Journal of Range Management

Publication of the Society for Range Management



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

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INSTRUCTIONS FOR AUTHORS appear on the inside back cover of each issue. A Style Manual is also available from the Society for Range Management at the above address @\$1.25 for single copies; \$1.00 each for 2 or more.

THE JOURNAL OF RANGE MANAGEMENT (ISSN 0022-409X) is published six times yearly for \$56.00 per year by the Society for Range Management, 2760 West Fifth Avenue, Denver, Colo. 80204. SECOND CLASS POSTAGE paid at Denver, Colo. **POSTMASTER: Return entire Journal with address change**—RETURN POSTAGE GUARANTEED—to Society for Range Management, 2760 West Fifth Avenue, Denver, Colo. 80204.

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Evaluation of Total Fecal Collection for Measuring Cattle Forage Intake

JERRY L. HOLECHEK, HELEN WOFFORD, DAVE ARTHUN, M.L. GALYEAN, AND JOE D. WALLACE

Abstract

Conventional digestibility trials with steers were conducted to evaluate relationships between actual forage intake and estimated forage intake using the total fecal collection procedure. Actual forage intake of 6 of the 9 forages fed was not accurately estimated by the widely used technique of dividing total fecal output by forage indigestibility estimated by in vitro procedures. This was because 48-h in vitro digestibility poorly estimated in vivo digestibility of 6 forages. Regression equations based on in vivo-in vitro digestibility relationships can reduce but not solve this problem because in vivo processes such as mastication and rumination are bypassed with in vitro techniques. The use of a 36-h microbial digestion period for nongrasses and a 72-96-h microbial digestion period for grasses shows potential to improve in vitro digestibility estimates of cattle in vivo digestibility. Another potential means of improving in vitro digestibility estimates is to select the highest digestibility value from forage or diet samples subjected to 36-, 48-, 60-, 72-, 84- and 96-h microbial digestion periods.

Although mechanisms controlling forage intake in ruminants have been described by Ellis (1978), Mertens (1977), Church (1979), Van Soest (1982), and Mertens and Ely (1982), present techniques to measure intake of pasture and range forages by ruminants are laborious, costly, and subject to numerous errors (Cordova et al. 1978, Kartchner and Campbell 1980). The total fecal collection method discussed by Van Dyne (1969) has become the most favored approach for estimating forage intake by domestic ruminants. Although this procedure has been widely used, evaluation of its accuracy is limited (Van Dyne and Meyer 1964). Our objective was to evaluate the total fecal collection/indigestibility method of Van Dyne (1969) for determining intake.

Methods

Two independent studies were conducted in 1980 and 1982 at the New Mexico State University farm. Details of each study will be reported separately.

Study 1

Three feeding trials were conducted between May and September of 1980. Steers were fed alfalfa (*Medicago sativa*) hay for 3 weeks before each trial. Five Hereford \times Angus yearling steers, weighing approximately 340 kg each, were used in each trial. Trials were 14 days long with 10 days for adaptation and 4 days for data collection. Schneider and Flatt (1975:124) concluded that a 5-day adjustment period was adequate to clear previously fed diets from the digestive tract; Dubose and Embry (1956) reported that a 4-day collection period was sufficient to quantify fecal excretion in steers and lambs.

Trials were in drylot pens where steers were fed ad libitum individually. Feed intake was determined by conventional handfed methods (Schneider and Flatt 1975:57). Steers were harnessed with fecal collection bags. Total fecal output was measured daily. Forages fed in the 3 drylot trials included milo hay (Sorghum vulgare) that had the heads removed, alfalfa hay, and oat hay (Avena sativa) that contained about 10% alfalfa. Feed was avail-

Manuscript accepted 4 June 1985.

able free choice throughout the day.

Five esophageal fistulated cows were used to collect diet samples in all 3 trials for diet in in vitro organic matter digestibility, crude protein, and fiber evaluation. In vivo organic matter digestibility of the milo, alfalfa, and oat hays was determined by the conventional procedure (Schneider and Flatt 1975).

Study 2

Study 2 was conducted with 6 yearling steers, weighing approximately 273 kg, in 6 digestion trials during the summer of 1982. Six different hays representing 2 forage classes (3 grasses and 3 nongrasses) were fed to the 6 steers in a Latin square design. All 6 hays were fed in each 15-day trial and randomized within rows and columns. Hays used were alfalfa, Eski sainfoin (Onobrychis viciaefolia), kochia (Kochia scoparia), millet (Panicum miliaceum), timothy (Phleum pratense), and silver bluestem (Bothriochloa saccharoides) prairie hay. Steers were confined to 6×15 m individual pens. Hays were chopped to a 2-4 cm particle size to reduce selective feeding.

Intake was determined by conventional hand-fed methods (Schneider and Flatt 1975:57) and estimated by the procedure of Van Dyne (1969) described in Study 1. Feed was available free choice daily, and intake was evaluated for each steer daily for 5 days after 10 days of adjustment to the feed.

We measured total fecal output in collection bags during the same 5 days we measured intake. During each 5 days of intake and fecal output measurement, samples of the feed offered to each steer were collected for laboratory analyses.

Nutritive Analysis

Preparation of samples for nutritive analysis and nutritive analysis procedures were the same for both studies. Feed and fecal samples were ground through a 1-mm screen in a Wiley laboratory mill and dry matter and ash content were determined following AOAC (1980). Feed samples (esophageal fistula samples in Study 1) for each steer/feed combination were analyzed for Kjeldahl N, P, and ether extract (AOAC 1980) and neutral detergent fiber, acid detergent fiber, and acid detergent lignin using Goering and Van Soest (1970) procedures. Crude protein (N $\% \times 6.25$), hemicellulose, and cellulose were calculated. In vitro digestibility was evaluated following Tilley and Terry (1963) as modified by Moore (1970) and Harris (1970). We composited rumen inoculum from 2 steers fed alfalfa hay. In vitro digestibility (48-h) of all samples was calculated from 3 replicates in each of 3 runs. In Study 2, microbial digestion periods of 0-, 4-, 8-, 24-, 36-, 60-, 72-, 84- and 96-h were used as well as the standard 48-h period. Two runs of triplicate tubes were used for all digestion periods in Study 2. Chemical composition of the 9 feeds is shown in Table 1.

For each feed we compared actual intake, estimated intake using total fecal output divided by in vivo indigestibility, and estimated intake using total fecal output divided by 48-h in vitro indigestibility using analysis of variance for a completely randomized design and LSD mean separation (Steel and Torrie 1960). Simple linear correlation was used to evaluate the relationship between in vivo and 48-h in in vitro digestibility.

Results and Discussion

Actual forage intake and estimated forage intake using the procedure of Van Dyne (1969) differed (P < .05) for 6 of the 9 forages in our study (Table 2). However, intakes estimated from

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Funding for the study was provided by the New Mexico Agr. Exp. Sta. This is journal article 1115 of the Agr. Exp. Sta., New Mexico State University, Las Cruces 88003.

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		Study 1				Stuc	ly 2		
Forage characteristics ^a	Milo hay	Alfalfa hay	Oat hay	Millet hay	Timothy hay	Bluestem hay	Alfalfa hay	Sainfoin hay	Kochia
Crude protein %	4.9	25.7	18.0	13.6	7.8	6.5	20.2	21.2	8.9
Phosphorus %	_	_	_	.20	.11	.10	.23	.40	.18
Ether extract %	1.75	1.76	2.00	2.01	2.22	2.19	1.98	1.94	1.62
Neutral detergent fiber %	76.9	48.1	74.2	68.7	70.2	77.9	44.4	52.3	68.1
Acid detergent fiber %	57.5	40.5	50.0	40.8	40.5	47.5	35.2	47.0	43.4
Acid detergent lignin %	8.4	9.6	11.3	3.2	5.3	6.2	7.5	9.3	6.8
Cellulose %	49.1	30.9	38.7	37.6	35.1	41.2	27.6	37.7	36.6
Hemicellulose %	19.4	7.6	24.2	27.9	29.7	30.4	9.2	5.3	24.7
Cellulose + Hemicellulose %	64.5	38.5	62.9	65.6	64.8	71.6	36.8	43.0	61.3
Digestibility % (in vivo)	54.0	71.0	67.0	72.0	69.0	60.0	69.0	70.0	59.0
Digestibility % (in vitro)	56.0	61.0	48.0	68.0	60.0	47.0	65.0	69.0	52.0
Organic matter intake (% body weight)	.87	1.98	2.00	2.55	2.23	1.21	2.74	2.32	1.18
Digestible organic matter intake									
(% body weight)	.47	1.41	1.34	1.84	1.54	.73	1.89	1.62	.70

"All forage nutritive quality data including in vitro and in vivo digestibility are on an organic matter basis.

Table 2. A comparison of actual forage intake (organic matter, % body weight) with forage intake estimated from total fecal output combined with in vivo and in vitro organic matter digestibilities.

	Actual ^a	intake	Estima intake (i digestil	ted ^{a,b} n vivo pility)	Estima intake (i digestil	ted ^{a,c} n vitro pility)
Study 1						
Milo	0.87 ^d	(9)	.78 ^d	(9)	.82 ^d	(8)
Alfalfa	1.98 ^d	(6)	2.07 ^d	(6)	1.54 ^e	(5)
Oat	2.00 ^d	(5)	2.12 ^d	(5)	1.35°	(6)
Study 2						
Millet	2.55 ^d	(2)	2.61 ^d	(2)	2.28 ^e	(3)
Timothy	2.23 ^d	(4)	2.23 ^d	(4)	1.77 ^e	(4)
Bluestem	1.21 ^d	(7)	1.10 ^d	(8)	.83°	(9)
Alfalfa	2.74 ^d	(1)	2.71ª	(1)	2.40 ^e	(2)
Sainfoin	2.32 ^d	(3)	2.57 ^d	(3)	2.48 ^d	à
Kochia	1.18 ^d	(8)	1.24 ^d	(7)	1.04 ^d	(7)

*Numbers in parenthesis represent ranking of intakes from highest (1) to lowest (9). Intake estimated using the equation: Organic matter intake (% BW) =

matter marce (% DW) =

(100) \times (total fecal organic matter output, % BW)

(100) - (% in vivo organic matter digestibility)

^cIntake estimated using the equation:

Organic matter intake (% BW) =

(100) × (total fecal organic matter output, % BW) (100) - (% in vivo organic matter digestibility)

^{d,e}Means in the row with different superscripts differ (P<.05).

total fecal output and in vivo digestibility were in close agreement with actual intake for all 9 forages (Table 2). We conclude that the procedure of Van Dyne (1969), which uses 48-h in vitro digestibility to estimate in vivo digestibility, may frequently be biased because in vivo and 48-h in vitro digestibilities may be poorly correlated (r = .65). We consider the regression Syx = (= 3.66)excessive for reasonable predictive accuracy of in vivo digestibility. With the exception of milo hay, in vitro digestibility underestimated in vivo digestibility in our study (Table 1). Studies with sheep (Wilkins and Grimes 1966, McLeod and Minson 1974), mule deer (Urness et al. 1977), goats (Sidahmed et al. 1981), and elk (Brooks and Urness 1984) have shown in vitro digestibility values from the Tilley and Terry (1963) technique can differ substantially (5 units or more) from in vivo digestibility for many feeds. In contrast, Scales et al. (1974) found in vivo digestibility values of 6 feeds fed to sheep were accurately evaluated by the Tilley and Terry (1963) technique.

A major problem with the Tilley and Terry (1963) procedures is that rumen retention time varies considerably among forages (Campling et al. 1961, Ingalls et al. 1966, Milchunas et al. 1978) and animal species (Poppi et al. 1980, Hendricksen et al. 1981). Ingalls et al. (1966) and Milchunas et al. (1978) indicated grasses have slower passage rates than dicots if their digestibilities are similar. Consequently, the 48-h microbial digestion period required by the Tilley and Terry (1963) technique may be too brief for grasses and too long for legumes. Table 3 shows 0-, 8-, 24-, 36-, 48-, 72-, 84- and 96-h microbial digestion periods and in vivo digestibility for the 6

Table 3. In vitro digestibility % for 9 periods of microbial digestion and in vivo digestibility % of the 6 forages in Study 2*.

						Feed % D	igestibilit	y				
	Alf	falfa	Sai	nfoin	Ko	chia	M	illet	Tin	nothy	Blue	stem
	x	SE	\overline{x}	SE	x	SE	x	SE	\bar{x}	SE	x	SE
Digestion												
Period (h)												
0	40	.52	34	.06	28	.12	28	1.58	25	.25	19	49
8	50	.50	50	.12	34	.17	37	1.31	28	.53	22	18
24	62	.40	63	.89	48	.49	55	1.96	49	.34	34	1 76
36	67	.41	67	1.24	52	2.01	67	1.44	56	1 35	42	65
48	65	.25	69	.86	51	.59	68	.78	60	1.00	47	.05
60	65	.38	69	.26	52	1.57	69	1.00	63	1 21	52	1.22
72	65	.47	68	.23	53	.60	70	1.04	64	1.37	51	11
84	65	.59	69	.61	54	.45	70	.05	65	.77	54	49
96	66	.53	70	.09	53	.39	71	.12	67	1.08	56	1.23
In vivo digestibility	69	.87	70	3.22	59	3.46	72	2.20	69	2.04	60	2 94

^aAll data are on an organic matter basis.

forages in Study 2. We surmise that a 36-h microbial digestion period for dicots and a 72-96-h microbial digestion period for grasses would provide more accurate estimates of cattle in vivo digestibility than the standard 48-h period. An alternative would be to observe 36-, 48-, 60-, 72-, 84-, and 96-h microbial digestions and select the highest in vitro digestibility value to estimate in vivo digestibility. The rationale for this approach is based on our observation that the time period giving the highest in vitro digestibility value for each feed in Study 2 also closely represented the in vivo digestion coefficient (Table 3). However, these procedures could inflate digestibility estimates of forages retained in the rumen for periods shorter than required for complete digestion. Because of its low fiber content and high intake (Table 1), the alfalfa in our study probably had a rapid passage rate. Its in vivo digestibility was estimated to within 2 units (Table 3) by both procedures we have suggested. Therefore, we believe these procedures have potential to improve in vitro estimates of in vivo digestibility. Information on mean rumen retention times of various range forages by cattle is needed to further establish the reliability of the procedures we have described.

Urness et al. (1977) and Brooks and Urness (1984) indicate the regression equations between in vivo and in vitro digestibilities can be used to improve the accuracy of in vitro digestibility estimates. However in vivo digestibility of many forages will still be poorly estimated even if regressions are used. The procedures we have described are much simpler than regression techniques and may be equal or superior in accuracy, particularly for forages with long retention times. Our suggestions appear to merit further study.

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Relationships among Soluble Phenolics, Insoluble Proanthocyanidins and Fiber in East African Browse Species

JESS D. REED

Abstract

Tannins and other phenolics interfere with the interpretation of results from the detergent system of forage analysis. Leaves and apices from browse can contain up to 50% of their organic matter as phenolics including tannins that are soluble in aqueous acetone. Leaves and apices from browse that contain soluble proanthocyanidins (condensed tannins) also contain proanthocyanidins that are insoluble in both aqueous acetone and neutral-detergent. The content of insoluble proanthocyanidins is positively correlated with neutral-detergent fiber (NDF) and fiber-bound nitrogen. Condensed tannins may bind protein and make it less soluble in neutral-detergent and increase the content of NDF. The behavior of phenolics and tannins in the detergent system of forage analysis is discussed in relationship to estimating the nutritive value of 17 East African browse species.

The detergent system of forage fiber analysis and the partitioning of cell wall from cell contents is widely used in determining the nutritive value of browse in the diets of mammalian herbivores (Van Soest 1967, 1982; Mould and Robbins 1981). Soluble phenolics and tannins can lower nutritive value of forages by toxic effects on the animal or through enzyme inhibition and substrate binding in the digestive tract (Wong 1973, Swain 1979). Insoluble proanthocyanidins (condensed tannins) occur in the leaves of legumes and other plant species (Bate-Smith 1973, 1975), but their effects on nutritive values have not been sufficiently studied. Insoluble proanthocyanidins may be involved in plant defense, associated with insoluble and enzyme resistant protein, and negatively associated with digestibility and palatability (Ford 1978, Stafford and Cheng 1980, Reed et al. 1982). An understanding of the relationship of tannins and other phenolics to the detergent system is essential to its use in predicting nutritive value of browse (Mould and Robbins 1981).

Materials and Methods

Browse samples were collected over a 9-month period, including 1 dry season and 2 wet seasons, in Kenya during a study on the nutritional ecology of game and cattle (Reed 1983). Leaves and apices from 17 species, 39 samples (Table 1), were air dried in a well-ventilated room. Due to low humidity drying occurred in 24 to 48 hours. The species sampled are important in the diets of wild and domestic ungulates.

Neutral-detergent fiber (NDF), acid-detergent fiber (ADF), acid-detergent lignin, hemicellulosc, and cellulosc were determined by the methods of Goering and Van Soest (1970), omitting decahydronaphthalene and sodium sulfite in the NDF procedure (Van Soest and Robertson 1980). Proanthocyanidins insoluble in neutral detergent were determined by methods described by Bate-Smith (1973) as modified by Reed et al. (1982). Five milligrams of NDF were placed in a test tube, 5 ml of 5% concentrated HCl in a n-butanol were added and the tubes heated at 100°C for 1 hour. Absorbance was read at 550 nm. If proanthocyanidins were present in the NDF, the n-butanol-HCl solution turned red when heated. Results were expressed as A_{550} per gram of NDF. Nitrogen in the NDF (NDF-N) of *Acacia* species was determined by a macro-Kjeldahl procedure using Na₂SO₄ and CuSO₄ in the diges-

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JOURNAL OF RANGE MANAGEMENT 39(1), January 1986

Table 1. Neutral-detergent fiber (NDF), soluble phenolics and insoluble proanthocyanidins in East African browse.

			Soluble	Insoluble Proantho-
		NDF	Phenolics	cyanidins
Species	Part	(%OM)	(%OM)	(A ₅₅₀ /g NDF)
Acacia albida	Leaves	39.9	21.5	17.3
Acacia brevispica	Leaves	42.7	18.4	16.9
Acacia drepanolobium	Leaves	42.5	24.8	31.5
Acacia drepanolobium	Leaves	47.3	18.7	47.5
Acacia drepanolobium	Apices	44.5	22.7	58.9
Acacia drepanolobium	Leaves	45.2	24.5	88.8
Acacia drepanolobium	Apcies	44.9	14.5	36.4
Acacia etbaica	Leaves	39.2	33.6	6.5
Acacia mellifera	Leaves	42.5	23.8	5.6
Acacia mellifera	Leaves	37.1	22.4	5.7
Acacia mellifera	Leaves	34.1	24.1	31.8
Acacia mellifera	Apices	37.0	18.0	32.8
Acacia nilotica	Leaves	20.1	59.4	2.6
Acacia nilotica	Leaves	23.7	56.1	2.7
Acacia nilotica	Apices	23.6	59.8	2.0
Acacia senegal	Leaves	41.2	15.4	4.1
Acacia seyal	Leaves	22.4	41.0	2.0
Acacia seyal	Apices	20.7	54.5	1.6
Acacia seyal	Leaves	20.4	46.5	2.9
Acacia seyal	Apices	18.7	51.9	3.7
Acacia xanthophloea	Leaves	39.2	25.6	47.2
Acacia xanthophloea	Leaves	43.4	25.1	106.8
Acacia xanthophloea	Apcies	45.1	31.0	57.8
Albizia harveyii	Leaves	64.4	14.4	420.5
Albizia harveyii	Leaves	58.8	22.5	370.0
Albizia harveyii	Apices	40.8	18.4	104.5
Carissa edulis	Leaves	38.1	30.6	153.3
Carissa edulis	Leaves	42.1	29.6	185.2
Carissa edulis	Apices	41.7	25.7	302.4
Commifera schimperi	Leaves	36.5	18.0	225.0
Grewia tembensis	Apices	43.5	17.3	37.8
Grewia tembensis	Apices	40.9	14.7	27.7
Ormocarpum		27.0	10.6	100.6
Ormoorganum	Leaves	37.0	19.0	109.0
Ormocurpum	A	22.0	22.5	02.4
Iracnycarpum Dhylanthus socialis	Apices	33.8 24 4	23.3	75.4 0.0
r nyummus septans	Aniores	34.0	14./	7.0 72 A
rnyianinus sepiaiis	Apices	21.5	10.3	23.4
Physical angle and a second se	Leaves	23.4	43.4	10.0
Rhus natalensis	Amicos	64.0	12.0	410.0
Knus natatensis	Apices	04.9	13.0	433.3
mean		38.7	27.4	90.6
standard deviation		11.9	13.7	127.8

tion mix and collecting the distillate in a boric acid solution. NDF-N was determined only in the *Acacia* species because these samples contained similar levels of total N. Phenolics and tannins soluble in aqueous acetone were determined by a gravimetric procedure based on precipitation by ytterbium acetate (Reed et al. 1985). All determinations were conducted in duplicate.

Results

Variation in the NDF, soluble phenolics, and insoluble proanthocyanidins was large (Table 1). There were only small differences

Table 2. Correlations between neutral-detergent fiber (NDF), acid-detergent fiber (ADF), hemicellulose (HEM), cellulose (CELL), lignin (LIG), soluble phenolics and insoluble proanthocyanidins (A550/g NDF) in leaves and apices of 17 East African browse species (39 samples).

	Soluble phenolics	Insoluble proanthocyanidins	NDF	ADF	HEM	CELL
A550/NDF	-0.39**					
NDF	-0.72***	0.75***				
ADF	-0.62***	0.75***	0.88***			
HEM	-0.58***	0.47***	0.79***	0.39**		
CELL	-0.66***	0.55***	0.68***	0.81***	0.26	
LIG	-0.40**	0.70***	0.79**	0.88***	0.37**	0.45**

***p*<0.01

in content of NDF between samples from the same part of the same species collected at different times of the year. Differences between browse species in content of NDF were related to differences in content of soluble phenolics and insoluble proanthocyanidins. Samples high in NDF were low to moderate in soluble phenolics and high in insoluble proanthocyanidins, such as *Rhus natalensis* and *Albizia harveyii*. Samples low in NDF were high in soluble phenolics and low in soluble proanthocyanidins, such as *Acacia seyal, Acacia nilotica,* and *Pterolobium stellatum.* These relationships led to a high negative correlation between soluble phenolics and NDF and a high positive correlation between soluble proanthocyanidins and NDF (Table 2) as shown in Figure 1. The relationships were similar for ADF (Table 2).

There was a low but significant negative correlation between soluble phenolics and insoluble proanthocyanidins (Table 2). Correlations of soluble phenolics and insoluble proanthocyanidins with other fiber components had the same signs as correlations with NDF and ADF.

Correlations between soluble phenolics, insoluble proanthocyanidins, and other fiber components in *Acacia* species were similar to those in the overall analysis, except the correlation between ADF and insoluble proanthocyanidins was low and non-significant (Table 3). NDF-N had a higher correlation with insoluble proanthocyanidins than with NDF. Correlations between NDF-N and hemicellulose and between hemicellulose and insoluble proanthocyanidins were high.

Discussion

In Acacia species, insoluble proanthocyanidins are associated with higher levels of detergent insoluble nitrogen which may result from formation of tannin-protein complexes. These complexes may be more soluble in acid detergent because insoluble proanthocyanidins form soluble anthocyanidins in acidic solutions (Bate-Smith 1975). Red solutions of anthocyanidins form when refluxing browse that contain proanthocyanidins in acid detergent. Since hemicellulose is assumed to be the difference between NDF and ADF in the detergent system, this property of insoluble proanthocyanidins would also contribute to higher hemicellulose values.

The behavior of phenolics and tannins in the detergent system is highly variable. Browse with high levels of soluble phenolics



Fig. 1. Relationship between neutral-detergent fiber (NDF) and soluble phenolics (A), and between NDF and insoluble proanthocyanidins (A₅₅₀/g NDF) (B) in leaves and apices of East African browse. Rhus natalensis and Albizia harveyii had high levels of insoluble proanthocyanidins and NDF and low levels of soluble phenolics. Acacia seyal, A. nilotica and Pterolobium stellatum had the opposite characteristics.

Table 3. Correlations between neutral-detergent fiber (NDF), acid-detergent fiber (ADF), hemicellulose (HEM), cellulose (CELL), lignin (LIG), neutral-detergent fiber-nitrogen (NDF-N), soluble phenolics and insoluble proanthocyanidins (A550/g NDF) in leaves and apices from 9*A cacia* species (17 samples).

	Soluble Pehnolics	Insoluble Proantho- cyanidins	NDF	ADF	HEM	CELL	LIG
A ₅₅₀ /g NDF	-0.28						
NDF	-0.89***	0.50**					
ADF	-0.78***	0.15	0.86***				
нем	-0.72***	0.74***	0.76***	0.32			
CELL	0.80***	0.07	0.80***	0.78***	0.50**		
LIG	-0.51**	0.20	0.69***	0.90***	0.13	0.44*	
NDF-N	-0.73***	0.80***	0.84***	0.52**	0.90***	0.43*	0.47*

p*<0.05 *p*<0.01

***p<0.001

(greater than 50% of the organic matter) have high levels of cell solubles. The assumption of high digestibility of cell solubles (Van Soest 1967) in these plants may be misleading and may confound methods for estimating nutritive value based on the summative equation. Large quantities of soluble phenolics may lead to an overestimation of energy value if absorbed and excreted in the urine. Soluble phenolics form indigestible protein and carbohydrate complexes in the digestive tract that increase apparent fiber and lignin excretion in the feces (Osbourn et al. 1971). Prediction of digestibility based on NDF, ADF, lignin or in vitro results need to be adjusted for the content of soluble phenolics.

The NDF from browse with high levels of insoluble proanthocyanidins contains condensed tannins and tannin-protein complexes. The assumption that NDF represents cell wall carbohydrates and lignin in these plants is incorrect. An estimate of the amount of insoluble proanthocyanidin associated with NDF can be obtained by heating NDF in n-butanol-HCl and measuring absorbance. However, converting absorbance to an equivalent amount of proanthocyanidin is difficult because standards are not available and proanthocyanidins differ widely in their reactivity toward n-butanol-HCl (Swain 1979).

Measurements of soluble phenolics and insoluble proanthocyanidins are essential to the determination of nutritive value because their presence in browse interferes with the detergent system of analysis. This problem needs much more research because the detergent system is widely used and has substantially contributed to understanding nutritional limitations in forages. Relationships among soluble phenolics, insoluble proanthocyanidins and fiber in browse species from the intermountain states (*Artemisia tridentata, Populus tremuloides, Prunus virginiana, Purshia tridentata, Salix brachycarpa, Salix planifolia* and Vaccinium spp.) were similar to those described for East African browse. These results will be reported in future publication.

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Nutrient Content of Sheep Diets on a Serpentine Barrens Range Site

R.E. ROSIERE AND CHARLES E. VAUGHN

Abstract

Nutritional composition of sheep diets from a serpentine barrens range site was determined at various seasons and stages of plant growth and compared to diets from 3 other annual range sites. Sheep diets from the serpentine site tended to be more nutritious, ranking in the highest pair of sites in digestibility, digestible energy, crude protein, and ether extract, and containing highest concentrations of magnesium. These differences were subtle and had limited application to management. Nutritional differences attributable to plant phenology were inconsistent but more dramatic than those due to site. Late summer and winter were potentially critical periods for brood ewes with protein and energy, respectively, likely to be marginal or possibly deficient. Contents of nutrients and nutritional properties did not differ between available herbage and forage selected by sheep from serpentine barrens.

Serpentine, igneous rock formed from peridotite as a complex of hydrous magnesium silicates existing essentially as H4MG3Si2O9 (Gilluly et al. 1975) is the parent material of several soils over an extensive area of the Pacific region including the Sierra Nevada and Coast Ranges of California, Siskiyou Mountains of Oregon, and Wenatchee Mountains of Washington (Whittaker 1954a). California serpentine was described by Kruckeberg (1984a and b). Serpentine soils are low in fertility due to either low levels of calcium (Vlamis and Jenny 1948); high levels of magnesium relative to calcium (Wildman et al. 1968); or low levels of nitrogen. phosphorus, or molybdenum and toxic levels of chromium or nickel (Walker 1954). Coupling these chemical properties with harsh physical factors such as shallowness, stoniness, and steepness creates an edaphic environment supporting such stunted and sparsely populated plants (many endemic) as to constitute a wasteland called "serpentine barrens" (Buol et al. 1980). While serpentine land has low potential for timber production (Storrie and Wieslander 1952), it is widely used as range particularly in coastal northern California where sheep ranching is a traditional livelihood. Sheep are in fact commonly observed grazing the readily distinguishable serpentine barrens apparently in preference to adjacent range sites.

This study was conducted to quantify and evaluate nutritional value of sheep diets from a serpentine range site and to explore causes for a generally perceived preference by sheep for vegetation growing in serpentine soil. To explain this apparent preference, nutritive values from the serpentine range site were compared to those from three nonserpentine range sites. Chemical compositions of soil from the 4 range sites were also determined because these were fundamental to differences among range sites and might explain nutritional differences detected among sheep diets from those sites.

Materials and Methods

Sheep diets were sampled at various seasons and plant phenolog-

ical stages (described under "Collection and Analysis of Diet Samples") in 1981 and 1982 on 4 range sites of annual range on the University of California Hopland Field Station situated in the Coast Mountain Range of northern California (about 160 km north of San Francisco Bay in Mendocino County).

Description of Study Sites

The 4 range sites (scrpentine barrens site, gravel slope site, loamy upland site, rock outcrop site) from which diets were sampled occurred on 4 Hopland sheep ranges. A description of each site follows.

Serpentine barrens site. Located on Hopland Range, Foster. Soil series was Montara¹ (Lithic Haploxeroll) having rapid drying and pronounced shrink-swell properties. Serpentine rocks ranged in size from gravel to stones. Rolling topography with mostly westward exposure.

Gravel slope site. Located on Hopland Range, Sl. Soil series were primarily Josephine (Typic Haploxerult) with some Laughlin (Ultic Haploxeroll), Los Gatos (Typic Argixeroll) and Sutherlin (Aquic Haploxeralf). Soils were clay loams with Josephine and Laughlin being shallow and gravely. Slope had south-west aspect.

Loamy upland site. Found on Hopland Range, S3. Soil was mostly Sutherlin plus some Josephine and Laughlin with lower gravel content than in the gravel slope site. Loamy upland occupied hill and ridgetops more than hillsides as in the previous range site.

Rocky outcrop site. Occurred on Hopland Range, D1. Soil was essentially all Sutherlin series with abundant outcroping of sedimentary rock. Topography was rolling with a northerly exposure.

Vegetation of gravel slope, loamy upland, and rock outcrop range sites would be best described as deciduous woodland savannah (Griffin 1977). These range sites were dominated by blue oak (Quercus douglasii)², black oak (Q. kelloggii), interior live oak (Q. wislizenii) and madrone (Arbutus menziesii) and, less conspicuous but locally more important, sclerophyllus shrubs such as chamise (Adenostoma fasciculatum) and manzanita (Arctostaphylos spp.). The 3 woodland range sites had herbaceous understories of naturalized annual grasses (mostly Bromus, Aira and Festuca spp.) and forbs (primarily Erodium and Trifolium spp.).

Vegetation of the serpentine barrens site was, by contrast, annual grassland (Heady 1977). This range site was populated by depauperate specimens of typical annual species and serpentineendemic herbs but largely devoid of woody plants.

Compositions of the herbaceous understories of plant communities were determined by step-point procedure (Evans and Love 1957) at period of peak standing crop and are shown in Table 1. Annual production of range biomass (Table 1) was calculated by clipping and weighing caged and grazed herbage periodically throughout the grazing year (fall germination to fall germination) by methodology described by Mannetje (1978). Grazing year degree of use was determined from these biomass data.

Collection and Analysis of Diet Samples

Samples of sheep diets were collected using 6 esophagealfistulated crossbred wool ewes. Collections were made during 6 seasons/plant phenological periods: (1) fall/start of green feed

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The authors express appreciation to B.E. Olsen and K.M. Rutz, research assistants, for gross energy determinations; A.H. Murphy, Superintendent Hopland Field Station, for administrative support; and Shu Geng, biometrician-California Agricultural Experiment Station, for statistical counsel.

This article is a contribution from the California Agricultural Experiment Station, Forestry Research Unit. Study supported as Hatch Project 3992. Manuscript accepted 9 May 1985.

¹Soil classification follows Soil Survey Staff (1975). ²Plant nomenclature from Munz and Keck (1973).

Table 1. Species^a composition^b (percent) and herbage yield^c (kg/ha) of four annual range sites in coastal northern California.

Serpentine barrens site		Nonserpentine sites:	Loamy upland	Gravel slope	Rock outcrop
Grasses:		Grasses:			
Soft chess		Silver hairgrass			
(Bromus mollis)	8	(Aira caryophyllea)	10	26	6
Gray's fescue		Wild oats			
(Festuca gravi)	4	Avena barbata & fatua)	7	1	2
Mouse barley		Soft chess			
(Hordeum leporinum)	7	(Bromus mollis)	27	33	52
		Ripgut brome			
Rush:		(Bromus rigidus)	10	5	2
(Juncus bolanderi)	Т	Red brome			
		(Bromus rubens)	1	3	-
Forbs:		Other annual Bromus		_	3
Mountain dandelion		Medusahead			
(Agoseris heterophylla)	8	(Elymus caput-medusae)	7	_	Т
Douglas sandwort		Annual fescues			
(Arenaria douglasii)	1	(Festuca spp.)	3	1	13
Goldfields		Wild barleys			
(Baeria chrysostoma)	16	(Hordeum spp.)	1	Т	6
Three-colored gilia		Other annual Gramineae	1	Т	1
(Gilia tricolor)	1	Purple needlegrass			
Common spikeweed		(Stipa pulchra)	1	-	Т
(Hemizonia pungens)	5				
Pepperweed		Forbs:			
(Lepedium nitidum)	Т	Filaree			
Microseris		(Erodium botrys & cicutarium)	16	11	Т
(Microseris douglasii)	11	Geranium			
California plantain		(Geranium dissectum & molle)	—		Т
(Plantago hookeriana		Lupine			
var <i>californica)</i>	14	(Lupinus spp.)	2	1	13
Plectritis		Clovers			
(Plectritis cilosa)	9	(Trifolium spp.)	4	8	2
Rancheria clover		Miscellaneous	10	11	13
(Trifolium albopurpureum)	6				
Miscellaneous	5				
Moss (Musci)	5				
Peak Standing Crop	441		1383	732	1399
Mean Herbage at Sampling					
Periods	282		1087	533	699

^aPlant names from Munz and Keck (1973).

^bDetermined at peak standing crop using step point method.

^cUnder grazing. T = Trace (less than 1%).

period (seedling stage), mid December; (2) winter/early green feed period (seedling-prebloom), early February; (3) early-mid spring/middle of green feed period (early bloom stage), early April; (4) late spring/peak standing crop (full-bloom), mid May; (5) mid summer/mature plants (seed ripe-seed shatter), mid July; (6) late summer/disintegrating plants (straw), mid September. Samples of available herbage were obtained during this same period by clipping (ground level) plants occurring in ten .09-m² plots. These plots were randomly located within areas from which forage samples were selected by the fistulated sheep. Collected samples were dried in large forced draft ovens (55°C) and then ground through a Wiley mill (1-mm screen). Nutritive analyses were done by procedures given by Association of Official Agricultural Chemists (1965) for dry matter, ash, ether extract, and crude protein. For in vitro organic matter digestibility, the two-stage procedure of Tilley and Terry (1963) was used. Fiber constituents (neutral detergent fiber, acid detergent fiber, acid detergent lignin, cellulose, hemicellulose, acid insoluble ash) were assayed by methods of Goering and Van Soest (1975). Heats of combustion were determined using adiabatic calorimetry (Parr Instrument Company, 1981). Digestible energy was estimated by multiplying gross energy by organic matter digestion coefficients. This was based on the assumption that digestibility of energy bearing components was approximately

equal to that of total organic matter content (Rosiere and Torell 1985). Mineral content was determined on nitric-perchloric acid digests; phosphorus with vanadate-molybdate yellow color development and calcium, magnesium, and potassium by atomic absorption spectrophotometry (Varian Techtron 1972).

Soil Analysis

Since edaphic features were the primary characteristics or bases for the 4 range sites studied, chemical compositions of their soils were determined (Table 2). Soil samples were collected from the surface 15 cm, air dried, and sieved (2 mm). Available soil P was determined by the Bray and Kurtz (1945) No. 1 method, available S was determined turbidimetrically on a calcium phosphate-acetic acid extract described by Hoeft et al. (1973), and available (or total inorganic) N was determined by the steam-distillation method described by Bremner (1965). Exchangeable soil Ca, Mg, K, and Na were determined by atomic absorption spectrophotometry following extraction with neutral N ammonium acetate. Exchange acidity was determined by a barium chloride-triethanolamine method (Peech, 1965). Soil pH was measured with a pH meter in a 1:2.5 soil water suspension.

Statistical Evaluation

Biometrical techniques were conducted according to Steel and

Torrie (1980). Effects of seasons on nutritional value of diets were analyzed by making comparisons between 6 periods of season and phenological stage, the treatments, in one-way analysis of variance (completely random design with unequal replication). Seasonal means of nutrients and energy, fiber, and digestibility were separated (P<.01) by Fisher's protected least significant difference (separation of means only if AOV F values were significant). Comparison of diets from serpentine barrens to those from other sites was made by viewing sites and seasonal periods as treatments in an unbalanced 4×6 factorial experiment using analysis of variance of completely randomized design. When F values were significant (P<.05) mean values were separated by Tukey's honestly significant difference procedure. Differences in nutritional variables between sheep diets and range herbage over all seasons were tested for significance using Student's t as were differences in utilization between serpentine and nonserpentine locations.

Dominant

Soil Series

Montara

Josephine

Sutherlin

Sutherlin

Range Site

Gravel Slope

Loamy upland

Rock outcrop

Serpentine barrens

Results and Discussion

Nutritive content of sheep diets from serpentine barrens is reported as organic matter digestibility, energy content, crude protein, ether extract, fiber constituents, and minerals (Table 3). Rosiere and Torell (1985) reported detailed nutritive composition of diets from the 3 nonserpentine range sites. Sheep diets from serpentine barrens varied significantly over seasons and from other sites. There were differences among sites for all nutrients, energy digestibility, and fiber portions except neutral detergent fiber and cellulose (Table 4). Highly significant seasonal differences occurred on serpentine range for all organic components except hemicellulose (Table 3). Significant site \times season interactions were detected for in vitro digestibility, digestible energy, ether extract, and acid detergent fiber.

pН

6.8

5.8

6.1

6.2

Available

P

ppm-

3

48

3

7

S

3.0

4.5

5.0

6.2

Ν

6.9

9.1

5.8

7.7

Differences in nutritional quality of sheep diets among sites over the 6 seasonal/phenological periods of this trial contrasted with data from a concurrent study by Rosiere and Torell (1985). They sampled during 8 periods, including early and late summer seasons of the previous year, and found no significant differences in dietary quality among the 3 nonserpentine ranges. Changes in nutrient content with progression of growing season and plant development were documented in the companion experiment.

Though statistical differences existed among diets from the 4 sites, these relations were general and inconsistent and their biological significance was unclear. Serpentine barrens tended to yield forage which was more nutritious than that from other range sites. It ranked in the highest pair of sites for digestibility, crude protein, and ether extract and was in the lower pair for lignin. It was in the highest pair for digestible energy on an organic matter basis but was intermediate in digestible energy when expressed as dry matter. The loamy upland site rated with serpentine barrens in digestibility and was high in digestible energy, but fell in the lowest pair of sites for crude protein and ether extract. Forage selected from the gravel slope site compared with that from serpentine barrens in ether extract but ranked in the lowest pair of sites for protein, energy, and digestibility. Diets from this steep, shallow site also contained significantly less hemicellulose than those from other sites and had the highest measured concentration of lignin. The rock outcrop site provided diets with nutritional contents interme-

Table 3. Nutritional composition^{ab} of ewe diets from a serpentine barrens range site in northern California at various seasons.

				Season		
	Fall	Winter	Mid Spring	Late Spring	Mid Summer	Late Summer
Crude Protein	16.2 ±2.5 ^{ef}	17.4 ±2.4°	13.2 ±1.5 ^{fg}	11.6 ± 1.3^{gh}	$9.1 \pm .4^{hi}$	7.6 ± 1.3^{i}
Ether Extract	$1.6 \pm .2^{fg}$	$1.5 \pm .2^{s}$	$2.0 \pm .1^{t}$	$2.5 \pm .0^{\circ}$	$2.1 \pm .1^{ef}$	$1.5 \pm .1^{s}$
Neutral Detergent Fiber	46.7 ± 2.4^{fg}	$50.8 \pm .5^{f}$	$41.8 \pm .7^{g}$	47.9 ±2.5 ^{tg}	59.0 ±2.7°	51.0 ± 1.6^{f}
Acid Detergent Fiber	32.0 ±1.5 ^s	$36.3 \pm .9^{f}$	$27.4 \pm .7^{h}$	32.0 ± 1.6^{g}	$42.2 \pm .9^{\circ}$	$38.2 \pm .5^{f}$
Acid Detergent Lignin	$4.3 \pm .3^{f}$	5.8 ±1.0 ^{•f}	$4.1 \pm .3^{f}$	$5.5 \pm .1^{ef}$	$6.9 \pm .3^{e}$	$5.1 \pm .7^{ef}$
Hemicellulose	$14.7 \pm .9$	14.5 ± 1.2	$14.3 \pm .5$	15.9 ±1.0	16.8 ±1.9	12.8 ±1.4
Cellulose	22.6 ± 1.8^{h}	24.3 ± 1.2^{g}	$19.8 \pm .6^{i}$	23.4 ± 1.7^{gh}	29.3 ±1.0 ^e	$27.8 \pm .6^{f}$
Ash ^c	14.40± .63	15.78± .37	13.62 ± 1.66	12.77±.41	13.72±.39	$13.24 \pm .22$
Calcium ^e	.17± .02	.32± .02	.25± .02	.28± .02	.29± .02	$.26 \pm .02$
Phosphorus ^c	.29± .02	.35± .02	.29± .02	.38± .01	.29± .04	.23±0
Potassium ^c	1.74± .17	$1.40 \pm .14$	$1.38 \pm .02$	1.51± .05	.71± .03	.47± .06
Magnesium	.58± .05	.65± .09	.58± .05	.76± .10	.49± .04	.81± .06
Silica ^a	5.29± .37	5.06± .43	3.46± .26	$3.12 \pm .22$	5.99±.36	5.29± .37
In vitro organic matter digestibility	62.7 ± 2.0^{ef}	$58.2 + 2.2^{fg}$	72.1 +1.9 ^e	62.5 ± 7.4^{f}	52.6 +2.2 ^g	60.6. ±1.7 ^{fg}
Gross energy (Mcal/kg drv						
matter)	4.41± .03°	4.35± .03°	4.28± .04°	4.10± .04 ^g	4.12± .07 ^{fg}	4.00± .02 ^g
Digestible energy (Mcal/kg dry matter)	2.95± .09 ^{ef}	2.53± .08 ^{fg}	3.08± .07 ^e	2.54± .11 ^{fg}	2.17± .06 ^h	2.43± .07 ^{gh}

^aMean + SE

(%) except gross and digestible energy; (dry matter basis) except in vitro digestibility.

Sheep saliva contained potassium, phosphorus and calcium at .056, .025 and .0025%, respectively.

^dMeasured as acid-insoluble ash. ^{efghi}Means in the same row having different superscripts differ (P < .01).

Table 2.	Some soil	chemica	characteristics	s of four typ	ical northe	rn Califori	nia annua	l range s	sites.
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Ca

1.2

4.2

3.4

2.0

Mg

24.2

1.1

6.8

11.4

Exchangeable

-meq/100 g-

0.3

0.4

0.4

0.4

Na

Tr.

Tr.

Tr.

Tr.

Н

6.3

6.3

4.8

4.7

Table 4. Mean contents^a of nutritional variables in ewe diets from four annual range sites (averaged over six seasons) in coastal northern California.

	Range Site							
Nutritional Variable	Serpentine Barrens	Gravel Slope	Loamy Upland	Rock Outcrop				
Organic Matter Digestibility	62.2 ^{bc}	62.6 ^b	55.6 ^d	58.7 ^{cd}				
Digestible Energy	2.62 ^{bc}	2.53°	2.76 ^b	2.67 ^b				
Crude Protein	12.5 ^b	9.9 ^{cd}	8.8 ^d	11.0 ^{bc}				
Ether Extract	1.9 ^{bc}	1.7 ^{cd}	2.2 ^b	1.5°				
Neutral Detergent Fiber	49.5	47.2	46.6	50.3				
Acid Detergent Fiber	34.7	34.3	37.0	34.8				
Acid Detergent Lignin	5.3°	5.8°	9.2 ^b	8.1 ^b				
Cellulose	24.6	25.6	25.7	24.2				
Hemicellulose	14.8 ^b	13.0 ^b	10.0°	15.5 ^b				
Magnesium	0.66 ^b	0.32 ^c	0.16 ^d	0.40 ^c				

^aAll values are percent (DM basis) except Digestible Energy (Mcal/kg dry matter). ^{bed}Means in the same row having different superscripts differ (P<.01).

Table 5. Mean contents^a of nutritional variables in ewe diets during six seasons (averages of four range sites) in coastal northern California.

	Season									
Nutritional Variable	Fall	Winter	Mid Spring	Late Spring	Mid Summer	Late Summer				
Organic Matter Digestibility	62.8 ^c	55.4 ^d	72.1 ^b	58.1°	53.4 ^d	57.9 ^d				
Digestible Energy	2.88°	2.4 ^d	3.17 ^b	2.49 ^d	2.33°	2.49 ^d				
Crude Protein	13.6 ^b	12.4 ^{bc}	12.0 ^{bc}	11.1°	7.4 ^{cd}	7.0 ^d				
Ether Extract	2.0 ^b	1.9 ^{bc}	2.1 ^b	2.1 ^b	1.4 ^{cd}	1.2 ^d				
Neutral Detergent Fiber	46.1°	52.8 ^b	41.9 ^c	45.0 ^c	53.5 ^b	51.9 ^b				
Acid Detergent Fiber	33.8°	38.7 ^b	28.8 ^d	31.7 ^{cd}	39.0 ^b	39.0 ^b				
Acid Detergent Lignin	5.9 ^{cd}	8.5 ^b	5.0 ^d	6.2 ^{cd}	7.9 ^{bc}	6.9 ^{bed}				
Cellulose	23.5 ^{cd}	25.4 ^{bc}	21.0 ^d	23.6 ^{cd}	27.9 ^b	28.5 ^b				
Hemicellulose	12.3	14.7	13.2	13.0	14.6	12.9				
Magnesium	.36°	.37 ^b	.40 ^b	.48 ^b	.32°	.42 ^b				

^aAll values are percent (DM basis) except Digestible Energy (Mcal/kg dry matter). ^{beds}Means in the same row having different superscripts differ (P<.01).

diate between loamy uplands and gravel slopes, but these were more similar to the latter, which appeared to furnish the least nutritious forage of the 4 range sites.

Seasonal variation in nutritional content for the 4 range sites (Table 5) followed characteristic changes coincident with advancement of plant growth and maturity (Van Soest 1982). However, these patterns and relations among nutritive characters within seasons/phenological stages were not clear-cut. Diets were most digestible and had highest contents of digestible energy in fall and mid spring when concentrations of cellulose and acid detergent fiber tended to be lowest. However, crude protein was higher in fall than in late spring and ether extract was lower in summer than in spring diets. Forage was least nutritious in summer periods when lowest digestible energy, crude protein, and digestibility coincided. This was not absolute, though, as digestibility was as great in late summer as in fall or late spring, and energy value in late spring (at peak standing crop) did not differ from that in late summer (least available herbage). Protein was clearly lowest (P < .01) at summer's end, but acid detergent fiber and lignin and ether extract at this period did not differ from that in winter forage.

The comparatively high contents of fiber and lignin in winter diets, together with relatively low digestibility and an intermediate energy level and a paucity of herbage, indicated that winter could be a nutritionally stressful season for sheep irrespective of high protein contents. Examination of winter diets from nonserpentine sites also suggested that winter could be a critical season (Rosiere and Torell 1985). Viewed generally, and in relation to probable low forage intakes due to limited herbage and high fiber/lignin levels, it seemed that nutritional deficiencies would be most likely in summer and winter with minimal factors being protein and energy, respectively. Likelihood of deficiencies would, of couse, depend on nutrient requirements as affected by reproductive status and performance. Crude protein levels in forage selected by ewes satisfied requirements, as stated by National Research Council (1975) in percentage of diet, for maintenance at all sampling periods except late summer, and for pregnancy or lactation except in mid and late summer. Digestible energy requirements (Mcal/kg) were met for ewe maintenance during all periods, but energy concentrations in summer periods were lower than late gestation and lactation standards. Problems with dietary deficiencies could be eliminated or reduced by scheduling breeding and marketing so that advanced pregnancy and lactation coincided with lower quality diets (summer and winter) for a minimum duration.

Minerals other than magnesium were not evaluated statistically because saliva from fistulated sheep contained quantities of elements (Table 3) which likely biased levels measured in esophageal extrusa. However, it was felt that an adequate characterization of sheep diets, especially on serpentine barrens noted for an unusual magnesium: calcium ratio, should include some mineral analyses. Magnesium contents were not contaminated by saliva and were highest on the serpentine site, lowest on the loamy upland site, and intermediate on outcrop and gravel slope sites (Table 4). Concentrations of magnesium were lowest in fall and midsummer diets but did not differ significantly among other seasons (Table 5). Magnesium concentrations in soil from serpentine barrens were measured at concentrations that averaged 3.7 times greater than that of nonserpentine soils (Table 2). Herbage from serpentine barrens contained 4.5 times more magnesium than herbage from loamy upland and gravel slope sites (.65 vs.14%). Magnesium in herbage from the rock outcrop site (.60%) did not differ from that in serpentine herbage. Magnesium contents of diets from all sites exceeded the .04-.08% requirement (National Research Council 1975) by at least four-fold. Calcium in forage selected from serpentine range (Table 3) was below upper levels of National Research Council requirements at all seasons and it must be assumed that contents were somewhat overestimated by salivary calcium. High levels of magnesium and low levels of calcium in serpentinederived soils detected in this and previous studies (Vlamis and Jenny 1948, Wildman et al. 1968) were reflected not only in composition of plants growing in serpentine soil but also in diets of animals eating these plants. These data indicated that ewe diets were marginal in calcium, but there were no signs of calcium deficiency in brood ewes grazing these ranges yearlong with no mineral supplementation.

These results agreed with findings from agronomic species grown on serpentine soils where plant productivity and foliage mineral contents were affected by calcium availability (Jones and Ruckman 1974) and calcium/magnesium ratios (Wallace et al. 1975, Jones et al. 1976), but deviated from outcomes seen by Wallace et al. (1975) for native shrubs which under greenhouse conditions were unaffected by adverse calcium/magnesium ratios and presence of heavy metals (lithium, nickel, chromium).

Selective grazing on the serpentine barrens site by sheep was not clearly substantiated in this investigation. There was no significant difference between range herbage and sheep-selected forage for any nutritional variable on an annual basis. This contrasted with sheep diets from other annual range sites. On both grass-woodland and improved grassland range, Rosiere and Torell (1985) documented grazing selectivity though it was infrequent and less pronounced than that reported by workers for other range types. On serpentine, relations between nutrient contents in sheep diets and those in range herbage varied with seasons, but statistical tests could not be conducted on a seasonal basis since there was no replication of the serpentine site. Magnesium, for instance, averaged two-fold greater in diets but was measured higher in herbage during half the sampling periods, so mean annual contents did not differ significantly between diets and herbage. Comparisons of animal-selected and available feed were further complicated by sampling, and the fact that on any given range theoretically there was only one composite of nutrients in herbage, but there were potentially as many diets as sheep grazing that range. Indiscriminate consumption of nutritional variables was consistent with the proposal of Arnold (1960) that there should be less selective grazing of more palatable species and less mature plants.

Limited selectivity in grazing yet obtainment of more nutritious diets on serpentine barrens may explain attractiveness of this site to sheep. They could obtain higher quality forage while grazing less discriminately and thus meet nutrient needs more effectively. though this might be offset by lower site productivity (Table 2) which could reduce forage intake or increase grazing time and energy expenditure. Less standing crop or low growth form of plants could also have been a factor in apparent preference for serpentine range. Throughout this trial sheep were frequently seen foraging in closely grazed or even bare areas while ignoring adjacent bounteous parcels. Spot-grazing often resulted in patchworks of nonuse even on heavily grazed rangeland where it resulted in partial starvation of sheep amongst plentiful feed supplies. This phenomenon was particularly conspicuous in the straw stage of the dormant period on range with serpentine sites and on rock outcrop sites with homogenous stands of soft chess (Bromus mollis), an annual grass widely regarded as more palatable at maturity than associated species (Bentley and Talbot 1951, George et al. 1983).

Endemic species may have been a further factor involved in attraction of sheep to serpentine sites. The unique serpentine plant community did, despite low standing crop, produce herbage that was more nutritious. Serpentine plants may have been more attractive to sheep because of a different chemical composition reflective of that in the soil (e.g., higher contents of magnesium).

Degree of use on the serpentine site during the 1981-1982 grazing was 69%, but approximately two-thirds of herbage remaining at

vear's end was unpalatable common spikeweek (Hemizonia pungens) so utilization of edible portions was realistically nearer to 90%. From 1958 to 1983 utilization of herbage on this site at peak standing crop averaged 62% compared to a mean of 39% (P<0.1) at 5 nonserpentine locations in Foster Range (A.H. Murphy unpublished data), indicating a preference by sheep for serpentine range. It was observed that heavy grazing had a probable effect on species composition or plant physiognomy of serpentine barrens communities. In exclosures and areas between rocks with limited exposure to grazing, purple needlegrass (Stipa pulchra), the perennial dominant of the original California bunchgrass region (Heady 1977), and California melic (Melica californica) were more conspicuous than in heavily grazed range populated with forbs and annual grasses. Latimer (1984) also noted that purple needlegrass was a conspicuous member of grassland communities on serpentine sites but was rare on nonserpentine soils. He found that soft chess and wild oats (Avena barbata) were the only annual grasses common on serpentine. From these observations it seemed likely that serpentine barrens under heavy grazing was partly a result of plant and animal interactions and not just a product of unusual pedological/mineralogical conditions. Groups of range plants associated with serpentine soils should probably be viewed from a perspective of grazing history as they may exist, using Daubenmire (1968) classification, as a "zoo-edaphic climax" (vegetation induced by animals as well as soil).

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Grazing Preferences of Cattle in Regenerating Aspen Forest

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Abstract

The relative preferences of cattle for the major plant species in regenerating aspen (Populus tremuloides) forest following burning were studied to assist in developing strategies for controlling aspen regrowth by grazing with cattle. The tendency of cattle to graze forest rather than grassland increased as grasses matured towards the end of the growing season. Within the forest, cattle preferred herbaceous species when they were present. Of the shrub species, generally wild rose (Rosa spp.) and wild raspberry (Rubus strigosus) were preferred over aspen but aspen was preferred over western snowberry (Symphoricarpos occidentalis). Aspen was grazed more readily late in the season than early. Similarly western snowberry, which was of consistently low acceptability, was relatively more acceptable late in the season. Cattle readily consumed wild raspberry in both years and both seasons. Wild rose was accepted early in the season in both years but was less preferred late in the season when it had relatively more woody growth.

Since aspen (*Populus tremuloides*) forest provides very little useful fodder for beef cattle, the carrying capacity of ranches that support areas of forest may be increased by replacing the forest with grassland. Following initial clearing operations such as clear cutting or burning, large numbers of new aspen suckers regenerate (Sampson 1919, Berry 1973, Perala 1979) but generally cattle consume very little of this material. Many beef producers consider that the foliage of aspen suckers is unpalatable to cattle, yet aspen is recognised as an important browse species for deer, elk and moose (Krebill 1972, Mueggler and Bartos 1977, Penner 1978, Parker and Morton 1978). In some situations browsing by ungulates has been heavy enough to threaten survival of aspen stands (Smith et al. 1972, Bartos and Mueggler 1979). If cattle would graze aspen suckers, then grazing might serve as a useful low-cost adjunct to other brush control practices, especially where logs and stumps prevent mechanical operations, and where cost is a limiting factor. Use of the grazing animal to remove regrowth offers the added advantage that the regenerating forest becomes a forage resource rather than simply something to be removed.

Sheep and cattle will graze aspen suckers under certain circumstances. Smith et al. (1972) reported that cattle grazed 18% of available aspen sprouts in the first year after clear cutting in Utah, but only 3 to 4% in the next 2 years. In Alberta, 3 years after herbicide treatment, Hilton and Bailey (1974) found that the consumption of available aspen by cattle with access to both grassland and regenerating forest varied between years from 3 to 43% by weight.

The reason for wide variation in utilization of aspen by cattle is not clear. The availability of alternative forages, and the phenologic stage of all species present, has a major influence on diets (Heady 1964). Rosiere et al. (1975) found that the diets of cattle on open grassland depended, partly, on the relative availability of the species present. Also the relative preference for various species changes through the season (Gammon 1978, Roath and Krueger 1982, Holechek et al. 1982).

Since these factors may influence the propensity of cattle to browse in a regenerating aspen forest, an experiment was conducted to determine the relative preference by cattle for the major species in a regenerating aspen forest seeded to forages and the adjacent grassland, as influenced by (1) season of grazing, (2) stand age and (3) defoliation of plant species present. The effects of grazing treatments on the botanical composition of the regenerat-

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The authors wish to thank Dr. W.D. Willms and Dr. R.T. Hardin for technical guidance and counsel, and Messrs. Holowaychuk, Taylor, Helland and Henry for assistance in the field. The senior author was supported financially by the University of Alberta and by the Department of Agriculture, N.S.W., Australia. Manuscript accepted 9 May 1985.



Fig. 1. Biomass estimates of grassland and forest (kg ha⁻¹) during early and late grazing in 1979 and 1980 showing 95% confidence intervals. In late-grazed forests 1979, only pre- and post-grazing estimates were available.

ing forest have been described by FitzGerald and Bailey (1984).

Methods

Experimental Site

The experiment was conducted during 1979 and 1980 on the University of Alberta Ranch at Kinsella, in the aspen parkland of Alberta. Average annual precipitation is 432 mm, 75% of which falls in the growing season. Precipitation in the growing season of 1979 and 1980 was 259 mm and 503 mm, respectively. The topography is strongly undulating, with aspen groves occupying most of the more mesic sites.

Experimental Procedure

A 7-year-old stand of aspen was burned on 15 May 1979. Fine fuel within the forest was estimated at 10 tonnes ha⁻¹ and total fuels at 40 tonnes ha⁻¹. With a wind speed of 2.4m sec⁻¹ and relative humidity of 40%, the fire (a headfire) consumed 15-20 tonnes of fuel and killed over 95% of all topgrowth. Three days after the fire, a seed mixture of 2.8 kg ha⁻¹ of alfalfa (*Medicago sativa* cv. Drylander) inoculated with rhizobium, and 7 kg ha⁻¹ each of bromegrass (*Bromus inermis* cv. Magna), orchard grass (*Dactylis*) glomerata cv. Kay), and creeping red fescue (Festuca rubra cv. Boreal) was broadcast into the ashes.

The area was subdivided into 6 paddocks, each 0.5 ha in size, to provide 3 replications each of the 2 grazing treatments. Approximately 30% of each paddock was native grassland; the remainder was regenerating aspen forest.

Cattle (cows and heifers) which had been maintained on aspen forest/fescue grassland were placed on the treatment paddocks either early or late in the growing seasons of 1979 and 1980. Each treatment paddock was grazed either early or late, not both. Cattle were retained in the treatment paddocks until all edible material had been consumed or trampled, in order to determine how their apparent preference responded to selective depletion of the various plant species present.

Grazing times were:		
1979 Early	July 5 to 17	(12 days)
Late	22 August to 1 September	(10 days)
1980 Early	31 May to 13 June	(13 days)
Late	August 15 to 23	(8 days)

The early grazing treatments took place when plant growth was



Fig. 2. Daily estimates of the biomass of aspen, wild rose, wild raspberry and western snowberry during early and late grazing trials in 1979 and 1980.

sufficient to support the smallest practical herd (3 animals) for 10 days. The late grazing treatments took place after elongation of aspen stems had ceased but before aspen leaves showed any yellowing prior to senescence. In 1979, complete defoliation within about 10 days required 8 animals ha⁻¹ for early grazing, and 25 animals ha⁻¹ for late grazing since there was more plant material to be removed. In 1980 the early treatment was grazed with 8 animals ha⁻¹, and the late treatment with 27 animals ha⁻¹.

Measurements

Herbage yield in the grassland was estimated prior to grazing and daily throughout the grazing period from the dry weight of plant material clipped from $6 (0.5-m^2)$ frames randomly placed in the grassland community in each paddock. Total yield of herbaceous and woody species within the forest was estimated prior to grazing and at intervals throughout the grazing period by harvesting all plant material within randomly placed 0.5-m² quadrats, 10 per paddock. In late-grazed forest in 1979, only pre- and post-grazing estimates were available.

To observe the differential grazing of individual species, 10 permanent $1-m^2$ quadrat sites were established randomly within the aspen forest in each paddock. The height and number of each species within these quadrats was measured prior to grazing and daily during the grazing period.

During the grazing trials in 1979, samples of the 4 major woody species in the regenerating forest were collected and used to establish relationships between plant height, entire or browsed, and above-ground plant weight, by the procedure described by Fitz-Gerald (1983). The process was repeated in 1980, for early-grazed aspen. Having estimated the mean weight of a species and recorded its density, the total above-ground weight (biomass) of that species could be calculated.

Statistical Analysis

The linear regression between biomass and days of grazing was computed within grazing period and species. Determination of differences among the regression coefficients of the 4 species within each grazing period was made using analysis of covariance homogeneity of regression procedures (Neter and Wasserman 1974, p. 702). Specific differences in species intercepts and slopes were computed according to Neter and Wasserman 1974, p. 166. The intercepts were estimates of species biomass before grazing.

Preference Index

Silen and Dimock (1978) developed a model to describe the relationship between plant palatability and availability. We used this model to develop a diet selection or preference index based on the changing level of availability of individual species through the grazing period.

The model employed a relative preference index (P), which encompassed the factors affecting an animal's response to a given species if availability of all species was equal. It also required an availability index (A), which was calculated as the biomass of a given species, expressed as a percentage of total biomass. The overall preference (P) for a given plant species could be determined from the re-arranged model as follows.

$$P = \frac{A_i}{n} \times \frac{P_i}{E_i} \times W_{(i-1)}$$

$$\sum_{i=1}^{N} \sum_{i=1}^{N} \sum_{i=1}^{N$$

where A_i = availability of a given species on the i th day. P_i = preference of the given species on the i th day. $W_{(i-1)}$ = total plant biomass at the beginning of the i th day. ΣA = availability of all plant species on the i th day. i=1 E_i = consumption of the given species on the i th day.

Daily consumption was assumed to be the weight of plant material removed each day. Material removed by trampling was assumed to be proportional to the amount consumed. The preference index was calculated for each day of grazing using an iterative computer program which substituted and readjusted estimated values of P.

The same analysis used for plant biomass was used to analyse apparent changes in relative species preference over the grazing period, the relative preference of plants on offer in an ungrazed forest, and their mean relative preference over the grazing period. For the latter, the preference index means adjusted to the covariate (days-grazing) mean were compared among species.

Results

Plant Community

The botanical composition of the regenerating forest estimated from height and density data in 1979, and direct sampling in 1980, is presented in Table 1. In addition to aspen, the major woody species were wild rose (*Rosa woodsii*), western snowberry (*Symphoricarpos occidentalis*) and wild raspberry (*Rubus strigosus*). Sown grasses became a significant component in 1980.

Habitat Selection

The biomass of regenerating aspen forest and adjacent grassland declined as it was consumed by cattle during the grazing periods in 1979 and 1980. (Fig. 1). In the early-grazing trial in 1979, cattle browsed very little in regenerating forest until the adjacent grassland yield had been reduced to 750 kg ha^{-1} . In the late-grazing trial, although measurement was limited to the beginning and end of the grazing period, field observations showed that the regenerating forest was utilized from the beginning of the grazing period and extensive browsing occurred when the grassland still yielded 180 kg ha⁻¹.

In 1980, a similar pattern of grassland and shrub removal was evident in the late grazing treatment but in the early grazing treatment the pattern changed. Consumption of 'forest' species up to day 4 was more rapid than consumption of grassland species.

Table 1. Botanical composition (%) and total biomass (kg ha⁻¹) of regenerating aspen forest in early and late grazed paddocks, estimated prior to grazing in 1979 and 1980.

	197	79†	19	80	
Aspen Rose Raspberry Snowberry Grass Other	Early	Late	Early	Late	
Aspen	23	36	29	2	
Rose	10	25	9	19	
Raspberry	17	14	2†	10†	
Snowberry	44	24	17	35	
Grass		_	28	18	
Other	6	1	15	16	
Total Biomass	450	3000	1400	2000	

†Estimated from density and height data.

The reason was that herbaceous species, mainly orchard grass, made up 30% of available forage in the regenerating forest under early grazing and animals grazed these preferentially. After day 4, the cattle preferred grassland, and reduced yields to about 300 kg ha⁻¹ by day 7. Dry weather prevailed in May 1980. On days 3, 4, and 5 of the early grazing period it rained. The effect of relief from drought on woody plants (as yet unbrowsed), produced a non-significant increase in available forest species from day 4 to day 9 (Fig. 1).

Forage Selection within Regenerating Forest

Aerial biomass of the 4 major woody species in the regenerating forest (Fig. 2) declined as it was consumed during each of the 4 grazing trials. Furthermore, the coefficients for the linear regressions of biomass on days grazing (Table 2-slope) showed significant differences among rates of decline of biomass during grazing. This analysis describes the rates of decline in biomass over the whole grazing period. In the early grazing period of both 1979 and 1980, there was little consumption of aspen in the first few days of grazing, after which it was consumed in preference to other species (Fig. 2). This was not evident in the late grazing periods.

Relative Preference Indices

Preference indices were calculated daily from each species by

Table 2. Estimates of the biomass (kg ha⁻¹) of four woody species at the commencement of grazing (intercepts) in early and late grazing treatments in 1979 and 1980, and coefficients (b) from the regression of species biomass on days grazing with grazing periods.

Grazing period	Spp.	Intercept (a)	Slope (b)	r ²
1979 Early	Aspen	130.1b	-11.1a	.33
·	Rose	44.1d	– 4.3c	.53
	Raspberry	81.4c	– 7.5b	.35
	Snowberry	189.4a	– 2.1c	.00
Std. Error		7.15	1.05	
1979 Late	Aspen	1079.9a	-24.9b	.16
	Rose	765.5c	-12.1c	.01
	Raspberry	432.2d	-21.8b	.52
	Snowberry	825.7b	-44.la	.39
Std. Error		14.6	2.16	
1980 Early	Aspen	487.5a	-16.7a	.06
	Rose	19.2c	– 1.3b	.16
	Raspberry	31.6c	– 2.6b	.27
	Snowberry	286.1b	– 2.5Ъ	.00
Std. Error		7.1	0.89	
1980 Late	Aspen	53.7d	- 5.6c	.05
	Rose	557.8Ъ	- 4.5c	.00
	Raspberry	352.3c	-17.3b	.06
	Snowberry	489.6a	-28.8a	.36
Std. Error	-	13.5	2.38	

a or b values within a grazing period followed by the same letter are not significantly different (P < 0.05).

 r^2 significant if greater than 0.12 (P < 0.05, 30 df).

Table 3. Preference index means adjusted to covariate zero (intercept), and to the covariate mean (mean), with standard errors, for linear regressions of preference index on days grazing.

Treatment	Intercept.	SEint	Mean	SE	r ²
1979 Early					
Aspen	.63b	.19	.70c	.08	.01
Rose	1.22a	.21	1.57a	.10	.16
Raspberry	1. 09a	.16	1.17Ъ	.07	.01
Snowberry	.23c	.24	.32d	.11	.00
1979 Late	· · · · · · · · ·				
Aspen	.79bс	.12	.50Ъ	.06	.53
Rose	1.05Ъ	.14	.59Ь	.06	.26
Raspberry	1.74a	.12	1.31a	.06	.24
Snowberry	.50c	.12	.96a	.06	.51
1980 Early					
Aspen	.12b	.21	.58c	.09	.18
Rose	2.07a	.24	1.88Ъ	.13	.05
Raspberry	2.44a	.25	3.18a	.14	.03
Snowberry	.18b	.39	.71c	.22	.17
1980 Late					
Aspen	2.25a	.25	2.22a	.11	.01
Rose	.67bс	.19	.36d	.09	.15
Raspberry	1.19b	.18	1.07Ъ	.08	.03
Snowberry	.10c	.23	.65c	.09	.47

Means within grazing periods followed by the same letter are not significantly different ($P \leq 0.05$).

r² significant if greater than 0.12 (P<0.05, 30 df).

grazing trial. These indices account for differences in the composition of the plant community and should be a more stable representation of preference than slopes that describe biomass disappearance.

Slopes of linear regressions of preference indices on daysgrazing were examined by least squares regression (Table 3). The least square means were adjusted to the covariate value zero (regression intercept) and to the covariate mean. The latter is an estimate of the preference index of each species over the whole grazing period at each time of grazing. Hence it is affected by preference characteristics of defoliated plants. The coefficients of determination (r^2) indicate the high degree of variability associated with these preference indices.

Preference for individual species at the onset of grazing (i.e., the intercept) was influenced by both season of grazing, and age of stand. Preference for aspen at commencement of grazing was lower early in the season than late. As early grazing proceeded and alternative species were removed, aspen became more acceptable to cattle, (Table 3-mean); but under late grazing it became progressively less acceptable as the more palatable portions were removed. Rose was relatively more acceptable to cattle early in the season than late. Its acceptance was lowest late in the second year, when rose had developed woody stems. Raspberry was preferred, regardless of season or stand age. This is not surprising, since, in 1980, regrowth consisted of new shoots from below ground. Snowberry was always among the least preferred species, but, like aspen, it became more acceptable as alternative species were removed.

To ensure that absence of some species towards the end of a grazing period was not resulting in unduly high mean preference indices for remaining species, the indices for the first 5 days of the grazing period were analysed separately. Results are not presented because they did not alter the relative preference rating of species, except the mean index for snowberry in late 1979 became equal to rose and aspen. Hence, the high relative preference of snowberry in late 1979 (Table 3) arose after day 5, when other forages were becoming scarce.

Discussion

Aspen was more acceptable to cattle when grazed late in the

season than grazed early. This is evident from both indices (intercepts, Table 3) and biomass curves. Similar findings have been reported by Bryant and Kuropat (1980), who showed that young shoots of woody shrubs were avoided by moose. Such shoots had a higher content of resins than older shoots and selection of shrubs by moose was strongly negatively correlated with the concentration of such resins. Smith et al. (1972) also observed that range cattle browsed aspen more readily in the second half of the growing season.

Snowberry was unpalatable in all seasons, but after initial avoidance, there was some evidence that it was grazed less reluctantly late in the season. Again, this may be related to concentration of resins in the foliage.

Rose and raspberry were highly preferred as young shoots in the first year. Raspberry continued to be favoured in the second year as it produced new tender shoots from underground rhizomes. Rose grew a woody stem from which small new shoots arose after each grazing period. This may account for differences in preference between these species late in the year.

Preference indices were calculated from data over the whole grazing period. It should be noted that such a calculation obscures changes in preference that may occur during the grazing period as a result of changes in the composition of the species on offer or changes in their character (e.g., proportion of leaf). Hence it is important when using preference indices either to interpret them in conjunction with species biomass curves, or to select grazing periods in which those curves are essentially linear; i.e., when there is little change in the character of the species on offer to the animals.

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Effects of Cattle Grazing on Mule Deer Diet and Area Selection

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Abstract

Split enclosures, half grazed and half ungrazed by cattle in summer, were compared for mule deer habitat use in late summer using tame deer. Diet composition, dietary nutrition, and area selected for grazing by mule deer were used as criteria to assess the grazing effects of cattle. Generally few dietary or nutritional differences were determined. Nonetheless, deer preferred to forage on areas ungrazed by livestock at low deer use levels, but this preference rapidly decreased as deer use increased.

Many reported studies have indicated proper livestock grazing maintains or improves habitat for mule deer (*Odocoileus hemionus*) (Smith 1949, Smith and Doell 1968, Jensen et al. 1972, Longhurst et al. 1979, Smith et al. 1979, Neal 1981, Urness 1981, Reiner and Urness 1982, and others). In such management situations short-term direct effects—primarily competition for forage and habitat—may adversely affect mule deer. Although many studies have dealt with dietary overlap between livestock and mule deer (Hansen and Reid 1975, Hubbard and Hansen 1976, Hansen et al. 1977, Vavra and Sneva 1978, Campbell and Johnson 1983, and others), few have determined changes in mule deer foraging behavior and quantified the results.

Previous study in this area (Austin and Urness 1985) determined forage production and plant variety were abundant in spring and early summer, and that forage selection by mule deer only became potentially restricted in late summer. Therefore the effects of livestock grazing on mule deer would also be expected to be most critical in late summer. Consequently it was the intent of this study to compare late summer diet and area preferences of mule deer on contiguous areas grazed and ungrazed by cattle.

Study Area

The study site was located in the Sheeprock Mountains of western Utah at 2,100 m elevation (Fig. 1). Precipitation averaged about 35 cm, received mostly as snow in winter. Typical of the scattered, north-south trending ranges within the Great Basin, the Sheeprock Mountains provide limited summer range, primarily comprised of broadleaved shrub communities which are the most extensive and important communities used by mule deer in this area.

The study site, comprised of mixed-browse communities, was managed by the U.S. Forest Service with a 3-pasture rest-rotation grazing system. During summer 1983, a grazing intensity of about 4.4 ha/AUM of cattle use was applied in the study area.



Fig. 1. Limited summer range, containing a diversity of plant communities, received heavy cattle use in the mixed browse vegetation of enclosure #1.

Methods

In spring 1983, prior to cattle use, four 0.2 ha sampling areas were established along 1.5 km of an east slope canyon. Half of each area, selected by coin toss, was fenced to 1.2 m height to exclude cattle. Use by wild deer continued throughout the summer, but the degree of use was not determined. Following the 1983 prescribed cattle grazing period ending in mid-August, the sampling areas were fenced to a height of 2.5 m, and the center dividing fence from each enclosure was removed (Austin et al. 1983).

Available forage production on each half of each enclosure was determined in August from 100 microplots (20×50 cm). The design consisted of 20 microplots spaced at meter intervals, along 5 evenly separated, parallel transects, established between opposite fence lines. Production of current annual growth was determined using weight-estimate by species with 1 in every 7 plots randomly selected, clipped, and forage weighed as a check for field estimates. Estimates were converted to an oven-dry basis via clipped samples.

Four tame mule deer, 3 adult bucks and 1 adult doe, were used to determine dietary and habitat choices in each enclosure. Deer were kept within a fifth enclosure to become acclimated to the available forage and area for 10 days prior to the first trial. In each enclosure

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This paper is a contribution of Utah State Division of Wildlife Resources, Federal Aid Project W-105-R.

Manuscript accepted 28 May 1985.

forage selection data were collected first, followed by area selection data. Dietary data were collected by leading individual deer into the enclosure, and then allowing the deer to graze freely until a minimum of 1,400 bites had been recorded. Bites taken on cattlegrazed and -ungrazed areas were recorded separately. After this first grazing period, all 4 deer were placed within the enclosure until an initial tame deer grazing pressure of about 20 deer-days/ha had been accumulated. During this period individual deer were observed on the grazed and/or ungrazed area to increase the number of bites. A minimum of 1,000 bites were collected on each half enclosure for each deer. Bites were converted to oven-dry weight via hand-plucked simulated bites (Neff 1974).

Selection for grazed and ungrazed treatments for foraging was determined by placing all 4 deer together in each enclosure for 24 hours. Scan sampling (Altmann 1974) at 4-minute intervals during the 14 daylight hours (6:32 a.m. to 8:28 p.m.) on 2 separate days was used. By the end of the first day about 40 deer-days/ha (includes initial grazing pressure) were accumulated, with about 60 deer-days/ha at the end of the trial. Foraging activity was recorded only during those instances when deer were selecting forage.

Following cattle grazing, but prior to the deer foraging trials, plant samples, based on observation of plant parts selected by deer during the acclimatization period, were collected from the grazed and ungrazed treatments. Percent crude protein (CP) and in vitro dry matter digestibility (IVDMD), using rumen inocula from elk fed alfalfa hay (Welch 1983, Brooks and Urness 1984) were determined from standard methods for species comprising 1% or more of mean diets from each enclosure treatment. All samples were run using a single inocula source with duplicates simultaneously. Dietary percent CP and IVDMD were weighted based on diet composition from individual deer.

Results

Grass production was generally uniform within the enclosures and since grass typically comprises a high proportion of cattle diets when available, the difference in available production between grazed and ungrazed areas was considered the major criterion defining the degree of cattle grazing. Most forbs were utilized by cattle at about the same degree as were grasses (Table 1); however, because forbs were distributed less evenly, particularly with respect to individual species, they were not used to assess cattle impacts. Total forage within browsing reach of mule deer on the areas ungrazed by cattle averaged 1,369 kg/ha with 294 kg/ha grass production; cattle use of grass averaged 66%.

Within enclosure 1 cattle removed about 76% of the available grass (Fig. 1). Use of palatable browse species, Utah serviceberry (Amelanchier utahensis Koehne) and mountain snowberry (Symphoricarpos oreophilus Gray), was visually apparent and sup-

Table 1. Available vegetal production (dry weight kg/ha) and mule deer diet composition (% dry weight ± SEm) of species comprising 1% or more of mule deer diets on split enclosures—half grazed and half ungrazed by cattle.

	Enclosure	#1				Enclosure	#2		
	Available	production	Diet co	mposition		Available	production	Diet con	nposition
Species	Grazed	ungrazed	Grazed	Ungrazed	Species	Grazed	Ungrazed	Grazed	Ungrazed
Amelanchier utahensis	3	75	31±8	18±5	Amelanchier utahensis	24	13	11 ± 4	14±3
Artemisia arbuscula	137	86	2 ± 1	Т	Rosa woodsi	3	6	5±1	2±1
Symphoricarpos oreophilus	70	206	23±6	17±4	Symphoricarpos oreophilus	367	282	36±9	25±11
7 other browse species	390	433	Т	Т	8 other browse species	1156	617	Т	Т
Total browse	600	800	56±3 •	** 35±5	Total browse	1550	918	52±10	41±12
Antennaria spp.	3	1	5±2	Т	Commandra umbellata	13	27	3±1	8±2
Commandra umbellata	5	38	2±1	15±6	Eriogonum racemosum	1	4	3±1	2±1
Eriogonum rasemosum	2	6	Т	5±2	Eriogonum umbellatum	3	3	1±T	Т
Eriogonum umbellatum	6	5	1±T	2 ± 1	Linum lewisii	Т	2	Т	5±2
Gavophytum spp.	Т*	Т	2 ± 1	Т	Lithospermum ruderale	2	Т	10±4	7±4
Linum lewisii	2	3	2 ± 1	1±1	Lupinus caudatus	167	106	3±2	3±1
Lithosperma ruderale	Т	Т	0	1±1	Polygonum douglasii	1	4	1±1 *	* 20±4
Polvgonum douglasii	2	6	22 ± 3	35±6	Solidago sparsiflora	4	8	14±5	10±4
Solidago sparsiflora	Т	Т	0	2±1	9 other forb species	11	54	1±1	1±1
10 other forb species	11	92	1±1	1±1	Total forbs	202	208	36±10	56±11
Total forbs	31	151	35±2 *	** 62±5	Total grasses	151	376	12±3	3±1
Total grasses	75	313	9±5	3±1	TOTĂL	1903	1502	100	100
TOTAL	706	1264	100	100					
	Enclosure	#3				Enclosure	#4		
	Available	production	Diet co	mposition		Available	production	Diet co	mposition
Species	Grazed	ungrazed	Grazed	Ungrazed	Species	Grazed	Ungrazed	Grazed	Ungrazed
Amelanchier utahensis	6	9	23±12	25±13	Amelanchier utahensis	12	18	3±3	6±2
Ouercus gambelii	284	282	49±12	2 39±6	Populus tremuloides	50	22	2±1	1±1
Symporicarpos oreophilus	210	207	16±4	10±4	Quercus gambelii	300	111	55±9	50±8
3 other browse species	129	95	0	Т	Rosa woodsii	14	16	5±2	7±2
Total browse	629	593	88±2	74±7	Symphoricarpos oreophilus	635	758	29±7	19±3
Eriogonum racemosum	1	4	Т	1±1	2 other browse species	418	205	Т	Т
Lupinus caudatus	91	317	4±2	2±1	Total browse	1429	1130	94±2	83±4
Polygonum douglasii	Т	2	Т	3±1	Chenopodium album	Т	1	Т	1±1
Solidago sparsiflora	Т	52	T'	** 15±4	Taraxacum officinale	5	14	2±1	12±7
Wyethia amplexicaulus	Т	4	0	2±1	17 other forb species	14	32	1±1	3±1
11 other forb species	12	75	1±1	1±1	Total forbs	19	47	3±2	16±8
Total forbs	104	454	5±2	24±7	Total grasses	28	175	3±1	1±1
Total grasses	173	312	7±3	2±1	TOTAL	1476	1352	100	100
TOTAL	906	1359	100	100					

*T = <.5

** Dietary contribution was significantly different (P<.05).

ported by available production data (Table 1). On the other 3 enclosures browse use by cattle was minor and was not readily observable. The heavier use of browse in enclosure 1 was attributed, in part, to being within 400 m of a major water source. No significant dietary differences for individual plant species were found between grazed and ungrazed areas because of the high variability of deer diets. However, the effect of cattle grazing did cause a significant (P < .05) shift from the forb-dominated diet selected by mule deer on the ungrazed area to a browse-dominated diet on the grazed area.

In enclosures 2 and 3 cattle removed about 60% and 45% of the grass production, respectively (Table 1). The only significant differences in deer diets between treatments in enclosures 2 and 3 occurred with 2 highly palatable forb species, goldenrod (*Solidago sparsiflora* Gray) and knotweed (*Polygonum douglasii* Greene).

Enclosure 4 contained the lowest production of grass, which led, in part, to the highest utilization level by cattle (84%). Available production and variety of browse species used by deer was highest in this enclosure, but no significant dietary differences occurred between cattle-grazed and -ungrazed areas.

Over all enclosures deer selected a significantly higher proportion of forbs on areas ungrazed by cattle (P < .05), whereas green grass and browse consistently contributed higher proportions on grazed areas (Table 1). Other browse as listed in Table 1 was unpalatable and highly dominated by big sagebrush (*Artemisia* tridentata Nutt.) in all enclosures.

Nutritionally, deer diets between cattle-grazed and -ungrazed areas showed few differences (Fig. 2). Crude protein values of deer



Fig. 2. Weighted % crude protein (CP) and % in vitro dry matter digestibility (DMD) from split enclosures—half grazed and half ungrazed by cattle.

diets were slightly and consistently, although not significantly, higher on the cattle-grazed areas, except enclosure 1 where a mean difference of 0.8% CP was significant (P < .05). In vitro dry matter digestibility averaged 58.0% on the grazed areas and 57.6% on the ungrazed areas. The only significant difference (P < .05) occurred in enclosure 2 where digestibility was over 60% for both grazed and ungrazed areas.

Upon first exposure to cattle-grazed and -ungrazed areas, individual deer selected forage in areas ungrazed by cattle (Fig. 3). During the initial dietary collection period (0-20 deer-days/ha) over all enclosures deer selected an average of 69.4% of the total bites in ungrazed areas and differences were significant (P < .05) in all enclosures.

Area selected for grazing when the 4 deer were placed together in the enclosures changed between days (Fig. 4). On the first day (20-40 deer-days/ha) deer spent a significantly (P <.05) higher percentage of time foraging in the cattle-ungrazed areas. Only in enclosure 3, where cattle grazing was lightest, was the difference not significant. In contrast, during the second day (40-60 deer-



Fig. 3. Percentage of bites selected by mule deer during the initial freeroaming grazing period on split enclosures—half grazed and half ungrazed by cattle.

days/ha) no significant differences were found.

Discussion

The influence of cattle grazing on mule deer was found to be variable depending on the intensity of cattle grazing and the criteria used to assess deer response. At levels of cattle grazing intensity where the primary impact was on understory vegetation, our data indicated that few individual species were altered in deer dietary composition, although deer diets were somewhat shifted in favor of browse and grass on grazed areas. The shift toward more grass and browse and fewer forbs in deer diets, which was significant only in enclosure 1 and over all enclosures combined, was probably primarily due to a lower abundance of forbs in cattle-grazed areas, and secondarily due to the sparse regrowth of grass. Nonetheless, neither CP nor IVDMD were significantly affected in deer diets.



Fig. 4. Percentage of grazing time spent by mule deer on split enclosures half grazed and ungrazed by cattle.

In contrast, deer did select areas ungrazed by cattle during initial foraging and subsequently during the first day of area selection observation. However, with increasing deer use during the second day of observation, selectivity for ungrazed areas was not found in any enclosure. When approximately 40 deer days/ha had accumulated, the selectivity for ungrazed areas was eliminated. At the heavier, probably excessive, level of cattle use where all classes of vegetation were significantly impacted, the effects on mule deer diet composition, area selection, and percent dietary CP were significant. Julander (1955) working on a similar nearby range indicated that proper use of grasses by cattle caused little effect on deer, but that over-grazing led to severe competition on the summer range.

Since mule deer and cattle diets often overlap by only 1-10% (Mackie 1981), including ranges similar to the Sheeprock Mountains (Lesperance et al. 1970), and social competition between deer and cattle is minor (Julander 1955, Kramer 1973, Skovlin et al. 1976, Willms et al. 1979), the relatively low level of significant differences due to cattle grazing found in this study is not surprising. Also the high mobility and forage selectivity of unconfined deer would tend to further reduce the effects of cattle grazing on deer diets (Lesperance et al. 1970) in contrast to our study where deer were restricted to small areas.

Parallel to our findings, Willms et al. (1980), using a similar experimental design, reported that deer diets between areas grazed and ungrazed by cattle were generally not different in the Douglas fir zone. They also indicated cattle grazing tended to shift deer diet selection toward heavier use of shrubs, and that with increasing deer use, differences between cattle-grazed and -ungrazed areas decreased. McMahan (1964) similarly found a shift in white-tailed deer diets toward more browse and grass, and less forb use on cattle-grazed areas in Texas.

We conclude the grazing effects of cattle, on mixed browse communities in the Great Basin, on mule deer diets and nutrition in summer are minor when intensity of cattle use is controlled such that cattle primarily use only understory vegetation. However, deer did prefer areas ungrazed by cattle at all levels of cattle grazing intensity studied when deer use was low; this preference was rapidly eliminated as deer use increased.

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Diet of Guanaco and Red Deer in Neuquen Province, Argentina

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Abstract

Spring and summer diets of guanaco (Lama guanicoe) and red deer (Cervus elaphus) in northern Patagonia were determined by the microhistological analysis of their droppings. Forbs were the main components of the guanaco diet both in spring and summer. Spring diet of deer was comprised mainly of grasses, whereas the summer was comprised equally of trees, shrubs, forbs and grasses. These results indicate differential use of the area by both species.

The 2 main wild ungulate species coexisting with domestic sheep in a large section of the southern Andean foothills are guanaco (*Lama guanicoe*) and red deer (*Cervus elaphus*). This area, called "precordillera," forms an ecotone between moist nothofagus forest to the west and arid steppe vegetation to the east (Anchorena 1978).

Sheep were first brought to the area toward the end of last century. Overgrazing by the sheep has been blamed for habitat deterioration. Guanaco is a species native to the area and widely distributed throughout all Patagonia. Its number have decreased considerably as a result of deterioriating habitat and excessive hunting (Raedeke 1980). Red deer were introduced in the area at the beginning of the century and have since increased considerably in number and area of distribution (Staudt 1978).

Guanaco, deer, and sheep diets have been determined separately in a variety of different habitats (Crocker 1959, Wardle et al. 1970, Mitchell et al. 1977, Bonvissuto and Moricz 1981, Ramīrez et al. 1981, Tilton and Willard 1981, Clutton-Brock et al. 1982, Bonvissuto et al. 1983). The purpose of this study was to expand the knowledge base by determining the spring and summer diet of guanaco and deer feeding on the same precordillera area.

Methods

The study was undertaken in Estancia Fortin Chacabuco, Depto. Los Lagos, province of Neuquén (41°S; 71°W). The climate in the area is cold, subhumid to dry. Altitude varies between 800 to 1,300 m. The study site is characterized by the predominance of grassland communities of "coirón" (*Stipa speciosa* var: *major*) and "coirón blanco" (*Festuca pallescens*) and shrub communities composed mainly of "neneo" (*Mulinum spinosum*) in a smaller proportion, interspersed by subantarctic gallery forests of "chacay" (*Chacaya trinervis*), "laura" (*Sochinus patagonicus*), "chapel" (*Escallonia virgata*), "pañil" (*Buddleja globosa*), "ñire" (*Nothofagus antarctica*), "parrilla" (*Ribes* spp.), "maitén" (*maytenus boaria*), alongside rivers and canyons.

Fecal samples were collected in October 1982 and January 1983 for microhistological analysis.

Each sample consisted of pellets from at least 10 different fecal groups in the case of deer, and from 10 different communal defecating areas used by guanacos. Because of the communal defecating habit of guanacos, it is impossible to sample for individual animals. All collected pellets were composited for season and species.

In addition, a composite sample of both old and new pellets deposited throughout the year was collected for each species, forming an annual sample of the diet composition in the area.

Samples were processed according to the method used by Willi-

ams (1969) and modified by Latour and Pelliza Sbriller (1981). For each sample, 400 microscopic fields were examined at 200x. The identification of the epidermic elements was undertaken using a key developed for the area by Latour and Pelliza Sbriller (1981). Relative frequencies, considered by Holechek and Gross (1982) to be the best estimators of dry weight, were determined for each of the species identified. These values represent the proportion of microscopic fields in which an individual species is present with respect to the total number of fields with identified species.

Relative frequency of species A: =

Number of Fields with species $A \times 100$

Number of fields with identified species

The sum of these values for all the species which comprise each group (trees and shrubs, forbs, grasses and grass-likes) represent the relative frequency of these groups.

Results and Discussion

Results of the microhistological examination of guanaco and deer feces collected during the spring and summer are given in tables 1 and 2. Table 3 shows the results of composite samples of feces of different deposition time throughout the year representative of the annual diet of guanaco and deer.

For guanaco, the main forages in the spring diet were Acaena spp. (38.3%), Festuca pallescens (13.8%) and Poa spp. (9.9%). Forbs accounted for 44.3% of the diet, grasses 32.4%, trees and shrubs 13.8% and grass like plants 6.7%. Major contributors to the summer diet were again Acaena spp. (50.0%), Poa spp. (11.5%) and Colletia spinosissima (5.7%). As with the spring diet, forbs were the major contributors at 50.2%, grasses next at 17.7%, trees and shrubs followed at 15.8% and grass-like plants last at 3.3%. Guanaco summer diets contained less grass and grass-like plants than the spring diets. In the composite fecal sample of old and new pellets deposited throughout the year, Mulinum spinosum (23.2%) and Colletia spinosissima (18.9%) were the main species consumed. Trees and shrubs accounted for the major part of the diet (59.6%) followed by forbs (15.4%) grasses (15.4%) and grass-like plants (5.6%). This differs from the spring and summer diet and would indicate an intensive use of trees and shrubs by the guanaco especially in the winter months.

For red deer, the main forages in the spring diet were *Festuca* pallescens (24.9%), Stipa sp. (35.1%) and Mulinum spinosum (5.4%). Grasses accounted for 66.8% of the diet, grass-like plants for 9.8%. Trees and shrubs 9.3% and forbs 5.4%. In summer, however, the most frequent species in the diet of the red deer were Stipa sp. (21.8%), Acaena spp. (20.1%), and Fabiana imbricata (8%). Trees and shrubs became more frequent (33.9%) followed by grasses (32.7%), forbs (24.7%) and grasslike species (5.2%). The composite fecal sample of old and new pellets deposited throughout the year showed an increased use of trees and shrubs (53.1%) followed by grasses (25.2%), grass-like plants (9.5%), and forbs (8.1%).

From this study it is clear that some spring diet overlap occurs between the two wild ungulate species, particularly in the grass group. Both consume significant amounts of *Festuca pallescens*.

Authors are with I.N.T.A. - E.E.R.A. Bariloche, C.C. 277 - Argentina. Manuscript accepted 11 June 1985.

 Table 1. Species composition of spring diet of guanaco and red deer in Neuquen.

	% Frequency	% Frequency
Species	Guanaco	Red Deer
Trees and shrubs	<u>.</u>	
Maytenus boaria	3.6	3.9
Fabiana imbricata	3.2	*
Buddleja globosa	2.8	_
Mulinum spinosum	2.8	_5.4
Berberis spp.	1.6	_
Forbs		
Acaena spp.	38.3	*
Verbascum thapsus	2.4	5.4
Erodium cicutarium	2.4	_
Heliotropium spp.	1.2	*
Grasses		
Festuca pallescens	13.8	24.9
Poa spp.	9.9	54
Bromus spp.	4.7	1.5
Stipa spp.	4.0	35.
Grass-likes		
Juncus balticus	4.0	5.9
Carex spp.	_	3.9
Compositae	2.8	+

*Species present with frequency below 1%.

However, only red deer consume significant quantities of *Stipa* sp. and very little of the guanaco's major food, *Acaena* spp. In general red deer spring diet is more dependant on grasses whereas guanacos depend on an even split between grasses and forbs. Forbs are consumed by both species in considerable quantities in summer, especially *Acaena* spp. The main grass species consumed by guana-

Table 2. Composition of summer diet of guanaco and red deer in Neuquen.

	% Frequency	% Frequency
Species	Guanaco	Red Deer
Trees and shrubs		
Colletia spinosissima	_5.7	6.9
Mulinum spinosum	3.3	1.1
Maytenus boaria	2.4	4.6
Berberis spp.	2.4	2.9
Fabiana imbricata	1.9	_8.0
Chacaya trinervis	+	3.4
Ephedra frustillata		6.9
Forbs		
Acaena spp.	50.0	20.1
Erodium cicutarium	10.5	_
Tetraglochin ameghinoi	_	1.1
Eryngium paniculatum	—	3.4
Grasses		
Poa spp.	11.5	2.9
Stipa spp.	3.3	21.8
Festuca pallescens	2.9	3.4
Rytidosperma virescens		2.3
Bromus spp.	—	2.3
Grass-likcs		
Juncus balticus	1.4	2.3
Eleocharis albibracteata	_	2.9
Compositae	1.9	*

*Species present with frequency below 1%.

Table 3. Species composition of annual diet of guanaco and red deer in Neuquen.

	% Frequency	% Frequency
Species	Guanaco	Red Deer
Trees and shrubs		
Mulinum spinosum	<u>23.2</u>	2.7
Colletia spinosissima	18.9	9.9
Berberis spp.	7.6	1.4
Fabiana imbricata	5.3	4.9
Ephedra frustillata	2.3	<u>21.1</u>
maytenus boaria	2.3	<u>10.4</u>
Chacaya trinervis	_	1.4
Adesmia spp.		1.4
Forbs		
Acaena spp.	<u>15.4</u>	*
Eryngium paniculatum	—	4.1
Ranunculus peduncularis		4.1
Grasses		
Poa spp.	8.1	3.6
Festuca pallescens	5.5	3.6
Bromus spp.	1.8	*
Stipa spp.	*	<u>18.0</u>
Grass-likes		
Juncus balticus	4.3	2.7
Carex spp.	1.3	5.4
Eleocharis albibracteata	*	1.4

*Species present with frequency below 1%.

cos in summer is *Poa* sp. whereas *Stipa* spp. is preferred by deer. Guanacos are more dependent on forbs in summer whereas red deer consume similar amounts of grasses, trees and shrubs, and forbs.

Trees and shrubs make up the major part of the diet of both species throughout the year; however, forbs are more important in the guanaco diet whereas grasses are for red deer.

Species composition of the guanaco diet would indicate a preference for gallery forest and shrub communities composed mainly of *Colletia spinosissima* and *Mulinum spinosum*, respectively, at an intermediate height on the slopes in the area. Deer, on the contrary, would make use of the low meadow communities in spring and of the intermediate height communities in summer and possibly the rest of the year.

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Dietary Selection by Goats and Sheep in a Deciduous Woodland of Northeastern Brazil

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Abstract

The dietary botanical composition of indigenous sheep and goats was determined in the semiarid tropics of northeastern Brazil, using esophageally fistulated animals. Sheep and goats selected similar diets during the dry season (May-Dec.). Main dietary components for both species were dried forbs and browse. Leaf litter from the deciduous trees provided the majority of dry season forage (500-1,500 kg/ha) and was a crucial element of dry season diets (20-70%). During the wet season (Jan.-Apr.), sheep selected mainly grasses and forbs, while goats rapidly shifted among grasses, forbs, and browse. By displaying attributes of both browsers and grazers, neither sheep nor goats conformed to traditionally rigid characterization. We found no indication that goats are better adapted for survival in this tropical environment than are sheep because of the botanical composition of their diets. Management implications of this study for the caatinga vegetation zone are discussed.

Although range science literature is replete with studies reporting detailed data on diets of cattle and sheep, few investigations have examined diets of goats grazing alone, or in common with other livestock (Malechek and Provenza 1983). Van Dyne et al. (1980) catalogued studies of livestock diets, and noted 5 and 38 such studies for goats and sheep, respectively. Only 3 studies listed in this paper compared dietary selections by goats and sheep grazing together on common ranges. No work has been done using esophageally fistulated animals to examine diets of either goats (*Capra hircus*) or sheep (*Ovis aries*) in northeastern Brazil.

Generally comparisons of the dietary selections of goats have been made with sheep of European origin. Little information is currently available on selectivity of tropical hair sheep or goats.

The authors wish to thank the personnel of the Centro National de Pesquisa de Caprinos for provision of physical facilities and assistance during the study. We are especially grateful to Venceslau Alves Costa, Animal Husbandryman, for his assistance. Manuscript preparation supported by Texas Tech University.

Manuscript accepted 25 April 1985.

Goats have acquired a reputation for survivability on harsh, degraded rangeland (Devendra 1978). This may be due, in part, to unique dietary selections made by goats (McCammon-Feldman et al. 1981). French (1970) maintained that high survivability by goats was related to their relatively unspecialized feeding habits. Increased specialization implies fewer plant species or parts eaten. Observations have indicated that goats eat a wider array of plant species than do other livestock (French 1970, Wilson et al. 1975).

Conversely, Van Soest (1980, 1982) stated that goats should display more specialized feeding habits than do sheep, based on body size, gastrointestinal capacity, nutrient requirements, and feeding strategy. He classified goats and sheep in 2 ways. First, goats are classified as forb- or browse- preferring intermediate (between browsers and grazers) feeders, and sheep as grasspreferring intermediate feeders. Van Soest's (1982:7) second classification lists goats as intermedite browsers, and sheep as grazers.

Livestock producers in northeastern Brazil prefer to raise sheep over goats (Gutierrez et al. 1981) because of many complex socioeconomic factors (Primov 1982). For instance, sheep do not require the less penetrable, more expensive fencing required for goats, especially adjacent to cropland. On the other hand, goats are often viewed by Brazilian producers as a form of drought insurance because of their reputed survivability and minimal requirements for supplemental feeds during droughts.

The objectives of this study were to determine the botanical composition of goat and sheep diets on a seasonal basis, and to evaluate the selective feeding strategies of goats and sheep. Such information would provide a basis for more sophisticated management and insight into the question of comparative adaptability of the 2 species.

Study Area

The 40-ha study area was situated on the Brazilian National Goat Research Center (CNPC), 10 km from Sobral, Ceara' state, Brazil. Sobral is located at 3.42° south latitude, 40.21° west longitude, at an elevation of 63 m. The landscape in the study area is slightly undulating. Soils are generally eroded, shallow clays (45-130 cm), underlain with crystalline bedrock.

Climate

The climate in the Northeast is characterized by distinct wet and

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Research was financed by USAID Grant No. AID/DSAN/XII-G-0049 as part of the Small Ruminant Collaborative Research Support Program in cooperation with Empresa Brasileira de Pesquisa Agropecuaria.

dry seasons. The dry season typically extends from June to December, although periodic droughts may extend the dry season to 11 months. The wet season usually extends from January through May. Periodic droughts are characteristic of this region (Freise 1938, Trewartha 1981).

The 30-year average precipitation in Sobral, and precipitation for 1981 and 1982 are 759, 538, and 650 mm, respectively. Variability in the annual amount, as well as the spatial and temporal distribution of moisture, is extreme (Freise 1938). Temperatures are hot, exceeding 32°C almost every day, with little seasonal variation.

Vegetation

The vegetation of this region is called *caatinga*, an Indian word meaning white forest (Ferri 1980), so-called because the deciduous woodlands have a whitish aspect during the dry season. *Caatinga* vegetation is not homogenous, but is a complex mix of deciduous trees and shrubs with an annual herbaceous understory (Ferri 1980, Pfister et al. 1983). The *caatinga* is noted for its density, diversity, and absence of perennial grass cover (Eiten and Goodland 1979).

The 40-ha pasture used in this study supported a stand of *caatinga* vegetation. These woodlands are areas of second or third growth that have not been recently cleared (i.e., within 20 to 40 years). Principal tree species on the study area are pau branco (Auxemma oncocalyx Taub.), sabia' (Mimosa caesalpiniaefolia Benth.) catinguera (Caesalpinia pyramidalis Benth.), marmeleiro (Croton hemiargyreus Muell. Clrg.), mororo' (Bauhinia forficata Link), and mofumbo (Combretum leprosum Mart.). Important annual herbaceous plants include Hyptis spp., Bainvillea spp., Phaseolus spp., and jitirana (Ipomoea spp.), a climbing vine. Dominant annual grasses are Paspalum spp., and Panicum spp., with numerous other genera represented (Pfister et al. 1983). The taxonomical classification of many plant species in this area has not been completed.

Methods

The native hair sheep and SRD (Sem Raca definida- without definite race) goats used in this study were about 2 years old and weighed about 18 kg when the sampling began. At approximately monthly intervals, 6 to 8 esophageally fistulated sheep or goats were used to collect diet samples in the 40-ha pasture. The 30

min. collections were done at 0530 hr for 3 consecutive days.

Extrusa samples obtained from fistulated animals were mixed and divided into 2 portions. One portion was frozen at -17° C, and the other dried at 40°C for 3 days. The latter was used for botanical determinations after pooling sub-samples over the 3 days for each individual animal.

Botanical composition was determined by the microscope point method of Harker et al. (1964). Plant tissue was systematically identified at 200 points per sample at 15x. Plants were identified by species, as leaf or stem, fruit or flower, or as unidentifiable.

Forage availability (kg/ha) was estimated by hand-harvesting all herbaceous vegetation within 30-40, $0.5m \times 0.6m$ randomly placed quadrats. Leaf litter was estimated by collecting dried leaves from these same quadrats. Tree foliage was estimated by stripping all leaves to a browsing height of 1.6 m from a sample population of the 4 major tree species: pau branco, sabia', catingueira, and mororo'. These 4 species were initially thought to be the only trees acceptable to livestock. Thirty individual trees of each species were randomly selected and stripped during each sampling period (except during September). Tree density was determined by counting individuals in 30 randomly placed $4m \times 10m$ plots, and availability of browse forage was calculated by multiplying the unit foliage per tree by the density estimate.

Data analysis was done using the statistical package Rummage (Bryce et al. 1980). The experimental design was a split-plot design with repeated measurements comparing sheep and goats, with individual animals nested (Gill 1978:203). Repeated measurements in 1981 were made during May 26-28, June 17-19, July 21-23, August 17-19, September 4-6, October 28-30, and December 14-16. Collection periods in 1982 were January 6-8, February 17-19, and April 26-28. Least squares analysis of variance was used for statistical analysis, with the protected LSD procedure used to compare individual means.

Results

Forage Availability

Leaf litter was clearly the dominant component of the available forage in the dry season (July-Dec., 1981) (Fig. 1). Peak amounts of leaf litter (1,500 kg/ha) were recorded in August. In October and December about 500 kg/ha of leaf litter was recorded. Herbaceous material and tree foliage contributed relatively little to the available forage after the early dry season (May-July).



Fig. 1. Biomass (kg/ha) of available forage during 10 sample periods, 1981 and 1982.

Table 1. Mean botanical composition (% and standard deviation) of goats' and sheep diets during 10 sample periods, 1981 and 1982 in northeastern Brazil.

	N	Aay	1	lune		July	A	ugust	Sep	tember
	sheep	goats								
Forbs										
Jitirana (Ipomoea spp.)	43.6 (9.8)	71.5(17.8)	9.6 (6.7)	21.3(15.2)	32.9(11.1)	71.6 (9.4)	58.6 (9.4)	55.1(19.7)	21.4 (4.5)	32.4(16.9)
Paco-Paco (Wissadula spp.)	0.0	0.0	2.2 (5.9)	0.0	4.2 (3.9)	2.0 (1.1)	2.3 (3.6)	6.1 (7.2)	0.0	0.0
Bambural branco (Bainvillea spp.)	0.0	0.0	0.0 ` ´	0.0	0.4 (0.5)	0.9 (1.2)	2.8 (2.5)	3.2 (3.4)	1.1 (1.7)	7.6(15.9)
Bambural verdadeiro (Hyptis spp.)	1.8 (1.8)	1.6 (3.9)	0.3 (0.7)	0.0	0.0	0.0	0.3 (0.6)	1.0 (1.0)	1.4 (1.7)	0.0
Bambural russarente (unclassified)	0.0 `	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mariana (Commelina spp.)	18.1 (8.0)	0.0	18.0(13.6)	3.1 (4.3)	0.4 (0.6)	0.3 (0.7)	0.8 (0.9)	0.8 (1.5)	0.0	0.0
Other forbs	8.8 (1.7)	3.8 (2.4)	8.8 (7.3)	3.9 (4.2)	0.1 (0.2)	0.5 (1.1)	7.0 (3.5)	4.4 (3.2)	2.3 (2.5)	0.4 (1.1)
Total forbs	72.3 (7.0)	76.9(14.8)	38.9(Ì8.4)	28.3(20.6)	38.0(12.0)	75.3 (9.6)	71.8 (9.7)	70.6(22.0)	26.2 (2.6)	40.4(19.8)
Browse										
Mororo' (Bauhinia forficata)	7.4 (4.2)	5.5 (5.2)	21.4(11.6)	42.6(19.9)	48.9(12.6)	9.4 (6.1)	14.6 (6.9)	22.6(22.1)	31.4 (5.9)	15.5(10.7)
Sabia' (Mimosa caesalpiniaefolia)	8.6 (6.1)	12.4(12.9)	10.3(10.6)	14.6(16.6)	5.1 (1.2)	2.6 (1.9)	3.7 (2.8)	1.4 (1.0)	8.0 (3.4)	8.9 (9.7)
Catingueira (Caesalpinia pyramidalis)	0.3 (0.7)	0.0	0.4 (0.8)	0.0	0.8 (0.9)	3.1 (6.3)	1.3 (1.1)	0.5 (0.6)	5.1 (1.9)	4.8 (4.5)
Marmeleiro (Croton hemiargyreus)	0.0	0.0	0.2 (0.7)	0.0	0.0	0.0	1.0 (1.4)	0.9 (2.3)	18.3 (5.3)	13.8 (9.4)
Mofumbo (Combretum leprosum)	0.1 (0.4)	1.3 (3.2)	0.2 (0.4)	0.1 (0.3)	0.3 (0.6)	1.1 (1.7)	0.1 (0.2)	0.7 (1.5)	1.4 (0.7)	0.7 (1.07)
Melosa (Ruellia asperula)	0.0	0.9 (2.1)	10.2 (9.1)	5.4 (6.7)	0.3 (0.4)	0.4 (1.0)	0.3 (0.5)	0.0	1.0 (0.5)	1.5 (2.3)
Pau branco (Auxemma oncocalyx)	0.4 (1.6)	0.6 (1.8)	0.0	0.0	0.2 (0.4)	0.1 (0.4)	0.1 (0.4)	0.1 (0.2)	1.5 (1.4)	1.0 (0.9)
Other browse	1.8 (2.3)	1.6 (1.0)	6.3 (2.1)	5.6 (3.2)	0.0 `	3.7 (2.6)	0.4 (0.5)	0.9 (1.2)	1.4 (1.7)	2.5 (1.8)
Total browse	19.7 (8.4)	22.3(15.0)	49.0(20.1)	68.3(23.4)	55.6(13.4)	20.4 (9.7)	21.5 (9.2)	27.1(21.6)	68.1 (4.9)	48.7(18.1)
Total grass	8.1 (7.9)	0.4 (0.7)	10.2 (7.6)	1.1 (2.3)	2.1 (1.6)	0.3 (0.5)	3.6 (1.7)	0.1 (0.2)	1.9 (2.2)	0.6 (1.0)
Unidentifiable	1.1 (1.1)	0.5 (0.5)	1.7 (1.4)	1.3 (2.4)	4.3 (3.9)	4.1 (1.8)	3.2 (2.6)	2.1 (1.5)	4.8 (3.7)	10.3 (8.0)
Leaf:stem ratio	2.9	2.9	7.1	11.2	8.2	4.0	2.8	3.1	5.0	3.0

	Oc	tober	December		January		February		April	
	sheep	goats	sheep	goats	sheep	goats	sheep	goats	sheep	goats
Forbs										
Jitirana (<i>Ipomoea</i> spp.)	16.3(10.2)	23.2(11.7)	17.6 (5.49)	21.9(14.4)	21.0(10.9)	9.9(11.8)	2.9 (3.0)	9.8 (5.9)	2.1 (2.3)	3.8 (3.9)
Paco-Paco (Wissadula spp.)	0.0	0.0	0.0	0.0	0.5 (0.7)	0.0	0.1 (0.3)	0.5 (1.4)	10.5(10.2)	8.3 (8.1)
Bambural branco (Bainvillea spp.)	0.3 (0.5)	0.1 (0.2)	0.2 (0.3)	0.1 (0.2)	8.0 (5.6)	1.4 (2.0)	1.4 (1.7)	0.6 (1.4)	4.8 (4.8)	25.8(21.7)
Bambural verdaderio (Hyptis spp.)	0.1 (0.2)	0.0	0.2 (0.3)	0.3 (0.6)	0.0	0.0	2.0 (4.2)	0.5 (1.0)	0.8 (1.2)	4.4 (2.9)
Bambural russarente (unclassified)	0.0	0.0	0.0	0.0	0.0	0.0	28.4(13.9)	13.6 (7.9)	0.0	0.4 (1.1)
Mariana (Commelina spp.)	2.0 (1.7)	0.6 (0.7)	0.8 (1.4)	0.0	9.5 (5.5)	0.8 (2.1)	5.6 (6.2)	0.6 (1.4)	1.3 (1.2)	0.0
Other forbs	0.6 (0.6)	0.4 (0.6)	0.1 (0.2)	0.1 (0.2)	16.1 (8.7)	12.4 (4.6)	4.8 (3.2)	9.0 (3.7)	10.4 (3.9)	6.6 (3.5)
Total forbs	19.3(10.8)	24.3(11.4)	18.9 (6.2)	22.4(14.2)	55.1 (5.6)	24.5(16.3)	45.2(21.7)	34.6(12.4)	29.9 (8.7)	49.3(18.9)
Browse										
Mororo' (Bauhinia forficata)	3.0 (2.1)	10.2(12.6)	5.8 (2.8)	17.9(17.0)	4.0 (2.6)	34.0(18.3)	0.1 (0.3)	4.4 (3.6)	2.1 (4.1)	6.5 (7.9)
Sabia' (Mimosa caesalpiniaefolia)	12.0 (5.9)	12.0 (5.6)	7.5 (2.3)	7.3(7.0)	1.0 (1.0)	22.6(11.7)	0.5 (1.1)	9.5(10.1)	1.0 (1.3)	12.0(10.4)
Catingueira (Caesalpinia pyramidalis)	27.8(14.3)	22.1(12.9)	38.1 (7.6)	22.3 (8.9)	0.6 (1.0)	5.6 (7.6)	0.0	0.0	0.0	0.0
Marmeleiro (Croton hemiargyreus)	3.8 (3.2)	8.9 (1.4)	7.8 (3.6)	12.8 (7.8)	0.0	0.0	0.0	0.0	0.0	0.0
Mofumbo (Combretum leprosum)	0.6 (1.6)	0.3 (0.4)	0.6 (1.0)	0.3 (0.4)	0.0	0.0	0.0	0.0	1.4 (1.7)	12.8 (6.7)
Melosa (Ruellia asperula)	3.9 (7.7)	2.0 (1.8)	1.4 (1.2)	3.6 (3.8)	1.4 (2.2)	1.4 (2.0)	1.1 (1.8)	8.0 (5.6)	44.1 (8.1)	1.9 (2.2)
Pau branco (Auxemma oncocalyx)	1.0 (1.4)	1.8 (1.8)	0.1 (0.3)	0.1 (0.2)	0.0	0.0	0.1 (0.3)	0.4 (0.7)	1.8 (1.8)	1.8 (3.4)
Other browse	1.2 (1.3)	1.9 (2.1)	3.7 (2.1)	3.4 (3.0)	3.4 (3.8)	3.5 (4.1)	0.3 (0.4)	4.5 (3.2)	7.1 (4.6)	10.8 (5.0)
Total browse	52.3(14.9)	59.2(13.6)	65.0 (7.3)	67.7(15.0)	10.4 (4.6)	67.1(17.1)	2.1 (2.0)	26.8(14.2)	57.5 (8.9)	45.8(18.0)
Total grass	13.0(11.4)	2.1 (1.2)	7.1 (3.8)	1.8 (1.7)	33.4 (6.7)	6.1 (6.9)	51.9(23.4)	37.9(13.2)	11.1 (9.6)	2.5 (3.2)
Unidentifiable	14.5 (5.8)	14.4 (4.4)	9.0 (3.5)	8.3 (6.1)	0.9 (1.5)	2.4 (2.8)	0.9 (0.8)	0.8 (0.7)	1.6 (1.1)	2.8 (2.4)
Leaf:stem ratio	2.4	2.5	3.1	3.2	2.9	7.3	5.5	4.6	2.7	3.8

The amount of forage available in the wet season showed a steady increase with forage maturation. Herbaceous annuals responded more quickly to precipitation than did the trees, increasing from January (1,976 kg/ha) to February (587 kg/ha). From February to April the biomass of tree foliage increased from about 160 kg/ha to 650 kg/ha.

Dietary Selection.

Both sheep and goats selected large but variable amounts of standing dead forb material and browse during the early dry season (May-Aug.). Two important species were jitirana, a climbing vine, and mororo', a leguminous tree (Table 1).

Relative amounts of leaf and stem consumed were highly variable during the May to August period (Table 1). There was a significant (P=.014) period by species interaction for leaf:stem ratios over all periods, and significant period by animal species interactions for browse, grass, and forbs in animal diets, reflecting seasonal fluctuations in selectivity. However, only for the amount of grass in diets was there a significant (P < 0.01) difference between animal species.

Diets of goats and sheep were similar during the late dry season period (Sep.-Dec.). The leaves of several tree species (catingueira,



Fig. 2. Quantities (%) of fruits and flowers in goats' and sheep diets during 10 sampling periods.

sabia', mororo', and marmeleiro), and jitirana were major dietary components. Leaf:stem ratios in these periods were consistently low (Table 1), reflecting large amounts of stem in the diets.

At the onset of the wet season in late December there was a divergence in composition of goats' and sheep diets. During January and February sheep selected large amounts of grass (30-50%) and forbs (45-55%). Little browse (2-10%) was consumed by sheep during these first 2 wet season periods. During April sheep began selecting more browse (55%) and less forbs and grass.

Goats initially selected browse in January (>65%) and then shifted to diets composed of nearly equal parts of browse, forbs, and grass in February. By April goats were selecting more browse and forbs. Grass was utilized very little.

Generally the plant species in the diets of sheep and goats were dissimilar during the wet season (Table 1). Sheep selected for large amounts of annual forbs, annual grasses, and the half-shrub, melosa (*Ruellia asperula* Lindau). Goats' diets consisted mainly of the tree species sabia' and mororo', annual grasses, annual forbs, and other browse species. Leaf:stem ratios during the wet season (Jan.-Apr.) indicated a significant (P < 0.1) difference between goats and sheep in January. Fruits and flowers were important dietary constituents sporadically during the study (Fig. 2).

Discussion

Dietary Selection

The degree of dietary overlap between sheep and goats was greatest in the dry season. Available leaf litter was largely pau branco, a tree species both goats and sheep found unacceptable. Discounting pau branco, there was only about 250 kg/ha of acceptable forage in the late dry season. Goats and sheep limited their grazing to the same approximate vertical space during the late dry season (Oct.-Dec.) (Pfister et al. 1985). Therefore, this study provided indirect evidence of severe inter-species competition during the dry season. Given the large amount of available forage during the wet season, differences between sheep and goats in partitioning their vertical grazing space, and dietary differences, competition was apparently reduced during the wet season. Diet studies have typically shown large seasonal variation in the diets of sheep and goats (Malechek and Leinweber 1972, Bryant et al. 1979). This study was no exception. Both sheep and goats demonstrated rapid changes in dietary selections. For example, grass, largely ignored during most of the year, became an important dietary component for goats during February (Table 1) and March (personal observation). Goats were especially attracted to the seedheads. Several other studies have reported the extensive, but highly seasonal, use of grass by goats (Malechek and Leinweber 1972, de Toit 1972, Nge'the and Box 1976, Bryant et al. 1979).

Leaf litter was a major dietary element for both sheep and goats during the dry season. During the late dry season, nearly 100% of the available forage was leaf litter. The decline in leaf litter biomass from August to October was apparently due to weathering and decomposition, trampling, and consumption by the grazing animals. Wilson et al. (1975) reported that dry leaves were important in goats' diets in Australia.

Fruits and flowers were seasonally important in animals' diets. Malechek (1982) and Malechek and Provenza (1983) have commented that these plant parts may be crucial to animal survival at times of nutritional stress. This may be true even though fruits or flowers represent a very small fraction of the diets, because these parts are often high in nutrients (Schwartz and Said 1981, Everitt and Alaniz 1981). For example, nutritional analysis of jitirana fruits indicated crude protein levels near 30% in August (Pfister 1983). Goats were especially adapt at prehending these fruits through use of a bipedal stance.

The native animals used in this study were apparently well adapted to the semiarid range conditions of northeast Brazil. Sheep and goats displayed attributes of both browsers and grazers. Van Soest's (1982:7) classification of goats as intermediate browsers, and sheep as grazers appears inappropriate in this area. Van Soest's earlier (1980) classification of goats as forb- or browsepreferring intermediate feeders, and sheep as grass-preferring intermediate feeders more closely resembles the pattern shown in this study.

We found large variability in dietary selectivity within groups of

sheep and goats during most months, and also seasonally. Other research has also indicated that genotypic variation in dietary selection within the species may be as large as that between species (Bryant et al. 1979; Warren et al. 1981, 1983). Such a selective strategy may be an important adaptive feature in the highly stochastic *caatinga* environment.

Management Implications

Slash and burn agriculture for subsistence cropping is widespread in the *caatinga* zone. Many ranchers feel that clearing the *caatinga* of trees allows more forage growth. However the longterm benefits of wholesale clearing are dubious. Walker (1979) maintained that trees in semiarid woodlands serve to reduce environmental fluctuations, even though trees produce less green foliage than annual plants. Complete clearing of the *caatinga* may favor short-term site productivity at the expense of long-term stability (Malechek 1982).

Selective clearing of the dominant tree species, pau branco, is recommended. Pau branco was not acceptable forage to goats and sheep during most of the year. This species coppices readily after cutting, and observations indicate that regrowth is more palatable to livestock than mature foliage. Selective clearing would remove some competition for light and moisture, yet retain sufficient quantity of the desirable trees. This would also provide opportunities for the introduction of more palatable plant species. In addition, this clearing could be done with readily available labor, and sales of the pau branco wood could provide cash benefits to landowners.

Sabia', catingueira, and mororo' should be protected from clearing. Sabia' and mororo' coppice readily after cutting, and sheep and goats severely browse the palatable regrowth, often killing young trees. Catingueira, on the other hand, is relatively unpalatable as green forage, but the dry tree leaves are nutritious and provide the bulk of the late dry season forage. These 3 trees provide wet season forage, but are best reserved as dry season forage.

The leaf litter from desirable trees plays a more important role than simply providing animal fodder. This material protects soil from erosion, especially when the area is most vulnerable at the end of the dry season. The first rains are usually very intense and annual plants give little protective ground cover. Without the tree and leaf litter cover, increased soil erosion is certain (Marinho et al. 1982).

Further research aimed at unravelling many complex plantanimal relationships in the *caatinga* is needed. The role of some "undesirable" tree species, such as the invader marmeleiro (*Croton* spp.), needs to be clarified. Considered a weedy species, marmeleiro provided animals forage at a critical time in the dry season during our study. Such information is important for formulation of ecologically sound management objectives, designed to halt the degradation of *caatinga* rangelands.

Although of limited duration, this study gave no indication that goats were superior to sheep for grazing *caatinga* vegetation of the type found near Sobral. Similarity of diets during the stressful dry season indicates that the question of goat and sheep survivability will be best addressed by examining nutritional aspects rather than botanical composition of their diets.

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Anagyrine in Western American Lupines

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Abstract

The teratogenic condition known as 'crooked calf disease' occurs when pregnant cows eat certain lupines with anagyrine concentrations at or above 1.44 g kg⁻¹ dry matter between the 40th and 70th day of pregnancy. Five of eight species collected in Oregon and Washington had accessions with anagyrine at or above the hazardous concentrations as determined by gas/liquid chromatography. A total of 14 species of lupine are now shown to contain accessions with potentially hazardous concentrations of anagyrine. Any range/livestock management system that will expose susceptible cattle to anagyrine-bearing lupines could result in serious calf crop losses.

Lupine species are distributed throughout the temperate regions of the world and are particularly rich in western North America. Speciation within the genus is extensive and confusing. Rydberg (1922) developed a list of 80 species in the Rocky Mountains and the adjacent plains, Tidestrom (1925) listed 53 from the Great Basin, and Hitchcock and Cronquist (1976) accepted 23 species in Washington. To further complicate species identification within the genus, Herman (1966) noted that hybridization among the species is a common occurrence.

Lupines have been considered good to poor feed, depending on their toxic principals, season of use, and class of livestock (Herman 1966). They have been shown to be a common source of the apparently teratogenic alkaloid anagyrine (Keeler 1976) and the extent of its occurrence is only partially understood. At least 9 species are reported to contain anagyrine in concentrations high enough to cause crooked calf disease (Davis 1982). The true extent of the teratogenic potential of this genus will not be known until the lupine species and ecotypes are more completely collected and analyzed. This study was undertaken to further the understanding of the distribution of the probable teratogen anagyrine in the native western American lupines.

Materials and Methods

The collection of native lupines (Tables 1 and 2) represents the native species commonly found in the rangelands of the Pacific Northwest. The procedures for field grown lupines were the same in this experiment as were employed by Davis (1982) and are not repeated here. This collection has been catalogued and entered in the USDA Plant Introduction system and seeds of all accessions that were used in this study are available for further testing, evaluation or breeding at the authors' address.

The accessions reported in Table 2 were grown in plastic greenhouse pots 9 inches in diameter and 9 inches high $(22 \text{ cm} \times 22 \text{ cm})$ containing 2.2 lb (1 kg) of air-dried soil mix, 1/3 soil, (Tucannon silt loam), 1/3 commercial peat, and 1/3 riverbank sand v/v. Each pot received 15 ml of a complete nutrient solution before planting, (Hoagland) and Arnon 1950). Twelve scarified lupine seeds were uniformly disturbed in the pot in 6 evenly distributed locations.

Reference samples of previously analyzed lupine tissue, as well as purified extracts of anagyrine were provided by Dr. Richard Keller, USDA Poisonous Plant Labora-tory, Logan, Utah 84321. Identification and quantification of the anagyrine peak, as well as the total alkaloids, was based on those samples. Manuscript accepted 11 June 1985.

and 4 pots were seeded to each accession for a total of 156 pots in the experiment. Each pot was thinned to 6 plants per pot as soon as the seedlings were well established. At 6, 12, and 18 weeks after emergence, an additional 15 ml of the same nutrient solution as initially used was injected into the soil of each pot with a repeating syringe. When the plants were 24 weeks old, the tops were cut to ground level. The plants from each pot were analyzed for anagyrine and total alkaloids by the procedures used by Davis (1982). Anagyrine and total alkaloid concentrations reported in Table 2 are the averages of 4 pots, each with 6 plants.

Results and Discussion

Six of the eight field-grown lupine species sampled contained identifiable amounts of anagyrine (Table 1). Five had concentrations high enough to be potentially teratogenic, i.e., greater than 1.44 g kg⁻¹ (Keeler 1976). The presence of anagyrine in toxic amounts was previously reported by Davis (1982) for all species in this trial except the seashore lupine⁶. Lupines contain many alkaloids in addition to anagyrine (Waller and Nowacki 1978). Anagyrine may be considered a minor alkaloid in most species when compared to the concentrations of sparteine, lupinine, and lupanine. These and other lupine alkaloids are responsible for the classic symptoms of lupine poisoning or toxicosis (Anon. 1968). The average highest total alkaloid concentration was found in silvery lupine, with a range of 11.4 to 50.2 g kg⁻¹. In contrast, the anagyrine content of spurred lupine, was only 0.1 g kg⁻¹ in the 2 collections that had detectable levels, but total alkaloid varied from 8 to 25 g kg⁻¹. The dry ground lupine, a low growing, moundlike, almost stemless lupine, was low in total alkaloids with a range of 4.2 to 18 g kg⁻¹ and no anagyrine was found. This species is morphologically similar to the prairie lupine, a recognized poisonous species, and is considered by some botanists to be a subspecies of the prairie lupine. Burke's lupine had anagyrine in 3 of the 4 accessions, but only 1 of these was high enough to be potentially teratogenic. Burke's lupine ranked second only to the silvery lupine in total alkaloids.

The tailcup lupine was the only species in which all of the accessions had anagyrine concentrations at or above the minimum teratogenic level of 1.44 g kg⁻¹. These concentrations verify the teratogenicity of this species as reported by Keeler (1976). Total alkaloids ranged from 6-12 g kg⁻¹ with anagyrine the principal alkaloid in this species, averaging 33.5% of the total alkaloid content. Other teratogenic lupines were the silky lupine, the velvet lupine and the seashore lupine.

Lupine species collected from Montana, Idaho, California, Oregon, and Washington were grown in the greenhouse and alkaloid levels are presented in Table 2. Eleven species were found to have accessions with anagyrine levels above the critical concentration of 1.44 g kg⁻¹. None of the annual species were found to contain anagyrine at teratogenic levels.

The cultivar 'Hederma' (sickle-keeled or pine lupine) is the only developed agronomic cultivar of a native western lupine. Ornamental cultivars have been bred from the Washington lupine, (Kelsey and Dayton 1942) and have been used for green manure in Europe. 'Hederma' has been fed to cattle and sheep with no teratogenic effects (James 1976). Foliage of 'Hederma' has been analyzed by the author and no anagyrine was found, but high concentrations of total alkaloids were present. By comparison 2 of the 3 wild collected accessions of sickle-keeled or pine lupine showed concen-

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This article is a contribution from Agricultural Research Service, U.S. Department of Agriculture, in cooperation with the College of Agriculture Research Center, Washington State University, Pullman 99164. Scientific Paper No. 6627

Table 1. Anagyrine and total alkaloid concentration in field grown lupine accessions from central Oregon and central Washington.

Lupinus	Number of	Number with	Number exceeding	Total alkaloids
species	accessions analyzed	anagyrine	1.44 g kg ⁻¹ anagyrine	$\mathbf{g} \mathbf{k} \mathbf{g}^{-1}$
arbustus Doug. (spurred lupine) ¹	4	2	0	17.1
argenteus Pursh (silvery lupine)	5	0	0	37.8
aridus Doug. (dry ground lupine)	6	0	0	8.0
burkei S. Wats. (Burke's lupine)	4	3	1@1.59	18.1
caudatus Kell. (tailcup lupine)	4	4	4 @ 2.94	8.75
leucophyllus Doug. (velvet lupine)	13	12	11 @ 2.90	8.38
littoralis Doug. (seashore lupine)	1	1	1 @ 3.31	8.68
sericeus Pursh. (silky lupine)	5	2	1 @ 3.46	10.00

'Common names follow Kelsey & Dayton (1942).

Table 2. Anagyrine and total alkaloid concentration in greenhouse grown lupine accessions from western America.

Lupinus	Number of	Number with	Number exceeding	Total alkaloids
species	accessions analyzed	anagyrine	1.44 g kg ² anagyrine	g kg '
albicaulis Doug (pine lupine)1	3	2	2 @ 2.08	11.43
albifrons Benth. (white face lupine)	2	0	0	8.48
alpestris A. Nels (mountain silvery lupine)	2	1	1@ 3.36	14.35
andersonii S. Wats. (Anderson's lupine)	1	1	1@ 3.15	10.20
argenteus Pursh. (silvery lupine)	5	4	3 @ 3.34	18.22
bicolor Lindl. (bicolor lupine)	I	0	0	8.19
burkei S. Wats. (Burke's lupine)	4	2	0	6.32
concinnus Agardh. (bajada lupine)	1	0	0	6.09
erectus Hend. (tall silvery lupine)	1	1	1@ 1.59	8.72
evermannii Rydb. (Everman's lupine)	I	1	1@ 4.62	21.52
hirsutissimus Benth. (stinging lupine)	1	0	0	2.99
humicola A. Nels. (lowland lupine)	1	1	0	18.99
latifolius Agardh. (broadleaf lupine)	1	1	1 @ 6.04	23.33
leucophyllus Dougl. (velvet lupine)	1	1	1@ 2.05	8.44
montigenus Heller (Mt. Rose lupine)	1	1	1 @ 10.27	19.54
nootkatensis Lindl. (Nootka lupine)	2	0	0	6.14
polyphyllus Lindl. (Washington lupine)	1	1	1@ 6.10	21.76
rivularis Doug. (stream lupine)	1	1	0	2.20
rothmalerii Klingk. (Rothmal's lupine)	1	0	0	10.00
ruber Heller. (red lupine)	1	1	0	13.59
sericeus Pursh. (silky lupine)	4	2	I @ 6.84	18.71
species	3	0	- 0	12.43

¹Common names follow Kelsey and Dayton, 1942.

trations of anagyrine in the teratogenic range. The single collection of Anderson's lupine was average in total alkaloids and had anagyrine concentrations well above the teratogenic minimum. The broadleaf lupine was above average in total alkaloids and had anagyrine concentrations similar to the Washington lupine and the silky lupine. The species with anagyrine at the highest concentration was the Mt. Rose lupine with anagyrine at 10.27 g kg⁻¹ and a total alkaloid concentration of 19.14 g kg⁻¹.

Based on these and previous findings of Davis (1982), the following species have produced accessions with anagyrine levels that are potentially teratogenic; the pine or sickle-keeled lupine, the mountain silvery lupine, Anderson's lupine, the silvery lupine, Burke's lupine, the tailcup lupine, the tall silvery lupine, Everman's lupine, the broadleafed lupine, the seashore lupine, the velvet lupine, the Mt. Rose lupine, the Washington lupine, and the silvery lupine.

This brings to 14 the known species with anagyrine at teratogenic concentrations. This number is variable depending on the system of speciation used and the synonomy that is present in the literature.

With the development of 'Hederma' as an anagyrine-free cultivar of the pine or sickle-keeled lupine, it follows that anagyrinefree cultivar development in other species should be possible. Concurrently the total alkaloids could be reduced and the palatability and forage quality should be improved. With extensive screening of widely collected germplasm, followed by intensive selection and breeding, accessions and possible new cultivars free of anagyrine with low total alkaloid content could be developed. They could be valuable additions to seeding mixtures where revegetation of depleted ranges is required. They could provide both forage and a nitrogen source to the range forage plant community.

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JOURNAL OF RANGE MANAGEMENT 39(1), January 1986

Small Mammals in Modified Pinyon-Juniper Woodlands, New Mexico

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Abstract

The effects of pinyon (Pinus edulis)-juniper (Juniperus spp.) treatments on rodent abundance, 13 to 18 years after treatment, were studied in southwestern New Mexico from 1981 to 1983. Treatments included bulldozing, bulldozing/piling/burning, thinning, and untreated woodland. The area had not been grazed by livestock since time of treatment but was subjected to light and irregular use by wild ungulates. Total rodent numbers were significantly greater ($P \ge 0.05$) on all treated areas compared to untreated woodlands but individual species and groups responded differently. Woodrats (Neotoma spp.) and brush mice (Peromyscus boylii) increased in abundance as slash accumulations increased, regardless of condition of overstory. Pinyon mice (P. truei) and rock mice (P. difficilus) numbers were also greater where slash was present, but only if the pinyon-juniper overstory was relatively intact. Grassland rodents, as a group, were more abundant on areas where the pinyon-juniper overstory and slash had been removed (bulldozed and bulldozed/piled/burned), but reduced numbers on buildozed plots where slash was left suggested slash accumulations may have detrimental effects on numbers of these species. Treatments did not influence number of different rodent species. Data indicate that numbers of individuals and proportions of rodent species can be affected by manipulation of pinyonjuniper overstory and method of slash disposal.

Pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occupy 20.5% and 18.0% of the land surface in Arizona and New Mexico, respectively (Short 1979). Mechanical methods such as chaining and bulldozing have been used to control large tracts of these woodlands (Springfield 1976) and generally have resulted in increased herbage production, but effects on wildlife habitats have been variable (Severson and Medina 1983).

Studies on effects of pinyon-juniper treatments on small mammals include the following: cottontails (*Sylvilagus audubonii*) (Kundaeli and Reynolds 1972) and white-throated woodrats (*Neotoma albigula*) (Turkowski and Watkins 1976) in New Mexico, and several species of small mammals in Utah (Baker and Frischknecht 1973, Smith and Urness 1984); Colorado (O'Meara et al. 1981); and Arizona (Turkowski and Reynolds 1970, Kruse et al. 1979). Most were conducted on areas grazed by livestock, and time intervals between treatment and study dates varied from 1 (Turkowski and Watkins 1976) to 25 years (Kruse et al. 1979).

The objective of this study was to test the hypotheses that there were no differences in number of rodent species, total individuals, and number of individuals of selected species and species groups on untreated pinyon-juniper woodland compared to woodlands subjected to mechanical control practices 13 to 18 years after treatment.

Study Area and Methods

The study was conducted on the Fort Bayard Allotment, Gila National Forest, 16 km east of Silver City, New Mexico. Important trees and shrubs include pinyon, one-seed juniper (Juniperus monosperma), alligator juniper (J. deppeana), gray oak (Quercus

Author would like to thank personnel of the Gila National Forest and the New Mexico Game and Fish Department for their assistance throughout the study and Dr. Bruce Hayward, Western New Mexico University, for identifying and weighing specimens. Special thanks are extended to Mary Gilbert and Gary Helbing for their assistance with collections.

Manuscript accepted 30 April 1985.

grisea), and hairy mountainmahogany (Cercocarpus breviflorus). More than 30 grass species occur on the allotment but two-thirds of the perennial grass production is from blue grama (Bouteloua gracilis) and sideoats grama (B. curtipendula). Over 50 species of forbs have been identified, but no single species is dominant. Common forb genera include globemallow (Sphaeralcea spp.), goosefoot (Chenopodium spp.), and buckwheat (Eriogonum spp.) (Kundaeli and Reynolds 1972).

Upland soils are primarily Lithic and Lithic Vertic Haplustolls while Aquic Haplustolls are common in lowland areas (Unpulished data, A.L. Medina, Rocky Mountain Forest and Range Experimental Station, Tempe, Ariz.).

Elevation ranges from 1,806 to 2,070 m. Annual precipitation averages 393 mm, 55% of which falls as rain from July through September. Annual precipitation for 1981, 1982, and 1983 was 427, 332, and 454 mm, respectively. Mean annual temperature is 12.8 °C, with mean monthly extremes of 3.5 °C (January) and 22.6 °C (July). Weather records are from Fort Bayard State Hospital on the southern edge of the study area.

The Allotment is part of the Fort Bayard military reservation which was established in 1869. Yearlong, excessive use by livestock resulted in deteriorated range conditions in 1937 when all livestock, except for a few pack and saddle animals, were removed (Reynolds 1964). The pinyon-juniper control treatments described in the following paragraph were established as part of a mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) habitat study. The areas used in the rodent study described herein have not been grazed by livestock since the treatments were applied. The military reservation, however, is within the range of 90 to 120 elk, about 100 mule deer, and about 75 white-tailed deer (*Odocoileus virginianus*). The area used for this study was approximately 10% of the entire reservation and use by wild ungulates was probably proportional.

Pinyon-juniper treatments were randomly established in each of 2 blocks. The lower block, at an elevation of 1,880 to 1,935 m, was treated in 1965 and the upper block, 1,935 to 2,040 m, in 1970. Treatments included (1) thinning (pinyon and junipers were cut to a minimum spacing of 6.1 m and left in place); (2) bulldozing (all pinyon and junipers were pushed over with a bulldozer and left in place); (3) bulldozing/piling/burning (trees were pushed and piled with a bulldozer, then burned); and (4) undisturbed woodland. All treated plots were approximately 120 ha.

During September 1981, each plot was divided into 6 sampling areas and a set of 2 transects was randomly placed in each. Each transect consisted of 17 trapping locations spaced 10 m apart. Each location consisted of 2 traps, a standard rat trap, and a museum special. Trapping was conducted during the second and third weeks of September each year. Traps were baited with a mixture of peanut butter, oatmeal, and an ant repellent, dimethylpthalate (Anderson and Ohmart 1977). Traps were run in one transect within each plot segment in 1981, the other in 1982, and the first transect again in 1983. Because of the time required to check and bait traps only 3 transects were run within each treatment for 4 consecutive days; then the traps were moved to 3 other transects and run for the next 4 consecutive days. Traps were left open for 24-hour trap sessions and were checked daily. Each of the 8 treatment areas received 816 trap-days effort per year. Captured individuals were tagged, placed in plastic bags, and frozen; then identified and weighed as time permitted.

Rodent data were analyzed with 3-factor analyses of variance (blocks, years, and treatments) with 6 observations per cell. Each

Author is research wildlife biologist, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. Research was conducted at the Station's Research Work Unit in Tempe, Ariz., in cooperation with Arizona State University. Station headquarters is in Fort Collins, Colo. Author would like to thank personnel of the Gila National Forest and the New
observation represented the total number of individuals captured on 1 transect in 1 year. Mean separation was by Newman-Keuls test (Zar 1984). All species could not be analyzed separately because of small sample sizes, so tests included the following species or species groups: (1) white-throated woodrat; (2) all woodrats, white-throated woodrat plus Stephens woodrat (N. stephensi), Mexican woodrat (N. mexicana), and a few specimens that could only be identified as woodrats; (3) brush mouse (Peromyscus boylii); (4) other woodland species, pinyon mouse (P. truei), and rock mouse (P. difficilis); (5) grassland species, which included white-footed mouse (P. leucopus), southern grasshopper mouse (Onychomys torridus), western harvest mouse (Reithrodontomys megalotis), and Ord's kangaroo rat (Dipodomys ordii); and (6) total individuals, which included all of the above. The null hypotheses tested was that there were no differences in number of species or number of individuals of each species (or species group) trapped among treatments. All statistical inferences were made at 0.05 probability level.

Densities of trees and shrubs were estimated by counting the number of individuals on 5- by 25-m sampling areas. Stein's twostage test (Steel and Torrie 1980) was used to determine the number of sampling areas per treatment, which varied from 25 to 55. Percentage slash cover was estimated by counting meters of slash intercept on twelve, 30-m transects, randomly located on rodent trapping transects in each treatment.

Plant and animal nomenclature follow Nickerson et al. (1976) and Hall (1981), respectively.

Results and Discussion

Vegetative Changes

Densities of pinyon and junipers were lowest on bulldozed/piled/burned and bulldozed treatments (Table 1). Pinyon has been reestablishing on all treated areas at a slightly faster rate than the junipers. Densities of broad-leaved shrub species tended to be greater under well-developed tree overstories.

Table 1. Densities of trees and shrubs (no./ha) and slash cover (%) in 4 pinyon-juniper treatments at Fort Bayard, New Mexico. Numbers are means \pm standard errors.

Tree/shrub	Untreated woodland	Bulldozed/ piled/ burned	Bulldozed	Thinned
	**********	Density (n	umber/ha)	
Junipers	107±13	10±3	35±10	142±19
Pinyon	252 ± 32	42±8	39±7	522 ± 71
Gray oak	385±44	156±17	209 ± 24	222±33
Hairy mountain-				
mahogany	235±29	80±14	154±25	206±30
Other	<u>214±28</u>	<u>66±14</u>	111 ± 18	53±12
Totals	1,193±83	354±34	548±43	1,145±107
		Cover	r (%)	
Slash	3±1	6±1	13±2	10±1

Slash accumulations were 2.5 to 3 times greater on the thinned and bulldozed plots than on untreated woodlands (Table 1). Most slash on untreated plots resulted from natural mortality. Intermediate accumulations on bulldozed/piled/burned areas resulted from incomplete burning of piled slash and trees or shrubs that were pushed over and crushed but not piled.

Small Mammal Diversity

Thirteen rodent species were trapped over the 3-year period and the number of species caught was similar among treatments. Ten rodent species were found on all treatments (Table 2). Two additional species, deer mouse (*Peromyscus maniculatus*) and silky pocket mouse (*Perognathus flavus*), were trapped in the bulldozed/piled/burned treatment but only 1 individual of each species was caught. An additional species found on the thinned treatment, cliff chipmunk (*Eutamias dorsalis*), was represented by 2 individuals.

Results of previous studies have been varied. Turkowski and Reynolds (1970), working in Arizona, reported more rodent species where pinyons and junipers had been bulldozed 3 to 7 years prior to sampling than on untreated areas. Conversely, O'Meara et al. (1981) showed species diversity to be greater in untreated pinyon-juniper woodlands than on chained areas sampled 1, 8, and 15 years after treatment in Colorado. Variable results among studies and differences of only 1 to 3 minor species, each represented by few individuals, between treated and untreated areas indicate that pinyon-juniper control has minimal effects on number of rodent species.

Number of Individuals

Significantly higher total numbers of individuals were trapped on treated than on untreated woodlands (Table 2), but there were no differences in total individuals among the areas subjected to pinyon-juniper control practices.

Significantly more white-throated woodrats and total woodrats were trapped on bulldozed and thinned areas than on untreated woodlands. Intermediate numbers occurred on bulldozed/piled/burned areas. Brush mice were significantly more numerous on the bulldozed and thinned treatments and less numerous on the bulldozed/piled/burned and untreated plots (Table 2). Slash appears an important habitat component for these species. Generally, highest numbers of woodrats and brush mice were found in treatments with high slash accumulations, i.e., bulldozed and thinned (Table 1). Intermediate number were found in treatments with intermediate amounts of slash (bulldozed/piled/burned) and fewest in treatments with least slash (untreated woodlands).

The addition of slash to the woodland character of the thinned plot accounted for the significantly greater number of woodland species (pinyon mice and rock mice) on the thinned as compared to untreated woodlands. The pinyon-juniper overstory was apparently more critical because these woodland species were least abundant on treatments where this overstory was removed (bulldozed and bulldozed/piled/burned areas) even if slash was present (Table 2).

Other investigators have also noted a preference for slash cover by rodents, particulary deer mice, voles (*Microtus* spp.) (Baker and Frischknecht 1973), and woodrats (Turkowski and Reynolds 1970, Turkowski and Watkins 1976). O'Meara et al. (1981) noted significantly more slash on areas chained 1 to 15 years previously compared to untreated sites, but attributed increases in deer mice, least chipmunks (*Eutamias minimus*), and plains pocket mice (*Perognathus flavescens*) on treated areas to increases in shrubs and perennial grasses. Slash may be especially important to woodrats because cover near the ground is important for shelter-site selection (Olsen 1973). Slash not only provides such cover but also furnishes the building materials (bark, pieces of wood, etc.) for shelter construction (Turkowski and Watkins 1976).

Not all species responded to the presence of slash, however. Grassland rodents (white-footed mice, southern grasshopper mice, western harvest mice, and Ord's kangaroo rats) were significantly more abundant on the bulldozed/piled/ burned treatment, indicating a preference for open stands of gray oak and hairy mountainmahogany. Reduced numbers on bulldozed plots indicate slash accumulations may have a detrimental effect on most of these species. Treatments leaving a pinyon-juniper overstory (untreated and thinned plots) had significantly fewer total individuals of this group (Table 2).

While grass and forb growth was not measured during trapping, Short et al. (1977), working on the same study areas, found total herbage production was greater (P<0.05) on bulldozed and bulldozed/piled/burned areas than on thinned and untreated woodTable 2. Total numbers of individuals of each rodent species and species group trapped on four pinyon-juniper treatments during 1981, 1982, and 1983 at Fort Bayard, New Mexico.

Rodent	Untreated woodland	Bulldozed/ piled/ burned	Bulldozed	Thinned
Stephen's woodrat	9	2	15	26
Mexican woodrat	2	4	6	12
White-throated woodrat	117a'	156ab	205Ь	183b
All woodrats ²	129a	168ab	229b	222b
Brush mouse	45a	57a	98Ь	1156
Pinyon mouse	24	1	4	48
Rock mouse	2	5	7	10
All woodland mice	<u>26a</u>	<u>6</u> b	11b	58c
White-footed mouse	9	50	9	14
Southern grasshopper mouse	13	66	30	3
Ord's kangaroo rat	16	31	10	11
Western harvest mouse	8	28	_46	7
Total grassland species	46a	175c	95b	35a
Total Individuals ³	246a	408b	433b	432b

Values within a row followed by same letter are not significantly different at the 0.05 probability level.

²Includes unidentified woodrats.

³Includes deer mice, silky pocket mice, and cliff chipmunks.

lands. No differences were found between the two cleared treatments or between thinned and untreated areas. Relative differences in herbage production were still apparent at time of trapping and may have contributed to increased numbers of grassland species and decreased numbers of woodland species (Table 2).

The only significant block differences were the number of whitethroated woodrats and total woodrats which were most numerous in the lower block and brush mice which were more abundant in the upper block. In the case of woodrats, Turkowski and Watkins (1976), working in the same study area, found more woodrat houses in the lower block than in the upper block prior to any treatments. These results, therefore, have been interpreted to be due to differences in elevation and related environmental factors rather than age of treatment.

Results from this study cannot be compared directly to those where livestock grazing was occuring on study plots. While use by wild ungulates had occurred since treatments were imposed, effects were likely small because such use was light and irregular. Any large ungulate has the potential to alter food and cover used by rodents, however. Black and Frischknecht (1971) noted differences in species composition of rodents when comparing ungrazed range with ranges that were heavily or moderately grazed by cattle. Sheep grazing on big sagebrush (Artemisia tridentata) ranges caused significant reductions in both diversity and density of small mammals, but only diversity was reduced on areas dominated by crested wheatgrass (Agropyron cristatum) (Reynolds and Trost 1980). No information is available relating livestock to slash reduction. It is probable, however, that large ungulates, particularly cattle, elk, and horses, could cause reductions in slash over a period of years through rubbing and trampling activities.

Conclusions and Management Implications

Controlling pinyon and juniper trees by bulldozing, bulldozing piling/burning, and thinning did not affect rodent species diversity but did result in increased numbers of individuals of several species and groups. Managers may have the option of influencing which species increase the most by manipulating slash. Treatments leaving slash, for example, yielded highest numbers of woodrats and brush mice regardless of whether the pinyon-juniper canopy was completely removed. Pinyon and rock mice, collectively, also responded favorably to slash accumulations but only if the pinyonjuniper canopy was relatively intact (e.g., thinned treatment). Grassland species, including white-footed mice, southern grasshopper mice, western harvest mice, and Ord's kangaroo rats, were most abundant where the pinyon-juniper overstory was removed and the slash piled and burned.

The study area had not been grazed by livestock since treatments were applied but has received light and sporadic use by deer and elk. Livestock likely influence rodent populations by altering food and cover; slash may even be affected by larger ungulates through rubbing and trampling activities. The degree of influence on rodent numbers depends on intensity and duration of livestock grazing. While caution should certainly be used in extending these results to areas that are grazed by livestock, there is no existing information that covers these interactions. One purpose of this study was to provide management with a series of options developed under a "no grazing" regime which can be used as a foundation for comparing results from similar studies where livestock grazing was present and defined.

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Forage Utilization Cost Differentials in a Ranch Operation: A Case Study

L. ALLEN TORELL, E. BRUCE GODFREY, AND DARWIN B. NIELSEN

Abstract

The total cost (fee and non-fee) of grazing BLM, FS, and private deeded rangeland was estimated by partial budgeting procedures from records kept by the Saval Ranch, a northeastern Nevada cow-calf operation. Private rangeland was estimated to be the most expensive forage source at \$24.99 per AUM. The total cost of grazing BLM land was estimated to be \$8.07 per AUM and FS was estimated to cost \$9.08 per AUM.

The use of America's federally administered rangelands has been associated with controversy for more then a century. One of the issues that has a long history involves the fees charged operators whose livestock are permitted to graze these lands. Numerous authors have discussed this issue (e.g., Nielsen and Workman 1971, Bergland and Andrus 1977, Roberts 1963, Roberts 1967, Nielsen 1982, Foss 1959, Dutton 1953, Gardner 1962, Kearl 1966, Kelso 1947) but much confusion concerning this issue continues today as evidenced by the studies currently being conducted by the Forest Service and Bureau of Land Management as required by the Public Rangeland Improvement Act (PRIA) of 1978. In fact, few issues associated with the use of federally administered lands has received as much attention in the literature. At the heart of this controversy is the general misunderstanding concerning grazing fees and the total costs of grazing public as well a privately owned lands.

Manuscript accepted 28 May 1985.

All users of public lands must incur 2 types of costs—fee and non-fee costs. For example, a hunter incurs travel costs (non-fee costs) and may also have to pay an access fee. Similar costs must also be borne by ranchers whose livestock graze public or private lands. Any differences between the total costs (fee and non-fee costs) of grazing 2 different but comparable parcels of land means that economic rents accrue to the parcel with the smallest total cost (see Gardner 1962, Roberts 1963, or Brokken and McCarl 1984).

Numerous studies (e.g., Nielsen and Workman 1971, Gardner 1962, Fowler and Gray 1980) have estimated the "permit value" due to cost differentials between grazing federal and private rangelands. Other studies have surveyed ranchers in an attempt to directly estimate the cost differential between public and private forage sources (e.g., Obermiller and Lambert 1984). No studies have attempted to estimate what differences in cost, if any, exist among the various types of land used by a particular ranching operation.

This case study estimates the costs of using Bureau of Land Management (BLM), Forest Service (FS), and deeded rangeland for a ranch in northeastern Nevada. The unique data from the Saval Ranch for 1982 can not be directly applied to other ranch operations. Furthermore, these costs would be expected to vary overtime. The partial-budgeting procedure outlined, however, can and should be used to estimate the costs of using any site grazed by domestic livestock. The partial-budgeting enterprise analysis described below is needed to make sound economic decisions about a particular site.

Study Area

The Saval Ranch is located approximately 72 km (45 mi) north of Elko, Nev. (Fig. 1). The ranch operation includes approximately 19,881 ha. (49,105 acres), including lands owned and managed privately (3,060 ha; 7,557 acres), by BLM (10,489 ha; 25,908 acres)

JOURNAL OF RANGE MANAGEMENT 39(1), January 1986

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This publication is: Utah Agricultural Experiment Station Journal paper no. 3069 and contribution number 6 of the Saval Ranch Research and Evaluation Project. Bureau of Land Management; Agricultural Research Service; Saval Ranch; College of Agriculture, University of Nevada-Reno; Forest Service, and Soil Conservation Service cooperating.



Fig. 1. Location of study area and general layout of the Saval grazing allotment.

and by FS (6,332 ha; 15,640 acres). Native rangeland pastures on BLM lands are fenced into parcels of about 1,620 ha (4,000 acres) (Fig. 1). The "Darling Seeding" crested wheatgrass pastures, which are managed by BLM, are somewhat smaller with an average of 644 ha (1,590 acres) per pasture. FS pastures are larger with 3,692 ha (9,120 acres) in the South Independence pasture and 2,640 ha (6,520 acres) in the North Independence pasture.

Elevation of the ranch varies from approximately 1,524 m (6,000 ft) at the Haystack Ranch to nearly 2,438 m (8,000 ft) on the FS pastures. BLM pastures are on gently sloping alluvial fans located at the base of the Independence Mountains. In contrast, FS pastures are in steep, mountainous terrain. Annual precipitation on the ranch ranges from approximately 3.5 cm (9 inches) at lower elevations to approximately 8.3 cm. (21 inches) at high mountain elevations.

Methods

The cost of grazing rangeland may be divided into 2 general categories—variable and fixed. '/ariable costs (e.g., salt, labor, supplies) were determined from the ranch's expense and labor records. Fixed costs (e.g., depreciation, interest on investment) were estimated based upon the curren market value of deeded land and Federal grazing permits.

To estimate the cost of grazing range forage requires that each source of forage be treated as a separate distinct enterprise. That is, total ranch expenses must be divided to allocate ranch expenses to the appropriate activity based on the allocation of labor and material inputs to various production activities. This information was obtained when Saval Ranch employees recorded how much labor each task required. This procedure was followed throughout the grazing season. The ranch manager also estimated labor requirements for the winter feeding period. For simplicity, ranch activities were grouped into the 11 general categories shown in Table 1.

Obviously, the allocation of some ranch expenses may result in some overlap of expense categories. To avoid double-counting, these "joint costs" were allocated to the expense category or categories for which most of the expense was incurred. For example, tractors were primarily used for hay production and winter feeding although they may occasionally be used to maintain fences, cattle

Table 1. Ranch activities performed under each general labor activity designation.

Winter Care of Cattle	Checking and doctoring cattle during the win- ter and spring months. Calving during the spring.
Winter Feeding	Feeding cattle hay during the winter months.
Ranch Maintenance	Repair of buildings, corrals, roads, and vehicles. Excludes range improvement main- tenance and repair of haying equipment.
Haying	Putting up grass hay for winter feeding. In- cludes repair of haying equipment.
Irrigating	Flood irrigation of meadowland. Includes ditch repair and construction.
Working Cattle	Branding, vaccinating, weaning, and market- ing of cattle.
Moving Cattle	Herding cattle between allotments. Excludes herding while on a particular pasture.
Range Improvement Maintenance	Maintenance of fences, cattle guards, and other range improvements on both Federal and private lands.
Summer Care of Cattle	Herding cattle for better distribution on the pasture, salting, and checking cattle on range. Includes travel time to and from the pasture.
Ranch Management	Management, bookkeeping, and office work.
Miscellaneous	Shoeing horses, going to town, and other odd jobs.

guards, and other range improvements. In this case, tractor expenses were allocated only to hay production and hay feeding.

Labor expenses were estimated by multiplying the number of hours per labor category times \$5.37 per hour—the average hourly ranch expense for labor, room, and board. Other cash costs for salt, fencing materials, and other inputs were recorded by the Saval Ranch manager. Vehicle mileage to and from allotments and pastures was estimated from topographic maps of the ranch. The number of trips to allotments was estimated from labor data. Trip mileage was then multiplied by \$.34 per km. (\$0.55 per mi.), the estimated average cost, including depreciation, of owning and operating a full-size pickup truck during 1982 (Hertz 1983).¹

Private range improvement depreciation and interest on private land investment also reflect "joint expenses." It was not possible to exactly allocate these expense categories between hay AUMs² and private range forage AUMs. Depreciation and interest expenses were allocated between hay production and private range forage production according to the proportion of hay and range forage AUMs produced on private rangeland and meadows (as hay aftermath). These depreciation and interest costs were not, however, used to determine the cost of harvesting forages.

Estimated range improvement depreciation costs were based on initial improvement investment using the straight-line method. Vehicle depreciation was included in the \$.34 per km. charge discussed above.

It was assumed that the Saval Ranch would accept a 10% return on the current market value of all land and range improvement investments. This represents an "opportunity" cost for funds invested in forage resources. Best estimates of current market value of various private lands on the Saval Ranch are \$1,500/ha(\$600/acre) for native meadows, \$187.50/ha. (\$75/ac.) for native rangeland, and \$250/ha (\$100/acre) for crested wheatgrass (personal communication, July 25, 1983, A. Steninger, Western Ranch Service, Elko, Nev.). Federal grazing allotments in Elko county have a

¹Hertz only compiles per mile driving costs—including insurance, licenses, fees, taxes, loan interest, maintenance, repairs, gasoline, oil and other service station charges, and depreciation—for cars. Trucks are not included. Thus, it was assumed that the per mile cost would be similar between a full-size car is reported by Hertz, and pickup trucks as used on the ranch.

²An animal unit month (AUM) is considered to be the amount of feed or forage required by one mature cow with calf (or the equivalent) for one month.

current market value of between \$30 and \$35 per AUM. A midrange value of \$32.50 per AUM was assumed in this study.

Forage use during the 1982 grazing season was estimated from BLM and FS grazing records, and actual use records kept by the ranch. **Results and Discussion**

Labor Input

The total annual labor input into the ranch operation was 12,859 hours during 1982. Of this total, 20.6% (2,646 hours) were for harvesting range forage. The largest portion of this time (1,429 hours) involved moving cattle to comply with BLM and FS grazing requirements. An additional 613 hours was spent maintaining range improvements, and 604 hours were required to care for cattle that were on rangelands. These 3 labor activities are highlighted in Figure 2. These activities result in labor costs that are not directly associated with livestock production but rather is a cost of harvesting range forage (e.g., getting the livestock to the pasture and maintaining improvements).

1982 Forage Use

The Saval Ranch did not maintain a constant cow herd during 1982. Herd size on the Saval Ranch declined during the year from a high of 1,310 head (including first-calf-heifers) on 31 March 1982, to 713 head on 1 January 1983. The reason for this reduction was the diagnosis of a discase problem that resulted in the sale open and late calving cows. Since these cows were sold after the grazing period (start of the winter feeding), this herd reduction did not affect the grazing costs reported below.

Annual forage use during the 1982 grazing season was estimated to be 9,410 Animal Unit Months (AUMs). Cattle were turned into the Lower Mahala Creek allotment the first of April³, then onto the

³Cattle were also fed during this time. Turn-out was allowed to provide protection from wind during calving. For a "normal" year, early turn-out is about April 15 onto crested wheatgrass pastures.

2194hrs. Winter Fe 1053hrs. Hayin 3230 **25.1%** 8 22 Winter Care Cattle 600hr 4.7% Misc 570hrs À 4 Z krigating 847hrs. 6.6% 86hrs 302 ummer Care Cattle 1333h 10.4% 604hrs. Impr. Maint. 87 oving Cattle 1429h

Ranch Maint.

Fig. 2. Ranch labor input by general labor activity.

"Darling" crested wheatgrass seeding, to higher-elevation native BLM range near the end of May, FS pastures the end of June, and back to privately owned fields and pastures during the fall (Fig. 3). Approximately 200 head of cows remained on private land throughout the summer.

During the 8-month grazing season, the Saval Ranch depended upon federal rangeland for 69% of livestock forage requirements. This included 658 AUMs of forage owned by the ranch but man-

					Per AUM Expense					
Land Type	Total Herding Time (Hours) ¹	Mile (Kilometer	eage rs)/(Miles)	Total AUMs Harvested (AUMs)	Labor Cost at \$5.37/hr. (\$/AUM)	Travel Cost at \$.34/kilometer (\$/AUM)	Horse Expense (\$/AUM)	Total Cost (\$/AUM)		
Private	331	180	(112)	2,956	.60	.02	.20	.82		
BLM	485	1,031	(641)	2,954	.88	.12	.20	1.20		
FS	613	1,434	(891)	3,500	.94	.14	.20	1.28		

¹The 311 hours spent in moving cattle from Upper Sheep/Mahala BLM allotments to the USFS South independence allotment (Fig. 3) was equally split between BLM and USFS forage sources.

Table 3. Range improvement maintenance costs.

				Per AUM Expense					
Land Type	Total Maintenance Time (Hours)	Mileage (Kilometers)/(Miles)	Total AUMs Harvested (AUMs)	Labor Cost at \$5.37/hr. (\$/AUM)	Travel Cost at \$34/Kilometers (\$AUM)	Fencing Materials (\$AUM)	Total Cost (\$/AUM)		
Private	444	734 (456)	2,956	.81	.08	.22	1.11		
BLM	60	352 (219)	2,954	.11	.04	.03	.18		
FS	109	631 (392)	3,500	.17	.06	.05	.28		

Table 4. Cost of caring for cattle while on range.

					Per AUM E	xpense	
Land Type	Total Time Time (Hours)	Mileage (Kilometers)/(Miles)	Total AUMs Harvested (AUMs)	Labor Cost at \$5.37/hr. (\$/AUM)	Travel Cost at \$34/Kilometers (\$AUM)	- Salt (\$AUM)	Total Cost (\$/AUM)
Private	37	269 (167)	2,956	.07	.03	.09	.18
BLM	62	592 (368)	2,954	.11	.07	.09	.27
FS	505	2,471 (1,536)	3,500	.77	.24	.09	1.10

Table 2. Livestock moving costs.



Fig. 3. Forage use during the 1982 grazing season and herding time between pastures.

aged by the BLM and FS under exchange of use agreements.

Specific Forage Utilization Costs

Moving Cattle

A total of 1,429 hours were spent moving cattle among allotments and pastures (Fig. 2). Table 2 shows that the largest amount of time (485 hours) was involved in moving of cattle to, from and between BLM pastures. A smaller amount of time was spent moving cattle onto/off and between FS pastures (613 hours) and private fields and pastures (331 hours). Labor costs accounted for approximately 73% of herding cost for all 3 forage resourcesprivate, BLM and FS.

Depreciation of 15 horses and a horse trailer used to haul these

horses added an additional \$.20 per AUM to the herding expense. Total average herding expense per AUM was estimated to be \$.82for private deeded rangeland, \$1.20 for BLM lands, and \$1.28 for FS lands.

There was a wide range in the herding costs for various BLM pastures. The herding expense for BLM pastures close to hay meadows (Darling seeding and Lower/Middle Mahla allotments) averaged only \$.76 per AUM while herding expenses for BLM allotments farther from the ranch headquarters (Upper Sheep and Upper Mahala allotments) averaged \$1.70 per AUM. This difference in cost primarily reflects differences in range productivity (ha/AUM), distance from the ranch headquarters, allotment size, and terrain.

Maintaining Range Improvements

Labor required to maintain range improvements amounted to 613 hours (Fig. 2). This included primarily the maintenance of fences and cattle guards because the Saval Ranch had no significant investment in water developments. Livestock primarily obtained water from creeks and streams located on allotments.

According to the Saval Ranch manager, relatively little labor and material was required to maintain range improvements during 1982. More maintenance will be required in the future to repair fences that are considered to be in a state of disrepair. Low beef prices and high interest rates did not make these investments possible during 1982. Therefore, the estimated maintenance costs per AUM (\$1.11 for private, \$.18 for BLM, and \$.28 for FS) should be considered to be minimal.

Approximately 72% of the labor input involved in range improvement maintenance was on private land. A total of 444 hours were spent fixing fences on private land (Table 3). Most of this time (363 hours) was spent maintaining fences around the hay meadows and stack yards to allow cattle to graze aftermath from hay meadows during the fall.

Care of Cattle on Range

A total of 604 hours were spent tending cattle on range. Most of this time (505 hours or 84% of the time) occurred during the period when cattle were on lands administered by the FS. A trip to check cattle on FS lands generally required a full day of work as a consequence of the steep topography and the rough roads that had to be traversed.

A large part of the 505 hours (Table 4) spent caring for cattle on FS lands involved herding. Cattle tended to congregate near sources of water and had to be moved to prevent overgrazing in riparian zones and to force grazing in other areas which would not have been grazed if extensive herding had not occurred.

BLM and private rangelands used by cattle on the Saval Ranch are relatively flat and require very little herding. As a result, much less time was spent moving, checking, and providing salt for cattle using private (37 hours) and BLM (62 hours) lands.

The relatively high herding costs required on the FS allotments used by Saval Ranch animals mean the cost of caring for cattle on FS land is nearly 4 times greater than on BLM land and over 6 times greater than for private land. Estimated costs of caring for cattle per AUM are \$.18 for private land, \$.27 on BLM land, and \$1.10 on FS land (Table 4).

Lost Animals

The Saval Ranch averages an estimated 3% annual death loss for all livestock classes. About half of the deaths occur during the winter. Death losses are similar for each type of land (i.e., private, BLM, FS) used by Saval Ranch cattle. Poisonous plants are not a problem on any of the pastures.

Death loss during 1982 was estimated to be worth \$12,341. Half of the deaths occurred during the period when cattle were using rangelands resulting in an estimated cost of \$1.31 per AUM.

Veterinary and Medicine

The ranch spent \$2,793 for veterinary services and medicine during 1982. Most of this expense was for vaccines and the treatment of calf scours. Cattle using rangelands required little medical attention. As a result, veterinary and medicine expenses during this period were considered as "livestock costs" and not a cost of grazing range forage.

Development Depreciation

Except for private rangeland and meadows, the Saval Ranch made few private investments for range improvements. The BLM and FS have, however, made substantial investments in range improvements on the Saval Ranch, more than on many other ranches. The estimated value of improvements implemented by federal agencies during 1981, 1982, and 1983 are \$149,381 (Torell et al. 1985). These investments add nothing to the cost of range forage from the perspective of the ranch except for improvement maintenance.

Approximately 51 km (32 mi) of fence on the ranch enclose hay meadows, private pastures, and rangeland. Assuming an initial investment of \$808 per km (\$1,300 per mi), 20 years of life, and no salvage value, the annual depreciation cost for the 51 km of fence is estimated to be \$2,080 or an average depreciation cost of \$.29/AUM.

Interest on Investment

The ranch utilizes approximately 691 ha (1,708 acres) of privately owned meadowland, 406 ha (1,003 acres) of private crested wheatgrass, and 1,962 ha (4,846 acres) of private rangeland. Total investment in private forage sources is estimated to be \$1,488,855. This represents a weighted average investment of approximately \$210 per private AUM. Interest costs on this investment are \$21 per AUM if an interest rate of 10% is assumed.

Estimated interest on the 51 km of privately owned and maintained fencing is estimated to be \$.29 per AUM while estimated interest on investment in federal allotments is \$3.25 per AUM.

Interest on investment and depreciation are "non-cash" costs, not "out-of-pocket" expenses, that many ranchers tend to ignore, at least in the short run. Failure to consider these "non-cash" costs greatly reduces the cost of grazing range forage.

Forage Cost Summary

If the "fixed" costs of forage use are not included, private deeded forage is the least expensive source of forage at \$3.42 per AUMless than federal forage by about the amount of the federal grazing fee (Table 5). When "fixed" costs are included (which they must be in the long run) private deeded forage is the most expensive source of forage (nearly \$25 per AUM) because interest on investment is 85% of this cost. While the cost of forage from this source appears to be very high for livestock grazing, forage from this land is essential to feed cattle year-round and it is necessary as "base property" to qualify for federal grazing permits. Furthermore, expensive hay harvested from private lands must be fed during the winter. Generally, western ranches must maintain at least some deeded property to utilize other cheaper sources of forage. In addition, few restrictions exist that limit the use of private lands. Landowners generally have the freedom to use, exclude, and transfer (sell) deeded property and also benefit from increases in property values.

The major advantages of grazing private land is the absence of regulations governing the use of these lands, including restrictions on season of use and stocking rates. Proposed changes in federal lands policy, which among other things could alter the season of use and reduce stocking rates on federal lands, could further enhance the advantage(s) attributable to private land ownership. The direct costs of complying with federal land policies (e.g., herding cattle out of riparian areas, extra herding to remove cattle from an allotment, seasonal use requirements) are included in the total cost figures presented above. Indirect costs, such as time required

Table 5. Forage cost summary.

Expense Item	Private Deeded (\$/AUM)	BLM (\$/AUM)	FS (\$/AUM)	Combined Federal (\$/AUM)
Variable Costs ¹				
Moving Cattle	.82	1.20	1.28	1.24
Range Improvement				
Maintenance	1.11	.18	.28	.23
Care of Cattle on				
Range	.18	.27	1.10	.72
Lost Animals	1.31	1.31	1.31	1.31
Grazing Fee	—	1.86	1.86	1.86
Subtotal	3.42	4.82	5.83	5.36
Fixed Costs Development				
Depreciation	.29	.00	.00	.00
Interest on				
Investment	21.28 ²	3.25	3.25	3.25
Subtotal	21.57	3.25	3.25	3.25
Total	\$24.99	\$8.07	\$9.08	\$8.61

Depreciation and "opportunity cost" charges on vehicles, which are "fixed" expenses, have been included as variable costs for simplicity. This results in a slight descrpancy between "variable" and "fixed" expense classifications.

This represents a weighted average based on 4136 AUM's from fed hay, 846 AUM's from private range and pasture and 2210 AUM's from grazing the aftermath on hay meadows.

to negotiate with federal agency personnel, are not included in the above cost estimates.

Forage from BLM lands appears to be the least expensive source of forage for the Saval Ranch (\$8.07 per AUM) if the 1982 grazing fee of \$1.86 per AUM is included. Approximately 52% of BLM non-fee cost is for interest on the ranch's investment in the BLM grazing permit.

The estimated non-fee cost of FS forage is more than \$1.00 per AUM higher than it is for BLM forage. Most of this difference is the result of additional care needed for cattle using FS lands including salting, checking cattle, and herding cattle for better distribution. Total non-fee costs for forage obtained from FS lands is estimated to be \$7.22 per AUM. The total cost of using FS lands is \$9.08 per AUM when the 1982 grazing fee is included. The weighted average cost of using federal lands by the Saval Ranch is estimated to be \$8.61 per AUM.

Discussion

The Saval Ranch headquarters are located closer to range forage than many other ranches. Since the headquarters are located adjacent to federal and private pastures, cattle do not need to be trucked except when sold. The ranch has very minimal private investments in range improvements on federal rangeland. As a result, this ranch's cost of grazing rangelands is probably less than those for other ranches who must truck and move cattle substantial distances, and/or have substantial investments in water developments, fencing, and other range improvements.

Results of this study suggest that a ranch incurs different costs when cattle graze different parcels of land. This suggests that the *net* returns obtained from grazing these differing parcels will also differ even if the same gross return is obtained from each area. As a result, average costs probably do not reflect the net value that results from grazing livestock in a particular area. Furthermore, the non-fee costs will commonly exceed the fees that are charged for using an area of rangeland.

The cost differences shown in this study can not be used as the basis for establishing a fee for the use of public or private lands because these costs do not reflect the value of forage. The value of grazing any area should be based on the performance of animals grazing these areas after the fee and non-fee costs of obtaining this forage have been subtracted. Fee and non-fee costs, such as those estimated above, would have to be subtracted from the revenues obtained from using an area before the value of forage obtained from any source of forage (e.g., BLM, FS, private) could be estimated.

The higher variable costs incurred when grazing public lands suggest that lease rates for use of private lands may be higher than those for using public lands. However, these higher fees could only be obtained if: (a) both types of lands yielded equal returns and (b) the opportunity costs of investments for private lands were ignored (or reduced significantly).

Even though grazing range forage is relatively inexpensive on the Saval, non-fee costs are still substantial. Variable costs for both BLM and FS lands are at least 1.5 times the grazing fee. Grazing fees comprise about 22% of this ranch's total estimated cost of grazing federal rangelands during 1982. This suggests that the "non-fee" costs of grazing federal rangeland must also be considered whenever changes in federal land grazing and pricing policies are proposed.

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SRM Election Results

The Elections Committee Chairman Don Smith, along with several other Colorado Section members, counted the ballots for new offices on Monday, December 9, 1985, at the Society for Range Management headquarters. Elected officers are:

Second Vice-President-William (Bill) A. Laycock

Directors (1986-1988)—Gary Donart and Tommy Welch

Directors Donart and Welch will replace retiring Directors Currie and Fischbach in February 1986.

Ballots and tally sheets are retained in the Denver office for one year for review. Approximately 28% of the membership voted.

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Statement of Ownership, Management, and Circulation

- (Act. of August 12, 1970, Sec. 3685, Title 39, United States Code)
- 1. Title of Publication: Journal of Range Management
- 2. Date of Filing: September 24, 1985
- 3. Frequency of Issue: Bimonthly
- 4. Location of Office of Publication: 2760 West Fifth Ave., Denver, Colo. 80204
- 5. Location of General Business Office: Same
- 6. Name and Address of: Publisher: Society for Range Management, 2760 West Fifth Ave., Denver, Colo. 80204 Editor: Patricia Smith 2760 West Fifth Ave., Denver, Colo. 80204

Managing Editor: Peter V. Jackson III 2760 West Fifth Ave., Denver, Colo. 80204

- 7. Owner: Society for Range Management, 2760 West Fifth Ave., Denver, Colo. 80204
- 8. Known Bondholders, Mortgagees, etc.: None
- 9. For Completion by Nonprofit Organizations Authorized to Mail at Special Rates: The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes have not changed during preceding 12 months.
- 10. Extent and Nature of Circulation

A Total coning printed	Avg. for 12 months	Actual for issue nearest filing date
A. Total Copies printed	0,039	0,700
b. Pala Circulation		
I. Dealers, counter sales	0	0
2. Mail subscriptions	5,914	5,868
C. Total paid circulation	5,914	5,868
D. Free distribution	20	15
E. Total distribution	5,934	5,883
F. Copies not distributed	925	817
G. Total	6,859	6,700

I certify that the statements made by me above are correct and complete.—*Peter V. Jackson*, Managing Editor.

Effects of Adenosine Monophosphate on Germination of Forage Species in Salt Solutions

D.J. UNDERSANDER

Seed germination can be a limiting step in the establishment of plant species on saline soils. There are indications that the level of adenosine monophosphate (AMP) in the seed may be a limiting factor in seed germination under stress. The objective of this research was to determine if added AMP would improve germination of grass and legume seeds under saline conditions. The seeds of tall fescue (Festuca arundinaceae Schreb. 'K-31'), bluegrama [Bouteloua gracilis (H.B.K.) Lag. ex Steud.], crested wheatgrass [Agropyron cristatum (L) Goertn 'Nordan'], switchgrass (Panicum virgatum L. 'Blackwell'), perennial ryegrass (Lolium perenne L. 'Lynn'), tall wheatgrass [Agropyron elongatum (Host) uv. 'Platte'], Russian wildrye (Elymus junceus Fisch.), western wheatgrass (Agropyron smithii Rydb.), and alfalfa (Medicago sativa L. 'Dawson') were germinated in petri dishes at varying levels of salinity with and without AMP. Time required for germination was shortened for all species, except switchgrass and western wheatgrass, with added AMP. Percent germination of alfalfa was increased with AMP at 14 days in 0.068 M sodium chloride and of tall fescue in the same concentration of sodium sulfate (dibasic). Perennial ryegrass, Russian wildrye and alfalfa demonstrated similar responses at 0.102 M sodium chloride. The germination of alfalfa was improved with AMP at 14 days in 0.034 M sodium sulfate. Adenosine monophosphate tended to have little effect when severe germination depression occurred from high salt concentrations.

Many thousands of hectares of soil have salt accumulations to the extent that seedling germination and vigor are reduced. Stand establishment on these soils is frequently very difficult. Germination is both delayed and final germination percentage reduced (Berstein and Wayward 1958). Holm and Miller (1972) reported that adenosine monophosphate (AMP) promoted germination of several weed seeds and that seed treatment with AMP accelerated germination (McDaniel and Taylor 1976). Pretreatment of cotton seeds with AMP hastened germination under saline conditions but no more than soaking in distilled water (Shannon and Francois 1977). Pretreatment of seeds with salt solutions has been found to increase salt tolerance during germination of wheat (Chaudhuri and Wiebe 1968).

Seedling germination involves the syntheses of RNA and proteins. This synthesis is dependent on the prior synthesis of adenosine triphosphate (ATP) in the seed (Anderson 1977a) but AMP may limit formation of ATP in seeds (Anderson 1977b). If AMP is a limiting factor in seedling germination, pretreatment of the seed with AMP may enhance germination. Anderson (1977a) reported that exogenously applied adenosine was incorporated into the embryonic axes of soybeans.

Under conditions of stress, AMP may be limiting germination and therefore, externally applied AMP may enhance germination. The objective of this research was to determine if pretreatment of rangeland seeds with AMP would enhance germination under saline conditions.

Methods

Germination studies in petri dishes were conducted on the following species: tall fescue (*Festuca arundinaceae* Schreb. 'K-31'), bluegrama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.], crested wheatgrass [*Agropyron cristatum* (L) Goertn 'Nordan'], switch-

Manuscript accepted 11 May 1985.

grass (*Panicum virgatum* L. 'Blackwell'), perennial ryegrass (*Lolium perenne* L. 'Lynn'), tall wheatgrass [*Agropyron elongatum* (Host) Beauv. 'Platte'], Russian wildrye (*Elymus junceus* Fisch.), western wheatgrass (*Agropyron smithii* Rydb.), and alfalfa (*Medicago sativa* L. 'Dawson').

Fifty seeds of each species in three replications were germinated in distilled water in the light ($20 \ \mu \text{ S}^{-1}\text{m}^{-2}$) at 25 °C to determine the rate and extent of germination under nonlimiting conditions. Seed pretreatment consisted of applying AMP (10^{-4} M in 10^{-2} M phosphate buffer pH 7) or an equal volume of distilled water to the seeds and immediately placing 50 seeds into petri dishes on filter paper to begin the trial. A preliminary study indicated that there was no effect on seed germination from inclusion of phosphate buffer alone in distilled water or saline solutions.

The salt treatments consisted of either sodium chloride or sodium sulfate (dibasic) at 0.034, 0.068, and 0.102 M. The salt solutions were added to the petri dishes. All treatments were replicated 3 times. Filter papers and salt solutions were changed every 3 days to reduce changes in salt concentration during the study. Treatments were incubated at 25 °C. Germination counts were taken every 2 to 3 days to determine rate of germination. Final germination was considered to be total germination at day 14.

Data were analyzed as a completely randomized design for the factors: species, salt type, salt concentration, and seed treatment and the results are presented in Table 1. Individual means of

Table 1. Analysis of variance of forage species germination in two salts at three concentrations with or without adenosine monophosphate (AMP).

DF	Sum or squares	F	PR>F
8	294332.26	212.84	0.0001
1	110254.70	637.82	0.0001
1	14495.30	93.85	0.0001
2	367159.92	1062.00	0.0001
6	179462.55	173.03	0.0001
8	39842.93	28.81	0.0001
3	9699.94	7.01	0.0001
16	99252.76	35.89	0.0001
1	455.15	2.63	0.1049
2	31729.81	91.78	0.0001
1460	252378.53		
	DF 8 1 2 6 8 3 16 1 2 1460	Sum or squares 8 294332.26 1 110254.70 1 14495.30 2 367159.92 6 179462.55 8 39842.93 3 9699.94 16 99252.76 1 455.15 2 31729.81 1460 252378.53	Sum or squares F 8 294332.26 212.84 1 110254.70 637.82 1 14495.30 93.85 2 367159.92 1062.00 6 179462.55 173.03 8 39842.93 28.81 3 9699.94 7.01 16 99252.76 35.89 1 455.15 2.63 2 31729.81 91.78 1460 252378.53 91.78

treated and untreated seeds for each day-salt type-salt concentration combination were separated with a t-test. The effect of days was analyzed by separated measures analysis.

Results and Discussion

The germination of all species increased with time. There was no germination of any grass species on the second day but, by day four, most live seeds of the tall fescue, bluegrama, crested wheatgrass, perennial ryegrass, and the tall wheatgrass had germinated in distilled water (Table 2). The germination of switchgrass was somewhat slower, being nearly complete by day six of the trial. Germination of Russian wildrye and western wheatgrass was largely completed by day eight of the trial. Germination of Dawson alfalfa was faster than that of any of the grasses and was largely completed by day two of the trial. The final germination of the

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Table 2. Germination of forage species in distilled water.

	Germination								
Species	Day 2	Day 4	Day 6	Day 8	Day 11	Day 14			
			%						
Tall fescue	0	93	93 ິ	_*	93	93			
Bluegrama	0	79	83	—	85	88			
Crested wheatgrass	0	87	89		90	91			
Switchgrass	0	23	41	_	48	53			
Perennial ryegrass	0	87	89		91	91			
Tall wheatgrass	Ō	87	91		92	- 92			
Russian wildrye	0	56		85	85	85			
Western wheatgrass	Ō	9	_	43	50	51			
Alfalfa	93	95	_	95	95	95			

S₂ = 2.6

*Data not collected.

species ranged from 85 to 95% with the exception of switchgrass and western wheatgrass, which had significantly lower (P = 0.01) final germinations of 53 and 51%, respectively.

Several generalizations can be made concerning the effect of salinity on germination of the species studied. The germination of tall fescue, perennial ryegrass, tall wheatgrass, and Russian wildrye was not affected by either sodium chloride or sodium sulfate at the 0.034 M (Tables 3 and 4). The results agree with the report by Mass and Hoffman (1977) that these grass species are more salt tolerant than most grass species. Other species were more sensitive to salt concentration and showed varying reductions in germination in the presence of 0.034 M salt concentration. Switchgrass and western wheatgrass appeared particularly sensitive to salt concentration, having 50% or greater reductions in germination at the lowest salt level. All species showed considerable reduction in germination at the 0.102 M salt concentration.

Sodium sulfate appeared to have a greater effect on germination than did sodium chloride. The germination of crested wheatgrass was reduced by the 0.034 and 0.068 M sodium sulfate treatments but not by equivalent levels of sodium chloride. Similarly, germi-

Table 3. Percentage germination of seeds of forage species with or without adenosine monophosphate (AMP).

					NaC1			Na2SO4			
Species	Salt concentration	AMP	Day 4	Day 6	Day 11	Day 14	Day 4	Day 6	Day 11	Day 14	
	M						_%				
Crested wheatgrass	.034	No Yes	70 89*	88 90	86 91	87 91	25 69*	45 77*	60 78	63 83	
	.068	No Yes	23 71*	65 77	78 81	81 84	13 16	27 40	27 41	38 60	
	.102	No Yes	13 27*	31 43	29 46	30 45	3 5	9 20	10 16	12 17	
Tall fescue	.034	No Yes	81 93	81 94	83 91	89 91	78 83	81 83	80 83	87 83	
	.068	No Yes	64 76*	64 77 *	61 77	76 78	10 9	19 12	17 13	19 40*	
	.102	No Yes	10 1	12 15	21 17	25 19	0 0	0 0	0 0	3 0	
Bluegrama	.034	No Yes	13 13	31 31	45 45	58 58	4 19*	16 33*	3 45	43 49	
	.068	No Yes	1 2	7 16 *	27 34	40 57	0 0	0 7	3 20*	4 19	
	.102	No Yes	0 0	0 7	23 21	31 23	0 0	1 1	1 1	1 2	
Perennial ryegrass	.034	No Yes	47 87 *	83 91*	92 92	91 93	38 84*	83 85*	77 88	78 89	
	.068	No Yes	28 37	85 85	86 85	86 87	11 27 *	39 53	60 55	60 57	
	.102	No Yes	11 19	60 77*	57 77 *	55 79*	3 12*	6 24*	33 25	36 21	
Tall wheatgrass	.034	No Yes	69 71	83 85	83 89	83 88	37 53*	78 81	81 83	81 84	
	.068	No Yes	17 23	52 72*	59 72	60 73	3 14	47 68*	60 72	60 73	
	.102	No Yes	5 11*	48 53	54 55	54 57	0 5	20 33*	37 37	38 39	
Switchgrass	.034	No Yes	3 11	25 22	31 25	31 23	2 4	18 19	26 23	25 25	
	.068	No Yes	2 5	13 14	23 18	23 19	0 1	5 7	10 13	12 14	
	.102	No Yes	0 0	4 5	9 11	10 11	0 0	1 1	3 3	3 4	

*Significantly higher germination (P<.05) than untreated, t-test.

nation of tall fescue, bluegrama, perennial ryegrass, Russian wildrye, and alfalfa was reduced to a greater extent by 0.068 M sodium sulfate than by the same concentration of sodium chloride. The difference between salts was probably due either to the higher concentration of sodium ions or to the slightly lower osmotic potential of sodium sulfate treatments but not by equivalent levels

The 0.034 M salt concentration did not reduce germination of tall fescue (Table 3). Thus, no effect of AMP would be anticipated. AMP treatments did have significantly (P=0.05) higher early germination for the 0.06 and 0.102 M concentrations of sodium chloride where the salt concentrations reduced germination. In both cases the rate of germination was enhanced while there was no significant (P=0.05) difference in the final germination at day 14. The AMP treatment did increase the final germination of tall fescue in sodium sulfate at 0.068 M where the final germination was 19% without AMP and 49% with AMP.

Salt concentrations of 0.034 M reduced germination of bluegrama to a greater extent than that of tall fescue (Table 3). Early germination of bluegrama was enhanced by AMP in the 0.034 M sodium sulfate and the 0.068 M sodium chloride. The AMP treatment had significantly (P=0.05) higher germination in the 0.068 M sodium sulfate solution by day 11. A similar trend continued for day 14 but the difference was not significant. There was no effect of AMP at the 0.102 M salt concentration where the salt concentration severely reduced germination.

The germination of crested wheatgrass was generally less effected at each salt level than the germination of other species (Table 3). AMP increased the early germination of the seeds germinated in sodium chloride at every salt concentration. Rate of germination of crested wheatgrass was also increased by AMP in 0.034 M sodium sulfate. In no case was there a significant increase in final germination due to the AMP treatments.

Similarly, perennial ryegrass was fairly tolerant of salinity during germination. Early germination of this species was increased by AMP at every level of sodium sulfate and at the 0.034 M sodium chloride treatment. Additionally, the final germination of perennial ryegrass was increased in 0.102 M sodium chloride with AMP (79 vs 55%).

The early germination of tall wheatgrass was increased with AMP at every level of sodium sulfate. Further, at the 0.068 and 0.102 M sodium chloride concentrations, early germination was enhanced with AMP.

The early germination of Russian wildrye was enhanced with the AMP treatment in sodium chloride at 0.034 M and 0.102 M. A similar trend was noted with sodium chloride at 0.068 M; however, the difference was not significant. Additionally, AMP enhanced the early germination of Russian wildrye in 0.102 M sodium sulfate. The final germination at 15 days of Russian wildrye was significantly increased from 38 to 63% in the 0.102 M sodium chloride.

As with crested wheatgrass, the early germination of alfalfa was increased by AMP at every concentration of sodium chloride. Also the final germination at 14 days was significantly increased by AMP in sodium chloride at 0.068 and 0.102 M salt concentration and in the sodium sulfate at 0.034 M.

As lack of significant salt type by treatment interaction (Table 1) indicates, treatment with AMP caused similar germination responses in both sodium chloride and sodium sulfate. The AMP seed treatment at no time had any effect on the seeds of switchgrass and western wheatgrass. The lack of response could be due to the lots of seed chosen for the study. As noted in Table 2, both species had low germinations in distilled water. Another possibility is that a metabolic difference may exist between these 2 species from the other species tested. Monocotyledons tend to have less salt tolerance than dicotyledons. However, differences occur in much more closely related species due to differences in membrane permeability, enzyme activity, or ability to synchronize compartmentalization (Greenway and Munns 1980). Both species showed a rapid decline in germination with increasing salinity even at the lowest levels in the experiment. As noted previously, few of the species responded when the salt concentration had greatly reduced

Table 4.	Percentage	germination of	of seeds of i	forage species	with or with	out adenosine	e monophosphate	(AMP).
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	Salt				NaC	1				Na ₂ SO ₄	ļ	
Species	Concen- tration	AMP	Day 2	Day 4	Day 8	Day 11	Day 14	Day 2	Day 4	Day 8	Day 11	Day 14
	M							%				
Russian wildrye	.034	No Yes	0 0	45 64*	76 75	77 83	78 83	0	33 47	75 68*	76 70	77 70
	.068	No Yes	0 0	35 45	72 73	73 73	74 74	0 0	7 13	29 39	39 41	39 42
	.102	No Yes	0 0	5 31*	37 51	38 61*	38 63*	0 0	0 1	0 23*	13 25	21 25
Western wheatgrass	.034	No Yes	0 0	2 4	17 13	22 15	23 16	0 0	0	7 12	9 13	11 13
	.068	No Yes	0 0	0 0	9 12	11 11	13 13	0 0	0 0	1 1	1 2	1 2
	.102	No Yes	0 0	0 0	0 5	1 6	1 6	0 0	0 0	0 0	0 0	0 0
Alfalfa	.034	No Yes	31 83*	76 92	90 93	92 93	92 93	19 27	56 79	67 90	69 91	66 91*
	.068	No Yes	11 49*	39 79*	79 93*	84 92*	85 91*	0 0	0 5	5 23*	6 22*	25 22
	.102	No Yes	2	6 23*	27 61*	29 62*	33 63*	0 0	0	0	0	0

*Significantly higher germination (P<.05) than untreated, t-test.

of sodium chloride.

germination.

Possibly, responses to AMP may be observed only at salt levels that moderately reduce overall germination.

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Germination of Fourwing Saltbush Seeds: Interaction of Temperature, Osmotic Potential, and pH

R.L. POTTER, D.N. UECKERT, J.L. PETERSEN, AND M.L. MCFARLAND

Abstract

Establishment of shrubs and other forage plants on arid and semiarid rangelands and salt-contaminated sites may be enhanced if ecotypes with ability to germinate and establish under moisture stress and high temperatures can be identified. The interactive effects of temperature, osmotic potential, and pH on germination were evaluated with seed from 4 populations of fourwing saltbush [Atriplex canescens (Pursh) Nutt.] from western Texas. Predicted optimum temperature (15 to 18°C) from osmotic potential by temperature response surfaces for germination of 3 populations (Valentine, Grandfalls, and San Angelo) were similar to those reported for populations of fourwing saltbush from other western states. Germination of seed collected near Texon, Texas was significantly (P < 0.01) affected by media pH range 6 to 9. Seed from the Texon population germinated under lower osmotic potentials compared to the other 3 populations. Total germination of all four populations was enhanced by osmotic potentials lower than 0 MPa. Seed from the Texon population may possess germination characteristics more suitable for arid-land seeding than those from populations near Valentine, Grandfalls, and San Angelo, Texas.

Fourwing saltbush [Atriplex canescens (Pursh) Nutt.], a native, evergreen shrub, is absent or rare on most western Texas rangeland, probably because of the prevalence of continuous, yearlong grazing by cattle, sheep, and/or goats. The species has been successfully used for rehabilitation of oilwell reserve pits where high concentrations of soluble salts and sodium prevented acceptable establishment or growth of other species.¹ Our preliminary grazing trials suggest that fourwing saltbush may be valuable for balancing the seasonal deficiencies of protein in native forages (D.N. Ueckert, unpublished data).

Fourwing saltbush frequently grows on relatively dry, saline

Manuscript accepted 28 May 1985.

soils, suggesting that its seed may be adapted for germinating under conditions of limited moisture. Springfield (1966) hypothesized capacity to germinate under dry field conditions may vary among geographic strains or ecotypes of fourwing saltbush. Therefore, ecotype selection should improve potential for revegetating arid and semiarid rangelands.

Fourwing saltbush germinates best at low temperatures (13 to 24°C). Light is not required unless seeds are less than 4 months old or under alternating temperature regimes (Springfield 1970). Fourwing saltbush emergence was adversely affected by high (53°C) compared to low (39°C) temperature regimes (Sosebee and Herbel 1969). Buffered pH in the range 3.0 to 8.0 did not affect germination of 6 Australian saltbush species (Beadle 1952). However, saltbushes are seldom found growing in acidic soils (Foiles 1974). Dewinging fourwing saltbush seed in a hammer mill hastens germination and is a standard practice. The bracts contain about 10% saponin, a germination inhibitor (Nord and Van Atta 1960).

Tolerance of fourwing saltbush seed to low media osmotic potential during germination may be genetically controlled. Spring-field (1966) reported fourwing saltbush seed germinated at -1.50 MPa of manitol-induced moisture stress, but total germination and germination rate decreased with increasing moisture stress. However, seeds of 3 of 6 seed accessions exhibited greater total germination at -0.30 MPa than at -0.03 MPa, and total germination of 2 accessions was greater at -0.70 MPa than at -0.03 MPa. Springfield concluded that additional research was needed to confirm whether germination of some fourwing saltbush strains was actually stimulated by low media osmotic potentials.

Fourwing saltbush seed tolerated greater levels of moisture stress during germination at 17°C than at higher or lower temperatures (Springfield 1966). This suggests that moisture stress may be less limiting to germination when temperatures are near optimum. Field germination of seeds can be better understood if the interactive effects of seedbed parameters are known (Kaufman and Ross 1970, Sharma 1976). Objectives of this study were to (1) evaluate the interaction of temperature, osmotic potential, and pH on germination of fourwing saltbush seeds, and (2) determine whether germination characteristics varied among naturally occurring populations of the species in western Texas.

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This article is approved by the Director, Texas Agricultural Experiment Station as TA-20556.

This research was partially funded by University Lands, the University of Texas System.

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¹McFarland, M.L. 1984. Revegetation of oilwell reserve pits in west Texas. MS Thesis, Texas A&M University, College Station.

Methods and Materials

Seed from about 100 native fourwing saltbush plants were handharvested in December 1981 at each of 4 sites in the western Edwards Plateau and Trans-Pecos resource areas of Texas, including: 1 km west of San Angelo (Tom Green County); Texon (Reagan County); 10 km south of Grandfalls (Pecos County); and 5 km northwest of Valentine (Jeff Davis County) (Table 1). Fourwing

Table 1. Collection sites of fourwing saltbush seeds used in evaluation of the interaction of temperature, osmotic potential and pH upon germination.

Location	°N Lat	°W Long	Elevation (m)	Avg annual precipitation (cm)
San Angelo	31°30′	100°25′	564	48
Texon	31°15′	101°40′	792	38
Grandfalls	31°15′	103°00'	792	30
Valentine	30° 35′	104°40'	1433	28

saltbush occurred on loam and clay loam soils of the Tulia and Angelo series (Calciorthidic Paleustalfs and Torrertic Calciustolls) at the San Angelo site (Wiedenfeld and Flores 1976), on Reagan silty clay loam soils (Ustollic Calciorthids) at the Texon site (SCS staff, personal communication), on Reakor silty clay loam soils (Typic Calciorthids) at the Grandfalls site (Rives 1980), and on Verhalen and Dalby clay soils (Mollic and Typic Torrerts) at the Valentine site (Turner 1977).

Soils at all sites except Texon were nonsaline, but characterized by some degree of disturbance. The Texon site was at the edge of an oilfield characterized by heavily eroded, barren soil and a shallow, saline water table with electrical conductivities of 100 to 200 dSm⁻¹. Fourwing saltbush seeds were collected from plants growing on the edge of this saline area. All seeds were oven-dried at 49°C for 24 hr, then dewinged in a modified hammer mill. Soil surface temperatures frequently exceed 49°C during summer in western Texas, thus we feel that there was no biologically significant effect caused by oven drying the seeds. The seeds were stored at room temperature in paper sacks until July 1982 when germination studies were initiated.

Germination trials were conducted in a factorial design with 3 replications. Constant temperature regimes were 12, 17, and 22°C. Polyethylene glycol (PEG) 6,000 was used to simulate low (-0.3 to -0.4 MPa), moderate (-0.6 to -0.8 MPa), and high (-1.3 to -2.2 MPa) osmotic potentials using the empirical formula and gravimetric procedures developed by Michel and Kaufmann (1973). Approximate concentrations (kg PEG/kg water) of PEG needed to achieve desired osmotic potentials at each temperature were calculated from the empirical formula. Exact concentrations of PEG were determined by drying 20 ml of buffered solution in a vacuum oven. Exact PEG concentrations were entered into the empirical formula to provide approximate values for media osmotic potentials. A 0 MPa treatment (distilled water plus buffer) was included in all experiments. Buffered pH levels were 6, 7, 8, and 9. Sorensen's phosphate buffers were used at pH 6 and 7 and tris(hydroxymethyl)aminomethane buffers were used at pH 8 and 9 (Henry 1979). Buffer solutions were added at 40 ml per liter of germination media. These buffers cause slightly lower osmotic potentials than those estimated from gravimetric determinations of PEG concentrations. Effects of the buffers on osmotic potentials were not determined.

A replication consisted of 50 seeds placed on 2 layers of filter paper in a petri dish and subjected to each combination of temperature, osmotic potential, and pH. Eight ml of the appropriate germination media was added to each dish. The dishes were randomly placed on several layers of blotter paper in covered glass boxes. The blotter paper was kept saturated with distilled water throughout the 4-week trials. This procedure minimizes changes in media osmotic potentials through time (Berkat and Briske 1982). Seeds were germinated in controlled environment chambers in darkness but were exposed to light when germination was evaluated weekly. Seeds were considered germinated when the length of the radicle exceeded the length of the seed (3.5 to 7.0 mm). Surplus PEG solutions were placed in bottles and stored with the seeds throughout the trials. The change in pH of the PEG solutions averaged ± 0.1 units at the end of the 4-week trials. The experiment was repeated in 2 controlled environment chambers (Puffer-Hubbard Model GL-10CT, Grand Haven, Mich., and Sherer Environmental Model RI-25LTP, Asheville, N. Carolina) and the data pooled for statistical analysis.

Germination was modeled by quadratic response surfaces or regression analysis (Evans et al. 1982). Quadratic response surfaces based on osmotic potential by pH were estimated for each fourwing saltbush population, temperature, and week on cumulative germination transformed by $\sin^{-1} \sqrt{p}$, where p = proportion of seeds germinated. Regression analysis was used to model germination responses where appropriate. All tests for significant main effects and interactions were at the $P \le .01$ probability level.

Results and Discussion

Effect of pH in the quadratic response surfaces based on osmotic potential by pH treatments was significant only within the Texon fourwing saltbush seeds at 22°C. Linear and quadratic effects of osmotic potential and pH were generally significant each week for the Texon seeds at 22°C. Since varying pH did not affect germination of the Texon seeds at 12 or 17°C, quadratic regression equations based on osmotic potential within temperatures were used to model weekly germination responses. Data were pooled over pH levels for the Valentine, Grandfalls, and San Angelo populations and quadratic response surfaces based on osmotic potential by temperature were used to model weekly germination responses.

Germination of seed from the Texon population at 22° C increased toward extremes in pH. Critical values were pH 7.6 to 7.7 and -0.3 to -0.4 MPa for each week. Total germination (week 4) was 22% in the saddlepoint at pH 7.7 and -0.4 MPa, and increased to 30 and 27% at pH 6 and 9, respectively.

Rapid germination is important for successful establishment of range seedings (Jordan 1983). The most rapid germination (week 1) at 12°C occurred at 0 MPa for the Texon seeds (Table 2). Greatest predicted germination of the Texon seeds after 1 week (27%) occurred at 17°C and -0.4 MPa. Discrete sets of temperature and media osmotic potentials produced maximum germination of seeds from the Valentine, Grandfalls, and San Angelo populations. Linear effects of temperature and quadratic effects of temperature and osmotic potential were statistically significant for each week. Linear effects of osmotic potential were present during weeks 3 and 4 in the Valentine population, week 2 in the Grandfalls population, and weeks 1 and 2 in the San Angelo population. More seeds from these populations germinated at 0 MPa than at lower osmotic potential during the first 2 weeks (Table 3).

Germination of the Texon seeds was significantly greater at media osmotic potentials less than 0 MPa than at 0 MPa for weeks 2, 3, and 4 at 12°C and each week at 17°C (Table 2). Maximum germination at 17°C occurred at -0.6 to -0.8 MPa, but the greatest total germination occurred at 12°C and -0.4 MPa. However, Texon seed germinated at considerably lower osmotic potentials at 17°C than at 12°C. Maximum germination after 4 weeks occurred at -0.1 MPa for the Grandfalls and San Angelo populations, compared to -0.3 MPa for the Valentine seeds (Table 3). Maximum germination after 1 week occurred at higher temperatures (16.7 to 17.9°C) than maximum germination after 2 weeks (15.1 to 16.4°C). Predicted optimum temperatures for maximum germination after 3 or 4 weeks were about 15 to 16°C for these 3 populations.

Wildland species can vary greatly in germination characteristics,

Table 2. Predicted germination (%) of fourwing saltbush seeds collected from a saline area near Texon, Texas at 12 and 17° C constant temperatures and selected media osmotic potentials (MPa).¹

	•••••••••••••••••	Osmotic Potential (MPa)								
Temperature	Week	0.0	-0.2	-0.4	-0.6	-0.8	-1.4	-1.8	SEE ²	
(°C)					(Germir	nation %)				
Ì2 Í	1	17	15	13	10	6	0	0	1	
	2	24	33	36	34	27	0	0	1	
	3	26	34	37	37	32	3	0	1	
	4	27	34	38	37	33	6	0	1	
17	1	24	26	27	26	24	13	4	1	
	2	26	30	33	34	33	21	8	1	
	3	27	31	34	35	34	24	11	1	
	4	27	31	34	35	35	25	13	1	

Germination values estimated from quadratic regression equations based on media osmotic potential. 2SEE = Standard error of the estimate.

Table 3. Predicted optimum germination (%) of fourwing saltbush seeds collected near Valentine, Grandfalls, and San Angelo, Texas and associated critical values of media osmotic potential (MPa) and temperature (°C) for each week of a 4-week trial.¹

		Critica	Critical values			
Population	Week	Osmotic potential (MPa)	Temperature (°C)	optimum response (% germination)		
Valentine	1	0.0	17.9	37		
	2	0.0	16.4	44		
	3	-0.2	16.2	45		
	4	-0.3	16.0	46		
Grandfalls	1	0.0	17.3	23		
	2	0.0	15.3	31		
	3	0.0	15.5	31		
	4	-0.1	15.5	31		
San Angelo	1	0.0	16.7	33		
-	2	0.0	15.1	45		
	3	0.0	15.2	45		
	4	0.1	15.2	45		

Germination and critical values estimated from quadratic response surfaces based on media osmotic potential by temperature. Critical values, in these cases, where those at which germination responses were maximum. The significant effect of media pH on germination of seed of the Texon ecotype prohibited estimation of a response surface based on these factors for this ecotype.

even within populations (Westoby 1981). Fourwing saltbush and other woody chenopods have the ability to evolve new ecotypes adapted to harsh site conditions (Stutz 1983). Adaptation to a saline environment may explain the unique germination characteristics of seed from the Texon ecotype in relation to pH and osmotic potential of the germination medium. However, the increased germination of seeds from the Texon ecotype at lower media osmotic potentials compared to the other 3 ecotypes might have been caused by the environment in which these seeds matured. Seeds that developed on plants growing on the saline soils at Texon may have taken up more salts (osmoticum) which allowed them to germinate at lower osmotic potentials.

A significant interaction between temperature and osmotic potential occurred with the Valentine population during the third and fourth weeks, whereas this interaction was generally absent from the Grandfalls and San Angelo populations. The interaction indicates that the nonadditivity for total germination occurs at lower (more negative) osmotic potentials and higher temperatures (Fig. 1).

A temperature by osmotic potential interaction exists for some species but not for all (Kaufmann and Ross 1970, Sharma 1976). Results of this study suggest that this interaction exists in some ecotypes of fourwing saltbush but not others. This interaction implies that when seeds are subjected to high temperatures (e.g., summer) the effect of limited moisture is more inhibitory to germination than when temperatures are near or below optimum (e.g.,



Fig. 1. Illustration of the significant ($P \le 0.01$) interaction between temperature (TEMP) and media osmotic potential (0.P.) for total germination of fourwing saltbush seeds collected from plants growing in a high elevation, desert grassland near Valentine, Texas. Maximum germination after 4 weeks occurred at 16.0° C and -0.3 MPa. Data generated from a quadratic equation were used for plotting by SAS/GRAPH.

spring or fall), whereas if moisture is not limited, these seeds germinate well over a broader range of temperatures. Fourwing saltbush from the Valentine population apparently has undergone selection resulting in plants that produce seed that do not germinate at high temperatures and low soil moisture contents. Conversely, the absence of this interaction from the San Angelo and Grandfalls populations suggests high and low temperatures inhibit germination equally as soil water contents vary.

Conclusions

Interactive effects of seedbed parameters upon germination varied considerably among ecotypes of fourwing saltbush. Optimum temperatures for germination varied among the populations, but were generally 15 to 18°C, which agrees with studies on other saltbush populations (Springfield 1966, 1970). The relative tolerance of the 4 populations of fourwing saltbush to moisture stress during germination was Texon > Valentine > Grandfalls = San Angelo. The effect of pH was relatively minor though it cannot be ignored as a factor affecting germination of seeds from the Texon population at 22°C.

Low media osmotic potential was less detrimental to germination at optimum germination temperature than at higher or lower temperatures. Increasing moisture stress delayed germination of 3 populations similar to the findings of Springfield (1966) and Sharma (1976). Total germination of seeds from the Texon site was significantly greater at osmotic potentials of -0.4 to -0.8 MPa than at 0 MPa, which suggests results observed by Springfield (1966) were not attributable simply to random variation. This result suggests seed from the Texon population might have more potential for arid land seedings compared to seed of the other populations.

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Population Dynamics of Seeded Species on Northeast Washington Semiarid Sites, 1948-1983

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Abstract

Fifty-one graminoid and 10 forb taxa commonly used in range seedings were planted at 3 semiarid northeast Washington sites, spring and fall seasons, in monospecific stands, on 5.5 m by 1.3 m plots, 1948 to 1951. Population dynamics and clipped yields were observed at irregular intervals from 1952 to 1983. Ten graminoid, but no forb, taxa are recommended for range seeding. Grass species differ markedly in fitness for the sites, as demonstrated in success of passing through the environmental sieve, recruiting posterity, and long-term survival. Species interactions were site specific, demonstrating characteristic and complex demographic schedules at each site. Hard fescue was the most aggressive competitor, progressively replacing many of the others at all sites. Crested wheatgrass taxa provided the highest yields. Species mixtures which developed were unstable in the long term (30 years), and are not recommended in seeding practice.

Manuscript accepted 4 June 1985.

Exotic graminoid species have been introduced onto semiarid sites in the western United States over the past century to restore valuable perennial forage plants where climax species have been removed. Eventual ecological adjustment of these extrinsic populations into the habitats which they have been introduced is frequently in doubt, because accurate long-term records have rarely been kept. Consequently, information necessary for selection of proper species to be used in future seeding activities is inadequate.

More than 30 years of records are now available for 3 sites in northeast Washington. The primary objective of these trials was to bracket the environments with exotic forage taxa having differing site requirements, as a means of selecting the highest producing, longest lived, and most competitive for each location. Sixty-one species and varieties (or cultivars), were included.

Although modern concepts of population ecology were not included in the original design, results provide a rare, if less than ideal, perception of population dynamics. Plant population ecology terms and concepts of Silverton (1982) are followed in this discussion. It is our purpose to report here both species fitness and demographic trends.

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Table 1. Site characteristics at three Northeast Washington species adaptation nurseries.

	Harrington	Republic	Riverside
Annual precipitation (inches) (see Fig. 1)	12.26	16.04	22.19
slope	1% SW	0–1% SW	2% SW
elevation (feet)	2167	2610	2200
latitude	47° 25′	48° 39'	47° 58′
longitude	118° 15′	118° 44'	117° 26′
Legal Description	NE4/SE4/Sec16, T23N, R36E	SE1/4NE1/4Sec20, T37N, R33E	NE1/4NE1/4Sec3, T28N, R43E
Soil	Benge silt loam	Chesaw sandy loam	Bonner gravelly silt loam
Landform	Dry terrace, well drained	Outwash terrace, well drained	Dry Outwash terrace well drained
Parent material	Loess over outwash gravel	Glacial outwash & volcanic ash	Glacial outwash & volcanic ash
	Calcic Haploxerolls	Entic Haploxerolls	Typic Haplorthods
Habitat type	Artemisia tripartita	Pinus ponderosa/	Pinus ponderosa/
	Festuca idahoensis	Agropyron spicatum	Stipa comata
		and P. ponderosa/	and P. ponderosa/
		Stipa comata	Agropyron spicatum

¹Climatological data from nearest weather station, at Deer Park, WA.

Hafenrichter et al. (1949) classified forages adapted to the Pacific Northwest into 10 major groups based on phenology, productivity, and utility of the species. Woolfolk and Harris (1951) listed forage taxa found to be best adapted to the nurseries discussed in this study and recommended proper seasons for seeding ranges typified by these sites. Evanko (1955) listed all taxa seeded in the three nurseries and rated them according to seedling establishment and survival through 1953, as well as recommended 8 taxa as superior. Earlier releases reported data on germination, phenology, and mortality, giving insight into success in passing the environmental sieve, recruitment, birth, and survival of taxa on these sites (Evanko 1952, 1954). Gates and Harris (1959) reported further on species adaptation at the 3 nurseries, including yields for 8 outstanding species and varieties. These were Nordan and commercial crested wheatgrass varieties (Agropyron desertorum Schult)¹, Fairway crested wheatgrass (A. cristatum [L.] Gaertn.), Whitmar variety bluebunch wheatgrass (A. spicatum [Pursh] Scribn. and Smith), tall wheatgrass (A. elongatum [Host] Beauv.), intermediate wheatgrass (A. intermedium [Host] Beauv.), hard fescue (Festuca ovina var. duriuscula [L.] Koch), and big bluegrass (Poa ampla Merr.).

Methods

Species adaptation trials were established on semiarid sites near Harrington, Republic, and Riverside in northeastern Washington (Table 1). Average annual precipitation data for the study period are given in Figure 1.



Fig. 1. Average annual precipitation, 1948-1978, for 3 northeast Washington locations near forage nurseries (De 2r Park is nearest climatological station to Riverside site).

One plot of each species was seeded at each site in fall 1948, spring and fall 1949 and 1950, and spring 1951. Sites were prepared by plowing, harrowing and packing immediately prior to seeding.

Scientific names follow USDA-Forest Service (1976) Northwest Plant Names. (See Dewey (1983) for proposed changes in Agropyron taxonomy).

Three 5.5-m rows, 45 cm apart, with 45-cm alleys between rows in adjacent plots, were seeded using a vegetable seed drill. Competing weed species were removed twice each growing season for 2 years following seeding.

Evaluations were made annually following germination until 1953, and at irregular intervals since that time. Yields, vigor, and area dominance are reported here for 1959, 1968, and 1978. Planted species were clipped 2 cm above the crown, from a 1-m randomly selected section of the center row of the plot, air dried, weighed, and the result converted to kg/ha. If the center row lacked established plants of the designated taxa, the clipped subplot was established on one of the outside rows or a nearby area having a stand. Nondesignated taxa clippings were kept separate, dried, and weighed. Vigor was estimated on a scale of 1 to 5, with ratings of 3 or above considered satisfactory. Area dominance maps were prepared indicating parts of the sites controlled by specific taxa. Areas of species dominance were established subjectively on the basis of coverage and vigor. Confirming observations of aggressive invasion, but no yield or vigor observations, were made in August, 1983.

In the beginning, all sites were fenced to prevent livestock grazing use. Fences were maintained regularly during early years, but repairs became infrequent as administrative responsibility was transferred between Forest Service, Agricultural Research Service, and Washington State University.

Results and Discussion

A majority of the taxa seeded proved not to be fitted to the environments found on the test sites. They either failed to pass the environmental sieve, or to effectively recruit a viable population (Table 2).

Six short-lived taxa are recommended as suitable for short-term range plantings on these sites. They establish quickly and produce large quantities of good quality forage. These include timothy (*Phleum pratense L.*), mountain brome (*Bromus marginatus* Nees), reed fescue (*Festuca arundinacea* Schreb.), and orchardgrass (*Dactylis glomerata L.*) at the Harrington and Republic sites, and green needlegrass (*Stipa viridula Trin.*) at Riverside.

Forb seedings had failed by 1953, except for ladak, creeping, and Siberian alfalfa (*Medicago sativa* L.) varieties at Harrington. These had disappeared also by 1959. Legumes are desired in range grass plantings on semiarid soils for their nitrogen fixing ability. However, none were found adapted to long-term competition in these trials.

Ten seeded species or varieties demonstrated sufficient fitness to be recommended for semipermanent or permanent range seedings Table 2. Taxa seeded in 1948-51, not recommended for long-term range seedings at three Northeast Washington sites.

Bluegross bulgenet	
Bluegrass, bulgous+	Kye, mountain
Bluegrass, Canada§ (2)	Ryegrass, perennial
Bluegrass, Canby	Timothy (2)
Bluegrass, Kentucky (2)	Wheatgrass, slender (4)
Brome, mountain	Wheatgrass, streambank (2)
Brome, smooth	Wheatgrass, western
Canarygrass, reed	Wildrye, blue
Fescue, Idaho (2)	Wildrye, Russian
Fescue, sheep	Alfalfa (3)
Fescue, tall	Burnet, small
Foxtail, creeping	Clover, alsike
Foxtail, meadow	Clover, strawberry
Needlegrass, green	Clover, white, ladino
Oatgrass, tall	Clover, yellow, sweet
Orchardgrass (3)	Trefoil, big, Granger
Redtop	Milkvetch, sicklepod
Ricegrass, Indian	

*For scientific names, variety names, or accession numbers, see Gates and Harris (1959) table 2

§Numbers in parentheses indicate number of varieties or accessions in trials, when more than one.

on these, or similar sites (Tables 3 and 4). They include Nordan, standard, and Fairway crested wheatgrasses; tall, intermediate, and bluebunch (Whitmar) wheatgrasses; hard fescue and big bluegrass; and Siberian wheatgrass (A. sibericum Beauv.) and pubescent wheatgrass (A. trachycaulum C. Richt.) The latter 2 are added in this report to the 8 previously recommended by Gates and Harris (1959), based on 1968-78 evaluations.

The 10 recommended species and varieties appear to be longlived. However the original seeded rows in none of the plots were clearly observable by 1983, and individual plants occurred at random where distinct rows had been earlier. This observation leads to questioning whether members of the original cohorts were still present, or replaced by newly recruited vegetative daughters and seedlings. The implication is that at least some individual plants of these species have longevity less than 30 years, and through recruitment of seedings or clones their populations may move about the site. On the other hand, seedings of commercial crested wheatgrass 30 years old have been observed on other sites in the west with rows clearly delineated, and essentially no recruitment between. The presence of new plants of the recommended species and varieties at these 3 sites, especially in competition with cheatgrass (B. tectorum L.) and other aggressive weeds, indicates close naturalization of these seeded perennial exotics to their new environments (Harris 1967).

Hard fescue was the most aggressive invader of all seeded taxa (Table 3). It controlled almost half of the area of the 3 sites after 30 years (1948-78). It became established after initial seeding at Riverside and Republic, but failed in early seedings at Harrington (Evanko 1955). However, once established there by later seedings, it progressively dominated Harrington, as well as the other sites.

Intermediate, pubescent, and crested wheatgrasses became well established by 1959, and spread aggressively into plots where competition was mild. Intermediate and pubescent spread by rhizomes as well as seeds. These 2 species are similar in appearance and ecologic site requirements, with pubescent being slightly more drought tolerant. Seeds of the 2 are frequently mixed in commercial lots. However, by 1978 these aggressive wheatgrasses had lost area dominance in competition with others, primarily hard fescue.

Bluebunch (Whitmar), Siberian, and tall wheatgrasses, and big bluegrass were the least aggressive of those listed in Table 3. They have proven useful in some situations, mostly as monospecific stands. Tall wheatgrass is ideally adapted to saline and alkaline subirrigated sites in this region where yields of 8 to 9 metric tons/hectare (7 short tons/acre) have been reported (Hafenrichter et al. 1949). Big bluegrass is slow to establish, and susceptible to uprooting during grazing.

Wheatgrasses were most successful in resisting the incursions of hard fescue at the Harrington site (Table 3 and Fig. 2, 5). Crested, intermediate, and pubescent wheatgrasses proved to be well

Table 3.	Changes in percent of	nursery site covered b	y major taxa on 3 successive dates.
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		Harrington			Republic			Riverside	
Planted Taxa	1948/ 1951§	1968	1978	1948/ 1951§	1968	1978	1951§	1968	1978
			********	%					
Crested wheatgrasses (mixed)	11	24	21	8	14	3	8	4	0
Tall whcatgrass	4	0	0	4	0	0	4	1	2
Intermediate wheatgrass	6	13	12	4	9	9	4	8	20
Siberian wheatgrass	4	6	0	1	7	0	2	0	0
Pubescent wheatgrass	4	11	12	4	14	6	3	11	10
Bluebunch wheatgrass (Whitmar)	2	2	0	7	6	2	4	0	0
Hard fescue	10	29	34	4	24	56	5	25	50
Big bluegrass	0	6	6	2	3	0	4	0	0
Major invading species									
Cheatgrass	*	6	12	*	4	2	*	8	2
Duffuse knapweed	*	0	0	*	0	2	*	0	0
St. Johnswort	*	0	0	*	1	17	*	0	0
Spanish clover	*	0	0	*	0	0	*	50	11
Major invading native species									
Bluebunch wheatgrass	*	0	0	*	Т	3	*	0	0
Silky lupine	*	t	Ŧ	*	ŧ	+	*	ŧ	Ť
Sandberg bluegrass	*	ò	ó	*	4	Ó	*	ò	ò
Canda bluegrass	*	0	0	*	0	0	*	4	2
Bottlebrush squirreltail	*	0	Ó	*	0	0	*	1	0
Needle-and-thread	*	Õ	Ő	*	10	0	+	Ō	Ō
% of site covered by above taxa	41	97	91	34	89	100	36	93	97

Second of original seeded site.
*Not reported.

[†]Scattered throughout site, without area dominance.

Table 4. Yields of ten best adapted grasses at three northeast Washington sites, 1959, 1968 and 1978.

			• •	Standi	ng Crop Yiel	d (kg/ha)		
Location and species		1959		1968		1978		Average Yield by species location
Harrington				,				
Fairway crested wheatgrass	AB*	2477(5)§	Α	1219(5)	AB	1861(5)	Α	1852
Commercial crested wheatgrass	AB	2464(6)	Α	1308(6)	AB	1971(6)	Α	1915
Nordan crested wheatgrass	Α	3311(4)	Α	1337(4)	AB	1643(4)	Α	2097
Tall wheatgrass	В	1320(1)	Α	1078(1)	В	000(1)	В	799
Intermediate wheatgrass	В	1563(9)	Α	939(9)	AB	1392(9)	AB	1298
Siberian wheatgrass	В	1848(5)	Α	873(5)	AB	1033(5)	AB	1252
Whitmar bluebunch wheatgrass	В	1500(3)	Α	476(3)	AB	394(3)	В	798
Pubescent wheatgrass	В	1499(4)	Α	898(4)	AB	1591(4)	AB	1330
Hard fescue	В	1705(4)	Α	798(4)	Α	2389(4)	AB	1597
Big bluegrass	AB	2642(2)	Α	1381(2)	AB	2065(2)	A	2029
Republic								
Fairway crested wheatgrass	CD	976(6)	CDE	679(6)	А	1822(6)	BC	1159
Commercial crested wheatgrass	В	1942(7)	AB	1515(7)	В	752(7)	AB	1403
Nordan crested wheatgrass	Ā	2766(2)	A	1637(2)	B	776(2)	A	1726
Tall wheatgrass	E	138(7)	DE	115(7)	B	000(7)	Ē	84
Intermediate wheatgrass	ĈD	1105(8)	BCD	877(8)	ĀB	889(8)	BCD	957
Siberian wheatgrass	DE	518(2)	E	000(2)	B	184(2)	F	234
Whitmar bluebunch wheatgrass	BC	1690(7)	ABC	1147(7)	ĀB	862(7)	ĀR	1233
Pubescent wheatgrass	BCD	1208(7)	CDE	729(7)	B	758(7)	BCD	898
Hard fescue	DE	555(7)	DE	363(7)	ĀB	975(7)	CDF	631
Big bluegrass	BCD	1276(4)	CDE	392(4)	В	000(4)	DE	556
Riverside								
Fairway crested wheatgrass	AB	932(5)	CD	129(5)	С	000(5)	CD	354
Commercial crested wheatgrass	AB	924(4)	ABC	445(4)	B	896(4)	BC	755
Nordan crested wheatgrass	AB	1129(5)	CD	118(5)	BC	768(5)	BC	671
Tall wheatgrass	ABC	632(5)	AB	559(5)	BC	507(5)	BC	566
Intermediate wheatgrass	A	1397(6)	ABC	474(6)	B	1172(6)	B	1014
Siberian wheatgrass	AB	795(4)	CD	76(4)	Ē	000(4)	ČD	290
Whitmar bluebunch wheatgrass	AB	989(4)	Ă	712(4)	Ă	3040(4)	A	1580
Pubescent wheatgrass	ABC	708(5)	CD	272(5)	B	1014(5)	BC	664
Hard fescue	BC	595(5)	ČD	120(5)	BC	678(5)	ČD	464
Big bluegrass	c	000(6)	D	000(6)	č	000(6)	D	0
Average yield by year	Α	1288	В	988	С	677		

*Duncan's multiple range. Yields with the same letter are not significantly different at the 5% level.

§Figures in parentheses are numbers of plots represented in yield means.



Fig. 2. Population dominance areas at Harrington site, 1968 and 1978.

adapted to that site and in the period between 1968 and 1978 lost only small areas to competition, although areas of dominance shifted within its boundaries. The unshaded parts (Fig. 2) were dominated primarily by cheatgrass and a mixture of seeded and native plants. Cheatgrass is well adapted to invade plots abandoned by unsuccessful taxa, or to vigorously compete with seedlings of all perennials (Harris 1967). Observations in 1983 revealed that hard fescue seedlings scattered over the site in 1968 and 1978 were actually the forerunners of an invading population of that taxa.

In 1968 at the Republic site all of the more aggressive taxa were invading nearby plot areas as well as adjacent native plant stands. Hard fescue had increased from 4% coverage in 1951 to 24% in 1968 (Table 3, Fig. 3 and 5). Crested, intermediate, Whitmar and pubescent wheatgrasses had likewise expanded coverage from their original seeded plots all across the site. Big bluegrass, smooth brome (*Bromus inermus* Leys), and western wheatgrass (*A. smithii* Rydb.) were evident in small amounts, located in the unshaded areas of Figure 3. St. Johnswort (*Hypericum perforatum* L.), was invading all seeded populations except hard fescue. Needle-andthread (*Stipa comata* Trin. and Rupr.), a native perennial grass common to secondary seres in this area, had become established in peripheral areas, along with Sandberg bluegrass (*Poa secunda* Presl.) a unbiguitous native understory species. Cheatgrass was scattered throughout the site, and in control of 4% of the area.

By 1978, hard fescue had expanded its control to more than half (56%) of the Republic site, displacing crested, intermediate, Whitmar, and pubescent wheatgrasses, as well as cheatgrass, needleand-thread, smooth brome, and western wheatgrass populations



Fig. 3. Population dominance areas at Republic site, 1968 and 1978.

from all or parts of areas dominated 10 years earlier (Fig. 3). St. Johnswort had substantially increased its presence, and diffuse knapweed (*Centauria diffusa* Lam.), another exotic perennial weed, had appeared on the site. Both noxious weeds demonstrated the capacity to thoroughly invade all but hard fescue populations. Hard fescue and these weeds had continued to further expand across the site when observed in 1983.

Fewer seeded taxa were fitted to the Riverside site than at Harrington or Republic (Fig. 4). At this site the taxa were arranged in plots so that as additions were made in successive seasons, the same taxa were planted in an adjacent row in the next column. Thus all the crested wheatgrass was planted across the top row of plots in Figure 4, and so on throughout the list of taxa. This gave the 1968 map a definite horizontal bias.

In 1968, 25% of the site was dominated by hard fescue. Pubescent, intermediate, and crested wheatgrass populations had expanded moderately since first planted. Tall wheatgrass, green needlegrass (*Stipa viridula* Trin.) and Idaho fescue (*F. idahoensis* Elmer) were present only on part of the plots where they were originally planted and are not considered to be well fitted to the site. Canada bluegrass (*P. compressa* L.) a native perennial, had invaded several plots where seeded taxa had failed. Spanish clover (*Lotus purshianus* [Benth] C. & C.) a native annual forb, competed vigorously and displaced cheatgrass in part. Bottlebrush squirreltail [*Sitanion hystrix* (Nutt.) S.G. Sm.] a native seral grass, invaded a small area on one side of the site. Most of the more than 50 taxa originally planted here were evaluated as maintaining satisfactory stands in 1953 (Evanko 1955).

By 1978 hard fescue controlled half of the entire Riverside site by invading and displacing stands of Spanish clover, Canada blue-

Fig. 4. Population dominance areas at Riverside site, 1968 and 1978.

grass, bottle-brush squirreltail, and cheatgrass. Intermediate wheatgrass had reduced crested wheatgrass and pubescent wheatgrass as dominants, and covered 20% of the site. However, 1983 observations found these 2 latter taxa still present and functioning as significant co-dominants with intermediate wheatgrass in areas mapped as intermediate in 1978 (Fig. 4). Also, as at the other sites, hard fescue continued to expand its area of dominance. Individual pioneer plants of hard fescue were scattered throughout the site, and their presence indicated continued expansion of this taxa when observed in 1983.



Fig. 5. Diagrams of 27 year changes in percent area dominance, 1951, '68, and '78, at three nursery sites (Hard fescue, solid line; crested wheatgrass, dashed; intermediate wheatgrass, dot-dash; pubescent wheatgrass, dotdot-dash). See Table 3 and Figures 2, 3, and 4.

Differences in population dynamics of the major seeded species are clearly evident in Figure 5. Again, it is obvious that hard fescue is more competitive in Republic and Riverside habitats than at Harrington. At Republic and Riverside, hard fescue dominance has increased at an accelerated rate to occupy 50% and more of these sites by 1978. In the future it might be expected that hard fescue curves in Figure 5 will flex and begin to level off as they

Table 5.	Average yields by	site and taxa, combined	plots and years,	1968 and 1978 (kg/ha).
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Таха	Harr	ington	Reput	olic	River	side	Average	•	
					Kg/ha				-
Commercial wheatgrass	Α	1915	AB	1403	BC	755	Α	1431	
Nordan wheatgrass	Α	2097	Α	1726	BC	671	Α	1382	
Whitmar wheatgrass	В	790	AB	1233	Α	1580	AB	1237	
Fairway wheatgrass	Α	1852	BC	1159	CD	354	ABC	1124	
Intermediate wheatgrass	AB	1298	BCD	957	В	1014	ABCD	1105	
Pubescent wheatgrass	AB	1330	BCD	898	BC	664	BCD	933	
Hard fescue	AB	1597	CDE	631	CD	464	CDE	821	
Big bluegrass	Α	2029	DE	556	D	00	EF	524	
Tall wheatgrass	В	800	Ε	84	BC	566	F	324	
Average	Α	1288	В	988	С	677			

'Yields with the same letters are not significantly different at .05 probability as determined by Duncan's multiple range.

approach 100% nursery area coverage. This is typical of logistic population development, and follows the classical sine curve. Of the 3 major competing wheatgrases, intermediate was more resistant to replacement, trailed by pubescent and crested wheatgrasses. Native and exotic species previously invading these sites have also receded before the recruitment pressure of hard fescue.

At Harrington site, hard fescue has been measureably less aggressive, and the wheatgrasses relatively more competitive. There has also been more competition exerted by other seeded native and exotic taxa (particularly by cheatgrass) for plot areas abandoned by unfit taxa. Total area dominated by taxa listed in Table 3 dropped from 97% in 1968 to 91% in 1978, including 6% increase in cheatgrass over this period. Superior soil texture and depth at Harrington site (Table 1) appear to reduce the differences in recruitment and survival ability between hard fescue and competing taxa. The flex point in the sine curve has apparently been passed for hard fescue at this site and maximum coverage will presumably level off below 50%.

Standing crop yield data for selected years are presented in Table 4. These yields were produced under conditions of intense interspecific or intraspecific competition (presumably for soil moisture and nutrients). By 1959, and thereafter, all of the bare soil spaces opened by site preparation and plot weeding activities had been reinvaded to full site capacity, under prevailing conditions, by aggressive seeded perennials, or annuals and perennials from adjacent borders. Thus, yield performance of a particular seeded taxa is inextricably confounded with differing intensities of competition imposed by an unknown variety of neighbors.

Examination of yield data in Table 4 in connection with site coverage data in Table 3 reveals that a few taxa show significant (P>.05) yields on sites where their site coverage is zero. Note, for example, big bluegrass yields and site coverage at Harrington and Republic in 1978. Yields in these examples, and a few others, were clipped from spots too small to be mapped out separately in the site coverage matrix at the scale used.

Average yields were greatest at Harrington and least at Riverside (Table 5). This was true for all taxa except Whitmar bluebunch wheatgrass, which reversed the general trend. The Harrington site received the least precipitation, but has the finest textured and deepest solum (Table 1 and Fig. 1) as noted above. Conversely, the Riverside site received the highest average annual precipitation but has the coarsest textured and shallowest soil. Inasmuch as competition for soil moisture and nutrients is known to be limiting on these sites, it may be assumed that differences in soil characteristics (primarily texture and underlying drainage structures) more than compensated for the increased precipitation received at Riverside, as expressed in standing crop yield.

Commercial and Nordan wheatgrass populations were highest producers overall, and tall wheatgrass the lowest (Table 5), although variability within taxa reduced statistical significance of differences noted. All recommended taxa yielded sufficient amounts to justify use in range seedings as one or more of the test sites, particularly in monospecific stands.

Conclusions

Grass species used in seeding semiarid ranges of northeast Washington differ significantly in ability to establish through the environmental sieve, recruit posterity, and survive in the longterm. Crested, desert, Whitmar bluebunch, intermediate, pubescent, Siberian and tall wheatgrass, big bluegrass, and hard fescue are recommended as sufficiently fitted to sites where tested to be useful in long-term range seedings if proper steps are taken in establishment. The other 51 taxa planted were much less successful, and are not recommended except in situations of predetermined site suitability.

Species interactions are highly site-specific. Each site demonstrated a different and complex schedule of dynamics. Hard fescue appears to be capable of fully dominating Republic and Riverside sites, but less so at Harrington. Crested wheatgrasses were highest standing crop producers, but all recommended taxa yielded sufficient amounts to be useful.

Among the 10 recommended, correct taxa selection may depend on individual species characteristics other than reported here. Hard fescue proved to have some outstanding demographic qualities, but palatability for livestock is low, as is yield. It is best suited for erosion control, ground cover, and to close sites to serious noxious weed invasion. The crested wheatgrasses are most valuable for early spring forage before becoming tough and unpalatable in early summer. Intermediate, tall, and Whitmar wheatgrasses extend the green forage season into mid-summer, but intermediate is the only highly palatable one of the 3.

Species mixtures in range seedings are unstable particularly in the longer-term. Hard fescue will eventually dominate most species complexes on sites reported here. It is suggested that monospecific populations of suitable species, selected to fit seasonal or other requirements, and fenced out separately, may be more economical to establish, and simpler to manage in grazing systems than species mixtures.

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Annual Medics and Related Species as Reseeding Legumes for Northern Utah Pastures

M.D. RUMBAUGH AND D.A. JOHNSON

Abstract

Legumes are beneficial in providing high quality forage and enhancing fertility levels in the soil by biological nitrogen fixation. Nonperennial Medicago species have a world-wide distribution and have been used successfully for grazing in Mediterranean-type environments. The feasibility of using nonperennial Medicago species as reseeding pasture legumes in the northern Utah area was evaluated at 2 locations in replicated plantings of 584 accessions representing 34 Medicago species. These nurseries were planted in the spring of 1981 and data were collected through the 1983 growing season. Most of the species were easily established at both test sites. Many grew more rapidly during the seeding year than did the perennial check, M. falcata L. However, no annual or biennial species was as well nodulated or reduced acetylene on a per plant basis as well as M. falcata. None of the populations matured, reproduced, and initiated soil seed bank at the droughtier of the 2 locations. M. laciniata (L.) Mill., M. lupulina L., M. murex Willd., and M. muricoleptis Tin. excelled in the numbers of seedlings per meter of area established by natural reseeding in the fall of the first year of test. However, only M. lupulina (black medic) produced abundant seedlings during the second year following seeding. Results indicated that M. lupulina could develop a soil seed bank more rapidly than the other species. Black medic also had superior ground cover characteristics during the second and third years after sowing. Adapted populations of M. lupulina appear to have long-term value for forage production in Utah rangeland pastures with suitable soils and adequate precipitation.

The genus *Medicago* consists of 1 shrub, 21 herbaceous perennials, and 34 herbaceous annual species (Lesins and Lesins 1979). It includes the world's most important forage legume, alfalfa (*Medicago falcata* L., *M. sativa* L., and their hybrids). The annual species are known collectively as "medics" or "burr clovers". Medics evolved in North Africa and the Middle-East where they grow over a wide range of soils, temperature regimes, and lengths of growing season (Ewing 1983).

Several species of medic now occur in North America, and some are occasionally cultivated in the United States. Spotted or Southern burr clover [M. arabica (L.) Huds.], Tifton burr clover (M. rigidula Desr.), barrel medic (M. truncatula Gaertn.), and California or toothed burr clover (*M. hispida* Gaertn.) are used as winter annual pasture legumes where temperatures are mild. Their distribution, however, is generally restricted to the southern states and the Pacific Coast west of the Cascade and Sierra Nevada mountain ranges. Cog-wheel burr clover (M. tuberculata Willd.) was recommended for pasture usage in the east central area of Texas (Henson and Hollowell 1960). Little burr clover (M. minima Bart.) has been reported to occur in several of the southern states. M. orbicularis Bart., called "button clover", grows wild in parts of Tennessee and has been seeded sporadically in northeastern Texas (Davis et al. 1957, Wheeler 1950). Forage yields and protein concentrations were increased when button clover was added to grass or cereal pastures. It should be noted that the common names often used for medics in the United States are not the same as those used in

Australia for the identical species.

Figure 1 illustrates the annual climatic patterns of precipitation and temperature at a locality where medics are indigenous (Tunis, Tunisia), and where they have been successfully introduced (Los Angeles, CA). Most medic species are winter annuals adapted to Mediterranean climates. Their usual life cycle is to germinate with the onset of the first fall rains in September to November and to grow rapidly while warm temperatures and precipitation coincide. While the growth rate may be reduced during winter, flowering usually is completed during April. In colder temperate climates, these species would have to be used as spring annuals.

Self-seeding annual legumes may be better adapted to arid rangelands than perennial legumes. Quinlivan (1971) showed that medics can survive many years of drought due to the hardseed mechanism. In addition, although annual medics have no means for evading dry seasonal conditions by earlier flowering, their phasic development can be accelerated by drought stress once flowering has begun (Clarkson and Russell 1976). Their successful adaptation to arid environments is evidenced by the presence of several medic species in regions of North Africa receiving less than 250 mm of annual precipitation (Francis 1981). Furthermore, Tadmor et al. (1971) considered medics to be among the best adapted plants for practical desert range development in the 80- to 100-mm winter rainfall region of the Negev Desert in Israel.

The objective of the present study was to evaluate the developmental characteristics of medics when used as spring and early summer reseeding annual legumes in a cold winter desert environment.

Materials and Methods

Seeds for experiments were obtained from the USDA Regional Plant Introduction Station, Experiment, Georgia, and from the South Australian Department of Agriculture, Adelaide, South Australia. A total of 584 *Medicago* accessions representing 34 species and originally collected in 39 countries were included. Two species (4 accessions) were long-lived perennials, 1 species (70 accessions) was a short-lived perennial, and the remainder were annuals. The species identifications designated by the seed source agencies were retained. All seeds were scarified and treated with commercial peat base inoculants of appropriate *Rhizobium meliloti* Dang. strains immediately prior to sowing.

Clean tilled nurseries were seeded in Cache Valley near Logan, Utah (41°45'N, 111°48'W, 1389 m) and Curlew Valley near Snowville, Utah (41°57'N, 112°42'W, 1411 m) on 6 April 1981 and 14 April 1981, respectively. Twenty-five seeds were hand planted in a single row within each meter-long plot. The plots were spaced J meter apart within rows and 2 meters apart between rows. The experimental designs at each location were 2 replicate randomized complete blocks with the randomization restricted so that all accessions of each species were retained together within incomplete blocks. Weeds were controlled throughout the experiments by hand cultivation. Relative maturities of the accessions were quantified by recording the date on which the first fully opened flower was observed in each plot. Seedlings were counted and ground cover visually estimated within a circular 1.0-m² frame centered on each plot. Plant widths and heights were measured on the widest and tallest plants within each plot and, therefore, are maximum values for the test environment. The degree of pod spininess was scored visually on a 1 to 3 scale and other traits scored on a 1 to 9

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The authors appreciate the helpful suggestions of E.J. Crawford, Senior Plant Introduction Officer, South Australian Dept. of Agriculture, Adelaide, while planning the research and for many of the seeds used in the experiments. The research is a contribution from the USDA-ARS and the Utah Agricultural Experiment Station, Logan. Journal Paper No. 3056.

Manuscript accepted 30 May 1985.



Fig. 1. Mean monthly temperature and precipitation at 2 locations with a Mediterranean climate (Tunis, Tunisia, and Los Angeles, Calif.) and at 2 locations with a cool desert climate (Logan, Utah, and Snowville, Utah). Modified from Walter and Lieth (1960).



Fig. 2. Precipitation in Cache Valley (Logan, Utah) and Curlew Valley (Snowville, Utah) for 1981 through 1983.

scale with the lowest figure representing the most desirable and the highest figure the least desirable expression of the traits.

During the third week of June 1981, one or more accessions within each species which exhibited above-average shoot biomass were sampled in the field to estimate nitrogen fixation activity. One plant within each plot was excavated with minimal disturbance of the adjacent plants. Nitrogen fixation activity and leaf water potential were estimated in the field by the acetylene reduction and pressure chamber techniques described by Johnson and Rumbaugh (1981) and by Scholander et al. (1965), respectively.

Results and Discussion

Long-term average precipitation at the U.S. weather stations nearest the plantings (Logan and Snowville, Utah) is shown in Figure 1 and that for the 3 years of study is presented in Figure 2. Both sites received low amounts of precipitation during July through September of 1981 with 4.1 and 0.5 cm of rainfall in Cache Valley and Curlew Valley, respectively. Maximum daily temperatures during the summer of 1981 exceeded recent historical averages for Cache Valley by only 0.1° C but those for Curlew Valley were 2.4° C above average (Table 1). The higher temperatures and

 Table 1. Average daily maximum temperatures (C) at the recording stations nearest the test sites.

	Cach	e Valley	Curlew Valley		
Month	1981	Average 1951-1980	1981	Average 1951-1980	
May	17.7	20.0	20.0	20.7	
June	24.8	25.1	28.1	26.4	
July	30.6	30.1	34.7	32.5	
August	31.1	29.5	35.5	31.0	
September	25.2	24.1	29.8	25.4	

lower precipitation during the first growing season resulted in greater potential drought stress at the Curlew Valley test site than at Cache Valley. The subsequent 2 years of the experiments, 1982 and 1983, were years of above-average precipitation.

Most of the *Medicago* species successfully germinated and emerged at both the Cache Valley and Curlew Valleys sites in the

Table 2. Developmental characteristics of Medicago species grown in Cache Valley, Utah.

	Number	•						Pod‡							
	of		50 seed	Initial‡	Shoot‡	1981 c	lay of	abun-	Spine§	Pla	ant	Seedling	density	c 1	(7)
	acces-	Growth†	weight	stand	biomass	first b	loom	dance	length	size (cm)*	_(numb	er/m)	Ground	cover (%)
	sions	habit	(g)	(score)	(score)	Numerical	Date	(score)	(score)	Width	Height	10-22-81	7-10-82	7-19-82	5-25-83
M. aculeata	6	Α	0.49	4.7	3.6	158	7 June	7. 9	3.0	91	12	182	7	39	8
M. arabica	13	Α	0.11	5.3	5.7	171	20 June	8.0	3.0	71	10	233	4	10	7
M. arborea	1	Р	0.35	8.0	8.0	—	—	9.0	_	63	28	1	2	0	0
M. achersoniana	1	Α	0.13	8.0	8.0	206	25 July	9.0	1.0	92	10	150	3	35	30
M. blancheana	3	Α	0.38	3.3	5.5	170	19 June	5.8	1.3	51	31	33	2	2	4
M. constricta	16	Α	0.23	4.8	6.8	174	23 June	7.3	3.0	102	11	256	9	20	38
M. disciformis	5	Α	0.16	5.7	6.6	181	30 June	8.2	3.0	92	12	158	4	14	8
M. falcata	3	Р	0.11	7.8	5.5	168	17 June	9.0	1.0	182	62	21	3	9	1
M. gerardii	2	Α	0.21	6.2	6.0	180	29 June	9.0	3.0	89	6	292	14	36	38
M. granadensis	1	A	0.55	5.0	4.5	188	7 July	9.0	3.0	76	26	114	4	30	0
M. intertexta	2	Α	0.65	2.0	1.2	183	2 July	8.2	3.0	85	25	55	8	8	0
M. laciniata	1	A	0.12	3.5	7.0	169	18 June	8.0	3.0	156	10	708	16	68	0
M. littoralis	14	A	0.13	3.7	5.0	160	9 June	6.4	2.6	95	16	276	13	19	2
M. lupulina	70	В	0.07	6.2	7.6	169	18 June	4.4	1.0	155	22	931	3,806	91	54
M. minima	13	A	0.08	6.2	7.5	160	9 June	5.5	2.9	78	14	299	91	25	12
M. murex	6	A	0.16	4.9	6.5	167	16 June	2.5	2.9	96	14	628	6	18	1
M. muricata	1	A	0.07	4.5	8.0	178	27 June	3.0	3.0	/9	20	2/1	3	18	15
M. muricoleptis	1	A	0.37	0.0	7.5	181	30 June	9.0	2.5	124	4	/90	3	18	U
M. noeana		A	0.18	3.5	6.5	181	30 June	8.4	1.4	94	24	141	10	21	0
M. obscura	100	A	0.18	4.8	5.8	173	22 June	5.5	2.0	121	21	300	10	22	0
M. ordicularis	100	A	0.18	/.0	1.5	180	5 July	1.1	1.0	79	10	157	4	14	0
м. polymorpna	111	A	0.18	4.5	5.6	157	6 June	3.0	2.7		20	242	9	15	3
M. praecox	1	A	0.09	4.5	8.0	1/2	21 June	3.3	3.0	00	10	119	0	10	15
M. raaiaia M. rigidula	59	A	0.22	0.2	7.2	109	18 June	0.0	1.0	105	12	252	4	10	14
M. rigiauia	20	A	0.22	4.0	1.2	1/2	21 June	7.5	2.9	57	13	333 70	0 2	51	10
M. TURNER	4	A A	0.50	4.0	4.2	137	20 June	5.1	2.5	04	20	207	51	27	2
M. rugosu M. sauvagei	1	A	0.40	2.5	75	171	5 June	1.0	2.0	40	15	111	1	27	0
M. soutellata	23	Δ	0.23	4.5	5.5	150	13 June	54	5.0	109	29	175	40	21	2
M tornata	25	Å	0.77	44	50	156	5 June	6.2	1.0	94	20	141	-0	8	1
M tribuloides	20	Δ	0.21	51	61	162	11 June	64	7.8	83	15	282	25	24	1
M truncatula	25	Å	0.15	3.8	5 3	164	13 June	71	2.0	72	14	116	25	12	Ô
M turberculata	23	Å	0.22	47	48	166	15 June	53	17	143	24	16	5	21	2
M. turbinata	22	Ă	0.39	6.0	5.7	158	7 June	8.0	2.3	105	14	149	6	22	6
Mean			0.21	5.1	6.4	157	6 June	5.9	2.2	93	17	274	413	26	12
L.S.D. (0.05)			0.05	0.9	0.6	23		1.1		16	4	190	151	11	8
(0.01)			0.06	1.2	0.9	31		1.5		20	5	251	167	15	11

†A=annual, B=biennial, P=perennial

1=most, 9=least

\$1=no spines; 2=moderate spines; 3=long curved spines

*Maximum distances measured on 24 September 1982

initial establishment year. However, only a few plants were found in the Curlew Valley experiment in 1982 and none in 1983. Therefore, second and third year results were available from Cache Valley only. There was a ninefold range in average seed size among the species tested (Table 2). M. aculeata Willd., M. granadensis Willd., M. intertexta Mill., M. rugosa Desr., and M. scutellata Mill. excelled in this trait, whereas the 50 seed weights of M. lupulina L., M. minima, M. muricata Willd., and M. praeco DC seeds were less than 0.1 g. Seedlings of large-seeded species were more vigorous and larger than seedlings of small-seeded species. This was reflected in the initial stand and shoot biomass scores recorded on 11 June 1981, 2 months after planting. The associations between seed weight and stand and shoot biomass resulted in significant simple correlation coefficients of r = 0.42 (P<0.05) and r = 0.66 ($P \le 0.01$), respectively. All of the 5 large-seeded species mentioned are adapted to heavy, wet, clay soils (Lesins and Lesins 1979). M. aculeata is considered by some authorities, including Urban (1873), to be a botanical variety of *M. turbinata* All.

The habits of the small-seeded species differ. *M. minima* is one of the most widely distributed and the most variable annual medic. It commonly is found growing in dry soils on rocky hillsides or in sands of the Mediterranean region. *M. muricata* was considered by Lesins and Lesins (1979) to be a form of the polymorphic species, *M. tornata* Mill.. In its natural habitat, it too is found on sandy soils or at least on sites with only a thin layer of dry, loose soil on top of rock. Similarly, *M. praecox* is best adapted to sandy soils of droughty sites. *M. lupulina* is quite different than the other small-seeded medics discussed because it grows best in moister soils and cooler temperatures than the expressly annual *Medicago* species. Most populations of black medic in northern Great Basin areas occur at elevations higher than approximately 1,400 m and are short-lived perennials.

Early maturity would be a desirable trait of species selected for northern Utah rangeland pastures so that plants could form seed pods prior to the summer drought stress period. Average date of first bloom of the medic species in 1981 varied from 5 June for *M.* sauvegei Negre and *M. tornata* to 25 July for *M. achersoniana* Urb. (Table 2). Accessions not flowering until July would usually be exposed to very restricted soil moisture availability during their reproductive development, and immature or aborted pods would result. This interpretation is supported by the pod abundance scores recorded on 7 July 1981. M. sauvagei, the earliest flowering species, produced more pods per plant than any other medic. The Pearson correlation coefficient for date of first bloom and pod abundance score was r = 0.53 ($P \le 0.01$).

Long pod spines, especially if they are curved, are undesirable because they may become caught in the wool of grazing sheep. Several medics have pods of that type but others do not (Table 2). There is ample genetic variation within a number of the species to select for types with less prominent spines.

Table 3. Characteristics related to nitrogen fixation activity of Medicago species when grown in Cache Valley, Utah.

	Plants tested	Leaf water potential		Plant v	veight (g)		Nodules per plant	Acetylene reduction activity [†]
Species	(number)	(-MPa)	Shoot	Root	Nodules	Total	(number)	nanomoles/h/plant
M. aculeata	6	0.66	6.98	0.19	0.0017	7.17	7.8	6.7
M. arabica	6	0.78	2.18	0.19	0.0012	2.37	13.5	9.4
M. arborea	3	0.62	0.17	0.04	0.0003	0.20	4.0	16.5
M. blancheana	6	0.94	2.76	0.09	0.0017	2.85	8.5	8.9
M. constricta	6	0.80	3.59	0.10	0.0003	3.69	3.5	4.9
M. disciformis	6	0.83	3.65	0.14	0.0003	3.78	2.5	7.4
M. falcata	3	0.80	2.22	0.52	0.0025	2.74	22.3	13.4
M. gerardii	3	0.95	6.66	0.40	0.0027	7.07	12.7	4.1
M. granadensis	5	0.70	5.58	0.19	0.0035	5.77	17.6	2.7
M. intertexta	6	0.70	4.07	0.21	0.0007	4.28	3.2	6.6
M. laciniata	6	0.94	1.93	0.09	0.0002	2.02	2.7	22
M. littoralis	6	0.94	4.60	0.14	0.0005	4.73	3.7	2.5
M. lupulina	6	0.86	1.44	0.10	0.0010	1.54	9.0	6.2
M. minima	5	1.04	2.68	0.11	0.0008	2.79	9.2	8.7
M. murex	5	0.80	1.92	0.09	0.0008	2.01	4.8	
M. muricata	6	0.94	1.40	0.10	0.0003	1.50	8.0	
M. muricoleptis	3	0.67	1.31	0.14	0.0004	1.45	6.7	2.1
M. noeana	6	1.02	2.28	0.09	0.0000	2.36	0.8	3.1
M. obscura	11	0.96	3.57	0.15	0.0004	3.72	3.5	3.6
M. orbicularis	6	0.98	6.50	0.15	0.0008	6.64	11.0	1.0
M. polymorpha	6	0.97	7.51	0.21	0.0026	7.72	12.8	41
M. praecox	5	1.01	0.75	0.05	0.0002	0.80	1.8	0.0
M. radiata	5	0.74	1.62	0.07	0.0004	1.70	1.4	
M. rigidula	3	1.03	1.96	0.08	0.0001	2.04	1.0	
M. rotata	6	0.88	4.06	0.15	0.0005	4.21	7.5	
M. rugosa	6	0.82	4.85	0.30	0.0040	5.16	16.0	59 3
M. sauvagei	5	1.22	1 04	0.05	0.0001	1 09	04	
M. scutellata	5	1.12	3.12	0.16	0.0015	3.28	5.4	0.6
M. tornata	6	1.26	7.64	0.16	0.0014	7 80	60	0.0
M. tribuloides	3	1.11	7.34	0.23	0.0027	7 57	73	35
M. truncatula	4	0.84	6.56	0.34	0.0005	6.90	4.8	
M. turberculata	6	1.00	4.21	0.18	0.0010	4.39	9.8	28.6
M. turbinata	5	1.08	7.86	0.30	0.0025	8.17	10.8	16.0
Mean	5	0.92	3.80	0.16	0.0011	3 96	71	65
L.S.D. (0.05)	- -	0.14	2.98	0.10	0.0010	3.05	70	N S
(0.01)		0.18	3.94	0.13	0.0014	4.03	9.2	N.S.

[†]Values were omitted when the background correction exceeded the sample activity.

Table 4. Characteristics related to nitre	gen fixation activity of Medical	go species when grown is	n Curlew Valley, Utah.
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Saccio	Plants tested	Leaf water potential		Plant v	veight (g)	Total	Nodules per plant	Acetylene reduction activity†
	(number)	(-MFa)	Shoot	Root	Nodules	10(8)	(number)	nanomoles/ n/ plant
M. aculeata	5	1.72	2.68	0.11	0.0155	2.81	16.2	9.0
M. arabica	1	1.70	0.55	0.04	0.0021	0.59	10.0	3.0
M. arborea	3	2.80	0.08	0.02	0.0000	0.10	0.0	
M. blancheana	4	—	0.09	0.01	0.0010	0.11	1.8	0.5
M. constricta	5	2.09	1.01	0.05	0.0013	1.06	7.6	2.4
M. disciformis	2	1.68	0.16	0.01	0.0000	0.17	1.0	1.7
M. falcata	1	_	0.19	0.01	0.0115	0.21	18.0	3.5
M. gerardii	4	1.85	1.60	0.12	0.0087	1.73	11.8	6.6
M. granadensis	3	1.35	2.08	0.12	0.0019	2.20	5.0	0.6
M. intertexta	5	2.45	0.34	0.06	0.0006	0.40	3.6	0.2
M. laciniata	1		0.00	0.01	0.0000	0.01	0.0	
M. littoralis	5	1.82	0.63	0.04	0.0014	0.69	4.2	1.4
M. lupulina	1	2.10	0.50	0.03	0.0019	0.53	4.0	2.2
M. minima	2	1.72	0.31	0.02	0.0000	0.33	0.0	
M. murex	5	1.71	0.22	0.02	0.0002	0.24	0.6	2.8
M. muricata	5	1.50	0.97	0.05	0.0005	1.02	1.2	3.0
M. muricoleptis	2		0.08	0.01	0.0000	0.10	0.0	—
M. noeana	4	1.95	0.37	0.03	0.0000	0.40	0.0	_
M. obscura	7	1.96	0.38	0.02	0.0015	0.40	2.6	0.6
M. orbicularis	6	2.35	0.28	0.02	0.0009	0.30	4.7	0.1
M. polymorpha	3		0.03	0.01	0.0000	0.04	0.0	_
M. praecox	3	_	0.11	0.02	0.0010	0.14	3.3	1.1
M. radiata	4		0.60	0.03	0.0008	0.63	2.2	0.6
M. rigidula	5	1.73	0.95	0.07	0.0005	1.02	0.8	
M. rotata	4	1.66	0.05	0.02	0.0000	0.07	0.0	<u> </u>
M. rugosa	5		0.09	0.03	0.0000	0.12	0.0	
M. sauvagei	5	2.10	0.96	0.05	0.0000	1.01	0.0	
M. scutellata	4	1.62	0.38	0.05	0.0079	0.44	10.2	1.8
M. tornata	4	2.01	0.64	0.02	0.0014	0.66	1.0	1.8
M. tribuloides	3	1.55	2.95	0.09	0.0008	3.04	3.7	1.1
M. truncatula	4	1.92	0.31	0.05	0.0038	0.37	5.5	0.7
M. turberculata	6	1.78	0.62	0.05	0.0029	0.67	5.7	2.2
M. turbinata	4	1.75	0.17	0.03	0.0010	0.20	1.2	—
Mean	4	1.89	0.67	0.04	0.0021	0.72	3.6	1.3
L.S.D. (0.05)	-	0.40	1.11	0.05	0.0056	0.37	7.5	N.S.
(0.01)		0.53	1.46	0.06	0.0074	0.49	9.9	N.S.

Values were omitted when the background correction exceeded the sample activity or when there were no nodules.

Mean plant width measured on 24 September 1981 varied from 34 to 182 cm (Table 2). Similarly, mean plant height varied among the species from 4 to 62 cm. The perennial, *M. falcata*, was larger than any of the annual or biennial species. *M. laciniata* (L.) Mill. was the widest and *M. blancheana* Boiss. the tallest of the annuals. *M. lupulina* was among the wider species but of moderate height.

Ability to reseed and seedling survival are absolutely essential for consideration of any plant population as a candidate for longterm pasture usage. Species excelling in number of seedlings per m^2 in the fall of the first year were *M. laciniata*, *M. lupulina*, *M. murex* Willd., and *M. muricoleptis* Tin. However, only *M. lupulina* had more than 100 seedlings per m^2 in the summer of the second year of the experiment. Medic seedlings usually overwinter at localities with Mediterranean climates (Fig. 1). This is less likely to occur in the Great Basin and sufficient hard seed must be formed to reestablish the population each spring. *M. lupulina* also was superior to the other species with respect to ground cover capability in both 1982 and 1983. This trait also is considered very important for legumes which are to be included in seed mixtures for range reseeding.

Physiological responses of the *Medicago* species to the environments of the 2 test sites in 1981 differed (Tables 3 and 4). Plants in Curlew Valley were smaller, possessed fewer nodules, fixed less nitrogen, and had lower leaf water potentials than plants of the same species in Cache Valley. Average total plant weights of the species at the 2 sites were positively and significantly (P < 0.05) associated but the correlation coefficient was low, r = 0.38. Analogous correlations for leaf water potentials and acetylene reduction activities were not significantly different from zero. These differences were interpreted as due to greater drought stress in the Curlew Valley nursery. Plants at that site often were visibly wilted, stunted, and died without forming seed. No plants were alive in the third year of experimentation at Curlew Valley but 25 species persisted into the third year in Cache Valley.

Despite large differences among the species in ability to reduce acetylene in the Cache Valley planting, the differences were not statistically significant (P>0.05). The acetylene reduction procedure often results in coefficients of variation of greater magnitude than many other agronomic and physiological measurements. However, assuming that the rankings of means provides a valid indication of relative ability to fix atmospheric nitrogen (Table 3), M. rugosa was more active than the other species while M. tuberculata ranked second. These values are similar in magnitude to those shown by Baltensperger and Smith (1984) for M. lupulina grown in a nitrogen-free medium in a greenhouse environment. The correlation of numbers of nodules and acetylene reduction activity on a per plant basis for species means was positive, r = 0.41 (P<0.05) (Table 5). The weights of plant parts also were significantly and positively associated, but only nodule weight significantly influenced acetylene reduction. As judged by the coefficient of determination, r^2 , variation in nodule weight accounted for 24% of the variation in nitrogen fixation capability. Either nodule number or nodule weight would be useful for evaluating the nitrogen fixation potential of legumes in selection nurseries or in rangeland pasture seeding experiments.

Table 5. Simple correlations (r) of Medicago traits associated with nodula tion and acetylene reduction activity in Cache Valley, Utah.

Associated traits	Nodules per plant (number)	Acetylene reduction activity (nanomoles/h/plant)
		[
50 seed weight (g)	0.08	0.24
Day of first bloom	0.05	-0.04
Leaf water potential (-MPa)	0.19	0.09
Shoot weight (g)	0.34*	0.04
Root weight (g)	0.70**	0.26
Nodule weight (g)	0.80**	0.49**
Total plant weight (g)	0.37*	0.05
Nodule number		0.41*

^{*}P<0.05

** P<0.01

Based on the data obtained in these experiments and summarized in Tables 2 and 3, M. lupulina apparently has more potential to improve pastures in environments similar to that of Cache Valley during 1981 through 1983 than the annual medics tested. The other species may be more useful in different environments, although none appeared to perform satisfactorily in Curlew Valley. M. lupulina exhibited superior reseeding and ground cover characteristics compared to the other species.

M. lupulina (black medic or yellow trefoil) is widely distributed in North American as well as throughout the other temperate and subtropical regions of the world. Annual, biennial, and short-lived perennial forms exist (Turkington and Cavers 1979). Many varieties have been described because of the morphological diversity of the species (Lammerink 1968). Each population from a single site consisted of a number of genotypes in varying proportions which may shift when the population is moved to other habitats or climates. Wheeler (1950) indicated that black medic hay yields of 4.5 to 6.7 ton/ha were possible but that this species seldom was cut for hay. Wherever it thrives, black medic is a valued constituent of spring and early summer pastures. Blaser and Stokes (1946) described the characteristics of several black medic strains grown in Florida. In the western United States, black medic was well nodulated and capable of fixing atmospheric nitrogen under range conditions (Baltensperger and Smith 1984; Johnson and Rumbaugh 1981; Smith and Baltensperger 1983, 1984). More detailed experiments showed fixation occurring even when soil water content reached as low as 8% (Holter 1978). Soil nitrogen accumulation in summer under medic swards can be independent of plant density or time of sowing and considerably higher than that in the absence of medics (Adem 1977). Koala and Sims (1982) reported that black medic increased wheat yields 92% and water use efficiency 81% in a ley farming experiment conducted near Bozeman, Mont.

Because M. lupulina is now distributed world-wide, natural selection probably would have differentiated the populations originating in different countries. Attributes of the M. lupulina populations tested are listed in Table 6. Introductions from Greece, Iran, Spain, U.S.S.R., and Yugoslavia excelled in reseeding ability. Individual accessions from some of the other countries also were able to reseed and also had high ground cover values. Most accessions were phenotypically heterogeneous and are expected to be genetically responsive to a variety of environmental circumstances (Lammerink 1968). An exceptionally broad and plastic germplasm base could be attained if several accessions or ecotypes were selected, the seed increased as separate populations, and the increase mechanically blended to form a seed mixture for pasture plantings or oversowing. Such a scheme would allow the release of one population with the capability of excelling in many kinds of sites (G.A. Gintzburger, unpublished).

Conclusions

Medicago lupulina (black medic) was better adapted to the environment of the northern Great Basin as exemplified by a Cache Valley, Utah, nursery site during the 3 years of experimentation than any of the annual species within that genus. While most medics grew well, were nodulated, and were capable of fixing atmospheric nitrogen, M. lupulina had superior reseeding and ground cover characteristics. Significant diversity was exhibited among the 70 M. lupulina introductions tested. Selected introduc-

Table 6. Characteristics of 70 Medicago lupulina accessions from 21 countries grown in Cache Valley, Utah.

	Number of	1981 day of	first bloom	Plant s	ize (cm)	Seedling densi	ty (number/m)	Ground	l cover (%)
Country	accessions	Numerical	Date	Width	Height	10-22-81	07-10-82	07-19-82	05-25-83
Afghanistan	13	168	17 June	154	22	1,118	3,765	89	55
Argentina	1	156	5 June	135	35	628	2,583	100	90
Australia	1	162	11 June	178	20	942	2,110	95	50
Austria	1	169	18 June	196	28	532	3,046	100	35
Czechoslovakia	1	169	18 June	129	29	1,304	3,003	100	70
Denmark	3	176	25 June	154	22	171	1,528	83	35
France	3	171	20 June	151	28	468	3,286	87	43
Great Britain	3	162	11 June	141	22	692	2,956	88	77
Greece	1	187	6 July	186	15	546	11,582	100	35
Hungary	1	169	18 June	150	37	434	3,810	100	75
Iran	4	172	21 June	174	20	918	5,051	98	41
Italy	2	166	15 June	173	22	672	3,794	100	42
Pakistan	2	162	11 June	102	16	2,213	2,093	88	68
Poland	1	174	23 June	187	26	10	1,787	95	50
Spain	6	169	18 June	160	19	1,158	6,946	97	46
Sweden	1	194	13 July	101	8	18	16	30	75
Switzerland	2	169	18 June	180	16	834	2,400	92	80
Turkey	17	169	18 June	154	20	755	3,206	88	50
Uruguay	2	162	11 June	134	33	1,517	2,756	88	45
U.S.S.R.	2	172	21 June	182	20	1,844	4,548	92	30
Yugoslavia	3	169	18 June	156	25	1,535	6,211	100	85
Mean	3.3	169	-	155	22	931	3,806	91	54
L.S.D. (0.05)	_	7	_	25	6	488	N.S.	N.S.	28
(0.01)		9		33	8	645	<u>N.S.</u>	N.S.	N.S.

tions could be propagated separately and the seeds blended to form a single population potentially adapted to many kinds of pasture and range sites.

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Alfalfa Survival and Vigor in Rangeland Grazed by Sheep

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Abstract

Few detailed comparisons have been made among alfalfa (Medicago spp.) cultivars and strains grazed in semiarid, rangeland environments. The objective of this study was to determine survival and vigor of alfalfa cultivars and experimental strains that were grown in association with rangeland grasses and grazed by sheep for 3 seasons. Three-month old seedlings of 5 cultivars and 6 experimental strains of winterhardy alfalfa were transplanted in June 1979 into grass sod on 0.9-m centers at a hillside site with a west-facing 16% slope and Amor loam (Typic Haploboroll) soil. Dominant vegetation was western wheatgrass (Pascopyrum smithii (Rydb.) Löve. Syn: Agropyron smithii (Rydb.)], blue grama [Bouteloua gracilis (H.B.K.) Lag.], and smooth bromegrass (Bromus inermis Leyss.). For 3 seasons after the establishment year, each replicate was grazed in sequence for 2 weeks at a stocking rate of 48 yearling ewes/ha during summer and then mowed to a height of 10 cm in September. Only 5 of the 11 entries had greater than 50% survival after the third season. Three germplasm pools derived from local alfalfa plantings that had persisted more than 50 years in association with rangeland grasses were highest in survival, ranging from 72-74%. Drylander and Roamer, 2 cultivars developed primarily for grazing in semiarid regions of western Canada, had 65 and 62% survival, respectively. Phenotypic variability found among surviving plants in this study will permit further genetic improvements in alfalfa for rangeland.

Interest in introducing alfalfa (Medicago spp.) into rangelands in western North America dates back to the early 1900's when N.E. Hansen of the South Dakota Agricultural Experiment Station described alfalfa that he collected from the dry steppes of Siberia (Hansen 1909). Low seed production and seed shattering have been major factors limiting widespread commercial use of these hardy, creeping rooting accessions of yellow-blossomed 'Siberian' alfalfa (M. falcata L.) collected by Hansen. Oakley and Garver (1917) reported that the greatest value of *M. falcata* lies in its ability to form fertile hybrids [M. sativa subsp. varia (Martyn) Arc.] with common, purple flowered alfalfa (M. sativa L. subsp. sativa). They further state that, "those who fail to see beyond M. falcata's agronomic defects as it exists in the natural state are missing an opportunity in the field of plant breeding." Major sustained efforts to develop alfalfa cultivars for rangeland in the semiarid Northern Plains region of North America did not materialize until breeding programs were initiated by Agriculture Canada at Swift Current, Saskatchewan, in 1938 (Heinrichs 1954) and by the South Dakota Agriculture Experiment Station in the 1940's (Adams 1956). Several winter and drought-hardy cultivars intended primarily for dryland grazing have been developed through these breeding programs. Most of the grazing management research and commercial usage of alfalfa in rangelands has been with seeded mixtures of alfalfa and various grass species (Lorenz 1982). Recent development of interseeding technology (Chisholm et al. 1982) has provided a means of introducing alfalfa into native range or into established stands of seeded grass.

This study compared survival and vigor of 11 alfalfa cultivars and experimental strains that were spaced-planted into rangeland and grazed by sheep for 3 seasons.

Materials and Methods

Seedlings of 5 cultivars and 6 germplasm pools of winterhardy alfalfa (Table 1) were started in peat pots in the greenhouse in March 1979 and transplanted 3 months later into sod on 0.9-m centers at a range site with a 16% west facing slope. The site was mowed to a height of 10 cm just prior to transplanting. Seedlings were hand watered immediately after transplanting and twice during August of the establishment year with sprinkler irrigation to encourage a high level of survival. No fertilizer was applied during the study. Soil was classified as an Amor loam (Typic Haploboroll), an upland soil fairly high in clay content typically found on slopes of 10-25%. Associated vegetation was primarily western wheatgrass [*Pascopyrum smithii* (Rydb.) Löve. Syn: *Agropyron smithii* Rydb.], blue grama [*Bouteloua gracilis* (H.B.K.) Lag.], and smooth bromegrass (*Bromus inermis* Leyss.).

Each of 4 replications was subdivided on a grid pattern into 144 5-plant \times 5-plant cells. Each cell contained 4 plants of the C-3, South Dakota, Mandan I, and Mandan II germplasm pools and 1 plant of each of the 7 remaining entries for a total of 23 plants per cell. Plants from all entries were randomly distributed within each cell with 2 of the 25 positions left vacant. We anticipated that the C-3, South Dakota, Mandan I, and Mandan II germplasm pools would contain unique genotypes that would be adapted to rangeland grazing. Thus, representation of these 4 germplasm pools in the plant cells was 4 times higher than the remaining 7 entries. This provided a valuable base population from which outstanding individual genotypes could be selected.

In 1980 through 1982, each replicate was grazed in sequence for 2 weeks at a heavy stocking rate of 48 yearling ewes/ha, beginning about 1 June with the first replicate and terminating about 1 August with the fourth replicate. The grazing sequence for the replicates was the same each season. Forage utilization after the 2-week period of grazing was approximately 75%. All replicates were mowed to a height of 10 cm in September each year. Annual precipitation was near the long-term average of 42 cm for the duration of the study, but early season precipitation was low in 3 years. March through June precipitation, which averages 20 cm, was 44, 37, and 56% of normal for 1979, 1980, and 1981, respectively.

Survival and vigor of each plant was recorded in August of the establishment year and after approximately 30 days regrowth had occurred following grazing in the 3 subsequent years. Vigor of live plants was visually rated on a scale from 1–9 where a score of 1 indicated highest vigor and 9 indicated a plant that appeared nearly dead. Survival and vigor data were analyzed using a randomized complete block design. Data included in the analysis were one plant, randomly selected by computer, from each of the 4 germ-plasm pools with 4 plants per cell and 1 plant from each of the 7 remaining entries that were represented by a single plant in each cell. This resulted in 144 plants per entry from the 144 5-plant \times 5-plant cells in each of 4 replications.

Not all portions of the study had uniform survival due to differences in soil type, associated vegetation, grazing intensity, and other factors. The 5-plant \times 5-plant cells were sorted into the following overall survival categories based on survival data recorded after 3 seasons of grazing: Category I (0-8 plants surviving within each cell), Category II (9-13), Category III (14-18), and Category IV (19-23). Summing over replications, the number of cells in Categories I through IV were 77, 158, 231, and 83, respec-

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Ballou, and R.A. Wald are gratefully acknowledged. Manuscript accepted 24 May 1985.

Table 1. Description and origin of cultivars and germplasm pools.

Entry	Description	Origin
Drylander	15 clone synthetic. Approximately 70% creeping rooted. Slow recovery and very persistent. Intended for overseeding rangeland, permanent or semipermanent pasture, or single-cut hay crop in semiarid regions of western Canada and northern U.S.	Agriculture Canada, Swift Current, Saskatchewan (Heinrichs 1971)
Roamer	7 clone synthetic. Approximately 60% creeping rooted. Faster recovery and higher seed yield than Drylander, but slightly less hardy. Intended use same as Drylander.	Agriculture Canada, Swift Current, Saskatchewan (Heinrichs 1967).
Spredor 2	Selected for creeping root habit, persistence, bacterial wilt resistance, seed production, and vigor. Intended primarily for overseeding range- land, permanent or semipermanent pasture, and dryland hay production in northern areas.	Northrup, King Co. (W.J. Knipe ¹ , personal communication)
Ramsey	4 clone synthetic. Selected for winterhardiness and multiple pest resistance. Area of adaptation similar to Vernal.	Minnesota Agr. Exp. Sta. and USDA, ARS (Elling et al. 1973).
Ladak 65	49 clone synthetic. Derived from older commercial stands of certified Ladak. Higher levels of bacterial wilt resistance and more persistent than Ladak in long-ferm stands.	Montana Agr. Exp. Sta. (Eslick et al. 1968).
KS-10 Germplasm Pool	95 clone synthetic derived from Ladak. Resistant to spotted alfalfa aphid (<i>Therioaphis maculata</i> Buckton), pea aphid (<i>Acyrthosiphon pisum</i> Harris), and bacterial wilt [<i>Corynebacterium insidiosum</i> (McCull.) H.L. Jens]. KS-10 has more rapid recovery and is less dormant than the parent variety, Ladak.	Kansas Agr. Exp. Sta. and USDA, ARS (Sorensen et. al. 1975)
C-3 Germplasm Pool	Genetically diverse population derived by intermating selections from 63 cultivars, experimental synthetics, and germplasm pools adapted to the central and northern Great Plains. Intended as a germplasm source for breeding cultivars adapted to semiarid regions.	Colorado Agr. Exp. Sta. and USDA, ARS (Townsend et al. 1976)
Alaska Germplasm Pool	Germplasm source population of <i>Medicago falcata</i> that has persisted for over 50 years at Palmer, Alaska.	Alaska Agr. Exp. Sta. and USDA, ARS (Roscoe L. Taylor ² , personal communication)
South Dakota Germplasm Pool	Germplasm source population derived by bulking open pollinated seed of selections from alfalfa-grass stands that have been grazed over 50 years at the N.G. Smith ranch, Perkins County, SD and the R. Schnell ranch, Adams County, ND. Primarily <i>M. falcata</i> tracing to introductions of N.E. Hansen.	USDA, ARS, Mandan, ND
Mandan I and Mandan II Germplasm Pools	Two germplasm source populations derived by bulking open pollinated seed of selections from alfalfa-grass stands at two sites. These alfalfa- grass stands have persisted under light grazing and hay production since 1922 at the Northern Great Plains Research Laboratory, Mandan, ND., and trace to bulk seed from source nurseries of N.E. Hansen. In each population, approximately 20% of the plants have typical <i>M. falcata</i> characteristics, 50% <i>M. sativa</i> subsp. varia, and 30% <i>M. sativa</i> L. subsp. sativa.	USDA, ARS, Mandan ND

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tively. Twenty-seven cells out of a total of 576 had less than 50% survival in the establishment year and were not included in statistical analyses. Number of surviving plants was evaluated in an 11×4 contingency table (11 entries $\times 4$ survival categories) with a chi square test for independence. The null hypothesis was that all entries had the same survival, relative to each other, in each of the 4 survival categories.

Results and Discussion

The Alaska germplasm pool, Spredor 2, and Ramsey had low survival and vigor during the establishment year relative to other entries (Table 2). Factors other than slow seedling development typical of *M. falcata* may have contributed to low survival of the Alaska germplasm pool. The South Dakota germplasm pool, primarily *M. falcata* but with some introgression from *M. sativa*, had high survival in the establishment year. The Alaska and South Dakota germplasm pools trace to a different genetic base (Rumbaugh 1980), and the relatively cool, moist environment in Alaska imposed different selection pressures than would be found in the semiarid environment of the northern Great Plains. The other 2 entries with relatively low survival in the establishment year, Spredor 2 and Ramsey, also were developed in more humid environments where little selection pressure likely was exerted for establishment capability under semiarid conditions.

Only 5 entries had above 50% survival after 3 seasons of grazing (Table 2). The Mandan I and II and South Dakota germplasm pools were nearly equal in survival and ranked above all other entries. The source material for these 3 germplasm pools had been subjected to some degree of grazing and had persisted in association with grass in local rangeland environments for over 50 years (Table 1). Some reseeding of the original M. falcata source material had undoubtedly occurred. The 2 Mandan germplasm pools had more introgression of M. sativa than the South Dakota germplasm pool. Drylander and Roamer, while relatively high in survival, ranked lower than the Mandan and South Dakota germplasm pools. Ramsey, a winterhardy cultivar developed for hay production, was significantly lower in survival than the other entries. Vigor scores of plants surviving 3 seasons of grazing did not differ appreciably among entries except for Ramsey, which was significantly less vigorous than most of the others.

Table 2. Survival percentages and vigor scores in the establishment year and after three seasons of grazing by sheep for 11 alfalfa cultivars or experimental strains transplanted on 0.9 m centers at a grassland site near Mandan, ND.

	Establishm	ent year	Grazed three seasons ³			
Entry	Survival Per- centage ¹	Vigor Score ²	Survival Per- centage	Vigor Score		
Mandan I Germ	-					
plasm Pool	93	6.5	74	6.0		
South Dakota Germplasm Pool	97	68	73	61		
Mandan II Germ	-	0.0	75	0.1		
plasm Pool	92	6.7	72	6.1		
Drylander	92	6.6	65	6.2		
Roamer	93	6.6	62	6.7		
C-3 Germ-						
plasm Pool	96	6.1	50	6.4		
Alaska Germ-						
plasm Pool	64	7.7	46	6.2		
Spredor 2	76	7.7	43	6.7		
KS-10 Germ-						
plasm Pool	93	6.4	43	6.7		
Ladak 65	91	6.4	42	6.5		
Ramsey	66	7.7	30	7.2		
S	2.7	0.2	4.0	0.2		
LŜD.06	7.7	0.5	11.7	0.6		

Each entry represented by 549 transplants.

²Vigor score ranges from 1-9 where 1 = most vigorous; dead plants not scored. Survival of 549 transplants per entry and vigor of live plants were assessed after 30 days regrowth had occurred following grazing.

The 5-plant \times 5-plant cells provided 549 microenvironments to compare entries for survival. Survival, expressed as a percentage of establishment year stands, was tabulated for each entry within 4 survival categories for plant cells (Table 3). A significant chi square test for independence indicated that the entries did not maintain the same survival, relative to each other, in all 4 survival categories.

The Alaska germplasm pool had relatively high survival when survival of other entries was low, but did not maintain this advantage in the categories with higher survival. Once established, the Alaska germplasm pool, with slow regrowth and early fall dormancy, was able to survive in microenvironments where less hardy germplasm did not. In microenvironments with high overall survival, most of the other entries had taller plants with faster regrowth than the Alaska germplasm pool and were equal or higher in survival. Survival of Ramsey was below the survival category mean in all categories. Ramsey is winterhardy (Elling et al. 1973), but the cultivar apparently was not well adapted to stresses associated with grazing and/or drought in this study. The Mandan I and II and South Dakota germplasm pools were apparently suited for grazing over the entire range of microenvironments found in this study, since they survived well in all 4 survival categories. Drylander, with slower regrowth than Roamer, had higher survival in Category I. Drylander and Roamer both ranked slightly above the survival category mean in the remaining 3 categories.

Stress factors that are representative of rangeland conditions are important in identifying superior alfalfa genotypes suited to rangeland grazing. Keller (1948) pointed out that selection of range plants should be made under conditions that represent, as closely as possible, the area where the species is expected to be used. Ries (1982) reported that alfalfa has to survive and produce under limited management in a wide variety of rangeland environments. He stated further that alfalfa is selectively grazed by livestock and wildlife and, even under proper stocking rates, grazing pressure could be quite heavy. Alfalfa in our study was subjected to a number of different stress factors typical of rangeland conditions. In addition to stress associated with grazing, other factors imposing selection pressure for survival on the alfalfa included a 16% west-facing slope, competition from associated vegetation, low early season precipitation in 3 out of 4 years, and the September clippings which probably resulted in low levels of carbohydrate reserves in root and crown tissue (Smith 1972) and reduced snow cover during winter.

The creeping rooted trait described by Heinrichs (1963) that enables plants to produce new shoots from horizontal rootstalks

Table 3. Survival percentages and ranking within four survival categories for 11 alfalfa cultivars or experimental strains transplanted on 0.9 m centers at a grassland site and grazed by sheep for three seasons near Mandan, ND.

· · · · · · · · · · · · · · · · · · ·	Survival expressed as percentage of establishment year stands									
	Category I ¹ (0-8 plants)		Category II (9-13 plants)		Category III (14-18)		Category IV (19-23 plants)		Overall Weighted	
Entry	survival	rank	survival	rank	survival	rank	survival	rank	Mean	rank
South Dakota Germplasm		_								
Pool	58	2	74	2	85	2	95	1	79	1
Mandan I Germplasm										
Pool	46	4	76	1	86	1	92	4	78	2
Mandan II Germplasm										
Pool	56	3	73	3	82	3	93	3	77	3
Alaska Germplasm		-								
Pool	75	1	61	4	72	5	85	9	70	4
Drylander	43	5	58	5	78 `	4	92	4	70	4
Roamer	30	6	58	5	72	5	90	6	65	6
Spredor 2	18	8	40	7	63	7	86	8	53	7
C-3 Germplasm Pool	15	9	40-	7	61	8	93	2	53	7
KS-10 Germplasm Pool	15	9	25	н	57	9	81	10	46	9
Ladak 65	14	11	29	10	52	10	87	7	45	10
Ramsey	26	7	34	9	46	11	79	11	44	11
x	36		52		69		88		62	
								S_	3.5	
									10.0	

Survival categories based on number of live plants in individual plant cells recorded after 30 days regrowth had occurred following the third season of grazing. Survival Categories 0 and 1V were represented by 77, 158, 231, and 83 plant cells, respectively. X² for independence = 96.0, $P = 0.0001^{**}$ 30d.f. [from 11 × 4 contingency table (11 entries × 4 survival categories) of number of surviving plants].

may be an important survival mechanism for alfalfa in rangeland. Other traits that Heinrichs (1975) found important to survival of alfalfa in semiarid rangeland of western Canada include deep-set crowns that protect plants from trampling, dormancy during long dry and cold periods, and slow regrowth after grazing. It was apparent in our study that plants with rapid regrowth after grazing and fall cutting tended to have low survival. Smith (1972) reported that root reserves in alfalfa are rapidly depleted by frequent cutting. Thus, slow regrowth could be an important factor contributing to maintenance of carbohydrate root reserves in rangeland alfalfa under grazing pressure.

Our primary breeding objectives in developing alfalfa for rangeland are high establishment capability and high levels of persistence under grazing. High regrowth potential under grazing and long-term persistence may be mutually exclusive. We are encouraged by the phenotypic variability found among surviving plants in this study and are optimistic that further genetic improvements can be made in alfalfa germplasm for rangeland.

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Early Root and Shoot Elongation of Selected Warm-season Perennial Grasses

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Abstract

Root length and root:shoot ratios are considered to be important survival factors of seedlings growing in areas of limited water. This study was conducted to determine early root elongation and root:shoot ratios during the germination to seedling stage of 'Premier' sideoats grama [Bouteloua curtipendula (Michx.) Torr.], 'Cochise' lovegrass (Eragrostis lehmanniana Nees × Eragrostis trichophora Coss and Dur.), 'A-130' blue panic (Panicum antidotale Retz.), and accessions PMT-1733-77 and NM-184 alkali sacaton (Sporobolus airoides Torr.). Root and shoot measurements were made approximately every 12 hr from seed planting to 190 hr and the results related to species success or failure in reported seeding trials. Sideoats grama root lengths were greater than those of all other species at all sample times. Root lengths among the other species were not different until about 5 days after planting when Cochise lovegrass root lengths were significantly $(P \le 0.05)$ less. Though there was no significant ($P \le 0.05$) difference in root lengths among accessions of alkali sacaton, accession 1733 root elongation continued after accession NM-184 root elongation ceased. Sideoats grama shoot lengths were significantly (P < 0.05) greater than those of all species until day 6, when sideoats grama and blue panic were not different. Average 7-day root:shoot ratios ranged from 2.9:1 for sideoats grama to 1.3:1 for blue panic. Rapid root elongation or comparatively high root:shoot ratios obtained for species in this study could not be directly related to reported success or failure in seedling establishment.

Root length and root:shoot ratios are considered important survival and environmental adaptations of plants (Troughton 1956). Perhaps the most critical period of a plant's life is the germination to early seedling stage (7 days) when moisture uptake is dependent on the seminal root (Mueller and Weaver 1942, Tapia and Schmutz 1971). In semiarid and arid climates, characterized by brief periods of soil moisture that are subjected to high potential evaporation rates, water potential in the surface 10 cm of soil is not maintained above -15 bars for extended periods in the summer (Noy-Meir 1973). Within only a few hours or days of germination. rapid seedling root elongation into relatively moist subsurface soil is a prerequisite to successful establishment (Tadmor and Cohen 1968). In arid and semiarid climates, seedling shoots are exposed to extremely dry air conditions while the seedling roots can be exposed to relatively moister soil conditions. Because high transpiration rates are associated with dry, hot air conditions, a seedling with a relatively large root: shoot ratio should experience less moisture stress (Wilson et al. 1976).

A limited number of studies have indicated species differences in root elongation rates. Wilson and Briske (1979) found that seminal root elongation rates of blue grama [Bouteloua gracilis (H.B.K.) Lag. ex. Griffiths] ranged from 6 to 10 mm per day. Sosebee and Herbel (1969) reported that 21 days after planting, sideoats grama [Bouteloua curtipendula (Michx.) Torr.] had an average root length of 96 mm and alkali sacaton (Sporobolus airoides Torr.) had an average length of 38 mm. However, no significant root:shoot ratio (by weight) difference existed between the 2 species. Dalrymple and Dwyer (1967) reported that root:shoot ratios (weight based) of sideoats grama decreased from 8:1 for 3-week old plants to 4.9:1 for 15-week old plants and that, as plant age increased, variation in root and shoot weights among species increased. These previous studies indicated species differences in root elongation and root:shoot ratios, but the results may not be comparable because the studies were conducted under various environmental conditions. Also, the critical period of germination to early seedling stage (7 days) was not extensively monitored.

The objectives of this study were: (1) to quantify root and shoot elongation and root:shoot ratios of several warm-season perennial range grass species during the germination to early seedling stage (7 days), and (2) to relate root elongation and root:shoot ratios to reported success and failures in seedling establishment trials.

Materials and Methods

Root and shoot lengths of 5 range grasses were determined at 12-hour intervals from seed germination to early seedling stage (7 days). The experimental design was completely randomized with 3 replications of 200 root and shoot observations for each grass. The experiment was conducted over a period of 5 months. Replications occurred randomly over time with all other conditions similar. Germination data were collected to indicate when to begin measurement of root and shoot lengths and to assist in interpretation of root and shoot length data.

Grass species studied were 'Premier' sideoats grama, 'Cochise' lovegrass (*Eragrostis lehmanniana* Nees × *Eragrostis trichophora* Coss and Dur.), 'A-130' blue panicgrass (*Panicum antidotale* Retz.), and accessions PMT-1733-77 and NM-184 alkali sacaton. These species have been used, with varying success, in many reseeding programs in the southwestern United States (Tromble 1974, Jordan 1981, Cox and Jordan 1983). The study was conducted in a light and temperature controlled growth chamber with alternating temperatures of 30 and 22° C ($\pm 2^{\circ}$ C) and relative humidity near 100%. High temperatures coincided with 14 hr of light and low temperatures with 10 hr of darkness. Light was supplied by both fluorescent and incandescent lamps that produced 35,300 lumens/m². These temperatures and light-dark sequences were similar to reported optima for germination and seedling growth of the species studied (Knipe 1967, Sosebee and Herbel 1969).

Seedlings were grown in cylinders made from 150-mm lengths of 25-mm diam polyvinylchloride pipe cut in half longitudinally. The 2 halves were held together with rubber bands to form a cylinder open at both ends. One hundred cylinders were placed upright in a holding tray and each filled to within 5 mm of its top with 135 g of 20-mesh, white, crystal silica. Silica was used to minimize variability in soil nutrient content, texture, and bulk density. One seed was placed in each half of the silica-filled cylinder, covered with 5 mm of silica, and watered with 15 ml of distilled water to bring the silica to field capacity. This initial watering was considered time zero for all subsequent measurements.

Seed germination for each replication was determined for each species using petri dish germination techniques. For each replication, 100 seeds were placed on Whatman No. 2 filter paper, watered with distilled water at time zero, and placed next to the root cylinder holding tray in the growth chamber. Germination counts were made every 12 hours $(\pm 2 hr)$ after initial watering. A seed was considered germinated when its radicle or plumule length was greater than or equal to the seed length.

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Manuscript accepted 13 May 1985.

Root and shoot length measurements were begun 12 hours after germination was first observed in the germination study and then every 12 hours (\pm 2 hr). At each measurement time, 10 cylinders were randomly taken from the holding tray for observation and measurement and 10 ml of water were applied to each remaining cylinder. Each of the 10 cylinders was separated and the seed from each half observed for germination. If the seed had germinated, its root and shoot lengths were measured to the nearest millimeter. If the seed had not germinated, it was placed in a petri dish with numbered areas on filter paper for later identification and determination of viability. If the identified seed germinated during the remainder of the replication sampling period, the seed was considered viable and zero root and shoot lengths would be recorded for the seed at its originally sampled time. If the seed did not germinate during the replication sampling period, the seed was considered nonviable and not included as a sample for its original sample time.

Analysis of variance and the Scheffe test (Snedecor and Cochran 1980) were used to test hypotheses of root and shoot length differences at common sample times among replication and species means at P < 0.05. Root:shoot ratios were determined using only nonzero values.

Results and Discussion

Analysis of variance indicated no significant (P < 0.05) differences among replications, so data were combined for analysis of variance among species. Sample times selected for root or shoot comparisons among species represent a range of ± 2 hours from times listed in the tables or figures. This range was necessary because of deviations in the planned 12-hour sampling schedule. A range less than ± 2 hours would have eliminated too many comparisons.

Root Lengths

Sideoats grama had significantly (P < 0.05) longer mean root lengths than the other species (Table 1). Mean root lengths among

Table 1. Mean root lengths of species for selected sample times.*

Time (hr)	Cochise Lovegrass	Alkali Sacaton NM-184	Blue Panic	Alkali Sacaton 1733	Sideoats Grama
			mm		
58	2.5a	3.9a	4.4a	1.6a	25.4Ь
70	6.2a	7.2a	6.2a	5.1a	30.6b
80	10.5a	12.1a	9.6a	9.4a	39.4b
92	13.8a	14.8a	12.5a	16.7a	44.4b
105	15.0a	19.3a	15.6a	_	48.9b
117	15.9a	19.5ab	18.2ab	21.8b	53.7c
129	16.8a	20.2ab	23.4b	24.1b	
140	17.2a	20.3ab	24.2b	25.7Ъ	64.3c
154	16.7a	20.6ab	29.1b	28.8b	
165	16.1a	21.0ab	32.3b	30.7b	66.8c

*Means in rows with different letters are significantly different ($P \leq 0.05$) according to the Scheffe test.

the other species were not significantly (P < 0.05) different until almost 117 hours (5 days) after initial watering. Root length differences among species became significant (P < 0.05) as the seedlings became older (Table 1), a finding similar to that of Dalrymple and Dwyer (1967).

The root length-time curves among species were distinctly different (Fig. 1). The root elongation rate of 'Cochise' lovegrass and alkali sacaton NM-184 decreased abruptly around 96 hours (4 days). The root elongation rate of alkali sacaton 1733 also decreased at 96 hours but the decrease was not as abrupt. The continued increase in root elongation of alkali sacaton 1733 after 96 hours, though not statistically different than the root elongation of NM-184, may partially explain why 1733 has been more successfully established than NM-184 (Cox, J.R., USDA-ARS, personal communication). Also, Briske and Wilson (1977) found that blue grama root lengths differed among accessions and suggested that accessions with the most rapid root elongation rate should be the easiest to establish. Blue panic and sideoats grama root elongation rates remained relatively constant throughout the sample period.

Sideoats grama had the longest root lengths at any measurement time. If rapid early root elongation is a prerequisite to successful establishment as reported by Tadmor and Cohen (1968), sideoats grama should be relatively easy to establish. Conversely, 'Cochise' lovegrass should be the most difficult to establish because its roots were shortest at any measurement time. However, Jordan (unpublished Bureau of Land Management Progress Reports) found in many reseeding trials in southeastern Arizona (Cochise County) that sideoats grama was very difficult to establish whereas 'Cochise' lovegrass was readily established. Jordan's findings were based on trials conducted in a 165-mm summer precipitation zone and when subsurface soil moisture was very low. Because roots will not grow into dry soil (Hendrickson and Veihmeyer 1931), the potential for rapid root elongation of sideoats grama would not be a beneficial attribute for successful seedling establishment under the dry subsurface soil conditions. Tromble (1974), working in a 190-mm summer precipitation zone, had excellent success in establishing sideoats grama on a root-plowed site in southeastern Arizona. Tromble drill seeded sideoats grama around mid-July after previous rains had been sufficient to wet subsurface soil zones. Under conditions of wet subsurface soil, sideoats grama will rapidly extend its seminal root into zones of subsurface soil moisture and not be totally dependent on soil moisture relations of the drastically changing upper soil zones.

Shoot Lengths

Seedling shoots are sites of carbohydrate synthesis and the larger the shoot the greater the opportunity for seedling growth (Kramer, 1983). Though large shoots promote food production, they also promote high rates of transpiration which are accentuated in dry, hot climates.

Mean shoot lengths of sideoats grama were significantly (P < 0.05) longer than those of all other species until almost 140 hours (6 days), when blue panic and sideoats grama shoot lengths were not significantly (P < 0.05) different but were still greater than the shoot lengths of the other species (Table 2). Shoot elongation of all

Table 2. Mean shoot lengths of species for selected sample times.*

Time (hr)	Cochise Lovegrass	Alkali Sacaton NM-184	Blue Panic	Alkali Sacaton 1733	Sideoats Grama
			mm		
58	1.2a	2.4a	3.0a	1.5a	9.2b
70	3.2a	4.1a	4.5a	2.7a	12.1b
80	6.9a	6.3a	6.7a	5.0a	16.2b
92	8.4a	7.8a	8.9a	6.7a	18.5b
105	9.2a	10.6ab	12.4b		18.7c
117	9.8a	10.9a	14.9Ъ	9.9a	20.6c
129	11.2a	12.3a	18.0b	11.1a	_
140	11.4a	12.1a	20.3b	12.0a	24.8b
154	12.5a	12.3a	22.7Ъ	12.9a	_
165	12.1a	12.2a	25.0b	13.8a	28.7Ь

*Means in rows with different letters are significantly different ($P \leq 0.05$) according to the Scheffe test.

species during the period of measurement lagged behind root elongation, a phenomenon found for seedlings of many plant species (Oppenheimer 1960, Wiese 1968, Evetts and Burnside 1973). Except for sideoats grama and alkali sacaton 1733, the shoot length-time curves had shapes similar to the root length-time curves (Fig. 1). Shoot elongation of sideoats grama and alkali sacaton 1733 declined much sooner than root elongation.

There was no significant ($P \le 0.05$) shoot length difference between accessions of alkali sacaton, and their shoot length-time curves resemble the shoot length-time curve of 'Cochise' lovegrass.


Fig. 1. Root and shoot lengths, and root:shoot ratios for various sample times of all species.

Germination

Because of the sampling method used, there was an interaction between the germination rate of each species and the time dependent root and shoot length measurements. This interaction is important if absolute growth rates are desired; but for this study, the interest was in determination of root and shoot lengths at various times from initial watering, so separation of germination rate from root or shoot length was not made.

Curves of average cumulative germination, based on number of seeds germinated for each species, indicated 3 groupings (Fig. 2).



Fig. 2. Curves of cumulative germination of seeds for all species.

These 3 groupings were also separated using a germination rate index (Evetts and Burnside 1972). The index reflects the overall germination rate of a species from time of watering to final germination count and compensates for percentage of seeds germinated. The germination rate index ranged from a high of 1.0 for sideoats grama to a low of 0.3 for blue panic. 'Cochise' lovegrass and the 2 accessions of alkali sacaton had an index of 0.4. Also, time to achieve 50% germination is commonly used to reflect rapidity of germination. The times to 50% germination of sideoats grama, alkali sacaton NM-184, 'Cochise' lovegrass, alkali sacaton 1733, and blue panic were 22, 46, 50, 52, and 80 hours, respectively.

Rapid germination is an important factor in the success or adaptability of a species (Whalley et al. 1966, Jordan 1981). However, in climates characterized by sporadic and often small rainfall events such as found in southeastern Arizona, rapid germination may be a detriment to a species. For example, the rapid germination of sideoats grama seed can be either a positive or negative factor in establishment, depending on the amount and temporal distribution of rainfall. Under favorable conditions, nearly all viable sideoats grama seeds would respond quickly to rainfall (Frasier et al. 1984). If the amount of rain was insufficient to adequately wet subsurface soil zones, the seeds would germinate but the rapid root growth characteristic of sideoats grama would be of little benefit because the root would grow into dry soil. Under the same conditions, a relatively smaller portion of viable 'Cochise' lovegrass seeds would respond because of their slower germination rate (Fraiser et al. 1984). If the moisture was inadequate to sustain

Root:Shoot Ratios

Root:shoot length ratios, were determined as a possible indicator of seedling drought resistance. Presumably, the larger the ratio, the more drought resistant the seedling (Oppenheimer 1960). Root:shoot ratios varied within and among species with time (Fig. 1) and the 7-day average root:shoot ratios were 2.9:1, 2.2:1, 1.8:1, 1.6:1, and 1.3:1 for sideoats grama, alkali sacaton 1733, alkali sacaton NM-184, 'Cochise' lovegrass, and blue panic, respectively.

Three time-related trends in root:shoot ratios were found among the species studied (Fig. 1). Root:shoot ratios of 'Cochise' lovegrass and alkali sacaton 1733 increased with time during the first 72 (3 days) to 96 hours (4 days) after initial watering and then decreased and became relatively constant. Blue panic and alkali sacaton NM-184 root:shoot ratios remained fairly constant throughout the evaluation period. The root:shoot ratio of sideoats grama was initially high (4.6:1) and decreased rapidly with time until about 72 hours (3 days) when the ratio became relatively constant (around 2.5:1). This decrease in the root:shoot ratio of older-aged sideoats grama plants also was found by Dalrymple and Dwyer (1967).

If a high root:shoot ratio is a morphological characteristic of drought resistance, as suggested by Wright and Streetman (1960), then sideoats grama should be the easiest to establish of the species studied. However, even though sideoats grama has the largest 7-day average root:shoot ratio, this species has been difficult to establish in the semiarid climates compared to 'Cochise' lovegrass and blue panic, whose initial root:shoot ratios are less than 2:1.

Conclusions

Comparatively high root:shoot ratios, very rapid germination, and rapid seminal root elongation have been reported to be positive seedling characteristics important for establishment in semiarid or arid environments. Even though these characteristics are found in sideoats grama, range managers have had limited success with this species in reseeding programs in southeastern Arizona where there was less than 190 mm summer rainfall, and when subsurface soil moisture was very low. 'Cochise' lovegrass has a relatively low root:shoot ratio, slow germination rate, and the slowest seminal root elongation rate of the species studied. However, 'Cochise' lovegrass has been successfully used in reseeding programs in the semiarid Southwest. Sideoats grama and 'Cochise' lovegrass show an interesting contrast of morphological characteristics and, of the species studied, probably represent the extremes in morphological and physiological adaptations to climatic conditions, respectively.

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Herbaceous Biomass Dynamics and Net Primary Production Following Chemical Control of Honey Mesquite

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Abstract

The effect of honey mesquite (Prosopis glandulosa var. glandulosa Torr.) control on herbaceous growth dynamics, forage production, and root and crown biomass was investigated in 1979 and 1980 on a site aerially treated with a 1:1 mixture of 2,4,5-T plus picloram at 0.6 kg/ha in May 1974. Density, height, and canopy of honey mesquite trees 5 years after treatment were 248 plants/ha, 0.9 m, and 3.1%, respectively, compared to 963 plants/ha, 2.2 m, and 34.6%, respectively, in the adjacent untreated control plot. Yet, there were no differences between sprayed and untreated plots after 6 and 7 growing seasons relative to species composition. growth dynamics, and production of herbaceous plants. Averaged across years and treatments, estimated aboveground net primary production was 2,525 kg/ha. Crown and root biomass in the top 10 cm of the soil profile averaged 685 and 3,837 kg/ha, respectively, with no significant treatment or year effects. Lack of treatment difference partially validates a conceptual model presently used for economic analysis of herbicide sprays for honey mesquite control. Further, it supports the hypothesis that honey mesquite trees provide critical habitat for the more productive midgrasses indigenous to this site; and that elimination of this habitat in sparse stands of the shrub subsequently limits post-treatment herbage response.

Dense stands of honey mesquite often suppress herbage production with the degree of suppression primarily a function of stand density and the innate productivity potential of the treated site (Scifres and Polk 1974, Dahl et al. 1978, McDaniels et al. 1978,

Manuscript accepted 9 May 1985.

Brock et al. 1978, Jacoby et al. 1982, Bedunah and Sosebee 1984). Degree of suppression is difficult to quantify because of spatial and temporal variation in herbage response following mesquite control. Major factors affecting herbage response are initial stand density, method of control, effectiveness of control, condition and composition of understory vegetation at the time of treatment, and post-treatment climatic and livestock grazing conditions (Scifres 1980).

Research in the Rolling Plains of Texas has indicated that the increase in herbaceous standing crop during the first 3 to 4 growing seasons following control of honey mesquite is generally accompanied by a shift in overall species composition toward more productive species (McDaniel et al. 1978, McDaniel et al. 1982). However, longer-term herbage responses in this region relative to seasonal growth dynamics, species composition, and aboveground net primary productivity (ANPP) have not been addressed. The objective of this study was to quantify these effects 6 and 7 growing seasons after treatment. Our central hypothesis was that control of honey mesquite would continue to enhance herbage production 6 and 7 years post-treatment.

Materials and Methods

Study Area

The study area was located 37 km southwest of Vernon, Texas, on the W.T. Waggoner Estate Ranch ($33^{\circ}50^{\circ}N.$, $99^{\circ}25^{\circ}W.$; elevation 384 m). Climate is continental and semiarid. Mean annual precipitation at Vernon is 65.2 cm. Peak rainfall months are May (11.9 cm) and October (7.7 cm). The average frost-free growing season is 224 days extending from late March to November (Koos et al. 1962). Mean annual air temperature is 17° C. Average daytime maximum and minimum temperatures range from 36° C in July to -2.5° C in January (U.S. Dep. Comm. 1980).

The study was conducted during the 1979 and 1980 growing

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Appreciation is extended to the E. Paul and Helen Buck, Waggoner Foundation, Inc. for financial support and the W.T. Waggoner Estate Ranch for study area and treatment installation.

Report is published with approval of the Director, Texas Agricultural Experiment Station, as TA 20218.

seasons. Precipitation at Vernon was slightly above the longterm average during the 1979 growing season (70.5 cm) and well below average during the 1980 growing season (41.1 cm). Ambient air temperatures were near the longterm average during the 1979 growing season. Temperatures during the 1980 growing season were above average with daytime maximums from June through September 1980 consistently exceeding 37.8° C with the maximum during the 42-day period from 23 June to 3 August never less than 37.8° C.

Experimental Area

Twice-replicated 0.25-ha subplots were located in two, 6.4-ha brush management treatment plots originally established in May 1974. Treatments were an untreated control and an aerial application of a 1:1 mixture of 2,4,5-T [2,4,5-(trichlorophenoxy)acetic acid] and picloram (4-amino-3,5,6-trichloropicolinic acid) in a diesel oil-water (1:3) emulsion at 0.6 kg/ha. The 4 four plots were located on Tillman clay loam soils. The Tillman series is a member of the fine, mixed, thermic family of Typic Paleustolls. It is a deep, well-drained, upland soil located on 0–1% slopes. Range site classification is clay loam. The plots were grazed as a unit by cattle at a light rate of stocking during each dormant season.

The native vegetation of the 6.4-ha treatment plots was characterized in early June 1974 prior to herbicide application (Haas 1978). Averaged across plots, honey mesquite canopy was 26%. Density of honey mesquite trees averaged 556 plants/ha. The understory vegetation was a mixture of short- and midgrass type communities. Based on June 1974 standing crop estimates, the dominant shortgrasses were buffalograss [Buchloe dactyloides (Nutt.) Englem.], a warm-season perennial, and little barley (Hordeum pusillum Nutt.), a cool-season annual. The dominant coolseason midgrass was Texas wintergrass (Stipa leucotricha Trin. and Rupr.). The dominant warm-season midgrasses were sand dropseed [Sporobolus cryptandrus (Torr.) Gray], white tridenns [Tridens albescens (Vasey) Woot. and Standl.], and red threeawn (Aristida longiseta Steud.). Total herbage standing crop in the untreated area averaged 1,147 kg/ha with 1,116 kg of grass and 31 kg of forbs. Total herbage standing crop in the treated area averaged 1,164 kg/ha with 1,138 kg of grass and 26 kg of forbs.

The pre-treatment herbaceous standing crop data gathered in 1974 was also stratified by community type. Communities delineated were midgrass upland, dense shortgrass, sparse shortgrass, and midgrass draw (Haas 1975). Based on percent composition by dry weight, the midgrass upland communities were dominated by buffalograss (27%) and Texas wintergrass (16%). The shortgrass dense communities were dominated by buffalograss (74%) while the shortgrass sparse communities were dominated by buffalograss (51%) and sand dropseed (14%). The midgrass draw communities were dominated by buffalograss (11%), western wheatgrass (Agropyron smithii Rydb.) (16%), sideoats grama [Bouteloua curtipendula (Michx.) Torr.] (31%), and various species of forbs (15%).

The honey mesquite canopy in the 6.4-ha untreated plots was 32.8% by 1976 (Haas 1973). Estimated canopy cover in the treated plots in 1976 was 2.2%. Estimated woody plant cover in 1979 in the untreated and treated subplots was 34.6% and 3.1%, respectively (Schultz 1982). Woody plant density in the untreated subplots in 1979 was 963 plants/ha as compared to 248 plants/ha in the treated subplots. Average tree height in the untreated plots was 2.2 m. Average tree height in the treated plots was 0.9 m. The dominant herbaceous species growing on the study area during the 1979 and 1980 growing seasons were buffalograss, Texas wintergrass, little barley, and Japanese brome (Bromus japonicus Thumb.), a coolseason annual grass. Other common warm-season perennial grasses were tumble windmillgrass (Chloris verticillata Nutt.), tumblegrass [Schedonnardus paniculatus (Nutt.) Trel.], red threeawn, and sand dropseed. Common sixweeks grass [Vulpia octoflora Rydb.] and rescuegrass [Bromus unioloides (Willd.) H.B.K.], 2 annual shortgrasses, were common during spring. Common perennial forbs were heath aster (Aster ericoides L.), western ragweed (Ambrosia psilostachya D.C.), silverleaf nightshade (Solanum elaeagnifolium Cav.), and American germander (Teducrium canadense L.). The most frequent annual forbs were common broomweed (Xanthocephalum dracunculoides D.C.) and woolly plantain (Plantago purshii R. & S. var. purshii).

Methods

On-site precipitation was measured with a standard rain gauge. Soil water content was determined gravimetrically from interspaces separating the shrubs in all subplots on a weekly basis. Samples were collected at 10-cm increments to a depth of 100 cm when possible. Extremely dry conditions during summer 1980 limited the sample depth to the top 10 cm of the soil profile.

Aboveground standing crop was sampled by the frequent harvest method utilizing ten, 0.25-m circular quadrats in each subplot on each sample date. Location of quadrats was entirely random. When individual honey mesquite trees physically restricted the placement of a quadrat, a second location was randomly selected. Vegetation was clipped at ground surface and dried at 60° C to a constant weight. All biomass was separated by species into 3 categories: live, recent dead (current year's dead), and old dead (previous year's dead). Harvest dates were approximately once a month from March through October in 1979 and from May through September in 1980.

Belowground biomass was sampled in June of both years to estimate vertical root distribution in 10-cm increments. An 80-cm core, 5.1 cm in diameter, was taken from the center of each quadrat after the aboveground herbaceous material was harvested. Four additional 7.5-cm diameter cores were collected in each harvest quadrat to estimate total root biomass in the top 10 cm of the soil profile. Cores were washed following the procedures outlined by Lauenroth and Whitman (1971). Samples were dried at 60° C to a constant weight, separated into either crown or root tissue, weighed, and ashed at 610° C to determine organic matter.

Aboveground net primary production (ANPP) was estimated by summing peak current year's (live + dead) standing crop by species and species group (Singh et al. 1975). Species groups consisted of all species contributing <5% to the total ANPP in either treatment in either year. Data were analyzed utilizing various analysis of variance models (Steel and Torrie 1960). Tukey's Q-values were utilized for mean separations when F-values were significant ($\alpha =$ 0.05). Arcsin transformations for percentage composition data were utilized when appropriate.

Results

Soil Water Content

Because soil water content did not differ among treatments, regardless of sampling date or depth, data were pooled across treatments to illustrate trends during the 2 growing seasons (Fig. 1). Soil water contents were closely coupled to amount and temporal distribution of rainfall, and were considerably less throughout the 1980 growing season when compared to 1979. Schultz (1982) found no differences between treatments in soil water potentials measured at 10-cm increments. He reported average soil water potentials of 0.03, 0.10, 0.50, and 1.5 (-MPa) occurred when soil water content in the top 10 cm of the soil profile averaged 20.8, 15.5, 12.0, and 11.2%, respectively.

Herbage Growth Dynamics

Vegetative growth was initiated in early spring in 1979 (Fig. 2). Peak live standing crop occurred in June in both treatments. Estimated peaks were 1,750 and 1,600 kg/ha in the untreated and sprayed plots, respectively. Live material was present throughout the 1979 growing season with approximately 700 kg/ha harvested from each treatment in October. Recent dead biomass began to accumulate in late April as the cool-season grasses and forbs began to senesce. Quantity of recent dead standing crop progressively increased thereafter as the warm-season plants matured. Quantity



Fig. 1. Monthly precipitation (cm) at Vernon (vertical lines) and soil water (%) in top 10 cm at study sites during 1979 and 1980 growing season.

of old dead standing crop decined rapidly during spring with only minimal amounts present by summer.

Herbage dynamics in 1980 were substantially different than in



Fig. 2. Aboveground biomass dynamics on untreated and treated plots during 1979 growing season.

1979 because the drought which began in late May (Fig. 1) effectively eliminated all vegetative growth after early June (Fig. 3). Peak live biomass in both treatments was approximately 40% less in 1980 than 1979 with no live material present in either treatment by late July. As the live plants senesced during the summer, dead material increased dramatically; however, quantity of recent dead standing crop declined during the late summer of 1980 as opposed to the steady increase observed in 1979. Decline in recent dead



Fig. 3. Aboveground biomass dynamics on untreated and treated plots during 1980 growing season.

standing crop indicates transfer of material into the litter component. Such a transfer in 1980 would be expected since the recent dead material in 1980 was probably considerably older than on comparable calendar dates in 1979. Dynamics of the old dead standing crop in 1980 were similar to 1979.

Statistical analyses of the live, recent dead, and old dead biomass estimates across dates generally indicated significant ($\alpha = 0.01$) species, date and species-by-date interaction effects regardless of tissue category. Treatment and treatment interaction effects, however, were not significant ($\alpha = 0.10$). We attributed the lack of significant treatment effects to a lack of differences between treatments in species composition. Buffalograss was the dominant species in both treatments and accounted for 70 to 80% of the total standing crop on any given harvest date on the untreated plots, and from 45 to 56% of the total standing crop harvested on any given sample date in the treated plots.

Aboveground Net Primary Production (ANPP)

ANPP varied significantly ($\alpha = 0.01$) between years and among species (Fig. 4). The year effect was caused by the 1980 drought, which reduced total ANPP 27% relative to 1979 estimates. The species effect resulted from differences among species in ANPP. A significant ($\alpha = 0.01$) year-by-species interaction effect reflected the influence of differences in growing conditions between years on the growth of the different species.

Belowground Biomass

Estimated root biomass in the top 10 cm of the soil profile was 3,837 kg/ha with differences between treatments and years not significant ($\alpha = 0.05$). Likewise, crown biomass (685 kg/ha) and vertical root distribution were unaffected by treatment or year. Approximately 38% of the roots to a depth of 80 cm occurred in the



Fig. 4. Estimated above ground net primary production (kg/ha) for individual species and/or species groups on untreated (Unt) and treated (Tr1) plots during 1979 and 1980. Species and species groups are Texas wintergrass (Stle), annual grasses (Angr), buffalograss (Buda), sand dropseed (Spcr), tumble windmillgrass (Chve), other warm-season grasses (Wsgr), common broomweed (Xadr), and other forbs (Forb).

top 10 cm of the soil profile, and about 55% occurred in the top 20 cm. Both the quality and pattern of distribution of roots were similar to those reported for other North American grasslands (Sims and Singh 1978).

Discussion and Conclusion

The results of this study indicate no difference in total herbage production between sprayed and unsprayed honey mesquite plots 6 and 7 growing seasons after treatment primarily because species composition was quite similar in both treatments. We believe the results provide strong ecological evidence in support of the conceptual models of post-treatment herbage response proposed by Whitson and Scifres (1982) for economic analyses of honey mesquite control. Our belief is based upon the rather broad generalization that the herbage response following control of honey mesquite in these grasslands is most often related to the response of those grasses growing beneath the canopy of the trees at the time of treatment (Brock et al. 1978, McDaniel et al. 1978, Jacoby et al. 1982, McDaniel et al. 1982). It follows that since these are generally the most productive grasses that grow on a site, the magnitude and duration of post-treatment herbage response is closely related to their response. It is therefore not surprising that control of sparse stands of honey mesquite and/or control of honey mesquite on sites with low productivity potential and/or in excellent range condition generally limit the magnitude of the herbage response following control, while post-treatment rainfall patterns and grazing intensity generally affect both the magnitude and duration of the response (Scifres and Polk 1974, Scifres et al. 1974, Dahl et al. 1978, McDaniel et al. 1978). Basically, our data suggest that the post-treatment response of midgrasses growing beneath the canopy at the time of treatment was of insufficient magnitude and/or duration to induce a statistically significant treatment effect 6 and 7 years after spraying.

An ecological explanation of these data must center on the basic concepts of habitat and succession. We hypothesize that the presence of honey mesquite trees on this site may be critical for the survival and propagation of substantial populations of midgrasses. The hypothesis is based on an assumption that the ameliorated micro-environment within the canopy area of the honey mesquite trees (Brock 1978) is the critical factor controlling the relative abundance of most midgrasses on this site. We found no evidence that would support the hypothesis that the honey mesquite trees growing on our study site were actually limiting the abundance of midgrasses in the interstitial areas. Rather, we believe that buffalograss would be the dominant grass species on this site in the presence or absence of honey mesquite trees regardless of livestock grazing regime. Results of Foster et al. (1984) further support this belief. They reported that buffalograss was the dominant grass on a Tillman clay loam site located about 5 km from our study site. Their site supported only a sparse stand of honey mesquite trees, and it had not been grazed by domestic livestock at other than a light rate during the dormant season for a minimum of 10 years.

The relative differences between years and treatments in the productivity of various species provide biological evidence in support of our hypothesis. For example, Texas wintergrass (Stle) production increased from 160 to 335 kg/ha in the untreated plots from 1979 to 1980 but decreased from 155 to 60 kg/ha in the treated plots (Fig. 4). We believe these differences, although not statistically significant, reflect the interaction effect of the 1980 drought and the presence or absence of mesquite trees. The preferred habitat of Texas wintergrass in this region is beneath the canopy of honey mesquite (Brock et a. 1978). Previous research has shown that the canopy area of both honey and velvet mesquite [P. glandulosa var. velutina (Woot.) Sarg.] tends to ameliorate the xeric environment characteristic of most rangelands (Tiedemann and Klemmedson 1973, Brock 1978). We assume in this instance that the honey mesquite canopies effectively reduced the severity of the 1980 drought within the canopy area which, in turn, enhanced Texas wintergrass production. Similar results have been reported in south Texas by Scifres et al. (1982). They found that grass production decreased following control of a sparse stand of huisache (Acacia farnesiana Willd.) in years of below-average rainfall. They attributed this decline primarily to an overall reduction in Texas wintergrass production which resulted because of the elimination of huisache canopy, the preferred habitat of Texas wintergrass.

The same interaction effect was also evidenced by the response of the other warm-season grasses (Wsgr) (Fig. 4), which were those midgrasses that grew primarily within honey mesquite canopy areas. The magnitude of their response, however, was less dramatic than that for Texas wintergrass.

In summary, we believe our interpretation of the results of this study provide a conceptual model that may enhance our ability to predict more accurately the magnitude and duration of herbage response following spraying of honey mesquite in north Texas. Hopefully, future studies will be undertaken at other locations to specifically test the validity of our hypothesis as an ecological explanation of post-treatment forage responses following mesquite control.

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Renovation of Seeded Warm-season Pastures with Atrazine

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Abstract

Numerous warm-season pastures have been established in the last 30 years in the central Great Plains. Some of these pastures are old enough to verify that they can be abused by overgrazing as easily as native tallgrass prairies. Overgrazed warm-season pastures are invaded and dominated by cool-season grasses such as smooth brome (Bromus inermis Leyss.) and Kentucky bluegrass (Poa pratensis L.), which diminishes the pasture productivity during the hot summer months. Since established warm-season grasses have greater tolerance to the herbicide atrazine than coolseason grasses, the effectiveness of atrazine applications in renovating invaded warm-season pastures was evaluated. A single, early spring application of atrazine (3.3 kg/ha) killed or sufficiently suppressed the cool-season grasses so that surviving warmseason remnants were able to effectively re-establish the warmseason pasture in a single growing season without any loss in total pasture forage production. Lower rates of atrazine were not as effective, particularly if smooth brome was the primary coolseason grass. The single atrazine application cost was approximately 25% of the seed cost associated with more conventional renovation. Pastures should not be grazed the treatment year but can be hayed at the end of the growing season. The success of the practice is dependent on the presence of warm-season grass remnants. Spraying test strips in small fenced areas would be advisable before treating entire pastures.

The eastern one-third of Nebraska was historically warm-season dominated True Prairie (Weaver 1965). Much of this land was plowed when the area was homesteaded for production of grain crops.

Many of these areas have been seeded into warm-season pastures during the last 30 years. Usual seed mixtures consist of big bluestem (Andropogon gerardii Vitman), switchgrass (Panicum virgatum L.), indiangrass (Sorghastrum nutans Nash.), sideoats grama [Bouteloua curtipendula (Michx.) Torr.], and little bluestem [Schizachyrium scoparium (Michx.) Nash]. These pastures and native rangeland are used primarily for spring and summer grazing for cow-calf herds. Some of the seeded pastures are old enough to verify that overgrazing is a factor on seeded pastures as well as on native tallgrass prairies. This results in invasion and dominance by smooth brome (Bromus inermis Leyss.) and Kentucky bluegrass (Poa pratensis L.).

Recently Samson and Moser (1982) demonstrated the effectiveness of a spring application of atrazine [2-chloro-4-(ethylamino)-6-(isopropyl amino)-s-triazine] in shifting the composition of native rangeland dominated by Kentucky bluegrass to warm-season remnant big bluestem and sod-seeded switchgrass in a single growing season. Waller and Schmidt (1983) also shifted species composition in native rangeland from a Kentucky bluegrass and smooth brome dominated mixture to one dominated by remnant warmseason grasses, primarily big bluestem, by a single spring applica-

Manuscript accepted 14 May 1985.

tion of atrazine.

The purpose of this study was to determine if the seeded warmseason pastures could be renovated by using atrazine to suppress cool-season competition. A second objective was to evaluate the use of atrazine in stands dominated by smooth brome rather than Kentucky bluegrass.

Materials and Methods

Study Area

This study was conducted in south central Nebraska 6.5 km west of Clay Center, on the Roman L. Hruska U.S. Meat Animal Research Center (MARC). The area is located within the True Prairie region of North America (Weaver 1965). The topography is gently rolling to nearly level. Soils are formed in deep windblown Peorian loess, with a subsoil of glacial outwash and till. The study site is mapped as Crete silt loam (fine, montmorillonitic, mesic, Pachic Arguistoll) thick solum, with 0 to 1% slope. Average annual precipitation is 69 cm with 80% occurring from April through September. Average growing season is 148 days and the normal grazing period on range is from 1 May to 31 October (Hammer et al. 1981).

Pasture History

There are 4,450 ha of seeded, warm-season grasses at MARC. The study areas were formerly cultivated areas with grasses seeded into milo [Sorghum bicolor (L.) Moench.] stubble in the spring of 1967. Seed mix species were 'Pawnee' big bluestem, 'Nebraska 54' indiangrass, 'Trailway' sideoats grama, 'Nebraska 27' sand lovegrass, [Eragrostis trichodes (Nutt.) Wood]; and a legume, 'Empire' birdsfoot trefoil (Lotus corniculatus L.). Annual spring and summer grazing was initiated in the spring of 1969 (L. Brownlee 1981, personal communication). Spring applications of 73 kg/ha ammonium nitrate (NH₄NO₃) were made in alternating years. The overgrazing required to maintain herd size in beef cattle genetic studies allowed smooth brome to dominate the pastures. Kentucky bluegrass and annual brome (Bromus spp.) also appeared.

The study area had been in smooth brome for many years and buried seed and rhizomes may have contributed to its occurrence. Additionally, roadside vegetation at MARC is a mixture of smooth brome and Kentucky bluegrass, providing a potential seed source. These cool-season grasses could exploit the wet springs when the seeded warm-season grasses were dormant.

A grazing exclosure in one pasture was used to statistically define treatment effects over a 2-year period following a single herbicide application. The grazed portion of the pasture was used to determine the magnitude of treatment response. Additional pastures were sprayed in 3 different years to qualitatively evaluate the year effect and provide evidence of repeatability of treatment response.

Grazing Exclosure

Treatments, an unsprayed control and 1.12.2, or 3.3 kg(ai)/haatrazine (AAtrex 4L), were applied on 2 April 1981 within the exclosure using a conventional pressurized boom (3 m) sprayer. The herbicide solution was mixed for the low rate using a carrier volume of 200 1/ha. Multiple passes were used to achieve the 2 higher treatments. Prior to growth initiation and before treatment application, the dormant standing crop was removed by mowing and raking. This is a common practice when dormant vegetation restricts the ease and efficiency of herbicide application. For easier data collection and to reduce the effect of shading from previous

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Research is based on a thesis presented by T.O. Dill to the faculty of the Graduate College of the Univ. of Nebraska in partial fulfillment of the requirements of the M.S. degree. This paper is published as Journal #7680 of the Nebraska Agricultural Experiment Station.

The authors express appreciation to Mr. LaMoine Brownlee, (retired) supervisory agronomist, Roman L. Hruska, U.S. Meat Animal Research Center, Clay Center, Neb., for his assistance in this research.

year's growth, standing crop was also removed prior to the 1982 growing season. The experimental design was a randomized complete block with 4 replications. Plots (experimental unit) were 3×6 m and separated by 3-m alleys.

Species composition data were obtained in May and October 1981 and 1982. Warm-season species were at the 2 to 5 leaf stage and easily distinguishable in May of both years. Stand density and potential production eliminated the use of more conventional line transects or ten-point frames. Ten 1-m rods used as line transects were randomly placed at right angles on either side of a line running lengthwise through the center of each plot. Relative species composition was estimated by counting basal culms of each species that intercepted the line (sampling rod). At the end of the second growing season, species composition was also determined in a similar manner outside the exclosure in the grazed portion of the pasture. Five randomly located transects (100 m) radiated away from the grazing exclosure and ten 1-m rods were randomly located perpendicular to each transect. The area immediately adjacent to the fencing was excluded.

Yield (above-ground biomass) was estimated by hand clipping individual species within 3 quadrats at ground level on 3 harvest date in 1981 and 1982. Quadrats (0.2 m^2) were randomly located in each plot on each harvest date. Quadrats clipped in a previous sampling were not resampled. Samples were ovendried in a forced air oven for 48 hours at 68° C and weighed.

Preplanned, orthogonal contrasts were used to compare treatment responses (Steel and Torrie 1980). Analyses were on plot means of above-ground biomass for warm-season grasses, coolseason grasses, and total herbage. Warm-season herbage was the sum of individual yields of the key species: big bluestem and indiangrass. Cool-season herbage was the sum of the individual yields of the prominent species: smooth brome, annual bromes, and Kentucky bluegrass. Total herbage was the sum of yields for warm-season grasses, cool-season grasses, and all other aboveground vegetation. Regression analysis was used to evaluate consistency of response. A multivariate analysis was used to determine significant treatment by time interactions for shifts in relative species composition (Stroup and Stubbendieck 1983).

Pasture Demonstration

During the 3 years following treatment of the grazing exclosure, 11 entire pastures (approximately 65 ha each) received a single spring application of atrazine. Each pasture selected was characteristic of the grazing exclosure. In 1982, 3 pastures were sprayed 10 April with 2.2 kg/ha atrazine. Five pastures were similarly treated in 1983. Three pastures were sprayed in 1984 with 2.8 kg/ha. Pasture demonstrations were used to determine repeatability of treatment response on a production scale.

Results and Discussion

Grazing Exclosure

Vegetation Composition

Approximately 74% of the vegetation on the untreated area was smooth brome, Kentucky bluegrass, and annual bromes (coolseason grass component). Big bluestem and indiangrass (warmseason grass component) comprised only 20% of the vegetation. Other warm-season grasses present in small amounts included little bluestem, switchgrass, sideoats grama, and stinkgrass [*Eragrostis cilianensis* (All.) E. Mosher].

Precipitation for the 1981 growing season was consistent with the long-term average for cool-season vegetation, warm-season vegetation and vegetative year (Table 1). Consequently, results for the year of treatment for the grazing exclosure were representative of expected vegetation response to atrazine applications.

In May, approximately 5 weeks following the herbicide application, treatment effects were apparent. The highest atrazine rate had more warm-season grass composition (P = .08) and less cool-season Table 1. Seasonal precipitation (cm) and long-term average at Clay Center, Nebraska in 1981 - 1984.¹

		Ye	ar		_
Season ²	1981	1982	1983	1984	Long-term average
Cool-season Warm-season	35.2 33.1	42.6 32.9	42.6 36.1	50.6 22.8	32.9 36.9
year	68.3	75.5	78.7	73.4	69.8

¹Data obtained from the Climatological Data for Nebraka, National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, North Carolina. The long-term average was based on data from 1951-1980.

²Cool-season precipitation is measured from the previous October through May. Warm-season precipitation is measured from June through September. Vegetative year precipitation is measured from the previous October through September.

grass composition (P=.09). This was apparently caused by the loss of annual brome from the treated areas. It was the most atrazine sensitive cool-season competitor, exhibiting mortality within 2 weeks. Visual observation indicated that perennial species required 4-6 weeks to exhibit an atrazine effect. However, regression analysis indicated a lack of consistency in response across treatments ($r^2 <.5$) for all variables.

In 1981 warm-season grass percent composition remained unchanged on the untreated plots between May and October (Fig. 1). On all areas treated with atrazine the warm-season composition





had increased approximately two-fold. Higher atrazine rates resulted in higher percent composition for warm-season grass composition (P = .01, $r^2 = .68$). There was an atrazine rate by time interaction (P = .03) for the proportions of warm- and cool-season grasses, verifying the shift in species composition following atrazine treatment. Samson and Moser (1982) observed a similar shift toward warm-season grasses within the first growing season after spring applications of atrazine (2.2 kg/ha) and paraquat (1,1¹ dimethyl-4,4¹ bypyridinium ion) (.03 kg/ha) on a Kentucky bluegrass dominated native warm-season pasture in eastern Nebraska. Additionally, Waller and Schmidt (1983) reported similar findings with atrazine (2.2 kg/ha) alone on native, warm-season pastures dominated by Kentucky bluegrass.

One year following treatment (May 1982), the untreated plots and those treated with 1.1 kg/ha had nearly equal percent composition of warm-season grasses (Fig. 1). The percentage of warmseason grasses was four-fold greater on the plots treated with 2.2 kg/ha and nearly eight-fold greater on those treated with the 3.3 kg/ha rate compared to untreated areas. Comparisons between October 1981 and May 1982 for the atrazine treated plots indicated the failure of the low atrazine rate to release warm-season remnants and the inability of the moderate atrazine rate to maintain adequate cool-season suppression the second year following application. However, the high atrazine rate supported the higher levels of warm-season grasses. These results observed with the moderate rate (2.2 kg/ha) of atrazine were similar to the results observed by Waller and Schmidt (1983) for smooth brome.

By the end of the second growing season (October 1982) the percent warm-season grasses had remained the same on the ungrazed, untreated areas and those treated with the low atrazine rate (Fig. 1). However, this level was approximately four-fold greater than May 1982 levels. The grazed control which was outside the exclosure had less than 50% of the warm-season grass composition compared to the untreated areas within the grazing exclosure. However, regression analysis indicated that only 50% or less of the variability within the grazing exclosure was a result of atrazine rate. This was a result of the similarity in warm-season grass composition on the untreated control and the lowest atrazine rate. The infuence of the grazing rest was also apparent on the untreated area, with warm-season grasses increasing from 19% in October 1981 to 36% in October 1983. However, this was less than half of the warm-season grass composition on the areas treated with 3.3 kg/ha of atrazine. It was apparent that the benefit of atrazine treatment compared to a grazing rest was related to the rate and magnitude of stand conversion.

The shifts in species composition observed in 1981 were not as dramatic in 1982 (atrazine level by time, P = .14). This indicated that the changes that occurred the first growing season in the

proportion of warm- and cool-season grasses had stabilized. However, the high rate of atrazine still resulted in two-fold greater warm-season grass composition than the ungrazed, untreated area and was over five-fold greater than the grazed area. Considering the favorable precipitation for cool-season species in 1982 and the below normal percepitation for the warm-season grasses (Table 1), the warm-season grass response would be expected to be even greater during the more favorable years.

Herbage Yield

Untreated and treated areas had similar warm-season grass yields at the initial harvest June 1981 (Table 2). Generally, coolseason grass yield was reduced with atrazine application. The herbicide had an immediate effect on cool-season grass yield, particularly the annual brome, while the warm-season response was delayed and variable across treatments. Total yield of the untreated area and that receiving the lowest atrazine rate was similar while the medium and high rates reduced total yield approximately 66 and 75% respectively.

By August of 1981 areas treated with the higher rates of atrazine had greater warm-season grass and lower cool-season grass yields compared to the untreated and low atrazine rate plots (Table 2). Trends in yield with increasing atrazine rate were consistent with the June harvest data. Total yield had recovered on the plots treated with the higher atrazine rates and there was no difference between treated and unteated areas. The loss of cool-season production in treated plots was compensated by the improved warmseason production.

At the end of the first growing season (October 1981), trends in yield of warm- and cool-season grasses remained unchanged (Table 2). The low rate of atrazine was insufficient to provide any shift in the yield components compared to the untreated area.

			For	age yield		· · · · · · · · · · · · · · · · · · ·
Category		A	trazine treatment	(kg/ha)		Linear contrast
	Month	Untreated	1.1	2.2	3.3	(P>F) ¹
						-1981-
	June					
Total		5120	5230	1820	1280	<.01
Warm-season		630	430	1030	700	.40
Cool-season		3970	4670	770	580	.01
	August					
Total		4970	4210	4710	4730	.72
Warm-season		960	900	3580	4320	.01
Cool-season		3480	3300	830	250	.01
	October					
Total		3810	3900	5060	5160	.13
Warm-season		1170	1070	4540	4920	.01
Cool-season		2610	2800	350	220	.01
						1092
	lune					-1982-
Total	Julie	2200	2100	2210	2200	92
Warm concor		2200	2190	1300	1710	.52
Cool sesson		1270	1900	810	450	.01
Cool-season	Inter	1270	1000	010	450	.02
Total	July	6600	5070	7120	8010	15
Warm and an		4240	3070	5000	7100	.15
Warm-season		4240	2/40	1120	760	.01
Cool-season	Santamban	2315	2550	1150	700	.01
T-4-1	September	6000	5620	4000	8110	22
Total		4000	3020	\$100	7200	.23
warm-season		4090	2510	3190	820	10.
Cool-season		1800	3100	1000	020	.01

Table 2. The effect of different levels of atrazine on big bluestem and indiangrass (warm-season), smooth brome and Kentucky bluegrass (cool-season) and total yield (kg/ha) sampled at three dates within each of two growing seasons. The linear contrast was used to describe the treatment effect.

¹Contrast coefficients for treatments 0, 1.1, 2.2, and 3.3 kg/ha were: linear =3-1 1 3



Fig. 2. This pasture was a seeded warm-season pasture which had been dominated by smooth brome and Kentucky bluegrass prior to atrazine application (2.2 kg/ha) in April 1982. The vegetation response was evident by July 1982 as indicated by the photograph. Bare ground represents Kentucky bluegrass and smooth brome patches which were suppressed with the herbicide. The estimated yield of warm-season grass was in excess of 5 MT/ha.

However, the 2.2 and 3.3 kg/ha rates of atrazine provided shifts from cool- to warm-season components of yield without reducing total yield. Differences between the low and medium atrazine rates were still greater than between the medium and high rates.

The changes during the first growing season in the vegetation yield following atrazine application were consistent with percent composition changes and indicated the complete modification of vegetation dynamics. The proportion of warm-season to cool-season grass yields increased at a much faster rate on the areas treated with the higher atrazine rates (treatment by month interaction, P = .02). The development of warm-season tillers was encouraged with the atrazine treatment and these tillers appeared vigorous and productive. The magnitude of this response would warrant having after a frost the year of treatment.

The relationship between yield and atrazine rates established during the first growing season remained 1 year following treatment (Table 2). However the relationship between the untreated area and the area treated with 1.1 kg/ha was altered with the untreated consistently having more warm-season and less coolseason grass yield than the area treated with 1.1 kg/ha. This was first indicated in June 1981 and was observed at all succeeding sample dates. Apparently, the low atrazine rate was sufficient to reduce annual bromes but was ineffective in reducing the vigor of the perennial brome. The very favorable cool-season precipitation for 1982 and reduced competition from annual brome resulted in a more vigorous stand of smooth brome than occurred on the untreated area where annual brome was still abundant. Consequently, smooth brome yield was enhanced by the removal of a cool-season competitor. The smooth brome was an excellent competitor and probably depleted soil moisture prior to warm-season growth initiation.

In July 1982 there was a marked increase in the amount of warm-season grass yield on the untreated area and a slight decrease in cool-season grass yield compared to that of August 1981 (Table 2). This was an indication of the response to a grazing rest. Also, it was apparent that the medium atrazine rate was not adequate to prevent the increase of smooth brome the year following treatment. The high atrazine rate resulted in continued improvement in the warm-season grass yield. At the end of the second growing season (September 1982), the relationship between yield components and increasing rates of atrazine was comparable to that of the July 1982 harvest data.

Pasture Demonstration

Cool-season precipitation was above normal for all 3 years of the pasture demonstration trial (Table 1). Warm-season precipitation

was below normal in 2 of the 3 years. Pastures receiving the moderate atrazine rate in 1982 and 1983 exhibited a similar response to that documented in the grazing exclosure (Fig. 2). In both years cool-season grass control was adequate. Kentucky bluegrass and annual bromes were eliminated and smooth brome was reduced by over 50% based on visual estimates. The warmseason grasses were the dominant vegetation by mid-summer in the year of treatment. However, the second year following treatment there was an increase of smooth brome in pastures, indicating that a single application of the moderate rate was inadequate (L. Brownlee 1984, personal communication). Pastures treated in 1984 at the higher rate had excellent smooth brome control. Visual observation of the pasture demonstrations did support the repeatability of treatment response documented in the grazing exclosure. The estimated cost for herbicide and application was \$25/ha. This compared to a seed cost alone of \$100/ha associated with reseeding native, warm-season grasses.

Conclusion

A single, spring application of atrazine (3.3. kg/ha) can renovate smooth brome dominated, seeded warm-season pastures when remmants such as big bluestem are present. It was apparent that seeded warm-season pasture remnants maintain sufficient vigor to respond to a suppression of cool-season competition and increased while cool-season grass percent composition was decreased. A low atrazine rate (1.1 kg/ha) was similar to a 2-year grazing rest in shifting percent composition from cool- to warm-season with the major changes occurring at the end of the second growing season. There was a benefit from the grazing rest alone; however, the addition of the higher rates of atrazine expedited the change. Vegetation treated with the higher rates would not require 2 years of grazing rest. It appeared that the medium atrazine rate was not sufficient to maintain improvement in warm-season grass composition during the second year, which would eventually necessitate a repeated herbicide application. Shifts in species composition were accomplished while maintaining or improving the total yield. This effectively converted a cool-season pasture to a warm-season pasture within 1 year and without a loss in total production.

The use of atrazine is a relatively inexpensive, fast method to convert an abused, seeded warm-season pasture from cool-season dominance to warm-season dominance. The herbicide application cost was less than \$25/ha while the seed cost alone for a conventional reseeding would exceed \$100/ha. When the major invading cool-season species was smooth brome, a high atrazine rate (3.3 kg/ha) was required for control. However, 2.2 kg/ha was effective the first year for smooth brome suppression and it was sufficient to control Kentucky bluegrass. The success of this practice is dependent on the presence of viable warm-season remnants. It would be advisable to apply the herbicide to small areas protected from grazing before treating entire pastures.

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Phytosociological Observations on the Vegetation of Burnt and Unburnt Areas Near Ibadan, Nigeria

B.M. SHARMA

Abstract

The area of study has a topography mainly of plains with occasional hills and is characterized by comparatively higher pH and conductivity on burnt sites. The weed communities existing on the unburnt sites were A xonopus-Eupatorium-Centrosema Community during the dry season (November to March) and Axonopus-Eupatorium-Commelina Community during the wet season (April to October). However, on the burnt sites, Imperata-Setaria-Panicum Community emerged. The dry season community on the unburnt site had comparatively the highest diversity index. Index of species association was high for Imperata cylindrica and Calapogonium mucumoides on burnt sites while for Axonopus compressus and Commelina diffusa during both dry and wet seasons on unburnt sites. The sominance-diversity relationships based on Simpson's Index were higher for the community on burnt sites. According to Kuchler's height classes, the height class 2 was predominant. The annual vegetation burning, in general, results in a preponderance of grasses and there were 12 grasses out of 29 species (41.4%) recorded on the burnt areas.

Plant community is an organized complex with a typical floristic composition and morphological structure which have resulted from the interaction of species populations through time (Shimwell 1971). The distribution of a species population depends upon several factors directly related to phenotypic plasticity; genotypic adaptability; and competitive, reproductive, and tolerance capacities of the species. The ecological amplitude of the species is thus quite important to its existence in a particular habitat. One such habitat is that which is burned during the dry season every year. It constitutes a good site to secondary plant succession.

Ahlgren (1974) recognized fire as one of the most dramatic of the natural forces shaping the biotic community over time. Some of the notable contributors in this field with regard to West Africa were Afolayan (1979), Egunjobi (1979, Hall (1975), Hopkins (1968), and others. Adeoye and Sharma (1981) worked on the vegetation disturbed by trampling while Sharma (1982) analysed the undisturbed weed community. This investigation was conducted during 1981-82 to phytosociologically analyze the herbaceous vegetation of burnt and unburnt sites during different seasons in Nigeria and to know the existing plant communities.

The study was conducted at Ibadan on an area of 1,032 hectares. The most extensive landform in the area is the plains with occasional hills and rock outcrops. The average elevation is 233 m (Oguntoyinbo 1982). The area experiences tropical climate with wet season (March to October) and dry season (November to February).

Materials and Methods

The sampling of vegetation was done with a 0.5-m² (1 $\times 0.5$ m) quadrat laid at random. Fifty quadrats were laid each in dry and wet season on the unburnt areas while 25 quadrats were laid on burnt sites during the dry season. Within each quadrat, the total number of individuals of each species was recorded to calculate density while frequency was expressed in percentage as the number of quadrats occupied by a given species (Phillips 1959, Traczyk and Tracyzk 1977). Their cover was determined with the help of sub-

squares (100 cm²) within the quadrat frame. Importance Value Index (IVI) for each species was derived by the addition of relative frequency, relative density and relative cover (Curtis and McIntosh 1951). The height and diameter (1 cm above soil level) of each species were noted based on 3 replicates. In addition, herbaceous plants occurring outside the quadrats were also listed for species diversity. Plants were identified with the help of regional and local flora (Hutchinson and Dalziel 1954, 1963, 1972; Stanfield 1970; Lowe and Stanfield 1974).

Composite soil samples from 0-10 cm depth were collected at the frequency of 1 sample for 5 quadrats during both the seasons. They were analysed for pH, conductivity, and organic matter. PH and conductivity were determined for 1:2 Soil: Water Suspension with Phillip-Harris meters while organic matter content was found by igniting the oven-dry soil sample in a muffle furnace at 500° C for 3 hours.

Results and Discussion

Climate and vegetation show a very close relationship and it is possible to regard vegetation as an indicator of climate and to utilize plant distribution for delimitation of climatic zones (Walter 1971). Salient climatic features of the area, based on the climatic data for 1981, were 1,135 mm of total annual precipitation with no rainfall in January and December, while less than 20 mm rain in November and March; 93 to 97% relative humidity at 0700 hr; and 86 to 214 hours of sunshine in August and January, respectively. The mean daily temperature varied from 25° C in August to 29° C in February. However, the extreme maximum and minimum temperatures were 37° C (February and March and 14° C (November) respectively.

Apart from the aerial environment, habitat also affects vegetation patterns, and the best documentation of the patterning comes from soil surveys. The analysis of soils from the area shows pH varying from 6.75 to 7.85, conductivity from 133.6×10^{-4} Sm⁻¹ to 267.1×10^{-4} Sm⁻¹ and organic matter from 3.8 to 12.3% during the dry season in the unburnt sites. However, in the same sites, the values range from 5.8 to 7.4, 104.9×10^{-4} Sm⁻¹ to 581.9×10^{-5} Sm⁻¹, and 4.1 to 14.1% during the wet season respectively. In general, the soil samples have a higher pH, conductivity, and organic matter during the dry season. In the burnt areas on the other hand, pH and conductivity were higher during the wet season. Comparing the unburnt and burnt sites, pH and conductivity were higher in the latter sites.

The prevailing vegetation displays the effects of environmental conditions. The phytosociological features of the unburnt areas on seasonal basis and burnt areas during dry season have been given in Table 1, 2, and 3. Various communities that emerged on the basis of the Importance Value Index (IVI) were Axonopus-Eupatorium-Centrosema community during dry season and Axonopus-Eupatorium-Commelina community during wet season, both on the unburnt areas, while Imperata-Setaria-Panicum community during the dry season on burnt sites.

Axonopus-Eupatorium-Centrosema Community (Unburnt site, dry season):

The IVI of 32 plants out of a total of 69 plants has been shown in Table 1. Forbs and grasses were 59 and 10 respectively. Codominant plants were *Tridax procumbens*, *Paspalum conjugatum*, *Sida*

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The author wishes to acknowledge Mr. Ikem, O.N. for help in collecting the field data, and to Mrs. J. Lowe for identification of plants. Manuscript accepted 15 June 1985.

Table 1. Phytosociological features of plant commun	ty on unburnt sites during di	y season (Number of o	quadrats = 50, IVI = Im	portance Value Index).
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	Mean	Mean		Density	Cover	
	Height	diameter	Frequency	per	per quadrat	
Name of plants	(Cm)	(Cm)	(%)	quadrat	(Cm ²)	IVI
Amaranthus viridis L.	81.3	1.03	6	0.1	34	2.5
Andropogon fastigiatus Sw.	56.0	0.4	2	0.5	26	2.4
Aspilia africana Pars.	50.0	0.4	2	0.2	42	2.1
Boerhavia coccinea Mill.	37.5	0.4	12	0.5	150	7.8
B. diffusa L.	39.1	0.5	14	0.6	200	9.8
Bryophyllum pinnatum (Lam.)						
Oken	18.6	0.6	6	1.3	98	7.2
Calopogonium mucunoides Desv.	31.5	0.2	6	0.1	20	2.3
Cardiospermum grandiflorum						
Swartz.	19.0	0.2	4	0.2	48	2.6
Centrosema pubescens Benth.	17.6	0.21	28	1.1	330	17.7
Commelina erecta L.	30.0	0.5	2	2.4	76	8.7
C. diffusa Burm. f.	21.3	0.4	24	1.3	58	10.8
Cyathula prostrata Blume	23.4	0.3	10	0.8	86	6.7
Cynodon dactylon (L.) Pers.	13.0	0.2	2	0.6	44	3.1
Desmodium scorpiurus (Sw.)						
Desv.	12.0	0.3	6	0.2	22	2.5
Dissotis rotundifolia (Sm.)						
Triana	121.0	0.4	2	0.3	52	2.6
Eupatorium odoratum L.	88.4	0.8	32	2.3	584	27.9
Euphorbia hirta L.	25.1	0.3	12	0.4	20	4.6
E. hyssopifolia L.	30.4	0.3	10	0.7	166	7.2
Ipomea involucrata P. Beauv.	10.0	0.3	4	0.1	38	2.2
Justicia flava (Forsk.) Vahl.	15.0	0.4	2	0.3	80	3.2
Kyllinga erecta Schumacher	40.5	0.3	4	0.6	44	3.7
Nelionia canescens (Lam.)						
Spreng.	19.0	0.3	4	0.4	22	2.5
Sida acuta Burm. f.	151.1	0.6	22	0.5	220	12.1
S. veronicifolia Lam.	12.3	0.2	8	0.4	30	3.7
Synedrella nodiflora Gaertn.	22.8	0.4	12	0.5	36	5.2
Talinum triangulare (Jacq.)						
Willd	22.5	0.5	12	0.7	68	6.3
Tridax procumbens L.	29.6	0.3	22	1.7	280	16.6
Waltheria indica L.	80.5	0.9	4	0.1	56	2.6
GRASSES						
Axonopus compressus Beauv.	39.0	0.4	16	7.2	288	30.1
Panicum maximum Jacq.	96.6	0.7	12	0.3	176	7.9
Paspalum conjugatum Berg.	50.0	0.6	2	4.0	100	13.6
Sporobolus pyramidalis	21.7	0.32	8	0.96	34	5.3

acuta and Commelina diffusa. They all have IVI above 10. Axonopus-Eupatorium-Commelina Community(Unburnt site, wet season):

The community comprised 65 species including 58 forbs and 17 grasses. Table 2 shows 35 main species. The codominant species were Commelina pubescens, T. procumbens and S. acuta. Axonopus compressus had the highest density in both seasons on the unburnt sites.

Imperata-Setaria-Panicum Community (Burnt Site, Dry Season):

The community had 29 species of which 23 are shown in Table 3. It included 12 grasses, and 3 of them were highly dominant. Other codominant species were Sporobolus pyramidalis, Paspalum orbiculare, T. procumbens, Calopogonium mucunoides, Eupatorium odoratum, Andropogon fastigiatus etc.

On comparing the 3 communities, certain features emerge which require consideration.

Frequency

It is one of the most commonly applied quantitative parameters for the analysis of communities. Raunkiaer (1934) grouped species frequency into 5 equal classes A to E (Table 4). It is seen that frequency class A has the highest number of species but comparatively they are lesser on burnt areas. However, there was a species -Imperata cylindrica on this site belonging to Class C. Species having 40% frequency belonging to frequency class B were Calopogonium mucunoides and Panicum maximum, both occurring on burnt sites. Moreover, frequency class B was the richest on burnt sites.

Index of Similarity:

Similarity relations between communities can be expressed mathematically. These mathematical expressions of community similarity are variously referred to as indices of similarity or community coefficients (Mueller-Dumbois and Ellenberg 1974). One of the more widely applied such index is by Sorensen (1948) which can be expressed as follows:

$$1S = \frac{2C}{A+B} \times 100 \text{ where}.$$

- C = number of species common to two communities
- A = total number of species in one releve
- **B** = total number of species in second releve.

Table 2. Phytosociological features of plant community on unburnt sites during Wet season (Number of quadrats = 50, IVI = Importance Value Index).

	Mean	Mean		Density	Cover	
Name of plants	Height (Cm)	diameter	Frequency	per	per quadrat	13./1
	(СШ)	(Ciii)	(%)	quautat	(CIII-)	1 1 1
FORBS						
Alternaninera sessilis						
K. Dr. ex Kotn.	23.5	0.3	4	0.2	68	2.8
Aspilla ajricana (Pers)						
C.D. Adams	49.4	0.5	10	1.2	179	8.3
Boernavia alijjusa L.	45.0	0.5	8	0.4	132	3.4
Centrosema pubescens Benth	38.9	0.2	28	1.2	258	14.1
Commetina benghalensis L.	39.5	0.4	8	0.4	12.5	2.3
C. ayjusa Burm. 1.	43.7	0.4	26	2.4	218	14.9
Cyathula prostrata L.	42.6	0.3	6	0.7	42	3.5
Cyperus dilatatus Schum. &.						
I honn.	64.0	0.4	10	1.7	84	7.2
Desmodium scorpiurus (Sw.)						
Desv.	10.0	0.1	4	1.5	18	4.1
Eupatorium odoratum L.	82.3	0.7	18	1.2	402	15.9
Euphorbia hirta L.	34.6	0.3	12	0.9	52	5.5
E. hyssopifolia L.	32.4	0.2	14	0.5	108	6.4
Kyllinga erecta Schumach	40.5	0.4	4	0.7	32	2.8
Mariscus alternifolius Vahl.	35.5	0.4	12	0.7	60	5.4
Sida acuta Burm.f.	39.1	0.5	16	0.6	280	10.6
S. veronicifolia Lam.	15.0	0.2	8	0.2	27	2.8
Spigelia anthelmia L.	39.7	0.4	8	0.4	28	3.2
Talinum triangulare (Jacq.) Willd.	41.1	0.5	14	0.3	107	6.0
Trianthema portulacastrum L.	37.5	0.6	8	0.3	152	5.5
Tridax procumbens L.	43.9	0.3	20	1.2	344	13.9
Walthria indica L.	78.0	0.7	4	0.1	42	2.01
GRASSES						
Andropogon fastigiatus Sw.	38.6	0.3	6	2.7	88	8.3
Axonopus compressus P. Beauv.	20.6	0.6	20	13.5	346	37.7
Brachiaria deflexa (Schumach.)						
C.E. Hubbard ex Robyns	51.0	0.3	6	0.7	56	3.8
Cynodon dactylon (L.) Pers.	14.5	0.2	4	2.2	94	4.1
Digitaria ciliaris (Retz.) Koel.	47.6	0.3	6	1.2	46	4.7
Eleusine indica Gaertn.	33.6	0.4	10	0.7	86	5.9
Imperata cylindrica P. Beauv.	51.5	0.3	12	1.6	108	8.1
Panicum maximum Jacq.	155.0	1.5	4	0.1	102	3.2
P. repens L.	47.0	0.4	4	0.9	44	3.5
Paspalum conjugatum Berg.	69.0	0.4	2	1.7	92	4.6
P. orbiculare Forst	54.4	0.3	10	1.4	120	7.5
Setaria barbata (Lam.) Kunth.	65.3	0.3	6	0.7	70	4.2
S. longiseta P. Beauv.	67.3	0.3	6	0.98	78	4.9
Sporobolus pyramidalis	61.3	0.3	14	1.7	134	9.5

Accordingly, the index comes as follows for different comparisons:

- 1. Dry and Wet Season Communities on unburnt areas 68.65%
- 2. Dry season community on burnt and that on burnt areas 40.82%
- 3. Wet season community on unburnt areas and dry season community of burnt areas 61.7%

It is seen that the dry season community on unburnt and that of burnt areas is considerably different. This is more likely due to change in the habitat composition.

Species Diversity.

Species diversity implies both the number of species and the number of individuals in a community. It is a measure of the amount of variability in the species composition of a community. Diversity is greatest if each individual belongs to a different species, the least if all individuals belong to one species. Man's activities usually diminish diversity. Using the logarithmic series

 $S = a \log_{e}(1 + N)$ where,

- S = number of species
- N = Number of individuals
- a = Index of diversity.

Computation of 'a' is avoided by using a graph from which 'a' is obtained directly (Lewis and Taylor 1967). Accordingly, the diversity index of the 3 communities is shown in Table 5. Although the number of species was highest during dry season and the number of individuals was highest during wet season, the diversity index was maximum during the dry season on unburnt areas. Mueller-Dombois and Ellenberg (1974) are of the opinion that regional species diversity does not appear to be merely a function of time and access of taxa, but is equally a function of the kind and *modus operandi* of the regional evolutionary stress factors.

Correlation between Species.

Treatment of vegetation samples through mathematical correlations leads to the conclusion that no 2 plant species have exactly the same ecological and sociological amplitude. However, some species are so similar in their distribution that they can be combined into groups. One can use coefficients for evaluating the similarity between 2 species with regard to their distribution by an index of association (IA). Jaccard's Index of Community Similarity can be applied as an index of species association (Mueller-Dombois and Ellenberg 1974). Table 3. Phytosociological features of plant community on burnt sites during dry season (Number of quadrats = 25, IVI = Importance Value Index).

	Mean Height	Mean	Frequency	Density	Cover per quadrat	
Name of plants	(Cm)	(Cm)	(%)	quadrat	(Cm ²)	IVI
FORBS						
Calopogonium mucunoides Desv.	19.5	0.3	40	1.5	432	19.8
Commelina benghalensis L.	36.0	0.4	8	0.2	40	2.9
C. diffusa Burm f.	5.0	0.4	4	0.6	68	3.3
Eupatorium odoratum L.	78.5	0.7	36	1.5	440	19.2
Euphorbia heterophylla L.	48.6	0.5	20	1.1	192	10.2
E. hirta L.	34.0	0.2	8	0.7	40	3.8
E. hyssopifolia L.	43.1	0.3	12	0.2	28	3.3
Phyllanthus amarus Schum, &						
Thonn.	38.5	0.3	8	0.2	12	2.4
Sida acuta Burm. f.	39.0	0.4	8	0.3	164	5.5
Spigelia anthelmia L.	37.2	0.5	20	1.8	148	10.7
Tridax procumbens L.	44.3	0.3	32	3.4	368	20.6
Waltheria indica L.	64.0	0.8	12	0.6	244	8.5
GRASSES						
Andropogon fastigiatus Sur.	14.7	0.3	12	2.8	152	11.1
Cynodon dactylon (L.) Pers.	34.6	0.3	12	3.1	72	10.1
Dactyloctenium aegyptium (L.)						
Willd.	43.6	0.3	12	1.1	72	6.0
Digitaria ciliaris (Retz.) Koel.	45.0	0.3	8	0.8	28	3.8
Eleusine indica Gaertn.	56.5	0.4	8	1.8	112	7.3
Imperata cylindrica P. Beauv.	59.7	0.4	56	0.8	588	42.5
Panicum maximum Jacq.	104.0	1.0	40	1.9	596	23.9
Paspalum orbiculare Forst.	60.8	0.1	28	4.6	332	21.4
Setaria barbata Kunth	53.6	0.4	36	3.3	296	26.2
S. longiseta P. Beauv.	58.5	0.3	8	1.4	80	5.9
Sporobolus pyramidalis			Ū			•••
P. Beauv.	57.1	0.4	32	5.2	396	21.8

Table 4. Percent frequency distribution of species belonging to three communities.

Table 5. Diversity index of the communities on burnt and unburnt areas.

		Unburr	Unburnt Areas		
		Dry season	Wet season	Dry season	
A	0-20	92.7	96.9	72.4	
B	21-40	7.2	3.1	24.1	
С	41-60	0.0	0.0	3.4	
D	61-80	0.0	0.0	0.0	
E	81-100	0.0	0.0	0.0	

IA = $\frac{C}{a+b+c} \times 100$ where,

- С = number of quadrats in which two species under comparison occur together,
- = number of quadrats in which one of the two species а occurs alone.
- b = number of quadrats in which the other species is found alone.

The IA values were calculated between the species having the highest IVI and all other species having IVI of 10 and above (Table 6). The highest IA was for I. cylindrica and C. mucunoides on burnt sites, and A. compressus and C. diffusa during both seasons on unburnt sites.

Dominance-Diversity Relations of Plant Communities.

The dominance-diversity relationships of land plant communities have been extensively studied by Whittaker (1965, 1970). The ranking of component plant species according to their importance values reflects the contribution by species towards their ability to utilize a fraction of the community's resources. From such information, one can appreciate the structural and functional role of the species in a community. One of the simplest measurements based on quantitative relationships of species is Simpson's Index, where

Community	Number of species	Number of individuals	Diversity index (%)
Unburnt areas			
Dry season	69	1868	14
Wet season	65	2592	12
Burnt areas			
Dry season	29	1349	7

the dominance concentration of the layers of a community (C) is derived from the sum of squares of importance values (y) divided by the total importance value (N) of the community. Accordingly, for unburnt areas the value was 11.8 and 11.4 for dry season and wet season communities respectively, while 19.8 for the community on burnt areas. Whittaker (1965) has shown that on arranging the species in a sequence from most to least important, they form a continuous progression from dominants through intermediates to rare species. However, most communities have a small group of dominants, a larger number of moderately important species, and a small number of rare species. In this study the dominance concentration is higher in the burnt area community. Shimwell (1971) is of the opinion that a community is a functional system of interacting species, each with their own structural and ecological niches and that the importance value progressions mirror the general structure of the vegetation in space and time.

Height and Diameter Measurements

The height of a plant is the perpendicular distance from the soil at its base to the height point reached with all its parts in their natural position (Heady 1957). Individuals of a plant species differ in height and diameter. Hence average measurements have been shown in Tables 1, 2, and 3. The principal value of such measurements expresses qualities such as vigour, stage of growth, competi-

Table 6. Percent Indices of Species Association (IA) based on the highest dominant species and the others having IVI of 10 and above.

IA of Axonopus compressus with others (refer Table 1)			
Commelina diffusa	33.33		
Centrosema pubescens	15.78		
Eupatorium odoratum	0.0		
Paspalum conjugatum	0.0		
Sida acuta	18.75		
Tridax procumbens	11.11		
IA of Axonopus compressus with others	(refer Table 2)		
Commelina diffusa	27.78		
Centrosema pubescens	4.35		
Eupatorium odoratum	11.76		
Sida acuta	5.88		
Tridax procumbens	5.55		

IA of Imperata cylindrica with others (refer Table 3)

Andropogon fastigiatus	6.25
Calopogonium mucunoides	33.33
Cynodon dactylon	6.25
Eupatorium odoratum	21.05
Euphorbia heterophylla	13.33
Panicum maximum	15.00
Paspalum orbiculare	16.67
Setaria barbata	21.05
Spigelia anthelmia	11.76
Sporobolus pyramidalis	22.22
Tridax procumbens	22.22

tion of range readiness, etc. Kuchler (1967) gave eight classes for height, namely, 1 = less than 0.1m; 2 = 0.1 - 0.5m; 3 = 0.5 - 2m; 4 = 2-5m etc. Accordingly, the different communities show certain pattern of height classes (Table 7). It is seen that the height class 2 is

Table 7. Height classes of plants in different communities.

		Height classes		
Community	l (≪0.1 m)	2 (0.1–0.5 m)	3 (0.5–2 m)	
Unburnt areas	4/5 0) 1		20(29.0)	
Dry season Wet season	4(5.8)* 0(0)	45(65.2) 48(73.8)	20(28.9)	
Burnt areas	2(6.9)	17(58.6)	10(34.5)	

*Actual number of individuals with percentage figure in parentheses.

predominant. The plants taller than 1 m were *Panicum maximum* and *Sida acuta* while comparatively maximum diameter was observed in *Amaranthus viridis* during dry season, and *P. maximum* during wet seson as well as on burnt areas.

According to Curtis and Partch (1950), flower production increased sixfold with about 60% accompanying increase in height in some grasses. The figures for height in this study with respect to the pioneer plants do indicate a rapid growth.

Effect of Fire.

One of the important factors is the annual vegetation burning during dry season in the sub-humid tropics and tropical savannas. According to Rogers (1979), it is an effective tool for clearing and keeping land free of encroaching woody growth, encouraging new grass flush as potential grazing material, and to remove coarse dry grass cover. In West Africa and many other parts of the world, extensive savannas are maintained as an anthropogenic fire climax (Collinson 1977). The pioneer plants recorded, a month following the fire, were species of *Calopogonium, Commelina, Eupatorium, Euphorbia, Panicum, Paspalum, Sporobolus*, etc. *Imperata cylindrica* was the dominant species. Ranjitsinh (1979) reports this grass to dominate as a result of successions of annual fires while McIlroy (1964) observed that growth of *Pennisetum purpureum*, *Panicum maximum* and *Paspalum* sp. is promoted by fire. This investigation also recorded these species coming up, particularly after burning. Martin (1966) reported higher values of frequency and density for species of *Sporobolus* and *Panicum* at burnt sites and this is also true for this study. In general, there was a preponderence of grasses at the burnt sites as is obvious from Table 3. The percentage of grasses in dry and wet season communities on unburnt areas and the community on burnt areas was 14.5, 26.1, and 41.4 respectively. The cause of the flush is still unclear but has been attributed to temperature stimulation at the effect of massive fertilization following ash deposits and dew fall becoming available to the plants.

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Modeling Evapotranspiration from Sagebrush-Grass Rangeland

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Abstract

Three models, CREAMS, SPAW, and ERHYM, were used to predict evapotranspiration (ET) from a sagebrush-grass range site in southwest Idaho. Model-predicted ET was compared with ET measured by a lysimeter and ET calculated with a water-balance equation using field-measured soil water and precipitation values. There was generally good agreement between the lysimeter and water-balance calculated ET and between these ET values and model-predicted ET. Maximum averaged daily ET rates were about 2.5 mm for April, May, and June with single day ET values from the lysimeter as high as 5.0 mm. Although the CREAMS predicted ET rates were generally higher than those predicted by SPAW and ERHYM or measured by the water-balanced method, all 3 models were functionally capable of simulating ET from sagebrush-grass range sites. ERHYM was the simplest of the 3 models to operate.

The sagebrush-grass ecosystem includes about 52.6 million ha in the western United States (U.S. Forest Service 1980). Although its productivity per unit area is low, the sagebrush ecosystem is a major resource in terms of livestock production, wildlife habitat, and as a watershed for onsite and downstream water resources. This ecosystem supplies an estimated 25 million animal unit months (AUM) of grazing for domestic livestock with a potential for 78 million AUMs with improved management and range condition (USDA-SEA-AR 1980).

Evapotranspiration (ET) is a major component of the soil water balance equation for semiarid rangelands. Branson et al. (1976) estimated that as much as 96% of the incoming precipitation was returned to the atmosphere as ET from such rangelands. Most estimates of ET from sagebrush-grass rangelands have been determined from field measurements of precipitation, soil water content, and runoff (Rawls et al. 1973, Sturgis 1979).

During the past decade, several water-balance, climate models have been developed that can be used to predict evapotranspiration from rangelands. Most of these models have been evaluated for the shortgrass and mixedgrass prairies (Innis 1978, Aase et al. 1973, Wight and Hanks 1981, de Jong and MacDonald 1975, Hanson 1976). Research on modeling ET from sagebrush-grasslands has been limited. Wight and Neff (1983) evaluated a water-balance, climate model in a sagebrush-grass community in southeastern Montana. Sonntag et al. (1982) developed an ecosystem model which included an ET component for a sagebrush-grass community in Nevada.

Accurate estimates of ET are essential in the development of effective hydrologic and plant growth models. This paper evaluates

Manuscript accepted 14 May 1985.

Study Area

The study site was located in southwestern Idaho on the Reynolds Creek Experimental Watershed (Robins et al. 1965) on a nearly flat ridge top, at an elevation of 1,649 m. The soil is a Searla gravely loam of the loamy, skeletal, mixed, frigid family of the Calcic Argixerolls subgroup. Soil in the area averages about 100 cm in depth over a basalt bedrock. Annual precipitation averaged 34.9 cm for the 1962-1982 period.

The site is dominated by low sagebrush (Artemisia arbuscula) with sandberg bluegrass (Poa sandbergii) and bottlebrush squirreltail (Sitanion hystrix) comprising the major grass species. Basal cover for the past 11 years averaged 24, 26, 28, and 22% for live plants, litter, rock, and bare ground, respectively. Foliar cover averaged 45%.

Methods

Lysimetry

The study lysimeter was installed in 1968. It enclosed an undisturbed cylindrical soil core 152 cm in diameter and 122 cm deep. Changes in weight were measured by electrical transducers and were recorded with a digital recorder.

Soil Water Measurements

Soil water was monitored biweekly throughout most of the growing season by the neutron scatter method. Water content was measured in the 0 to 23, 23 to 46, 46 to 76, and 76 to 106-cm soil layers, respectively, in the lysimeter and an adjacent area. ET from the adjacent area was calculated as the sum of the change in soil water content and precipitation that occurred during soil measurement intervals. This method assumes no runoff. Observations of the area indicated that runoff is generally negligible. The soil water values at the beginning of the growing season were used to initialize model simulations each year.

Model-predicted ET

Three models were used to predict ET for the period 1976-1981: (1) SPAW (Soil-Plant-Air-Water) (Saxton et al. 1974); (2) CREAMS Chemicals, Runoff and Erosion from Agricultural Management Systems) (Knisel 1980); and (3) ERHYM (Ekalaka Rangeland Hydrology and Yield Model) (Wight and Neff 1983). The models were parameterized with soil and soil water data from the area adjacent to the lysimeter. Comparative model performance over the 6-year period was similar and only the results from 1977, 1978, and 1979, low, above average, and average production years, respectively, are discussed in detail. The SPAW and CREAMS ET

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components were developed for cropland applications. The ERHYM ET component was originally developed for cropland application, but it has been modified for use on rangelands. The models were applied with essentially no "fitting" or calibration.

Each model uses a different procedure for calculating potential evapotranspiration (ET_p) , potential transpiration (T_p) , and potential soil evaporation (E_p) (Table 1). Actual transpiration (T) in each

Table 1. Methods of calculating potential evapotranspiration (ET_p), potential transpiration (T_p), and potential soil evaporation (E_p).

Model	EΤ _p	Tp	E _p *
SPAW	(E _{pan}) (PC)	(ET _p)(CF)(PF)	(ET_p) $(ET_p)(e^{-0.4LAI})$ ET_p-T_p
CREAMS	Ritchie†	(ET _p)(LAI/3)‡	
ERHYM	(ET _{J-H})(K _c)	(ET _p)(TRC)(RGC)	

PC = Pan coefficient

CF = Cover factor

PF = Phenology factor

LAI = Leaf area index

TRC = Transpiration coefficient = 0.0213 + 0.0162 (average site yield, $lb/acre)^{1/2}$ RGC = A relative growth curve that varies between 0.0 and 1.0

ETJ-H = Jensen-Haise calculated ETp

* E_p is never allowed to exceed ET_p - T_p

†From Ritchie (1972). ‡For LAI values >3.0, T_p = ET

 $\$For LAI values < 1.70, E_p = 0.5 ET_p$

model is controlled by available soil water as indicated in Figures 1a, 1b, and 1c. Water movement and root distribution vary among models. All models operated on a daily time scale.

SPAW

SPAW is a fairly comprehensive crop model that utilizes pan evaporation and a pan coefficient (PC) to calculate ET_p . Water added to the soil moves through the profile along hydraulic gradiants. Water in excess of field capacity is drained through the soil as percolate. T_p is controlled by a plant cover factor (CF), a phenology factor (PF), and available by soil water (Fig. 1a). Soil evaporation is represented by an inclusion of a separate thin (1.3 cm) upper boundary layer (evaporation layer of soil in the soil profile). Water is evaporated from this layer and is limited only by ET_p and water content. Water content of this layer varies between air dry and field capacity and water is replenished by upward movement from the second soil layer driven by a Darcian type equation. The SPAWET model is the most process oriented of the 3 models evaluated.

CREAMS

The hydrologic component of CREAMS utilizes an ET routine developed by Ritchie (1972). ET_p is calculated from solar radiation, average air temperature, albedo, a psychometric constant, and a leaf area index. T equals T_p until 75% of the available water is removed (Fig. 1b). Transpiration demand is distributed down through the profile based on a root distribution that is described by an exponential function. Soil evaporation is calculated by the two-stage drying process and is limited to the top 15-cm layer of soil profile.

ERHYM

This model calculates ET_p as the product of the Jensen-Haise calculated ET_p (alfalfa as the reference crop) and a crop coefficient (K_c) (Jensen and Haise 1963). In addition to water content (Fig. 1c), transpiration from specific soil layers is controlled by the product of a transpiration coefficient, soil temperature, and a root density factor. The transpiration coefficient represents the portion of ET which can be T at peak standing crop. Soil temperatures are obtained from a soil temperature simulation routine. The root density factor is a recent modification of the original model which controls rate of water uptake based on the density of roots in each soil layer. Soil evaporation is limited to the top 30 cm of the soil profile and utilizes a one-stage drying process.



Fig. 1a. The relationship between $T/T_{\rm P}$ and available soil water as used in SPAW where curves A, B, C, and D represent different levels of atmospheric demand (potential ET). (From Saxton and McGuiness 1982.)



Fig. 1b. The relationship between T/T_p and soil water as used in CREAMS.



Fig. 1c. The relationship between T/T_p and available soil water as used in ERHYM.

Results and Discussion

A typical set of growing season ET_p curves as calculated by the 3 models is presented in Figure 2. The CREAMS and SPAW ET_p are



Fig. 2. Cumulative potential evapotranspiration as calculated by SPAW, CREAMS, and ERHYM. Reynolds Creek, 1977.

	April	May	June	July	August	September	BSW†
	(mm/day)						
1977							
Lysimeter	nd*	1.98	2.67	1.59	0.96	1.14	18
Water balance	0.34	1.42	1.63	1.28	0.32	0.92	2
SPAW	0.62	1.65	1.67	0.48	0.35	0.56	2
CREAMS	1. 46	2.80	2.01	0.39	0.81	0.22	2
ERHYM	0.46	1.32	2.24	0.70	0.27	0.28	2
Precipitation (mm/month)	2	63	47	10	15	14	
1978							
Lysimeter	2.40	1.77	2.53	1.15	0.88	1 11	110
Water balance	2.57	1.63	2.15	1 14	0.00	0.67	86
SPAW	2.32	3 14	1.58	0.91	0.41	0.07	86
CREAMS	2 82	3.01	1.62	0.67	0.41	0.75	00
ERHYM	1.01	1.83	2.57	1.13	0.62	0.58	86
Precipitation	84	18	17	12	12	22	
1979							
Lysimeter	1.35	2.45	2.41	0.69	1 25	0.55	120
Water balance	0.97	1.39	1 37	0.82	1.04	0.55	54
SPAW	2 16	1.65	0.52	0.16	0.76	0.12	54
CREAMS	2.00	2 43	0.92	0.10	1.00	0.15	54
ERHYM	0.89	1.83	1.45	0.32	1.09	0.57	54
Precipitation	20	28	11	5	49	2	21

Table 2. Model-predicted and field-measured evapotranspiration, beginning soil water content, and monthly precipitation for 3 growing seasons at the Reynolds Creek study site.

*nd = no data available.

[†]Amount of available plant soil water in the root zone at the beginning of the growing season (approximately April 1).

considerably higher than the ERHYM ET_p . The Jensen-Haise based ET_p in ERHYM is calculated by an empirical equation which was developed using alfalfa as a reference crop. For this study, a crop coefficient (K_c) of 0.85 was used to convert the Jensen-Haise ET_p to a rangeland ET_p . This K_c value was determined using lysimeter data from a mixed prairie grassland in eastern Montana (Wight and Hanks 1981).

Alfalfa requires relatively warm weather before it begins growth in the spring, thus the ET_p based on the Jensen-Haise method is limited by cool weather and this is reflected by the low values calculated for the early spring. Similar limitations would occur during the fall and winter periods.

In addition to solar radiation and temperature, CREAMS uses an albedo input in calculating potential evaporation. An average albedo of 0.15 for the study site area was reported by Belt (unpublished data 1972). Dirmhirn and Belt (1971) reported an albedo of 0.13 for a similar site in southeastern Idaho. These albedo values represented midday measurements and are somewhat lower than would be expected for daily averages. The low albedo helps account for the high ET_p values calculated by CREAMS.

Average daily ET rates for each month as measured by the lysimeter and water-balance methods and the model-predicted ET values are presented in Table 2. The good agreement between lysimeter and water-balanced measured ET values supports the reliability of the water-balance ET data. The major differences between the 2 methods were due to differences in soil water contents at the beginning of the growing season. These differences were probably due to seepage of rain water along the inside walls of the lysimeter and/or the restriction to drainage through the lysimeter. Maximum averaged daily ET rates were about 2.5 mm/day for April, May, and June. The availability of soil water significantly limited ET during the remainder of the growing season. ET values from the lysimeter on days following significant precipitation reached maximum values of 4.5 to 5.00 mm in the summer months.

For most of the growing season, the SPAW, ERHYM, and lysimeter cumulative ET curves were parallel, indicating good

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agreement on daily ET rates (Fig. 3). The CREAMS ET values were a little higher than the values determined by the other methods, but the seasonal dynamics were very similar. The high ET rates measured by the lysimeter at the beginning of the growing season (Julian days 124 to 128) indicate a weakness of the models in



Fig. 3. Model-predicted and lysimeter-measured evapotranspiration. Reynolds Creek, 1977.

accounting for ET under some weather conditions. Wet cool weather prevailed during the period Julian day 121 to 131 with numerous precipitation events totaling about 5 cm and mean daily temperatures averaging about 6° C. During this period both the lysimeter and the evaporation pan measured about 3 cm of ET and evaporation, respectively. The model-predicted values were significantly lower than the lysimeter-measured values. Apparently, the models underpredicted the evaporation from an essentially free water surface that occurred during this period. Also, the model ET_p may have been unrealistically low, possibly due to very low temperatures.

Comparisons of model-predicted and water-balance-calculated ET for the area adjacent to the lysimeter are presented in Figures 4a, 4b, and 4c. For the average and below-average production years, CREAMS predicted higher ET than did ERHYM or SPAW,



Fig. 4a. Seasonal evapotranspiration as determined by the models and water-balance method. Reynolds Creek, 1977.



Fig. 4b. Seasonal evapotranspiration as determined by the models and water-balance method. Reynolds Creek, 1979.



Fig. 4c. Seasonal evapotranspiration as determined by the models and water-balance method. Reynolds Creek, 1978.

which were in general agreement with the field-measured values. For the above-average production year (1978), both CREAMSand SPAW-predicted ET were in good agreement with the fieldmeasured ET, while ERHYM-predicted ET was slightly lower than the field-measured ET. Differences in ET rates were most pronounced early in the growing season when soil water was most plentiful.

The CREAMS ET routine allows up to 75% of the available water to be removed before water content limits T (Fig. 1b). This is reflected by a higher percentage of ET attributed to T by the CREAMS model than by the other 2 models (Table 3). By allowing only 30% of the available soil water to be removed before water content limits T as suggested by de Jong and MacDonald (1975) for native grass, ET was reduced 10% during the first 60 days of the growing season, making it more in line with the other models and field-measured values. Such modifications are simple to make and should be considered before applying CREAMS type ET routines to rangeland sites.

The models partitioned ET into E and T somewhat differently (Table 3). The SPAW model predicted little or no T in August and September, while CREAMS predicted relatively high T rates during those 2 months. These extreme values probably reflect some of the difficulties in the direct application of cropland ET models to rangeland plant communities. Quantification of crop-developed parameters such as leaf area index and phenological, or plant cover curves for rangeland conditions would realistically take a little calibration and tuning.

Model-predicted ET was regressed on the water balancecalculated ET for the periods that coincided with the soil water measurements (approximately 2-week intervals) and the coefficients of determination (r^2 values) were calculated (Table 4). The slopes and y-intercepts of the regression lines indicate that SPAW and ERHYM simulated ET a little better than did CREAMS. However, with some adjustments of the ET controlling parameters, all models may have been equal in performance.

As would be expected, the model-predicted and field-measured ET rates all approached zero at the end of the season, indicating that all available water had been evapotranspired. For semiarid rangeland, this is normally the case and is an advantage in longterm simulations in that the models are "zeroed out" each year, preventing cumulative errors in soil water accounting.

Conclusions

All 3 models appeared to be functionally capable of simulating ET from sagebrush-grass rangelands. Major differences in the models' performance were generally at the beginning of the growing season and during the below-average and average production years. Performance of the 3 models probably could have been improved by tuning or calibration through the adjustment of soil and vegetation parameters. All vegetation parameters were based on average conditions and were not sensitive to the annual variations of a native plant community. Of the 3 models tested, SPAW and ERHYM were best able to simulate ET from the study site. Compared to SPAW and CREAMS, ERHYM is simpler to operate and the required input data were more readily available.

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Table 3. Percent of model-predicted evapotranspiration attributed to transpiration at Reynolds Creek.

	April	May	June	July	August	September	Seasonal
1977							
SPAW	72	36	47	29	0	0	37
CREAMS	54	60	43	23	31	38	50
ERHYM	29	45	34	9	9	0	32
1978							
SPAW	34	67	73	51	3	0	51
CREAMS	36	68	73	45	29	38	53
ERHYM	14	66	59	57	36	16	51
1979							
SPAW	50	67	27	0	0	0	43
CREAMS	37	73	70	48	28	38	52
ERHYM	47	62	44	52	26	3	44
Mean							
SPAW	52	57	49	27	3	0	44
CREAMS	42	67	62	39	29	38	52
ERHYM	30	58	46	39	24	6	42

Table 4. Means, slopes, Y-intercepts, and r² values for the regressions of model-predicted evapotranspiration on water-balance ET measured at bi-weekly intervals* during the growing season.

	Water-Balance			SPAW				CREAMS			ERHYM				
	1977	1978	1979	Mean	1977	1 9 78	1979 Mean	1977	1978	1979	Mean	1977	1978	1979	Mean
Mean (mm)	3.32	7.09	3.92	4.78	3.56	7.50	4.32 5.12	5.64	7.93	5.45	6.34	3.62	5.84	4.13	4.53
Slope			_	_	0.90	0.99	0.73 0.87	1.26	0.99	1.07	1.10	1.03	0.93	1.04	1.00
Y-intercept (mm)		_	_		0.57	0.51	1.47 0.85	1.44	0.90	1.23	1.19	.19	-0.74	0.07	0.33
r ²	—	_			0.96	0.98	0.88 0.94	0.92	0.97	0.94	0.94	0.97	0.98	0.99	0.98

*N for 1977, 1978, and 1979 was 13, 12, and 13, respectively.

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Observations on Herbage Growth, Disappearance, and Accumulation under Livestock Grazing

D.L. SCARNECCHIA AND M.M. KOTHMANN

Abstract

Expressing the effects of grazing animals on herbage requires explicitly defined variables describing herbage growth and herbage disappearance, as well as variables describing net changes in herbage. This paper presents a mathematical framework on variables describing herbage growth, disappearance, and accumulation, which can be used to model herbage dynamics, and to develop and present field research.

Describing herbage dynamics with or without livestock grazing requires measurement of both herbage growth and disappearance. Sequential measurements of standing crop define net changes in standing crop but do not indicate the changes that occurred in growth and disappearance. Often this distinction is essential in understanding and comparing effects of grazing management on herbage dynamics. We often hear that grazing systems (Society for Range Management 1974) such as short-duration grazing will maintain or increase growth rate of herbage, but less is said about effects on herbage disappearance. Similarly, in sampling during grazing studies, we usually emphasize standing crop measurements, while growth and disappearance measurements are often ignored. In general, while growth and disappearance have been frequently described and modeled in plant sciences, there is a need to mathematically formalize basic variables for application in grazing research. Quantification of dry-weight changes per unit area in standing crop, herbage growth, and herbage disappearance requires clearly defined variables developed from principles of systems analysis. Relationships among these variables should be clear and mathematical description of each variable explicit. This paper (1) defines concepts of herbage growth, herbage disappearance, and herbage accumulation; (2) offers a mathematically defined terminology for describing components of standing crop dynamics, and examines its relationship to previous papers on herbage terminology; and (3) discusses the importance of measuring herbage growth and disappearance in evaluating herbage dynamics in field grazing research.

Herbage Growth

Herbage growth has been defined by Hodgson (1979) as the development and increase in size and weight of new leaf and stem tissue. This is a functional definition of herbage growth for pasture research. Assume that during the dormant season all herbage is removed from a pasture by fire or another means, and the growth of herbage during the subsequent growing season is measured. Herbage increases in dry weight per unit area at some herbage growth rate (HGR) (Table 1) which we could measure in kg/haday. HGR is a rate of new growth; it says nothing about disappearance. This variable is equivalent to what Thomas (1980) defined as the gross crop growth rate, but for range and pasture work the term herbage growth rate seems more appropriate. HGR may be differentiated with respect to time to give a rate of change in HGR, which is nonzero any time the herbage growth rate is not constant. Integration of HGR over time gives the total summed

growth of herbage, the cumulative herbage growth (CHG), which has units of kg/ha. Because CHG is an integration over time, there is a period of time (t-t₀) implicit in its calculation, where t and to are the end points of integration. Thus, cumulative herbage growth. herbage growth rate, and rate of change in herbage growth rate are a complete time-dynamic description of herbage growth.

Herbage Disappearance

Aspects of herbage disappearance have been studied in a number of field studies, e.g., Pearson (1975), Abouguendia and Whitman (1979), Ohiagu and Wood (1979), Deshmukh and Baig (1983), Important papers on range and pasture terminology (Society for Range Management 1974, Hodgson 1979, Thomas 1980) have not addressed the subject in detail. To concisely define herbage disappearance, we first must define two other terms. The above-ground herbage mass (Hodgson 1979) or the standing crop (Society for Range Management 1974) are the total mass of herbage per unit area of ground at any time. Standing crop is measured from ground level, and is equivalent to herbage mass if the latter is measured from ground level (Hodgson 1979). We can then define herbage disappearance as the loss of herbage from the standing crop associated with senescence, harvest, grazing, trampling, defecation, decay, weather, or other causes. More will be said later about standing crop, but given a standing crop, the herbage disappearance rate (HDR) can be defined as the rate per unit area of herbage dry-weight loss from the above causes and can be expressed in kg/ha-day (Table 1). By differentiation and integration of HDR with respect to time, the rate of change in HDR and the cumulative herbage disappearance (CHD), respectively, can be derived (Table 1). Thus, cumulative herbage disappearance, herbage disappearance rate, and rate of change in herbage disappearance rate are a complete time-dynamic description of herbage disappearance.

Herbage Accumulation

With 3 variables each describing herbage growth and herbage disappearance, 3 others can be derived describing the net differences between corresponding pairs of variables. Thus, we define net herbage accumulation rate (NHAR) as the difference between herbage growth rate and herbage disappearance rate, i.e., NHAR = HGR – HDR (Table 1). NHAR is equivalent to net crop growth rate as defined by Thomas (1980). Differentiation of NHAR with respect to time gives the rate of change in NHAR, with units of kg/ha-day². Integration of NHAR over time gives the net herbage accumulation (NHA), which has units of kg/ha. Net herbage accumulation expresses the difference between cumulative herbage growth and cumulative herbage disappearance over a period of time (Table 1). Thus, the growth and disappearance columns of Table 1 are basic variables used to derive corresponding variables in the accumulation column. Measurement of any 2 variables in a row (Table 1) allows calculation of the third variable in that row.

Classification of Variables

The variables described in Table 1 are useful for describing herbage dynamics in modeling or field research (the rate of change variables in row 3 are useful mainly in modeling). Forrester (1961) described features of system structure, including 2 of importance here, level and rate. He defined levels as accumulations within a system, and rates as instantaneous flows between levels in a system.

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GROWTH DISAPPEARANCE ACCUMULATION **CUMULATIVE HERBAGE** CUMULATIVE HERBAGE NET HERBAGE LEVEL ACCUMULATION (NHA) CHG - CHD **GROWTH (CHG) DISAPPEARANCE (CHD)** ∫HGR • dt {HDR • dt ∫NHAR • dt Units: kg/ha Units: kg/ha Units: kg/ha HERBAGE GROWTH HERBAGE DISAPPEARANCE NET HERBAGE ACCUMULATION RATE RATE (HGR) RATE (HDR) RATE (NHAR) HGR - HDR Units: kg/ha-day Units: kg/ha-day Units: kg/ha-day **RATE OF CHANGE IN** RATE OF CHANGE IN RATE OF CHANGE IN RATE OF HERBAGE DISAPPEARANCE HERBAGE NHAR (RCNHAR) **GROWTH RATE (RCHGR)** CHANGE RATE (RCHDR) **RCHGR - RCHDR** IN RATE d (HGR) d(HDR) d(NHAR) dt dt đt Units: kg/ha-day² Units: kg/ha-day² Units: kg/ha-day²

Table 1. Summary of basic variables with appropriate units describing herbage growth, disappearance, and net accumulation.

If a system is brought to rest, levels continue to exist but rates do not (Forrester 1961). In modeling herbage dynamics with the variables in Table 1, cumulative herbage growth, cumulative herbage disappearance, and net herbage accumulation would normally be level variables. HGR, HDR, and NHAR are rate variables, and the variables in row 3 are rates of change in rates.

Standing Crop and Herbage Mass

Standing crop (Society for Range Management 1974) or herbage mass (Hodgson 1979) can be expressed in terms of variables in Table 1. Standing crop is the amount of herbage per unit area at any time, and can be expressed as $SC = SC_0 + NHA$, where SC_0 is initial standing crop at time to, SC is the standing crop at time t, and NHA is net herbage accumulation during the period of time t-to. Standing crop is a measure of the state of a sward (Hodgson 1981). It is also normally a level as defined by Forrester (1961), because it exists if an herbage system is brought to rest, and because conceptually it is an accumulation. Unlike cumulative herbage growth, cumulative herbage disappearance, and net herbage accumulation, which are calculated over some implicit or explicit period of time, standing crop is defined at one point in time. A change in standing crop (Δ SC) over some period of time (t-t₀) equals NHA, as can be seen by rearranging the equation above, i.e., $\Delta SC = SC - SC_0 =$ NHA.

Uses in Research

Because growth and disappearance are continuous in most swards, and because they respond differently to variations in management, simple estimates of net changes in herbage may not adequately describe the effects of environment or management (Hodgson 1981). To describe and compare effects of different grazing systems, we need independent measurements of herbage growth and disappearance. This usually involves measurements of life histories of individual plants along with spatial and temporal patterns of defoliation of individual shoots and plant parts (Hodgson 1981). There have been several recent studies (Gammon and Roberts 1978, Briske and Stuth 1982) of defoliation under different types of grazing management. Measurements of herbage defoliation, herbage senescence, and other factors contributing to disappearance should be made as a matter of course in field grazing studies. Where herbage disappearance is difficult to measure directly, indirect calculation of disappearance is possible if accumulation and growth are measured. With accumulation measurements alone, indirect calculation of disappearance is not possible. Without measurement of growth or disappearance, measurement of net herbage accumulation by a series of standing crop measurements says little about the effects of different management practices on growth and disappearance of herbage. In range research, we have frequently been concerned with measuring changes in standing crop and have learned comparatively little about herbage dynamics. The variables in Table 1 provide a framework for mathematically describing and comparing herbage dynamics under different grazing systems. More attention spent measuring variables in columns 1 and 2 will allow better interpretation of standing crop and the variables in column 3. Consideration and execution of these more detailed measurements within a mathematical framework as described here would be an important refinement in our grazing research.

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Combination of Weight Estimates with Clipped Sample Data

VILMA CARANDE AND DONALD A. JAMESON

Abstract

Weight estimation is a common procedure to determine range forage production. In this method clipped samples are used to train an observer, to make periodic checks on observer performances, and to compute estimated/clipped conversion factors. The clipped sample data are then discarded. This is in contrast to a double sampling procedure where both clipped values and estimated values are used in computation of sample variance. However, if both estimated values and clipped plots are taken at random, they can be combined to compute sample means and variances by using techniques appropriate to combining data of different variances. The efficiency of the combined sample appears to be greater than that of formal double sampling and also has the advantage that plots clipped for training and checking can also be used as part of the sample.

Sampling for forage production occupies a very important position in range research studies. The choices of basic approaches are few: (1) clipping, (2) some "indirect" method such as weight estimation, or (3) a combination of (1) or (2).

Clipping is generally considered to be the superior method but has 2 commonly understood drawbacks: (1) it may be very time consuming compared to indirect methods and (2) it is destructive. In addition, clipping itself, although commonly accepted as the least prone to measurement errors, does, in fact, contain such errors (in addition to sampling errors).

For indirect methods this discussion will focus on weight estimation, although the concepts also apply to other "indirect" methods. Weight estimation is often preferred to clipping because it is both less time consuming and nondestructive (Pechanec and Pickford 1937). It is generally understood that the weight estimates are less exact than clipped samples.

In order to capture some of the advantages of both, weight estimation and clipping are sometimes combined in "double sampling." Double sampling was first discussed in the range management literature by Wilm et al. (1944) and more recently by Francis et al. (1979) and Ahmed et al. (1983). Double sampling uses an optimum ratio of estimated to clipped plots, considering both the relative costs and relative variances of the 2 methods.

Whether the method used is double sampling or weight estimation alone, the weight estimates are converted to either dry or wet clipped weight equivalent by computing a linear regression or ratio. For linear regression

$$y = a + bx \tag{1}$$

where y is the clipped weight, x is the estimated weight, a is the value of y when x = 0, and b is the slope of the regression line. For ratio sampling a is equated to 0 and

$$y = Rx \tag{2}$$

where R is the ratio estimator.

Equation (1) always results in a lower variance estimate than Equation (2) (Ahmed et al. 1983), but nonzero values of the constant a may create difficulties. Therefore, linear regression is recommended for species (or other taxa) with few zero estimates, and ratio sampling is recommended when zero estimates are com-

mon enough that assigning the value a to plots estimated as zero would be bothersome (Francis et al. 1979).

Although theoretically sound, the double sampling procedure has some drawbacks. If the optimum ratio of estimated plots to clipped plots is to be calculated, a presample must be collected to compute the needed variances. Generally a standardized ratio rather than an optimum ratio of estimated plots per clipped plot is used for each study; this will, of course, result in some loss in efficiency. The computations require a strict discipline in proportion of plots clipped, and plots clipped for training purposes are not used in the statistical calculations.

Perhaps more commonly used than double sampling is weight estimation where the estimates are controlled by reference to clipped plots. In this method some plots are both clipped and estimated in order to train the observers. After training is judged to be sufficient, the clipped and estimated values are used to compute a linear regression or ratio correction. Although the clipped plots are used for training and for calculating the correction factor, they are not considered part of the actual sample. The sampling variance from the corrected estimates is considered to be appropriate for determining sample size.

Although clipping is usually considered to be the superior method, it is usually the case that for a set of plots that are both clipped and estimated the variance of the estimated plots S_x^2 is less than the variance of the clipped plots S_y^2 . Primarily, this is caused by the fact that most observers estimate a smaller range of values than the corresponding clipped values. In the extreme, an observer could always estimate a constant value, resulting in a zero variance for the corrected values, which is not a superior result. If low variance is equated with a superior method, an anomaly is thereby created: the use of weight estimates may result in a procedure where poor estimates are rewarded by a lower variance.

A major concern is to compute an appropriate variance for the estimated plots, designated here as S_{\bullet}^2 . The variance for estimated plots S_{\bullet}^2 should not be less than S_{Ψ}^2 . An appropriate method for developing S_{\bullet}^2 which meets this requirement is shown in the Appendix.

In the usual weight estimate method the clipped values are discarded once the correction factors are computed. This could represent a considerable loss of information, particularly if a great deal of clipping is needed for adequate training and control. If both the clipped values and the estimated values are random samples, both could be used; but each set of values may have a different variance. If the clipped plots are from a sample with variance S_{e}^{y} and estimated plots are from a sample with variance assigned as S_{e}^{2} , a variance appropriate to the pooled value of a single estimated plot and a single clipped plot can be computed by

$$\frac{1}{S_p^2} = \frac{1}{S_e^2} + \frac{1}{S_y^2}$$
(3)

where S_p^2 is the pooled variance (Maybeck 1979). For more than one datum value, S_e^2 and S_y^2 would be replaced by the appropriate square of the standard error of the mean. A weighting factor g can be calculated from S_e^2 and S_y^2 :

$$g = \frac{S_{e}^{2}}{S_{e}^{2} + S_{v}^{2}}$$
(4.1)

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Manuscript accepted 28 May 1985.

The weighted mean using the two methods is computed by

$$\mathbf{x}' = \mathbf{g}\overline{\mathbf{y}} + (1 - \mathbf{g})\overline{\mathbf{x}} \tag{4.2}$$

where \overline{y} is the mean of clipped plots, \overline{x} the mean of the estimated plots, and x' the combined best estimate (Gelb 1974, Maybeck 1979). To avoid double counting of plots that are both estimated and clipped, \overline{x} should include only those plots which do not have clipped values.

Numerical Example

Data for this example were collected in the oakbrush type of southwestern Colorado. One hundred eighteen plots were both clipped and estimated, and an additional 600 plots were estimated only. A ratio correction (i.e., y = Rx) was used.

For this example:

variance of clipped plots;
$$S_y^2 = 1311$$
 (5.1)

variance of estimated plots;
$$S_x^2 = 1221$$
 (5.2)

variance of estimated plots independent of clipped plots; $S_{x,y}^2 = 219(5.3)$

$$S_{\phi}^{2} = S_{y}^{2} + S_{x,y}^{2} = 1530$$
 (5.4)

Based on the equations of Francis et al. (1979) and Cochran (1977), the optimum ratio of estimated to clipped plots was 6.8. Taken to the nearest integer, the optimum ratio would have been 7:1. The appropriate variance from Francis et al. (1979) is 389. (The equations for double sampling calculations are not shown here because they are not part of the method being described; double sampling results are only included for comparison.)

For comparison purposes the same ratio of clipped to estimated plots will be used in the combined method (in practice a constant ratio does not have to be maintained. For plots estimated but not clipped, the variance S_e^2 is 1530 (Equation 5.4). For 6 such plots the appropriate square of the standard error of the mean is 1530/6 = 255. From Equation (4.1) the weighting factor g to combine the 6 estimated (but not clipped) plots with 1 clipped plot is

$$g = \frac{255}{255 + 1311} = 0.163$$
 (6)

The pooled variance of clipped and estimated plots from Equation (3) is

$$\frac{1}{S_p^2} = \frac{1}{255} + \frac{1}{1311} = .004684 \quad (7.1)$$

$$S_p^2 = 213$$
 (7.2)

If all 7 plots had been clipped, the appropriate square of the standard error of the mean would have been 1311/7 = 187. Assuming that the cost of clipping a plot was 10 units of time and the cost of estimating a plot was 1 unit of time, the following error terms and costs can be compared:

	Error	
Type of Sampling	Term	Cost
7 estimated plots using S_x^2/n	175	7
7 clipped plots using S_y^2/n	187	70
1 clipped plot and 6 estimated plots		
combined	213	17
(the clipped plot is also estimted)		
double sampling, 7:1 ratio	389	17

Conclusion

Both the estimated values and clipped control plots of the weight estimation procedure can be used to compute sample means and variances using techniques appropriate to combining data of different variances. In the numerical example analyzed here, the combination of the clipped and estimated plots resulted in an error term which is only slightly higher than that of clipping alone and considerably less than the error term from double sampling. Since the variance of the estimated plots is assumed to be $(S_y^2 + S_{x,y}^2)$, the error term is more conservative than would have been the case had only clipping been used. Thus, the combination of clipped and estimated plots results in a procedure that has a relatively low cost and a conservative estimate of variance.

Appendix

Proportioning S_x^2 for the linear regression method is shown by:

$$S_{x,y}^2 = (1-r^2)S_x^2$$
 (A1)

where $S_{x,y}^2$ is the variance of x independent of y and r is the correlation coefficient between clipped and estimated plots. For the ratio method the equations of Francis ct al. (1979) and Cochran (1977) are modified to find the variance of x independent of y:

$$S_{x,y}^2 = S_x^2 - 2RS_{yx} + R^2 S_y^2$$
 (A2)

where R is the ratio estimator for x = Ry and S_{xy}^2 is the covariance between x and y.

We propose that an appropriate calculation of variance for estimated plots is a combined variance term S_{\bullet}^2 , where S_{\bullet}^2 is defined by

$$S_{e}^{2} = S_{y}^{2} + S_{x,y}^{2}$$
 (A3)

Equation (A3) will have the following results for a "perfect" estimate:

$$S_{x,y}^2 \to 0 \text{ and } S_e^2 \to S_y^2$$
 (A4)

for constant clipped plot weights:

$$S_y^2 \to 0, \ S_{x,y}^2 \to S_x^2 \text{ and } S_e^2 \to S_x^2$$
 (A5)

and for a completely "useless" estimate:

$$S_{\mathbf{x},\mathbf{y}}^2 \rightarrow S_{\mathbf{x}}^2 \text{ and } \rightarrow S_{\mathbf{x}}^2 + S_{\mathbf{y}}^2$$
 (A6)

Equation (A4) indicates that as the agreement between clipped and estimated values improves, S_e^2 will more closely approach S_y^2 . Equation (A5) indicates that as the clipped plots more closely approach a constant, the variance of the estimated values around the constant clipped weight will remain and $S_{x,y}^2$ will approach S_x^2 . Equation (A6) would provide a large penalty for a completely "useless" estimate, but this condition would seldom be expected. Under any conditions S_e^2 calculated by Equation (A3) provides no reward for having poor estimates and is more conservative than using either S_x^2 or S_y^2 .

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Technical Notes:

Estimating Ratios of Live and Dead Plant Material in Clipped Plots

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Abstract

Hand separation of live and dead material from clipped plots is tedious and relatively expensive. Live and dead plant materials are easily distinguished under a microscope and can be quickly quantified. After clipping and drying, a sample can be separated in about 10 minutes.

Estimating the proportions of live and dead materials from vegetation plots is necessary for accurate determinations of forage production and is usually accomplished by hand separation. However, hand separation is expensive, especially when a large number of samples need to be separated. If an accurate method for estimating the live/dead ratio were available, large numbers of samples could be handled with greater efficiency. The purpose of this paper is to report a technique for subsampling and estimating live/dead ratios in vegetative samples.

Materials and Methods

Live and dead grass (Sorghum halepense) was collected and placed in a forced air drying oven until constant weights were obtained. Dry plant materials were ground with a Wiley mill to pass through 1.0-mm mesh sieve. Mixtures of the dried materials were made in a variety of proportions and were analyzed by the microscopic method described by Sparks and Malechek (1968). Only the occurrence of a live or dead fragment in a microscope field was recorded; the number of fragments per field was ignored. Two microscope slides were made for each mixture and 20 fields were analyzed for each slide. The process was repeated 3 times so that variation could be evaluated. All slides were examined at $10 \times$ magnification.

When the microscope method is used for determining relative botanical compositions, plant materials are usually cleared to remove plant pigments (Cavender and Hansen 1970). After clearing, live and dead plant fragments are similarly colorless. During the present study, plant fragments were not cleared of pigments but were easily distinguished as green and brown fragments, respectively. In addition, slides were analyzed immediately following preparation. Because wet mounts were made, slides were rinsed clean after analysis and used again. Data expressed herein are means \pm standard errors.

Results and Discussion

Mixtures containing 20 to 65% live plant material were analyzed. Known and estimated percentages were highly correlated (r = 0.98) and on the average estimates were only 3.5 ± 0.7 percentage points different from the known values (Fig. 1). The slope of a straight line describing the data was not significantly different from 1.0 so that for practical purposes there was a 1:1 relationship between known (Y) and estimated (X) values. Variation in the data for each mixture was small and occurred above and below known values, indicating a lack of technique bias for the experiment.



Fig. 1. Comparison of known and estimated proportions of live plant material in ground mixtures of live and dead Johnson grass (Sorghum halepense).

Estimation of live versus dead plant material by the method described here is reasonably accurate.

About 6 minutes were required to analyze the 40 microscope fields used to quantify the samples. If 4 minutes are allowed for grinding vegetation samples, then it is reasonable to assume that about 10 minutes are required for complete analysis. If another 10 minutes per hour are allowed for technician activities between samples, then it is reasonable to expect that 5 samples could be analyzed each hour.

The technique described here is an accurate and economical alternative to hand separation of live and dead vegetation. Since the difference between live and dead material is easy to distinguish, little training is necessary before technicians become competent to perform the analysis.

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This research was supported in part by the U.S. Forest Service under agreement number 19-276. Tammy Wray and Kathy Johnson provided technical assistance in the laboratory.

Manuscript accepted 4 June 1985.

Relationships of the Error Associated with Ocular Estimation and Actual Total Cover

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Abstract

The relationship between the error associated with the ocular estimation of cover and the magnitude of actual cover was examined by estimation of artificially constructed images of known cover under laboratory conditions. Estimation error varied with actual cover in a manner suggesting that cover classes should be relatively narrow at the extremes of actual cover.

Ocular estimation of plant cover is a fundamental and widely employed method for the evaluation of plant dominance, succession and treatment response in vegetation studies. Relationships between error incurred with such estimates and the magnitude of percent cover are, however, lacking in the literature. While this function may be largely circumvented by the use of estimation classes (Daubenmire 1959, Braun-Blanquet 1965, Domin and Krajina (in Mueller-Dombois and Ellenberg 1974)), the width and distribution of these classes has been intuitive. The purpose of this investigation was to better define the relationship between actual percent cover and the error associated with ocular estimation.

The ocular estimation of plant cover is complicated by the great variety of life forms, surface contrasts, and canopy relationships. It is unrealistic to examine estimation of error over an infinite combination of these variables. In addition, the parametric values for cover in natural populations is seldom known and is often unstable. Rather, this study focused upon the basic relationship between error and cover, controlling for the aforementioned factors through the use of an artificial population of two-dimensional images of known coverage. The implicit compromises that this approach entails are the restrictions of no overlap and nonrandomness at the edge of field (Schultz et al. 1961). By taking this approach, however, we may interpret our findings in terms of a "best case" situation, upon which future investigations dealing with more complex situations may build.

Materials and Methods

The artificial population used in this study consisted of 20 twodimensional images of known coverage. The images consisted of irregular, entire, light-green colored paper figures mounted with varying degrees of aggregation on white posterboard, arranged to avoid any overlap among the figures or with a round 0.25-meters square quadrat boundary. The choice of quadrat size and shape, as well as image color, was largely arbitrary and these factors were held constant. Paper figures for any one image were cut out of a single sheet of paper of known area in a complex, jigsaw fashion. The coverage of these images ranged from 0.36 to 97.30%; actual cover percentages of the artificial images were designed to cover this range at roughly equivalent intervals. At 4 actual coverage levels, 2 replicates were constructed with the same percent cover but with unique configurations and degrees of aggregation.

Twenty-four graduate students and faculty of the Utah State University College of Natural Resources estimated total percent cover for the 20 quadrats under laboratory conditions. All participants were instructed to make their estimates at the highest degree of precision possible, based on actual total cover; that is, only the

The authors wish to thank the faculty and graduate students of the Utah State College of Natural Resources for their cooperation and participation in this study. This research was supported by a Grant DEB81-01827 from the National Science Foundation to J.A. MacMahon.

Manuscript accepted 2 October 1985.

area covered by the figures themselves, as opposed to the polygon method of Daubenmire (1959).

The standard error of estimate and coefficient of variation were calculated for the mean of observer estimates for each quadrat. Least squares second order polynomial regressions were derived to estimate the strength of the relationship between error and the magnitude of actual cover.

Results and Discussion

Table 1 shows the actual cover values along with the corresponding means of 24 observer estimates and the standard errors of those mean estimates. The least squares linear regression line for actual cover (X) versus mean estimated cover (Y) is:

$$Y = -0.33 + 1.00(X)$$

The coefficient of determination (r^2) for this equation is 0.99 (p<0.001) and the y-intercept is not significant (p>0.1).

Table 1. Actual cover, mean estimated cover, and the standard error of mean estimated cover for twenty two-dimensional, artificial paper images.

Actual cover (%)	Mean estimated cover (%)	Standard error of mean estimates (%)
0.36	0.83	0.11
1.45	2.30	0.26
2.32	3.02	0.39
5.79	6.10	0.61
11.58	11.63	0.75
11.58	10.83	0.78
23.17	24.12	1.18
30.12	29.13	0.60
34.75	33.42	1.36
34.75	33.42	1.81
40.55	38.79	1.15
46.34	44.63	1.56
52.13	51.75	1.54
52.13	51.21	1.02
57.92	58.29	1.39
57.92	55.08	1.82
63.72	63.83	1.51
81.09	81.63	1.48
86.89	89.92	0.98
97.31	97.54	0.27

Figure 1 shows the relationship between the coefficient of variation and actual cover. The least squares polynomial function produced an r^2 of 0.85 (p < 0.001). Error expressed as a function of the mean declined rapidly to about 40% actual cover, and more slowly thereafter. Note that the curve does not extend to the limits of actual cover.

Figure 2 shows the relationship between the standard error of estimate and actual cover. The least squares polynomial function produced an r^2 of 0.75 (p < 0.001). The magnitude of the standard error peaked at approximately 55% actual cover, and declined in a roughly symmetric fashion with increasing or decreasing actual cover. Again note that the curve does not extend to the limits of actual cover.

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Fig. 1. The relationship between the coefficient of variation for mean estimated cover and actual cover of a two-dimensional population of artificial paper images.

The standard deviation expressed as a percentage of the mean, or coefficient of variation, increases rapidly below 40% cover, reflecting the limits of precision of the observers. For example, if the average observer cannot estimate cover to a precision less than 0.5%, then this will have much less effect on the coefficient of variation at 50% actual cover than at 1% actual cover. The behavior of this relationship at the limits of actual cover is not entirely clear. Presumably, an observer under these conditions should be able to perfectly estimate zero and 100% actual cover, and thus the coefficient of variation should go to zero at these limits. At the upper limit, this seems to agree with our empirically-determined relationship. As one approaches zero, however, the coefficient of variation approaches the value 0/0, and is thus mathematically unstable. Though it is unlikely that this would ever be of any practical concern in field ecology, the theoretical behavior at this limit remains unclear.

When error is expressed as the standard error of the mean, which carries the same units as the original value (in this case, percent cover), we find a slightly skewed-left parabolic curve, with a peak error at approximately 55% actual cover. This suggests that extremes of cover may be estimated with less error than intermediate cover levels (the fitted curve does not extend to the limits of actual cover because these extremes were not empirically tested, though in theory the standard error of estimate should go to zero at zero and 100% actual cover). On this basis, cover estimation classes should ideally be relatively narrow at the extremes and wider for the intermediate ranges of cover. The Daubenmire (1959) cover classes (0-5, 5-25, 25-50, 50-75, 75-95, and 95-100%) reflect this near-symmetrical decrease in observer error at the extremes of actual cover. A modification of this scale by Bailey and Poulton (1968) separates the 0-5% cover class into two classes (0-1 and 1-5%), and perhaps better reflects the slightly skewed-left nature of



Fig. 2. The relationship between the standard error of mean cover estimations and the actual cover of a two-dimensional population of artificial paper images.

our empirical curve. The Domin-Krajina (in Mueller-Dombois and Ellenberg 1974) scale (<1, 1-5, 5-10, 10-25, 25-33, 33-50, 50-75, 75-95 and 95-100%) has narrower cover classes at the extremes, but is more skewed-left than the standard error curve based on our empirical data. The Braun-Blanquet (1965) (<1, 1-5, 5-25, 25-50, 50-75, and >75%) is asymmetric, lacking a narrow cover class at the upper end of the scale.

The actual ability of observers to estimate cover will, of course, vary under the complicated conditions encountered in the field. This study focused on total cover, and controlled for canopy overlap and height, as well as for edge effects. Such complications may be expected to increase observer error at any given level of actual cover, though we expect the relationships found in this study to hold, at least in a relative way, over the range of cover values. The artificial population used in this study did vary in the degree of aggregation of the paper figure, and is thus more extensible to field situations than a population with random distributions of figures (Schultz et al. 1961).

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Construction of an Inexpensive Liquid Resin Esophageal Cannula for Goats

EDUARDO G. GRÜNWALDT AND ROBERTO SOSA

Abstract

A simple method for construction of esophageal cannulas for goats employing liquid polyestyrenic resin is described. They were made with easily available and low cost materials.

Difficulties occur in research carried out with grazing livestock, one of them being determination of the botanical and chemical composition of ingested matter. One of the existing practical techniques to obtain representative samples of the diet selected by ruminants is esophageal fistulation (Torell 1954). Others have reported modifications in cannula construction aimed at reducing costs, weight, animal stress, and ulcerations in the esophageal mucosa, as well as increasing efficiency and durability (Denney 1981, Taylor and Bryant 1977, Bishop and Froseth 1971). Different types of cannulas have been adequately described by Van Dyne and Torell (1964). A variety of materials have been used in their construction, such as steel, wood, rubber, polyethylene. The objective of this technical note is to describe the construction of an esophageal cannula manufactured with liquid resin.

Material and Method

Figure 1 shows a schematic model of the cannula. The different components of the mould can be seen in Figure 2. The body (A) is made of hard wood, polished by a surface finishing, in which a semicylindrical groove was made with a universal milling machine. This mould has a cover with a drain (B), made of galvanized plate. The connection of (A) and (B) is made with screws (C). Liquid polyestyrenic resin¹ with the catalyst at 1.5% concentration (cobalt accelerator), polymerizable at room temperature, is poured in the assembled mould (Fig. 3).

After 50 minutes, the mould is disassembled and there results one half of the entire esophageal tampon. All components are linked by means of a bronze screw and wing nut (Fig. 4). A groove is carved with an emery stone on the parts of the plug which are introduced in the esophagus. The objective of this groove is to facilitate the passing of the ingested food. Figure 5 shows a cannula occluding a goat fistula.

Final considerations

In order to obtain an increase in the cannula diameter, rubber plates of different thickness may be added between both bodies, as a wedge, avoiding the loss of saliva. This alternative replaces the other solution, which is having cannulas of tampons of different diameters, which should be periodically exchanged according to circumstances.

This model has been successfully used for more than 24 months in esophageal fistulas in goats: the cannula was not swallowed, there was no mucosal ulceration or accumulation of forage material, in spite of removal every 20-30 days. Excellent results were also obtained when occasionally used as a ruminal cannula in goats. It may be assumed that there would be no difficulties for application in sheep. A bigger model may be considered possible, for esophageal fistulas in cattle.

- Authors belong to the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).
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Resin, type 2800 "POLIPERL"®. Haití 1598, Martínez, Buenos Aires, Argentina..



Fig. 1. Cannula schematic model (dimensions in mm)



Fig. 2. Component parts of mould.

Cannulas made out of polyestyrenic resin, according to the described method, can be considered adequate for the occlusion of esophageal fistula because of: (a) their resistance (they bear occasional falls on hard floor, when dropped by the person handling the animals); (b) light weight (27 g); (c) low cost; (d) simple construction, and (e) manufacturing with easily available materials.



Fig. 3. Assembled mould.



Fig. 5. Cannula occluding the esophageal fistula.

The cost of this cannula in Argentina, excluding the bronze screw and wing nut, is US \$0.10.

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Fig. 4. Assembled cannula and its components.



Book Reviews:

The Primary Production in the Sahel (PPS) Project. 1984.

Editors H. Breman and P.W.J. Withol. Center for Agrobiological Research (CABO), P.O. Box 14, 6700 Wageningen, the Netherlands. 113 p. pamphlet.

This is a report of various projects mainly carried out in Mali 1976-81 by the Netherlands and Ministry of Rurals Development of Mali. In January 1981, a three-day symposium was held in Bamako. Three courses were given and ten posters illustrated research results. Included are the problems, aims, and results of various studies. The annotated bibliography includes 73 studies with abstracts in English. A manual of good management based on these studies in being prepared by the Department of Soil Science—Agr. U. Wageningen, Int. Livestock Center and the Sahel Institute. This and the above report should be of vital interest to all Sahelian range or land managers. —John L. Schwendiman.

Oaks of North America, 1985. Howard A. Miller and Samuel H. Lamb. Published by Naturegraph Publishers Inc., P.O. Box 1075, Happy Camp, Cal. 327 pp. ill., paperback, \$9.95.

It begins with a brief history of the economic importance of oaks in Europe, England, and then America. It includes information of early lumber production, forest cover types, wildlife uses, pests, and opportunities in management.

The 100th meridian is used as a division line between the eastern and western oaks. The eastern groups include 43 species and varieties with taxonomic keys based on growing season characteristics. Identification is difficult because there are many more hybirds than distinct species. Each species description includes a distribution map, as well as photos of mature leaves, acorns, twigs, tree trunk, and bark.

The western oaks are divided into three groups: West Texas, Southwest oaks, and Pacific oaks. Maps and photos are again abundant and useful. There is appended a list of oaks that occur in Mexico, with a key to their identification. Included also is glossary of botanical terms, a list of common and scientific names, and suggested readings. This book should prove useful to all interested in, and working with, oak forests.—John L. Schwendiman, Pullman, Washington,

For Love of the Land. 1985. R. Neil Sampson. National Association of Conservation, Districts, League City, Texas 77573. 360 pp. ill., hardcover, \$14.95.

This book is essentially a history of the National Association of Conservation Districts. Its release coincides with the 50th anniversary of the founding of the Soil Conservation Service. Hugh Bennett is recognized as the "Father of the Soil Conservation Movement." He was influential in establishing a series of soil erosion experiement stations and demonstration projects. During the dustbowl days of 1935, under President Roosevelt, public law #46 created the U.S.D.A. Soil Conservation Service and established a national conservation policy. The book vividly describes the strains and stresses of getting this new movement going. It describes one of the outstanding success stories of the "New Deal Era," where local landowners organized to tackle the job of conserving the nations' soils and waters.

After the first district was organized in 1937, the movement gained momentum until by January, 1944, there was a total of 900 districts in the U.S. The NACD organization followed in 1946, with representation from 17 states. It had the support of many national farm organizations and chemical and implement compan-

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ies, as well as responsible district officials.

Biographies of many state and national leaders are included. Hundreds of names are mentioned. As the organization developed, it spun off a ladies auxilliary, a newsletter, an awards program, and a national office providing many other services. Biographies are listed by states, and a chronology by years gives important events and accomplishments.

Love of the Land is a history of "democracy in action," or how to get things done without the force of law. It should be required reading for every conservationist and citizen who has an interest in the preservation of our land heritage.—John L. Schwendiman Pullman, WA

BOOKS RECEIVED FOR REVIEW

Complimentary copies available to volunteer reviewers. Contact Dr. Grant A. Harris, Department of Forestry and Range Management, Pullman, Wash. 99164.

- Management of migratory shore and upland game birds in North America. 1977. Edited by Glen C. Sanderson. International Association of Fish and Wildlife Agencies. University of Illinois, Urbana-Champagin (Price ?).
- Wildlife management of your land. 1985. Charles L. Cadieux, Stackpole Books, Cameron and Kelker Streets, P.O. Box 1831, Harrisburg, PA 17105. \$29.95.
- Agroforestry in the southern United States. 1984. School of Forestry, Wildlife, and Fishery. Louisiana Agr. Exp. Sta., Baton Rouge, LA 70803. \$12.50. Rcd 1/5/85 L.E. Linnartz, M.K. Johnson, Ed. (Paper)
- Photosynthesis. Energy conversion by plant and bacteria. Vol.1, 1982. Academic Press Inc., Orlando, FL 32887. Ed. Govindjee.
- Vol. II. Development, carbon metabolism, and plant productivity. Ed Govindjee. \$65.00 hc.
- Home rule on the range. Early days of the grazing service. 1984. Vantage Press, 516 West 34th St., NY, NY 10001. \$10.95.
- Enviromental planning and management. 1985. John H. Baldwin. Westview Press, 5500 Central Ave., Boulder, CO 80301. \$42.50 hc, \$18.50 paper.
- Experimental behavioral ecology and sociobiology. 1985 Ed., B. Holldobler and M. Lindauer. Sinauer Associates, Inc., c/o Publisher Storage and Shipping, 231 Industrial Park, Fitchburg, MA 01420 (Price?).
- Introduction to wildlife management. 1985. James Shaw, McGraw-Hill, 1221 Avenue of the Americas, New York, NY 10020
- Mathematical programming for natural resource management. Dennis P. Dykstra. McGraw-Hill Book Company, 1221 Avenue of the Americas, New York, NY 10020. Price?.
- Yearbook of agriculture. 1984 Animal Health, Livestock and Pets. U.S. Department of Ag. Washington, D.C. Supt. Doc. (free from congressman).
- North american game birds and mammals. 1984. A. Starker Leopold, Ralph J. Gutierrez and Michael T. Bronson. Charles Scribner's Sons, 597 5th Avenue, New York, NY 10017. \$12.95 paper.
- Soil reclamation processes, microbiological analyses and applications. 1985. Edited by Robert L. Tate, 3rd, and Donald A. Klein. Marcell Dekker, Inc., 270 Madison Avenue, New York, NY 10016. (Price ?).
- Land classification for land uses, management, and valuation. 1983. Marion E. Everhart. Todd Publishing, Inc., P.O. Box 5837, Scottsdale, AZ 85261. \$18 cloth.
- Bibliographies on chaparral and the fire ecology of other mediterranean systems. 1984. Jon E. Keeley. California Water Resources center. Report No 58, Univ. Cal Davis 95616 (no price listed)
- Washington state grazing land assessment. 1984. Grant A. Harris and Martha Chaney. Soil Conservation Service, U.S. Court House Room 360, Spokane, WA 99201. 136 p (free)
- Enviromental planning and management. 1985. John H. Baldwin Westview Press, 5500 Central Ave. Boulder, CO 80301. 336 p \$42.50 hc, \$18.50 paper.
- Behavior of domestic animals. 1985. Benjamin L. Hart. W.H. Freeman and Company, 41 Madison Ave, New York, NY 10010. 390 p, \$29.95
- Photosynthesis. 1982. Volume I, Energy conversion by plants and bacteria.
 Volume II, Development, carbon metabolism, and plant productivity.
 1983. Ed. Govindjee. Academic Press, Inc. Orlando FL 32887. Vol. 1, 799 p, \$79.00; Vol II, 558 p. \$65.00.
- Ecological systems of the geobioshphere, Vol. I, ecological principles in global perspective. 1985. Heinrich Walter. Springer Verlag, New York, NY (translated to English by Sheils Gruber,) (no price given).

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