-23,768	-357,041		
Long-term debt payment[1]	0	0	-15,627	-207,490		
60-year average	26,665		10,794			
NPV		366,194		150,847	Out of business	
Large						
Optimal average returns over variable costs	$81,493	$1,144,213	$80,014	$1,098,415	Out of business	
Off-ranch income	13,500	202,796	13,500	202,796		
Family living expense	-12,085	-181,540	-12,085	-181,540		
Fixed costs and capital replacment	-36,737	-551,860	-36,737	-551,860		
Long-term debt payment[1]	0	0	-30,779	-408,674		
60-year average	46,171		13,913			Out of business
NPV		613,609		159,137		

[1] Long-term debt payment is only incurred during the first 30 days of the analysis.

Medium Ranches

The model results for the no-debt medium size ranch with grazing fees of $1.92/AUM versus $3.96/AUM were similar to those of the small ranch. The optimal strategy would be to pay the higher fee unless forced out of business by cash flow restrictions. Net returns would decrease by the amount of the added grazing fee payment, $5,163/year.

The medium-size ranch with a 20% debt/asset ratio would have to increase the amount of borrowed funds and switch to intermediate-term borrowing during some years to meet cash flow restrictions. Because of increased interest payments, the average change in annual net returns would be -$5,511/year, an amount greater than the increase in grazing fees.

With the defined situation the medium ranch model was infeasible at the high-debt level even at the 1992 federal fee rate of $1.92/AUM. Additional computer runs indicate the cash flow restrictions of the model could not be met even if the grazing fee were zero.

Large Ranches

With the grazing fee increase to $3.96/AUM, the large ranch with no debt would have to borrow about $11,000 during selected years when beef prices were relatively low. There was a slight change in marketing strategies between years but as a 60-year average only 4 fewer animal units yearlong (AUY) were produced each year. An annual average of 193 USFS AUMs would go unused.

Similar to the large ranch model with 40% debt, which was infeasible even at the current fee, the large ranch with a 20% debt/asset ratio became infeasible at the $3.96/AUM fee. Large size Gila National Forest (GNF) ranches with intermediate debt, approximately 11% of the current GNF ranches (Table 5), could not meet cash flow restrictions if grazing fees were increased to $3.96/AUM. As indicated by additional computer runs, cash flow restrictions could be fulfilled with a grazing fee of about $3.50/AUM.

Optimal Production Strategies: Synar Proposal

With the Synar proposed fee of $8.70/AUM, production strategies were similar for the 3 ranch sizes; in most cases there would be no production. Cash flow restrictions could not be met by any of the ranches with debt, and for those ranches with no debt, major changes in production would be optimal. Livestock production would be cyclic with USFS AUMs going unused in low beef price years but used fully when beef prices were relatively high. Averaged over all years, for the small no-debt ranch, optimal herd size was reduced from 113 AUY with the PRIA fee to 92 AUY with the $8.70/AUM fee. Similarly, optimal herd size was reduced from 301 AUY to 273 AUY for the medium no-debt ranch, and from 667 AUY to 424 AUY for the large no-debt ranch.

Short and intermediate-term borrowing would optimally be used to cover annual expense shortfalls and to purchase brood stock as herd size was adjusted to changing economic conditions. By making these adjustments, the reduction in net returns from the higher fee was minimized. The small no-debt ranch, for example, would have realized an annual decrease in net returns of $8,495 ($6.78/AUM fee increase x 1,253 AUMs) if grazing fees had been paid on all USFS AUMs. By letting some AUMs go unused in selected years, the average decrease in net returns was reduced to $8,391/year.

Table 7. Total number of current GNF ranchers () and AUM use by these ranchers at alternative fee rates.

Ranch Size	Debt			
	No debt	20%	40%	Total
Base run $1.92/AUM fee				
		1992 GNF permitted AUM use		
Small	(16) 19,769	(23) 28,555	(5) 6,590	(44) 54,914
Medium	(14) 35,584	(20) 51,399	(5) 11,861	(39) 98,845
Large	(14) 76,441	(20) 110,414	(4) 25,480	(38) 212,335
Total				(121) 366,094
		Optimal GNF use ($1.92/AUM)		
Small	(16) 19,769	(23) 28,555	(5) 6,590	(44) 54,914
Medium	(14) 35,584	(20) 51,399	(0) 0	(34) 86,984
Large	(14) 76,140	(20) 110,079	(0) 0	(34) 186,219
Total				(112) 328,117
		Change in AUM use		
Small	0	0	0	0
Medium	0	0	–11,861	–11,861
Large	–300	–335	–25,480	–26,116
Total				–37,977
Rangeland Reform '94				
		Optimal GNF use ($3.96/AUM)		
Small	(16) 19,769	(23) 28,555	(0) 0	(39) 48,324
Medium	(14) 35,458	(20) 51,278	(0) 0	(34) 86,735
Large	(14) 73,423	(0) 0	(0) 0	(14) 73,423
Total				(87) 208,483
		Change in optimal AUM use from $1.92/AUM		
Small	0	0	–6,590	–6,590
Medium	–127	–122	0	–248
Large	–2,717	–110,079	0	–112,796
Total				–119,634
H.R. 944 (Synar)				
		Optimal GNF use ($8.70/AUM)		
Small	(16) 16,093	(0) 0	(0) 0	(16) 16,093
Medium	(14) 31,577	(0) 0	(0) 0	(14) 31,577
Large	(14) 37,859	(0) 0	(0) 0	(14) 37,859
Total				(44) 85,529
		Change in optimal AUM use from $1.92/AUM		
Small	–3,676	–28,555	–6,590	–38,821
Medium	–4,007	–51,399	0	–55,406
Large	–38,282	–110,079	0	–148,361
Total				–242,588

Total Impacts to Current GNF Permit Holders

Ranch Numbers.

The estimated number of current GNF ranches that would be producing under alternative grazing fee proposals is shown in Table 7. The medium and large 40% debt/asset ratio ranch models could not meet cash flow restrictions at the current grazing fee and are estimated to be on their way out of business without additional off-ranch income. The loss of these ranches is expected with or without increased grazing fees and altered land-use policies. It would be expected that the equivalent number of current Gila National Forest (GNF) ranches would decrease from 121 to 112 under current grazing fee policy.

With an increase in federal grazing fees to $3.96/AUM, the small 40% debt/asset ranch and the large 20% debt/asset ranch were estimated to go out of business. With these 2 ranch categories no longer operating, the number of equivalent ranches would decrease to 87. A still higher fee of $8.70/AUM would decrease the number to 44 ranches.

The only ranches still producing at the $8.70/AUM fee would be those with no debt. This assumes remaining ranchers would continue in business and not decide that other investments would be more advantageous.

It might be expected that with increased grazing fees and with added regulations, ranchers other than those forced out of business would choose to quit. But, as a counter point, because grazing permit values should decrease by an amount equal to or greater than the loss in discounted net returns, new ranchers should be able to buy Gila National Forest (GNF) ranches at a much lower price and still cash flow the investment, provided large debts are not incurred to make the ranch purchase. The grazing permit could also be attached to another existing ranch. Thus, the exact number of ranches using the GNF with different fees cannot be determined. The estimates provided here refer only to the expected change in production from current ranchers, given their defined size, production levels, and debt structure.

GNF AUM Use and Grazing Fee Receipts

Total Gila National Forest (GNF) permitted use during 1992 was estimated to be 366,094 AUMs (Table 5). Actual use averaged 71% (259,306 AUMs) of this amount from 1986 to 1991. The optimal annual use by current permit holders, as estimated from the linear programming (LP) analysis, would average 328,117 AUMs (Table 7). Optimal average USFS use at the $3.96/AUM fee was 208,483 AUMs. It dropped substantially to only 85,529 AUMs at a fee of $8.70/AUM, as only ranchers with little if any debt would remain in business at this fee.

Even though Gila National Forest (GNF) AUM use by current permit holders would decrease with higher grazing fees, optimal forage use was price inelastic (the % decrease in quantity of forage demanded was less than the % increase in price) with GNF revenue increasing at the higher fees. Relative to the 1992 $1.92/AUM fee, average annual grazing fee receipts would increase by $195,798 at $3.96/AUM and by $118,877 at the $8.70/AUM fee. Because grazing fee receipts would be higher at the $3.96/AUM fee, not the $8.70/AUM fee, the demand for GNF forage is estimated to be price elastic over this higher price range. The price elasticity of demand was estimated to be -0.64 (a 1% increase in price caused a 0.64% decrease in AUM use) for the fee change from $1.92/AUM to $3.96/AUM, and -1.11 for the change from $3.96/AUM to $8.70/AUM.

Livestock Receipts

Optimal average annual livestock receipts from current GNF ranchers at the $1.92/AUM PRIA fee totaled $9,988,307 (Table 8). This decreased to $6,300,637 at the $3.96/AUM fee, a 37% decrease. Optimal annual livestock receipts for current GNF ranchers at a grazing fee of $8.70/AUM would average $3,452,686, a 65% decrease.

Net Ranch Income

Average annual net ranch income for current GNF ranchers at the $1.92/AUM fee level was estimated to be $4,797,640 (Table 9). It dropped to $2,703,426 (44% decrease) with a $3.96/AUM fee and to $916,062 (81% decrease) with an $8.70/AUM fee. The reduction in NRI was about equal to the fee increase if ranchers remained in business.

Conclusions and Discussion

Higher grazing fees will reduce ranch income and net worth. Some ranchers will go out of business, but if the grazing fee remained at or below the $3.96/AUM rate proposed in Rangeland Reform '94 the optimal strategy would be to pay the higher fee unless high current debt created cash flow limitations. If permit values fall because of higher grazing fees and new regulations, as

Table 8. Annual average livestock receipts from current GNF ranchers at alternative fee leve

	Debt			
Ranch Size	No debt	20%	40%	Total
Base run $1.92/AUM fee				
	Optimal livestock receipts ($ Total @ $1.92/AUM fee)			
Small	$466,048	$673,180	$159,862	$1,299,089
Medium	1,113,036	1,623,173	0	2,736,209
Large	2,391,830	3,561,178	0	5,953,009
Total				9,988,307
Rangeland Reform '94				
	Optimal livestock receipts ($ Total @ $3.96/AUM fee)			
Small	$465,937	$673,225	$0	$1,139,163
Medium	1,112,727	1,657,026	0	2,769,753
Large	2,391,721	0	0	2,391,721
Total				6,300,637
	Average change in livestock receipts from $1.92/AUM ($ Total)			
Small	–$110	$46	–$159,862	–$159,926
Medium	–309	33,853	0	33,544
Large	–109	–3,561,178	0	–3,561,288
Total				–3,687,670
H.R. 944 (Synar)				
	Optimal livestock receipts ($ Total @ $8.70/AUM fee)			
Small	$451,706	$0	$0	$451,706
Medium	1,084,777	0	0	1,084,777
Large	1,916,203	0	0	1,916,203
Total				3,452,686
	Average change in livestock receipts from $1.92/AUM ($ Total)			
Small	–$14,342	–$673,180	–$159,862	–$847,383
Medium	–28,259	–1,623,173	0	–1,651,432
Large	–475,627	–3,561,178	0	–4,036,806
Total				–6,535,621

Table 9. Average annual net ranch income (NRI) for GNF ranchers at alternative fee levels.

Ranch Size		Debt			
		No debt	20%	40%	Total
Base run $1.92/AUM fee					
		Optimal average NRI ($ Total @$1.92/AUM fee)			
Small		$249,661	$360,622	$81,285	$691,568
Medium		581,129	834,453	0	1,415,582
Extra-large		1,112,587	1,577,904	0	2,690,490
Total					4,797,640
Rangeland Reform “94					
		Optimal average NRI ($ Total @ $3.96/AUM fee)			
Small		$210,502	$303.944	$0	$514,446
Medium		510,678	722,557	0	1,233,234
Extra-large		955,746	0	0	955,746
Total					2,703,426
		Average change in NRI from $1.92/AUM ($ Total)			
Small		($39,159)	($56,678)	($81,285)	($177,122)
Medium		(70,451)	(111,897)	0	(182,348)
Extra-large		(156,840)	(1,577,904)	0	(1,734,744)
Total					(2,094,214)
	Average fee Increase	Average change in NRI ($/AUM of 1992 GNF permitted use)			
Small	$2.04	($1.98)	($1.98)	($12.34)	($3.23)
Medium	2.04	(1.98)	(2.18)	0.00	(1.84)
Extra-large	2.04	(2.05)	(14.29)	0.00	(8.17)
H.R. 944 (Synar)					
		Optimal average NRI ($ Total @ $8.70/AUM fee)			
Small		$117,272	$0	$0	$117,272
Medium		338,311	0	0	338,311
Extra-large		460,479	0	0	460,479
Total					916,062
		Average change in NRI from $1.92/AUM ($ Total)			
Small		($132,389)	($360,622)	($81,285)	(574,296)
Medium		(242,818)	(834,453)	0	(1,077,272)
Extra-large		(652,108)	(1,577,904)	0	(2,230,011)
Total					(3,881,578)
	Average fee Increase	Average change in NRI ($/AUM of 1992 GNF permitted use)			
Small	$6.78	($6.70)	($12.63)	($12.34)	($10.46)
Medium	6.78	(6.82)	(16.23)	0.00	(10.90)
Extra-large	6.78	(8.53)	(14.29)	0.00	(10.50)

would be expected, proposed policy changes might mean an opportunity for new ranchers to lease these permits without a large purchase cost for the permit.

The ones who lose with higher grazing fees are current public land ranchers. In addition to decreased net annual returns, these producers would likely see a major decline in ranch value as earning potential decreases. Because debt load was found to be a major determinant of the ability to cash flow the ranching business, the implications for bankers and lenders is significant. Further, it is not small size ranch units that would most likely go out of business, as is widely believed; rather, it is those with high to intermediate debt obligations. Off-ranch income is a major part of family income for small part-time ranchers. Because higher debt is generally held by younger farmers and ranchers (NMDA 1990) this group would potentially be most impacted from increased grazing fees.

In this analysis a modeling and cash flow evaluation was conducted with specific assumptions about debt load, off-ranch income, production rates, and costs. When income was insufficient to pay all annual production expenses, a minimal family living allowance, and debt obligations, the ranch was considered to be “out of business.” As shown, with grazing fees in the range of $3 to $4/AUM some ranchers will leave the livestock business, especially those with high debt. Still others would be expected to enter and leave the business as ranch values and the economics of ranching change from altered land-use policies and market conditions.

The conclusion that the fee proposals of Rangeland Reform ‘94 will force some ranchers out of business is different than that reached by Richardson et al. (1993). These authors found that the proposed fees of Rangeland Reform ‘94 would not force representative ranches out of business over the next 6 years. The difference in conclusions might be because the previous study considered ranches that graze rangelands on a seasonal basis and are less dependent on federal lands for grazing capacity.

Grazing fees averaging $8.70/AUM would force many ranchers out of business and grazing fee receipts would be less than what could be obtained at a lower fee. This fee is too high if continued grazing use of public lands is desired.

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Technical Note
A digital technique for recording of plant population data in permanent plots

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Abstract

A mobile system to rapidly record demographic and spatial data of plant populations on permanent plots has been developed based on digital image processing equipment for personal computers. It offers considerable savings in field and data handling time and can record data from large plots. This system will facilitate broader application of plant demographic studies to arid and semi-arid ecosystems.

Resúmen

Se desarrollo un sistema móvil y rápido para recabar datos sobre vegetacion en parcelas fijas utilizando un equipo de procesamiento digital de imagenes, para P.C. ofrece grandes ventajas en tiempo y costo, facilitando los estudios demograficos de la vegetacion en ecosistemas áridos y semiaridos.

Key Words: VIVA, population data, digital data, image analysis

Demographic approaches to understanding change in plant populations have been advocated by Austin (1981) and others. However, few studies of plant population dynamics in arid and semi-arid environments have involved large numbers of plants and data sets have often been inadequate (Gardiner and Norton 1983). Logistic constraints in collecting plant demographic data using the more common techniques, chart mapping and the pantograph, have resulted in sampling being carried out on a limited number of quadrats, often 1 m^2 or less in size.

Photographic techniques have been used on rangelands to increase the spatial scale and speed of data collection (Hacker 1978, Owens et al. 1985). However, these require manual transfer of individual elements in the photographic image onto charts, and the computation of Cartesian coordinates if spatial data are required for subsequent analyses. This is time consuming and requires a second trip into the field to collate the basic data. Mack and Pyke (1979) developed a portable digitizer to plot the location of individual plants in the field. While this reduced sampling to a single operation, the apparatus is restricted to very small quadrat sizes.

With the advent of powerful, portable micro computers digitized image analysis is increasingly being used for a range of research purposes outside the laboratory. To date most of the applications that have been developed are based on the discrimination of elements in a photographic or video image for the measurement of area or density. The same equipment also provides a matrix on which coordinates can be plotted and can greatly increase the speed and objectivity with which plant demographic and spatial data are collected. Thus the VIVA (Video Imaging of Vegetation Attributes) system was developed to collect time series data on individual plants and cover measurements on permanent plots.

The VIVA System

The VIVA system uses video technology to collect data from live video images, photographs and other image formats. It is a menu-driven, PC-based program that records the position and attributes of individual plants on permanent plots or measures the cover values of elements that can be highlighted in an image. As data are collected they are formatted and saved to the database in the 1 operation, negating the need to transpose data into Cartesian coordinates or to return to the plot to interpret and annotate photographs.

The VIVA system comprises a personal computer with a hard disk that is capable of running Microsoft Windows 3.x, a video frame grabber, a video camera and lens, an RGB (Red/Green/Blue) monitor, and a gantry to support the video camera above the plot (Fig.1). The software has on-line help. A video frame grabber is a hardware add-on to a PC, used to capture images from a video camera into the computer's memory. The frame grabber used by the VIVA system has an image resolution of 512 × 512 pixels, or picture elements (Table 1). Data can be collected from photographic prints using a digitizing tablet, or photographic transparencies using a light box and video

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The development of this system owes much to the encouragement and assistance of Mr. O.R. Southwood, Mr. Hans Lohri of Leica (Aust) Pty. Ltd. Dr. D.G. Saville, Dr. G.W. King and Mr. J.W.A. Evans. The support of the Australian Wool Research and Development Corporation is gratefully acknowledged.
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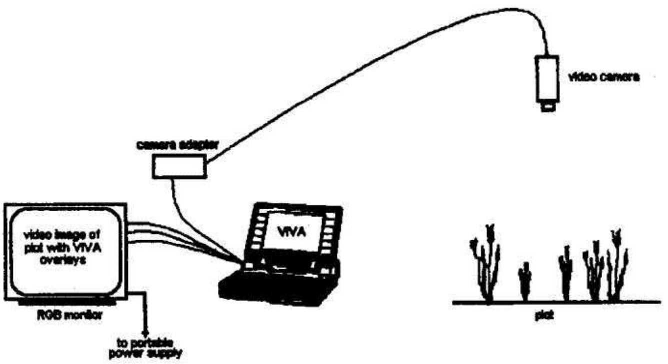


Fig. 1. The hardware setup to run the VIVA software in the field (see Table 1 for specifications).

The system has 4 subroutines: (a) the Sample Species subroutine enters site descriptions and quadrat co-ordinates, locates individuals, records individual plant attributes, displays previous samples on the RGB monitor and can recall individual plant attributes from previous samples; (b) the Edit Species Details subroutine lists descriptive data about the species to be measured; (c) the Plot Data subroutine produces charts of the location and diameter of individual plants for particular species or dates, and (d) the Thresholding subroutine enables absolute and percentage cover values for individual elements in the image to be determined for the whole image area or for the area that lies within the boundaries of the plot. Other subroutines enable data to be edited and sampling to be halted and resumed. All data are stored in separate files in dBase IV format.

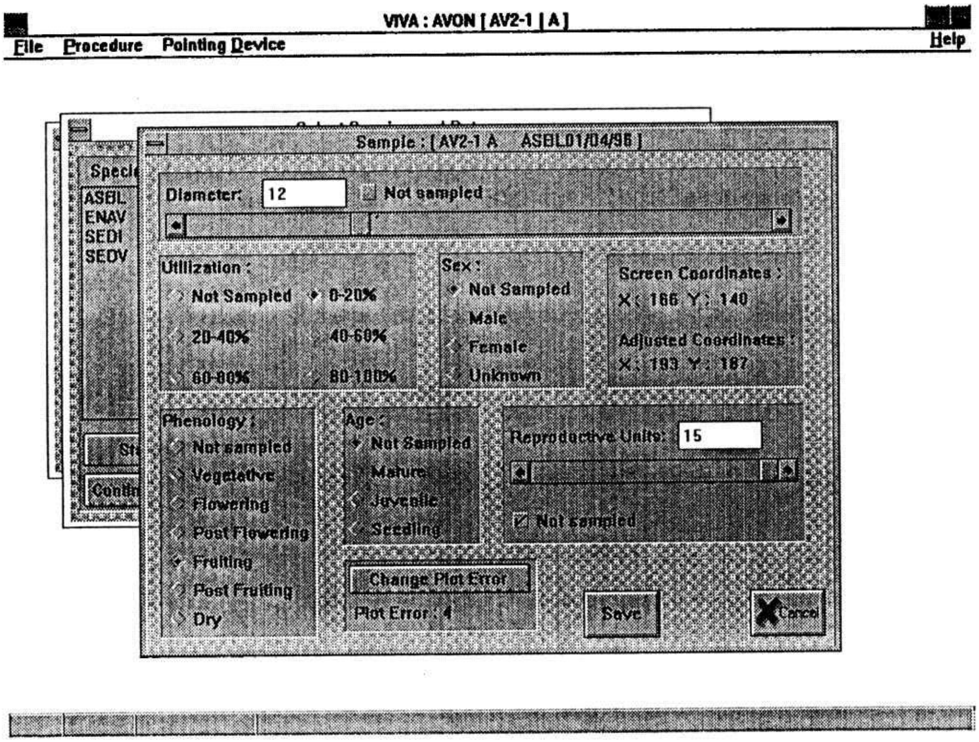
Table 1. Equipment used to run VIVA software in the field.

Computer:	Toshiba T5200
Framegrabber:	PC Vision Plus, Imaging Technology Inc., Massachusetts.
Video camera:	Sony ADC-D5CE
Camera lens:	Fujinon HF8B-SND4-1 1:1.4/8
RGB monitor:	Sony Trinitron PVM-1371QM
Power inverter:	PC300S, Power Conversions Pty.Ltd. Melbourne.

Operational Procedure

Site name, plot name and a code for the species to be sampled are entered or selected from the menus. Once set up over the plot to be charted the system displays a live video image and cursor on the RGB monitor. Four permanent markers on the plot are located in the image with the cursor and algorithms calculate adjustments to translation, rotation and scale. Plants recorded at the previous sampling are then written to their correct screen co-ordinates with respect to the current position of the markers.

Individuals that were recorded on the previous sampling appear on the screen as a red square. Plants that were sampled at a previous sampling but not the one immediately before the current sampling appear as an open red box. These will continue to appear for any number of months up to 10 years depending on the time specified in the Edit Species Details subroutine. The ability to display on the screen the location of previously sampled individuals for any specified time and recall their attributes is particularly useful for rhizomatous species such as *Astrebla lappacea* (Lindl.) Domin which may have no parts above the soil surface for many months. If a large, mature looking plant suddenly appears during



Sample : [AV2-1 A ASBL01/04/96]

ASBL
ENAV
SEDI
SEDV

Diameter: 12
☐ Not sampled

Utilization :
○ Not Sampled ● 0-20%
○ 20-40% ○ 40-60%
○ 60-80% ○ 80-100%

Sex :
● Not Sampled
○ Male
○ Female
○ Unknown

Screen Coordinates :
X : 166 Y : 140
Adjusted Coordinates :
X : 193 Y : 187

Phenology :
○ Not sampled
○ Vegetative
○ Flowering
○ Post Flowering
● Fruiting
○ Post Fruiting
○ Dry

Age :
● Not Sampled
○ Mature
○ Juvenile
○ Seedling

Reproductive Units: 15
☑ Not sampled

Plot Error : 4

Fig. 2. The data entry screen of the Sample Species subroutine.

Fig. 3. Photograph of mobile system used to map large plots in western New South Wales.

a sampling it can be quickly ascertained whether an individual of the same species has occupied that location previously. This feature negates the possibility of recording an individual plant as new when that individual has been recorded in a previous sampling.

Once located with the cursor a new plant appears as a green square and attributes of that individual can be entered through a menu system. Age (seedling/juvenile/adult), phenological stage (vegetative/preflowering/flowering/fruiting/post-fruiting/dry), sex (male/female/unknown), diameter, number of reproductive units, and an estimate of percent utilization can be recorded (Fig. 2). If an attribute is not sampled or is inappropriate for that species, eg. sex, a "Not Sampled" option is available and the data appears in the data file as "null" for text fields and "–1" for numeric fields.

If the plant has been sampled previously clicking on the red square or open red box will change the symbol to a green square and the previous values of the attributes being measured recalled. These values can then easily be edited and saved to the current sampling.

The VIVA system was used to study the population dynamics of 4 grasses and 3 shrubs in the chenopod shrublands of western New South Wales, Australia. This study required the regular sampling of 120 large (4 × 3 m) permanent quadrats and produced 58,000 records in 2 1/2 years. The system requires 2 people to collect data from large plots, 1 in the vehicle operating the computer and the second pointing out individuals in the plot and determining their attributes. For mobility in the field, a gantry has been developed which can be mounted on the front of a vehicle (Fig. 3). This system can be set up for operation or dismantled for travel to the next site in 3 to 5 minutes. To operate in the field a 300 watt inverter is required to power the system from batteries.

Speed in the field depends on the density of the target species. For most species between 150 and 200 individual plants can be located and their attributes recorded per hour. The number of records per hour increases with density as search time for the next individual of that species deceases. At the point where the distance between individuals approaches the resolution of the system the rate of recording may decrease as greater effort is needed in distinguishing one individual from another. With the above field setup, testing of the location accuracy of the system under ideal conditions resulted in a plotting error that was on average less than 1 pixel, ie. 8 mm. Inaccuracies in the field can occur because of operator error, flex in the gantry, and wind buffeting. These occasionally magnified errors in the initial location of an individual to 1 1/2–2 cm. However, this is a rare occurrence and has caused few problems in the re-identification of individual plants. Indeed, the system is so accurate that individuals that normally would not be recognized as extant plants can be relocated.

If spatial data only are required ground-based or aerial photographic images can be used to collect it. The VIVA software will provide coordinates for any identifiable element in the image relative to permanent markers on the ground. The algorithms contained within the software allow correction for orientation and scale between subsequent images of the same plot.

The measurement of cover values using the Thresholding subroutine involves the highlighting of elements in the image and the measurement of those elements in relation to the total image area. Each image appears on the RGB monitor as a grey-scale image consisting of 256 grey levels between white and black. Grey levels can be highlighted above, below or between any 2 specified values enabling dark, light or in-between elements in the image to be highlighted and measured. The element highlighted may be a soil surface feature, total vegetation cover, or a subcomponent of either. A feature of the VIVA software is that the area measured can be determined for the whole image area or only for that area which lies within the boundaries of the plot.

Discussion

The VIVA system has a number of data handling advantages over chart mapping, pantograph, and photographic techniques and allows a considerable increase in quadrat size over the digitizer used by Mack and Pyke (1979). The photographic technique of Owens et al. (1985) was also designed to collect plant demographic data from large plots in semi-arid environments. A major advantage of the VIVA system has over their technique is that demographic data can be downloaded directly to a database upon returning from the field without the need for data to be transposed from images. In comparison to the technique of Owens et al. (1985), VIVA also saves equipment establishment time, 3–5 minutes compared to 45 minutes, ground truthing time, and travel time. Sampling time will be dependent on the number of target species and vegetation structure. For the above-mentioned study this ranged between 5 and 140 minutes. Errors due to plants being missed during the initial sampling were slightly less than that of Owens et al. (1985) using their photographic technique. A total of 410 plants (3% of the total sample) were recorded for the first time at the second sampling, although they were large enough to have been present at the first sampling. The occurrence of this type of error will vary with the type of vegetation and the experience of the observer. Errors due to recording of artifacts do not occur with this system.

The image analysis capabilities of VIVA have not been tested in any systematic way, however, the principles of this methodology are well established in the fields of medical and ecological research. For example, image analysis techniques have been used to measure tree crown defoliation (Lee et al. 1983), disease impact in crops (Gerten and Wiese 1987), and tree root biomass (Ruark and Bockheim 1988).

Provided individual plants are identifiable on permanent plots, the VIVA system can be used at any spatial scale, and will facilitate broader application of plant demographic studies to arid and semi-arid ecosystems. The VIVA software is currently being commercialised and enquiries should be directed to the Manager Technology Transfer, NSW Agriculture, LMB 21, Orange NSW 2800, Australia.

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Book Reviews

Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Edited by F.B. Samson and F.L. Knopf. 1996. Island Press, Washington, D.C. 339 p. US$28.00 paper. ISBN 1-55963-428-6.

Concern for endangered and threatened species has been increasingly acted upon in the U.S. over the past few decades. Most of this activity has been focused on systems other than rangeland systems, e.g., tropical rainforests, the Florida Everglades, Pacific Northwest forests. The Endangered Species Act (ESA) is another of the top-down, command and control approaches to conservation that came largely from Washington, D.C. Such legislation and the bureaucratic attitudes they generated could be foisted off on public lands states in the West, whether the locals liked it or not. In the private land states of the Midwest, South, and East, however, the impacts of ESA have been slower to take effect. The historic impression of power brokers on the two coasts that the nation's midsection was deficient ("fly-over country") in potential for preserving or restoring biodiversity has also led that least appreciated part of the country–the prairies–to be the last part of America where biodiversity has been considered in land management planning. Thus, relatively little basic information on biodiversity exists to properly address these issues in the prairie states. The volume being reviewed was designed to begin filling these gaps and encourage more attention to biodiversity in the prairie region.

The book is organized into 4 main sections. The first is composed of 2 chapters, one on the place of prairie in our culture, where Dan Flores makes a very articulate argument that the prairie is the center of our national identity. The second chapter shows how economic values of unplowed prairie can extend way beyond our past assumptions.

The second section explores the sub-regional variation in ecosystem structure and function and its dependence on biodiversity. This reviewer was surprised to not find contributions here by the major groups of ecologists working at the Long Term Ecological Research sites in the region. Their participation could have strengthened this important section.

The third section has five chapters outlining the contributions of five groups of animals to the biodiversity of the region. It is nice to see that invertebrates and fishes have gotten their own chapters. Plants and microbes could have merited similar additional attention.

The fourth section is composed of 9 chapters that illustrate current agency or partnership approaches to begin dealing with biodiversity-landuse interactions in subsets of our prairie, including those in Canada. These all emphasize the local, bottom-up approach that is required if any positive action is to occur on landscapes where private ownership and human needs to make a living are integrated into the planning.

The concluding chapter, a synthesis of the preceding and prospectus of the future, by Paul Risser reminds us that prairies have evolved under the triple impacts of drought, grazing, and fire. In fact, these are necessary disturbances. Recent re-inventory of the Wisconsin prairie fragments by Leach and Givinish (*Science* 273:1555–1558), first inventoried by John Curtis in the 1940–50's, has shown an 8 to 60% reduction in plant species lists in those unmanaged remnants. This vividly demonstrates the folly of non-interventional preservation and points to the necessity of pro-active management to sustain the greatest amount of biodiversity possible. Members of SRM could have important roles in demonstrating this truism elsewhere in the prairie region.–*Neil E. West,* Utah State University, Logan, Utah.

Natural Capital and Human Economic Survival. By Thomas Prugh. 1995. International Society for Ecological Economics, Solomons, MD. 216 p. Distributed by Sinauer Associates, Inc., Sunderland, MA. US$18.95 paper. ISBN 1-8874900-02-7.

The appropriate role of economics, both in scientific inquiries into and policy formulation regarding ecological issues, continues to be a thorny issue among those interested in natural resource management. *Natural Capital and Human Economic Survival* makes a useful contribution to helping readers understand these complex issues. Additionally, it provides possible strategies that readers may wish to consider when choosing among alternative economic and natural resource policies. Readers having introductory courses in both micro- and macroeconomics and a course in natural resource economics should have little difficulty handling the material in this book. The International Society for Ecological Economics has performed a useful role in sponsoring this and two related books. Although this book could be used as a standalone text, it draws heavily upon the companion book, *Introduction to Ecological Economics*, by Robert Contanza.

The book is divided into 3 sections and a brief Afterword. Section I contains two chapters devoted to comparing and contrasting classical and neoclassical economics with ecological economics. This condensation of 2 complex topics is accomplished rather nicely, but an in depth comprehension will require the reader to have either a substantial background in economics or the use of supporting economics texts.

Chapter 2, along with the 2 chapters of Section II, are key to understanding the author's position regarding policies pertaining to ecological economics. The central topics are the definition and role of natural capital, the role of technology in the development of substitutes for natural capital and an alleged failure of contemporary accounting systems, and therefore markets, to reflect the "correct" price of natural capital.

Section III is concerned with the management of natural capital to achieve resource sustainability. Chapter 5 treats the need to invest in natural capital and contrasts command and control systems with incentive-based systems for maintaining sustainability in ecosystems. Chapter 6 then develops a number of strategies for investment in natural capital that combine features of both command and control and incentive-based systems. The treatments are non-technical and case studies from the Netherlands and Costa Rica are provided to illustrate approaches to achievement of resource sustainability. A brief Afterword provides the reader with some value issues that have been raised in the body of the text. Section III and the Afterword provide excellent material for classroom discussions that could go across numerous disciplinary boundaries.

Although economists may find this book lacking in rigor, many non-economists will find that the text provides a concise and rather understandable treatment of concepts important to the management of natural capital.–*LeRoy Rogers,* Washington State University, Pullman, Washington.