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Aspects of coyote predation on Angora Goats

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Abstract

A study to assess characteristics of coyotes (*Canis latrans* Say) that attack livestock was conducted in southern New Mexico. During 4–16 April 1991, 38 Angora does (*Capra hircus* L.) and their 34 offspring (kids) were exposed to coyote predation in 3 small experimental free-ranging flocks on the study area. One doe and 14 kids were killed by predators, including at least 12 cases of coyote predation. Coyotes selectively preyed on the smaller kids, and on goats in relatively small groups. Remains of 11 kids killed by predators were cached within the core areas of territorial coyotes. Six of 8 territorial coyotes and 5 of 9 transients (nonterritorial coyotes), with ranges that overlapped the distribution of flocks, consumed goats.

Key Words: *Canis latrans*, food cache, predation management

A contemporary goal in predation management is selective control of specific animals responsible for predatory attacks. However, a disputed question is whether episodes of predation on livestock are attributable to all coyotes (*Canis latrans* Say), or only a few individuals within populations (Wagner 1988). Published information about characteristics of depredating individuals is limited to observations of captive coyotes (Connolly et al. 1976), anecdotal accounts (Young and Jackson 1951), and sparse data from tangential studies (Althoff and Gipson 1981, Todd 1985, Gese and Grothe 1995).

Analyses of relative vulnerability to trapping indicate that there are significant biases toward capture of transient and younger coyotes in populations (Windberg and Knowlton 1990). The effect of these biases on management efforts to selectively target coyotes that prey on livestock is unknown. Also, an assumption that coyotes usually prey on livestock while foraging within their familiar ranges has not been validated. The locations of predatory attacks on livestock may have implications for targeting depredating individuals because coyotes have relatively low vulnerability to capture within their ranges (Windberg and Knowlton 1990).

Our objectives were to describe the age, sex, and territorial classes of coyotes that attack free-ranging Angora goats (*Capra hircus* L.), the location of successful attacks (kills) on goats by coyotes in relation to coyote territories, and any discernible patterns of predation on goats.

Methods

The 75 km^2 study area was located on the northern portion of the USDA-ARS Jornada Experimental Range (JER), 40 km north of Las Cruces, Dona Ana County, New Mexico (32°40'N 106°44'W, elev. 1,400 m). The JER (783 km^2) is used primarily for grazing by cattle, although experimental flocks of sheep (*Ovis aries* L.) were located in pastures 3 km south of the study area. The JER is characterized by basin topography representative of the northern Chihuahuan desert (Hennessy et al. 1983). The climate is arid, with mean annual precipitation of 231 mm concentrated in late-summer (Hennessy et al. 1983). Mesquite (*Prosopis glandulosa*) is the predominant woody species and large dunefields have formed on the sandy soils (Buffington and Herbel 1965). Rogers (1965) found that lagomorphs and rodents were primary prey of coyotes in the region during winter-spring 1964–1965, and our cursory examination of coyote feces indicated that they were the staple prey during this study.

Based on similar rates of coyote predation on sheep and goats during preliminary trials we conducted in 1988–1989, the more manageable Angora goats were selected as the representative experimental livestock for this study. The goats were purchased locally and were adapted to foraging in range conditions comparable with those on the study area. Most does were near the end of their reproductive lives (84% were ≥4 years of age based on replacement pattern of incisor teeth). The kids were 1–3 weeks of age, except for 2 individuals which were 4–6 weeks old. The goats were inspected and certified free of diseases by the New Mexico Livestock Board at time of purchase. Immediately prior to transport to the study area on 26 March 1991, all goats were administered an antibiotic (ceftiofur sodium) (Naxcel, The Upjohn Co., Kalamazoo, Mich.) to prevent shipping-fever and general respiratory infection. On 27 March, all goats were examined to record their general health and physical condition, marked with colored and numbered plastic eartags, and administered iver-

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The protocol for this study was approved by the Institutional Animal Care and Use Committee (Denver Wildlife Research Center). Identification of specific products or services does not imply endorsement or recommendation by the USDA over similar companies or products not mentioned.

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mectin (Ivomec, MSD Agvet, Rahway, N.J.) for broad-spectrum therapeutic treatment of internal and external parasites. Second and third doses of antibiotic were administered to all goats on 27–28 March; they received a second treatment with ivermectin on 6–7 April. On 1 April, the goats were examined for symptoms of diseases by a veterinarian. Ten kids diagnosed with contagious ecthyma (soremouth disease) were excluded from the study. Three flocks of goats (Table 1) were confined in enclosures on the study area for 3-5 days to establish social bonds prior to release.

One day before release of flocks on the study area, a Physiologic Marking Collar (PMC) (Connolly 1990) was mounted on each goat to identify coyotes that attacked them. Large (60 ml) and small (30 ml) PMCs contained radioisotopes (30 µCi of Cesium-134 and 60 µCi of Zinc-65, respectively) in a dyed (1% tartrazine, Burns and Savarie 1989) water solution. The concentrations of radioisotopes in PMCs were calculated to provide physiologic marks for ≥ 6 months based on quantities of solution ingested and absorbed during trials with captive coyotes (Knowlton and Ebbert 1991) and the physical and biological half-lives of the radioisotopes. Each PMC had a radio-transmitter with a 1-hour inactivity (mortality) sensor affixed to the rear strap. Each goat (does and kids) was also injected intramuscularly with 300 mg of iophenoxic acid for physiological identification of coyotes that consumed goat flesh (Knowlton and S. R. Olmstead, unpub. data). The iophenoxic acid was dissolved in ethyl alcohol (95%) at a concentration of 188 mg/ml, which yielded a 1.6 ml dose of IA-ethanol solution per goat. Body mass of kids was measured with a spring-balance scale 1 day before release.

After release of flocks from enclosures onto the study area, we attempted to locate all goats twice daily (early-morning and late-afternoon) using radio-tracking procedures. We also attempted to obtain a visual observation of each goat daily to ascertain that they were in satisfactory condition. The location of each group of goats observed visually was plotted on a map of the study area. Dead goats were identified by radio-transmitter signals in mortality mode, and the carcasses were located with radio-telemetry equipment. The carcass and the surrounding area were examined for evidence of the cause of death (Wade and Bowns 1982). Carcasses were typically recovered within 24 hours after death and all remains found were removed from the study area. The radio-transmitter was subsequently placed at an elevated position near the recovery site to estimate its location, as derived by 2 or 3 azimuths from fixed radio-telemetry receiving-stations.

Coyotes were captured with foothold traps and collared with radio-transmitters from 19 February to 21 March 1991. Data for point-estimates of locations of radio-collared coyotes were collected by fixed-station triangulation from 30 March to 29 May and analyzed using program HOME RANGE (Ackerman et al. 1990). Radio-collared coyotes were classified as territorial or transient (nonterritorial) based on the areal distribution of radio-telemetry locations (i.e., exclusive core areas of ranges) as described by Windberg and Knowlton (1988). Thirty-two radio-collared individuals, and 4 unmarked coyotes associated with them, were recovered by shooting during 29–31 May. Their carcasses were necropsied to collect tissue samples of blood, kidney, liver, and skeletal muscle for subsequent analyses for presence of physiologic markers (Knowlton et al. 1988, 1989). The tissues were assayed for radiation energies of Zinc-65 and Cesium-134 using a germanium detector attached to a pulse-height multichannel analyzer. Coyotes that fed on flesh of goats injected with iophenoxic acid were identified by an elevated concentration of protein-bound iodine in blood-serum (Knowlton et al. 1988) from analyses conducted by SmithKline Bio-Science Laboratories (Van Nuys, Calif.). Serum iodine levels >15 µg/100 ml were considered positive evidence that coyotes consumed goat flesh (Knowlton and Olmstead, unpub. data).

Ages of coyotes were estimated by patterns of cementum layers in microscopic sections of canine, or first-premolar, teeth prepared by Matson's Laboratory (Milltown, Mont.). Frequency data for predation on goats were analyzed with Fisher's exact tests. Mean mass of kids killed by predators was compared by *t*-test.

Results and Discussion

Forty one coyotes (26 males and 15 females) were marked with radio-collars. This sample comprised a low proportion of younger coyotes as only 7% were juveniles and 12% were 2 years old. Thirteen coyotes were classed as territorial and 12 as transients. There were insufficient data for classification of other radio-collared coyotes. Core areas (Ackerman et al. 1990) of 11 coyote territorial ranges were identified in the vicinity of the free-ranging flocks of goats (Fig. 1). We considered radio-collared coyotes to have been exposed to goats if the 85% harmonic-mean estimate (Ackerman et al. 1990) of their activity areas overlapped the distribution of a flock. Eight territorial and 9 transient coyotes were exposed to goats during the study.

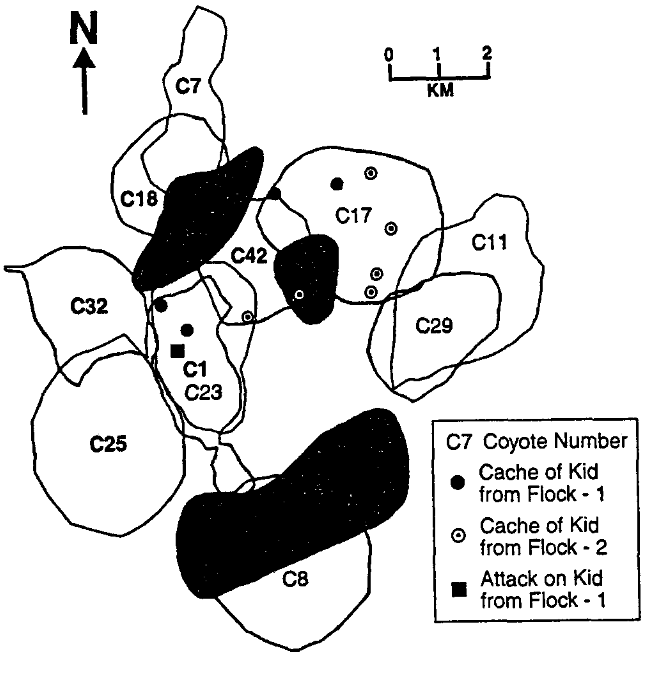

Fig. 1. Distribution of 12 food caches of Angora kids, and 1 site of attack, by coyotes in relation to core areas of coyote territorial ranges. Shaded areas represent minimum observed ranges of 3 flocks of goats (Flock-1 = upper, Flock-2 = middle, Flock-3 = lower). Coyote identification numbers in boldface print indicate individuals that consumed goat.

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The 3 flocks of Angora goats were released on 4–6 April and generally remained within 1 km of their enclosures for 4–6 days. Because the flocks were reluctant to range from their enclosures to forage, we discontinued providing supplemental food there on 10 April and the flocks immediately began ranging farther away. Extremely strong winds also began on 10 April and continued unabated for 3 successive days resulting in disruption and dispersal of the flocks. We subsequently discontinued exposure of goats to coyote predation on the study area on 16 April.

One doe and 14 kids were killed by predators during 8–15 April (Table 1). Twelve of the mortalities were confirmed as coyote predation based on evidence associated with the carcass (tracks, wounds, food cache). Predation was the cause of death for the other 3 goats and, although the specific predators could not be positively identified, also appeared attributable to coyotes. Four additional goats (3 kids and 1 doe) died during the same period but the causes were undetermined because they were recovered outside the study area several days after death.

Table 1. Flock size, exposure time, and predation on Angora goats on the JER study area, April 1991.

Flock number	Initial size of flocks		Period of exposure to predation	Days exposure of goats [1]		Goats[2] killed by predators
	Doe	Kid		Doe	Kid	
	- - - (No.) - - -			- - - (No.) - - -		– (No.) –
1	13	11	6–16 Apr	91	71	8
2	12	12	4–16 Apr.	120	90	6
3	13	11	5–16 Apr.	137	82	1
Total	38	34	4–16 Apr.	348	243	15

[1] Corrected for mortalities and absence of individuals from study area.

[2] All were kids except for 1 doe from Flock-1.

The cumulative exposure time for goats on the study area was 348 days for does and 243 days for kids (Table 1). Predation loss was notably less for Flock-3 than the other flocks (Table 1). The only predation in Flock-3 occurred when a doe and 2 kids moved 5 km northeast of their flock. Most predation (12 of 15 cases) occurred after the flocks splintered into smaller groups. In 11 cases, the victim was associated with only 1–4 other goats on the day prior to the attack. Only 3 cases of predation occurred when goats were in flocks (≥ 10 individuals) during a cumulative exposure of 22 days, whereas 12 goats were killed by predators from smaller groups (≤ 7 individuals) during 25 cumulative days of exposure ($\underline{P} = 0.08$).

At least 41% of the 34 Angora kids were killed by predators during 12 days of exposure on the study area. This remarkably high rate of predation occurred despite no recent (>7 years) exposure of goats, or sheep, as prey on our study area (R.P. Gibbens, USDA-ARS, JER, pers. com.). Further, the predation occurred before the peak of the pup-rearing season when additional food demands to provision litters might result in increased coyote predation on livestock (Till and Knowlton 1983). Although the coyote population around much of the JER was considered to be lightly exploited by humans (Howard and del Frate 1991), there was no recent history of control, harvest, or other exploitation of coyotes on our study area (C.C. Yarbrough, USDA-ARS, JER, pers. com.). Hence, the immediate and high coyote predation on goats observed during this study is contrary to speculation in the popular press (Milstein 1991, Smith 1993) that unexploited coyote populations pose less risk to livestock. However, most kids killed by coyotes were in atypically small groups instead of larger flocks characteristic of many goat production operations. Guthery and Beasom (1978) also reported that Angora kids were readily killed by naive coyotes in Zavala County, Tex., and that most were killed during their first days of life before joining the flock. This pattern of coyotes selectively preying on goats disassociated from flocks may identify a limitation in the use of guarding animals for livestock protection (Green et al. 1984).

Predation losses of 41% of kids versus 3% of does ($P < 0.001$) showed a distinct selection of kids over adults. Mean body mass of 14 kids killed by predators ($\bar{x} = 5.8$ kg, SE = 0.3) was less ($P = 0.03$) than mass of 15 kids surviving exposure to predators ($\bar{x} = 7.6$ kg, SE = 0.7). Further analysis of predation rates for 3 size classes (≤ 5.0 kg, 5.1-8.9 kg, ≥ 9.0 kg) of kids revealed a significantly greater ($P < 0.01$) proportion (0.36 vs 0.07) of smaller kids (≤ 5 kg) killed by predators whereas a greater proportion (0.33 vs 0) of larger kids (≥ 9 kg) survived. Thus, coyotes selectively preyed on the smallest goats available during our study. Henne (1977) and Guthery and Beasom (1978) also noted that predators selected the youngest lambs and goats during their studies, although supporting data were not provided.

Of 15 goats killed by predators, remains of their carcasses were located at the site of attack in only 2 cases. Portions of the carcasses of 12 kids and 1 doe were found in food caches made by coyotes. The cached remains of kids ranged from entire carcasses ($n = 2$) to only the head and cape ($n = 2$). Most caches ($n = 8$) were composed of anterior halves of carcasses, including the front legs. We only recovered the cached head of the doe killed by coyotes. Because the radio-transmitters were attached to the PMC strapped around the head, we were able to find caches of the anterior portion of carcasses whereas any additional caches of other portions could not be readily located. The tendency for coyotes to begin feeding on the posterior portion of livestock carcasses (Wade and Bowns 1982) suggests that the remains we located may have been the primary caches. The relationship between the locations of caches and the sites of predatory attacks were undetermined. During a preliminary trial in western Texas in spring 1989, 6 of 11 radio-collared kids and lambs killed by predators were cached, including 2 caches of Angora kids killed by coyotes found 1.4 and 2.1 km from the location of their flock (Windberg, unpub. data). Our recovery of most remains of goats killed by predators in well-disguised caches provides strong support for the contention of others (Nesse 1974, Guthery and Beasom 1978, Wagner 1988) that many unexplained losses of sheep and goats were attributable to coyote predation even though carcasses were not found.

The only documented site of a coyote attack on a kid within the study area was located near the center of a territorial core area shared by 2 coyotes (C1 and C23) (Fig. 1). Twelve caches of kids were located on the study area (Fig. 1). Two caches were in the core areas of the 2 coyotes (C1 and C23) in which the kill site was located. Based on analyses for protein-bound iodine in their serum, the 4-year-old male (C1) had consumed goat flesh, whereas the 3-year-old female (C23) had not. Two caches were in the core area of a 3-year-old female (C42), which had consumed goat, and an additional cache was in a portion of her core area that partially overlapped the core area of coyote-C1. Six caches were within the core area of a 6-year-old female (C17) that died before recovery, which precluded analysis for iodine residue. The remaining cache was slightly outside the core area, but within the 75% harmonic-mean estimate of the range of a 2-year-old female (C18), which had consumed goat. A 1-year-old male (C7) which shared part of the core area with coyote-C18 had also consumed goat (Fig. 1). The cached head of the doe was 1 km north of the area where coyote territorial ranges were delineated. During the period of exposure, Flock-1 and Flock-2 entered the ranges of 4 coyotes in which caches of carcasses were located (Fig. 1). Flock-3 ranged in the core area of a 4-year-old territorial female (C8) which had not consumed goat (Fig. 1). Some small groups of goats dispersed beyond the ranges of the main flocks, and 2 additional coyotes (C25 and C32) with core areas west of the flocks had also consumed goats.

The relatively small size of most kids made it difficult to maintain the PMCs in the proper position to be punctured during coyote attacks. The PMCs became dislocated (i.e., hanging loosely around neck) on 7 of the 14 kids killed by predators. Although all 14 kids killed by predators had tooth punctures in their neck (predominantly the anterior portion), only 2 of the PMCs were punctured. In contrast, 5 of 7 properly-mounted PMCs on older kids (7–10 weeks of age) were punctured by predators during a preliminary trial in 1989 (Windberg, unpub. data). The PMC on the doe killed by coyotes was punctured. Additionally, the PMC on 1 of 4 goats that died from undetermined causes was punctured. Assays of tissues (liver, kidney, muscle) from 36 coyotes recovered on the area after the study yielded no evidence of radioisotopes to associate them with puncture of PMCs during attacks on goats.

Of the radio-collared coyotes with ranges overlapping the distribution of goat flocks, 6 of 8 territorial individuals and 5 of 9 transients consumed goats. From this sample, we detected no difference ($P = 0.62$) between the proportion of territorial and transient coyotes that consumed Angora goats. There was no difference ($P = 0.99$) in the proportion of young (1–2 years) coyotes that consumed goats (3 of 11) versus those that did not consume goats (1 of 6). A greater proportion ($P = 0.05$) of coyotes that consumed goats were males (8 of 11) compared with coyotes that were exposed to but did not consume goats (1 of 6). Observations of sheep-attacking behavior among captive coyotes by Connolly et al. (1976) found most sheep killed by males. Gese and Grothe (1995) observed alpha male coyotes leading 8 of 9 attacks on deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*). Also, Young and Jackson (1951) stated that tracks of male coyotes were more evident than those of females at kill sites of lambs, and Todd (1985) noted a trend for diets of male coyotes to include more ungulates than females.

The nature of our data precludes definitive statements directly connecting coyotes that consumed goat flesh to their actual predation on goats. Coyote predation was judged to be the probable cause of 15 goat mortalities during the study. We believe it is reasonable to assume that coyotes which killed goats subsequently consumed a full meal of their flesh. The concentration of protein-bound iodine ranged from 320 to 750 μg/100 ml in serum of 10 coyotes, which suggested that each consumed a large meal of goat flesh (Knowlton and Olmstead, unpub. data). The mean mass of kids lost to predation (5.8 kg) represented approximately 4 meals for coyotes (Lindsey 1987). We removed about half of the total mass of kid carcasses <24 hours after death. Hence, at least 1 additional meal from each predated kid potentially remained available on the study area. This excess flesh from carcasses may have been consumed by coyotes associated with the killing individual, or cached. We had no data to associate the locations of caches of goats with specific coyotes. Foxes (*Vulpes vulpes*) that made food caches were observed to be the individual that retrieved them (Macdonald 1976) and 4 African wild dogs (*Lycaon pictus*) retrieved their caches ≤1 day later (Malcolm 1980). Because coyotes that cached unrecovered remains probably retrieved them, we believe it is reasonable to assume that the majority of coyotes which consumed goats during this study were responsible for or involved in their predation.

In 2 cases, we recovered an unmarked male coyote with a radio-collared territorial female (C18 and C32), suggesting that the pairs were territorial associates. Both these males had also consumed goat flesh, suggesting that sharing of carcasses by territorial groups occurred. If so, our data for the proportion of coyotes that consumed goats may be biased toward territorial individuals because transients tend to be primarily solitary (Camenzind 1978, Crabtree 1988). Further, the relative exposure to goats as prey was less for the radio-collared transients than territorial coyotes due to their larger ranges (Windberg and Knowlton 1988). Nevertheless, at least 5 transient coyotes consumed goats. About half of the caches were located along the apparent edges of core areas of coyote territories (Fig. 1). Some of those caches may have been made by transient coyotes because Windberg and Knowlton (1988) found that transients tended to be located in interstices of territories.

Conclusions

Coyotes began preying on Angora goats almost immediately after they were released on the JER study area during April 1991. Most coyote predation was directed at small disassociated groups of goats (≤7) instead of the larger flocks (10–24 goats). Coyote predation during the 12-day period of goat exposure was predominantly on kids, with a preference for smaller kids. We noted a trend for greater consumption of goats by male coyotes, but detected no differences in the propensity of various age or territorial classes of coyotes to consume goats. Therefore, our results suggest that management measures used to protect livestock during periods of exposure of highly vulnerable kids or lambs may be best directed at local coyote populations rather than at particular cohorts or individuals within the population.

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Technical Note: Comparison of simulated ground nest types for grazing/trampling research

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Abstract

Ornithologists often use simulated nests consisting of game bird or domestic poultry eggs to study nest survival. Researchers investigating cattle trampling of ground nests have sometimes used clay targets instead of actual eggs to avoid the confounding effects of nest depredation. To determine whether livestock respond similarly to clay targets and egg nests, we compared inadvertent trampling and intentional disturbance of clay targets versus clutches of 3 pheasant eggs by Angus × Holstein heifers. Overall trampling levels for clay target- and egg-nests were similar (35 and 36%, respectively). Cattle noticed and responded to both types of nests. When noticed, simulated nests were kicked, sniffed, licked, or picked up in the mouth. Cattle disturbed an average of 25% of the clay targets and 8% of the egg nests during 4 trials. Our results suggest that cattle are as likely to inadvertently trample egg nests as they are clay targets, but targets are more likely to attract attention and are therefore disturbed more often than egg nests. The greater likelihood of intentional disturbance of clay targets by cattle reduces the confidence of extrapolating the fate of this type of simulated nest to that of actual nests.

Key Words: artificial nests, cattle, clay targets, dummy nests, game birds, intensive rotational grazing, IRG, nest survival

Simulated nests are commonly used to study the effects of predation and other factors on nest survival (Henry 1969). Use of simulated nests ensures an adequate sample size for statistical testing, eliminates time-consuming nest searching, and allows study of some aspects of avian breeding ecology without disturbing nesting birds.

Most frequently, researchers use eggs of domestic poultry or pen-reared game birds to simulate ground nests (Henry 1969, Horkel et al. 1978, Bareiss et al. 1986). Where clutches of eggs are used as simulated nests for cattle trampling research, predation can confound estimates of trampling damage (Koerth et al. 1983, Bareiss et al. 1986). Some researchers have used clay pigeon shooting targets to simulate ground nests because they do not attract predators, but are as fragile as eggs, providing evidence of trampling (Koerth et al. 1983, Jensen et al. 1990). The appearance and odor of clay targets are unlike natural nests; these characteristics may result in a different animal response when nests are encountered in the pasture (N.J. Silvy, Texas A&M Univ., pers. commun.).

We conducted this study to determine which simulated nest type would be more appropriate for a planned study of ground nest trampling under intensive rotational grazing in the midwestern United States (Paine et al. 1996). During the nesting season, vegetation height in rotationally grazed, cool-season grass pastures varies from 5 to 40 cm. Nesting species include those that nest in sparse cover such as killdeer (*Charadrius vociferus* L.) as well as those that require more dense cover such as pheasant (*Phasianus colchicus* L.). Our objective was to determine if inadvertent and intentional disturbance of clay targets by cattle is similar to that of simulated nests of pheasant eggs, and if these simulated nest types can be used interchangeably.

Study Area and Methods

This study was conducted at the University of Wisconsin's Lancaster Agricultural Research Station (LARS) in southwestern Wisconsin. A 2.4 ha pasture, of approximately 15% slope was used. Pasture vegetation included smooth bromegrass (*Bromus inermis* L.), orchard grass (*Dactylis glomerata* L.), quackgrass (*Agropyron repens* L.), Kentucky bluegrass (*Poa pratensis* L.), and red clover (*Trifolium pratense* L.). The trial was conducted in late April 1993, when vegetation was <10 cm in height.

One hundred twenty nest sites were located in a 10 by 12 row grid in the pasture. Nest sites were about 12 m apart. We randomly placed 60 of each nest type on the grid. Nest types were a 10-

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cm diameter clay pigeon shooting target, placed paint side down; or a clutch of 3 unwashed pheasant eggs. Nest density was 50 nests ha^{-1}, much higher than has been recorded for natural nests (Buhnerkempe 1979, George et al. 1979). No effort was made to create a "nest bowl" or to conceal the simulated nests in vegetation. The purpose of the study design was not to simulate natural conditions, but to ensure cattle would encounter nests in the pasture so intentional and inadvertent animal disturbance of the 2 nest types could be assessed.

The grazing treatment was applied using LARS's herd of 130 Angus × Holstein heifers. The resulting stocking density of 54 animal units (AU) ha^{-1} is typical of an intensive rotational grazing system for dairy cattle (Undersander et al. 1991). The cattle occupied the pasture for 7 hours each day on 2 consecutive days. Two nest observations were made each day following rumination (trials 1 and 3) and grazing periods (trials 2 and 4). The herd was let into the pasture each morning at approximately 0900 and, after a period of exploration and grazing, settled down to ruminate. Nest checks for trials 1 and 3 were made after about 5 hours, when the cattle began grazing in early afternoon. Trials 2 and 4 ran from the start of afternoon grazing until late afternoon. Nest checks for trials 2 and 4 were made after the cattle had grazed for about 2 hours and were removed from the pasture.

We recorded 1 of 3 fates for each nest: trampled, disturbed, or intact. Targets that were broken into several pieces were recorded as trampled. Targets were recorded as disturbed if they were flipped over, moved from their original grid position, chipped or were covered with saliva, mud, and pieces of grass. For egg nests, the number of eggs crushed was recorded. For comparison with targets, an egg nest with ≥1 eggs crushed was considered trampled. Egg nests were recorded as disturbed if ≥1 eggs were moved from the nest site, were separated within the nest site, or were covered with saliva, mud, and pieces of grass. After each nest check, we replaced nests that were disturbed or trampled, so the number of intact nests would be equal at the start of each trial.

Each trial was analyzed separately and nest types were compared for trampled, disturbed, and intact nests using a simple Z-statistic formula, with significance at $P<0.05$. Because trials varied in length, we also compared hourly rates of trampling and disturbance during each of the 4 trials using the Z-statistic with significance at $P<0.05$.

Results and Discussion

Trampling Damage

While there were differences in trampling damage among the 4 trials, we recorded similar overall totals for the 2 nest types. Total amounts of trampling damage for the 4 trials were 36% and 35% for the egg nests and clay targets, respectively. Trampled targets were most often smashed into many pieces, whereas egg nests had varying levels of damage. Approximately two-thirds of trampled egg nests had ≥1 of the 3 eggs intact; half of these had 2 of the 3 eggs intact (data not shown).

For trials 1 and 4, the number of egg nests and targets that were trampled were similar (Fig. 1a). Slightly less than half of the 60 nests of each type were trampled during each of these trials. For trial 2, the number of targets trampled (25%) was more than twice the number of egg nests trampled (10%); however, for trial 3, more egg nests (48%) were trampled than targets (35%). These results suggest that chance plays a major role in inadvertent trampling of ground nests.

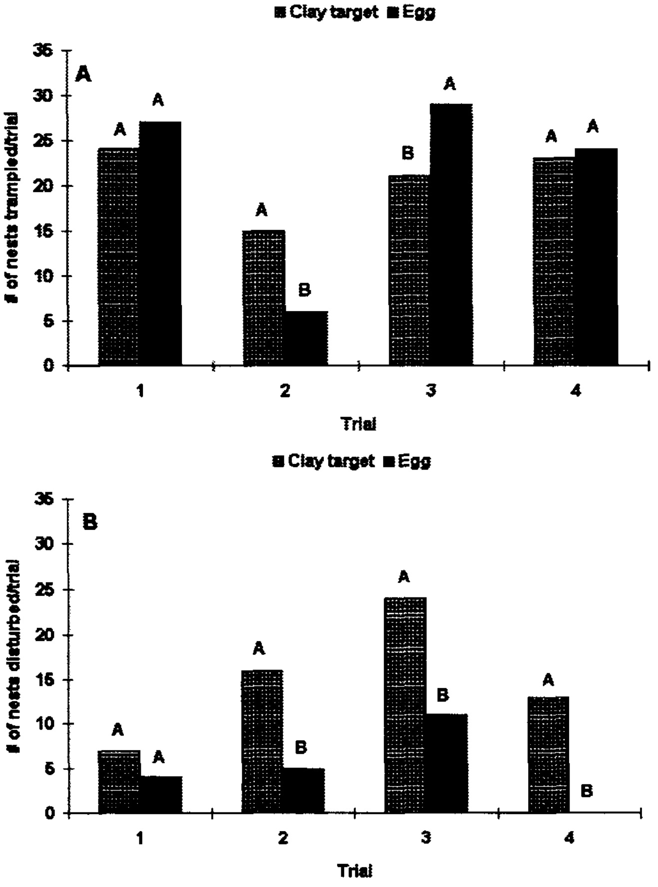

Fig. 1. Total number of simulated nests trampled (A) or disturbed (B) during 4 grazing trials. Nest types were a clay target (hatched bar) or a clutch of 3 unwashed pheasant eggs (solid bar). For each trial, 60 of each nest type were located randomly within a grid in a 2.4 ha. paddock. Differing letters within trials indicate significant differences ($P \leq 0.05$) by LSD.

For all trials except trial 2, trampling rates per hour were similar for targets and egg nests. In trial 2, we recorded a greater trampling rate per hour for targets than for egg nests (Fig. 2a). Animal inactivity during this trial resulted in a lower total number of trampled targets and egg nests compared to the other trials. Differences both in trampling rates and in overall damage among trials reflect the randomness of individual animal grazing/ruminating behavior and movement within the pasture (Smith et al. 1986).

Nest Disturbance

Cattle were observed to notice and respond to both types of nests. Both targets and eggs were sniffed, licked, or occasionally picked up in the mouth. One animal's interest in a simulated nest often attracted the attention of nearby animals. We informally observed 30 instances of cattle disturbance of nests. Of these, 23 were instances of cattle investigating targets, picking them up in their mouths and carrying them from the nest site. We observed 7

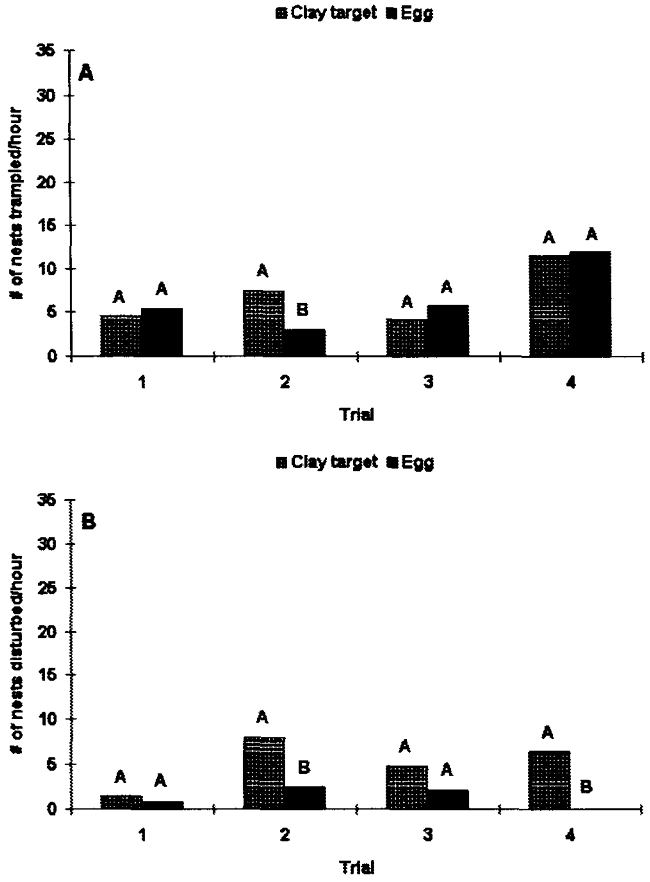

Fig. 2. Number of simulated nests trampled (A) or disturbed (B) per hour during 4 grazing trials. Nest types were a clay target (hatched bar) or a clutch of 3 unwashed pheasant eggs (solid bar). For each trial, 60 of each nest type were located randomly within a grid in a 2.4 ha. paddock. Differing letters within trials indicate significant differences ($P \leq 0.05$) by LSD.

instances of egg nests attracting such attention. In some cases, cattle picked up individual eggs in their mouths and moved them several feet from the nest site without damaging them.

Nest check data support our informal observations of nest disturbance (Fig. 1b). For all trials, more targets than egg nests were disturbed. Disturbance of targets was >3 times higher than egg nests in both afternoon trials (2 and 4). For trial 3, >2 times as many targets were disturbed as egg nests. For trial 1, the difference was not significant. Overall, 25% of the target nests were disturbed in the 4 trials, compared to 8% of egg nests.

In general, hourly rates of disturbance during the afternoon trials were higher than during the morning trials (Fig. 2b). The hourly rate of disturbance of targets was significantly higher than that of egg nests for the afternoon trials but not for the morning trials. During the morning trials, which encompassed a rumination period, the cattle were less likely to encounter simulated nests in the paddock because they were inactive. During the afternoon trials, the herd was actively grazing and was more likely to encounter simulated nests. The higher level of disturbance of targets than egg nests during active grazing suggests that clay targets are more likely to be noticed by grazing cattle than are egg nests.

Trampling and Disturbance Patterns

There were no obvious spatial patterns of nest trampling or disturbance either within a trial or among trials. One hundred eleven of the 120 nest sites (93%) were trampled or disturbed ≥1 times during the 4 trials. At 40 of the 120 nest sites, 2 trampling or disturbance events were recorded during the 4 trials. One and 3 events were recorded at 27 and 34 nest sites, respectively, and less than 10% of the sites had 4 events recorded. Within the grid of 120 nest sites, 9 sites (7%) were never trampled during the 4 trials. The locations of these sites within the grid appeared random, suggesting that chance was responsible for their survival.

Conclusions

In this comparison of clay pigeon shooting targets and clutches of pheasant eggs used as simulated ground nests, we found more clay targets were intentionally disturbed than egg nests, whereas inadvertent trampling of the 2 nest types was similar. The heifers in our study appeared to take a particular interest in clay targets when encountered in pastures. Both our recorded nest disturbance data and our informal observations suggest that unconcealed simulated nests of pheasant eggs attracted less attention than clay targets. We conclude the use of clay targets as simulated nests may generate biased data in rotationally grazed, cool-season grass pastures in the Midwest. The disturbance of clay targets by cattle reduces the confidence with which one can extrapolate from the fate of this type of simulated nest to that of natural ground nests.

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50:234–238

Seasonal variation of locomotion and energy expenditure in goats under range grazing conditions

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Abstract

Energy cost of various activities can be used in conjunction with direct field observations to estimate energy expended in the daily activities of free-ranging animals. The objective of this study was to estimate the energy expenditure due to locomotion of goats on open range. The study was carried out at the 130-ha "Los Pajares" pilot zone, located in the Filabres mountain-range, Almería. Average elevation is 865 m above sea level. The area has a Mediterranean climate. The mean annual precipitation is 324 mm. The average daily temperatures range from 8.9°C in January to 23.0°C in August. The landscape is characterized by woody plants and perennial grasses.

The experimental flock was grazed on its customary routes for 2 days during 4 seasons. The goats were released to graze during the day and then returned to an enclosed shed. Direct observation was used to simulate the total distance walked, the vertical ascent or descent, and to quantify other grazing activities. The energy expenditure of locomotion was calculated from the horizontal and vertical components of travel and the corresponding costs, which had been previously obtained by calorimetry. Daily travel distances by goats on range fluctuated from 5,763 m in summer to 3,482 m in autumn, with an annual average of 4,295 m, which represents a mean speed of 10.8 m/min. The mean annual vertical ascent or descent was 168 m. Estimated heat production due to locomotion ranged from 56.9 to 34.8 kJ/kg$^{0.75}$ per day in summer and autumn respectively. These values account for an increased energy requirement at pasture above maintenance of 14.2 and 8.7%, respectively.

Key Words: goats, locomotion, grazing, heat production

Goats are well adapted to the hot and dry conditions of the semi-arid areas of southern Spain, being the domestic animal species with the greatest productivity in such climatic conditions. Goats are able to obtain an adequate diet even when forage is scarce and they can feed over rugged and otherwise inaccesible terrain. The distance travelled by the grazing goat has important bearing on its productive performance and may be influenced by seasonal variation in grazing activities.

Ruminants expend much more energy outdoors than indoors. Animals on range spend considerably more time walking, eating, and foraging for food than confined animals which magnify their energy expenditure. The maintenance energy requirements of grazing ruminants has been reported (Table 1) to be from 0 > 100% greater than for animals in confinement, with the cost of travel contributing substantially to this increase. In arid lands, goats have to travel long distances for adequate food and water, and thus, their energy expenditure increase severalfold.

There have been several attemps to measure energy expenditure of grazing animals (Osuji 1974, Whitelaw 1974, Brockway 1978 and Prieto et al. 1992). Data on the energy requirements of grazing animals have been derived from estimates of feed intakes for constant liveweight (Wallace 1955, Reid 1958, Corbett et al. 1961, Coop and Hill 1962, Hutton 1962, Lambourne and Reardon

Table 1. The energy requirements for maintenance in ruminants. Comparison between estimates made with animals housed indoors and those of similar animals at pasture.

	MEm (MJ/d)			
	Indoors	At pasture	Increase	References
			(%)	
Cattle				
	—	—	15.0	[1]Blaxter (1967)
	50.6	50.6	0	[1]Corbett et al. (1961)
	50.6	77.8	53.8	[1]Reid (1958)
	50.6	88.3	74.4	[1]Wallace (1955)
	50.6	77.0-104.6	52.2-106.7	[1]Hutton (1962)
Sheep				
	—	—	11.0	[1]Blaxter(1967)
	6.7	8.4	25.4	[1]Langlands et al. (1963)
	5.9	9.6-11.3	62.7-91.5	[1]Coop and Hill (1962)
	5.9	8.8	49.2	[1]Lambournen and Reardon(1963)
	—	—	60.0-70.0	[2]Young and Corbett (1972)
	5.3	7.0	32.1	[3]Osuji (1974)
Goat				
	—	—	25/50/75	[4]NRC (1981)
	6.3	7.0	11.1	[5]Present work

[1] Estimates of feed intake for constant live weight.
[2] Direct measurements at pasture (CERT and MIC).
[3] By using the energy cost of different activities and their duration at pasture.
[4] Maintenance plus low, medium or high level of activity.
[5] Taking into account the extra costs associated to locomotion at pasture.

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1963, Langlands et al. 1963, Blaxter 1967) or by direct measurement on range (Young and Corbett 1972, Sánchez and Morris 1984). Because of the uncertainties about the reliability of these techniques, energy cost of various activities estimated using calorimetric techniques can be used in conjunction with direct field observations to estimate energy expended in daily activities of free-ranging animals. The usual procedure is a factorial method, whereby the energy expenditure is estimated from calorimetric determination of the energy cost of various activities. The energy cost of each activity is then multiplied by the total time spent by free-ranging animals in that activity and total daily extra energy expended is calculated by summation. Most of the energy required by the grazing animal is due to standing, eating, and locomotion. The contributions of other activities are usually considered negligible. Data on energy expenditure of goats (Lachica 1993) are scarce. Most recommendations have been obtained by feeding trials (i.e. NRC 1981) or have been derived from other ruminant species which have been proved to be misleading (Prieto et al. 1990, Aguilera et al. 1990). Our objectives were to observe and quantify the grazing activities of goats and to estimate their energy expenditure on open range.

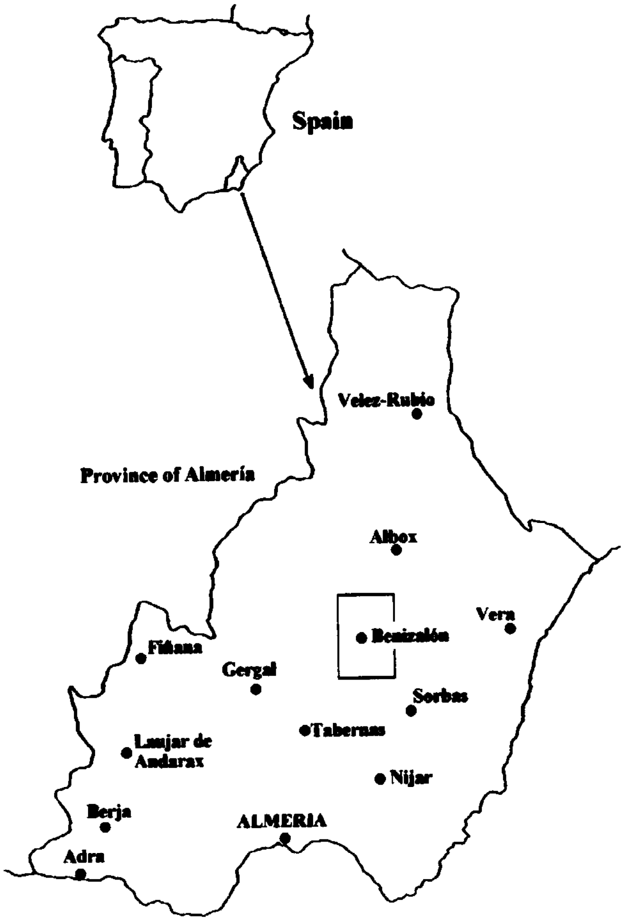

Fig. 1. Study area.

Study Area

The study was carried out at the 130-ha "Los Pajares" pilot zone, in a small valley located in the Filabres mountain-range, near Benizal6n, in the province of Almería, in southern Spain (Fig. 1) (latitude 37° 11' 40" N and longitude 2° 15' W). The topography is rugged, with small hollows and slopes of up to 70%. Average elevation is 865 m above sea level, with local elevation variations of 735 to 1,025 m. The climate is Mediterranean of semi-arid characteristics (De Martonne index: 12.8), consisting of hot, dry summers and mild winters. The mean annual precipitation is 324 mm. Summer is characteristically dry, with the minimum average precipitation being 2.2 mm in July. Seasonal temperatures range from 8.9°C in January to 23.0°C in August, with mean maximum temperature values in the hottest month of up to 35–40°C.

The landscape is characterized by woody plants and perennial grasses resulting from the degradation of the native Mediterranean communities. The vegetation is dominated by *Anthyllis cytisoides*, *Artemisia barrelieri* and *Stipa tenacisimae*. The most abundant plant species of interest for goat production are listed in Table 2. A catalogue of the vegetation of the area has been published by Robles (1990). The study area was chosen because of its geographical location, plant diversity, and representative flock of goats.

Materials and Methods

The experimental flock was composed of 72 head (2 males and 70 lactating females) in Autumn 1990 and of 87 head (3 males, 65 lactating females and 19 growing goats) from Summer 1991. The goats were of the "Granadina", "Malagueña" and "Serrana" breeds and their respective cross-breeds. After morning milking, the goats grazed once (winter) or twice (autumn, spring, and summer) during the day under the supervision of a shepherd and his family and then returned to an enclosed shed, in which they spent

Table 2. Plant species of interest for goat production in "Los Pajares" pilot zone.

Woody plants		
	Larger	*Anthyllis cytisoides, Artemisia barrelieri, Ephedra fragilis, Retama sphaerocarpa, Rhamnus lycioides*
	Smaller	*Fumana laebipes, Fumana thimifolia, Lavandula multifida, Phagnalon saxatile*
Herbaceous		
	Perennial	
		Lathyrus clymenum, Plantago albicans, Dactylis glomerata
	Annual	
		Erucastrum virgatum, Sanguisorba minor, Astragalus hamosus, Astragalus sesameus, Biserrula pelecinus, Lupinus angustifolius, Ornithopus compressus, Trifolium glomeratum Trifolium campestre, Vicia sativa, Sonchus oleraceus, Poa bulbosa
Exotic agricultural plants		
		Prunus dulcis, Olea europaea, Opuntia ficus-indica

the night. Concentrates were provided in autumn and winter. The type of goat management is considered as semi-extensive, for commercial milk production (annual average of 280 liters) and meat (especially carcasses of young kids).

Direct observation (Prieto et al. 1991a, 1991b) was used to measure total distance walked, vertical ascent, or descent, and other grazing activities. The track of a randomly selected lactating female was followed on foot by one observer for 10 minutes for locomotion or for 1 minute by another observer for grazing. This single animal was assumed to be a reliable indicator of flock activity under grazing conditions. At the end of the observation period the nearest goat was followed in a similar way. The procedure was repeated many times during the day throughout 2 consecutive days during each of 4 seasons. In total, 2 observers were used for locomotion measurements (summer values of one observer are missing) and a third observer was used for other grazing activities, such as behaviour and feeding habits (Barroso et al. 1991). The method allows a number of animals to be monitored with minimal labor. Goats had gentle dispositions and were easily approached while grazing. Experiments were conducted from October 1990 to July 1991.

For locomotion studies, each observer carried 1 pedometer and 1 altimeter. The pedometer (Walkman, Walk, and Jog Meter WJ-531, Yamax Corporation, Yokohama, Japan) was attached vertically to the observer's belt. The distance travelled is recorded on a digital indicator and subdivided from 25 m up to 100 km. A stride indicator allows adjustement of the instrument to the step length of the bearer. Several tests of the accuracy of the pedometers were conducted, at the beginning of each trial. The corresponding calibration factors of the instruments were obtained by dividing a known distance walked by the pedometer reading. These values were employed to convert pedometer readings into actual distances walked. The altimeters employed to determine the vertical ascent or descent (Altiplus N1, Pretel, France) are electronic instruments with several functions (altitude, altitude variation, temperature, barometric pressure). Altitude is calculated from atmospheric pressure with a resolution of 1 meter and ranged from -256 to 9,999 m. Temperature ranged from –25°C to 55°C, with an accuracy of about 1°C.

The energy expenditure of locomotion was calculated from both the horizontal and vertical (ascent and descent) components of goat's travel (by means of pedometer and altimeter readings) and the corresponding energy cost (3.35 and 31.1 $J \cdot kg^{-1} \cdot m^{-1}$ for horizontal travel and vertical ascent, respectively) and energy recovery (–13.6 $J \cdot kg^{-1} \cdot m^{-1}$ for vertical descent), which had been obtained by calorimetry with a confinement respiration chamber (Lachica 1993). The results were extrapolated to total time spent by the goats on range during each of 4 seasons and expressed in terms of animals of average live-weight. For example, a 38kg goat travelling an horizontal distance of H m, ascending A m and descending D m in the course of 24 hours would expend 38 × (H×3.35 + A×31.1 - D×13.6) J. The energy expenditure was then compared with the energy requirements for maintenance of the goat, which was previously determined by open-circuit calorimetry (401 $kJ/kg^{0.75}$ per day; Aguilera et al. 1990). From these data the increased energy requirements above maintenance due to activity of grazing goats were calculated.

Treatment effects on locomotion activities within each season were analyzed from data taken by 2 observers throughout 2 consecutive days by means of the one-way analysis of variance, where season was used as error for the analysis, and because the data set was unbalanced in summer, due to the lack of data from 1 observer, Bonferroni's test was used to determine significant diferences ($P<0.05$) among means.

The total phytomass and forage phytomass of pilot zone (130 ha) was evaluated in a previous work (Robles et al. 1991). The method of Point-Centred Quarter (Mueller-Dambois and Ellenberg 1974) and the allometric relationship phytomass/phytovolume were used for shrubs and the plot method for herbaceous biotipes. The values of total phytomass and forage phytomass were estimated as 987.9 and 541.4 kg/ha, the latter value corresponding to 3,435.9 MJ ME/year/ha.

Results and Discussion

Activities were divided into several major categories: grazing, defined as the time spent searching for and ingesting forage; walking, defined as the movement from one place to another without grazing; resting, defined as no activity (standing or lying); and others (socializing, etc.). Grazing, walking, and standing were the primary activities of the goats throughout the study period (values of activities other than walking in summer are missing), accounting for, on average, 57, 27, and 13% of the animal-day period, respectively (Table 3). Distinct seasonal trends are apparent in the data. Grazing activity climbed to a peak (70%) in winter and declined over spring and autumn (52 and 48%, respectively). A similar trend was observed for walking (26, 22 and 21% throughout winter, spring and autumn). Animal travel increased during the dry season (summer, 37%).

Table 3. Seasonal changes in daily activities (%) of the goat on range. (Values are means of 2 days of observation)

	Grazing	Walking	Standing	Lying	Others
			(%)		
Autumn	48.4	20.9	19.0	11.5	0.2
Winter	70.0	26.4	2.2	0	1.5
Spring	51.5	22.0	18.5	7.4	0.7
Summer	–	36.8	–	–	–
$\bar{x} \pm \sigma/\sqrt{n}$	56.6±5.51	26.5±3.14	13.2±4.51	6.3±2.75	0.8±0.31

Previous work on feeding habits in the same pilot zone (Barroso et al. 1991) demonstrated that a goat's diet changes depending on seasonal availability. Annually, 54% of daily feed intake corresponded to woody plants. Grassland use was high throughout the seasons, being greatest in summer (46%) and lowest in winter (36%).

No differences ($P>0.05$) were found when comparing locomotion activities from 2 observers, so pooled values of the different activities were calculated. Somlo et al. (1991) concluded that pedometers are inaccurate when carried by goats and were only adequate to measure distances when used by humans. The average pedometer calibration factors (distance travelled/distance recorded) and their coefficients of variation indicate the reliability of the

Table 4. Mean daily locomotion activities of the goat at pasture in the study area. (Values are means of 2 observers throughout 2 consecutive days)*

	Time spent at pasture	Distance travelled	Vertical ascent or descent	Mean speed
	(h)	(m)	(m)	(m/min)
Autumn	5.7^{a}	3482^{a}	139^{a}	10.2^{a}
Winter	6.0^{ab}	4137^{ab}	181^{a}	11.5^{a}
Spring	7.7^{b}	3799^{a}	197^{a}	8.2^{a}
Summer	7.2^{ab}	5763^{b}	153^{a}	13.3^{a}
Annual mean	6.7	4295	168	10.8
Pooled std. error	0.22	153.5	11.2	0.50
Range	(5.1–8.7)	(2982–6725)	(104–253)	(5.7–15.6)

*Within the same column values bearing different superscripts are significantly different ($P<0.05$).

records of distances walked in the present work ($\bar{x}_1 = 1.005 \pm 0.0213$, CV = 7.33%, n = 12; $\bar{x}_2 = 0.984 \pm 0.0459$, CV = 16.18%, n = 12; for pedometers 1 and 2, respectively). Distance travelled daily by goats on range (Table 4) fluctuated from 5,763 m in summer to 3,482 m in autumn, with an annual average of 4,295 m, which represents a mean annual daily speed of 10.8 m/min. These data were calculated over the whole day, not over the time spent walking. Travel activity peaked in summer and then declined in the other seasons, with a minimum in autumn. The mean annual vertical ascent or descent was 168 m.

Estimated heat production due to locomotion (Table 5) ranged from 56.9 to 34.8 kJ/kg$^{0.75}$ per day in summer and autumn, respectively, with an annual mean value of 43.5 kJ/kg$^{0.75}$ per day. Assuming a metabolisable energy requirement for maintenance of 401 kJ/kg$^{0.75}$ per day (Aguilera et al. 1990) and the corresponding average live weight, these values account for an estimated increased heat production above maintenance on range of 14.2 and 8.7% in summer and autumn, respectively ($\bar{x}$ = 10.8%). This agrees with the mean increase of 11% estimated for free ranging sheep by Blaxter (1967) but is markedly lower than values reported for free ranging cattle and sheep grazing (Table 1). For goats, the National Research Council (NRC 1981) considers a mean value of 424 kJ ME/kg$^{0.75}$, which is slightly greater than our experimental value, to determine their maintenance requeriments and then makes an extra allowance of energy to be added to the maintenance requeriments. For increased muscular activity of animals under grazing conditions: a 25% increment in the case of light activity, a 50% increment on semiarid rangeland pasture and on slightly hilly land, and a 75% increment in case of long-distance travel on sparsely vegetated grassland or on mountainous transhumance pasture was used. The application of these tabulated values to our data would overestimate the results when compared with the experimental values found. This indicates that it is inapropriate to extrapolate theorical allowances for activity to all conditions. A direct estimation of the additional expenditure of energy under grazing conditions, as done in this work, would be more advisable.

Table 5. The energy cost of locomotion of the goat at pasture in the study area during the different seasons. (Values are means of 2 observers throughout 2 consecutive days)[1]

	Live weight	Heat production (HP)	Estimated increased HP over maintenance[2]
	(kg)	(kJ/kg$^{0.75}$)	(%)
Autumn	37	34.8^{a}	8.7^{a}
Winter	35	41.4^{ab}	10.3^{ab}
Spring	40	40.7^{ab}	10.1^{ab}
Summer	45	56.9^{b}	14.2^{b}
Annual mean	38	43.5	10.8
Pooled std. error	0.0	1.57	0.39

[1] Within the same column values bearing different superscripts are significantly different ($P<0.05$).

[2] MEm=401 kJ/kg$^{0.75}$ per day (Aguilera et al., 1990).

Conclusions

The method used appear to be adequate to simulate and quantify grazing activities of goats on open range by means of direct observation. It is simple and easy to apply to field conditions, requiring only 1 observer for locomotion studies. The results also showed that the energy cost of locomotion represented a substantial contribution to the energy expenditure of goats on range. This study will facilitate a more accurate estimation of the stocking rate in the study area.

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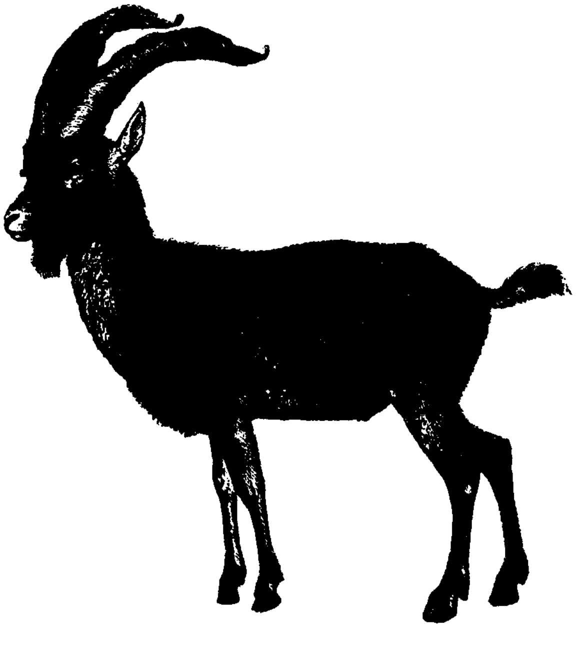

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Cattle as dispersers of hound's-tongue on rangeland in southeastern British Columbia

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Abstract

Hound's-tongue (*Cynoglossum officinale* L.) is a noxious weed on forested range of western North America (N.A.), which produces barbed nutlets (burrs) that attach to animals. There is anecdotal evidence that cattle are important dispersers of hound's-tongue in N.A., although European studies suggest animal dispersal of hound's-tongue burrs is minimal. The objectives of this research were to examine the role of cattle as hound's-tongue dispersers, and to develop a method of estimating hound's-tongue burr and plant density on rangeland that may be useful to researchers and range managers. To determine the movement of burrs onto cattle, the number of burrs on marked stalks, before and after grazing, were counted. In 1993 and 1994, about 65% of the burrs stalk^{-1} were picked up by grazing cattle, whereas, only 14% of the burrs stalk^{-1} were lost in a paddock ungrazed by cattle in 1994. Individual cows were monitored for burr gains and losses during monthly moves between paddocks by photographing their faces, and counting the burrs face^{-1} from projected slides. Cattle also were photographed every 2 weeks while in-situ on paddocks. Within 2 to 4 weeks, cows acquired and then lost burrs as they moved within and between paddocks. These experiments suggest that cattle are major dispersers of hound's-tongue on rangelands. There was a positive, linear relationship (R^2 =0.77; p<0.001, N=13) between the mean number of burrs face^{-1} and the number of burr stalks ha^{-1} of paddock. A relationship between the percent of photographed cattle with burrs and stalk density was best described by a hyperbolic model (R^2 = 0.83). With refinement, these relationships between burrs on cattle and hound's-tongue density on paddocks may be useful in monitoring hound's-tongue populations.

Key Words: adhesive fruits, burrs, monitoring weed populations, noxious range weed, seed dispersal, weed biocontrol

Hound's-tongue (*Cynoglossum officinale* L.) is a noxious rangeland weed in western Canada and United States that was introduced to our continent from Eurasia (Scoggan 1978, Upadhyaya et al. 1988). It is particularly abundant in the Interior Douglas Fir and Ponderosa Pine-Bunchgrass biogeoclimatic zones of British Columbia (B.C.) (Upadhyaya et al. 1988), where cattlemen consider hound's-tongue second only to the knapweeds as a priority for control (Upadhyaya and Cranston 1991). Hound's-tongue is a concern because it hinders the establishment of forage on newly-created pastures, and its barbed seeds or burrs attach to cattle, causing irritation and potential market losses (Upadhyaya and Cranston 1991). Hound's-tongue also is toxic to livestock (Knight et al. 1984, Baker et al. 1989). Chemical and cultural controls are being used to a limited degree in British Columbia (Upadhyaya and Cranston 1991). Several European insects that feed on hound's-tongue are being tested as potential biocontrol agents, but have yet to be approved for release in North America.

Detailed studies on the ecology of hound's-tongue are needed to enhance the likelihood of its successful control, but such studies have only been done on European populations of this weed. In the Netherlands, hound's-tongue has been described as a biennial or short-lived perennial that depends on both the continual creation of disturbed habitats and the dispersal of its seed to these habitats for either population maintenance or growth (Van der Meijden et al. 1992). However, large-scale disturbances and the dispersal of hound's-tongue burrs beyond a few metres were rare in English and Dutch studies of hound's-tongue ecology (Boorman and Fuller 1984, Van der Meijden et al. 1992). Furthermore, the largest animals thought responsible for burr dispersal were rabbits (De Jong and Klinkhamer 1988), and there were doubts as to their efficacy as dispersers (Boorman and Fuller 1984). It is likely the success of hound's-tongue on the forested rangelands of North America is due to ample disturbed habitats caused by logging and other man-related activities, and the availability of large dispersal agents such as cattle. However, the role of cattle and/or wildlife in the dispersal of hound's-tongue is largely anecdotal.

The objectives of this study were: 1) to examine the role of cattle in dispersing hound's-tongue on forested rangeland, and 2) to test the relationship between the number of burrs on cattle and the density of hound's-tongue burr stalks on paddocks. If a significant relationship is found to exist, surveys of burrs on cattle would be useful to range managers attempting to predict the spread and increase of hound's-tongue, or to researchers monitoring the impact of control methods.

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Materials and Methods

Study Area

The study was conducted on 3 contiguous range units in the Cranbrook Forest District, British Columbia. Each range unit is divided into 5 to 6 fenced paddocks, 195 to 660 ha in area, and cattle are rotated on a monthly basis between paddocks within each range unit from May to September/October. All paddocks were within the Interior Douglas Fir biogeoclimatic zone.

Hound's-tongue infestations ranged from low to high among the paddocks. The majority of plants were situated in patches of less than 100 to several thousand individuals on logged areas that ranged from 1 to 15 ha in size. Individual hound's-tongue plants typically produce from 1 to 8 flower stalks, which are 30–120 cm high (Upadhyaya et al. 1988) and determinate in growth. Each stalk is capable of producing several hundred hound's-tongue seeds or burrs, which ripen near-concurrently in June or July. In B.C., the majority of ripe burrs remain on stalks until detached by passing animals.

Role of Cattle in Hound's-tongue Seed Dispersal

Two sets of experiments were conducted to determine the role of cattle in moving hound's-tongue burrs among paddocks. One set examined the movement of burrs onto cattle from hound's-tongue plants, while the other examined the gains and losses of burrs from cattle over time.

The study of burr movement onto cattle took place in 1993 and 1994, on 2 separate range units, respectively, where hound's-tongue burrs had recently ripened on stalks. Before cattle were released in 1993, 60 hound's-tongue stalks were randomly chosen and tagged within a 100 m radius on a paddock and the total number of burrs stalk^{-1} were counted. Within 1 week, cattle were allowed to graze the paddock. Six weeks later, after cattle had ranged throughout the paddock, a second count of burrs was made for the stalks that could be relocated (i.e., 47 stalks). Signs of cattle disturbance, such as cropping of grass, fresh hoof prints, and manure, were noted. Since deer and elk also occurred in the area, a control paddock was added to the experiment in 1994. A logged area with hound's-tongue was chosen that spanned 2 paddocks on a range unit. Whereas the paddock on 1 side of the fence was grazed by cattle, the control paddock was ungrazed. Fifty hound's-tongue burr stalks were randomly chosen within a 100 m radius on each side of the fence separating the 2 paddocks. These were tagged and the number of burrs stalk^{-1} were counted before cattle were released in the cattle treatment paddock. Burrs were counted 4 weeks later on those stalks that could be relocated (i.e., 44 stalks on grazed paddock and 50 on control paddock). Fresh signs of cattle and deer/elk were noted for both paddocks during the second visit. A paired T-test was used on the 1993 data to detect significant differences in the mean number of burrs stalk^{-1} before and after grazing. The 1994 data were analysed using a repeated measures ANOVA with treatment (i.e., control versus grazed paddock) as a grouping factor. Post hoc contrasts of means were conducted on before and after grazing data using univariate repeated measures F-tests (Systat 1992). Stalks that could not be relocated for the second count were eliminated from the data sets.

To determine the fate of burrs that were attached to cattle, gains and losses of burrs were monitored on individual animals from 1 range unit. In 1992, 52 to 143 cows were photographed monthly from June to September using a 35 mm camera fitted with a 100–300 mm telephoto zoom lens. Cattle were photographed when they were moved between paddocks during the normal rotation schedule. Photographs were frontal views of the cow face, and included the forehead, nose, and the forward-pointing surface of both ears. Photographic slides were projected, and the number of visible burrs face^{-1} were counted. The face was used as a sample unit because it is a good indicator of when cattle have been grazing in hound's-tongue patches, and the facial view provides identification in the form of an ear tag number. Hence, the same animals could be followed in successive photo sessions. By random chance, a total of 26 animals were photographed consecutively each month from June to September. Differences in the mean number of burrs face^{-1} among months were detected using a one-way repeated measures ANOVA, followed by univariate repeated measures F-tests to compare consecutive months (Systat 1992).

In 1994, 31 to 70 animals from a herd were randomly photographed every 2 weeks while on each of 2 different paddocks that were consecutive in the rotation schedule (Wapiti Lake and Horseshoe). These animals were photographed in situ on the paddocks and not during round-up. To detect significant differences in mean burr numbers face^{-1}, a two-way ANOVA was conducted, with paddock and photography period as grouping factors. This was followed by Tukey HSD multiple comparisons (Systat 1992) to detect pairwise differences in means.

Hound's-tongue Density and Burr Numbers on Cattle

The relationship between hound's-tongue stalk density on paddocks and the number of burrs on cattle faces was studied from 1992 to 1994, on the 3 contiguous range units mentioned previously (see Study Area). In total, 13 photography sessions of cattle were conducted, involving paddocks with a wide range in hound's-tongue density. None of the paddocks had been previously grazed in the rotation schedules. In 9 cases, the cattle were photographed in a holding corral after being removed from a paddock where they had grazed for 3 to 4 weeks. In 4 cases the cattle were photographed while still in the paddock. As many cows as possible were photographed each time (i.e., 33 to 149 depending on the size of the herd), and an average number of burrs face^{-1} paddock^{-1} was determined from projected slides. The number of hound's-tongue stalks paddock^{-1} was estimated by thoroughly searching disturbed areas and counting all stalks. The count was expected to be a close approximation of the total number of stalks in each paddock, because hound's-tongue only grows on disturbed areas. To standardize for differences in paddock size, the number of counted burr stalks ha^{-1} was calculated for each paddock. The relationship between the mean number of burrs face^{-1} of cows that had been grazing in hound's-tongue infested paddocks and the number of burr stalks ha^{-1} was described with a regression equation. The percent of photographed cattle with burrs also was related to the number of stalks ha^{-1} using a non-linear regression program (Pcnonlin, 1992).

Results

Role of Cattle in Hound's-tongue Seed Dispersal

Hound's-tongue burrs were reduced on stalks by cattle activity (Fig. 1). In 1993, an average loss of 226.7±6.7 (SE) burrs stalk^{-1} was noted after cattle had grazed the paddock (df=46, t=13.60, p<0.001; before vs. after cattle). This represented a 65% reduction in burrs. Only 1 out of the 47 tagged stalks (2%) that were relocated had not lost burrs. In 1994, there was a significant effect of both treatment ($F_{1,92}$=56.51, p<0.001; grazed vs. control) and time ($F_{1,92}$=110.03, p<0.001; before vs. after cattle) on burr losses from stalks (Fig. 1). On the paddock where cattle had grazed, 140.1±14.0 burrs stalk^{-1} were removed, representing a loss of 67%. Only 52.9±11.8 burrs stalk^{-1}, or 14%, were lost from the hound's-tongue stalks in the control paddock where cattle were absent (Fig. 1). In the control paddock, 36% of the stalks had retained all burrs, while in the grazed paddock, only 2% of the tagged stalks had retained all burrs.

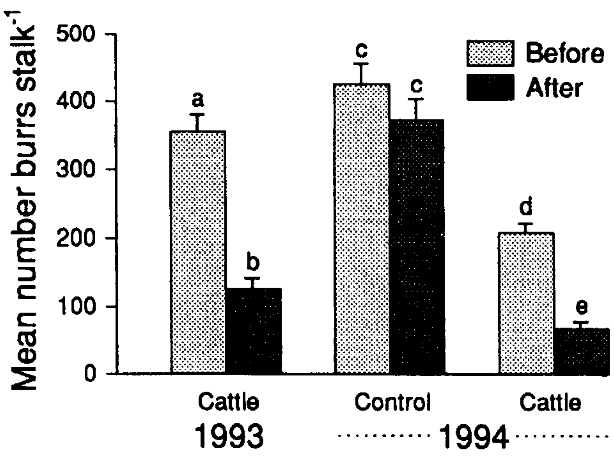

Fig. 1. Burr counts on tagged stalks before and after a cattle treatment in 1993 on a paddock where cattle had grazed, and in 1994 on a paddock where cattle had grazed, and a paddock where cattle were excluded (control). Vertical lines indicate SE of the mean. Paired bars with different letters are significantly different at p<0.05.

When the same cows were photographed repeatedly from June to September, it was evident that they were gaining and losing burrs on a monthly basis (Fig. 2). For instance, 73% (19/26) of the cattle photographed consecutively had gained burrs on their faces between June and July, and of these, 89% (17/19) had lost all of their facial burrs by August. The burr losses ranged from 1 to 202 burrs face^{-1} (Fig. 2). Between August and September, 46% (12/26) of the cattle showed gains that ranged from 1 to 93 burrs, 12% (3/26) showed losses ranging from 10 to 23, and the remaining 42% (11/26) had no facial burrs on both dates. Out of the 26 cattle photographed consecutively, 3 showed no gains across all photography dates. Mean changes in burr numbers were significant among months ($F_{3,75}$=5.49, p=0.002; Fig. 2).

Cattle photographed 2 weeks apart on 2 consecutive paddocks in a rotation, demonstrated slight fluctuations in burrs over the short-term (Fig. 3). There was no significant difference in the mean number of burrs face^{-1} between photography sessions on either paddock ($F_{1,174}$=0.02, p=0.89). However, there were differences in burr accumulation between paddocks ($F_{1,174}$=4.34, p=0.04).

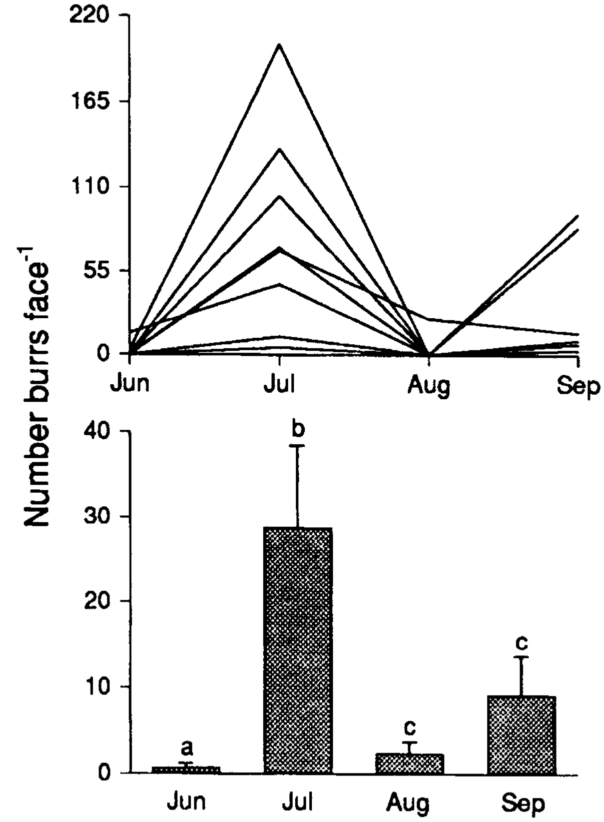

Fig. 2. Burr gains and losses on the faces of cattle photographed consecutively during monthly moves between paddocks. Top: Total number of burrs on the faces of 10 individual cows (1 curve cow^{-1}) purposely chosen to depict the range in monthly changes which occurred. Bottom: Mean number of burrs face^{-1} for all 26 cows photographed consecutively. Vertical lines indicate SE of the mean. Any 2 consecutive bars with different letters are significantly different at p<0.05.

Hound's-tongue Density and Burr Accumulation on Cattle

There was a significant, positive relationship between the mean number of burrs face^{-1} and the number of hound's-tongue stalks on grazed paddocks (Fig. 4). The correlation coefficient was larger when those cattle photographed in situ in paddocks were removed from the regression (Fig. 4). However, inclusion of these data points also produced a significant relationship.

The relationship between percent of photographed cattle with burrs on their faces and the number of stalks ha^{-1} of paddock was best described by a non-linear model of the form; $f(x) = ax/b+x$ (i.e., a hyperbolic curve; Fig. 5). The percent of photographed cattle with burrs is "f(x), and "x" is the density of burr stalks ha^{-1}. There are 2 estimated parameters in the equation, "a" and "b", which respectively represent the maximum percentage of cattle within a herd that may acquire burrs, and the stalk density at which 50% of the cattle in a herd acquire burrs. In fitting a curve to the data, the program Pcnonlin (1992) estimated a=99.3 and b=11.0.

Discussion

The results of the present study indicate that cattle are important dispersers of hound's-tongue seed. They are not only efficient in picking up ripe burrs from standing hound's-tongue stalks (Fig. 1), but within a relatively short period can lose accumulated burrs while in the same or a different paddock (Figs. 2 and 3). Burrs adhere to cattle that are grazing or walking among standing hound's-tongue stalks on logged areas and along logging/range roads. The mature burrs can attach to any part of the cow's body, but tend to be concentrated on the head, chest, and underside of animals. Burrs probably drop from cattle as they pass through underbrush, and when they rub against each other or objects such as trees, rocks, or posts. The latter behavior was commonly observed and, not surprisingly, hound's-tongue plants often are found ringing favorite cattle rubbing areas (pers. obs.).

Sequential photographs of cows document that cattle can quickly remove a large percentage of the burrs gained. Some cows had about 50 to 200 burrs on their faces during the July photography session, but no burrs in August after a stay in a paddock relatively clean of hound's-tongue (Fig. 2). Although these data reflect burr gains and losses on 1 part of the cow's body, they serve to illustrate the potential for large numbers of burrs to be carried to new areas by cattle. The fruits of hound's-tongue are covered in short barbed prickles (Upadhyaya and Cranston 1991), and do not seem to adhere as tightly to cattle hair as the burrs of some other plants, such as burdock (*Arctium minus* (Hill) Bernh.). Only if the hound's-tongue burrs become matted in the long hairs of the ears, forehead, or tail, is long-term adherence expected.

Despite the short-term adherence of burrs to cattle, they are capable of long-distance dispersal of burrs. Given that the individual paddocks under study were up to 660 ha in area, cattle are capable of moving burrs much further than 1 to 5 meters, which was the typical dispersal range of hound's-tongue seed in the Netherlands and England (Van Leeuwen and Van Breemen 1980, Boorman and Fuller 1984). Furthermore, if cattle with burrs are transported any distance to market, the weed may spread much further than from paddock to paddock within a range unit.

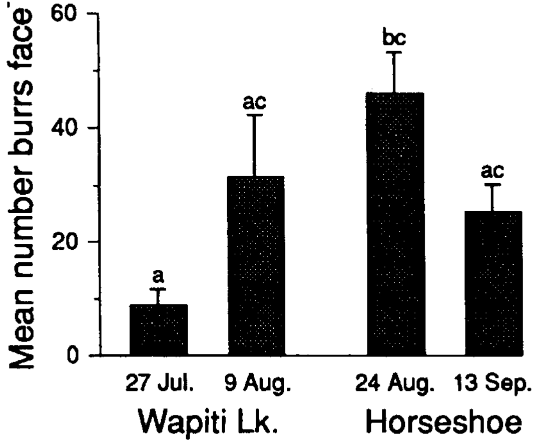

Fig. 3. Mean burr gains and losses on the faces of cows photographed every 2 weeks on 2 consecutive paddocks (Wapiti Lk. and Horseshoe) in a rotation. Cattle were moved on 19 August. Vertical bars indicate SE of the mean. Bars with different letters are significantly different at $p<0.05$.

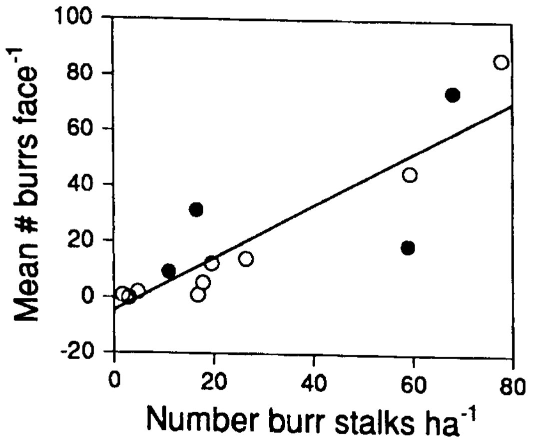

Fig. 4. Relationship between the mean number of burrs cow face^{-1} and the number of hound's-tongue burr stalks ha^{-1}. Filled circles depict cattle that were photographed in-situ on paddocks. Open circles depict cattle that were photographed immediately after round-up, when being moved to another paddock in their rotation. Regression through all circles (line shown), $Y=0.945X-4.568$, $R^2=0.773$, $p<0.001$, $n=13$. Regression through open circles, $Y=1.067X-8.379$, $R^2=0.929$, $p<0.001$, $n=9$.

Wildlife, such as deer and elk, also may contribute to hound's-tongue seed dispersal, although it is suspected that their role as dispersers is minor relative to that of cattle. In the experiment investigating the loss of ripe burrs from hound's-tongue stalks in paddocks, few burrs were lost from the tagged stalks of the control paddock in 1994 (Fig. 1), despite fresh signs that deer had gone through the hound's-tongue patch. However, there also was evidence of minimal livestock activity, possibly due to the presence of stray cattle. Hence, final conclusions on the role of wildlife as hound's-tongue dispersers cannot be made without further study.

Further investigation also is required of the role of cattle in acquiring hound's-tongue seed if generalizations are to be made for a broader geographic area, and different management regimes. Despite the fact that only 1 location in each of 1993 and 1994 was used for study of cattle acquisition of burrs, similar results were obtained involving 2 different range units (Fig. 1). Cattle definitely were involved in acquiring a large percentage of the burrs produced by hound's-tongue plants on the paddocks where they had grazed. Stock density probably is another factor affecting the movement of burrs between sites, and should be included in further studies.

An understanding of the role of cattle in dispersing hound's-tongue seed on rangelands together with information on the weed's ecological requirements, may be important in curtailing the spread of hound's-tongue to new areas. European studies indicate that hound's-tongue requires ground disturbance to become established (Boorman and Fuller 1984, Klinkhamer and De Jong 1988). In the interior of B.C., hound's-tongue grows particularly well on logged sites which become paddocks for cattle (Upadhyaya and Cranston 1991). Hence, cattle not only pick up burrs from previously-logged sites with dense stands of hound's-

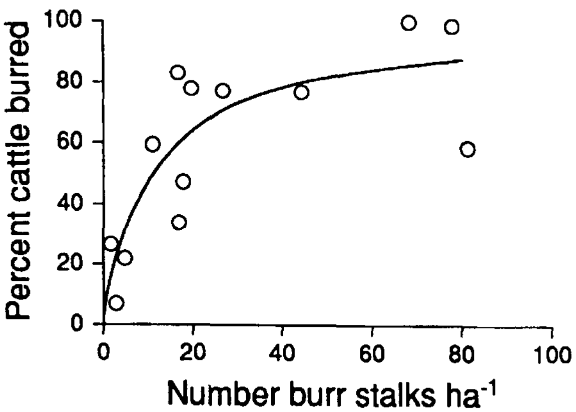

Fig. 5. Relationship between percent photographed cattle with burrs on their faces and number of burr stalks ha^{-1} of grazed paddock. The curve is described by the hyperbolic equation, % cattle with burrs = 99.3x/(11.0 + x), where "x" = number of burr stalks ha^{-1}. R^2=0.828.

tongue, but then introduce the seed to the recently disturbed sites of new paddocks. Cleaning cattle before they are moved to new paddocks or range units would help prevent or slow the spread and increase of this noxious weed.

There was a relationship between the numbers of burrs on cattle and the size of hound's-tongue infestations on paddocks. When cattle were on paddocks with low amounts of hound's-tongue, the cattle had low numbers of burrs on their faces. Conversely, cattle that came off of paddocks with large amounts of hound's-tongue, tended to have high numbers of burrs. Subsequent investigation of the relationship between burr numbers on cattle and burr stalk densities on paddocks indicated that a positive, linear relationship exists (Fig. 4). Furthermore, the strength of the relationship was greater if the regression only included data from cattle photographed soon after being moved off of a paddock versus those photographed while still in a paddock. A possible explanation for this phenomenon is that during a round-up cattle are typically exposed to a large area of paddock in a short period of time, and tend to be moved down the trails and roads where hound's-tongue occurs. Hence, the burrs gained after a cattle move would be a better reflection of hound's-tongue density over a large part of the paddock. Further information on exposure time of cattle to hound's-tongue is required to fully understand the relationship between burr numbers on cattle and stalk densities.

The relationship between burrs on cattle and hound's-tongue density on paddocks could be of potential use in monitoring hound's-tongue infestations. The measurement of burrs, either through photography or recording the percent of burred cattle, would be a much easier and less time-consuming method of determining the density of hound's-tongue on paddocks than actually counting stalks or plants. The data obtained could then be used to estimate the impact of various controls, including biocontrol, on either stalk density or burr numbers on cattle, or to potentially determine the rate of spread of the weed. Further research is needed, however, to refine the relationships among these methods and the actual measures of hound's-tongue populations.

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Landscape structure and change in a hardwood forest-tallgrass prairie ecotone

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Abstract

Temporal changes in land use, vegetation cover types, and landscape structure were examined in a hardwood forest-tallgrass prairie ecotone in northern Oklahoma using a Geographic Information System. Our objective was to examine relationships between human activity, changes in land use and vegetation cover type, and landscape structure in rural landscapes between 1966 and 1990. Cover types in most of the high density rural population landscape in this study require more intensive inputs and management, which resulted in a landscape with lower diversity, higher homogeneity, and greater patch fragmentation compared to the low density rural population landscape. Both native grasslands and forests were less fragmented in the low density rural population landscape whereas forests were increasingly fragmented in the high density rural population landscape. Native grasslands were less fragmented than forests for all years in both the low density rural population and high density rural population landscapes. Our study suggests conservationists should focus their concerns on fragmentation and losses in biological diversity that accompany increased human activity in densely populated rural landscapes that surround urban centers. Extensively managed landscapes dominated by native vegetation that are under less pressure from expanding human influence are in less peril.

Key Words: geographic information system, landscape structure, urbanization, vegetation cover type

Agricultural development of the Great Plains since the 1870's has caused a dramatic decline of tallgrass prairie, with the reduction of area occupied by this ecosystem exceeding any other in North America (Samson and Knopf 1994). Large, extensively managed blocks of native vegetation have been fragmented into smaller blocks of intensively managed introduced pastures and cropland. Urban sprawl into rural landscapes may exacerbate these changes in land use and vegetation cover type thereby further altering landscape structure and diversity. Replacing natural vegetation with managed systems of altered structure often reduce ecosystem diversity on a regional scale (Krummel et al. 1987, McNeeley et al. 1990). Such anthropogenic changes have caused concern about preserving and managing for biological diversity (Grove and Hohmann 1992, Urban et al. 1992, West 1993).

Although scientific literature contains extensive research on the effects of urbanization and fragmentation of contiguous forests, research is lacking in native grasslands (Samson and Knopf 1994) and grassland-forest ecotones (Risser 1990). Ecotones provide valuable insight to the complex dynamics of ecosystems including temporal changes in landscape structure and function (Wiens et al. 1985, Hardt and Forman 1989). Although ecotones are dynamic and typically have high community diversity (Risser 1990, Johnston et al. 1992), anthropogenic influences on change have not been well documented.

Changes in landscape structure may affect a wide variety of ecological processes (Turner 1989); but, relatively little is known about how components of landscape change over time (Baker 1992). Therefore, descriptions of changing landscape patterns form an important component of our understanding of ecological dynamics necessary to integrate the often conflicting demands of wildlife habitat, recreation, agriculture, and development. We chose 2 landscapes that differed in rural population density to test the hypothesis that human activity alters cover types and structure of landscapes in rural areas. Specifically, we hypothesized that 1) high density rural population and low density rural population landscapes differ in temporal change in land use, vegetation cover types, and landscape structure; and 2) structure of native grasslands have changed more than forests because of greater human activity in native grasslands.

Study Site

Our study was centered around suburban Tulsa, Okla., and the surrounding rural areas in northeastern Osage and southern Washington Counties. We selected 2 U.S. Fish and Wildlife Service Breeding Bird Survey routes, 024 (Collinsville) and 026 (Bartlesville) (Fig. 1) (Baumgartner and Baumgartner 1992), to represent the suburban to rural transition lying within the ecotonal area of the Cherokee Prairie grassland formation and oak-hickory savanna of the Cross Timbers (Bruner 1931, Soil

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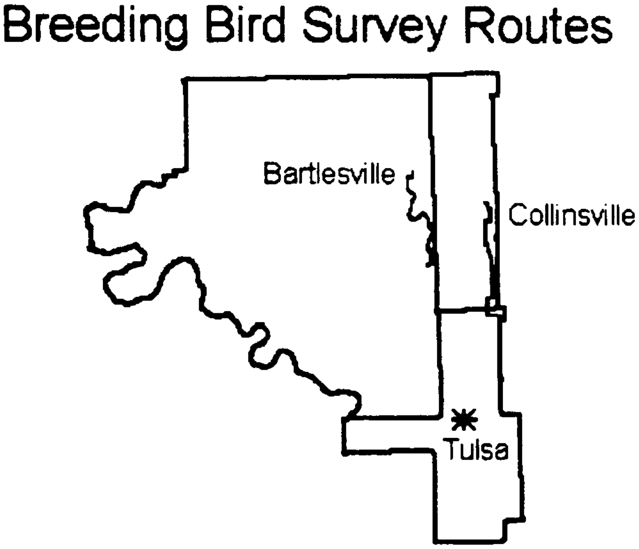

Fig. 1. The 2 U.S. Fish and Wildlife Service Breeding Bird Survey routes located in northern Oklahoma used for the study area.

Conservation Service 1981). The Cherokee Prairie extends as a long, narrow strip, 240 km southward from the Kansas state line with a width ranging from 48 to 96 km throughout most of its length. The area is better adapted to support grasses than forests because of climate and underlying geology (Harlan 1957). The Cross Timbers lie west of the Cherokee Prairie and the Lower Arkansas Valley, extending 288 km southward from Kansas with a width of 80 km. The region is a transitional oak forest with interspersed grasslands (Bruner 1931, Gray and Galloway 1959).

Survey routes varied in their proximity to Tulsa, a major metropolitan area in northern Oklahoma with an estimated population of 361,628 (U.S. Department of Commerce 1990). The Collinsville route is located in Washington County and the Bartlesville route is located in Osage County. Human population density of Washington and Osage County in 1990 was 3,340 km^{-2} and 520 km^{-2}, respectively. In addition, rural population density of Washington and Osage County in 1990 was 10.3 km^{-2} and 4.9 km^{-2}, respectively. Rural population is defined by the U.S. Department of Commerce (1990) as residing in communities of less than 2,500 people. Hence, from this point forward, the 2 landscapes will be discussed as high density rural population or low density rural population.

Methods

Data Collection

We used aerial photography for 1966, 1973, 1980, and 1990 as the data set for addressing the relationships between human activity (i.e. population density) and changes in land use, vegetation cover type, and landscape structure. Black and white aerial photographs were obtained from the U.S. Department of Agriculture, ASCS, Aerial Photography Field Office, Salt Lake City, Ut. Photographs were 60.96 × 60.96-cm enlargements with a representative fraction of 1:7,920. We used portions of photography that covered breeding bird survey routes (40.2 km in length) and 0.8-km on each side of the route boundary. The resulting coverage was approximately 6,430 ha for each route.

Topographic quadrangel maps, photo inspected in 1976, showed the natural and man-made features of the land at 1:24,000 scale and were obtained from the Oklahoma Geological Survey, Norman, Okla. The quadrangles indicate both geographical coordinates and specific features such as vegetation, water, roads, and towns. These maps were used for both geo-registration of the photography and to aid in photo-interpretation.

Features identified on each photograph included: breeding bird survey route, roads, buildings and houses, oil and gas facilities, land use, and vegetation cover types. Land use and vegetation cover types were interpreted based on the classification scheme of Stoms et al. (1983) (Table 1). All interpreted polygons of interest were traced on overlying acetate and the results of supervised photo interpretation for 1966, 1973, and 1980 were compared to those from the 1990 photography.

Table 1. Classification system used to map land use and vegetation cover types (adapted from Stoms et al. 1983).

Land use and cover type	Description
Developed area	Land occupied by residential, industrial, or other human structures and non-agricultural activities. Also includes transportation and utility facilities
Roads	Black top, gravel, dirt roads and driveways
Water	Ponds, lakes, streams, and rivers
Cropland	Land cultivated for row crops and cereal grains but excluding grazing lands
Pasture land and hay meadows	Includes pasture land (seeded, grasslands used for grazing by cattle, sheep, goats, and horses) and hay meadows
Native grassland	Native grasslands with less than 10% cover by shrubs or trees
Deciduous forest	Vegetation dominated (>10%) by cover of broadleaf hardwoods. Mostly post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*)
Brush-treated land	Native vegetation subjected to herbicides, fire, or chaining to control woody brush encroachment
Bare ground	Land with less than 5% vegetative cover

Completed polygons were digitized using a digital scanner. Scanned images were edited, rectified, and vectorized using LTPlus (Line Trace Plus, version 2.22) and imported into the Geographic Information System GRASS (Geographic Resource Analysis Support System) (Shapiro et al. 1992). Vector maps were then patched together to form the complete route, labeled, and converted to a raster map with 5-m resolution.

Data Analysis

Within the Geographic Information System, changes in land use and vegetation cover types over the last 24 years were examined. Landscape analysis was performed using the raster landscape ecological spatial analysis package within GRASS (Baker and Cai 1992). This package was developed for quantitative analysis of landscape structure. The raster landscape ecological programs were used to generate landscape measures of mean patch size, fractal dimension, richness, Shannon diversity index, dominance index, contagion, angular second moment, and contrast.

Mean patch size is the mean area (ha) of patches in the sampling area and serves as an index of fragmentation. It is calculated for all patches in the sampling area by dividing sample area size by the number of patches (Baker and Cai 1992). As patches become smaller because of fragmentation, mean patch size decreases. Fractal dimension is a measure of fractal geometry or patch shape complexity of a landscape (Mandelbrot 1983, Krummel et al. 1987). Fractal dimension was calculated by regressing polygon area against perimeter length for each landscape patch. Values for fractal dimension range from 1 to 2. Landscapes dominated by simple patterns (circles and squares) have low fractal dimension values while landscapes dominated by complex or convoluted patterns have high fractal dimension values (Krummel et al. 1987).

Shannon's diversity index combines richness and evenness. Richness refers to the number of patch attributes present in the sampling area and evenness refers to the distribution of area among different patch types (Turner 1990a, 1990b). Richness and evenness are the compositional and structural components of diversity, respectively (McGarigal and Marks 1994). Larger values for Shannon's diversity index indicate a more diverse landscape (O'Neill et al. 1988). The dominance index is based on the Shannon-Weaver diversity index (Shannon and Weaver 1962) but emphasizes deviation from evenness. The dominance index measures the extent that specific land uses (or vegetative cover types) dominate the landscape (O'Neill et al. 1988). Large dominance index values indicate a landscape dominated by 1 or few cover types while low dominance index values indicate a landscape with many cover types represented in approximately equal proportions (Turner 1990a).

Three texture measures were calculated for the regional landscape which included contagion, angular second moment, and contrast using eight-neighbor analysis to quantify the adjacency of similar patch types. Contagion measures the extent to which cover types are aggregated or clumped in contiguous patches (O'Neill et al. 1988). A landscape with well interspersed patch types will have a lower contagion compared to a landscape with poorly interspersed patch types (McGarigal and Marks 1994). Angular second moment is a measure of landscape homogeneity. Larger values for angular second moment indicate more homogeneity (McGarigal and Marks 1994). Contrast measures local variation present in the landscape (Baker 1994).

Comparisons between 1966 and 1990 were made between Collinsville and Bartlesville to assess the effects of human activity on vegetation cover types and landscape structure. Mean patch size and fractal dimension were also determined for native grasslands and forests within both Collinsville and Bartlesville to assess the effects of human activity on structure of these cover types.

Results and Discussion

Effects of Human Activity

Temporal Changes in Cover Types

Developed areas increased markedly in the high density rural population landscape (Collinsville) whereas developed areas decreased in the low density rural population landscape (Bartlesville) between 1966 and 1990 (Table 2). Therefore, these landscapes provided excellent study areas for investigation of the effects of human activity in rural landscapes on vegetation change and landscape structure. Because the high density rural population landscape was located near Tulsa, it experienced a greater amount of human influence over the past 25 years compared to the low density rural population landscape and resulted in different temporal changes in vegetation cover types.

Table 2. Temporal changes in vegetation cover types (ha) and percent change from 1966 of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990.

Index	Year				Change
	1966	1973	1980	1990	
	(ha)				-(%)-
High density rural population (Collinsville)					
Developed areas	16	7	25	24	50
Roads	88	92	101	87	-1
Water	53	76	58	71	34
Cropland	556	453	208	120	-78
Pasture land and hay meadows	676	672	850	999	48
Native grassland	1,432	1,601	1,546	1,508	5
Deciduous forest	449	294	398	377	-16
Brush-treated land	0	41	4	5	—
Bare ground	2	6	2	2	0
Low density rural population (Bartlesville)					
Developed areas	23	18	16	22	-4
Roads	108	94	121	118	9
Water	27	39	30	38	41
Cropland	25	41	12	13	-48
Pasture land and hay meadows	90	50	25	49	-46
Native grassland	1,375	1,308	1,120	1,117	-19
Deciduous forest	1,184	980	950	887	-26
Brush-treated land	397	616	877	878	121
Bare ground	20	7	10	8	-60

Land in the high density rural population landscape was subject to more intensive management practices, such as cropland and pasture land and hay meadows., than the low density rural population landscape. Cropland accounted for 17% of the area of the high density rural population landscape and only 1% of the low density rural population landscape in 1966. Both landscapes had a reduction in cropland between 1966 and 1990; however, the rate of loss in cropland was greater for high density rural population landscape compared to the low density rural population landscape (Table 2). Cropland in the high density rural population landscape was converted primarily to pasture land and hay meadows. Pasture land and hay meadows, which accounted for 21% of the area of the high density rural population landscape and only 3% of the low density rural population landscape in 1966, subsequently increased in the high density rural population landscape but decreased in the low density rural population landscape (Table 2). The increase in pasture land and hay meadows in the high density rural population landscape, which resulted from the conversion of native grassland, cropland, and forests, suggests the cover types on the high density rural population landscape require more intensive inputs and management compared to the cover types on the low density rural population landscape.

Deciduous forests accounted for 37% of the area of the low density rural population landscape and only 13% of the high density rural population landscape in 1966 (Table 2). Forests were converted primarily to brush-treated lands in the low density rural population landscape and to pasture land and hay meadows in the high density rural population landscape from 1966 to 1990. However, the rate of decline in forest was greater for the low density rural population landscape than the high density rural population landscape. Brush-treated lands accounted for 12% of the area of the low density rural population landscape and only 1% of the high density rural population landscape in 1966. Furthermore, area of brush-treated lands increased dramatically from 1966 to 1990 in the low density rural population landscape but not on the high density rural population landscape (Table 2).

Native grasslands were the dominant cover type on both landscapes in all years (Table 2). However, native grasslands changed little on the high density rural population landscape whereas native grasslands declined on the low density rural population landscape from 1966 to 1990. The decline in native grasslands along the low density rural population landscape may be misleading because native grasslands subjected to either herbicides or fire were photo-interpreted as brush-treated lands. Maintenance of tallgrass prairie dominance in this region requires fire or herbicides to prevent encroachment of woody species (Bragg and Hulbert 1976, Knight et al. 1994).

Temporal Changes in Landscape Structure

Landscape structure can be characterized by the composition and relative abundance of vegetation cover types and their spatial arrangement or geometry (Freemark et al. 1993). Because natural and anthropogenic disturbances alter landscape structure and may have important ecological implications (Turner 1990b), temporal changes in landscape structure must be considered in quantitative landscape studies (Dunn et al. 1990). Temporal changes observed in land use and vegetation cover types in our study resulted in altered landscape structure.

Mean patch size is generally large in areas of natural vegetation with minimal influence from human activities (Pickett and Thompson 1978). With increased human activity, mean patch size decreases because the landscape is generally subdivided into smaller patches (Forman and Boerner 1981). Measures of mean patch size in our study indicate the high density rural population landscape became more fragmented than the low density rural population landscape since 1973 (Table 3), and because mean patch size declined by 29% in the high density rural population landscape and only 7% in the low density rural population landscape from 1966 to 1990, landscape fragmentation was 4 times greater in the high density rural population landscape over the entire period. Human activities related to crop production and urban development also tend to simplify patch shapes which reduces fractal dimension (Krummel et al. 1987, O'Neill 1988). However, patch complexity as measured by fractal dimension was similar between landscapes and slightly increased in both landscapes after 1973 (Table 3). This suggests that natural disturbance regimes, including climate, may have influenced patch complexity to a larger degree than human activities.

Table 3. Measures of landscape pattern and percent change from 1966 of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990.

Index	Year				Change
	1966	1973	1980	1990	
					-(%)-
High density rural population (Collinsville)					
Mean patch size (ha)	4.16	3.93	3.22	2.96	- 29
Fractal dimension	1.23	1.25	1.27	1.28	+ 4
Shannon diversity	1.43	1.39	1.33	1.28	- 11
Dominance	0.65	0.75	0.81	0.86	+ 32
Contagion	2.69	2.83	2.85	2.91	+ 8
Angular second moment	0.27	0.30	0.30	0.32	+ 19
Contrast	0.33	0.46	0.50	0.50	+ 52
Low density rural population (Bartlesville)					
Mean patch size (ha)	3.96	4.29	3.63	3.42	- 8
Fractal dimension	1.27	1.24	1.27	1.30	+ 2
Shannon diversity	1.21	1.29	1.29	1.31	+ 8
Dominance	0.93	0.78	0.78	0.83	- 11
Contagion	2.99	2.82	2.81	2.88	- 4
Angular second moment	0.35	0.30	0.29	0.29	-17
Contrast	0.41	0.35	0.35	0.42	+ 2

Human activity typically decreases diversity by increasing landscape fragmentation, homogeneity, and dominance (Davis and Glick 1978). Landscape dominance increased in the high density rural population landscape (Table 3) suggesting a general trend for the landscape to be dominated by fewer land uses or vegetation cover types (O'Neill et al. 1988). Landscape dominance decreased in the low density rural population landscape suggesting a general trend toward land uses or vegetation cover types represented in more equal proportions. In addition, angular second moment increased from 1966 to 1990 in the high density rural population landscape suggesting a homogeneous, less diverse landscape. In contrast, angular second moment decreased from 1966 to 1990 in the low density rural population landscape indicating a landscape becoming more heterogeneous suggesting an increase in landscape diversity. Although landscape diversity was 15% greater in the high density rural population landscape compared to the low density rural population landscape in 1966, landscape diversity declined by 11% in the high density rural population landscape while landscape diversity increased by 8% in the low density rural population landscape from 1966 to 1990 (Table 3). Overall, the high density rural population landscape became less diverse, but the low density rural population landscape became more diverse since 1966.

Our results suggest that in the absence of societal pressure to halt increased human activity in rural landscapes still dominated by native vegetation, fragmentation will continue and biological diversity will most likely degrade in an accelerated fashion. For example, avian community structure as an indication of biological diversity, diverged over time in the high density rural population and low density rural population landscapes because of different land use and agriculture practices associated with each landscape (Boren 1995). Temporal shifts in avian community structure were reflected in increasing prairie habitat and generalist habitat associated species in the low density rural population and high density rural population landscapes, respectively. More neotropical migrants were lost from the high density rural population landscape compared to the low density rural population landscape (Boren 1995). A decrease in landscape quality, especially with regard to increased landscape fragmentation, may account for the observed loss of neotropical migrants from the high rural population density landscape (Johnson and Temple 1986).

Structure of Native Grasslands and Forests

Human activity tends to simplify patch complexity and increase fragmentation of contiguous forests (Godron and Forman 1983). The fractal dimension indicates forest patches were more complex in shape compared to native grassland patches in the high density rural population landscape (Table 4), suggesting greater human impact in native grasslands than in forests. In contrast, native grassland fragmentation remained relatively unchanged while fragmentation of forest increased from 1966 to 1990 (Table 4). Therefore, extrapolation of relationships between urbanization, patch complexity, and fragmentation to other ecosystems may not always be appropriate.

Table 4. Measures of landscape pattern and percent change from 1966 of native grassland and forest of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990.

Index	Year				Change
	1966	1973	1980	1990	
					-(%)-
High density rural population (Collinsville)					
Native grassland					
Mean patch size (ha)	15.24	15.37	12.52	15.25	0
Fractal dimension	1.25	1.27	1.26	1.25	0
Forest					
Mean patch size (ha)	2.72	1.75	1.69	2.01	- 26
Fractal dimension	1.36	1.39	1.36	1.35	- 1
Low density rural population (Bartlesville)					
Native grassland					
Mean patch size (ha)	11.83	9.81	12.81	18.55	+ 57
Fractal dimension	1.35	1.29	1.35	1.41	+ 4
Forest					
Mean patch size (ha)	3.99	6.21	4.43	5.47	+ 37
Fractal dimension	1.25	1.24	1.24	1.31	+ 5

Native grassland patches were more complex in shape compared to forest patches in the low density rural population landscape for all years (Table 4), which we attribute to fire and other brush treatment practices. Disturbance patches created by prescribed burning can increase landscape heterogeneity and patch complexity because fire effects differ with respect to topography, fuel type, fuel load, climate, and season (Godron and Forman 1983, Biondini et al. 1989, Baker 1992, Urban 1994). In addition, fragmentation decreased in both native grasslands and forests in the low density rural population landscape from 1966 to 1990 (Table 4).

Table 5. Percentage of native grassland and forest on a relative basis adjacent to human impact areas for the high density rural population and low density rural population landscapes for 4 separate years.

Cover type	Year			
	1966	1973	1980	1990
	----------	(%)	----------	
High density rural population (Collinsville)				
Native grassland	25	28	50	48
Deciduous forest	13	7	35	38
Low density rural population (Bartlesville)				
Native grassland	36	34	44	47
Deciduous forest	40	46	32	47

In both high rural population density and low rural population density routes there was relatively little change in the complexity of patch shape in either native grasslands or forests over time (Table 4). In addition, native grasslands were less fragmented than forests for all years based on mean patch size in both landscapes. Because native grasslands were less fragmented than forests one would expect to find increased road and residential growth in the forests compared to the native grasslands. However, our data indicated that roads were developed randomly with respect to cover type in the landscape. Human impact areas, including residential development, were primarily located in native grasslands in the high density rural population landscape in 1966 (Table 5). However, forests were increasingly selected for human development from 1973 to 1990 (Table 5). This may account for the observed temporal increase in fragmentation of forests. However, human impact areas were more evenly distributed between native grasslands and forests for all years in the low density rural population landscape (Table 5). Forests were more fragmented than native grasslands for both landscapes as early as 1900 (Criner 1996), which indicates differences in fragmentation between cover types is most likely a function of geomorphologic processes such as soils and natural disturbance regimes including climate and fire (Godron and Forman 1983).

Conclusions

High density rural population and low density rural population landscapes differed in temporal change in vegetation cover types and landscape structure. Native grasslands were less fragmented than forests in both landscapes. However, we found landscape quality, as defined by increased landscape fragmentation and decreased landscape diversity, has recently eroded in a densely populated rural landscape. In contrast, landscape quality improved in a low density rural population landscape dominated by ranching enterprises. Differences in landscape quality between landscapes (high density rural population vs. low density rural population) can be attributed to differences in land use and associated management practices. Maintenance of the tallgrass prairie by extensive management practices including prescribed burning, herbicide application, and grazing management most likely accounts for the observed improvement in landscape quality in a low density rural population landscape whereas an increase in more intensive management practices associated with seeded pasture land and hay meadows accounts for an observed reduction in landscape quality in a high density rural population landscape. These and other similar landscapes likely will continue to diverge in landscape quality in the absence of societal pressure to halt the spread of human activity into rural landscapes dominated by native vegetation. Our study suggests conservationists should focus their concerns on fragmentation and losses in biological diversity that accompany increased human activity in densely populated rural landscapes that surround urban centers. Extensively managed landscapes dominated by native vegetation that are under less pressure from expanding human influence are in less peril.

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Research observation: Influence of over-wintering feed regimen on consumption of locoweed by steers

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Abstract

Many producers believe cattle grazing wheat pasture during the winter are likely to graze actively growing locoweed when turned onto short-grass prairie in the spring. White locoweed (*Oxytropis sericea* Nutt, ex T&G) consumption was compared in a spring grazing study between steers wintered on irrigated 'TAM 105' wheat (*Triticum aestivum* L.) pasture (Wheat) and steers wintered on native range (Range). Range steers consumed locoweed for 43% of bites compared to 17% for the Wheat steers, and began eating locoweed before steers in the Wheat group. We rejected the hypothesis that steers wintered on wheat are more inclined to graze locoweed than steers wintered on native range.

Key Words: poisonous plant, *Oxytropis sericea*, beef cattle, grazing

The High Plains region of northeastern New Mexico, eastern Colorado, and the Oklahoma and Texas panhandles is an important grazing area for stocker steers and heifers. Many stocker cattle are wintered on wheat pasture then shipped to the High Plains region to graze rangeland for the summer. When cattle arrive in May, warm-season perennial grasses typically have not initiated growth, but white locoweed (*Oxytropis sericea* Nutt, ex T&G), a cool-season species, is generally in full bloom.

Ranchers speculate that cattle previously grazed on wheat pasture are likely to graze the green, actively growing locoweed in preference to dormant warm-season grasses, because they are conditioned to eating succulent forage. Conversely, cattle that are native to the area and wintered on dormant range should be more familiar with the vegetation community and conditioned to grazing dry grasses, and thus avoid grazing locoweed. The objective of our study was to test the hypothesis that steers wintered on native range would avoid locoweed, while steers wintered on wheat pasture would readily graze locoweed in the spring.

Methods

Phase 1, Winter Grazing of Wheat or Native Range.

Twelve Hereford steers (160 kg) were purchased in November 1993 from a ranch near Des Moines, N.M. and allotted randomly to wheat or native range winter feeding regimens at the New Mexico State Univ. Livestock Research Center at Clayton, N.M. Six steers were placed on irrigated 'TAM 105' wheat (*Triticum aestivum* L.) pasture from 10 January until 29 March (Wheat group). The wheat pasture was 50 ha and the steers were grazed with 95 other steers and heifers. The other 6 steers were wintered on 25 ha native range (Range group) adjacent to the wheat pasture, and supplemented with 0.45 kg/day protein supplement (95% soybean meal, 5% molasses, DM basis). Both groups received a salt/mineral mix (salt 20%, limestone 15%, dicalcium phosphate 29%, magnesium oxide 22%, soybean meal 9%, and other trace minerals) free choice throughout the winter and during the spring locoweed grazing trial. At the end of the winter conditioning period, steers on Wheat weighed 236 ± 8 (SE) kg, and those on Range weighed 226 ± 18 kg.

Phase 2, Spring Locoweed Grazing Trial

The site of the spring grazing trial was 16 km south of Des Moines, N.M. on a silty clay loam soil that was previously cultivated but reverted to short-grass prairie. Dominant species included bluegrama [*Bouteloua gracilis* (H.B.K.) lag. ex Steudel], western wheatgrass [*Elymus smithii* (Rybd.) Gould], squirreltail [*E. elymoides* (Raf.) Swezey], and white locoweed.

Four triangular pastures (3.4 ha each), which radiated out from a central set of corrals, were arranged in 2 blocks (2 pastures per block) with a 15-m alley separating the 2 blocks. Treatment groups were allotted randomly to blocks, and the 6 steers in each group were allotted randomly to 2 pastures (replications) within each block (3 steers per pasture). Blocks were separated to prevent steers in one treatment group from observing steers in the other treatment group, since social facilitation is a strong force that influences animal's diet selection (Ralphs et al. 1994a). Individual steers served as experimental units, whereas the pastures were merely the area where the effects of the treatment were expressed. Groups were rotated to the pastures in the other block midway through the study to minimize any pasture differences in diet selection.

Steer diets were estimated using a bite count technique (Lehner 1987). Each steer was observed for 5-min periods during the major morning and evening grazing periods each day. Generally, 3 to 6 observation periods were obtained from each steer every day. The number of bites of each forage class (cool-season grass, warm-season grass, forb, or locoweed) was recorded and the percentage of each class in the diet was calculated.

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Standing crop was sampled at the beginning and end of the study. Ten 1 m X .25 m plots were systematically located at 20-step intervals along a transect in each pasture. Forage classes were clipped, dried in a forced-air oven at 60°C for 48 hours, and weighed. White locoweed samples were analyzed for swainsonine concentration (Molyneux et al. 1989).

Blood samples were drawn from the jugular vein of each steer at the beginning and end of the trial, and serum was separated by centrifuge and frozen. Swainsonine concentration in the serum was measured by an α-mannosidase inhibition assay (Stegelmeier et al. 1995) to estimate intoxication level. Correlations were made between percentage of locoweed bites and swainsonine concentration in the blood.

Percentage of each forage class in the diet was compared between groups and over days of the trial in a split-plot analysis of variance. We tested the hypothesis that the Wheat steers would consume more locoweed than the Range steers (1-tailed test). Groups were the main plot and differences were tested by the steer within group factor. Day was the split plot in time, and day and the day X treatment interaction were tested by the residual error. Differences in percentage of locoweed bites between pastures was tested to verify that there was no pasture bias.

Results

At the beginning of the spring grazing trial, white locoweed was growing rapidly, new leaves of cool-season grasses western wheatgrass and squirreltail were 5 to 10 cm long, and few forbs other than locoweed were growing. Standing crop at the beginning of the study for dormant warm-season grasses was 306 (± 19 SE) kg ha^{-1}, cool-season grasses was 66 (± 13 SE) kg ha^{-1}, locoweed was 152 (±18 SE) kg ha^{-1}, other forbs was 70 (± 16 SE) kg ha^{-1}, and snakeweed was 49 (± 11 SE) kg ha^{-1}. The stocking rate during the 21-day trial was 1.13 ha/steer. A moderate stocking rate for this region is 6 ha/steer for a 5-month grazing season.

Steers from both groups preferred the cool-season grasses at the beginning of the study (50 to 70% of bites). After the first week, Range steers began eating locoweed and consumed it for 50 to 80% of their bites (Fig. 1). Steers assigned to the Wheat group started eating locoweed after the second week, and consumed similar amounts of locoweed as steers in the Range group for the remainder of the trial. Mean locoweed consumption by the Range steers was 43% of bites, compared to 17% by steers in the Wheat group ($P < 0.01$, Table 1). There was also a treatment X day interaction ($P = 0.02$), which verified that the Range steers began eating locoweed before the Wheat steers (Fig. 1). There were no differences in percentage of locoweed bites between pastures ($P > 0.10$).

Swainsonine concentration in blood serum of the Range steers was three-fold greater than in the Wheat steers (387 vs 126 ng ml^{-1}, $P = 0.001$) at the end of the trial, which indicated that Range steers were more severely intoxicated than the Wheat steers. There was a strong correlation between percentage of locoweed bites and swainsonine level in the blood ($r = 0.90$). Swainsonine concentration in white locoweed increased from 0.012% (air dry weight) at the beginning of the trial when locoweed was vegetative, to 0.028% at the end when it was in the flower bud stage of development.

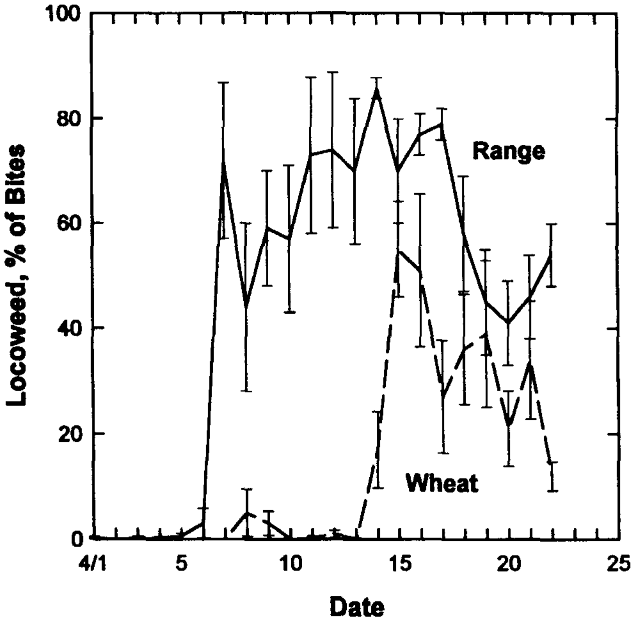

Fig. 1. Percentage bites of locoweed (bars are standard errors) for steers grazing short grass prairies after wintering on wheat pasture (Wheat) or native range (Range).

Steers from both groups continued to graze on the site for a subsequent aversion trial (Ralphs et al. 1997), and became lethargic and visibly intoxicated. However, they ceased grazing locoweed when warm-season grasses began rapid growth in late May. There was no swainsonine in blood serum at the end of the aversion trial when measured on 6 June 1994.

Management Implications

Our original hypothesis was that cattle wintered on native range would avoid grazing locoweed, while cattle wintered on wheat pasture would readily graze actively growing locoweed in the spring. Based on data from this trial, we reject this hypothesis. Steers wintered on native range began eating locoweed before those wintered on wheat pasture and consumed more of it in the spring.

We do not suggest that cattle wintered on range are more likely to consume locoweed compared to those wintered on wheat pasture. During the last part of the study, both groups of steers grazed similar amounts of locoweed and were visibly intoxicated. Results from previous research using native, mature cows (Ralphs et al. 1993, 1994b) clearly demonstrated that cattle will select large amounts of locoweed in the spring when warm-season grasses are still dormant. However, steers in this study, and all cattle in previous grazing trials, ceased grazing locoweed

Table 1. Means of forage classes in steer diets in spring grazing trial (% ± SE).

Winter treatment	Cool season grass	Warm-season grass	Locoweed	Forbs
	---------------	--------------- % of bites	---------------	---------------
Range	41a ± 3	13a ± 2	43a + 4	2a ± .2
Wheat	46a ± 2	33b ± 3	17b + 5	5a ± .6

^{ab}Means in a column followed by different letters are different ($P < 0.025$).

when warm-season grasses began growth. These data reinforce the management recommendation (Ralphs et al. 1993) to wait until warm-season grasses are growing and abundant before moving stocker cattle to locoweed-infested short-grass prairie on the High Plains.

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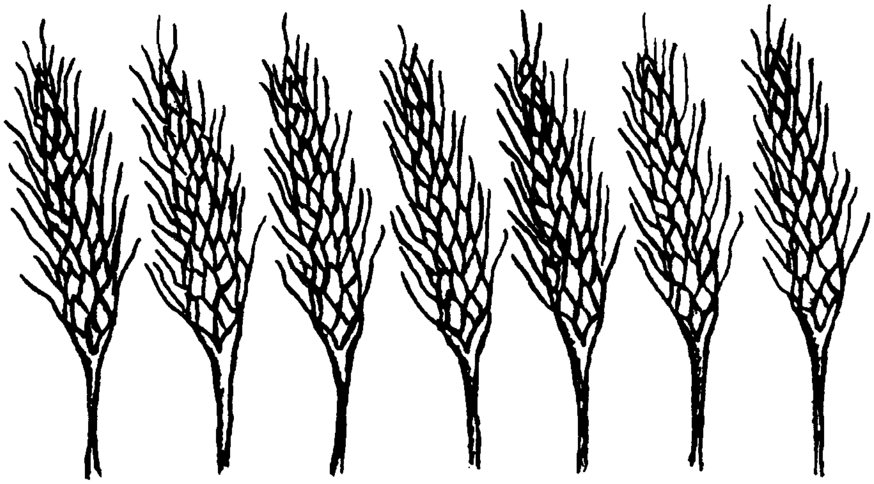

J. Range Manage.
50:253–257

Observations of white-tailed deer and cattle diets in Mexico

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Abstract

Most rangelands in northern Nuevo Leon, Mexico, have been grazed intensely for more than 10 years simultaneously by cattle and white-tailed deer (*Odocoileus virginianus texanus*). There is a lack of information concerning diet selection of white-tailed deer and cattle in this region. We observed the dietary preferences of these ungulates in northeastern Nuevo Leon for a 6 month period. Two adjacent areas were subjected to rotational grazing (RG) and continuous cattle grazing (CG). Fecal analysis was used to determine dietary overlap of these 2 sympatric ruminants. Cattle diets averaged 70% grasses, 23% browse, and 4% forbs. Deer diets were 63% browse, 24% forbs and 12% grasses in both areas. The preferred species for cattle in both areas were grasses. Deer preferred forbs on the continuous grazed area and grasses on rotational grazed area. Zacate toboso [*Hilaria mutica* (Buckl.] Benth.) was the most preferred species by both ruminants in both management systems. Differences between cattle and deer diets were significant ($P < 0.05$). The similarity index was higher on the rotational grazed (23%) than on the continuous grazed area (15%) ($P < 0.05$). The higher similarity index in RG area may have been a result of the altered forage preferences of deer. Zacate toboso under RG could be an important feed resource in those areas where white-tailed deer and cattle graze in common.

Key Words: cevrides, livestock, forage preferences, grazing methods, tobosa grass

During the past decade the use of rotational grazing (RG) has increased in northeastern Mexico. Some of this area has been grazed intensely with cattle (*Bos taurus, Bos indicus*) and white-tailed deer (*Odocoileus virginianus texanus*) during this period. Under rotational grazing it is common that a single herd of livestock rotates rapidly through several relatively small pastures. Grazing periods typically last 1–5 days, with rest periods of 30–60 days (Savory and Parsons 1980), depending on the rate of plant growth. Intensive management of deer requires a thorough understanding of the effects of different grazing methods such as rotational grazing. Cohen et al. (1989a, 1989b) compared the effects of rotational grazing and continuous yearlong grazing (CG) on home ranges, movement indices of female white-tailed deer, and forage availability in the Coastal Bend region of Texas. Many studies have been conducted on the food habits of white-tailed deer and cattle in South Texas (Davis and Winkler 1968; Chamrad and Box 1968; Drawe 1968; Everitt and Drawe 1974; Arnold and Drawe 1979). Quintanilla (1989) studied the dietary preferences of white-tailed deer in North Nuevo Leon, Mexico. Few investigations have examined diets of cattle in common with deer for different grazing methods. In northeastern Mexico, no study has been conducted of diet overlap between cattle and white-tailed deer.

The objectives of the study were to determine the botanical composition of cattle and deer diets and to observe differences in dietary overlap of both ruminants between rotational grazing and continuous grazing.

Materials and Methods

The study was conducted on 2 adjacent ranches located on the Rio Grande Plains in Anahuac, Nuevo Leon, Mexico, at an elevation of 150 m, approximately 89 km south from Nuevo Laredo, Tamaulipas. The annual average precipitation is 55 cm. Average daily temperature is 15°C. Four soil types are present but the principal soil of the 2 ranches is a sandy loam type. The chaparral-mixed grass community contains moderately dense stands of mixed shrub species including chaparro prieto [*Acacia rigidula*, Benth], mesquite [*Prosopis glandulosa*, Torr.], huizache [*Acacia farnensiana*, (L.) Willd.], granjeno [*Celtis pallida*, Torr.], cenizo [*Leucophyllum frutescens* (Berl.) Johnst.] and nopal [*Opuntia* spp.]. Dominant herbaceous plants are zacate Buffel [*Cenchrus ciliaris*, L.], zacate toboso [*Hilaria mutica*, (Buckl.) Benth], saladilla [*Varilla texana*, Gray], and croton [*Croton leucophyllus*, Muell.].

The rotational grazing method was implemented 8 years prior to the study by subdividing a 3,100 ha ranch into 64 equal sized paddocks. Each paddock was grazed from 3 to 6 days and rested 32 to 47 days, depending on vegetation response. The rotational grazing area was stocked at a rate of 3.1 ha/AUY. The continuous grazing area was a 3,300-ha ranch stocked at a rate of 10 ha/AUY.

Botanical composition of diets was determined monthly by microscopic examination of fresh fecal material period (Sparks

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and Malechek 1968) during a 6 month period. Fecal samples from deer in the rotational grazed area collected from 19 belt transects (300m × 4m) and from 10 belt transects in the continuous grazed area using 300m × 4m (19 in the RG; 10 in CG). Cattle fecal samples were collected using 4 animals randomly selected at the beginning of the study. Each analyzed sample was a composite of feces collected by animal during a 5 day period.

Botanical composition of the experimental pastures was determined monthly utilizing the line intercept method (Canfield 1941). The percentage of foliar cover of grasses, shrubs, and forbs was 41%, 42%, and 16% in the rotational grazed area and 25%, 67%, and 6% in the continuous grazed area. Dietary similarities were calculated using Kulczynski's formula (Oosting 1956) in which

$$\text{Similarity index} = \frac{2\,w}{(a+b)} * 100,$$

where w is the smaller percentage of 1 plant species in the diet of 2 different animal species and (a+b) is the sum of the 2 percentages of intake of 1 plant species. Similarity indices were separated by a standard t-test.

Preference indices were calculated by a ratio described by Taylor et al. (1980):

PR= (% in the diet –% in standing crop)/(% in the diet + % in standing crop).

Data were analyzed as a completely randomized design. One ANOVA model with crossed factor was used to examine the differences in the diet composition of both ruminant species. Student's t was used to detect differences ($P<0.05$).

Results

Species Composition of Cattle Diets

Thirty-four plant species were identified in the fecal samples of cattle. Two species were not identified. Species composition of cattle diets are shown by grazing method areas in Table 1 the mean diet of cattle in both areas was grasses 71%, shrubs 235, and forbs 4%. In average grasses, shrubs, and forbs formed 71%, 23%, and 4%. (Fig. 1). In the rotational grazing area the diet of cattle was formed for 33 plant species. The principal grasses consumed were zacate buffel (22%), zacate toboso (17%), and panizo texano [*Panicum texanum*, Buckl.] (14%). Shrubs were the second most abundant class of plants in the diet of cattle (16%) and the major species were nopal (8%), brazil [*Condalia hookeri*, M.C. Johnst.] (2%), escobilla butterfly-bush [*Buddieia scorioides*, H.B.K.] (2%), and granjeno (1%). Forbs composed only 4% of the diet.

In the continuous grazed area, cattle diets were higher in shrubs and lower in grasses and forbs than in rotational grazed area (Fig. 1). The diversity in the diet of cattle was lower in the continuous grazed areas (29 species). Grasses were the dominant component in the diet (67%). The major species were zacate buffel (17%), zacate toboso (14%), and panizo texano (13%). Shrubs were consumed at a relatively high average (27%). The most important shrubs species were nopal (17%), cenizo (4%), guajillo (2%), and escobilla butterfly-bush (2%). Forbs were rarely consumed (4%).

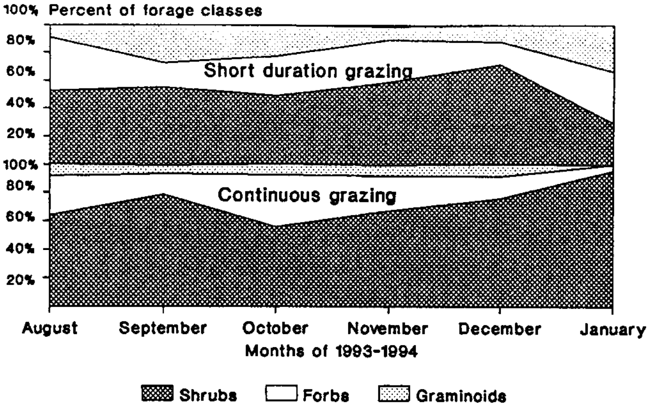

Fig. 1. Percent of forage classes in the diet of cattle in a rotationally grazed and a continuously grazed area.

Species Composition of Deer Diets

A total of 46 species, (20 forbs, 19 shrubs, and 7 grasses) were identified as eaten by white-tailed deer in this study. Species composition in deer diets are shown by grazing method (Fig. 2). In the rotational grazed area, 45 forage species were identified and shrubs were the dominant component (53%). The major browse species used by white-tailed deer were cenizo (16%), panalero [*Schaefferia cuneifolia*, A. Gray] (14%) and guajillo (7%). Forbs averaged 28% of diets. The most important forb species were *Physalis viscosa*, L. (5%). sangre de drago [*Jatropha dioica*, Sessé] (3%) and *Malva* spp. (3%). Grasses comprised 19% of the diet, and the most important species were zacate toboso (9%), alkali sacaton (3%), and zacate buffel (3%).

In the continuous grazed area, the diversity of deer diets were relatively lower (38 forage species). Deer diets were higher in shrubs, and lower in grasses and forbs than in the rotational grazed area (Fig. 2). Shrubs comprised 73% of deer diets. The

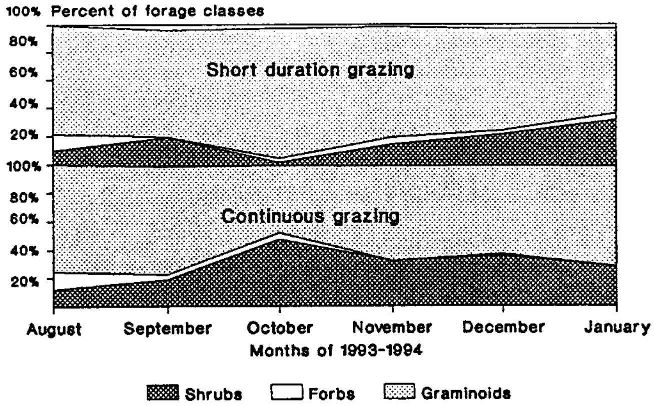

Fig. 2. Percent of forage classes in the diet of deer in a rotationally grazed and a continuously grazed area.

Table 1. Botanical composition of rotational grazed (RG) and continuous grazed (CG) areas, diets of cattle and white-tailed deer in each area, and calculated relative preferences.

	RG				CG			
Species	Cattle	Deer	Cattle	Deer	Cattle	Deer	Cattle	Deer
	Composition%		Preference ratio		Composition%		Preference ratio	
Grasses								
Bouteloa barbata	1	1	.4	–.2	4.4	.2	–.8	.5
Bouteloa trifida	.1	—	-1	—	.2	-	—	–.7
Cenchrus ciliaris	22	3	—		17	1.3	.5	1
Cynodon dactylon	6	—	.5	—	5	—	—	.6
Erinoeuron spp.	.7	—	1	—	3	—	—	1
Hilaria mutica	17	8.5	1	1	14	2.2	1	1
Panicum texanum	14	1.2	1	.6	13.5	1.7	–.2	.7
Sporobulus asper	4	2	.4	.2	1.7	—	—	1
S. airoides	7	3.1	.8	.7	7.8	–.4	.6	
Stipia spp.	1.2	.1	1	.8	.1	—	—	.9
Σ	73	18.9			65.9	6.2		
Shrubs								
Acacia berlandieri	1	7.5	.6	1	2.3	7.8	.5	—
A. farnesiana	—	.2	—	.9	—	1.9	.4	—
A. rigidula	—	8	–1	–.5	.09	2.7	–.6	–.1
A. wrightii	—	.04	—	–.8	—	.2	.9	—
Aloysia gratissima	—	—	.2	—	—	.4	-1	—
Atriplex cenescens	—	.6	—	.13	—	—	—	—
Buddleia scorioides	2	—	2	—	2.3	—	—	1
Bumelia languinosa	.5	.2	.3	–.3	.2	.3	.06	.2
Celtis pallida	1.3	2	–.3	.05	—	2.7	—	–.1
Condalia hookeri	1.9	1	.7	.5	1.4	.3	.3	–.4
Ephedra aspera	—	.1	—	–.7	—	—	—	—
Karwinskia humbodtiana	—	3	–.7	.8	.1	2.3	–.8	.2
Larra tridentata	—	.3	—	–.3	—	.2	–.9	—
Leucophyllum fructescens	.5	16	.3	1	3.5	31	7	1
Lycium berlandieri	—	.2	—	–.6	.02	—	-1	—
Opuntia spp.	8.5	1	—	–.8	16.7	.6	.4	–.8
Porlieria angustifolia	—	—	—	–.9	—	.3	—	–.84
Prosopis glandulosa	—	4	—	–.6	—	4.4	-	–.6
P. reptans	1	1	–.9	.07	—	1.5	—	.6
Schafferia cuneifolia	.2	14	.4	1	—	16	—	1
Σ	16.9	59.1			26.6	72.6		
Forbs								
Astragalus spp.	—	—	—	.7	—	—	—	—
Chenopodium hians	—	1	—	.9	—	.4	1	—
Croton dioicus	—	—	—	—	—	.6	.3	—
Croton leucophyllum	—	.7	—	1	—	.4	.7	—
Ephedra aspera	1	—	–.8	—	—	—	—	—
Euphorbia prostrata	1	—	–.7	—	—	—	—	—
Hibiscus cardiophyllus	.1	1	–.1	–.8	.6	1	1	1
Isocoma coronopifolia	.5	2	.8	1	.2	2.5	.1	–.9
Jatropha dioica	.02	3	–.1	.6	—	1.07	1	—
Lantana macropoda	—	.7	—	.4	—	.1	-1	—
Malva spp. 1	1	3	–.1	1	1.08	3.8	.9	.6
Malva spp. 2	1	3	–.3	.2	.4	.8	.9	.8
Malvella leprosa	2.1	2	1	1	.07	.07	.7	.7
Parthenium confertum	—	.08	—	–.8	.3	.1	.8	1
Physalis viscosa	.3	5	1	1	.5	3.5	1	.8
Ruellia runyonii	—	.5	—	3	—	.9	.8	—
Salsola iberica	1	.7	1	–.04	.6	—	—	.8
Solanum elaeagnifolium	.3	.9	–.08	1	—	1.4	1	—
Tiquilia canescens	—	1	—	1	—	1.3	.9	—
Varilla texana	—	2	—	–.6	—	2	–.7	—
Xanthocepalum texanum	—	5	—	–.6	—	—	—	—
Zenhyranthes longifolia	—	2	—	.6	—	.7	1	—
Σ	12.8	28.6			3.7			

[1] Botanical composition (%), 2 preference ratio, ((—) not found in the diet or in the vegetation)

major browse species were cenizo (31%), panalero (16%) and guajillo (8%). Forbs were the second most abundant plant class (21%). *Malva* spp., *Physalis viscosa*, L. (4%), and *Isocoma coronopifolia*, (Gay) Greene (2%) were the most important forbs. Grasses composed only the 6% of the deer diet. Zacate toboso, panizo texano, and zacate buffel were the most consumed grass species with 2%, 2%, and 1% respectively.

Preference Indices

Grasses were the preferred forage class by cattle in both areas, and zacate toboso was the most preferred species. The shrub escobilla butterfly-bush was the second most preferred species by cattle. However, deer preferred forbs in the rotational grazed area, and forbs and grasses in the continuous grazed area. One grass, zacate toboso, was the most preferred species by deer in both areas (Table 1).

Dietary overlap

Of the 55 taxa identified in the collective diets of cattle and white-tailed deer in the 2 experimental areas, 27 were used in common. Dietary overlap in the rotational grazed area (23%) was higher ($P<0.05$) than in the continuous grazed area (15%) (Fig. 3). Fluctuations were inconsistent during the 6 month period between the 2 experimental areas (Fig. 3). Regarding the 6 month basis, overlap in the rotational grazed area ranged from 17% to 36%. Diet similarity of cattle and white-tailed deer were greatest during January in the rotational grazed area. January data indicated white-tailed deer and cattle both consumed zacate toboso, guajillo, zacate buffel, and *Isocoma coropifolia*, (Gay) Greene. During September and October, the dietary overlap was similar. Common use of zacate toboso, panizo texano, granjeno, and nopal formed more than the 50% of the total overlap. In the continuous grazed area, dietary overlap ranged from 7% to 21% (Fig. 3). Diets were most similar during August (18%) and November (21%). Common species were zacate buffel and alkali sacaton during November.

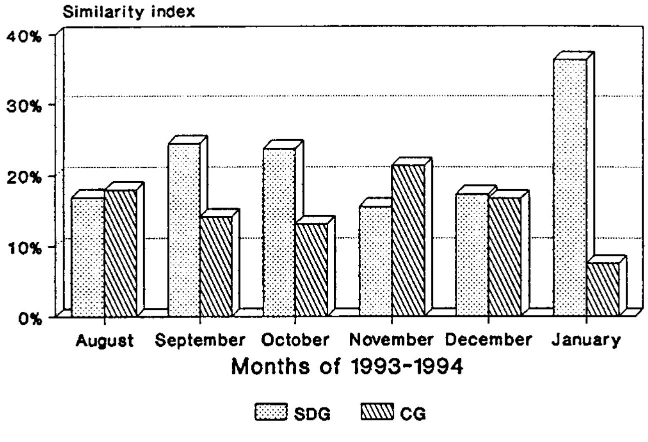

Fig. 3. Percent of dietary overlap between cattle and deer in the areas grazed differently.

Discussion

Cattle ate predominantly grasses in both grazing methods. Grasses have been reported to be the dominant forage class in cattle diets (Cook et al. 1963; Thetford et al. 1971; Galt et al. 1982). However, in this study the browse component of cattle diets was relatively high (23%). This result may have local significance because browse can be important as a complementary dietary resource in the diet of cattle. Usually, local farmers, who have no interest in deer hunting, completely clear the shrub vegetation in order to plant grasses for cattle grazing. Releasing or planting some brush species in the pastures could result in ecological and economical benefices. Further investigation of agroforestry systems involving native woody species should be done in these areas.

The most commonly preferred species for cattle and deer was the grass zacate toboso. The phenological state of zacate toboso was not quantified but it was observed to be actively growing. Culms become coarse and relatively unpalatable with increasing maturity (Paulsen and Ares 1962). One important result is that preference for and the amount of zacate toboso consumed was higher in the rotational grazed area than in the continuous grazed area. In comparison with continuous grazing, rotational grazing appeared to improve the total usage of zacate toboso by maintaining palatable culms (Senock et al. 1993). The use of zacate toboso in the pastures under a rotational grazing system can be recommended for the common production of cattle and white-tailed deer in this region.

Thirty-four plant species are composed in the diet of cattle in the present study. A total of 27 plant species were found in the rumen forage samples from cattle on mesquite and mesquite-free desert rangeland neat Tucson, Arizona (Galt et al. 1982). However at the La Michilia Durango, Mexico cattle consumed 84 plant species (Morales cited by Gallina 1993). Differences in the diversity of the botanical composition of the pastures may be the cause of this difference. Deer diet was more diverse than cattle diets (46 plant species). Deer can exercise a higher degree of selectivity than cattle because of the smaller mouth size and body size (Hanley 1982).

The major browse species used by white-tailed deer in both grazing methods were in order of major contribution: cenizo, panalero, and guajillo. In contrast to our results, chaparro prieto was the major component of the diet of white-tailed deer in 3 pastures close to our area (Quintanilla 1989). In the present study, the proportion of chaparro prieto in the diet was less than in the forage on the other, indicating selection against this species.

The diversity of diets was lower in the continuous grazed area. Plant diversity was greater in the rotational grazed area. In south Texas rotational grade promoted greater herbaceous species richness, diminished plant litter accumulation, and increased forb cover in comparison with deferred rotation grazing (Wilkins and Wendell 1992).

Our results contrast south Texas, cattle use of vegetation types was more uniform under rotation grazing than continuous grazing (DeYoung et al. 1988). Difference in plant diversity between the pastures before the implementation of the grazing systems and differences in the management of the continuous grazed pastures may be the reason for different results between these experiments.

Dietary overlap was significantly higher in the rotation grazed area than in the continuous grazed area. Cattle and deer share in this pasture more grass and forbs species in the rotational grazed area. During January the relatively high similarity index determined in the rotational grazed area would indicate minimal competition. However, dietary overlap is not sufficient evidence for competition (Colwell and Futuyma, 1971), and consequences of overlap depend upon availability of the resource. The reason for this difference may be the presence during January in the rotational grazing of plants with a higher proportion of cells content. In January in the rotational grazed area deer consumed the highest amount of grasses of the whole study. In contrast, in the continuous grazed area during the same month deer did not select any grasses.

Conclusions

The results of this study support the observation that cattle prefer grasses and deer prefer browse and forbs. However on Chaparral-mixed grass range under both continuous grazing and rotational grazing some species of different plant groups like prickly pear in the diet of cattle or zacate toboso in the diet of deer could be very important components in the diets of ruminants with different foraging strategies. The higher plant diversity within the rotational grazing area was responsible for the higher dietary diversity for both ruminants. Our results suggest that the use of zacate toboso in the pastures under the rotational grazing method can be recommended for common production of cattle and white-tailed deer on a shrub mixed grass savanna of the Rio Grande Plains.

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Relationships among Idaho fescue defoliation, soil water, and spotted knapweed emergence and growth

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Abstract

Developing rangeland management strategies to minimize spotted knapweed (*Centaurea maculosa* Lam.) invasion will require understanding the effects of intensity, frequency, and season of grazing on weed establishment. We studied the effects of hand-clipping 2-year-old Idaho fescue (*Festuca idahoensis* Elmer) plants 0, 30, 60, or 90%, 1, 2, or 3 times (14-day intervals) on spotted knapweed seedling emergence and growth in pots watered with 150 ml once weekly or 50 ml 3 times weekly. Pots were seeded with 5,000 spotted knapweed seeds m^{-2}, replicated twice, and placed in a growth chamber in a completely randomized design. The experiment was repeated once. Plants were harvested after 50 days. Treatment effects on soil moisture, Idaho fescue and spotted knapweed shoot and root weight, and leaf area were compared using analysis of variance and regression analysis. At final harvest, Idaho fescue shoot weight and leaf area decreased with increasing defoliation level and frequency. Idaho fescue root weight was not affected by any treatment. A single Idaho fescue defoliation at 30% and 90% increased spotted knapweed weight and numbers per pot respectively, over those pots with undefoliated plants. The level of defoliation necessary to enhance spotted knapweed numbers was lower as defoliation frequency increased. As defoliation level and frequency increased, soil water content increased resulting in a corresponding increase in spotted knapweed emergence and growth.

Key Words: *Centaurea maculosa* Lam., *Festuca idahoensis*, Elmer, clipping, weed invasion, grazing management

Spotted knapweed (*Centaurea maculosa* Lam.), an alien weed, has been spreading rapidly into Idaho fescue (*Festuca idahoensis* Elmer.), rough fescue (*Festuca scabrella* Torr.), and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith) dominated rangeland throughout the western United States (Roché and Talbott 1986) and Canada (Watson and Renney 1974). Herbarium records indicate a 4-fold increase in the number of counties with new introductions of this weed in 5 northwestern states during the past 20 years. In Montana, spotted knapweed has been spreading at a rate of 27% per year, infests about 2.2 million hectares, and has the potential to invade a total of 15 million hectares (Chicoine et al. 1985). Spotted knapweed reduces livestock and wildlife forage production (Bucher 1984; Spoon et al. 1983), increases surface water runoff and soil sedimentation (Lacey et al. 1989), and lowers plant diversity (Tyser and Key 1988).

Although spotted knapweed can invade in the absence of livestock grazing (Tyser and Key 1988), rapid invasion of rangelands by knapweeds is commonly associated with improper grazing. Invasion may be enhanced by selective and excessive grazing of desirable forage species (Lacey et al. 1990). The relationship between grass defoliation and spotted knapweed establishment may depend on the level and frequency of grass defoliation and the amount and frequency of precipitation during the establishment period. In a field study, a single grass defoliation greater than 60% of the canopy increased diffuse knapweed (*Centaurea diffusa* Lam.) establishment (Sheley et al. 1997). In that study, high spring precipitation appeared to favor knapweed seedling establishment. Similarly, spotted knapweed seedling emergence increased with increasing soil moisture in a controlled environment (Spears et al. 1980). Grass species have different responses to defoliation frequency (Alexander and Thompson 1982); however, most studies show increasing defoliation frequency reduces yield (Cook et al. 1958, Undersander and Naylor 1987). Interactions between defoliation level and defoliation frequency and their effects on spotted knapweed establishment have not been studied.

Developing strategies to minimize weed invasion requires understanding the relationship between the intensity, frequency, and season of grass defoliation on establishment and growth of spotted knapweed. The objective of this study was to determine the effect of Idaho fescue defoliation level and frequency under 2 watering regimes on soil water content and spotted knapweed seedling emergence and growth. We hypothesized that as defoliation level and frequency increase, soil water content will increase, resulting in a corresponding increase in spotted knapweed emergence and growth.

Materials and Methods

Experimental Design

Idaho fescue plants were established from seeds in 63 mm diameter × 250 mm depth (600 cm^3) pots consisting of 1/3 Farland silt loam (fine-silty, mixed Typic Argiboroll), 1/3 peat,

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and 1/3 sand. Seeds were collected in 1992 from Sanders County, Mont. Grasses were grown for 18 months in a greenhouse until leaf material covered more than 50% of the soil and their roots completely occupied the pots.

Treatments (4 defoliation levels, 3 frequencies, 2 watering regimes) were replicated twice in a completely randomized design and repeated once. Defoliation treatments were applied by hand-clipping grasses in each pot. Defoliation levels were 0, 30, 60, or 90% of above-ground biomass. Defoliation levels were calibrated by clipping a sample of potted plants at estimated levels and comparing their weights with weights of grass clipped to the soil surface. Plants clipped twice were re-clipped at the same level 14 days after the initial clipping, and plants clipped 3 times were re-clipped at the same level 14 and 28 days after the initial clipping.

After initial defoliation treatments, spotted knapweed seeds were evenly broadcast onto the soil surface. Seeds were collected in 1988 from Deer Lodge County, Mont. Seeding rate was 5,000 m^{-2} (16 seeds per pot) which is within the range of spotted knapweed seed production on rangeland in Washington and Idaho (Schirman 1981). Four pots without Idaho fescue plants (bare ground) were also seeded. Pots were placed in a growth chamber with 12°C day and 8°C night temperatures and a 12-hour photoperiod at 200 uE m^{-2} s^{-1} intensity.

Watering treatments were initiated after spotted knapweed was seeded. Two complete replicates of defoliation, frequency and bare ground treatments were watered with 50 ml on Mondays, Wednesdays, and Fridays, and another pair of replicates were watered with 150 ml on Monday only.

Soil Water Content

Volumetric soil water content (cm^3 cm^{-3}) was measured gravimetrically. After seeding with spotted knapweed, pots were saturated with water and allowed to drain to pot capacity, and weighed. Pots were re-weighed (total pot weight) weekly throughout the duration of the experiment. At harvest, soil volume and weights of all plant material, pots, and dried soil were determined. Soil water weight was calculated by subtracting the sum of the dried soil, plant, and pot weights from the total pot weight. Soil water weight was converted to volumetric water content by dividing by soil volume. Soil water contents of each treatment were averaged over the duration of the experiment and used in the analysis.

Sampling

After 50 days of growth, all plant material was harvested. Soil plugs were pulled from the pots, soil volume determined, and the soil was washed from the roots. Soil was dried at 60°C to a constant weight and weighed. Spotted knapweed seedlings were counted, their roots were separated from those of Idaho fescue, and spotted knapweed shoots were separated from their roots. Spotted knapweed leaf areas were measured using a Li-Cor leaf area meter. Shoots were dried at 60°C to a constant weight and weighed. Root length was measured using a Comair root-length scanner, then roots were dried at 60°C to a constant weight and weighed. Idaho fescue plants were harvested as described for spotted knapweed above. Leaves were separated from roots, leaf areas measured, and the leaves were dried and weighed. Roots were also dried and weighed, but not measured for root length.

Data Analysis

Data from the 2 experimental repeats were analyzed for homogeneity of variance using Pearson's chi-square test (SAS 1988). Variances were homogeneous and data were combined and analyzed using multiple linear regression (least squares) and analysis of variance. Regression models were used to predict average soil water content, spotted knapweed number, shoot weight, root weight, leaf area, and root length. Those models used Idaho fescue shoot weight or leaf area as independent variables. Regression models predicting spotted knapweed number and total weight used average soil water content as the independent variable. Models using defoliation level, defoliation frequency, frequency of watering, and their interactions as independent variables did not fit linear or curvilinear models. Those data were analyzed using analysis of variance. Main effects were defoliation level, defoliation frequency, and frequency of watering. Interactions included defoliation level by defoliation frequency, defoliation level by frequency of watering, defoliation frequency by frequency of watering, and defoliation level by defoliation frequency by frequency of watering.

Results and Discussion

Idaho Fescue Response

Defoliation level and frequency interacted to affect both Idaho fescue final shoot weight and leaf area (Fig. 1). When clipped once, there was no difference between 0 and 30% defoliation, and Idaho fescue progressively produced less final shoot weight and leaf area at 60 and 90% than at lower defoliation levels. When clipped 2 or 3 times, final shoot weights and leaf areas were reduced with each increase in defoliation level. Three defoliations had a greater impact on Idaho fescue than 1 or 2 defoliations at 30 and 60%. Ninety percent defoliation clipped 2 times produced similar final shoot weights and leaf areas to 90% clipped 3 times. These results are consistent with defoliated bluebunch wheatgrass (Mueggler, 1972), crested wheatgrass (*Agropyron desertorum* [Fisch.] Schult.)(Cooke et. al., 1958), and tall wheatgrass (*Agropyron elongatum* [Host] Beauv. 'Jose') (Undersander and Naylor, 1987).

Idaho fescue root weights were not affected by defoliation ($P>0.1$). In addition, watering frequency had no effect on Idaho fescue shoot weight, leaf area, or root growth ($P>0.1$). Similarly, Caldwell et al. (1981) found that shoot growth, but not root growth, of bluebunch wheatgrass was reduced by defoliation.

Average Soil Water Content

Linear regression showed soil water content was negatively related to final Idaho fescue leaf area and shoot weight (Fig. 2). Regression models using Idaho fescue root weight were not significant. We assume lower leaf areas reduced transpiration (Kramer and Boyer 1995). These results indicate grass defoliation, and potentially grazing, will leave soil water available to neighboring plants.

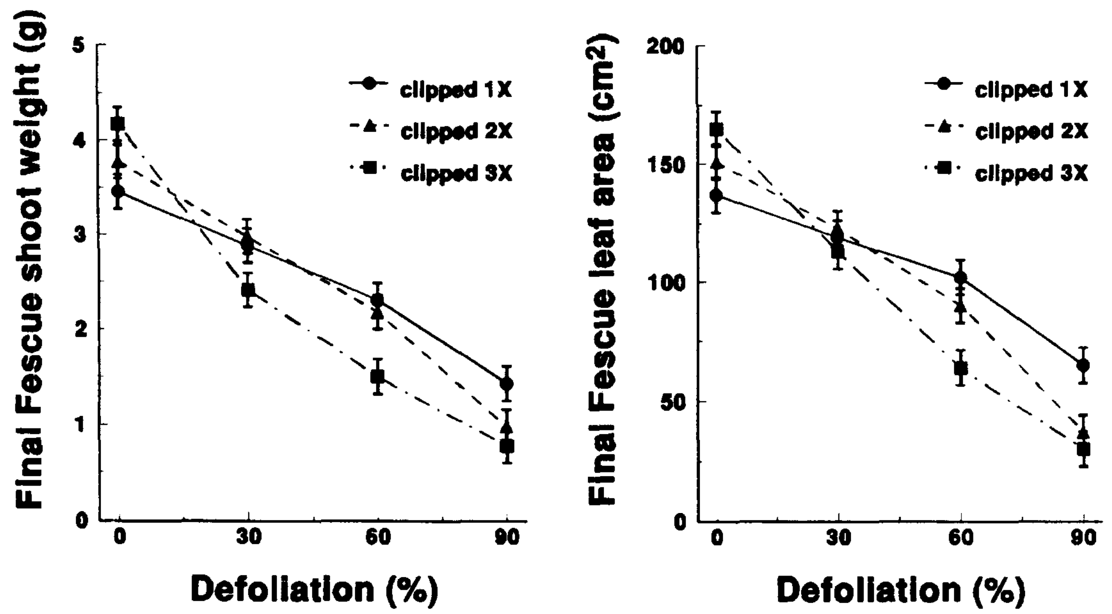

Fig. 1. Effect of defoliation level and frequency on Idaho fescue shoot weight (g) and leaf area (cm^2)^1. ^{1} Error bars represent ± 1SE.

Spotted Knapweed Emergence and Growth

Defoliation level and frequency interacted to affect spotted knapweed seedling numbers (Fig. 3). When Idaho fescue plants were clipped once, only those clipped at 90% had more spotted knapweed seedlings than the other defoliation levels, which responded similarly. Idaho fescue plants clipped twice produced similar spotted knapweed numbers as those clipped 3 times. At these defoliation frequencies, spotted knapweed numbers increased at each defoliation level. Spotted knapweed numbers after grass defoliation at 60%, clipped 2 or 3 times, were similar to those after a single defoliation at 90%.

There was also an interaction between defoliation level and watering frequency on spotted knapweed seedling numbers (P=0.08, Fig. 3). Idaho fescue defoliation levels of 60 and 90% had more spotted knapweed seedlings when watered 3 times per week than when watered once per week. Sheley and Larson (1996) suggested that knapweeds are able to capitalize on frequent but minimal periods of precipitation characteristic of arid

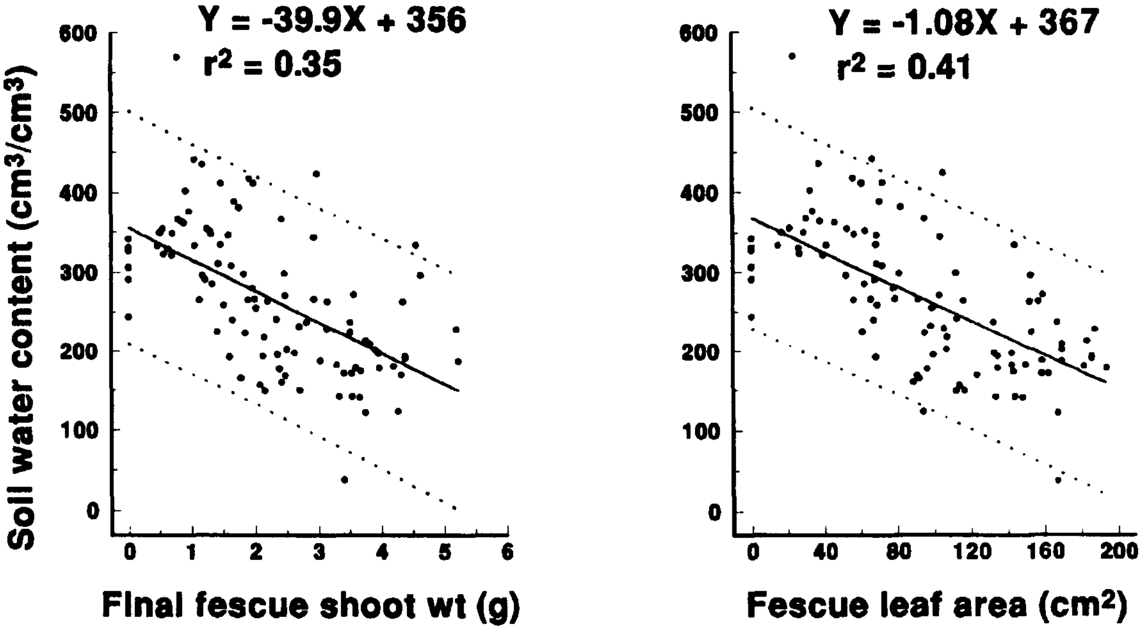

Fig. 2. Relationship between soil water content (cm^3 cm^{-3}) and Idaho fescue shoot weight (g) and leaf area (cm^2). Dashed lines are 95% confidence intervals.

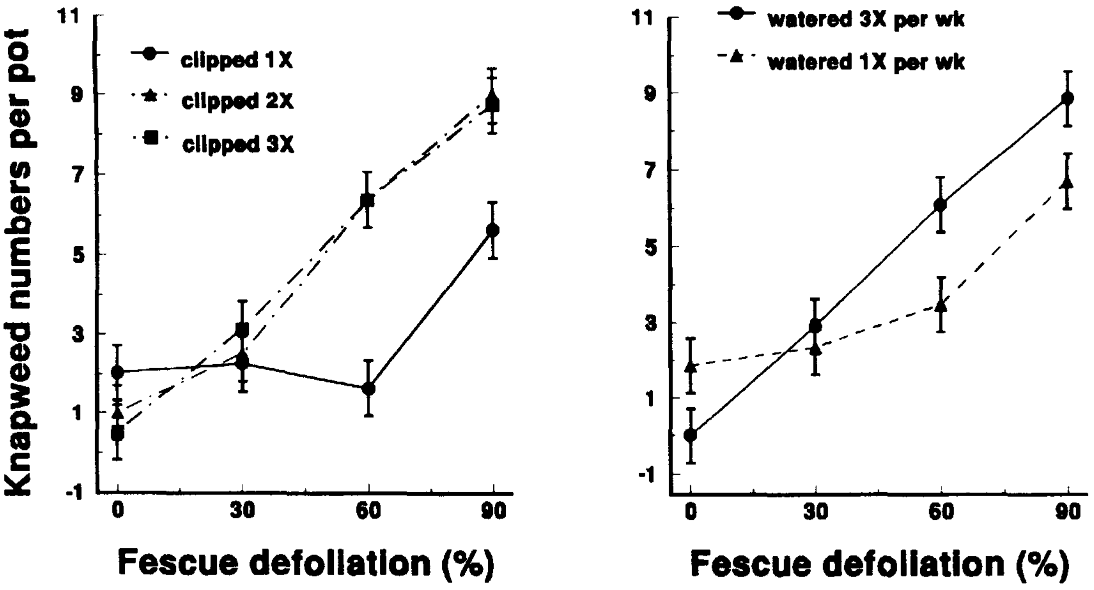

Fig. 3. Effect of defoliation level and frequency, and defoliation level and watering frequency on spotted knapweed number per pot[1]. [1] Error bars represent ± 1SE.

lands. This allows them to occupy and control safe sites as they become available. Our results indicate that severe defoliation together with frequent precipitation opens niches for spotted knapweed germination and emergence.

Defoliation level, defoliation frequency and frequency of watering did not interact to affect spotted knapweed growth, however main effects were significant. Increasing defoliation level of Idaho fescue caused an increase in spotted knapweed growth. Spotted knapweed growth in pots with grass clipped at 30% or more was greater than in pots with unclipped grass (Table 1). Grass defoliation greater than 60% produced greater spotted knapweed growth than lower defoliation levels. Sheley et al. (1997) found crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and bluebunch wheatgrass defoliation greater than 60% increased diffuse knapweed weight. Kennett et al. (1992), found that root crown and foliage growth of spotted knapweed were limited by competition from bluebunch wheatgrass. Our results indicate that even moderate defoliation (30%) may allow greater spotted knapweed growth on Idaho fescue rangeland.

Table 1. Spotted knapweed growth parameters at 4 Idaho fescue defoliation levels (%).

Defoliation	Total weight	Shoot weight	Leaf area	Root weight	Root length
(%)	(g)	(g)	(cm^2)	(g)	(m)
0	0.53	0.5	0.008	0.04	1.5
30	1.60	1.45	0.023	0.15	15.7
60	1.85	1.64	0.031	0.21	20.3
90	2.85	2.28	0.041	0.57	23.9
SE[1]	0.22	0.20	0.003	0.06	3.7

[1]Standard error of least squares means.

Increased clipping frequency also increased spotted knapweed weight, root length and leaf area (Table 2). Clipping more than once allowed greater spotted knapweed growth than a single clipping. However, clipping twice had a similar effect on spotted knapweed weight as clipping 3 times. Increasing grazing frequency may increase spotted knapweed invasion on Idaho fescue dominated rangeland.

Table 2. Spotted knapweed growth parameters at 3 Idaho fescue defoliation frequencies (number of defoliations).

Defoliation	Total weight	Shoot weight	Leaf area	Root weight	Root length
Frequency	(g)	(g)	(cm^2)	(g)	(m)
1	1.09	0.95	0.019	0.13	15.2
2	1.87	1.60	0.028	0.28	14.2
3	2.17	1.85	0.030	0.31	16.7
SE[1]	0.19	0.17	0.003	0.05	3.2

[1]Standard error of least squares means.

Spotted knapweed root weights and leaf areas were greater in pots watered 3 times per week than pots watered once per week (Table 3). Watering did not affect Idaho fescue plants, suggesting watering once per week was sufficient to maintain fescue growth, but was limiting for spotted knapweed seedling growth.

Regressions showed spotted knapweed numbers and total weight increased in pots where Idaho fescue clipping resulted in

Table 3. Spotted knapweed growth parameters at 2 watering frequencies (number of waterings per week).

Defoliation	Total weight	Shoot weight	Leaf area	Root weight	Root length
Frequency	(g)	(g)	(cm^2)	(g)	(m)
1	1.50	1.32	0.022	0.18	12.5
3	1.92	1.62	0.030	0.30	18.2
SE[1]	0.15	0.14	0.002	0.04	2.59

[1]Standard error of least squares means.

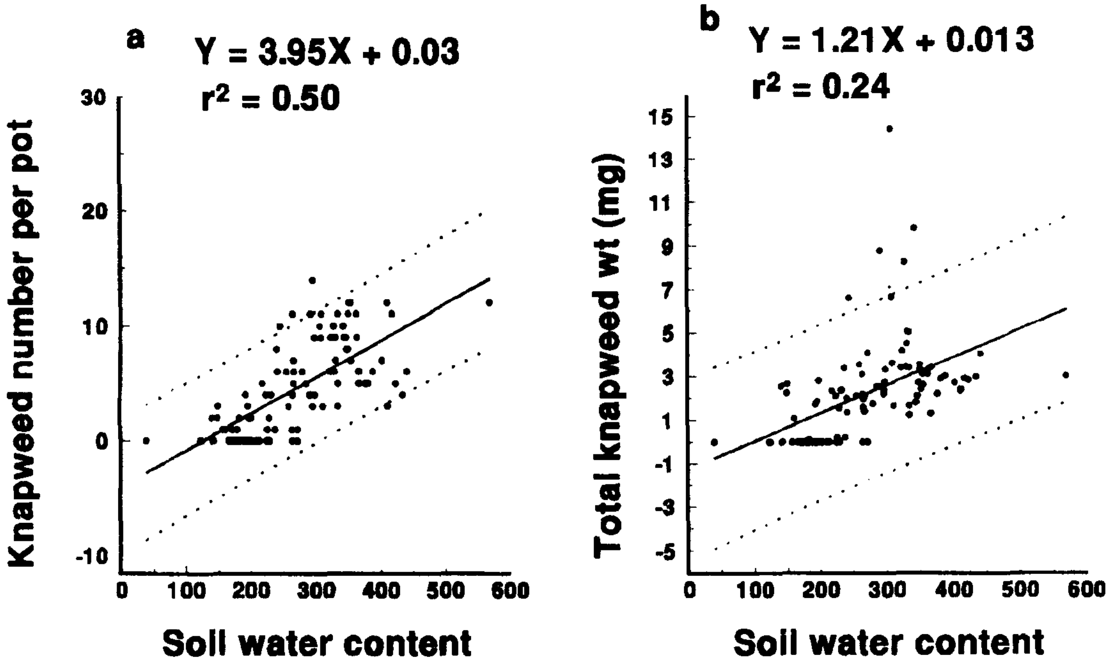

Fig. 4. Relationship between spotted knapweed number per pot or total weight and soil water content (cm^3 cm^{-3}). Dashed lines are 95% confidence intervals.

higher soil water content (Fig. 4). R^2 values indicate soil water content had a greater effect on seedling emergence than seedling growth. Thus, other factors, such as shading, influenced spotted knapweed growth.

Increasing both defoliation level and frequency on Idaho fescue plants caused the soil water content to increase, resulting in a corresponding increase in spotted knapweed emergence and growth. These results suggest that moderate intensity and infrequent grazing can minimize spotted knapweed invasion by maximizing soil water use by Idaho fescue.

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Response of spotted knapweed and grass to picloram and fertilizer combinations

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Abstract

Spotted knapweed (*Centaurea maculosa* Lam.) has reduced forage production, increased soil erosion, and lowered biodiversity on millions of hectares of rangeland throughout the western United States. Objectives of this study were to quantify the interaction between picloram (4-amino-3,5,6-trichloropicolinic acid) and fertilizer on spotted knapweed density and grass yield. Four picloram rates (0.0, 0.14, 0.28, and 0.42 kg ha^{-1}) and 4 fertilizer rates (N+P: 0.0+0.0, 10.5+12.2, 21.1+26.4, and 31.7+39.6 kg ha^{-1}) were applied to 3 spotted knapweed infested rangeland sites in a factorial combination arranged in a randomized–complete–block design during the spring of 1994. Grass yield and spotted knapweed density were measured at peak standing grass crop in 1994 and 1995. Data were analyzed as a split-plot in time using analysis of variance. Picloram and fertilizer did not interact to affect either spotted knapweed density or grass yield. All picloram treatments reduced spotted knapweed density to nearly zero. By 1995, all picloram treatments increased grass yield by an average of 1,500 kg ha^{-1}. Fertilization did not affect spotted knapweed density, but the highest rates increased grass yield on those sites with a substantial residual grass understory. Combining fertilizer with picloram may enhance grass yield on sites with a residual of highly productive grasses.

Key Words: *Centaurea maculosa*, spotted knapweed control, integrated weed management, forage production

In the grasslands of Montana and the Pacific Northwest, the decline of forage grasses, such as Idaho fescue (*Festuca idahoensis* Elmer) has been accompanied by dramatic increases in spotted knapweed (*Centaurea maculosa* Lam). Spotted knapweed, a deeply taprooted perennial, was introduced into North America around 1900 (Roché and Talbott 1986) and has become established in 133 counties in 5 northwestern states (Rice. 1994. Invaders data base software, Univ. of Montana, Missoula, Mont. 59812) and 2 Canadian provinces (Lacey et al. 1989). This weed has the potential to invade about 50% (20 million ha) of rangeland in Montana alone (Chicoine et al. 1985). Spotted knapweed is detrimental to soil and water resources (Lacey et al. 1989), reduces wildlife and livestock forage production (Watson and Renney 1974, Spoon et al. 1983) and lowers biodiversity (Tyser and Key 1988).

Most broadleaf herbicides are effective in killing spotted knapweed, but new seedlings usually emerge within a year (Fay et al. 1989). Picloram (4-amino-3,5,6-trichloropicolinic acid) applied at a rate of 0.28 kg ha^{-1} provides control for 2 to 5 years (Davis 1990). Although the persistence of picloram in the soil affects weeds for 12 to 30 months (Hamaker et al. 1967, Lacey 1985), extended control is enhanced by competition from residual perennial grasses that are released by the herbicide application (Hubbard 1975, Chicoine 1984, Sheley et al. 1984, Roché 1988). Although herbicide application and fertilization have increased forage production on rangelands (Dwyer and Schickendanz 1971, Hart et al. 1995), little is known about combining them to control knapweed and enhance forage production.

Integrating picloram and fertilizers may have a synergistic effect on providing spotted knapweed control and enhanced grass production. In a pilot study, Sheley and Roché (1982) combined picloram (0.28 kg ha^{-1}) and fertilizer (N+P: 17.9+22.4 kg ha^{-1}) which increased grass yield from about 275 (control) and 660 (picloram alone) to over 2,200 (picloram plus fertilizer) kg ha^{-1} 2 years after application. In that study, knapweed control was greater where picloram was combined with fertilization.

Ranchers and other land managers need a better understanding of the potential for using picloram and fertilizer combinations to manage spotted knapweed infested rangeland. This study used a 4 (picloram rates) by 4 (fertilizer rates) factorial design at 3 sites with varying residual grass species to quantify the interaction between picloram and fertilizer on spotted knapweed and residual grass.

Materials and Method

Study Sites

Field studies were conducted during 1994 and 1995 on 3 sites in western Montana to evaluate the effect of combining picloram and fertilizer to control spotted knapweed and enhance grass yield. Study sites 1 and 2 were located near Bozeman, Mont. (111° 5' 36" W, 45° 36' 26" N) and were adjacent to one another. Site 3 was located 30 km west of Ronan, Mont. (114° 20' 0" W, 47° 2' 06" N). All sites were within a bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith)–Idaho fescue habitat type (Daubenmire 1970), and were dominated by spotted knapweed.

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Site 1 was an abandoned hayfield. Spotted knapweed densities were 470 plants m^{-2} (SD=140). The residual grass understory was co-dominated by 2 introduced species, smooth bromegrass (*Bromus inermis* Leys) and timothy (*Phleum pratense* L.). The understory on Site 2 was dominated by the invader, Kentucky bluegrass (*Poa pratensis* L.). Spotted knapweed density was 140 plants m^{-2} (SD=107). The soil, a complex consisting of 70% Beaverton cobbly loam (loamy-skeletal over sandy or sandy-skeletal, mixed, Typic Argiborolls) and 30% Hyalite loam (fine-loamy, mixed, Typic Argiborolls) had zero slope and an elevation of 1,340 m. Annual precipitation ranges from 381 to 483 mm and the frost-free period ranges from 90 to 110 days. Precipitation during 1994 and 1995 was 451 and 447 mm, respectively.

The understory on site 3 was dominated by cheatgrass (*Bromus tectorum* L.), Canada bluegrass (*Poa compressa* L.) and Kentucky bluegrass. Spotted knapweed density was 420 plants m^{-2} (SD=142). Compared to sites 1 and 2, site 3 was severely degraded. The soil at this study site was a Dryfork-Selow silt loam (coarse-silty, mixed, frigid Calcixbrollic Xerochretts) with zero slope. Annual precipitation ranges from 254 to 356 mm. Precipitation during 1994 and 1995 was 321 and 280 mm, respectively. The frost-free period ranges from 120 to 150 days.

Experimental Design

Sixteen treatments (4 picloram rates, 4 fertilizer rates) were applied to 4 by 4 m (site 1 and 2) or 6 by 6 m (site 3) plots and factorially arranged in a randomized-complete-block design. The experiment was replicated 4 times at each site. Picloram rates of 0.0, 0.14, 0.28, and 0.42 kg ha^{-1} were applied in the spring of 1994 using a 6 nozzle backpack sprayer (site 1 and 2) or a 6 nozzle 4-wheel ATV (site 3) delivering 130 liters/ha spray solution. Granular fertilizer was broadcast at N+P rates of 0.0+0.0, 10.5+13.2, 21.1+26.4, and 31.7+39.6 kg ha^{-1} (source: 16-20-0, N-P-K; material: 0.0, 66, 132, 198 kg ha^{-1}) using a hand-cyclone applicator. Sites 1 and 2 were treated on May 2, 1994. Air temperature, soil temperature (surface), and relative humidity were 15.5°C, 21°C, 58%, respectively at the time of application. Winds were calm (<5 km hr^{-1}). Site 3 was treated on May 13, 1994. Air temperature, soil temperature (surface), relative humidity, were 17.5°C, 21°C, and 90%, respectively at the time of application. Winds ranged from 0 to 6 km hr^{-1}. Individual plots were spatially separated from each other by a 2.1 m buffer zone treated with 0.28 kg ha^{-1} picloram to prevent spotted knapweed seed contamination from neighboring plots. Spotted knapweed was in the rosette growth stage at this time.

Sampling

At peak standing crop (August), above-ground grass biomass within a 1 m^2 frame was harvested from each plot in both 1994 and 1995. Grass samples were dried at 60°C until weights were constant and then weighed. Spotted knapweed density (plants m^{-2}) was counted in two 0.1 m (2 × 5 dm) Daubenmire (1970) frames at each site at the time of harvest.

Data Analysis

Data were first analyzed with multiple linear regression (least squares) models using picloram and fertilizer as independent variables. Scatterplots of the residual versus the standardized predicted values indicated that most of the data did not fit a linear model. Therefore, all data were analyzed using standard analysis of variance procedures.

Each site was analyzed separately. The model used was a split-plot in time with herbicide, fertilizer, and herbicide × fertilizer as the wholeplots. Wholeplots were tested using the pooled mean square of block × herbicide, block × fertilizer, and block × herbicide × fertilizer as the error term. Year, year × herbicide, year × fertilizer, and year × herbicide × fertilizer were included in the subplot analysis. Subplots were tested using the pooled mean square of year × block, year × block × herbicide, year × block × fertilizer, and year × block × herbicide × fertilizer as the error term. When a significant ($P<0.05$) F-test was calculated, differences among means were tested using least significant differences procedures.

Results and Discussion

Analysis of variance shows picloram and fertilizer did not interact to affect either grass yield or spotted knapweed density (Table 1). On site 1 (smooth bromegrass/timothy) and site 3 (cheatgrass), the effect of picloram on spotted knapweed density and grass yield was dependent on year. On these sites, spotted

Table 1. Model components, degrees of freedom (df) and mean squares for grass yield (Gyd) and spotted knapweed density (Skn).

Component	df	Mean square					
		Site 1		Site 2		Site 3	
		Gyd	Skn	Gyd	Skn	Gyd	Skn
Herbicide	3	19,482,625*	3,060,953*	2,519,947*	148,292*	10,316,317*	448,378*
Fertilizer	3	3,513,076*	28,165	665,041**	7,172	1,585,529**	1,705
Herbicide x fertilizer	9	568,976	30,083	299,061	7,182	780,418	856
Whole plot error	45	623,998	45,355	248,490	7,028	683,886	4,884
Year	1	59,430,519*	409,635*	16,891,634*	1,070	87,321,086*	243,315*
Year x herbicide	9	3,345,441*	489,601*	616,418	1,273	8,651,164*	214,590*
Year x fertilizer	9	466,457	36,390	532,832	1,026	1,826,007*	747
Year x herbicide x fertilizer	27	280,330	43,437	252,428	928	806,931	284
Subplot error		419,600	50,845	374,732	2,003	713,823	5,216
Subplot df		47	47	48	48	48	48

*, ** significant at the 5% and 10% levels of probability, respectively.

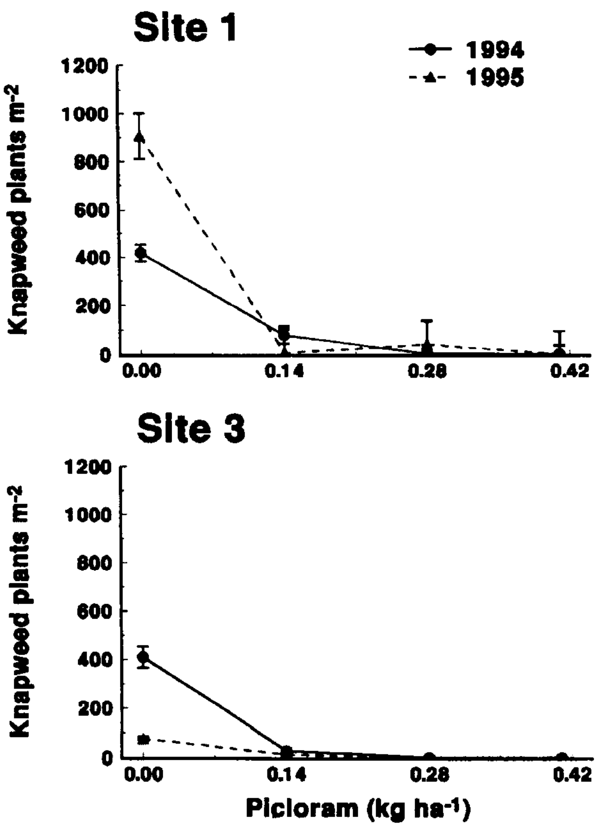

Fig. 1. Effect of year by picloram on spotted knapweed density (plants m^{-2})[1] on site 1 (smooth bromegrass/timothy) and site 3 (cheatgrass). [1]Error bars represent ± 1SE.

knapweed density in plots without picloram were affected by year, which accounted for the interaction (Fig. 1). All picloram treatments reduced spotted knapweed density equally on all 3 sites (Figs. 1 and 2).

In 1994, picloram increased grass yield over those treatments without the herbicide on sites 1 (Fig. 3) and 2 (Fig. 4), but not on site 3 (Fig. 3). On site 3, we believe that cheatgrass, Kentucky bluegrass, and Canada bluegrass were suppressed to the point where they were unable to respond to knapweed control that year. In addition, the early maturing cheatgrass may have completed its life-cycle before it could benefit from knapweed control.

By 1995, picloram increased grass yield on all sites (Figs. 3 and 4). On sites 1 and 3, those plots treated with picloram had lower grass yield in 1994 than in 1995. In all cases, increasing picloram rate had no effect on grass yield.

In Montana, the current recommended rate for controlling spotted knapweed using picloram is 0.28 kg ha^{-1} (Fay et al. 1995). In an 8 year study, Davis (1990) found 0.14 kg ha^{-1} provided 100% spotted knapweed control for at least 3 years, and provided similar control and grass yield to that of picloram at higher rates (0.22, 0.25, and 0.28 kg ha^{-1}) throughout the study. Effective long-term control of spotted knapweed requires periodic applications of picloram which are only cost-effective on highly productive range sites with a substantial grass understory (Griffith and Lacey 1991). Using the 0.14 kg ha^{-1} picloram rate may allow landowners a more cost-effective spotted knapweed control pro-

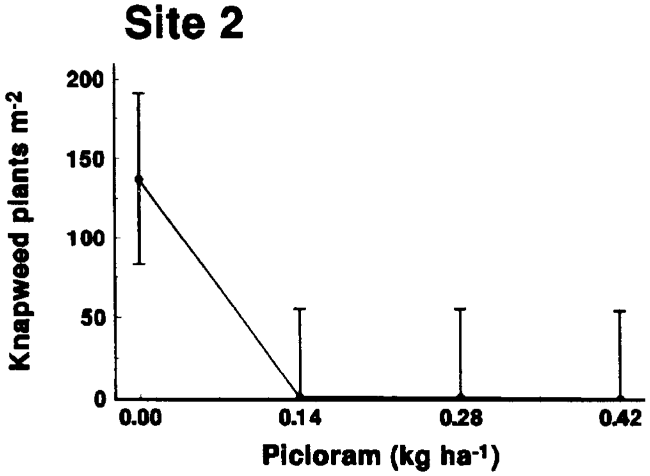

Fig. 2. Main effect of picloram on spotted knapweed density (plants m^{-2})[1] on site 2 (Kentucky bluegrass). [1]Error bars represent ± 1SE.

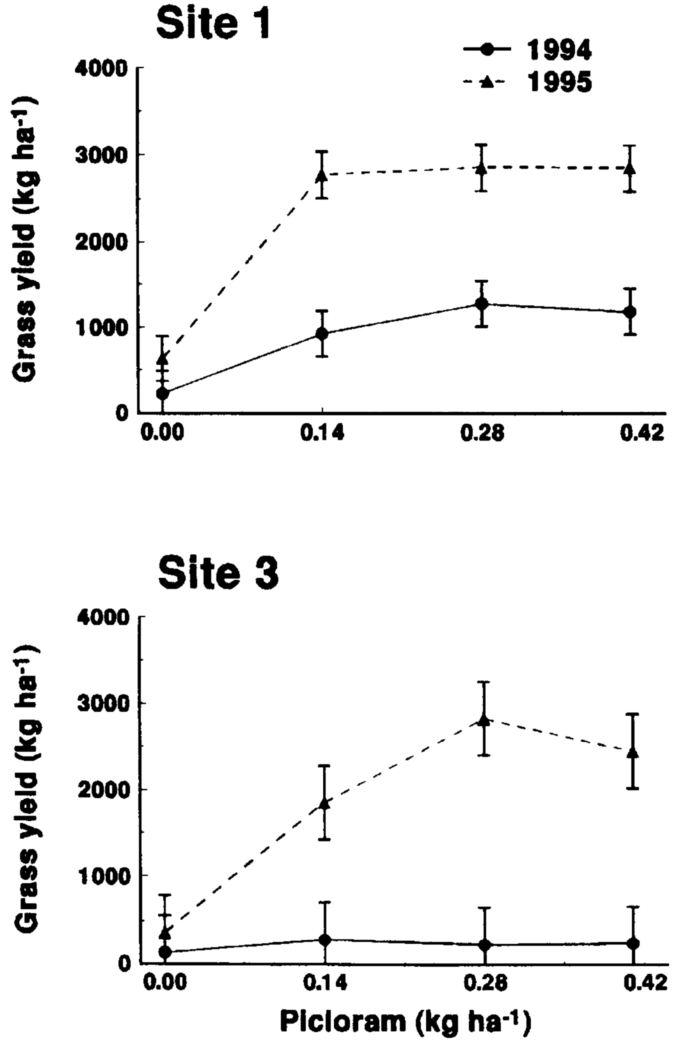

Fig. 3. Effect of year by picloram on grass yield (Kg ha^{-1})[1] on site 1 (smooth bromegrass/timothy) and site 3 (cheatgrass). [1]Error bars represent ± 1SE.

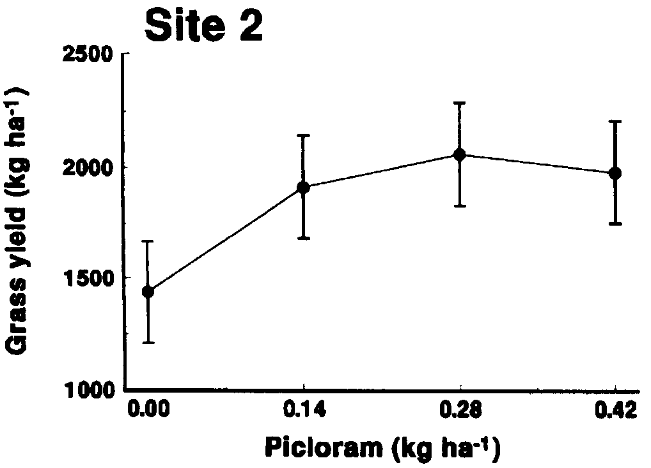

Fig. 4. Main effect of picloram on grass yield (Kg ha^{-1})[1] on site 2 (Kentucky bluegrass). [1] Error bars represent ± 1SE.

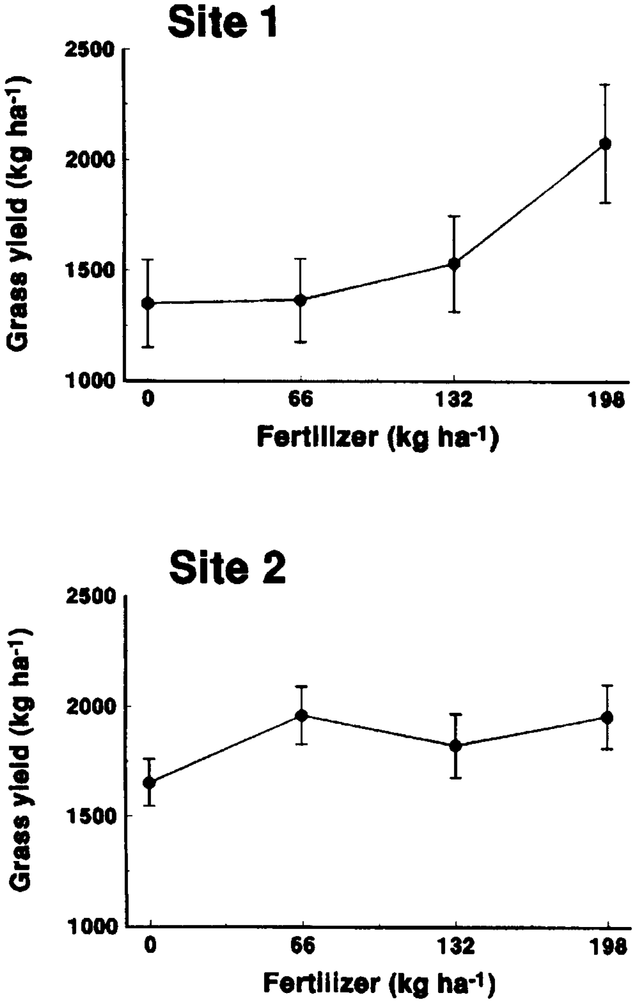

Fig. 5. Main effect of fertilizer (material: 0.0, 66 (10.5N+13.2P), 132 (21.1N+26.4P), 198 (31.7N+39.6P) kg ha^{-1}; source: 16-20-0 N-P-K) on grass yield (kg ha^{-1})[1] on site 1 (smooth bromegrass/timothy) and site 2 (Kentucky bluegrass). [1] Error bars represent ± 1SE.

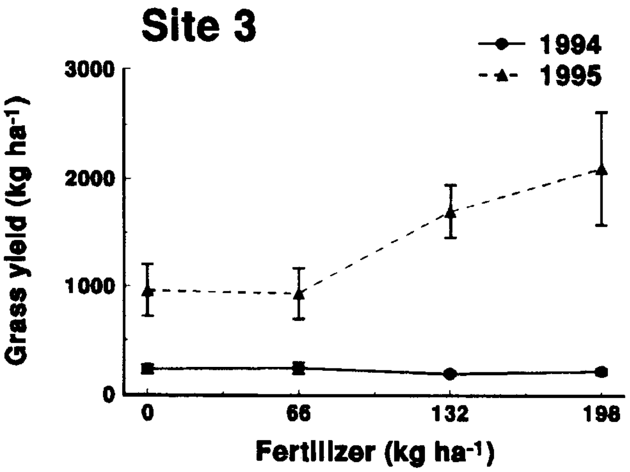

Fig. 6. Effect of year by fertilizer (material: 0.0, 66 (10.5N+13.2P), 132 (21.1N+26.4P), 198 (31.7N+39.6P) kg ha^{-1}; source: 16-20-0 N-P-K) on grass yield (kg ha^{-1})[1] on site 3 (cheatgrass). [1] Error bars represent ± 1SE.

gram on marginally productive range sites. However, we believe that picloram applications must be carefully timed with plant phenology and weather conditions to ensure adequate control at this reduced rate.

Fertilizer had no effect on spotted knapweed density (Table 1). Fertilizer (main effect) increased grass yield on sites 1 and 2 (Fig. 5). On site 1, only N+P applied at 31.7+37.6 kg ha^{-1} increased grass yield. Fertilizer applied at N+P rates of 10.5+13.2 and 31.7+39.6 kg ha^{-1} slightly increased grass yield over those treatments without these chemicals on site 2 (P=0.1). All fertilizer rates other than zero produced similar grass yield on that site. Similar results were obtained by Sheley et al. (1984) in Idaho.

On site 3, which was dominated by cheatgrass, the effects of fertilizer was dependent on year (Table 1). Grass yield was unaffected by fertilizer in 1994. In 1995, N+P rates of 21.1+26.4 and 31.7+39.6 kg ha^{-1} increased grass yield over 0.0+0.0 and 10.5+13.2 kg ha^{-1} (Fig. 6).

Although fertilizer did not interact with picloram to enhance grass yield, high rates substantially increased grass yield on the smooth bromegrass/timothy and cheatgrass sites. Sheley and Roché (1982) found an interaction between picloram and fertilizer, resulting in both greater spotted knapweed control and grass production. However, that study was conducted on an abandoned hayfield receiving about 762 mm of precipitation annually. If the increased grass yield indicates increased competitiveness, spotted knapweed reinvasion should be slowed. Managing for increased forage production combined with longer knapweed control could be cost-effective in some situations.

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Soil depth and fertility effects on biomass and nutrient allocation in jaraguagrass

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Abstract

The African perennial C_4 grass *Hyparrhenia rufa* (Nees) Stapf has successfully invaded the lowland non-flooded savannas of Venezuela except in isolated sites with a shallow lithoplinthic hardpan. To study the mechanism of this invasion process, an experiment was designed to determine the effect of soil fertility and depth of the lithoplinthic hardpan on growth, biomass, and nutrient allocation of *H. rufa*. The main treatments were fertilization with nitrogen, phosphorus and potassium and mechanical disruption of the lithoplinthic horizon prior to seeding with *H. rufa* at the beginning of the rainy season.

Soil fertility rather than soil depth is the predominant abiotic variable regulating the invasion and growth of H. rufa in savanna sites with a shallow lithoplinthic horizon. *H. rufa* exhibited flexibility in phenology, morphology, productivity and biomass allocation patterns in response to nutrient availability. These responses are typical of successful invader plants. Fertilization significantly increased plant growth through increased tillering and leaf production. Fertilization increased total and organ biomass by ~ 1,000% and the highest proportion was allocated to reproductive tillers. In unfertilized plants, live leaves comprised the highest fraction (~ 40%) of total biomass whereas the root/shoot ratio was about 0.3 in all treatments. N concentration was ~ 50% higher in roots and rhizomes than in other organs at the beginning of the dry season and under all treatments. Live leaves of unfertilized plants had higher N concentration than leaves of fertilized plants. Phosphorus and K concentrations were similar among vegetative organs but ~ 400% greater in reproductive tillers of fertilized plants. Fertilized plants had the greatest total content of mineral nutrients due to increased biomass production.

Key Words: biomass production, *Hyparrhenia rufa*; Neotropical savannas, plant invasion tropical soils

The lowland savannas of Venezuela have been used extensively for cattle grazing in spite of their low primary productivity, which is attributed to low soil fertility, seasonal drought and fire (Sarmiento 1984, Frost et al. 1986). Several African grasses, such as *Hyparrhenia rufa* (Nees) Stapf, have been introduced into Venezuela to improve forage quality. This species has spread aggressively and has displaced native plants from the most fertile habitats of the savanna (Parsons 1972, Baruch, and Fernández 1993).

Hyparrhenia rufa is a tufted, perennial, C_4 grass which has higher productivity and marginally better nutritive quality than most native grasses. It is also considered to be fire and drought tolerant (Daubenmire 1972, Parsons 1972, Bogdan 1977). Its annual growth cycle starts with rains in May and peak biomass is attained by August–September. Flowering occurs during the short days of November–December and its aboveground live biomass decreases to a minimum during the dry season

The superior competitive ability of *H. rufa*, as compared to native species, has been attributed to its greater: (a) net photosynthetic rate (Baruch et al. 1985); (b) higher water and nutrient use efficiency (Bilbao and Medina 1990, Baruch and Fernández 1993, Baruch and Gómez 1996); (c) proportion of assimilates allocated to leaves (Baruch et al. 1989, Simoes and Baruch 1991); (d) tolerance to defoliation (Simoes and Baruch 1991) and (e) germination potential (Z. Baruch, unpublished results). The invasion of *H. rufa* has not occurred uniformly within the savanna. *H. rufa* is absent in sites with a surface lithoplinthic horizon although it may dominate deeper soils nearby. The former soils (called "arrecife" or "ripio" in Venezuela) are the least productive of the Venezuelan savannas due to very low fertility and restricted root penetration (García-Miragaya and Cáceres 1990). The objective of this study, which was part of a program to understand the success of African grasses in Neotropical savannas, was to investigate the effects of soil fertility and impedance to root penetration on the invasion and growth of *H. rufa*.

Materials and Methods

Field work was done at the Estación Biológica de los Llanos (8° 53' N and 67° 19' W, 80 m above sea level) 10 km south of Calabozo (Guárico State, Venezuela), on an area that had been protected from fire and grazing for the last 30 years. The climate is warm throughout the year (mean = 27.6°C) and rainfall is strongly seasonal from May to November (annual mean = 1,300 mm). Soils of the study site originated from alluvial sediments ranging from clays to sands to cemented iron oxides. The latter constitute a reddish lithoplinthic hardpan at variable depths that is typical of the non-flooded savannas (López et al. 1971). In general, the soils are acidic, their nutrient and organic matter contents

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are low, and they are high in exchangeable aluminum (García-Miragaya and Cáceres 1990, Medina 1982). At the study site, depth of the lithoplinthic hardpan determines the vegetation pattern: where it occurs at ~ 20 cm or deeper, the native graminoid genera *Trachypogon*, *Axonopus*, *Andropogon*, *Aristida*, and *Bulbostylis* are dominant (Ramia 1967). *H. rufa* invaded these relatively deep soils between 1969 and 1977 (San José and Fariñas 1991) and the native vegetation was displaced by a homogeneous cover of the alien grass (Baruch and Fernández 1993). However, where the lithoplinthic horizon is near the surface, a sparse native community (~ 35% cover) dominated by *Trachypogon plumosus* and *Bulbostylis* sp. persists and *H. rufa* is absent.

Five sites with a surface lithoplinthic horizon (R1-R5) were selected for the experiment. One additional site with lithoplinthic horizon at least 30 cm deep and 100% covered by *H. rufa* (SH) was also sampled for comparison. Soil samples were taken from each site to analyze for bulk density, the soil fraction > 2 mm in diameter and soil texture (Cox 1976). The available elements were extracted with the North Carolina solution (Murphy and Riley 1963); P was determined by the molybdic–blue method (Murphy and Riley 1963), and the cations by flame spectrophotometry. Total soil N was extracted by digestion with concentrated H_2SO_4 and 30% H_2O_2, and determined by titration with 0.01N HCl (Jackson 1982). Organic matter was determined by the Walkley–Black method and pH was measured in water with a 2:5 soil:water ratio (Jackson 1982).

At each R site, four 2m × 2m plots, separated by 50 cm wide buffers, were established and all plants were manually removed. One of the following treatments was applied to each plot: (i) surface fertilization with 70 kg. ha^{-1} each of N as urea, P as triple superphosphate and K as KCl (treatment F); (ii) mechanical rupture of the lithoplinthic horizon with a pickaxe to a depth of 20 cm, and removal of pebbles > 5 cm in diameter which increased the effective soil depth (treatment D); (iii) fertilization + mechanical rupture (treatments D + F) and (iv) control, where only the plants were removed (treatment C). Assignment of the treatments to the plots of each site (block), was at random, resulting in a randomized complete block design. In addition, two 2 m × 2 m plots were established in the SH site where only the dense cover of *H. rufa* was removed.

On 29 June 1991, 250 g of commercial *H. rufa* seeds were surface applied to each plot. Germination occurred 1 week later and by 30 July, all except 7 seedlings (which was the lowest number of surviving seedlings) per plot were manually removed. Sampling started on 12 August. The first 3 samplings were 2 weeks apart, the next 4 were 3 weeks apart, and the last 2 samplings were 4 weeks apart. At each sampling, total number of leaves (live and dead) and culms or tillers on each plant were counted and invading plants were removed. On 9 January 1992, after the plants had reached their maximum seasonal growth, plots of sites R1, R2 and R3 and one of the SH plots were harvested. The remaining plots were harvested 4 weeks later due to logistic limitations. Each of the 7 plants in the plots was sampled. Belowground biomass was collected by excavating 15-cm deep and 10-cm in diameter around the base of the plant. This sampling probably recovered only part of the root systems. The plants were taken to the laboratory, separated into: (i) live leaves; (ii) dead leaves; (iii) culms; (iv) belowground organs (roots and rhizomes), and (v) reproductive organs (racemes). All parts were ovendried at 75°C and weighed. The organs of the plants from each plot were thoroughly mixed and ground through a 60-mesh sieve for N, P, and K determinations as described above. Soil samples were taken again for N, P, and K determination as described. Data were subjected to a two-way ANOVA and means were separated by the multiple rank Duncan test where appropriate (Sokal and Rohlf 1968). Statistical significance was assumed when $p<0.05$. Soil and plant results from the 2 SH plots could not be statistically evaluated and are included and discussed for comparative purposes only.

Results

During the year of the experiment, rainfall was greater than the average for the previous 20 years (1,440 mm vs. 1,300 mm) and 89% of it fell between May and December. Pan evaporation was more than 100% greater than rainfall (2,994 mm) and annual mean air temperature was 27.9°C (Ministerio del Ambiente, Venezuela). Before fertilization, soil P, K, Mg, organic matter and pH were similar in the experimental sites (R1–R5) and in the site dominated by *H. rufa* (SH). However, N and Ca were higher in the SH site (Table 1). The soils were sandy and the pH was acidic in all sites, but the soil fraction > 2 mm in diameter and soil bulk density were greater in the R sites (Table 1). Soil analyses after harvest showed that fertilization had increased P and K significantly (by 466% and 139%, respectively) but total N was not affected and remained around 2 mg g^{-1}.

The number of live leaves increased exponentially in the first 3 samplings of the fertilized R plots, whereas in the unfertilized treatments the increase was much slower. The plants from the SH site showed an intermediate behavior (Fig. 1). Tiller numbers were significantly higher in fertilized plants (Table 2). The difference in growth among treatments caused a difference in pheno-

Table 1. Mean and SD (in parentheses) of the soil physical and chemical variables corresponding to the experimental sites (R) and the SH site (savanna dominated by *H. rufa*, average of 2 plots). Total soil nitrogen values are reported. B. D. = bulk density; F > 2mm. = fraction of soil > than 2mm in diameter.

Site	Variable N	P	K	Ca	Mg	O. M.	pH	Clay	Sand	Loam	B.D.	F > 2mm
	(ppm)					(%)		(%)			(g cm^{-3})	
R	1700	4.1	32.2	16.1	18.2	1.4	5.1	12.0	59.7	19.8	0.8	0.7
	(600)	(0.3)	(4.9)	(5.3)	(2.4)	(0.1)	(0.1)	(1.5)	(1.9)	(1.8)	(0.1)	(0.1)
S. H.	2600	3.6	28.2	32.8	18.4	1.3	5.1	15.2	55.2	21.3	0.5	0.4

Table 2. Mean and SD (in parentheses) of total and organ biomass (g plant^{-1}) corresponding to the treatments and S.H. (savanna dominated by *H. rufa*). Included are the two-way ANOVA significant differences (*) at $p<0.05$. C=control; F=fertilization effect; D=depth effect; I=interaction (F×D). For each variable, values followed by the same letter are not statistically different at $p<0.05$. Data for SH (*Hyparrhenia rufa* savanna) is the mean of 2 plots, was not subjected to statistical analysis, and is shown only for comparison.

Variable	Treatment						
	C	D	F	D+F	F(2,12)	ANOVA	S.H.
	---------------- (g. plant^{-1})-			---------------			
Live Leaves	1.1a (0.2)	0.7a (0.3)	4.0b (0.4)	4.3b (0.5)	60.3	F*, I, D	1.7
Dead Leaves	0.6a (0.2)	0.7a (0.4)	4.7b (1.4)	3.4b (0.8)	13.8	F*, I, D	4.4
Culms	0.1a (0.0)	0.2a (0.1)	8.5b (3.4)	5.5b (0.9)	13.1	F*, I, D	2.6
Roots and Rhizomes	0.6a (0.1)	0.7a (0.3)	6.4b (1.6)	5.0b (0.5)	32.1	F*, I, D	3.6
Reproductive Organs	0.1a (0.2)	0.1a (0.3)	2.5b (0.8)	2.4b (0.6)	23.2	F*, I, D	0.6
Total Biomass	2.6a (0.4)	2.5a (1.7)	26.2b (7.0)	20.6b (2.2)	27.1	F*, I, D	12.3
Root/Shoot Ratio	0.3a (0.06)	0.3a (0.10)	0.3a (0.08)	0.3a (0.06)	0.6	F, I, D	0.3
Tillers/plant	13.1a (3.3)	11.9a (1.6)	25.2b (2.5)	24.4b (4.3)	10.9	F*, I, D	14.4

logical development: leaf and tiller numbers peaked 30–45 days earlier in the fertilized plants (Fig. 1). However, leaf death occurred simultaneously in all treatments and the SH site at the beginning of the dry season (January 1992).

Neither plant biomass nor nutrient concentration differed significantly between the 2 harvests, thus the data were pooled for statistical analysis. Fertilization was the only statistically significant effect. Total plant and organ biomass were consistently and significantly higher in fertilization treatments (Table 2). The plants from the SH site generally had intermediate biomass which was closer to that of fertilized plants (Table 2). The highest proportion of total biomass was represented by live leaves in unfertilized plants and by roots and rhizomes in fertilized plants (Fig. 2). The fraction of culms and reproductive structures was signifi-

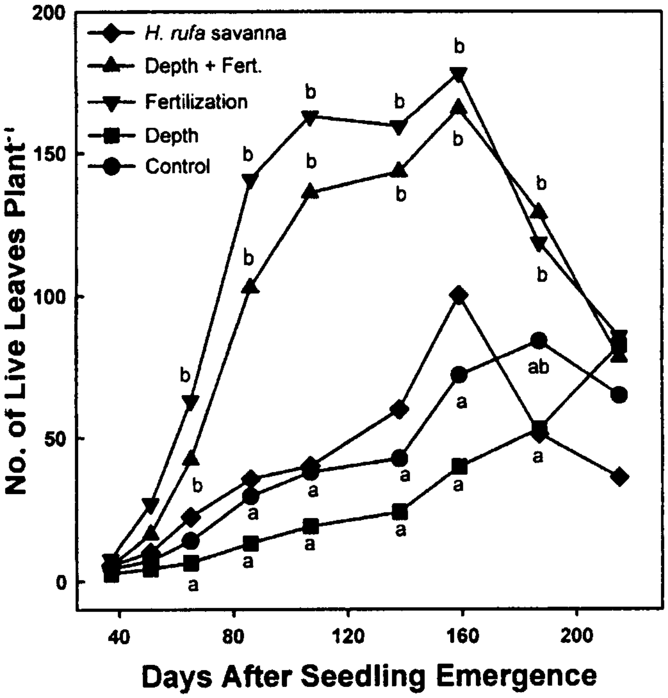

Fig. 1. Number of live leaves. plant-1 for each treatment and for the SH sites. For each sampling, treatments marked with the same letter are not statistically different at P < 0.05. (Data from the *H. rufa* savanna are from 2 plots and are shown only for comparison).

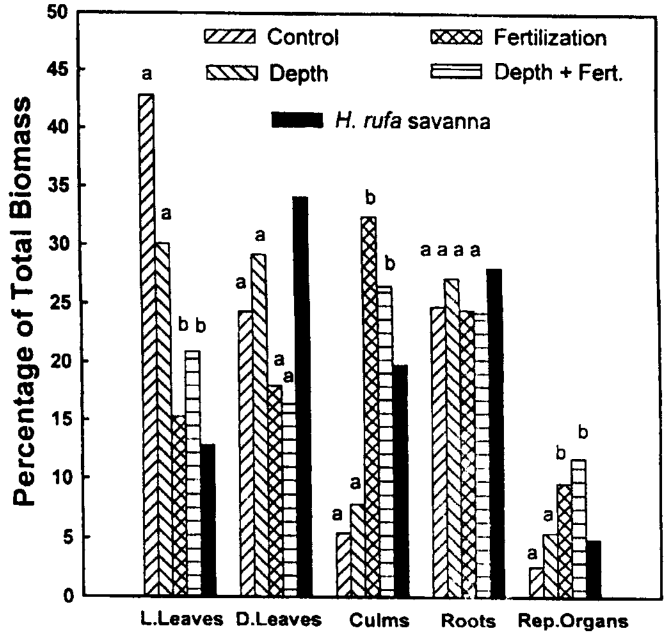

Fig. 2. Organ biomass as percent of total biomass under each treatment and the S.H. site (Data from the *H. rufu* savanna are from 2 plots and are shown only for comparison). For each organ, treatments marked with the same letter are not statistically different al P < 0.05.

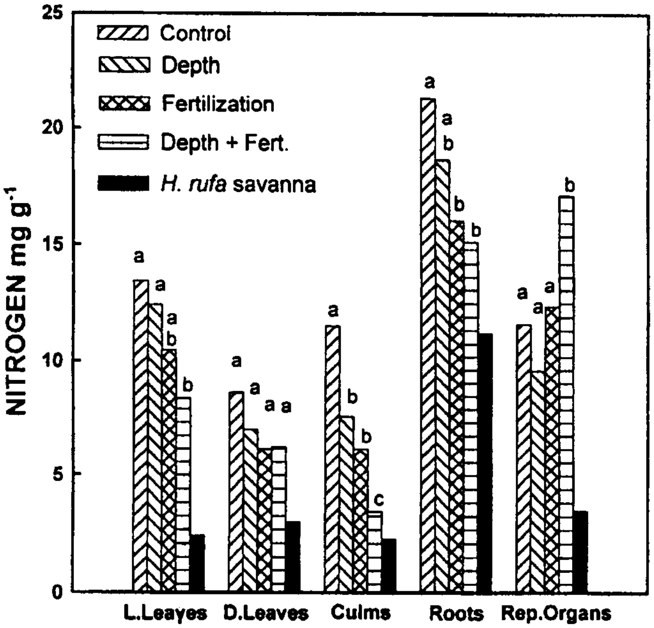

Fig. 3. Nitrogen concentration of the organs for each treatment and the S.H. site. Comments, symbols and statistics as in Fig. 2.

cantly higher in fertilized plants (Fig. 2). These allocation patterns resulted in a root/shoot ratio which was similar in all treatments (Table 2).

Among vegetative tissues, N concentration was significantly higher in underground organs in all treatments. Dead leaves had ~ 40% less N than live leaves except in plants from the SH site (Fig. 3). Vegetative organs of unfertilized plants had higher N concentrations than those of fertilized plants (Fig. 3). Total N content per plant organ was similar to biomass pattern, i. e. highest in the fertilization treatments, lowest in unfertilized plants and intermediate in SH plants. Phosphorus was more evenly distributed among vegetative organs than N in all treatments and SH. However, reproductive organs of both fertilized treatments had 100% greater P concentrations than vegetative organs (Fig. 4). In contrast to N, the P present in live leaves remained there until they senesced. Total P content per plant had the same pattern as N. Potassium concentration ranged from 5 to 10 mg g^{-1} in all organs and treatments except in reproductive organs of fertilized plants where the concentration was ~ 500 % higher (data not shown).

Discussion

The results show that growth and biomass production of *H. rufa* were more related to nutrient availability than to effective soil depth of the lithoplinthic soils typical of the well-drained savannas of Venezuela. Although only soil N and Ca concentrations were higher in the SH site, its lower bulk density and greater depth probably allowed the roots of *H. rufa* to exploit a larger volume of soil than in the R sites. Also, in the R sites, a high proportion of soil particles (~ 70%) was > 2 mm in diameter which was not analyzed for nutrient content. This fraction, composed of quartz pebbles and the lithoplinthic hardpan rich in iron oxides, has an extremely low nutrient concentration (García-Miragaya and Cáceres 1990). Therefore, the difference in total nutrient availability between R and SH soils would be greater than our data on concentration suggest. This greater nutrient availability in the deeper SH soils apparently favors the invasion and growth of *H. rufa*. Added nutrients had contrasting behavior, P and K remained in the soil longer than N which probably was either leached or absorbed by plants.

Hyparrhenia rufa in fertilized plots grew larger and produced more leaves and culms than those in unfertilized plots due probably by increased carbon assimilation as found by Coughenour et al. (1985) in *Hyparrhenia filipendula*. Also, leaf and culm production was accelerated by fertilization. This faster vegetative growth probably aided sexual reproduction as fertilized plants flowered earlier and produced more reproductive biomass than unfertilized plants. This might have been largely due to P availability. High biomass accumulation, as found in fertilized *H. rufa* is typical of fast-growing species in fertile environments (Chapin 1980) and of invader plants (Bazzaz 1986). In contrast, native savanna grass production responds less to fertilization, whereas N and P concentrations in their live biomass increase (Medina et al. 1977, Bilbao and Medina 1990).

At harvest, the highest fraction of total biomass of unfertilized plants was live leaves, which suggests a delay in their annual growth cycle and reproduction or that soil P levels were inadequate for reproduction. The root/shoot ratio was similar in all treatments indicating a high degree of rigidity in biomass allocation. This result should be interpreted with caution due to possible incomplete recovery of root biomass. Although nutrient availability regulated the growth of *H. rufa*, its effect was probably modulated by water availability. This was evidenced by leaf mortality which occurred synchronously in all treatments and in the

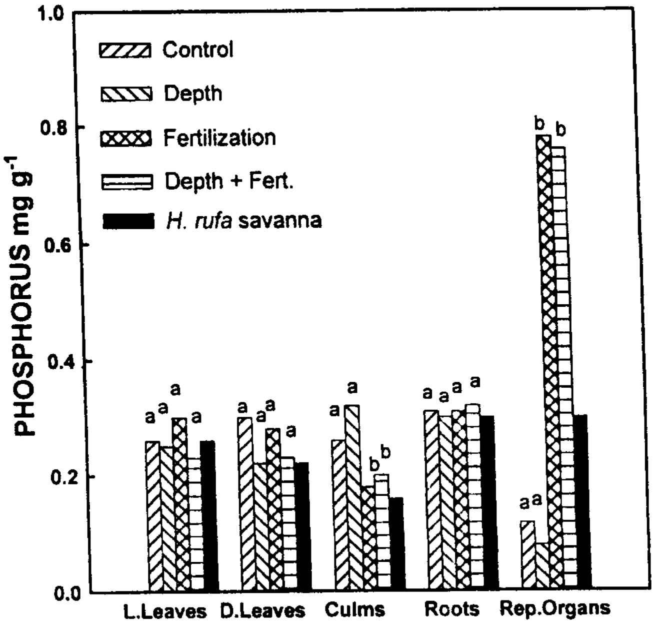

Fig. 4. Phosphorus concentration of the organs for each treatment and the S.H. site. Comments, symbols and statistics as in Fig. 2.

SH site at the beginning of the dry season. Early leaf senescence is an important drought-evasion strategy in *H. rufa* (Baruch and Fernandez 1993).

Fertilization increased total nutrient content per organ due to increased biomass but nutrient concentration was more affected by internal allocation. Nitrogen concentration, was highest in the roots and rhizomes of all treatments and SH, suggesting that they were the main N sink during the dry season and an important N source for the next growing season (Tergas and Blue 1971, Chapin 1988, Chapin et al. 1990). The low N concentration in dead leaves suggested that downward translocation of N from senescing leaves to roots and rhizomes took place. However, low N concentration in dead leaves of SH plants was not evident. The seasonal translocation has been reported in *H. rufa* and other tropical (Sarmiento 1992, Baruch and Gómez 1996) and temperate (Heckathorn and De Lucia 1994) grasses. The higher leaf N concentration in unfertilized as compared to fertilized plants could be caused by 3 mechanisms whose relative importance is difficult to distinguish: (i) Fertilization increased leaf biomass in *H. rufa* thus diluting N concentration (Medina et al. 1977, Chapin 1980); (ii) In unfertilized plants leaf N was not involved in growth due to P shortage (Bilbao and Medina 1990) and (iii) As discussed above, unfertilized plants were still vegetative and N translocation to roots and to reproductive organs was delayed. The low N concentration in SH plants as compared to unfertilized plants in R sites was probably caused by dilution of tissue N in the former due to its faster biomass production.

The uniform distribution of P among vegetative organs of the plants in all treatments contrasts to that of N and indicates the lack of preferential accumulation and partitioning of this element as postulated by Medina (1993). This is interesting, particularly in unfertilized plants, since the existence of a strategy that permits the economy of P should have been selected for in tropical savannas where P is strongly limiting (Medina et al. 1977, Medina 1982, 1993). The contrasting behavior of N and P could be clarified considering that *H. rufa* evolved in African savannas (Clayton 1969; Bogdan 1977) on soils where P is less limiting than N (Anderson and Talbot 1965, Medina 1993). On the other hand, the high P concentration in reproductive organs of fertilized plants is prominent and probably contributes, through increased reserves, to faster seedling growth after germination.

The results of this study indicate that *H. rufa* can establish on sites with shallow lithoplinthic hardpans if the competing vegetation is removed. Subsequently, soil fertility rather than effective depth regulated the permanence and growth of *H. rufa* on these sites. *H. rufa* showed flexibility in its phenological, architectural, productivity and biomass partitioning patterns in response to soil nutrient availability. Fertilization increased plant size and biomass whereas the absorbed nutrients were invested in growth and reproduction and reserves were accumulated in roots and rhizomes during the dry season. Low production of unfertilized plants induced N buildup in leaves and their vegetative growth period was longer which seemed to prevent the accumulation of sufficient reserves for sexual reproduction before the beginning of the dry season. This type of flexible response for nutrient use, plus the intrinsic high growth potential and the opportunistic use of water (Baruch et al. 1985, Baruch and Fernández 1993, Baruch 1996) partially explain the success of *H. rufa* in the non-flooded savannas of Venezuela.

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Post–burn recovery in the flooding Pampa: Impact of an invasive legume

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Abstract

Winter burning of *Paspalum quadrifarium* Lam. stands ("pajonales") promotes colonization of denuded spaces by several alien species. *Lotus tenuis* Waldst et Kit. ("lotus"), a recent invader of the region, is able to reach very high densities between the resprouting bunches of the dominant species. Results of a removal experiment performed to evaluate the impact of natural establishment of lotus on post-burn colonization of pajonal stands are reported. Seedlings of lotus were removed shortly after their emergence between burned bunches of *P. quadrifarium*. Eighty days after burning, approximately 30% of the soil surface remained uncovered within removal plots, whereas canopy cover was complete within controls. Furthermore, final (137 days post-burn) total aboveground biomass was 2.7 times higher in control than in removal plots. Removal of lotus significantly ($P<0.05$) increased the cover of an annual native grass (*Phalaris angusta Nees*, ex Trin.) and the final biomass of an alien thistle (*Carduus acanthoides* L.). A spatial association analysis provided additional evidence about the negative impact of lotus on colonization success of *C. acanthoides*. Weed colonization may be reduced, if not prevented, by managing the colonization processes of other new and useful invaders.

Key Words: *Paspalum quadrifarium*, removal experiment, fire, colonization, weeds, *Lotus tenuis*, Argentina

Paspalum quadrifarium Lam. ("paja colorada", thereafter "paspalum") is a bunch grass (1.50 m tall) that, under low disturbance regimes, excludes other species and forms dense patchy stands locally called "pajonal". Pajonal stands were probably responsible for the physiognomy of an important portion of the pre-settlement flooding pampa (Argentina); 25 years ago, the pajonal still occupied 14,000 km^2 of that region (Vervoorst 1967, León 1991). An important but unmeasured area of remnant pajonal persist today, mainly restricted to non-arable soils.

Winter burning of pajonal stands increases cattle stocking rates, but also promotes important infestations of exotic weeds, particularly of thistles (Cauhépé 1990, Sacido et al. 1995). In mature pajonal stands (those with a tall and dense canopy), the basal area of paspalum is generally less than 30%. Therefore, winter burning creates open spaces for seedling recruitment (Laterra et al. 1994). Spear thistle (*Cirsium vulgare (*Savi.Ten.) welted thistle (*Carduus acanthoides* L.), and narrowleaf birdsfoot trefoil (*Lotus tenuis* Waldst et Kit, thereafter "lotus") are common exotic colonizers of such spaces. However, annually burned experimental plots with high lotus biomass, showed lower colonization by thistles than plots with low lotus biomass (Laterra et al. unpublished data). Thus, interference (competitive and/or non-competitive, Hall 1974) effects, like those reported between other fugitive species (e.g. Platt and Weis 1985) are likely between lotus and thistles, as well between lotus and other colonizer species. The potential ability of lotus to reduce thistle establishment in burned stands has a particular management relevance because the former species represents an exceptional forage resource for these legume-poor grasslands (Montes 1988), and because thistles are unpalatable weeds without forage value.

Lotus is a warm-season, perennial legume from Europe that became naturalized in the flooding pampa only a few decades ago (Montes 1988). In contrast, thistle abundance in the region was noted by several travellers in the early past century (Vervoorst 1967). Studies regarding invasions of rangelands by alien plants are generally focused on their impact on native species (e.g. Parsons 1972, Musil 1993, but see Sheley and Larson 1994). The lotus-thistles case represents an interesting opportunity to assess the impact of a new invader on the established alien flora.

Results of an experiment performed to evaluate the impact of lotus on the post-burn development of pajonal stands are reported. This study sought to quantify: (1) the effects of post–burn occupation of pajonal stands by lotus on colonization by thistles and other colonizer species, and (2) the effects of colonization by lotus on canopy recovery rate and biomass production between bunches of paspalum after burning. Additional evidence of the influence of lotus is provided by analysing the spatial association between the presence of adult plants of welted thistle and the abundance of lotus. This study focused on welted thistle because the results of the removal experiment suggested it was one of the species most affected by the presence of lotus, and because welted thistle is a serious pest species in burned pajonal stands.

Materials and Methods

Study Site

The study was carried out in a rangeland located at San Ignacio, 20 km south of Ayacucho, Argentina, in the southeastern

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part of the flooding pampa. This is a 58,000 km^2 region characterized by flat poorly drained soils having a general deficiency of available phosphorus, and a temperate climate with frequent winter-spring floods and summer droughts (León 1991). Median annual precipitation for Ayacucho is 1029 mm, and the precipitation during the experimental period (September–February 1993-1994) equaled the median amount of the past 10 year median (549 mm and 550.5 mm, respectively) (Ayacucho Agency of the Instituto Nacional de Tecnología Agropecuaria, unpublished).

The pajonal stands of San Ignacio occur as patches associated with slight topographic elevations. One patch of nearly 3 ha was selected for a long term experiment about fire effects on pajonal community structure. The present data were obtained from a 0.7 ha plot belonging to that experiment, selected according to its topographic, soil and physiognomic uniformities. The plot was burned in the early spring 1990 (11 October) and late winter 1992 (26 August) and was lightly grazed during each post–burn summer. This management caused lotus to become a codominant species of the pajonal stand, with an important seed bank of 2.2 viable seeds/cm^2 by the time of the second burning (Maceri et al., unpublished data).

Field Methods

The complete study sector was burned again with a backfire on 10 September 1993. At that time, adults of paspalum had a mean height of 45.6 cm (SE=0.2, N=28), the standing biomass had a mean dry weight of 118.2 g/m^2 (SE=5.2, N=16) which was 37% green (SE=0.9, N=16). Humidity content of green and senesced biomass was 85 and 61%, respectively. Wind speed during burning was less than 25 km/h, and air relative humidity was 37%. The mean maximum fire temperatures, estimated with Tempilsticks (R) (Big Three Industries, Inc. Hamilton Blvd, South Plainfield, N.J. 07080, USA) placed at the soil level between paspalum bunches, was 189°C (SE=7.2, N=19). Only the tiller bases of paspalum and crowns of lotus remained unburned; the inter–bunch spaces were completely denuded. Since previous studies at the same site showed that, unless grazed, fast post–burn regeneration of the pajonal canopy caused low establishment of paspalum and any other species (Laterra et al. 1993, 1994), the entire pajonal patch (3 ha) was grazed with 10 cows, during 3 discontinuous days, between December 1993, and January 1994.

Removal Experiment

One month after the fire (early spring), thirty 30 × 50 cm permanent plots were randomly placed between bunches within a 400 m^2 square area at the center of the pajonal patch, excluding a few sites occupied by 1 or more adult plants (established before the last fire) of lotus or any other species. Half of those plots were randomly assigned to a removal treatment while the rest were left intact. At this time, seedlings of lotus which had emerged after the fire had only 1 or 2 leaves; all of the lotus seedlings within the removal plots were cut at the soil level. Clipping of a new established cohort of lotus seedlings was performed at a similar growth stage 1 month later. Seedling density of lotus was estimated on vertical photographs of 4 additional 30 × 50 cm plots, randomly taken in the study area at the time of the first clipping. Seedlings were clipped instead of uprooting to minimize soil disturbance. Eighty days after burning, at the beginning of summer, each plot was photographed vertically from a height of 1.50 m, and the plants were identified to species level. At this time, regrowth of paspalum bunches wasn´t extended over the plots. Canopy cover was estimated for each species using the photographs, by recording the length of intersections along 15 random transects totalling 3.25 m per plot. After 137 days post–burn (early summer), all aboveground biomass was harvested, oven dried and weighed.

Removal response coefficients (C) were calculated for each species, as:

$$C = (N_r - N_c) / N_r$$

where N_c is the mean biomass or cover of the target species in the control plots and N_r is the mean biomass or cover of the target species in the removal plots. Coefficient values from $-\infty$ to 1 represent increasing site preemption plus interference intensity experienced by the target species due to lotus. However, results of removal experiments may also be affected by indirect interactions (Aarsen and Epp 1990), and negative values of C can only be explained by them.

Statistical analysis of cover variables was accomplished using Student's t-test on untransformed data. Variance heterogeneity and/or lack of normality in biomass of some species could not be normalized through data transformations, so, they were analyzed using the Kruskal–Wallis's test.

Spatial association

In late summer (170 days post-burn), all adults of lotus and welted thistle were counted within 60 circular plots each 30 cm in diameter within the study sector. Half of the plots were randomly placed and the other half were centered on single adult plants of welted thistle growing among bunches of paspalum. The same procedure was repeated using 60 cm diameter plots, centered on the previous ones. The hypothesis of independence of plant density as a function of proximity to welted thistle, was examined using the Chi-square test.

Results and Discussion

No grass seedlings, a few thistle seedlings at cotyledonary stage, and many lotus seedlings were observed within the experimental plots at the first clipping date. Mean lotus seedling density was 34 seedling. dm^{-2} (SD=10.6, N=4) at the time of the first clipping. Clipping was not effective in completely excluding lotus from the plots since 80 days after burning this species had reestablished from both seeds germinated within plots and from plants growing immediately adjacent to the plots (Table 1). However, clipping the initial growth affected the recovery rate and species composition between bunches. Eighty days after burning, nearly 30% of soil remained uncovered within removal plots, whereas control plots were completely covered.

Removal of lotus enhanced the cover of all the species present at the first sampling date, as reflected by the positive and high

Table 1. Canopy cover (means ± 1 S.D.) in the interspace between adult plants of *Paspalum quadrifarium* 80 days after burning for the *Lotus tenuis* removal and control treatments. Only species with mean relative canopy cover equal to or greater than 1% in any treatment are shown. C is the removal response coefficient (see text for explanation). P is the significance level of the Kruskal-Wallis test.

Species	C	Canopy cover Removal	 Control	P
		- - - - - (%) - - - - - -		
Lotus tenuis	—	19 ± 9	91 ± 5	<0.001
Phalaris angusta	0.85	30 ± 16	4 ± 4	<0.001
Trifolium repens	0.75	9 ± 13	2 ± 4	0.027
Cirsium vulgare	0.83	5 ± 10	1 ± 2	0.571
Carduus acanthoides	0.91	2 ± 3	1 ± 1	0.086
Crepis capilaris l (Wall.)	0.95	2 ± 5	1 ± 1	0.272
Carduus nutans L.	1.00	1 ± 1	1 ± 1	0.165
C. vulgaris plus *C. acanthoides*	0.87	8 ± 9	1 ± 2	0.006
Total	—	68 ± 1	99± 1	<0.001

removal coefficients, suggesting an indiscriminated or diffuse interference effect of lotus between the principal colonizer species. However, this effect was significant only for the annual native grass *Phalaris angusta* Nees, ex Trin., for the exotic legume *Trifolium repens* L., and for the combined cover of the 2 most abundant thistles (both aliens), spear thistle and welted thistle. In contrast, the effect of lotus removal on the final biomass of the inter-bunch colonizers was less diffuse. Removal coefficients varied from welted thistle, the only species which showed a positive and significant treatment effect, to other species like *T. repens* which showed a negative but non-significant effect (Table 2). No pattern was found between removal coefficients and characteristics of target species like origin (native or exotics), taxon (monocots or dicots) or life history (annuals or perennials). The species that showed the most significant response in the first sampling, *P. angusta*, also showed positive but non-significant effects of removal treatment at the end of the experiment. Together with *Vulpia dertonensis* (all.) Gola, an annual exotic grass, they have a winter-spring cycle and only senescent tissues of these species were present at the time of the final harvest (summer).

As was said above, the experimental design applied here did not provide control for indirect interaction effects, which could be influencing both the positive and negative results. Thus, indirect influences from herbivores or soil microflora (e.g. Bergelson 1990, Holt 1977), cannot be assessed.

Consistent with the above results, the natural variation in lotus abundance explained a significant portion of the spatial pattern of welted thistle, both at 30 and 60 cm scales (Chi-square=14.9; 1 d.f.; p<0.001, and Chi-square=14.4; 2 d.f.; p<0.001, respectively). For example, for plots of 30 cm in diameter, frequency of this thistle was 2.7 times lower than expected when there was more than 3 lotus plants within the same plot (Fig. 1).

Table 2. Aboveground biomass of colonizing species (means ± 1 S.D.) in the interspace between adult plants of *Paspalum quadrifarium* 137 days after burning for the *Lotus tenuis* removal and control treatments. P is the significance level for the Student's t test, except for *Vulpia dertonensis*, *Phalaris angusta* and *Carduus acanthoides* L. where P is the significance level of the Kruskal-Wallis test. Biomass of species lower than 0.5 g/m² were pooled under the "other species" category. Total biomass includes all the species biomass plus non-identified plant residues. C is the removal response coefficient (see text for explanation).

Species	C	Biomass Removal	 Control	P
		- - - - - - - (g/m²) - - - - - - -		
Lotus tenuis	—	26.0 ± 10.7	192.9 ± 72.9	<0.001
Phalaris angusta	0.43	20.1 ± 17.4	11.4 ± 17.7	0.218
Carduus acanthoides	0.85	10.7 ± 14.5	1.5 ± 1.5	0.046
Trifolium repens	-0.63	7.8 ± 9.3	12.7 ± 24.0	0.793
Stipa spp.(1)	0.25	4.8 ± 7.4	5.9 ± 6.7	0.675
Vulpia dertonensis	0.99	3.7 ± 12.7	0.1 ± 0.2	0.312
Paspalum quadrifarium	0.01	0.6 ± 1.0	0.6 ± 0.8	0.967
other species(2)	-0.80	3.5 ± 5.1	6.4 ± 7.1	0.255
Total	—	90.2 ± 32.7	242.6 ± 71.1	<0.001

(1) mostly *S. neesiana*, *S. philippii*, and *S. formicarum*

(2) mostly *Carex* spp., *Plantago lanceolata* and *Picris echioides*

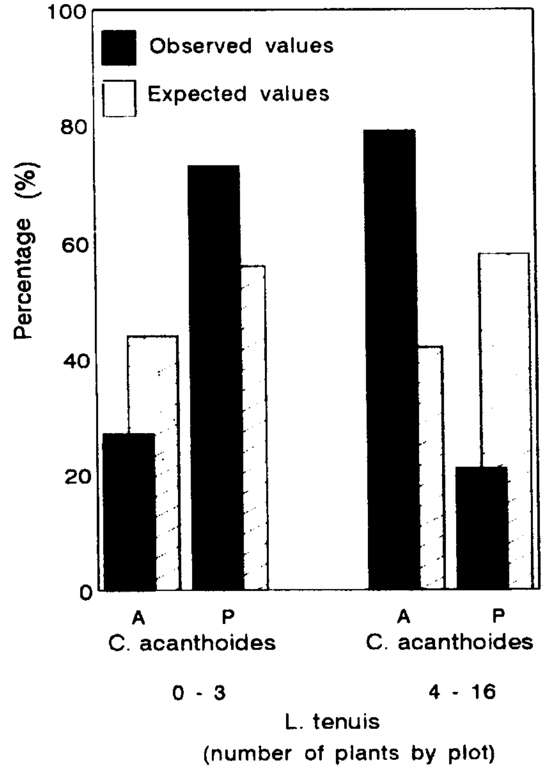

Fig. 1. Percentages of 30 cm diameter plots in which *Carduus acanthoides* was absent (A) or present (P) (1 to 3 adult plants), when *Lotus tenuis* had different number of adult plants within the same plots. The expected values are the calculated percentage of plots according to the independence hypothesis between the spatial distribution of both species.

Altering rates of resource supply is one of the most important effects of biological invasions at the ecosystem level (D'Antonio and Vitousek 1992). A reduction of 64% in the lotus contribution to final total biomass (from 79.3% in control plots to 28.9% in removal plots), reduced the final total biomass in a similar proportion (63%) (Table 2). Similar results were recently observed by Insausti, Soriano, and Quinos (unpublished data) in other grasslands of the flooding pampa (without *P. quadrifarium*), where the introduction of lotus after selective removal of all other broad-leaved herbs determined two-fold increments in leaf area index and biomass of the entire community. Thus, the rapid and complete covering of soil and/or the symbiotic nitrogen fixation by lotus, may have contributed to a greater resource uptake by the community, at least within the inter-bunch areas.

Like most legumes, lotus has high innate seed dormancy (Mujica and Rumi 1993), and thus the soil seed bank may be capable of persisting through long periods in which the habitat is occupied by a closed canopy cover. The heat from fire breaks innate seed dormancy of legumes by mechanical alteration of the seed-coat (Bradstock and Auld 1995), promoting massive germination of the buried seeds. Since both spear thistle and welted thistles do not form permanent seed banks (Soriano and Eilberg 1970, Roberts and Chancellor 1979, Klinhamer and De Jong 1993), their colonization of burned patches would mainly depend on immigration of seeds from previously disturbed patches, like it occurs with other ephemeral fugitives (e.g. Theaker et al. 1995). These life history differences suggest that seed production by thistles (annual or biennial life cycle) may have a faster post-burn decline than seed production by the perennial lotus. Thus, there may be an optimal fire frequency which could deplete or reduce the transient seed banks of thistles, while the seed bank of lotus is replenished or even increased. This burning frequency would cause dense establishment of lotus after fire, diminishing the opportunities for colonization by thistles from edge sources.

Conclusions

Colonization patterns of burned pajonal grasslands by lotus partially explained post-fire structure of the community. Increased abundance of this species reduced colonization by some thistles and annual grasses. These results illustrate that colonization of certain weeds may be reduced, if not prevented, by other new and useful invaders. Furthermore, colonization by lotus increased the plant biomass in the inter-bunch areas of the pajonal. Fire regime, as well as initial population structure of the principal colonizer species, may be important factors affecting the success of using selected invaders to manage other invaders.

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Viewpoint: Atmospheric CO_2, soil water, and shrub/grass ratios on rangelands

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Abstract

The abundance of woody plants on grasslands and savannas often is controlled by the availability of water and its location in soil. Water availability to plants is limited by precipitation, but the distribution of soil water and period over which it is available in these ecosystems are influenced by the transpiration rates of grasses. We discuss implications of recent and projected increases in atmospheric CO_2 concentration for transpiration, soil water availability, and the balance of grasses and shrubs. An increase in CO_2 concentration often reduces potential transpiration/leaf area by reducing stomatal conductance. On grasslands where effects of stomatal closure on transpiration are not negated by an increase in leaf temperature and leaf area, rising CO_2 concentration should slow the depletion of soil water by grasses and potentially favor shrubs and other species that might otherwise succumb to water stress. Predicted effects of CO_2 are supported by results from CO_2-enrichment studies in the field and are compatible with recent models of interactions between resource levels and vegetation pattern and structure.

Key Words: C_4 grasses, competition, rooting depth, stomatal conductance, transpiration

The importance of water availability to the geographic distribution of vegetation types (Whittaker 1975, Woodward 1987, Stephenson 1990) and their productivities is widely-recognized (Rosenzweig 1968, Webb et al. 1983, Sala et al. 1988). Soil water balance, thus, is a key component of current models to predict effects of climatic and atmospheric change on vegetation (Woodward 1993, Neilson and Marks 1994). On grasslands and savannas, where plant productivity is strongly coupled to precipitation (Webb et al. 1983, Sala et al. 1988, Pandey and Singh 1992), water availability in space and time exerts a dominant climatic control on the balance between grasses and woody species. In his study of southern African savannas, Tinley (1982) concluded that soil water availability was the most important factor controlling the relative abundances of grasses and trees or shrubs. Similar conclusions have been drawn in other tropical savannas (Medina and Silva 1990) where most grasses possess the C_4 photosynthetic pathway. Water balance, however, also affects shrub/grass ratios in temperate and subtropical regions where the two growth forms coexist (Williams et al. 1987). These and other studies (e.g., Neilson 1986, Sala et al. 1992) suggest that relatively small changes in water balance may cause relatively large changes in the structure of grassland ecosystems.

Atmospheric CO_2 concentration has nearly doubled since the last Ice Age, 18,000 years ago (Delmas et al. 1980), and has increased from about 275 ppm (parts per million; Neftel et al. 1985, Raynaud and Barnola 1985) to the present concentration near 355 ppm during the last 200 years. It may rise to twice the current level during the next century (Trabalka et al. 1986). Stomatal conductance usually declines as atmospheric CO_2 concentration rises (Morison 1987). On grasslands, a decline in stomatal conductance that reduces transpiration rate will increase soil water availability during intervals between rainfall. Woody or other plants that were previously excluded by low water availability may be favored as a result.

We review effects of atmospheric CO_2 concentration on stomatal conductance and processes at the leaf, canopy, and higher scales that regulate the effect of stomatal closure on transpiration. We then discuss consequences of slower transpiration for soil water levels and the balance between grasses and shrubs on grasslands and savannas. Effects of climatic changes that may accompany rising CO_2 concentration on grassland vegetation are addressed elsewhere (Parton et al. 1994). Influences of fire, browsing, grazing, and edaphic factors, other than soil water, that affect woody abundance also are not reviewed (Belsky 1990, Archer 1994, Archer et al. 1995). C_4 species dominate many warm temperate and tropical grasslands and savannas. We, therefore, emphasize possible effects of CO_2 on C_4-dominated ecosystems like rangelands of the central and southern Great Plains and southwestern U.S. Consequences of rising CO_2 for transpiration and soil water balance on C_3-dominated grasslands are briefly discussed.

Interactions Between CO_2 Concentration and Transpiration

One of the more consistent, though not universal, effects of an increase in atmospheric CO_2 concentration is a decrease in leaf or stomatal conductance (Morison 1987, Field et al. 1995). Morison and Gifford (1984a) found that leaf conductance of 16, mostly

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C_3, agricultural and horticultural species declined a mean 36% when grown at double the present CO_2 concentration. Few studies report stomatal conductance or resistance of C_4 plants grown at different atmospheric CO_2 concentrations. In our review of the stomatal responses of C_4 plants to CO_2, conductance was reduced an average 34% across 16 observations and 29% across 12 species by an approximate doubling of the current CO_2 concentration (Table 1). Little is known of the stomatal responses of plants grown at lower-than-current CO_2 levels. Available evidence suggests, however, that stomatal conductance may be more sensitive to a given change in CO_2 over subambient than elevated concentrations (Fig. 1; Polley et al. 1996a).

It is important to recognize that conductance is typically measured on sunlit leaves near the tops of well-watered plants. Absolute differences in conductance between CO_2 treatments are usually reduced by water stress (Gifford and Morison 1985), low light levels such as those found within canopies (Knapp et al. 1994), and high leaf–to–air vapor pressure deficits (Morison and Gifford 1983, Bunce 1993).

A decrease in conductance tends to reduce transpiration and lessen the rate at which soil water is depleted in a given environment. For these changes to occur, however, effects of stomatal closure on transpiration must not be offset by an increase in leaf area or leaf temperature, or by feedbacks between transpiration and evaporative demand of the atmosphere.

Most C_3 plants grow and accumulate leaf area faster when atmospheric CO_2 concentration is increased (Poorter 1993), partly because higher CO_2 stimulates photosynthesis. This is particularly true when plants have adequate nutrition and are grown alone or in stands of low density (Bazzaz 1990). There are exceptions (Morgan et al. 1994), but photosynthesis, growth, and leaf area of C_4 plants are relatively unaffected by increases in CO_2 concentration when the soil is wet (Morison and Gifford 1984b, Curtis et al. 1989, 1990, Polley et al. 1994, Dippery et al. 1995, Polley et al. 1996a). Water conserved by closing stomates, however, may allow plants at high CO_2 concentration to continue growth longer into drought (Gifford and Morison 1985, Owensby et al. 1993b, Samarakoon and Gifford 1995). Higher CO_2 levels may also speed physiological recovery of some plants from drought (Knapp et al. 1993b).

Leaf growth and area in both C_3 and C_4 plants may be limited by resources other than water or CO_2. Low nitrogen availability frequently limits production on C_4 grasslands (Seastedt et al. 1991). The growth response of C_4-dominated tallgrass prairie to elevated CO_2 was limited by low nitrogen availability more during a dry year than during a relatively wet year (Owensby et al. 1994). Production of ungrazed tallgrasses may also be limited by light (Knapp et al. 1993a). These limitations may partially be offset if resource utilization efficiency rises as CO_2 concentration increases. Biomass production per unit of nitrogen increases as CO_2 concentration rises for both C_3 and C_4 species (Owensby et al. 1993a, Polley et al. 1994, Polley et al. 1995). Rising CO_2 increases the amount of carbon fixed per unit of absorbed light in C_3 (Long and Drake 1991), but not C_4 plants (Knapp et al. 1993b).

Other feedbacks may reduce effects of stomatal closure on transpiration. Leaf temperatures may increase when stomates close because less energy will be dissipated by transpiration (Morison and Gifford 1984a). The resulting increase in leaf-to-air vapor pressure gradient will lessen water savings from a decrease in conductance. Transpiration is also influenced by the temperature and humidity of air around and immediately above a plant canopy. When air in this canopy "boundary" layer does not mix with that higher in the atmosphere, its temperature and humidity become highly dependent on transpiration itself. Slower transpiration reduces humidity of the air in the boundary layer and increases the amount of energy that heats the air (Jarvis and McNaughton 1986, McNaughton and Jarvis 1991, de Bruin and Jacobs 1993). These changes, in turn, increase the evaporative demand of air and reduce water savings from stomatal closure. Stable boundary layers develop most frequently above well-

Table 1. The percentage change in stomatal conductance (gs) of well–watered C_4 plants caused by an approximate doubling of the current CO_2 concentration. Stomatal conductance was measured at or near the CO_2 level at which plants were grown. Conductance was reduced by a mean 34% across observations. CTC=closed–top chamber, OTC=open–top chamber, GC=growth chamber.

Species	Growth CO_2	Growth Condition	Change in g_s	Reference
	(ppm)		(%)	
Andropogon gerardii	337/658	CTC, Field	–42	Kirkham et al. 1991
Andropogon gerardii	354/716	CTC, Field	–36	Nie et al. 1992a
Andropogon gerardii	Ambient/2X Ambient	OTC, Field	–51	Knapp et al. 1993b
Andropogon gerardii	Ambient/2X Ambient	OTC, Field	–51	Knapp et al. 1994
Andropogon gerardii	Ambient/2X Ambient	OTC, Field	–51	Ham et al. 1995
Andropogon glomeratus	350/650	GC, Pot	+11	Bowman and Strain 1987
Andropogon virginicus	380/650	GC, Pot	–13	Wray and Strain 1986
Amaranthus retroflexus + Setaria faberii	350/700	GC, Pot	–55	Garbutt et al. 1990
Atriplex canescens	360/680	GC, Pot	–20	Polley et al. 1996a
Echinochloa crus–galli	350/675	GC, Pot	0	Potvin and Strain 1985
Eleusine indica	350/675	GC, Pot	0	Potvin and Strain 1985
Eragrostis orcuttiana	340/680	GC, Pot	–71	Smith et al. 1987
Paspalum plicatulum	340/590	GC, Pot	–37	Gifford and Morison 1985
Schizachyrium scoparium	360/680	GC, Pot	–58	Polley et al. 1996a
Sorghum bicolor	330/660	CTC, Field	–12	Chaudhuri et al. 1986
Zea mays	340/718	OTC, Pot	–51	Rogers et al. 1983

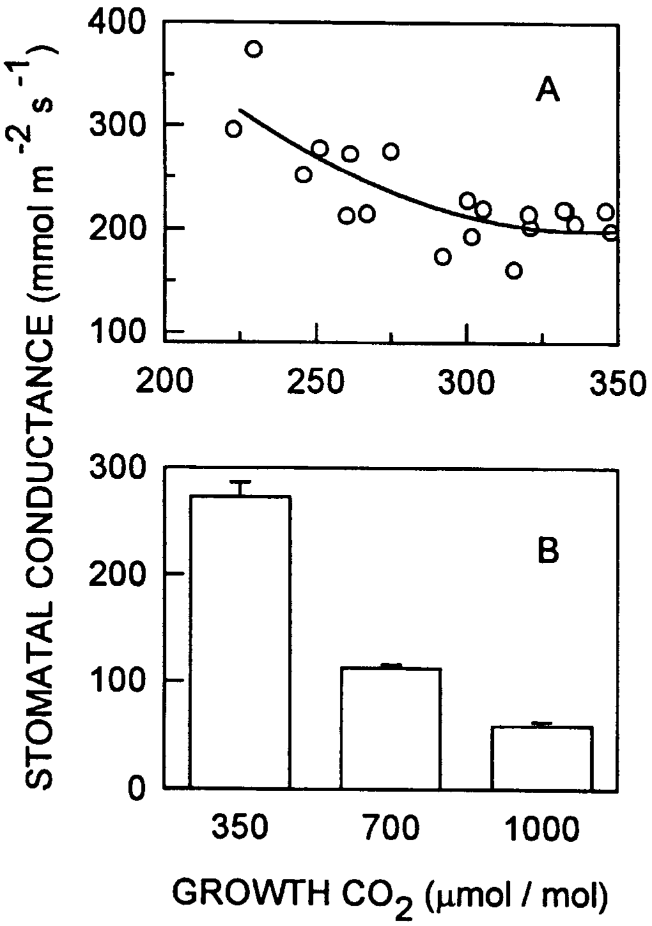

Fig. 1. Stomatal conductance of sunlit leaf blades of the C_4 grass *Schizachyrium scoparium* (little bluestem) as a function of the CO_2 concentration at which plants were grown. (A) The line is a regression through single measurements per plant with an infrared gas analyzer (Polley et al. 1994). (B) Vertical bars denote 1 standard error of the mean of 18 daily averages of leaf (blade) conductance. Conductance was measured during a separate experiment on 5 plants from each CO_2 treatment. Note that the scale of the y-axis differs in A and B.

watered agricultural crops with plant canopy conductances in excess of 20 mm sec^{-1} (McNaughton and Jarvis 1991). Canopy conductances are smaller, and stomatal control of transpiration is greater, in most grasslands and other extensively–managed vegetation in arid and semi–arid regions (e.g., Valentini et al. 1995).

Atmospheric CO_2 and Evapotranspiration: Field Studies

Extensive data are now available from CO_2 enrichment studies on salt marsh in Maryland, USA (Drake 1992) and tallgrass prairie in Kansas, USA (Owensby et al. 1993b). These data can be used to evaluate impacts of elevated CO_2 on the water balance of C_4-dominated ecosystems. Doubling CO_2 caused little increase in leaf or canopy photosynthesis of C_4 grasses in either ecosystem, except during or shortly following drought (Ziska et al. 1990, Drake and Leadley 1991, Drake 1992, Kirkham et al. 1991, Nie et al. 1992a, 1992b, Knapp et al. 1993b), but reduced potential water loss by halving stomatal conductance (Kirkham et al. 1991, Knapp et al. 1994).

Water savings expected from the decline in conductance at elevated CO_2 concentration were partly offset in Kansas by higher leaf temperatures (Kirkham et al. 1991) and, in years with below normal precipitation, greater leaf area (Owensby et al. 1993b). In spite of these negative feedbacks on transpiration, water loss/soil surface area was significantly reduced by elevated CO_2 in both salt marsh and tallgrass prairie. Evapotranspiration was reduced even during drought periods when C_4 growth was stimulated by CO_2. Doubling CO_2 concentration reduced evapotranspiration from C_4 cord grass (*Spartina patens* (Ait.) Muhl.) communities in salt marsh by 28% to 29% in each of 2 years (Drake 1992). Kirkham et al. (1991) calculated that during a 1-month period in 1989, doubling atmospheric CO_2 concentrations reduced evapotranspiration 15% from C_4-dominated tallgrass prairie that was watered weekly to field capacity, and 7% when watered weekly to one-half of field capacity. Average rates of evapotranspiration per unit soil surface were reduced 18% under well-watered conditions and 8% when supplemental water was withheld the following year (Nie et al. 1992b). Similarly, daily evapotranspiration from tallgrass prairie near peak biomass was reduced 22% during a relatively wet year by doubling the current CO_2 concentration (Ham et al. 1995). As a result of the decline in evapotranspiration, soil water levels in tallgrass prairie were consistently higher at elevated CO_2 concentration (Kirkham et al. 1991), even during periods of relatively severe drought (Owensby et al. 1993b).

Similar changes in soil water balance are possible in C_3-dominated communities as CO_2 rises, if leaf growth is limited by nitrogen availability (Hatton et al. 1992, Polley et al. 1995), phenology, or other factors. Jackson et al. (1994) found that doubling the current CO_2 concentration on a C_3 grassland reduced stomatal conductance and transpiration of the dominant species, wild oat (*Avena barbata* Brot.), by about 50%. The decline in water use per unit leaf area at elevated CO_2 was not offset by an increase in leaf area, and soil water content increased 34% by season's end.

Field estimates of the amount of water that might be saved on more arid grasslands as CO_2 rises are not available. Rates of water loss will almost certainly depend on the size, intensity, and temporal pattern of precipitation events. Generally, however, effects of CO_2 concentration on soil water balance should be smaller in arid than in relatively mesic ecosystems (Table 2).

Table 2. Predicted effects of rising atmospheric CO_2 concentration on transpiration, soil water availability, and the balance of shrubs and grasses on arid and relatively mesic grasslands and savannas.

Parameter	Mesic Grassland	Arid Grassland
Transpiration/Leaf area	Reduced	Reduced
Leaf Area	Increased during dry periods	Increased
Total Transpiration	Reduced	Small or no reduction
Change in Soil Water Content		
Shallow	Increased	Little change
Deep	Potentially Increased	No change
Shrub/Grass Ratio of Vegetation	Increased (especially if most precipitation falls when plants are active)	Little change?

Most precipitation events in arid and semi-arid environments are small and a high proportion of water from small rainfall events is lost to evaporation (Noy-Meir 1973, Sala et al. 1992). Rising CO_2 concentration consistently increases growth and leaf expansion of C_4 grasses when water becomes limiting (Gifford and Morison 1985, Owensby et al. 1993b). Transpiration rates of C_4 species, therefore, may also decline less, as CO_2 rises, in arid than in more mesic ecosystems. Whether the smaller absolute effect of CO_2 on soil water balance in arid than in more mesic ecosystems will prove important to vegetation dynamics remains to be determined.

Potential Consequences of Lower Evapotranspiration to the Species Composition of Grasslands and Savannas

Grasses may prolong growth into periods without rainfall by reducing transpiration and effectively conserving soil water. There are at least 2 ways, however, in which water saved by grasses could benefit woody and other plants (Fig. 2). First, the water could be used by plants that share rooting space with grasses. Seedlings of shrubs and other plants depend at least initially on water in the rooting zone of grasses (Williams and Hobbs 1989, Harrington 1991, O'Connor 1995). Even large woody plants may compete directly with grasses for water and other resources (Carlson et al. 1990, Dugas and Mayeux 1991, Belsky 1994, Le Roux et al. 1995, Montaña et al. 1995). Secondly, water conservation by grasses could increase deep percolation of subsequent rainfall. Shrubs and other plants that root more deeply than grasses (Knoop and Walker 1985, Sala et al. 1989, Medina and Silva 1990, Brown and Archer 1990, Sala et al. 1992, Axmann and Knapp 1993, Bragg et al. 1993, Nizinski et al. 1994) would be favored as a result. The depth to which precipitation moves depends partially on soil water content (Hanks and Ashcroft 1980). Deep percolation should increase, therefore, if the water content of upper soil layers remains higher for longer periods. Generally, this should occur more often in relatively–mesic than in arid grasslands.

Water at depth is recharged on some grasslands largely by rainfall during the dormant season of grasses (e.g., Cable 1969). In these ecosystems, changes in grass transpiration probably will not greatly affect growth of deeply–rooting shrubs. On many grasslands and savannas, however, shrubs depend on deep percolation of water during the period that grasses are growing (Knoop and Walker 1985), and could benefit from a positive feedback of rising CO_2 on soil water content.

The importance of the vertical distribution of soil water to shrub/grass ratios on savannas is well-recognized and has been conceptualized in a "two–layer" model of shrub/grass competition (Walter 1971, Walker et al. 1981, Walker and Noy-Meir 1982). Shallowly-rooting grasses are assumed to have primary access to, and to be superior competitors for, water in upper soil layers. The more deeply–rooting shrubs primarily access water below the roots of most grasses. The model does not consider influences of fire, browsing or grazing, and edaphic factors, other than soil moisture and soil texture, that could influence shrub/grass ratios (Belsky 1990, Archer 1994). It is, however, supported by studies in tropical savannas (Knoop and Walker 1985, Sala et al. 1989, Medina and Silva 1990), and is consistent with the observed influence of topography and drainage on woody cover (Tinley 1982, Coughenour and Ellis 1993).

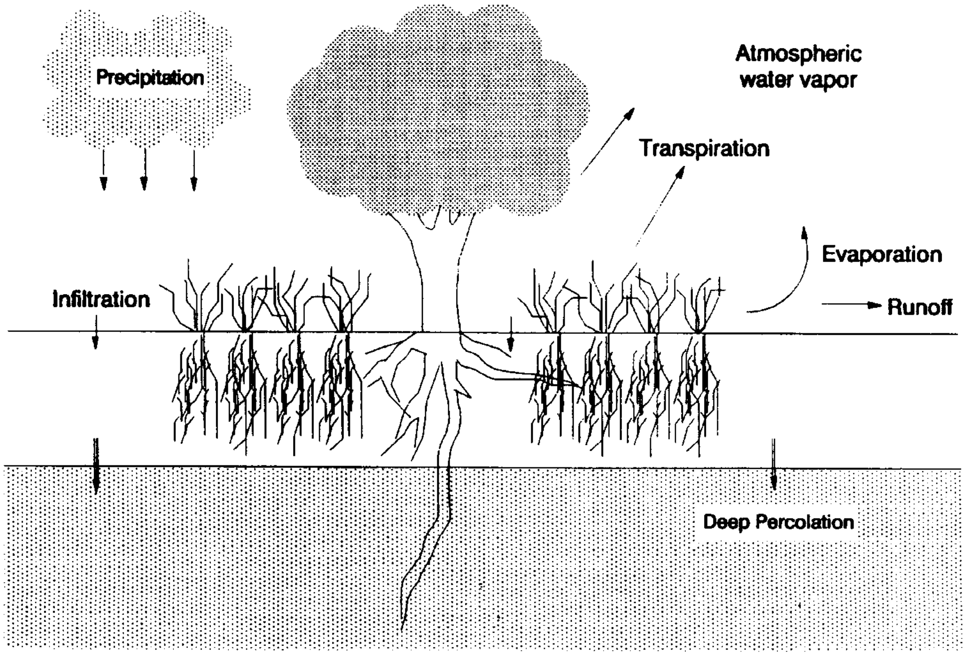

Fig. 2. Schematic diagram showing major pathways of water flux for grasslands and savannas. Rising atmospheric CO_2 concentration is predicted to reduce transpiration from shallowly–rooting grasses and other species, increase the duration of water in upper soil layers, and, in some ecosystems, increase percolation to soil layers occupied by deeply–rooting species like shrubs.

Results from a CO_2-enrichment study on tallgrass prairie in Kansas, USA are consistent with the prediction that some plants will benefit from changes in soil water balance at elevated CO_2. Although the mechanism has not been established, basal cover of forbs increased concurrently with soil water content following a doubling of the current CO_2 concentration (Owensby et al. 1993b). In the absence of fire or browsing, woody plants would likewise be expected to increase in size and abundance by exploiting the greater availability of soil water.

Woody ingress on grasslands may generate a series of positive feedbacks on ecosystem hydrology that reinforce the shift in growth form composition (Joffre and Rambal 1993). Grass production and transpiration often decline following woody invasion, resulting in higher soil water levels and, in some ecosytems, greater infiltration to soil depths where woody roots are concentrated (Knoop and Walker 1985, Sala et al. 1989). Heavy grazing or other factors that reduce leaf area and transpiration of grasses may also increase soil water content. Alternatively, water may move through woody roots from deep, moist soil to surface layers where it can be used by grasses (Richards and Caldwell 1987, Dawson 1993).

Relationship to Other Ecosystems and Other Hypotheses/Models

A progressive shift to taller plants as CO_2 concentration and average levels of soil water increase is compatible with predictions from the vegetation models of Tilman (1988) and Smith and Huston (1989). In both of these models, vegetation change through time or over spatial resource gradients is driven by the relationship between soil resource (water and nitrogen) availability and potential plant height. As soil water availability increases, competition for light favors an increase in the mean height at which leaf area is displayed (Smith and Huston 1989).

Vegetation dynamics on grasslands may, therefore, be increasingly driven by competition for light or other soil resources as soil water availability increases. Not all competitors of grasses will be favored. Perhaps only plants that can grow above the grass canopy, or that are competitive for the limited nitrogen on many grasslands, will benefit. Basal cover of *Poa pratensis* L. on tallgrass prairie declined at elevated CO_2, apparently because the short-statured grass was shaded by taller species or was limited by low nitrogen availability (Owensby et al. 1993b). Fertility and other soil characteristics are important determinants of shrub/grass ratios on some grasslands and savannas (Walker 1993). Saline or poorly–drained soils limit woody invasion (Belsky 1990), but soil fertility commonly determines the type (evergreen, sclerophyllous vs. deciduous, mesophyllous) of woody invader that is successful.

Variation in soil water content across landscapes also influences species composition on some grasslands and savannas (Coughenour and Ellis 1993, Walker 1993). Drainages, or sites that receive runon, may have a greater abundance of shrubs than adjacent areas. It is, of course, difficult to predict effects of rising CO_2 on the spatial distribution of water on grasslands with complex terrain. Hydrologic simulations for a forested catchment, however, indicated that elevating CO_2 altered the spatial distribution of soil water by increasing the number of areas with moist soil (Hatton et al. 1992).

Summary and Conclusion

Water availability exerts an important control on the composition of vegetation on grasslands and savannas where evaporative demand often exceeds precipitation. Rising atmospheric CO_2 concentration increases plant production per unit of transpiration (Morison 1993, Polley et al. 1993), perhaps allowing plants to grow and reproduce on less water than was formerly required. These changes alone could alter species distributions and local abundances (Idso and Quinn 1983). On some grasslands and savannas, plant composition may also respond to indirect impacts of CO_2 on soil water balance. A CO_2-caused decrease in canopy transpiration rate should generally favor more mesophytic species by slowing soil water depletion and, in some ecosystems, may benefit more–deeply–rooting plants by increasing percolation. Effects of rising CO_2 on individual species, however, will remain difficult to predict. Species dynamics in any community depend on dispersal rates, seedling establishment, and other factors, including grazing and fire, that may vary independently of CO_2 concentration (Belsky 1990, Archer 1994, Archer et al. 1995, Polley et al. 1996b).

Effects of CO_2 concentration on soil water availability and vegetation dynamics in the future will also depend on accompanying changes in climate. Temperature–caused increases in evapotranspiration may offset predicted increases in precipitation in some regions (Neilson and Marks 1994) and reduce positive effects of higher CO_2 concentration on soil water balance. Given the sensitivity of species composition on grasslands to precipitation and soil water balance, interactions between climatic change and rising CO_2 concentration must be more clearly understood before we will be able to predict the future dynamics of vegetation in these ecosystems.

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Gas exchange of Idaho fescue in response to defoliation and grazing history

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Abstract

We tested the hypothesis that prior grazing history would influence the defoliation responses of Idaho fescue (*Festuca idahoensis*) growing in a common garden environment. Plants were taken from a grazed pasture and adjacent exclosure which had not been grazed since 1937, and established in a common garden at 1 m spacings during spring of 1989. Plants from defoliated and nondefoliated treatments within the 2 populations were sampled during 1992 and 1993. Photosynthesis, conductance to H_2O, and xylem potentials were measured during the 2 growing seasons, and carbon isotope ratio ($\delta^{13}C$) was measured for senescent leaf tissue. Both within exclosure and outside exclosure defoliated plants exhibited compensatory photosynthesis that averaged a 12% increase the first year, and a 52% increase during the second year, compared with nondefoliated plants. No differences in photosynthesis occurred between the 2 collections. However, outside exclosure plants had higher stomatal conductance than did exclosure plants for the dry year 1992. Also, outside exclosure plants exhibited more negative $\delta^{13}C$ (thus lower water use efficiency) than exclosure plants for 1992 and 1993. We suggest that the higher conductance of previously-grazed plants relative to nongrazed plant populations may be an adaptive response to greater soil moisture often found in grazed sites.

Key Words: photosynthesis, water use efficiency, *Festuca idahoensis*

There has been a marked decline in the abundance and distribution of caespitose grasses of the shrub steppe region of western North America over the past 100 years (Mack and Thompson 1982). One of the reasons often cited for this reduction is that these grasses did not co–evolve with large populations of wild ungulates and were thus not able to tolerate high levels of livestock grazing. For example, bluebunch wheatgrass (*Agropyron spicatum* (Pursh) (syn. *Pseudoroegneria spicata* (Pursh) A. Love)) a grazing–intolerant species shows slow rates of foliar regrowth and allocates relatively more photosynthate to root development rather than to reestablishment of top following defoliation when compared to the grazing tolerant exotic bunchgrass, crested wheatgrass (*Agropyron desertorum* (Fish. ex Link) Schult.) (Caldwell et al. 1981, Richards 1984, Mueller and Richards 1986). Response shown by the high seral species Idaho fescue (*Festuca idahoensis* (Elmer)) indicates a higher level of grazing resistance. Jaindl et al. (1994) demonstrated that field–grown Idaho fescue exhibited high rates of foliar regrowth following defoliation. Species or ecotypes that evolved with large populations of herbivores rapidly reestablish leaf area following defoliation (McNaughton 1979, Caldwell et al. 1981, Etherington 1984, Wallace et al. 1984, Polley and Detling 1988).

This research was designed to determine if compensatory photosynthesis occurs in Idaho fescue that had been partially defoliated during the vegetative stage of growth. Compensatory photosynthesis of remaining leaves may be a mechanism that aids in reestablishment of leaf area following defoliation (Detling et al. 1979, Wallace et al. 1984). In addition, we compared plants which have been excluded from livestock grazing since 1937 with plants from an adjacent area that have been grazed. Measurements taken included photosynthesis, stomatal conductance to H_2O, xylem potential, and carbon isotope ratios ($\delta^{13}C$) of leaves collected at the end of the growing season.

Materials and Methods

Idaho fescue plants were transplanted to a common garden at the Northern Great Basin Experimental Range, 64 km west of Burns, Oregon, USA (1,370 m elevation). Soils at the common garden site were loamy alluvium weathered from rhyolite, andesite, and basalt bedrock, and are typically found on broad stream floodplains and terraces with 0–2 % slopes (Lentz and Simonson 1986). Long-term precipitation (1950–1993) averaged 283 mm for the crop year (September to August). Most precipitation occurs between November and May as snow and rain, and mean daily temperatures have been –0.6 and 17.6°C for winter and summer. Crop year precipitation for the 1992 and 1993 seasons were 245 and 523 mm, respectively.

Twenty-five individual Idaho fescue plants were collected in May 1989 from inside and outside an exclosure in an *Artemisia*

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tridentata ssp *wyomingensis*/*Festuca idahoensis* plant community (Doescher et al. 1986), located within 2 km of the common garden site. Plants were originally collected within approximately 25 m of each other and transplanted 1 m apart in a completely randomized design. To provide uniform root competition for the border rows and to isolate the garden from the surrounding area, an additional row of Idaho fescue was established around the perimeter of the grid. Broadleaf weeds were controlled throughout the experiment using herbicides the first year of establishment, and mechanical means thereafter.

Ten plants from each collection area were selected at random and assigned to either a defoliation or no defoliation treatment (5 plants for each treatment). Approximately 60–70% of the tillers of plants in the defoliated treatment were clipped on 22 April 1992 and 19 May 1993. Defoliated plants were clipped at 5 cm above the ground to simulate livestock grazing, which rarely removes all tillers on the plant (Briske and Stuth 1982). Leaf photosynthesis, stomatal conductance to H_2O, and xylem potentials were measured for defoliated and nondefoliated plants on 24 April, 6 May, 23 June, and 6 July 1992; and on 17 June and 28 July 1993. Measurements were taken on leaves of vegetative tillers that remained undefoliated. We selected tillers that had been recruited at the onset of the growing season to ensure consistency of tiller age among treatments.

Xylem potentials, stomatal conductance to H_2O, and net photosynthesis were measured between 1100 and 1300 hours on each of the sampling days. Xylem potentials were determined using a Model 3005 plant water status console (Soilmoisture Equipment Corp., Santa Barbara, Calif.) for 2 or more leaves from the south side of each plant. Leaf photosynthesis and conductance were measured on 5–12 leaves per plant using an LI 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Neb.). The portion of leaves within the cuvette were excised and measured for leaf area so that photosynthesis and conductance could be expressed on a leaf area basis. We measured leaf length and diameter, and used the equation for surface of a cylinder to calculate leaf area.

Values of $\delta^{13}C$ were determined on samples collected for leaf area determination during the final photosynthesis sampling of each season. Leaf material was collected from nondefoliated tillers on clipped and unclipped plants and also from regrowth on defoliated plants. Dried samples were ground and the $\delta^{13}C$ values were determined with an isotope ratio mass spectrometer at the Department of Biology, Stable Isotope Lab, Boston University. Results are expressed as:

$$\delta^{13}C(^0/_{00}) = (R_{sample}/R_{standard}-1) * 1000. \qquad (1)$$

The $\delta^{13}C$ values reflect seasonal water use efficiency (Ehleringer and Osmond 1989). There is an inverse relationship between water use efficiency and discrimination against $^{13}CO_2$ (Farquhar et al. 1989). Thus, less negative values of $\delta^{13}C$ indicate higher water use efficiency.

Data for net photosynthesis, conductance, and xylem water potentials were evaluated separately for each year using analysis of variance (ANOVA) for a completely randomized 3-factor (population * defoliation * time) design with repeated measures on collection and defoliation treatment in any 1 year. Individual plants served as replications. Differences in $\delta^{13}C$ were evaluated using analysis of variance (ANOVA) in a completely randomized 3 factor (population * defoliation * year) design with repeated measures on collection and defoliation (Winer et al. 1991). Significant differences ($P<0.05$) among 3 or more means were separated using Waller and Duncan's BLSD mean separate procedure (Steel and Torrie 1980). Only significant differences ($P<0.05$) are reported in the text.

Results

Photosynthesis

The only significant interaction for net photosynthesis measurements was time by defoliation in 1993 (Table 1). Photosynthesis was initially higher for defoliated than nondefoliated plants during the May 1993 sampling, but declined rapidly with time (Fig. 1). Defoliated plants usually maintained higher leaf photosynthetic rates during the growing season than did nondefoliated plants (Fig. 1). Photosynthetic rates averaged 8.8 and 9.9 µmole CO_2 m^{-2} sec^{-1} (12% increase) during the 1992 season and 6.5 and 9.9 µmole m^{-2} sec^{-1} (52% increase) in the 1993 season for leaves from the nondefoliated and defoliated plants, respectively. There was no statistical difference in photosynthetic rate between plants collected inside or outside of the exclosure.

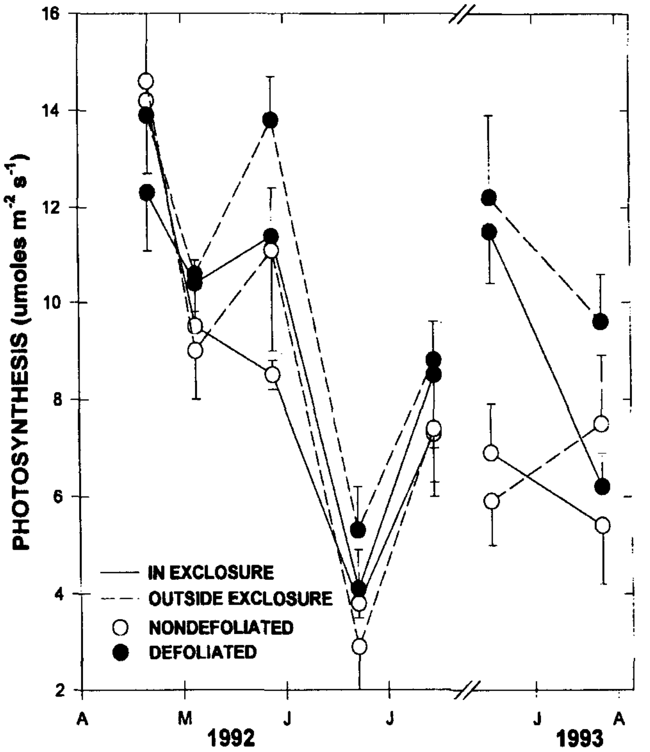

Fig. 1. Net photosynthetic rates of defoliated and nondefoliated *Festuca idahoensis* plants with a prior history of grazing (outside exclosure) or no grazing (in exclosure). Vertical lines are 1 standard error of the mean.

Conductance

Stomatal conductance to H_2O was greater for plants from outside the exclosure as compared with plants taken inside the exclosure during 1992 (Fig. 2). Defoliated plants also had greater conductance than did nondefoliated plants. No interactions were detected

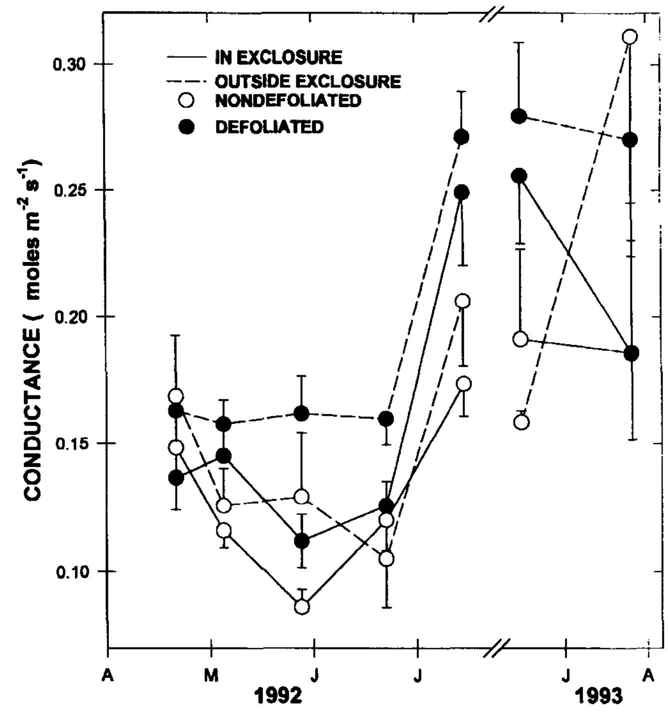

Fig. 2. Conductance of defoliated and nondefoliated *Festuca idahoensis* plants with a prior history of grazing (outside exclosure) or no grazing (in exclosure). Vertical lines are 1 standard error of the mean.

for stomatal conductance in 1992 (Table 1). Conductance values averaged 0.14 and 0.17 mole m^{-2}sec^{-1} for plants from the exclosure and outside the exclosure, respectively, and 0.14 and 0.17 mole m^{-2} sec^{-1} for nondefoliated and defoliated plants, respectively. There was a significant time by defoliation treatment interaction in 1993 (Table 1).

Xylem Potentials

Xylem water potentials varied significantly ($p<0.01$) over time in both years (Fig. 3), but did not differ consistently between populations or defoliation treatments. Values were highest during the spring of 1992, and lowest during late June of 1992; and were less negative during June 1993 than values measured in June 1992 (but not in July).

Carbon Isotope Ratios

There was a significant year by collection interaction for $\delta^{13}C$. The interaction apparently resulted from larger differences between collections in 1992 (below-average precipitation) compared to 1993 (well above-average precipitation). Defoliated plants had lower $\delta^{13}C$ values than control plants in 1992, but not in 1993 (Table 2). Plants collected from inside the exclosure had less negative $\delta^{13}C$ values than did those collected from outside the exclosure for both years. This indicated the exclosure plants had higher water use efficiency than did plants that had been grazed previously.

Discussion

Grasses that have coevolved with herbivory often exhibit compensatory photosynthesis of remaining leaf tissue following defoliation (Detling et al. 1979, McNaughton 1979, Painter and Detling 1981, Wallace et al. 1984). We measured compensatory photosynthesis in Idaho fescue plant populations that had been either grazed or protected from grazing since 1937. The increase in photosynthetic rate for defoliated plants of Idaho fescue ranged from about 10 to 50%. This response may help explain the high regrowth potential found in a previous study of defoliated Idaho fescue (Jaindl et al. 1994). A recent study of Idaho fescue (Merrill et al. 1994) documented overcompensation as defined by Brown and Allen (1989). Merrill et al. (1994) found that Idaho fescue plants that had been defoliated in early spring attained aboveground biomass levels that were similar to ungrazed control plants by the end of the growing season. Bluebunch wheatgrass with a similar evolutionary history to grazing as Idaho fescue, also exhibited compensatory photosynthesis (Nowak and Caldwell 1984). Rapid reestablishment of the canopy may be important for both recovery from defoliation and for competitive ability (Richards 1984). This grass is thought to have evolved under relatively light herbivore pressure (Mack and Thompson 1982). Compensatory photosynthesis following defoliation may be a common response in rangeland grasses (Senock et al. 1991), although Nowak and Caldwell (1984) questioned the importance of compensatory photosynthesis for herbivory tolerance in grasses they studied.

Table 1. Statistical analysis (ANOVA) of photosynthesis, conductance, and midday xylem potential for Idaho fescue plants for populations (grazed vs non-grazed), defoliation treatment (defoliated or not), time, and interaction effects.

	Main effects and interaction				Time effects and interactions				
	MSE	Collection	Collection x Defoliation	Defoliation	MSE	Time	Time x Collection	Time x Defoliation	Time x Collection x Defoliation
1992									
Photosynthesis	6.3	NS	*	NS	5.4	**	NS	NS	NS
Conductance	0.002	*	**	NS	0.001	**	NS	NS	NS
Xylem Potential	44.1	NS	NS	NS	31.8	**	NS	NS	NS
1993									
Photosynthesis	7.9	NS	**	NS	5.8	*	NS	*	NS
Conductance	0.008	NS	NS	NS	0.007	NS	NS	*	NS
Xylem Potential	24.5	*	NS	NS	7.5	**	NS	**	*

*Indicates statistical significance at ($P<0.05$).
**Indicates statistical significance at ($P<0.01$).
NS indicates not statistically significant ($P>0.05$).

Table 2. Carbon isotope ratios ($\delta^{13}C$) and standard errors (S.E.) of the means for leaves of Idaho fescue populations that were historically grazed (outside exclosure) or not grazed (exclosure) and defoliated once per year or not defoliated during the study. Precipitation was slightly below average in 1992 and nearly twice the average in 1993.

	Defoliation Treatment			
	None Mature Leaf	60–70% Mature Leaf	60–70% Regrowth	Mean
1992		($\delta^{13}C$)		
Exclosure	–25.2	–25.9	–26.6	–25.9a[1]
Outside Exclosure	–26.3	–26.3	26.6	26.4b
Mean	–25.8x	–26.1y	–26.6z	
1993				
Exclosure	–26.0	–26.6	–26.3	–26.3a
Outside Exclosure	–26.4	–26.4	–26.6	–26.5b
Mean	–26.2	–26.5	–26.5	

[1] Means within a column or row followed by different letters are significantly different within the same year ($P < 0.05$).

Defoliated plants generally exhibited higher stomatal conductance to H_2O than did controls (Fig. 2), which may help explain higher photosynthetic rates for plants that had been defoliated. Wallace et al. (1984) found similar results and attributed increased photosynthetic rates following clipping to increased stomatal conductance. The higher conductances of defoliated plants may also explain their reduced water use efficiency (WUE) relative to nondefoliated control plants in 1992. Greater stomatal opening following defoliation allows for greater discrimination against ^{13}C, which is inversely correlated with WUE (Farquhar et al. 1989). In a comparison of 2 cold desert bunchgrasses, Anderson and Toft (1993) found that *Leymus cinereus* utilized soil water to a lower level and maintained higher conductance and photosynthesis, but had reduced WUE. The situation for defoliated and nondefoliated Idaho fescue appears comparable. Defoliated plants maintained higher levels of photosynthesis and conductance, but slightly lower WUE than did nondefoliated plants. If reestablishment of a photosynthetically active canopy is a beneficial adaptive response to defoliation, then maintenance of carbon uptake and allocation of carbon to leaves may be more critical than WUE. In a competitive environment, the advantage of conserving soil water via high WUE is questionable (Jones 1980). Tilman (1988) suggested that resource consumption was the mechanism responsible for competitive displacement in cases where several species were limited by a single resource. Thus, conservation of soil water would seem to put a species at a competitive disadvantage.

It did not appear that xylem water potential was influenced by either defoliation treatment or past grazing history. Although during the wet year, outside exclosure plants had more negative xylem potential (Table 1; Fig. 3). Photosynthesis followed a similar seasonal trend to that of xylem potential, but photosynthesis is probably controlled more by soil water than by leaf water potential (Gollan et al. 1986, Davies and Zhang 1991, Tardieu et al. 1992). Defoliation may have reduced soil water extraction, but not enough to increase leaf water potential. In a native community the density of Idaho fescue plants would generally be higher than 1 plant m^{-2} in our spaced-plant nursery. Thus, the potential effect of defoliation on soil moisture would be greater in a natural community relative to our experimental setting. Previous studies have demonstrated that sufficient soil water can be conserved by reduced leaf area to increase plant water potential with heavy grazing (Svejcar and Christiansen 1987, Wraith et al. 1987).

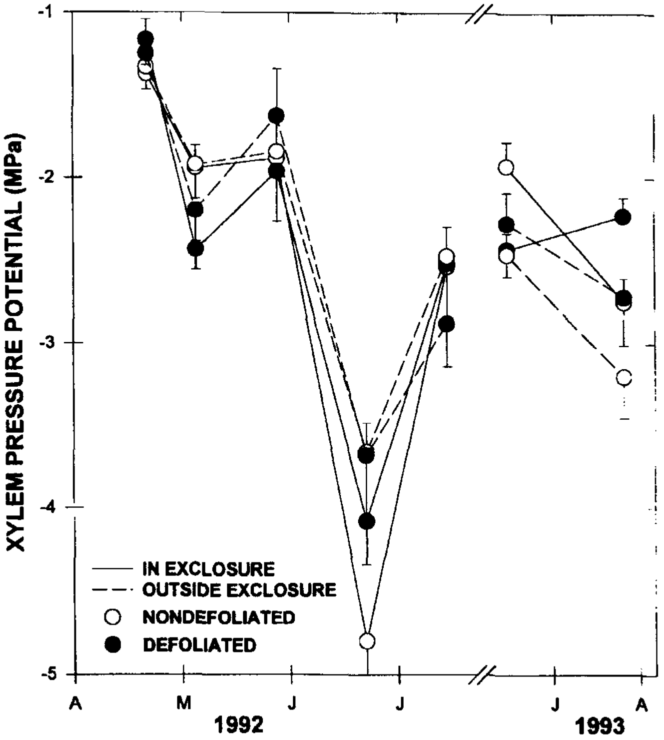

Fig. 3. Leaf xylem potential of defoliated and nondefoliated *Festuca idahoensis* plants with a prior history of grazing (outside exclosure) or no grazing (in exclosure). Vertical lines are 1 standard error of the mean.

Assuming the plants from within and outside the exclosure had a similar history of heavy grazing prior to 1937, our research indicates that divergence in stomatal conductance has occurred between these 2 Idaho fescue populations. At least the 2 populations differed during 1992 when rainfall was slightly less than normal. The 1993 season is difficult to interpret because of the limited sampling dates and precipitation that was nearly double the long-term average. Previous work has shown morphological differences in populations with and without a long-term history of grazing (Peterson 1962, Detling and Painter 1983, Etherington 1984, Carman 1985, Butler and Briske 1988, Polley and Detling 1988, 1990, McKinney and Fowler 1991, Briske and Anderson 1992). However, little morphological change was shown for Indian ricegrass (*Oryzopsis hymenoides*) protected for 50 years from heavy grazing (Trlica and Oradho 1989, Orodho and Trlica 1990). Wallace et al. (1984) speculated that morphological characteristics require shorter evolutionary time periods to respond to herbivory than do physiological characteristics. Zangerl and Bazzaz (1984) found rapid short-term selection for both morphological and physiological characteristics in annual species subjected to controlled environmental gradients. Briske and Anderson (1992) measured morphological variation of *Schizachyrium scoparium* in response to about 25 years of livestock grazing, and we measured differences in conductance within 50 years. Our results may indicate relatively rapid evolutionary response in Idaho fescue in grazed environments.

Conclusion

In conclusion, we measured compensatory photosynthesis in Idaho fescue and differences in water use efficiency and stomatal conductance between grazed and ungrazed populations. Why the outside and inside exclosure populations have diverged since 1937, and how herbivory influences the genetics of this species, are areas that require additional study.

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Estimation of Green-Ampt effective hydraulic conductivity for rangelands

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Abstract

Effective hydraulic conductivity (K_e) is an important parameter for the prediction of infiltration and runoff volume from storms. The Water Erosion Prediction Project (WEPP) model, which uses a modified Green-Ampt equation, is sensitive to the hydraulic conductivity parameter in the prediction of runoff volume and peak discharge. Two sets of algorithms developed from cropland data to predict K_e have previsouly been used in the WEPP model. When tested with data collected on rangelands, these equations resulted in low predictions of K_e which significantly over-estimated runoff volume. The errors in runoff prediction were propagated through the model and resulted in poor predictions of peak discharge and sediment yield. The objective of this research was to develop a new predictive equation to calculate K_e specifically for use on rangelands using field data collected in 8 western states on 15 different soil/vegetation complexes. A distinction was made between ground cover parameters located outside and underneath plant canopy in an effort to account for the significant spatial variability that occurs on most rangelands. Optimized K_e values were determined using the WEPP model and observed runoff data. A regression model (r^2=0.60) was then developed to predict K_e using measured soil, canopy cover, and spatially distributed ground cover data from 44 plots. Independent rangeland data sets are now required to test the new equation to determine how well the relationships developed from the data used in this study extend to other rangeland areas.

Key Words: WEPP, infiltration, runoff, hydrologic modeling, spatial variability, ground cover

The Water Erosion Prediction Project (WEPP) model (Lane and Nearing 1989) was developed to provide process-based erosion prediction technology for croplands, rangelands, and forests to organizations involved in soil and water conservation and environmental assessment. To be successful in predicting erosion, the model must first succeed in predicting infiltration and surface runoff. The infiltration component of the WEPP model uses the Green-Ampt equation (Green and Ampt 1911) as modified by Mein and Larson (1973) to obtain the time to ponding and infiltration rates for steady rainfall. This equation was further modified by Chu (1978) to simulate infiltration for unsteady rainfall events, allowing for alternating periods of ponded and unponded conditions.

Although this latest technology for modeling runoff and erosion represents a major improvement over older models, significant problems still exist as a result of the techniques used to estimate model parameters under rangeland conditions. This is particularly true in modeling infiltration. Estimates of hydraulic conductivity change with the scale of measurement as a result of the high spatial and temporal variability that exists in natural systems (Dunne et al. 1991). Current methods for measuring hydraulic properties in the field are expensive and time consuming and therefore alternative techniques are needed to estimate model parameters and improve model results for rangelands.

The approach used in WEPP to simplify parameterization is to estimate hydraulic properties by relating them to soil and vegetation data that are commonly collected and readily available. The objectives of this research are to evaluate 2 existing sets of algorithms used in the WEPP model to predict effective hydraulic conductivity (K_e) and to develop an alternative method. All 3 methods are compared to optimized K_e parameters determined with the WEPP model.

Infiltration Model Description

Green-Ampt Equation

The form of the Green-Ampt equation used in WEPP to calculate the infiltration rate after ponding occurs is:

$$f = K_e \left(1 + \frac{N_s}{F}\right) \tag{1}$$

where f is the infiltration rate (mm hr^{-1}), K_e is effective saturated hydraulic conductivity (m sec^{-1}), N_s is the effective capillary pressure head at the wetting front (m), and F is the cumulative infiltration depth (m). Cumulative infiltration depth is calculated as:

$$K_e t = F - N_s \ln \left(1 + \frac{F}{N_s}\right) \qquad (t > t_p) \tag{2}$$

where t is time (sec) and t_p is time to ponding (sec). Effective capillary pressure head at the wetting front is:

$$N_s = (\eta_e - \theta_v)(\psi - h_0) \tag{3}$$

where η_e is field-saturated porosity (m^3 m^{-3}), θ_v is initial volu-

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metric water content (m^3 m^{-3}), ψ is the average capillary pressure head across the wetting front (m), and h_0 is the depth of ponding over the soil surface. The average capillary pressure head is estimated internally in WEPP as a function of soil properties (Rawls and Brakensiek 1983).

Prior to surface ponding the infiltration rate is equal to the rainfall rate and cumulative infiltration is equal to cumulative rainfall. The infiltration rate starts to decline when ponding begins, decreasing as the depth of wetted soil increases. If rainfall continues for a sufficient period, infiltration generally approaches a final, constant, steady rate.

For this study, volumetric water content was calculated as:

$$\theta_v = w \, \rho_b \, \rho_w^{-1} \tag{4}$$

where w is initial soil water content by weight (g g^{-1}), ρ_b is dry bulk density (gm cm^{-3}), and ρ_w is the density of water (about 1 gm cm^{-3}). Effective field-saturated porosity was calculated as:

$$\eta_e = 0.9 \, (1 - \rho_b \, \rho_s^{-1}) \tag{5}$$

where ρ_s is soil particle density, and is typically 2.65 gm cm^{-3} for a mineral soil.

Parameter Estimation

The importance of hydraulic conductivity in the calculation of infiltration with the Green-Ampt equation has been well documented. Brakensiek and Onstad (1977) found that the effective conductivity parameters have a major influence on infiltration and runoff amounts and rates. Moore (1981) showed that both the rate and amount of infiltration are more sensitive to hydraulic conductivity and available porosity than to the wetting front capillary potential. Tiscareno-Lopez et al. (1993) concluded that both the runoff volume and peak runoff rate computed by the WEPP model are very sensitive to the hydraulic conductivity parameters in the Green-Ampt equation.

One approach to estimating Green-Ampt hydraulic conductivity is to use an average or effective value, thus ignoring the variable and random nature of the physical processes. Green-Ampt effective hydraulic conductivity (K_e) is a lumped parameter that integrates a soil's ability to infiltrate water under variable soil pore structure, surface microtopography, and rainfall amount and intensity distributions. The K_e value derived in this study provides a single integrated value to represent an entire plot.

Most research to date has focused on saturated hydraulic conductivity (K_s), the ability of a soil to transmit water under fully saturated conditions (Klute and Dirksen 1986), rather than K_e, because it is comparatively easy to measure under laboratory and field conditions. One approach consists of correlating hydraulic conductivity with easily measurable soil properties such as soil texture, effective porosity, bulk density, and coarse fragments in the soil.

Rawls and Brakensiek (1989) evaluated a number of physical factors that are important in the estimation of K_s. Their findings were incorporated in the algorithms used to calculate K_e in early versions of WEPP (Rawls et al. 1989). This was accomplished by adjusting K_s to account for the weight of coarse rock fragments in the soil, frozen soil, soil crusting, soil macroporosity, and soil cover, using the following equation:

$$K_e = K_b \, [C_f [((B_c A_c^{-1}) \, C_r) + M_f((1 - B_c) \, A_c^{-1})] + (B_o A_c^{-1}) \, C_r + M_f((1 - B_o) \, A_o^{-1})] \tag{6}$$

where K_b is baseline hydraulic conductivity (m sec^{-1}), C_f is a canopy correction factor (fraction), B_c is bare area under canopy (fraction), A_c is total canopy area (fraction), B_o is bare area outside canopy (fraction), A_o is total area outside canopy (fraction), C_r is a crust reduction factor (unitless), and M_f is a macroporosity factor (m m^{-1}). C_r is calculated as a function of the average wetting front depth, soil crust thickness, a correction factor for partial saturation of the subcrust soil, and a crust factor. M_f is computed as a function of sand and clay content. The equations used to calculate these variables were developed by Brakensiek and Rawls (1983) for plowed agricultural soils with a constant crust thickness of 0.005m.

Baseline hydraulic conductivity is given by (Rawls et al. 1989):

$$K_b = K_s \, (1 - M_{cf}) \, FS_a \tag{7}$$

where K_s is saturated hydraulic conductivity (m sec^{-1}), M_{cf} is the fraction of course fragments in the soil, and FS_a is a frozen soil factor (unitless). The equation used to calculate K_s was developed from an extensive agricultural soils database (Rawls and Brakensiek 1985) and is:

$$K_s = Q_e^3 [(1 - Q_t)^2 \, (0.001 \, p_t \, O_r^{-1})^2 \, 0.00020 \, C^2]^{-1} \tag{8}$$

where Q_e is effective soil porosity (m^3 m^{-3}), Q_t is total soil porosity (m^3 m^{-3}), p_t is soil bulk density (mg m^{-3}), O_r is soil water content (m^3 m^{-3}), and C is an adjustment factor for soil texture (unitless).

The approach outlined above is complex and involves several levels of nested regression equations. In some cases the parameters overlap and thus an error at 1 level can be propagated through to the final prediction of K_e. Wilcox et al. (1992) reported a poor correlation between predicted and observed runoff using these empirical equations with rangeland data from rainfall simulation experiments conducted in southwestern Idaho. Savabi et al. (1995) reported that WEPP underestimated runoff from naturally vegetated plots in Texas using the Rawls equation for estimating K_s (Eq. 8).

In subsequent versions of the WEPP model, a different set of algorithms replaced Eq. 6 for predicting K_e. With these algorithms, developed by Risse et al. (1995), K_e is calculated directly from basic soil properties. They are based on WEPP model optimization runs of both measured and curve number predicted runoff quantities on agricultural soils. A number of soil properties including sand, clay, silt, very fine sand, field capacity, wilting point, organic matter, CEC, and rock fragments were investigated through regression analysis to determine which could best be used in the prediction of K_e.

For soils with a clay content less than or equal to 40%, K_e is calculated as:

$$K_e = -0.46 + 0.05 \, Sa^{1.25} + 9.44 \, CEC^{-0.69} \tag{9}$$

where Sa is percent sand and CEC is the cation exchange capacity (meq/100g of soil) in the surface soil layer. If the cation exchange capacity is less than or equal to 1.0, K_e is:

$$K_e = 8.98 + 0.05 \, \mathrm{Sa}^{1.25} \tag{10}$$

If clay content is greater than 40%, K_e is given by:

$$K_e = -0.016 \, e^{171 \mathrm{Cl}^{-1}} \tag{11}$$

where Cl is percent clay in the surface soil layer.

The combination of equations outlined above resulted in an r^2 of 0.78 for the test data set which was comprised of 43 different soil series. The selected equations were chosen as a result of their simplicity and the standard error of their estimates.

Materials and Methods

Study Sites

Field data collected during the 1987 and 1988 USDA WEPP rangeland field study from 15 sites with a total of 44 plots in the Western and Great Plains regions of the United States (Simanton et al. 1987; 1991) were used for the research described in this paper. Abiotic and biotic descriptive data for each site are presented in Tables 1 and 2.

Experimental Design and Sampling Methods

Simulated rainfall was applied to undisturbed, paired plots measuring 3.05 by 10.67 meters using a rotating boom simulator developed by Swanson (1965). Plots were located in the same soil and vegetation type at each site. Rainfall simulations were made on each plot representing dry and wet antecedent moisture conditions. During the dry run, water was applied at a rate of 60 mm hr^{-1} for 1 hour. The wet run was made 24 hours later at a rate of 60 mm hr^{-1} for 30 minutes.

Total rainfall amount and distribution were measured with 6 non-recording raingages positioned around each plot. Rainfall intensity was measured with a recording raingage located between the paired plots. Runoff passed through a pre-calibrated supercritical flume at the downslope end of each plot, flow depths were measured with a pressure transducer bubble gage, and continuous hydrographs were developed using the flume's depth/discharge rating table (Simanton et al. 1987).

A major objective of vegetation data collection was to provide an estimate of spatial distribution of canopy and ground surface cover. Measured ground cover characteristics were bare soil, rock (mineral particles greater than 2 mm), litter (organic material in direct contact with the soil surface), cryptogams (algae, moss and lichens), and plant basal cover. Vegetation composition (i.e. grass, shrub, forb, cactus), canopy cover, ground surface characteristics, and surface roughness were measured before rainfall simulation using a 49-pin point frame placed perpendicular to the plot slope at 10 evenly spaced transects along the plot border. A steel pin was lowered vertically at 5 cm intervals along the point frame. If the pin touched a plant aerial part, the lifeform was recorded. The pin was then lowered to the plot surface and the first characteristic touched was recorded for that point for determination of ground cover. It is often difficult to determine where canopy cover ends and plant basal area begins for areas that have been heavily grazed, for many prostrate growth form plant types, and on sites with high surface roughness and pedestalled plants. For this work, *canopy cover* is defined as any plant part elevated 2.5 cm or more from the soil surface. A plant part in contact with the pinpoint within 2.5 cm of the soil surface is considered to be *basal cover.*

Areas located directly underneath plant canopy are referred to as *under-canopy* areas while areas located between plants (i.e. no canopy cover directly above) are referred to as *interspace* areas (Fig. 1a). Total under-canopy ground cover is calculated as the sum of the fraction of each ground cover component located under vegetative canopy (as defined above), while total interspace cover is calculated as the sum of the fraction of each ground cover component located outside of plant canopy. For example, if 30% of a plot is covered by rocks, and 40% of those rocks are in interspace areas while 60% are under-canopy, then total rock cover in the interspaces is 12% {(40 X 30)/100}. Similarly, total rock cover under-canopy is 18% {(60 X 30)/100}. Distributions of litter, basal vegetation, and cryptogams are similarly calculated. Total interspace and under-canopy area are calculated by summing the cover for the individual components located in their respective areas. Plant nomenclature used throughout the discussion follows Gould (1975).

Model Configuration and Optimization

Measured topographic, precipitation, vegetation and soils data from the WEPP rangeland field study were used to run the WEPP model for a single rainfall event. Topographic data included plot length, width, and slope values. Measured precipitation data con-

Table 1. Abiotic site characteristics from the WEPP rangeland field experiments.

	Site	Soil Family	Soil series	Surface texture	Slope	Elevation
					(%)	(m)
1)	Tombstone, Ariz.	Ustochreptic calciorthid	Stronghold	Sandy loam	10	1,377
2)	Tombstone, Ariz.	Ustollic haplargid	Forest	Sandy clay loam	4	1,420
3)	Susanville, Calif.	Typic argixeroll	Jauriga	Sandy loam	13	1,769
4)	Susanville, Calif.	Typic argixeroll	Jauriga	Sandy loam	13	1,769
5)	Meeker, Colo.	Typic camborthid	Degater	Silty clay	10	1,760
6)	Sidney, Mont.	Typic argiboroll	Vida	Loam	10	N/A
7)	Los Alamos, N.M.	Aridic haplustalf	Hackroy	Sandy loam	7	2,144
8)	Cuba, N.M.	Ustollic camborthid	Querencia	Sandy loam	7	1,928
9)	Chickasha, Okla.	Udic argiustoll	Grant	Loam	5	378
10)	Chickasha, Okla.	Udic arguistoll	Grant	Sandy loam[1]	5	369
11)	Woodward, Okla.	Typic ustochrept	Quinlan	Loam	6	615
12)	Freedom, Okla.	Typic ustochrept	Woodward	Loam	6	553
13)	Cottonwood, S.Dak.	Typic torrert	Pierre	Clay	8	744
14)	Cottonwood, S. Dak.	Typic torrert	Pierre	Clay	12	744
15)	Sonora, Tex.	Thermic calciustoll	Perves	Cobbly clay	8	650

[1] Farm land abandoned during the 1930's that had returned to rangeland. The majority of the 'A' horizon had been previously eroded.

Table 2. Biotic mean site characteristics from the WEPP rangeland field experiments.

	Site	Rangeland cover type[1]	Range site	Ecological status[2]	Cover		Standing Biomass
					Canopy	Ground	
					------ (%) -------		(kg ha^{-1})
1)	Tombstone, Ariz.	Creosotebush-Tarbush	Limy upland	38	32	82	775
2)	Tombstone, Ariz.	Grama-Tobosa-Shrub	Loamy upland	55	18	40	752
3)	Susanville, Calif.	Basin Big Brush	Loamy	55	29	84	5,743
4)	Susanville, Calif.	Basin Big Brush	Loamy	55	18	76	5,743
5)	Meeker, Colo.	Wyoming bib sagebrush	Clayey slopes	60	11	42	1,583
6)	Sidney, Mont.	Wheatgrass-Grama-Needlegrass	Silty	58	12	81	2,141
7)	Los Alamos, N.M.	Juniper-Pinyon Woodland	Woodland community	NA[3]	16	72	1,382
8)	Cuba, N.M.	Blue grama-Galleta	Loamy	47	13	62	817
9)	Chickasha, Okla.	Bkuestem prairie	Loamy prairie	60	46	94	2,010
10)	Chickasha, Okla.	Bluestem prairie	Eroded prairie	40	14	70	396
11)	Woodward, Okla.	Bluestem-Grama	Shallow prairie	28	45	62	1,505
12)	Freedom, Okla.	Bluestem prairie	Loamy prairie	30	39	72	1,223
13)	Cottonwood, S.Dak.	Wheatgrass-Needlegrass	Clayey west central	100	46	68	2,049
14)	Cottonwood, S.Dak.	Blue grama Buffalograsse	Clayey west central	30	34	81	529
15)	Sonora, Tex.	Juniper-Oak	Shallow	35	39	68	2,461

[1] Shiflet (1994).
[2] Ecological status is a similarity index that expresses the degree to which the composition of the present plant community is a reflection of the historic climax plant community. This similarity index may be used with other site criterion or characteristics to determine rangeland health. Four classes are used to express the percentage of the historic climax plant community on the site: I 76-100; II 51-75; III 26-50; IV 0-25 (USDA, National Resources Conservation Service (1995).
[3] NA - Ecological status indices are not appropriate for woodland and annual grassland communities.

sisted of rainfall volume, intensity, and duration. Values used to characterize vegetation included total ground cover by each component, their distributions between interspace and under-canopy areas, and total canopy cover. Complete soil pedon descriptions, sampling, and analysis were made by the USDA-Natural Resource Conservation Service (NRCS) Soil Survey Laboratory at each of the rangeland sites as a part of the WEPP Rangeland Field Study. Measured values of sand, clay, organic matter, bulk density and cation exchange capacity from the surface horizon from a single pedon were used. The same values determined from 1 pedon were used to define the soil parameters for all plots at a particular site.

The rainfall simulation plots were prewet with 60 mm of water and allowed to drain for 24 hours to minimize antecedent soil water content differences. Soil water content was measured at 3 locations on the plot: top, middle, and bottom before the rainfall simulation runs. Soil water content was at or near field capacity for all sites. Saturation by volume was calculated using the following equation (Hillel 1980):

$$s = \theta_v \eta_e^{-1} \tag{12}$$

where s is the degree of saturation by volume, θ_v is the volumetric water content, and η_e is effective soil porosity.

The WEPP model was used to generate an optimized K_e value and a corresponding predicted runoff value for each of the 44 plots in the data set under a single storm simulation using data from the wet run. The model was run for a range of values of K_e for each plot, and corresponding model predicted runoff volume was generated. An optimization program, based on a least squares analysis, was used to interpolate between 2 values of K_e until the best fit was found.

Data Analysis

Data from the WEPP field studies were used to evaluate Eq. 6 (Rawls et al. 1989) and Eqs. 9–11 (Risse et al. 1995). K_e values were calculated with both equations and compared with the optimized K_e values for each plot. The WEPP model was used to generate runoff volume for both sets of predicted K_e values. Predicted runoff volume corresponding to each set of predicted K_e values was then compared with observed runoff volume.

A regression equation was developed and tested using measured soil and cover data from all of the plots. Maximum r^2 regression analysis was used to generate regression equations within an 85% confidence range for the dependent variable (optimized K_e). The soil parameters included in the analysis were percent sand, silt, and clay, cation exchange capacity (meq 100 g^{-1} soil), bulk density (g cm^{-3}), and organic matter (percent by volume). The components of ground cover that were evaluated include basal vegetation, litter (plant residue), rock, and cryptogams. Both the total cover values

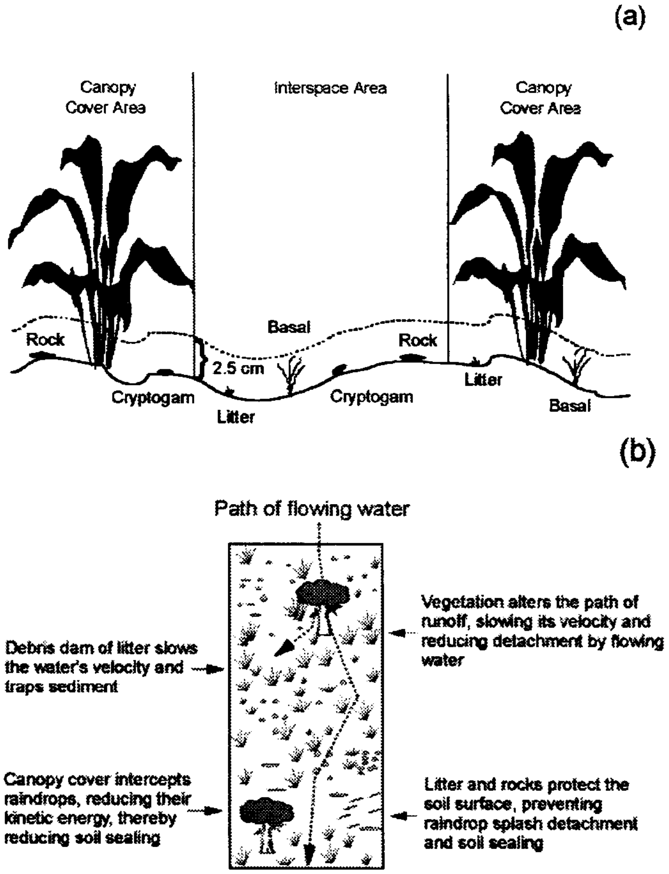

Fig. 1. (a) Distinction between under-canopy and interspace areas used in point frame sampling to define spatial attributes of canopy and ground cover components. Canopy cover is greater than 2.5 cm in height; (b) Influence of vegetation and surface cover on surface runoff.

for each component of ground cover and the cover values for each component measured in interspace and under-canopy areas were considered.

Regression equations with 6 terms or more were discarded due to the complexity involved in understanding the physical interactions that would occur with so many terms. Equations with terms that were codependant were also rejected. Those equations that had variables that were significant at $p \leq 0.1$ were retained. The remaining regression equations were then tested with the data set used throughout this analysis. All statistical analyses were conducted with version 6.2 of the SAS for Windows statistical software package (SAS Institute Inc. 1985)[1].

Results and Discussion

Values of observed runoff volume and optimized effective hydraulic conductivity are presented in Table 3. The new linear equation developed to predict K_e (mm hr^{-1}), with an r^2 of 0.60 and standard error of 3.72, is:

$$K_e = 21.45 - 30.00Cl + 11.66L_r - 45.12B_r + 75.89R_i \quad \textbf{(13)}$$

where Cl is clay content (fraction), L_r is litter cover in interspace areas (fraction), B_r is basal cover in interspace areas (fraction), and R_i is rock cover in under-canopy areas (fraction). As with all equations developed with regression analysis, Eq. 13 should only be used within the spread of the data that were used to derive it or unreasonable results may be obtained. From a physical standpoint, the independence of the 4 terms is an attractive feature of the equation.

Correlation coefficients for each variable used in the multiple regression analysis were calculated. Of all the terms tested, clay

Table 3. Observed runoff volume and optimized hydraulic conductivity (K_e) from the WEPP rangeland field experiements.

	Site	Plot	Year	Observed Runoff	Optimized K_e
				(mm)	(mm hr^{-1})
1)	Tombstone, Ariz.	33	87	1.5	24.5
		36	87	2.5	32.9
2)	Tombstone, Ariz.	52	87	12.8	13.8
		54	87	16.2	3.6
3)	Susanville, Calif.	137	87	0.4	15.3
		140	87	0.2	15.9
		137	88	0.1	17.0
		140	88	0.8	18.7
4)	Susanville, Calif.	141	87	0.4	13.8
		142	87	0.2	15.4
		143	87	1.0	20.1
		144	87	2.0	15.3
		143	88	2.0	18.4
		144	88	2.0	20.3
5)	Meeker, Colo.	107	87	1.5	10.8
		112	87	4.6	5.2
6)	Sidney, Mont.	103	87	1.0	26.5
		106	87	0.3	18.4
7)	Los Alamos, N.M.	128	87	8.1	5.2
		129	87	8.8	7.3
8)	Cuba, N.M.	132	87	4.5	14.5
		133	87	1.3	18.5
9)	Chickasha, Okla.	71	87	17.0	9.4
		76	87	11.5	11.5
		71	88	5.6	22.7
		76	88	0.6	27.7
10)	Chickasha, Okla.	77	87	11.6	10.4
		80	87	10.7	8.8
		77	88	6.6	18.8
		80	88	6.3	16.5
11)	Woodward, Okla.	91	87	0.2	25.9
		94	87	3.3	15.5
		91	88	0.6	18.2
		94	88	1.9	22.0
12)	Freedom, Okla.	156	88	1.5	16.8
		158	88	3.0	13.0
13)	Cottonwood, S. Dak.	113	88	1.5	10.0
		118	88	3.0	8.6
14)	Cottonwood, S. Dak.	119	87	5.0	4.2
		122	87	7.6	3.0
		119	88	8.5	2.7
		122	88	6.8	4.4
15)	Sonora, Tex.	67	87	16.5	0.8
		70	87	6.9	3.7

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[1] The USDA neither guarantees nor warrants the standard of the product, and the use of the name by the USDA implies no approval of the product to the exclusion of others that may also be suitable.

content was shown to have the strongest relationship with K_e with a moderate negative correlation (R = -0.53) at the 95% significance level. Conversely, sand content showed a moderate positive correlation (R = 0.48). It has been documented that soil texture is related to hydraulic conductivity on homogeneous soils, with increased sand content associated with increased conductivity (Rawls et al. 1982). In semiarid watersheds in Nevada, Blackburn (1975) found a significant relationship between infiltration rates and soil texture. He reported negative correlations between clay and silt-sized particles and infiltration, and a positive correlation between sand and infiltration.

Litter cover in interspace areas is represented by a positive term in Eq. 13, indicating that K_e increases as litter cover in the interspaces increases. Litter cover in interspace areas ranged from 2.6 to 61.4% on the 44 plots evaluated, and in general was the most prevalent ground cover type (Table 4). Litter has long been recognized as effective in reducing soil erosion on rangelands (Singer et al. 1981, Khan et al. 1988, and Meyer et al. 1970). Litter cover at the soil surface intercepts raindrops and dissipates their energy (Fig. 1b). This reduces the clogging of soil pores with sediment, reducing sealing and crusting, thus enabling more infiltration. Litter cover also increases potential for debris dam

Table 4. Spatial cover data (%) from the WEPP rangeland field experiments.

			Total Under-Canopy Cover:				Total Interspace Cover:			
Site	Plot	Yr	Litter	Rock	Cryp[1]	Basal	Litter	Rock	Cryp	Basal
			(%)							
1) Tombstone, Ariz.	33	87	9.2	13.3	0.0	0.0	7.3	48.7	0.0	2.4
	36		12.7	13.1	0.0	0.0	8.1	48.1	0.0	2.2
2) Tombstone, Ariz	52	87	5.7	0.0	0.0	0.8	11.0	3.5	0.0	14.9
	54		4.5	0.2	0.0	2.0	13.1	3.1	0.0	19.8
3) Susanville, Calif.	137	87	24.9	1.2	0.0	2.0	39.2	7.8	0.0	10.2
	140		17.6	1.2	0.0	2.4	35.9	15.1	0.0	11.1
	137	88	21.8	0.0	0.0	6.8	35.9	14.5	0.0	4.6
	140		18.6	0.0	0.0	6.4	37.3	17.7	0.0	3.6
4) Susanville, Calif.	141	87	6.5	2.4	0.0	0.8	42.9	19.2	0.0	8.2
	142		9.8	2.4	0.0	0.4	45.7	18.0	0.0	4.5
	143		0.0	0.0	0.0	0.0	61.8	20.9	0.0	0.0
	144		0.0	0.0	0.0	0.0	51.8	23.6	0.0	0.0
	143	88	6.4	0.0	0.0	4.1	27.2	30.9	0.0	1.4
	144		4.1	0.0	0.0	6.8	24.1	27.7	0.0	2.7
5) Meeker, Colo.	107	87	8.8	0.0	0.0	0.0	2.6	0.0	0.0	11.0
	112		5.9	0.0	0.0	0.4	22.7	0.0	1.2	11.6
6) Sidney, Mont.	103	87	5.1	0.0	3.7	0.6	25.1	0.0	25.3	19.0
	106		4.5	0.2	5.5	0.6	21.0	0.4	38.8	12.5
7) Los Alamos, N.M.	128	87	7.1	0.0	6.5	0.8	12.1	0.6	31.5	15.1
	129		7.3	0.0	3.7	0.6	16.4	0.4	25.7	16.5
8) Cuba, N.M.	132	87	3.7	0.0	5.3	0.0	19.2	0.0	14.3	20.8
	133		4.1	0.0	4.1	0.8	17.9	0.0	10.2	22.9
9) Chickasha, Okla.	71	87	40.6	0.0	0.0	0.8	24.9	0.0	0.0	6.3
	76		53.1	0.0	0.0	0.4	26.3	0.4	0.0	17.4
	71	88	20.5	0.0	0.0	18.6	50.9	0.0	0.0	8.5
	76		21.0	0.0	0.0	18.6	56.1	0.0	0.0	3.8
10) Chickasha, Okla.	77	87	7.8	0.0	0.4	0.0	30.8	0.0	4.3	15.7
	80		8.6	0.0	0.2	0.0	25.1	0.0	1.4	18.3
	77	88	4.8	0.0	0.5	1.4	52.8	0.5	4.3	12.9
	80		4.3	0.0	0.5	0.5	61.4	0.0	3.3	20.5
11) Woodward, Okla.	91	87	22.2	0.2	0.0	0.6	13.1	0.2	2.0	6.3
	94		16.5	0.0	0.4	0.6	9.0	0.0	4.9	6.5
	91	88	23.3	0.0	1.9	20.5	18.6	0.5	0.5	4.3
	94		23.3	0.0	5.2	19.0	26.7	0.0	10.0	2.4
12) Freedom, Okla.	156	88	20.5	0.0	1.9	10.0	30.5	0.5	6.7	6.7
	158		19.5	0.0	1.0	12.4	28.1	0.0	1.9	2.4
13) Cottonwood, S.Dak.	113	88	15.2	0.0	0.0	19.0	27.2	0.5	0.0	1.5
	118		21.0	0.0	2.9	12.4	30.0	1.4	0.4	5.2
14) Cottonwood, S.Dak.	119	87	14.7	1.2	0.0	0.8	35.1	1.2	2.0	27.0
	122		13.9	0.4	0.0	0.4	37.1	1.2	0.8	21.2
	119	88	13.8	0.0	1.9	34.3	20.0	2.4	2.9	9.5
	122		7.6	0.0	0.5	32.9	27.2	0.5	1.4	10.0
15) Sonora, Tex.	67	87	8.8	5.1	1.0	0.2	11.8	22.7	5.1	16.3
	70		26.1	1.4	2.7	0.8	16.3	1.9	1.2	15.5

[1] Cryp is cryptogams, defined here as all moss, lichens, and algae.

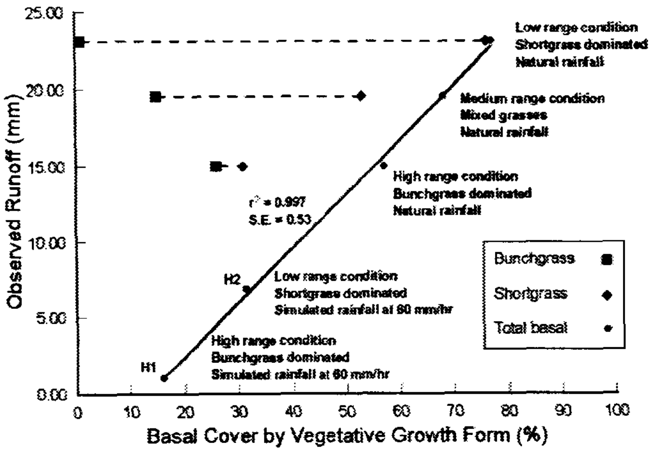

Fig. 2. Mean annual runoff plotted against basal cover by vegetative growth form (short grasses and bunch grasses) based on a study by Hanson et al. (1978). As represented by the dashed line, bunchgrass and shortgrass basal cover sum to give the total basal cover for each of the 3 watersheds (low, medium, and high range conditions). Also plotted are observed runoff vs. mean total basal cover from rainfall simulations conducted by the WEPP rangeland study team (Simanton et al. 1987; 1991) within the low and high range condition watersheds evaluated by Hanson et al. (1978).

formation, providing an obstacle to the flow of water. The result is increased tortuosity and hydraulic roughness which reduces runoff velocity, increasing ponding and infiltration.

Vegetal cover is generally positively correlated to infiltration and negatively correlated to interrill erosion, whereas bare soil is generally associated with a decrease in infiltration (Packer 1951, Dadkhah and Gifford 1980). Many researchers have found higher infiltration rates under plant canopies than in the interspaces (Wood and Blackburn 1981, Thurow et al. 1986, and Tromble et al. 1974). Canopy cover tends to provide protection from raindrop impact, preventing the formation of a soil crust and dislodged soil particles from clogging soil pores, but all plants do not have the same impact in influencing infiltration rates.

In this study, basal cover in the interspace was found to be negatively correlated to K_e and correlation analysis revealed a moderate negative relationship between the 2 ($R = -0.48$). This relationship appears contrary to much of the previous hydrologic work in which increases in plant cover were related to decreases in runoff and increases in the apparent infiltration rate. However, the relation between plant community parameters (e.g., basal cover) and hydrologic response of uplands is a complex function that changes depending on the type of plant community being evaluated. Within a plant community, where the vegetative growth form remains constant and only the density of plants changes, the literature consistently indicates that infiltration rate increases as canopy cover increases (Packer 1951, Dadkhah and Gifford 1980). When the vegetative growth form shifts (e.g., from bunchgrass to shortgrass, or woodland to grassland), the relationship between basal and canopy cover and infiltration and runoff appears to shift. That is, equal amounts of vegetative cover within each of the different plant communities do not necessarily have the same relationship to apparent infiltration rates and runoff.

Hanson et al. (1978) initiated a ten-year study of hydrologic response as a function of grazing intensity at Cottonwood, South Dakota. They constructed 4 watersheds (0.9 ha each) in 3 different pastures representing low, medium, and high range condition for a total of 12 watersheds. The low condition pasture was dominated by shortgrasses such as *Bouteloua gracilis* (H.B.K.) Lag. (blue grama) and *Buchloe dactyloides* (Nutt.) Engelm. (buffalograss). The high condition pasture was dominated by bunchgrasses including *Agropyron smithii* (Rydb.) (western wheatgrass) and *Stipa viridula* (Trin.) (green needlegrass). The fair pasture had a mixture of all 4 grass species. The authors reported that total annual runoff and runoff from summer convective storms increased as basal area increased from the bunchgrass-dominated pasture to the shortgrass-dominated pasture (Fig. 2). Our data from the Cottonwood research station shows similar results. The shortgrass-dominated community has a lower apparent infiltration rate than the bunchgrass-dominated site for both years they were evaluated. All 3 of these watersheds are located on a Pierre clay soil and no significant differences were found in bulk density, cation exchange capacity, organic matter, or depth of the A horizon. The main differences between the sites are in the type of plant species and the amount of plant biomass present.

Other researchers have reported that changes in vegetative growth form or plant species result in changes in the relationship between plant attributes of cover and basal area and apparent infiltration rates and runoff. Thurow et al. (1986) reported that areas dominated by bunchgrass species had greater infiltration rates than shortgrass dominated areas in the Edwards Plateau area in Texas. Rauzi et al. (1968) reported that infiltration rates and runoff were correlated to plant community type with mid and tall grass plant communities having higher infiltration rates and lower runoff rates than shortgrass plant communities using data from the northern and southern Great Plains regions. Thomas and Young (1954) found *Hilaria mutica* (Buckl.) Benth. (tobosa) sites had higher infiltration rates than did *Buchloe dactyloides* (Nutt.) Engelm. (buffalograss) sites. Weltz and Wood (1986) reported that *Muhlenbergia richardsonis* [Trin.] Rydb. (mat muhly) dominated sites had higher infiltration rates than *Bouteloua gracilis* (H.B.K.) Lag. (blue grama) dominated sites at Ft. Stanton, N. M.

The plants that dominated the interspaces in this study were small annual forbs and grasses. The highest total interspace cover by basal vegetation for any plot in this data set was only 27%, and most plots had less than 20% cover (Table 4). The exact mechanism for the reduction of infiltration associated with these plants is not fully understand. It has been hypothesized that the reduction in infiltration rate is a function of increased bulk density, reduced organic matter content of the soil, or the difference in root distribution and biomass between short, mixed, and tall grass species. Root biomass in the top 10 cm of the soil was negatively correlated to K_e in this study ($R = -0.47$). Short grasses tend to have a more lateral, matted root structure as compared to the deeper reaching roots of the mid and tall grasses, resulting in differences in soil pore structure (Weaver and Harmon 1935). These differences might affect the ability of water to infiltrate the soil, resulting in increased runoff from shortgrass dominated sites. Although root biomass is not a term in Eq. 13, it has a similar negative relationship to K_e to that of basal area. We hypothesize that basal cover may be a surrogate for addressing the variability of soil pore orientation and structure resulting from the lateral root orientation associated with short grass species.

Blackburn et al. (1992) reported that vegetative growth form (e.g., shrub, bunchgrass, sodgrass) is one of the primary factors influencing the spatial and temporal variability of surface soil processes that control infiltration on rangelands. To improve our ability to predict infiltration and runoff for these systems, we must first recognize that they are spatially and temporally influenced by growth form, amount, and distribution of native vegetation. Before predictive models can provide realistic estimates of the influence of alternative land management practices on infiltration and runoff they must be able to account for vegetation-induced spatial and temporal variability of soil surface factors. To accomplish this, new techniques are needed to develop better infiltration equations and parameters that address the inherent variability that exists on native and managed rangeland ecosystems, and additional research is required to develop a better understanding of the relationship between plant species and the infiltration process.

Cooke and Warren (1973) proposed that in a semiarid environment, as vegetal cover decreases, if rocks are present in the soil, rock cover should increase as a result of the removal of fine particles by raindrop impact and overland flow, leaving the coarse particles behind. This relationship is seen in the data in this study. Correlation analysis revealed a moderate negative relationship between basal cover and rock cover ($R = -0.57$). The negative relationship found between basal cover in the interspaces and K_e could, therefore, be a secondary effect of low or no rock cover on those plots.

Rock cover under plant canopy is also positively related to K_e in Eq. 13, and correlation analysis revealed a moderate positive relationship ($R = 0.31$). Only 13 of the 44 plots had any rock cover under plant canopy, however, and in most cases the percentage of such cover was very small (Table 4). Rock cover outside of plant canopy was present on 30 of the plots, and the percentage of rock cover on these plots was higher than that under plant canopy, in general, particularly on the shrub sites. Interspace rock cover and total rock cover were also positively correlated to K_e ($R = 0.38$ for both terms), suggesting that the location of the cover is less important than the actual absence or presence of rock cover itself.

The literature on the relationship between rock cover and infiltration and erosion is contradictory. A number of investigators have reported a negative relationship between rock cover and infiltration (Tromble et al. 1974, Abrahams and Parsons 1991, Brakensiek et al. 1986, Haupt 1967, Wilcox et al. 1988), while others have found a positive relationship (Lane et al. 1987, Simanton et al. 1984, Meyer et al. 1970). These contradictory results could be explained by the position of rock fragments in relation to the soil surface. In a laboratory rainfall simulator study, Poesen et al. (1990) concluded that rock fragment position in top soils greatly affects water infiltration. They found that if the rock fragments rested on the top soil, water intake increased and runoff decreased. If the rock fragments were embedded in the top soil, however, infiltration rates were reduced and runoff generation was increased. Such a theory could help to explain the positive correlation we found.

The fact that 3 of the model terms in Eq. 13 are ground cover characteristics and that they represent the distribution of those characteristics as a percentage of either interspace and under-canopy area suggests the importance of considering areas underneath and outside plant canopy independently. In semiarid areas, infiltration and erosion rates are a complex function of plant, soil, and storm characteristics (Gifford 1984). Although infiltration is a soil driven process, vegetation influences are great. Spatial vegetation characteristics such as root density may act as surrogates for soil characteristics such as bulk density and organic matter. Many studies have shown that the spatial distribution and the amount and type of ground cover are important factors influencing both spatial and temporal variations in infiltration and interrill erosion rates on rangelands (Blackburn et al. 1992, Dunne et al. 1991, Knight et al. 1984, Thurow et al. 1986). In considering K_e, intended to evaluate hydraulic conductivity for an entire plot, the apparent importance of ground cover on its prediction is not surprising. Given the variability in microtopography within many of these plots, the interception of flow by ground cover could have a potentially large impact on infiltration.

It is important to point out that the new predictive equation was solved for experimental rainfall events with a constant rainfall intensity of 60 mm hr^{-1}, and therefore a constant K_e was predicted for each site. In reality, the effective hydraulic conductivity of a hillslope is a nonlinear function of rainfall intensity, initial soil water content, and the distribution and quantity of canopy and ground cover. Lane et al. (1978) reported that significant errors in estimating runoff are possible if it is assumed that a watershed contributes runoff uniformly over the entire area when only a small area within the watershed is actually contributing all of the runoff. Hawkins (1982) observed that the apparent infiltration rate is a nonnegative function of rainfall intensity. The apparent infiltration rate will define the mean areal loss rate only when the maximum infiltration rate has been defined (i.e., when the rainfall intensity equals or exceeds the maximum infiltration rate of any portion of the hillslope or watershed).

The interaction of micro-topography and vegetation on surface storage capacity is one of the major factors that creates confusion between rainfall simulator results and data from natural rainfall induced runoff. For many rangeland areas, rainfall consists of bursts of high rainfall rates followed by reduced rainfall or brief periods of no rainfall followed by intense rainfall rates. During the periods of high intensity rainfall, the surface storage areas overtop and runoff is produced. During periods of lower rainfall intensity, water in surface storage areas infiltrates and must be filled again during the next high rainfall burst. These fluctuations in rainfall intensities contributes to the phenomenon of apparent infiltration rate changing as a function of rainfall intensity (Morin and Kosovsky 1995). In addition, runoff generated in bare interspace areas does not generally flow long distances down slope before being intercepted by vegetation clumps where all or part of the runoff is absorbed depending on the infiltration capacity of the soil. Rainfall simulators with uniform high intensities mask these processes. New research with variable intensity rainfall simulators that can reproduce the natural variability in rainfall intensity are required before rainfall simulator rainfall/runoff results on plots can be accurately related to natural hillslope or watershed runoff responses.

The K_e values predicted by both the Rawls (Eq. 6) and Risse (Eqs. 9–11) equations are plotted against corresponding optimized values for each plot (Fig. 3a). Both seriously underpredicted K_e for this data set. The Rawls model resulted in a coefficient of determination very close to 0. A lower limit of 0.07 mm hr^{-1} was set for K_e in versions of the WEPP model that used the Rawls equations to eliminate the physically impossible case of a negative K_e. Model predicted K_e defaulted to this minimum value for all of the rangeland plots in this study. The Risse equations showed little improvement, resulting in a coefficient of determination of 0.22.

The estimation of K_e improved when Eq. 13 was tested with the plot data used throughout this study (Fig. 3b), although there is still a bias in underpredicting K_e. Use of this equation results in an r^2 of 0.60. The observed value of the F statistic used to test the appropriateness of the linear regression is 14.84 with an associated $p>0.0001$. Each of the 4 terms in the equation are individually significant at the 95% confidence level.

Figs. 3c and 3d show runoff volume predicted by the WEPP model using the Rawls (Eq. 6) and Risse (Eqs. 9–11) equations plotted against observed runoff volume and the new equation (Eq. 13) plotted against observed runoff volume, respectively. As expected, runoff volume predicted using the new K_e equation showed improvement over that predicted by the Rawls and Risse equations since the same data set that was used to develop the new equation was also used to test it. Independent rangeland data sets must now be used to test Eq. 13.

Conclusions

The Green-Ampt equation is sensitive to the effective hydraulic conductivity parameter; therefore, its accurate estimation is important to model results. The algorithms developed by Rawls et al. (1989) and Risse et al. (1995) to calculate effective hydraulic conductivity using data collected from agricultural systems were found to be unsatisfactory for rangeland systems. Using either set of equations, the hydrologic component of WEPP is unable to accurately predict runoff volume.

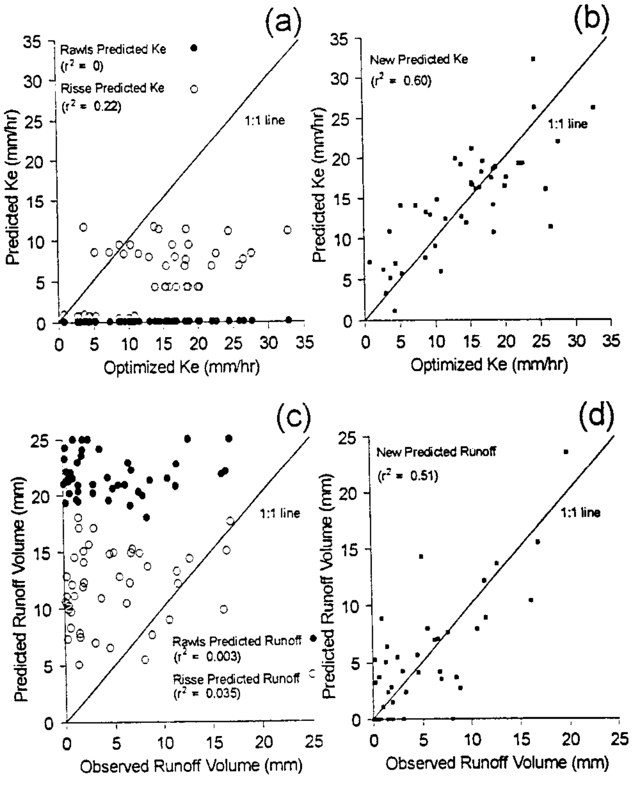

Fig. 3. (a) Observed vs. predicted values of effective hydraulic conductivity (K_e) using algorithms developed by Rawls et al. (1989) and Risse et al. (1993); (b) Observed vs. predicted values of effective hydraulic conductivity (K_e) using new algorithm developed in this research; (c) Observed vs. predicted runoff volume generated with WEPP using predictive K_e algorithms developed by Rawls et al. (1989) and Risse et al. (1993); (d) Observed vs. predicted runoff volume generated with WEPP using predictive K_e algorithm developed in this research.

Although natural systems are complex, adding increasing complexity to physically based models doesn't always improve model predictions (Beven 1989). Sometimes it is better to use simpler regression equations based on interactions of physical characteristics. Such was the logic used to develop the predictive equation presented in this paper. The regression model is well balanced in that it contains a term representing soil texture (clay) and 3 terms representing the distribution of ground cover (litter and basal cover in interspace and rock cover in under-canopy areas). This lends credence to the idea that the spatial distribution of ground cover is an important factor in hydrologic modeling. The equation presented here is recommended for further testing under rangeland conditions for the purpose of independent validation. Further testing is also required to determine its robustness under a broader range of soil and vegetative conditions.

Equation 13 may not be suitable over a continuum of rainfall events with different intensities. Development of the equation was based on the assumption that all other model inputs are correct and model formulation of the effective capillary pressure head at the wetting front in correct. The approach taken herein evaluates spatial variation in cover across the slope, but not down the slope. More work is required to evaluate down slope processes such as flow path continuity and tortuosity.

Finally, the equation was fitted over a relatively large area (35 m^2) in an attempt to incorporate the spatial variaion of the area into 1 value. There is still a need to define spatial variability of infiltration and runoff along a hillslope, considering also the cumulative total runoff volume at the end of the hillslope using new research methodologies and techniques.

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Comparison of forage value on private and public grazing leases

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Abstract

Federal land grazing fees have been set by a formula that uses a base rate developed from a 1966 study comparing total grazing costs on private and public lands. A similar market comparison was recently conducted in Idaho, New Mexico, and Wyoming. Total grazing costs were gathered through personal interviews from 258 ranchers using 245 public grazing permits and 149 private leases. Public land grazing permit values were also estimated in each state. This study demonstrated that many public land ranchers have been willing to pay more for grazing than the apparent value implied from the private forage market. With the 1992 grazing fee of $1.92/animal unit month (AUM), 34% of Bureau of Land Management (BLM) cattle producers, 62% of U.S. Forest Service (USFS) cattle producers, 60% of BLM sheep producers and 92% of USFS sheep producers paid more for grazing public lands than did those grazing privately leased lands. Estimated forage values averaged $3.63/AUM for cattle grazing BLM land, and were negative for cattle using USFS lands and for sheep using both BLM and USFS allotments. Using a 3.35% interest rate to amortize permit value, the annual value of public land forage was estimated to be from $3 to $5/AUM. Doubts were cast about the standard assumptions that ranchers have profit maximization as their primary goal, that permit value measures only excess forage value, and that sufficient private leases are available for a valid comparison between private and public forage markets.

Key Words: grazing fees, permit value, profit maximization, public land policy, land use

Fees for grazing public lands were first assessed in 1906 by the U.S. Forest Service (USFS) and in 1936 by the Bureau of Land Management (BLM). The authorization to graze livestock on federal lands was controlled by issuing grazing permits to those who could meet the "prior–use" and "commensurability" requirements. To encourage use and private investment on the rangelands the original permits were freely given to ranchers, with grazing fees set at low levels. The difference between the cost of utilizing federal rangelands and the value of the forage was quickly capitalized into the value of the base ranch (Roberts 1963).

Since the first administered grazing fee, numerous attempts have been made to establish a fair market price for public land forage (Kearl 1989). Because federal grazing fees are set by a formula and are not open market transactions between willing buyers and sellers, no direct estimate of market value is obtainable and indirect valuation procedures are necessary. One method frequently used is to compare grazing fees on public lands to private land lease rates. Private land lease rates were used to imply the value of National Forest lands as early as 1915 (Rachford 1924). Recent federal grazing fee studies have relied on market price comparisons to establish forage value. Grazing fee studies conducted during the 1960's (USDA/USDI 1977) and 1980's (Obermiller 1992) compared the total cost of grazing public and private lands. Studies conducted in the 1980's (USDA/USDI 1986) and updated in 1992 (USDA/USDI 1992) used a market rental appraisal of private land leases to imply forage value. LaFrance and Watts (1995) also used the private grazing market to examine forces that influence private grazing fees across western states and draw implications to public grazing policy. A main inference of these studies was that considerable variation exists in forage value both within and between selected areas.

The objective of this study was to examine the value of public forage in Idaho, New Mexico, and Wyoming by comparing the total costs of grazing public and private leases (total cost approach). A further objective was to examine the value of federal grazing permits in each state and compare the capitalized value of permits with the forage value obtained from the total cost approach. This second objective not only provides an estimate of the rancher's "willingness–to–pay" for federal forage, but also provides a verification on the theoretical "correctness" of the total costs approach.

Theoretical Justification

The theoretical justification for using the private forage market to imply equitable federal land grazing fees is founded in economic models developed in the 1960's at Utah State University (Roberts 1963, Jensen and Thomas 1967, Nielsen and Wennergren 1970). The "Utah model" assumes private and public

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land forage are direct substitutes and that the marginal productivity of the 2 inputs are equal (Nielsen and Wennergren 1970). This implies the amount a profit maximizing rancher should be willing to pay for the 2 types of forage would also be equal.

The marginal factor costs of grazing leased land are comprised of fee (FEE) and non-fee (NFEE) costs. Fee costs are the fees paid to the lessor for the forage utilized and services provided. Non-fee costs are supplementary costs incurred by the lessee to utilize the leased forage. Examples of non-fee costs are transportation of livestock to the lease site, maintenance of fences and facilities, and care of livestock while on the lease.

The total cost approach of determining the value of federal forage compares the fee and non-fee costs of grazing both private and public rangelands. Theoretically, it is the marginal factor costs of the forages, or the amount the rancher was willing to pay for grazing the last unit of forage, that should be equated. What is obtainable from ranchers is their current level of production and the total cost of grazing the allotment. Grazing fees derived from the total cost approach have therefore been based on average rather than marginal costs (USDA/USDI 1977).

To apply the total cost method, total costs of grazing public lands (excluding the grazing fee) are subtracted from the total costs of grazing private lands (including the lease rate) to estimate the grazing fee that equates total grazing costs on private and public lands. This is equivalent to equating costs of utilizing public grazing to private grazing costs by adjusting the public land grazing fee. The estimated grazing fee would be

$$\mathrm{FEE}_{\mathrm{public}} = (\mathrm{FEE}_{\mathrm{private}} + \mathrm{NFEE}_{\mathrm{private}}) - (\mathrm{NFEE}_{\mathrm{public}}). \qquad (1)$$

Estimation of the variables defined in equation [1] resulted in the $1.23/AUM base charge established in the Public Rangeland Improvement Act of 1978 (PRIA) fee formula[1]. The estimated difference in total grazing costs ($1.23/AUM) was considered to be the "average" grazing fee that should be charged to equate grazing costs (USDA/USDI 1977).

It should be noted that valuing forage by comparing total grazing costs does not provide a direct estimate of net forage value, but rather an estimate of the net value of public land grazing. Total private grazing costs define the amount willingly paid for the total grazing package, including services. Subtracting non–fee grazing costs on public lands from this amount results in an estimate of the amount that could be paid for public land forage while maintaining total private and public grazing costs at the same level.

The fee charged to graze public land has historically been less than the value of its marginal product and the rancher who had access to federal land grazing realized a surplus economic value known as permit value. Permit value (PERMIT) is said to be the capitalized cost advantage that public land ranchers have over those grazing on private lands or

$$\mathrm{PERMIT}_{\mathrm{public}} = \frac{(\mathrm{FEE}_{\mathrm{private}} + \mathrm{NFEE}_{\mathrm{private}} - (\mathrm{FEE}_{\mathrm{public}}\ \mathrm{NFEE}_{\mathrm{public}})}{r}$$

$$= \frac{\mathrm{COSTADV}}{r} \qquad (2)$$

This capitalization formula calculates the present value of a perpetual flow of any cost advantage (COSTADV) that may accrue from grazing on public lands. This formula is sensitive to the capitalization or interest rate, r, that is assumed. The greater the r, the smaller the present value of the perpetual flow. The capitalization formula also assumes the decision maker has an infinite planning horizon and determines the permit value accordingly. A finite planning horizon would suggest a smaller permit value. An infinite planning horizon is typically justified even when a rancher maintains the permit for a finite time since the rancher can sell the rights to utilize the permit. The capitalization formula would not be valid if the rancher anticipated the grazing rights would be appropriated by the federal government without just compensation.

Because access to grazing is embodied in the grazing permit, the surplus value became a marketable item that was transferred when the permit was sold (Nielsen and Wennergren 1970). As the cost differential between grazing public and private lands fluctuates, in the presence of a competitive market, the changing value of the grazing permit theoretically eliminates the cost advantage that public land ranchers have. When a public land rancher buys the grazing permit, total grazing costs are equated and the cost advantage is eliminated (Workman 1988; Torell and Doll 1991).

Obermiller (1992) argued that permit value is not a capitalized cost advantage, but rather the capitalized value of cost savings realized through economies of size when federal grazing permits are attached to the ranch unit. Complementarity between different seasonal forage sources is also cited as a reason for permit value. Some combination of these factors may be appropriate.

Because grazing permits can be purchased and sold[2], a direct estimate of the annual value of public land grazing can be obtained by computing a rate of return on grazing permit investment and adding this to the current grazing fee (Nielsen and Wennergren 1970). This can be seen by rearranging equation [2] as

$$\mathrm{COSTADV} = \mathrm{PERMIT}_{\mathrm{public}} \times r \qquad (3)$$

and then adding COSTADV to the current grazing fee to obtain the annual value of public land grazing. This procedure gives a site-specific estimate of forage value while directly considering the costs, forage quality, level of improvement, and characteristics of specific public land ranches. More productive and/or lower cost ranches should theoretically have a higher valued grazing permit, implying a higher forage value.

Theoretical Inference

If permit values arise only because of a capitalized cost advantage for public land grazing, determining the annual forage value from permit values should provide a verification of the forage value determined from the total cost approach. However, if permit values are influenced by factors other than expected livestock returns, valid estimates of forage value will not necessarily be obtained using this method. Jensen and Thomas (1967) found that factors associated with grazing cattle on public ranges explained only 55% of the variation in permit sales value. Similarly, Torell and Doll (1991) found that permit values have not provided a consistent estimate of the value of public land forage. They found that permit values contributed more to the value of the ranch in the early 1980's than the capitalized cost advantage of public land grazing would justify. After 1987, public lands contributed less to the value than the simple capitalization formula would suggest. Thus, permit values may not be a sensitive and consistent indicator of forage value.

Approach

To identify public and private grazing costs, a survey of ranchers in Idaho, New Mexico, and Wyoming was conducted. Non–fee grazing cost data were gathered on the cost items identified in the 1966 grazing fee study (Refer to Table 1 for a listing of cost items. A more detailed variable description of the study design is provided in Torell et al. (1993) and Bartlett et al. (1993)).

Range improvement investments (development depreciation) on public lands were determined from BLM and USFS records and from the interview process. Only the rancher's share of cost was considered and investments on non–federal land were prorated by the percentage of time or use on the federal allotment.

Sampling Procedures

A random sample of public permittees and private lessees in the 3 states were personally interviewed to solicit estimates of fee and non–fee grazing costs. Lists of public land permittees were obtained from BLM and USFS records for each state. Lists of private forage lessees were available from prior grazing lease surveys, from USDA/National Agricultural Statistics Service, stockgrower organizations, and County Extension faculty.

Surveys were conducted in the 3 states during October through December 1992. The grazing cost data were obtained from 77 ranchers in Idaho, 85 ranchers in New Mexico, and 99 ranchers in Wyoming. The three–state data base included information on 173 BLM allotments, 72 USFS allotments, and 151 private leases.

Of the federal allotments surveyed, 44 provided grazing for sheep. Sheep grazing on private rangeland was not common. The survey included only 3 private sheep leases in Idaho, 3 in New Mexico, and 9 in Wyoming. Recognition of limited sample size should be given when interpreting sheep grazing costs and forage values.

Statistical Analysis

Total grazing costs were calculated for each lease using the labor and mileage rates and other assumptions detailed in Bartlett et al. (1993). Total costs were converted to a $/AUM value and non–fee grazing costs were spread over all AUMs on the allotment or lease, regardless of land ownership.

Grazing cost calculations and analysis were completed using appropriate statistical routines found in the SAS statistical program (SAS Institute, Inc. 1988). Variation in grazing costs were analyzed using an unbalanced analysis of variance (ANOVA) with a three-way design and interaction. Differences in the size of leases and sample size between states and classes of livestock were accounted for in the least squares means (LSM) computed with the statistical models. Forage value estimates are presented as mean values followed by 90% confidence limits about the mean. A more complete description of the model used in the analysis is given in Bartlett et al. (1993).

Permit Values

Ranch sales data were collected in Idaho and Wyoming from Farm Credit Services (FCS) for the period 1986 through 1992. Summary statistics were compiled from 129 BLM and 38 USFS permit ranch sales in Idaho, and 290 BLM and 35 USFS sales in Wyoming. Sales data compiled included an appraiser's allocation of the contribution that public and state AUMs made to the market value of recent ranch sales. These estimates of permit value were recorded from FCS sales sheets and averaged over the 1986–92 period. The reported averages were weighted by the number of federal AUMs leased.

A previously developed land value model was used to estimate New Mexico grazing permit values. The model used FCS ranch sales data for 1987 through March 1993. Average 1992 permit values were determined using the estimated regression equation developed from 378 ranch sales (Torell and Kincaid 1996). This was done by estimating the January 1992 market value of a 300 AUY ranch totally dependent on BLM or USFS for grazing capacity. The regression model has historically given permit values consistent with the appraisers values used to obtain permit values for Idaho and Wyoming (Torell and Fowler 1986).

Using the permit value approach, annual forage value was estimated by multiplying average permit values by a capitalization rate of 3.35% and adding this to the 1992 grazing fee of $1.92/AUM. The result is the annual amount that ranchers have paid in the market place for public land grazing (Torell and Doll 1991). The 3.35% capitalization rate is consistent with long–term rates of return realized from western public land ranches (Agee 1972, Madsen et al. 1982, Workman 1986). Obviously, annual forage value will vary considerably depending on the interest rate. This is a limitation of using permit values to imply forage value.

Results

Three-State Average Grazing Costs

Grazing costs were estimated for BLM and USFS allotments, and compared to costs for private leased lands in the 3 states (Table 1). Different cost categories are shown for both cattle and sheep. They were estimated across states after adjusting for differences in lease size through the ANOVA process. Total non–fee grazing costs were estimated to be $15.41/AUM for cattle on BLM, $21.89 for cattle on USFS, $23.23 for sheep on BLM, and $32.68 for sheep on USFS. By comparison, the same costs on private leased lands totalled $19.04/AUM for cattle and $20.46/AUM for sheep, including the private land lease rate.

Nearly all cost categories were significantly higher on public lands than on private leased lands (Table 1). This is consistent with the perception commonly expressed by public land ranchers that non-fee costs for grazing public lands are higher than on private lands. Major cost items for private and public land grazing included lost animals, moving and herding livestock, salt and feed, and range improvement maintenance. The private lease rate averaged $7.71/AUM for cattle producers and $7.18/AUM for sheep producers. The lease rate was a major part of the total cost of grazing on private leased lands, accounting for over 34% of total grazing costs. Total grazing costs were statistically different between private and public cattle producers and between private and USFS sheep producers (Table 1).

BLM vs. USFS

As previously noted, cattle grazing costs were estimated to be higher on USFS land than BLM administered land (Table 1). This is similar to what Obermiller (1992) found for eastern Oregon

Table 1. Average grazing costs per AUM on BLM, USFS, and private leased lands in Idaho, New Mexico, and Wyoming combined (adjusted for differences in lease size), 1992.

	Cattle			Sheep		
	BLM	USFS	Private	BLM	USFS	Private
Sample size (n)	141	60	134	32	12	15
Lost animals	3.09^{a}	4.49^{b}	2.10^{c}	5.16^{b}	6.05^{b}	$2.63^{a,c}$
	(0.31)	(0.41)	(0.28)	(0.69)	(0.95)	(0.87)
Association fees	0.20^{a}	1.07^{c}	0.01^{b}	0.17^{a}	0.00^{b}	$0.00^{a,b}$
	(0.08)	(0.10)	(0.07)	(0.17)	(0.24)	(0.22)
Veterinary	0.08^{a}	0.12^{a}	0.12^{a}	0.16^{a}	0.37^{b}	0.20^{a}
	(0.03)	(0.04)	(0.03)	(0.07)	(0.10)	(0.09)
Moving livestock	2.61^{a}	4.49^{b}	1.93^{c}	3.97^{b}	5.97^{d}	$2.51^{a,b,c}$
	(0.29)	(0.38)	(0.26)	(0.64)	(0.88)	(0.81)
Herding	3.63^{a}	5.00^{c}	2.94^{a}	7.30^{b}	13.49^{d}	3.05^{a}
	(0.37)	(0.49)	(0.33)	(0.83)	(1.13)	(1.04)
Misc. labor and mileage	0.61^{a}	0.77^{a}	0.18^{b}	0.73^{a}	1.13^{c}	$0.34^{a,b}$
	(0.08)	(0.10)	(0.07)	(0.17)	(0.23)	(0.21)
Salt and feed	1.41^{a}	1.12^{a}	1.80^{a}	1.81^{a}	1.06^{a}	1.53^{a}
	(0.27)	(0.36)	(0.24)	(0.60)	(0.82)	(0.75)
Water	0.47^{a}	0.24^{b}	0.11^{b}	$0.51^{a,b}$	0.38^{a}	$0.16^{a,b}$
	(0.07)	(0.09)	(0.06)	(0.16)	(0.22)	(0.20)
Horse	0.22^{a}	0.45^{b}	0.15^{a}	0.34^{a}	0.78^{c}	0.22^{a}
	(0.03)	(0.04)	(0.03)	(0.07)	(0.10)	(0.09)
Improvement maintenance	2.86^{a}	3.41^{a}	1.84^{b}	$2.33^{a,b}$	$2.26^{a,b}$	$2.22^{a,b}$
	(0.29)	(0.37)	(0.25)	(0.63)	(0.86)	(0.79)
Development depreciation						
Federal land	0.30^{a}	0.39^{d}	0.00^{c}	0.14^{b}	$0.24^{a,b,d}$	$0.02^{b,c}$
	(0.03)	(0.04)	(0.03)	(0.07)	(0.10)	(0.09)
Private land	0.16^{a}	0.07^{a}	0.15^{a}	0.11^{a}	0.02^{a}	0.22^{a}
	(0.05)	(0.06)	(0.04)	(0.11)	(0.15)	(0.13)
Other costs	0.23^{a}	0.50^{c}	0.11^{a}	1.01^{b}	1.89^{d}	0.35^{a}
	(0.09)	(0.11)	(0.08)	(0.19)	(0.26)	(0.24)
Private land lease rate	—	—	7.71^{a}	—	—	7.18^{a}
			(0.34)			(1.07)
Total cost	15.41^{a}	21.89^{b}	19.04^{c}	23.23^{b}	32.68^{d}	20.46^{b}
	(0.99)	(1.30)	(0.88)	(2.19)	(3.00)	(2.74)
Forage Value	3.63 ± 2.42	–2.86 ± 2.59		–2.77 ± 6.22	–12.22 ± 6.94	
	(1.47)	(1.58)		(3.71)	(4.07)	

Note: Means on the same row followed by the same letter are not statistically different at P = 0.10. The number in parenthesis is the standard error of the mean. Individual cost items may not add up to the total cost because the mean for each cost item was estimated using an independent linear statistical model and is not the simple average for the cost category. Least-squares or adjusted means are presented which give the average value had there been a balanced design for class variables and with all covariates set at their mean value (SAS 1989, p. 948). Forage value is shown as the mean value with 90% confidence limits about the mean.

where, on average, utilization of USFS land was the most expensive lease, followed by private land, and then BLM. The 1966 grazing cost survey did not find USFS grazing costs to be higher than private land leases when averaged across all forests and BLM districts. Part of the reason for this insignificance was the considerable variation that was found within a forest and region. The 1966 study found the average cost of grazing USFS land was $0.62/AUM higher than BLM land, but again, this difference was not statistically significant (Houseman et al. 1968. Special report on the grazing fee survey. Unpublished Report. USDA/Statistical Reporting Service).

Major cost categories explaining the higher cost of grazing USFS lands included lost animals, association fees, moving and herding livestock, miscellaneous labor, vehicle expenses, and horse costs. Other cost categories, including miscellaneous expenses and development depreciation on federal lands, were significantly higher on USFS administered lands in some cases but contributed little to the higher cost of USFS grazing.

Several explanations are possible for the relatively high cost estimated for grazing USFS lands and the negative estimate of forage value for these lands.

1. Private leases included in the grazing cost survey were considered comparable to BLM and state trust lands with respect to proximity and physical characteristics. However, few leases were found that were directly comparable to USFS lands with respect to vegetation types, climate, and water resources. Had similar substitutes been identified for USFS grazing, the value of private lease costs might have been higher that the non–fee costs of using USFS grazing.
2. If the estimated cost of using USFS lands is correct, USFS permittees are spending more to graze than ranchers who use private lands. This would suggest that USFS permits should have low or zero value. The total cost approach, though, may not capture all elements of value associated with USFS permits. For example, USFS permittees may be willing to pay higher costs to graze in scenic remote areas and maintain a

way of life or accept a below–market wage rate and return on investment (Bartlett et al. 1989, Harper and Eastman 1980, Smith and Martin 1972).

3. In New Mexico, some of the cost increases could be explained by culture and the high value placed on the agrarian way of life. Of the 21 USFS ranchers interviewed in New Mexico, 10 had relatively small herds and were Hispanic ranchers, mostly in north–central New Mexico. Grazing costs, especially the value of unpaid family labor, were higher for these individuals.
4. Market–price comparisons for valuing forage assumes ranchers have numerous alternatives available to them. Private and public forage are assumed to be direct substitutes. In reality, most private forage sources remain leased and federal leases are not accessible to the general public unless transferred with the base ranch. Ranchers are therefore forced to use higher–cost alternatives (e.g., USFS allotments) if they want to be in the livestock business. However, this does not mean that ranchers who utilize USFS forage are losing money or are not profitable, only that their costs are higher on average.

Cattle vs. Sheep

The total cost of grazing sheep on public lands was significantly higher than for cattle. When the values in Table 1 are weighted by the number of AUMs and averaged for federal lands, the total cost of grazing sheep on public land was estimated to average \$7.72/AUM more than grazing cattle on public land and \$1.42/AUM more for private–land sheep producers compared to private–land cattle producers.

Sheep grazing costs were also the most variable. Because of this variability and the relatively small sample size for sheep producers, especially on private lands, the confidence intervals estimated for sheep forage values are over twice that estimated for cattle production. As shown in Table 1, some of the variability is explained by differences between BLM and USFS.

Permit Value

Table 2 shows estimated permit values for Idaho, New Mexico, and Wyoming and the 1992 forage value implied from these values. Average permit values ranged from \$36/AUM for BLM in Wyoming to \$89/AUM for BLM in New Mexico. BLM and USFS permit values were significantly different in Wyoming but not in Idaho or New Mexico. Implied forage value using the permit valuation method was highest in New Mexico (\$4.90/AUM for BLM and \$4.33/AUM for USFS). Forage value was estimated to be from \$3.00 to \$3.50/AUM for the permits in Idaho and Wyoming. Permits in New Mexico may be more expensive because of their yearlong use compared to the seasonal permits found in Idaho and Wyoming.

If, as economic theory suggests, permit value constitutes a surplus economic value created because the fee charged to graze public land has been less than the value of the marginal product (VMP) of the forage, the forage value obtained from the total cost approach should equal the amortized value of the permit (yearly surplus) plus the federal grazing fee. The theory appears to hold for BLM cattle permits as the forage value obtained from the total cost approach approximates the total value ranchers were willing to pay for the permit while also paying the federal grazing fee. For the remaining public leases, the total cost approach shows that public lands do not have a capitalized cost advantage over grazing on private lands. By comparison, the permit value approach demonstrates that ranchers were willing to pay a premium for federal grazing permits in the land resource market. This dichotomy suggests permit values are comprised of more than a capitalized cost advantage for public land. As previously discussed, cost savings realized through economies of size, complementarity between different seasonal forage sources, or the utility a rancher receives from managing cattle in scenic remote areas may also contribute to permit value.

Table 2. Grazing permit value and forage value implied from average permit values in Idaho, New Mexico, and Wyoming (\$/AUM).

	Permit Value		Forage Value[1]	
State	BLM	USFS	BLM	USFS
Idaho	37a	42a	3.16	3.32
	(1.31, 129)	(2.71,38)		
New Mexico	89a	72a	4.90	4.33
Wyoming	36a	47b	3.13	3.50
	(1.01, 359)	(3.47, 43)		

Note: Permit value means in the same row that are followed by the same letter are not statistically different at $P = 0.10$. Means in the same column are not compared statistically. The numbers in parenthesis are the standard error of the mean and the sample size. The standard error is not shown for New Mexico because the mean value is estimated from a regression model.

[1] Estimated as permit value × 3.35% + \$1.92/AUM 1992 grazing fee.

Theoretically, grazing fees equal to the forage value estimates in Table 2 should eliminate permit value. Yet, permit value estimates in New Mexico for state trust lands indicate this may not always be the case. Torell and Doll (1991) estimated that as New Mexico state land grazing fees went from \$1.60/AUM in 1986 to \$3.13/AUM in 1989 the value of state land grazing permits decreased by about \$30/AUM for every \$1/AUM increase in the fee. State land permits went from the most valuable permit to the least valuable permit in 6 years. New regression estimates indicate that New Mexico state land permits have recently increased in value relative to BLM and USFS (Torell and Kincaid 1996). This is true even though New Mexico state land fees are nearly double those on federal lands and USFS total grazing costs were estimated to be considerably higher than those on BLM land. Security of lease and certainty concerning fee policy and other public land policies, then, may be important considerations in determining the price paid for a public grazing permit.

Discussion and Conclusions

A comparison to the private forage market has historically been used to estimate the value of public land forage. Results of this study indicate grazing values that equate public and private lease costs fall, with $P = .10$, between \$6.05 and \$1.21 for BLM cattle permits, - \$0.27 and –\$5.45 for USFS cattle, \$3.45 and –\$8.99 for BLM sheep, and between –\$5.28 and –\$19.16 for USFS sheep permits.

Theoretical justification for the total cost valuation method comes from the standard economic models and principles that describe the motives of profit maximizing firms (ranches). These methods are justified based on certain limiting assumptions: 1) ranchers are profit maximizers, 2) ranchers have at their disposal numerous alternative forage sources and leasing alternatives, 3) private and public forage are direct substitutes, and 4) rational and profit-motivated livestock producers are willing to pay a price equal to the value of forage in production. If the competitive forage market were efficient, the capitalized value of the grazing permit would theoretically eliminate any cost differentials, thus equating the total cost of public and private grazing.

If only forage values for cattle grazing BLM land are considered, this economic scenario would appear to hold. Non–fee grazing costs on BLM lands were found to average \$3.63/AUM less than grazing costs on private leased lands after adjusting to the same lease size and averaging across all 3 states. Given the 1992 public land grazing fee of \$1.92/AUM, an excess value of \$1.71/AUM (\$3.63/AUM–\$1.92/AUM = \$1.71/AUM) was apparently capitalized into a grazing permit value and ranchers were paying equal amounts for grazing public and private lands[3]. The implied permit value is consistent with the value found for BLM grazing permits using a capitalization rate of about 4.75% for Idaho and Wyoming, and 2% for New Mexico.

Negative forage value estimates for USFS and BLM sheep allotments do not support the total cost approach whereby grazing permit value is the factor that equates total grazing costs. In these cases, grazing costs were found to be higher, on average, than for private lands. Theoretically, profit–motivated ranchers should not be willing to pay more for grazing public lands if private leases are available at a lower cost. The fact that USFS permits and some sheep permits[4] continue to have a market value furthers the argument that comparison with the private market fails to account for several factors. The total cost approach requires one to make several assumptions that apparently are not valid. First, profit may not be the most important motive of public land ranchers. This is consistent with the results of Bartlett et al. (1989), Harper and Eastman (1980), Young and Shumway (1991), and Smith and Martin (1992). The implication is all livestock producers cannot be treated as profit maximizers since ranch resources generate both production and consumption outputs. Second, private leases may not be directly comparable to public leases in attributes that affect value. For example, the limited number of private leases that were truly comparable to USFS lands leads one to question the validity of the total cost approach in determining forage value for USFS lands. Third, in many areas of the west, private land is in short supply, leaving few economical alternatives to public land forage. Rejecting the total cost approach as a method of valuing forage does not mean that grazing cost comparisons that were made between private and public land ranchers are not useful. The cost differential for public and private leases has changed since the 1966 Western Livestock Grazing Survey. It was estimated that with the 1992 grazing fee of \$1.92/AUM, 34% of cattle producers on BLM land, 62% of USFS cattle producers, 60% of BLM sheep producers and 92% of USFS sheep producers paid more for grazing public lands than did those leasing private lands (Bartlett et al. 1993; Torell et al. 1993). Additional investments were also made to buy the grazing permit. The common belief that public land ranchers pay less on average than those leasing private lands is not true.

This study confirms results by Houseman et al. (1968. Special report on the grazing fee survey. Unpublished Report. USDA/Statistical Reporting Service), Obermiller (1992) and LaFrance and Watts (1995) that no singular value exists for federal forage. Results suggest that forage value varies by season of use, type of use, and other variables. As a result, any effort to determine a single value for federal forage is futile. Approaches that allow the value of forage to vary such as competitive bidding have been suggested (Gardner 1963). LaFrance and Watts (1995) recommended the permanent transfer of grazing rights to current permit holders. They suggest privatization of permits would provide incentives for good stewardship and allow permits to be sold to parties who value them most.

Other methodologies such as linear programming or budgeting could be used to determine the value of specific forage types in an area, but results are sensitive to assumptions concerning the rate of return given to other resources used on the ranch. An effort to determine public grazing fees on a site–by–site basis using such modeling approaches would also be very expensive and time consuming.

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Endnotes

1. The PRIA fee formula is:

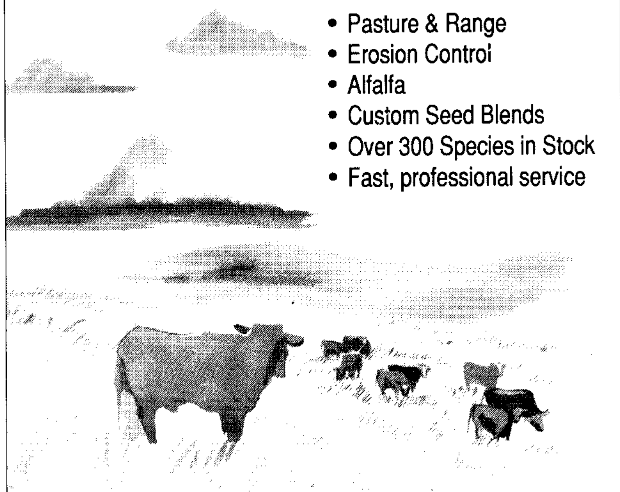
$$\text{Fee} = \$1.23 \left(\frac{\text{FVI} + \text{BCPI} - \text{PPI}}{100}\right)$$

The $1.23 base forage value is the estimated difference in total fee and non–fee costs of grazing private and public rangeland using data collected by a 1966 Western Livestock Grazing Survey (USDA/USDI 1977, p. 2-22). The base is adjusted by annual changes in private grazing land lease rates (FVI), costs of beef production (PPI) and prices received for beef cattle (BCPI).

2. Gardner (1962) hypothesized that transfer retrictions for grazing permits including commensurate property and priority requirements impeded the market for grazing permits. Nielson and Wennergren (1970) and Torell and Doll (1991) concluded that even given these transfer restrictions a resonable amount of competition exists and that a relatively free market exists for permits to graze public lands.

3. Much variability was found, however, and grazing cost estimates for individual grazing allotments ranged from -$74/AUM to + $20/AUM (Bartlett et al. 1993, Torell et al. 1993). Permit values also vary considerably.

4. It appears that some sheep permits do not have economic value. Vacant sheep allotments exist in nearly all of the western states. The uncertainty about grazing fee policy and other public land policies has reduced permit values (Torell and Doll 1991).



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Techniques for computer–assisted mapping of rangeland change

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Abstract

Management of grasslands subject to replacement by woody species requires an understanding of the scales and patterns of change and how to detect and express them. We used the Jornada del Muerto Basin of southern New Mexico as a case study, testing the suitability of Landsat Multi-Spectral Scanner (MSS) data for detecting vegetation changes. Cycles of drought and heavy grazing have apparently changed the once extensive grasslands of the upland Jornada and surrounding areas gradually into a patchwork of shrublands and relict grasslands. Integrated remote sensing and geographic information system (GIS) techniques can facilitate automated detection of these rangeland changes. A GIS was used to store and process two 4-band, co–registered multi–temporal Landsat MSS scenes collected in July 1983 and August 1992. Scene-to-scene radiometric calibration was performed using a regression technique. The data were then evaluated for changes 3 different ways using algorithms based on 1) differences between the 'red' (chlorophyll absorption) bands for the 2 scenes; 2) the Euclidean distances between the 'red' and 'near-infrared' bands for the 2 scenes; and 3) a standardized principal components analysis using all 8 MSS bands. A threshold of 3 standard deviations above the mean was applied to each of the 3 resulting 'change' images to represent areas of extreme change. Correlations among these images ranged between 0.83 and 0.95. We conclude these techniques can identify successfully the patterns and extent of extreme change, and thus have potential value for management of our rangelands resources.

Key Words: remote sensing, GIS, change detection, range management

Arid rangelands cover nearly 50% of earth's terrestrial surface (Williams et al. 1968). Before the turn of the century, perennial grasslands ranged across the northern Chihuahuan Desert (Buffington and Herbel 1965). Human and natural forces have transformed these once seamless rangelands into shrublands (Gibbens and Beck 1988, Grover and Musick 1990, Schlesinger et al. 1990) that extend from southeastern Arizona (Bahre 1991) to western and southern Texas (Archer et al. 1988, Ritchie et al. 1992). Ungulate grazing has been cited as responsible, in part, for this change, and for resulting ecosystem instability (West 1993).

Remote sensing techniques have assisted mapping and monitoring rangeland change (Warren and Hutchinson 1984, Smith et al. 1990, Franklin and Turner 1992). Changes observed in remotely–sensed data can complement ecological assessments of restorable rangelands. Both restoration and long–term management efforts require location and monitoring of the spatial patterns of change. Regional maps of rangeland vegetation change provide range managers with information for setting long–term grazing practices.

We demonstrate in this paper how integrated observations from the Landsat Multi–Spectral Scanner (MSS), and change-detection techniques, can be combined within a GIS to map apparent changes produced by climatic and human forces (e.g., drought, grazing, urbanization) in the Jornada Basin. The Basin is located in the southwestern corner of New Mexico at the northern limit of the Chihuahuan Desert. Arid lands such as the Jornada appear particularly subject to change due to narrow–range climate regimes and lack of soil nutrient reserves (Mabbutt 1984). Field studies by Jornada ecologists offer explanations why change has occurred in this former grassland ecosystem, but these changes have been observed at relatively fine scales (i.e., the individual plant or community) and have not been extended to broader scales (i.e., the Basin). Our focus is on extreme change at regional scales. Any detected change greater than 3 standard deviations above the mean is considered extreme, representing, for example, a change of grassland to barren.

Background and Study Area

The Jornada Basin lies in south central New Mexico (Fig. 1). Once-abundant Jornada grasslands attracted early pioneer cattle ranchers to the Basin. Only 150 years ago, uplands of the Jornada Basin were dominated by black grama (*Bouteloua eriopada*). Before the advent of drilling technology in the 1880's, ranchers limited livestock to populations that could be supported by the natural springs in the bordering mountains. Around the 1880's, wells were able to tap groundwater reserves. Technology brought water to the surface, which increased livestock numbers and opened the land up to heavy grazing.

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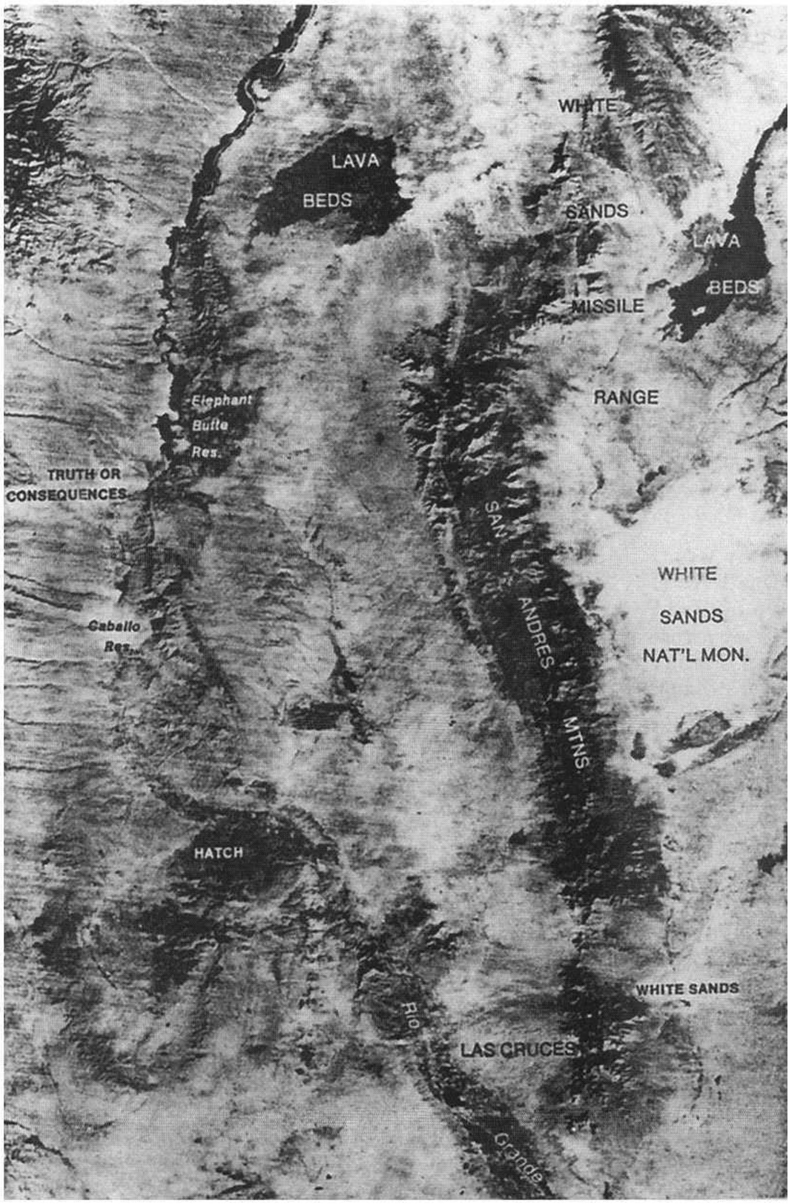

Fig. 1. Location map of the study area. This map shows the Jornada Basin, west of the San Andres Mountains, trending southeastward towards Las Cruces. The right-most of the 2 lava beds (with the panhandle) is the Valley of Fires lava flow. Elephant Butte Resvoir can be seen along the left edge of this map. (Source: Photo Geographic International).

The ecological mechanisms behind the species changes remain controversial (Hennessey et al. 1983, Schlesinger et al. 1990). Episodic drought and heavy grazing have apparently promoted the conversion of grass into shrublands (Schlesinger et al., 1990, West 1993). The fragmented pattern of change detected in the southern Jornada Basin imagery supports, at the comparatively broad scale of Landsat MSS, the patchy spatial patterns seen by ecologists looking at relatively finer scales. Specifically, Schlesinger et al. (1990) reported, though at the scale of individual plants, formation of 'islands of fertility' by shrubs recruiting nutrients from nearby soils. Resulting nutrient–poor soils were subsequently eroded, or ceased to support perennials.

Materials and Methods

For this work, we make 2 basic assumptions: 1) Vegetation change modifies spectral responses; and 2) Vegetation changes are sufficient to be detected. Although digital manipulation of remotely sensed data can yield more accurate change detection than visual inspection of the images, there are cautions, particularly in the early stages of image acquisition and processing. The main factors that complicate detection of bona fide vegetation changes using multi–temporal, multi–spectral data sets obtained with the same sensor system are: 1) image registration; and 2) time–dependent differences in radiometric responses.

Selection and Registration of Multitemporal Data Sets

One of the basic requirements for vegetation change detection is the availability of at least 2 'anniversary' images of the same land area, to avoid confusion with phenological cycles. In this study, the 2 Landsat MSS data sets were acquired within 3 weeks of the same date: 14 July 1983 and 7 August 1992. These dates occur during the summer monsoon season, which produces locally heavy, spatially–variable rainfall.

Image rectification and registration were performed using the Arc/INFO GIS software. A network of ground control points was selected throughout both data sets. A nearest–neighbor re-sampling approach, which preserves recorded radiances, was used because it is important in change detection studies to compare original values (Jensen 1996).

Registration error of approximately 1 pixel is typically tolerance for change detection studies (Eastman and McKendry 1991). After our registration was complete, scene–wide comparisons between datasets produced a root–mean–square registration error of 1.16 MSS pixels (i.e., 92 m). Given the homogeneity common to this and other arid landscapes, an average error just above 1 pixel was considered sufficient to represent significant trends in the spatial patterns of vegetation change.

Radiometric Correction of Multi-Sensor Data

We performed radiometric correction of the 1983 and 1992 Landsat data sets to adjust for different sensor gains and offsets between Landsats 4 and 5, and to standardize the datasets for differing sun angle and atmospheric effects. Correction of atmospheric effects is important in change detection studies, because detection of land cover can be affected adversely when uncorrected images from different years are compared. We evaluated 4 correction methods: 1) Dark Body Subtraction; 2) Empirical Line Adjustment; 3) Image Regression; and 4) Radiative transfer modeling.

Dark–body subtraction requires pixels of known zero-ground radiance, while the empirical-line technique regresses known ground reflectance to pixel-reflectance values (Chavez 1975, Marsh and Lyon 1980). Though the empirical line technique is reliable, ground reflectance data were unavailable for this study. Radiative transfer models involve a complex mixture of data and assumptions (Chavez 1975) and we consider these models less accurate compared with image-based methods.

After review, image regression was selected. Image regression normalizes one data set to another, using a standard linear regression algorithm to relate the values of pixels at corresponding locations between 2 image dates. We considered the 1992 Landsat 5 data the independent variable, and the 1983 Landsat 4 data, the dependent variable. The 1992 data were the favored independent variable due to the currency and assumed greater radiometric fidelity of Landsat 5 compared with Landsat 4. The logic used here is the dependent variable can be considered an adjusted image of the independent variable (Eastman and McKendry 1991). Thus the difference between the 2 is one of offset and gain. Image regression standardizes this offset and gain, and further processing using change detection methods may then be used to discern actual changes in vegetation.

Validation of Change using Spatial Correlation

Given the main objective of this work was identification of extreme vegetation changes, we used different change–detection algorithms to cross–validate detected extremes. Specifically, 3 mutually–exclusive change–detection methods (Euclidean distance, Red–Band 'Differencing' and Standardized Principal Components (SPCA)) were cross–correlated to confirm locations of detected changes. Visual inspection and computer analysis of the cross–correlated images produced significant agreement. Use of spatial correlation not only validates detected change; knowing the precise coordinates of altered areas also makes subsequent ground surveys cost-effective.

Landsat Data and Change Detection Methods

The Landsat MSS images have a nominal spatial resolution of 79m (Price 1987). After geometric and radiometric standardization, a 2209 × 1726 pixel rectangle was extracted from the July 1983 (Fig. 2) and August 1992 (Fig. 3) data sets.

Since the launch of the first Landsat, in

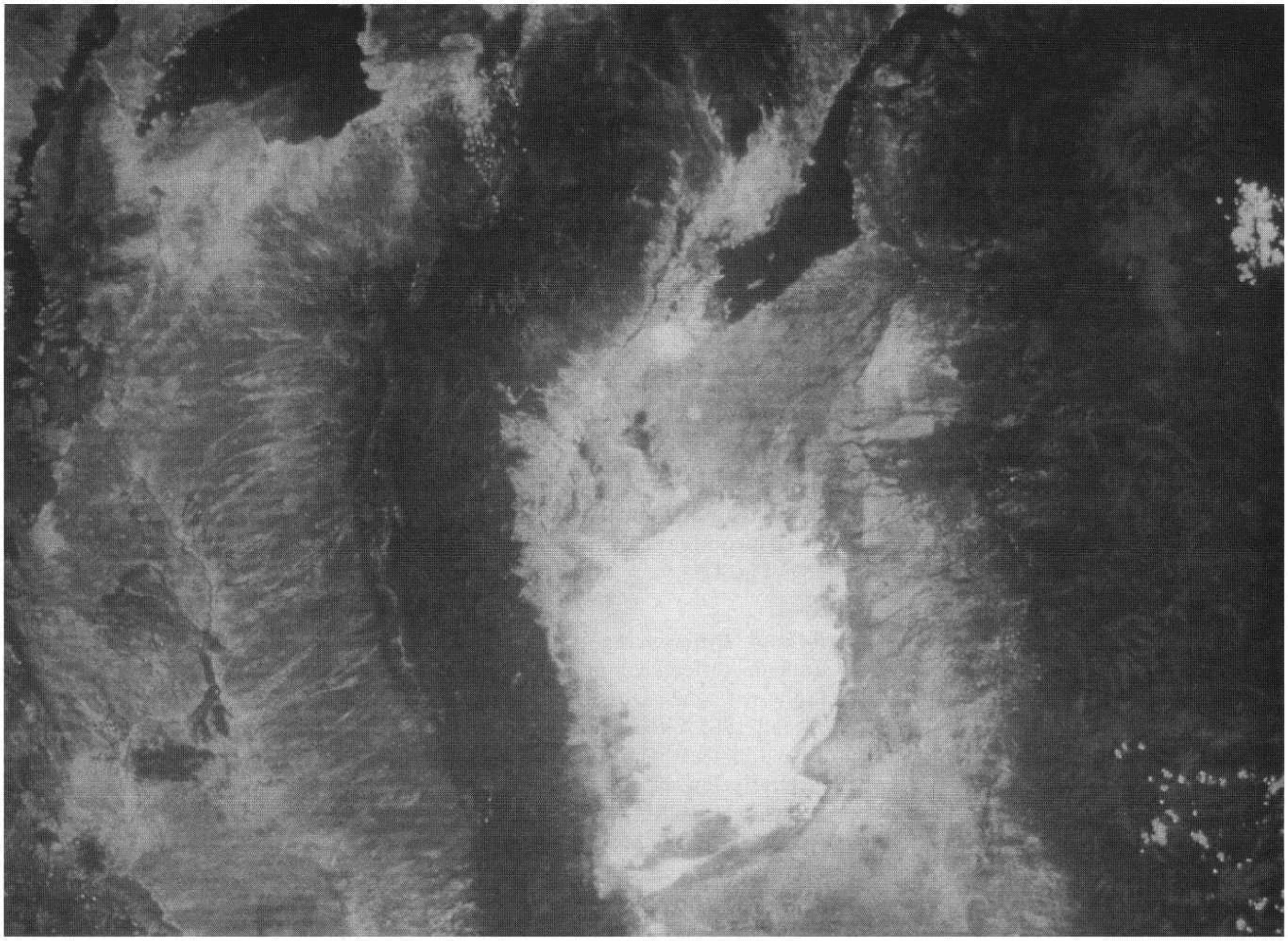

Fig. 2. Gray-scale representation of July 1983 Landsat MSS false-color composite image.

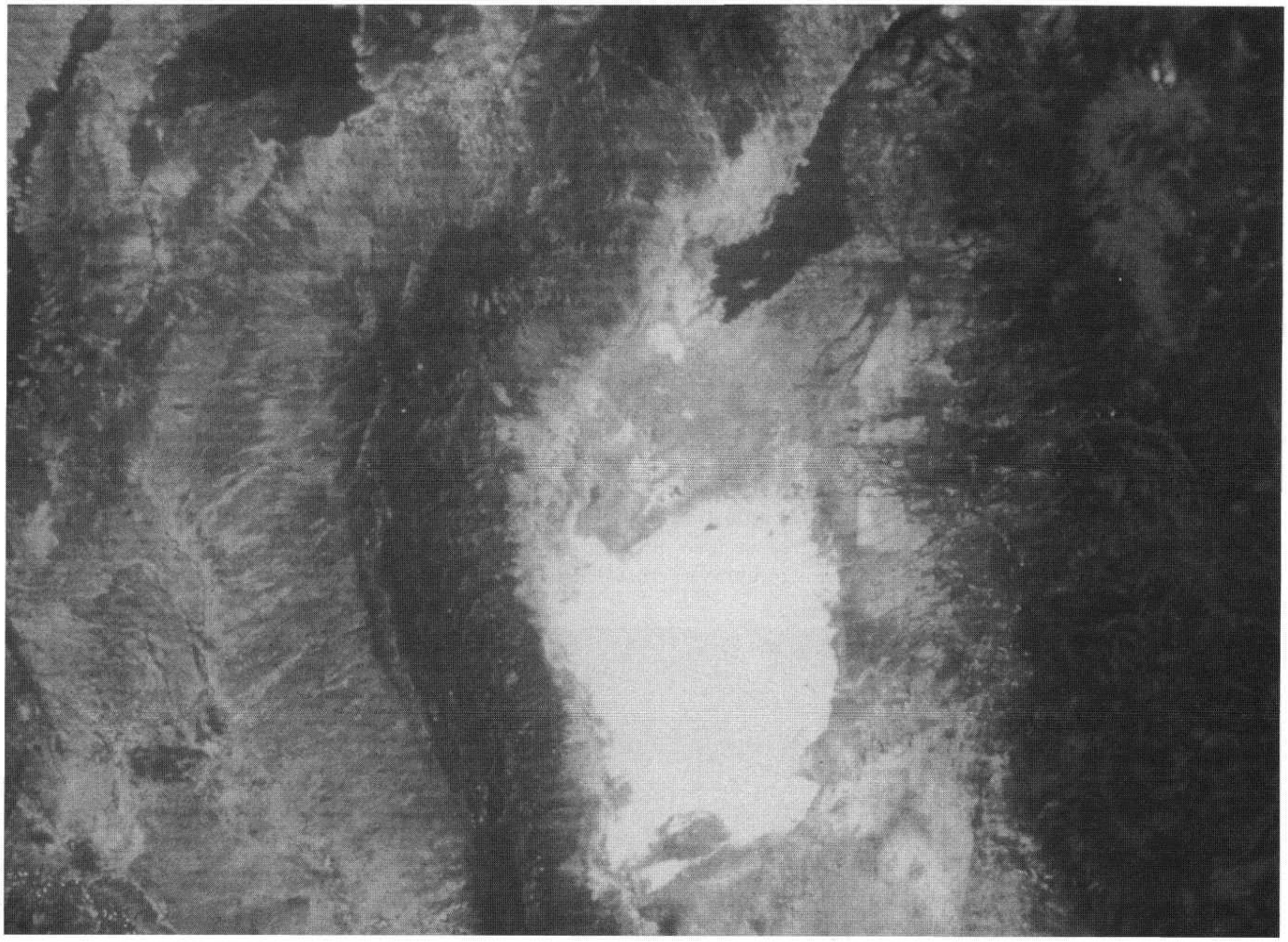

Fig. 3. Gray-scale representation of August 1992 Landsat MSS false-color composite image.

1972, the most common method of detecting land cover change has been visual interpretation of multi-temporal MSS images. Visual interpretation is still widely used and is a direct, fast, manual change detection strategy. The computer-assisted techniques described next provide the opportunity to automate change detection over large areas.

Euclidean Distance

Vegetation leaf pigments typically absorb red light, while the cell structures reflect near-infrared (NIR) light. If these pigment and structural properties change with time, the amount of this change can be expressed as the Euclidean distances in the red and near-infrared brightness values before and after the changes:

$$D = \mathrm{SQRT}[\,(\mathrm{NIR}_2 - \mathrm{NIR}_1)^2 + (\mathrm{Red}_2 - \mathrm{Red}_1)^2]$$

where D = Euclidean Distance, and the subscripts refer to time 1 (1983) and time 2 (1992).

Computed Euclidean distances can be used to produce an image depicting change (Fig. 4).

Red-Band 'Differencing'

A simple 'difference' image was created from the red band digital counts from the 1992 and 1983 Landsat MSS scenes. In arid environments where vegetation cover is generally low, the red band typically provides best results for mapping green leaf cover (Ringrose and Matheson 1991). Both soils and vegetation usually have high reflectances in the near-infrared spectral bands. As a result, reflectance differences in the near-infrared are typically small for soils and vegetation (Franklin et al. 1993, Chavez and MacKinnon 1994). In arid environments a 'difference' image between the red bands from 2 image dates (Fig. 5) may, therefore, detect vegetation change more effectively than can the near-infrared band difference or vegetation indexes such as the Normalized Difference Vegetation Index (NDVI).

Standardized Principal Components Analysis (SPCA)

Principal components analysis (PCA) has been used typically for data compression (Jensen 1996), but also has been suggested for change detection (Fung and LeDrew 1987). Unstandardized PCA uses the variance/co-variance matrix to compute the eigenvalues and eigenvectors. In contrast, Standardized Principal Components Analysis (SPCA) uses the correlation matrix, which standardizes the principal components to zero mean and equal (unit) variance. This standardization produces even loadings on all of the spectral bands, which is considered important for the resolution of change (Fung and LeDrew 1987).

Using SPCA, all 8 bands from the 2 MSS scenes were merged to create 8 Standardized Principal Component (SPC) images (i.e., SPC1, SPC2, etc. representing the standardized principal component 1 image, the standardized principal component 2 image, etc.). We follow the suggestion of Eastman (1992) who found that SPC1 represents the status quo. Because SPC1 and SPC2 are uncorrelated, SPC2 represents change information.

Table 1. Correlation matrix of change-detection images produced using Standardized Principal Component 2 (SPC2), red-band 'difference' and Euclidean distance change-detection methods. Correlations where produced using the entire 2209 × 1726-pixel image (i.e., n = 3,821,734)

	SPC2 Diff.	Red-Band Dist.	Euclid
SPC2	1		
Red-Band Diff.	0.828	1	
Euclid. Dist.	0.824	0.948	1

Results and Discussion

Correlation analysis among the techniques produced significant relationships (Table 1). Correlation of the 'change' images showed direct relationships between the Euclidean distance and SPC2 images (0.824), the red-band 'difference' and SPC2 images (0.828), and the Euclidean distance and red-band 'difference' images (0.948). Consequently, all 3 methods produced similar image outputs, though each used a different pathway to discriminate changed areas. The red-band 'difference' method is the simplest computationally and, based on this criterion, appears most favored among change detection methods we tested.

To produce 'change' strata, all images were divided into 6 levels according to

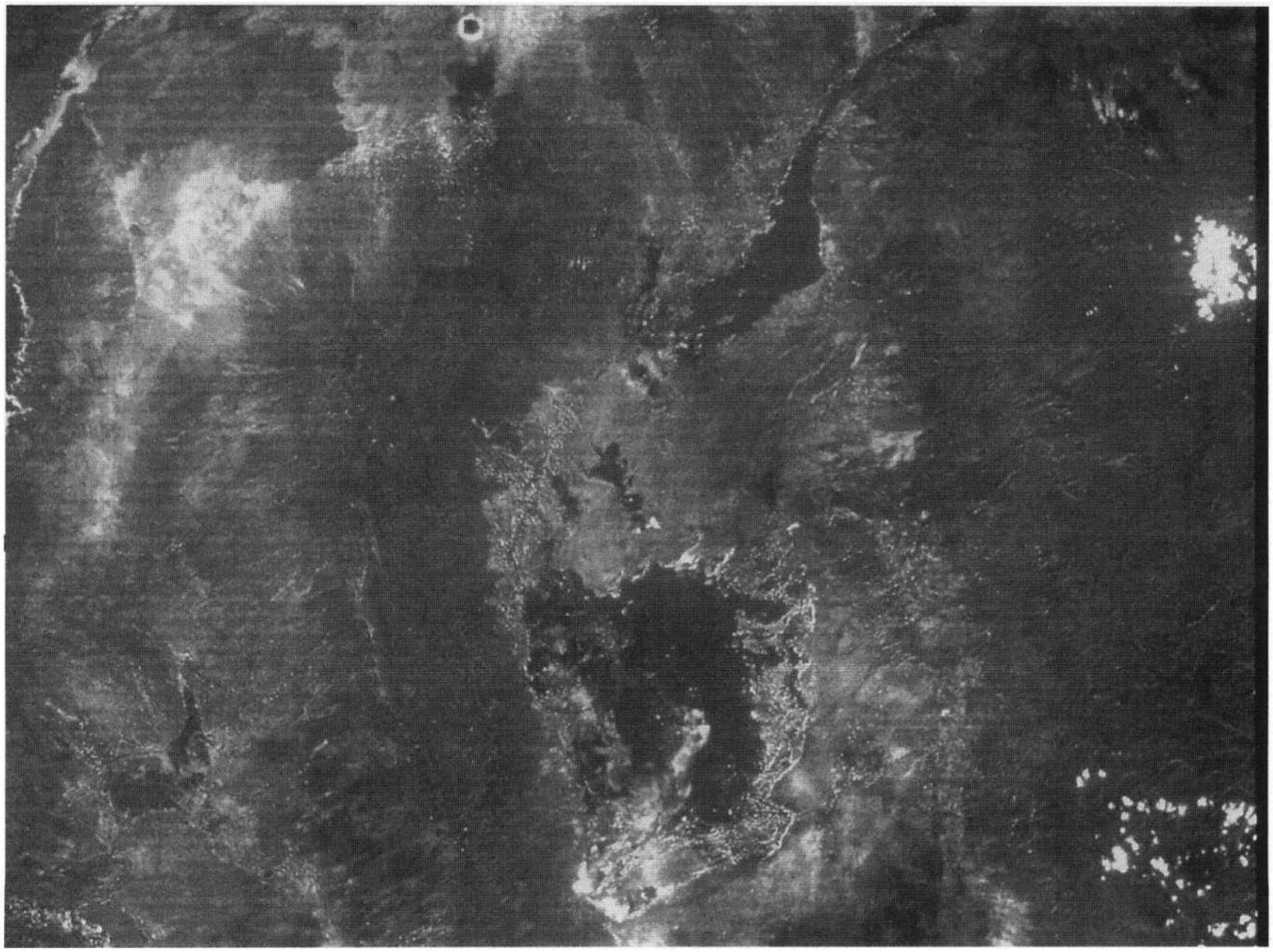

Fig. 4. Euclidean distance 'change' image using MSS2 (Red, 0.6–0.7 μm) and MSS4 (Near-Infrared, 0.8–1.1 μm). Whitest areas indicate greatest change, showing where vegetation cover is sparser on the 1992 than the 1983 images.

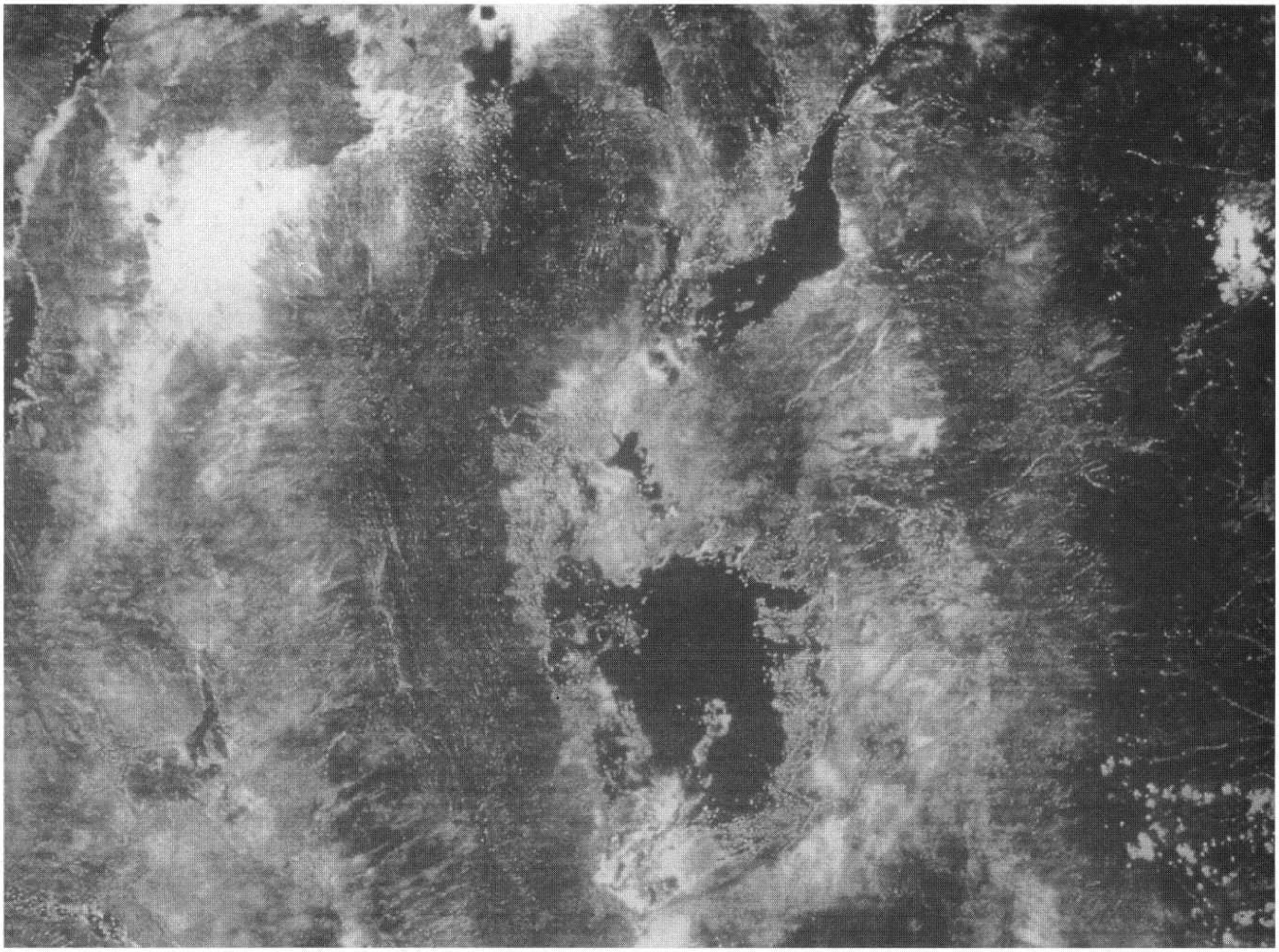

Fig. 5. 'Differenced' Red Bands, 1983 vs. 1992. Whitest areas indicate greatest change. Note the lava beds are dark, indicating little or no vegetation change. We found the dynamic range produced using 'differenced' red bands was greater than produced from 'differenced' NDVI images.

their standard deviations, 3 standard deviations above and below their means. Binary images of 'extreme' change were produced by 'thresholding' them to display only changes greater than 3 standard deviations above their means (Fig. 6 and 7). In these images, areas of extreme change are white. Note the spatial correspondence of the white places in both images.

Areas of known stability and change were used to check the reliability of detected changes. Two areas of apparent stability are the White Sands National Monument and the lava beds. These areas are dark on the Figures 6 and 7, suggesting little or no change. We noted during scene-to-scene registration a change in water levels of Elephant Butte Reservoir (upper left corner on the images) on the July 1983 data set (lower level) and August 1992 data set (higher level). This known change can be seen in the images as the white-outlined shoreline of the reservoir. Finally, the spatial patterns of change seen along the Rio Grande River, in the southwest corner of the images, are associated with known changes in crop rotation.

Consistent spatial patterns of change are evident in all processed images, where all white areas indicate less vegetation in the 1992 scene than in 1983 scene. One region showing change extends as a large swath south of the large lava flow, east of Elephant Butte Reservoir. Continuing south in the Basin towards Las Cruces, the pattern of decreased vegetation appears more fragmented.

The 'islands of fertility' hypothesis attributed to Schlesinger et al. (1990) was posed at the scale of the individual plant, and suggested increased fragmentation of vegetation. With 79m pixels, the Landsat MSS data carried insufficient spatial resolution to confirm Schlesinger's hypothesis. General trends cited by Schlesinger et al (1990), however, including increased heterogeneity of soil resources in arid lands as they evolve into shrubby 'oases', are consistent with the discontinuous patterns of vegetation change detected around the Monument boundary and in the southern reaches of the basin, where overgrazing has been significant (Buffington and Herbel 1965). Finally, this pattern is consistent with documented evidence of wind-induced mesquite dunes in this region (Gibbens et al. 1983).

Conclusions

With the increased concern about grassland replacement by woody plants, rangeland managers must consider how to

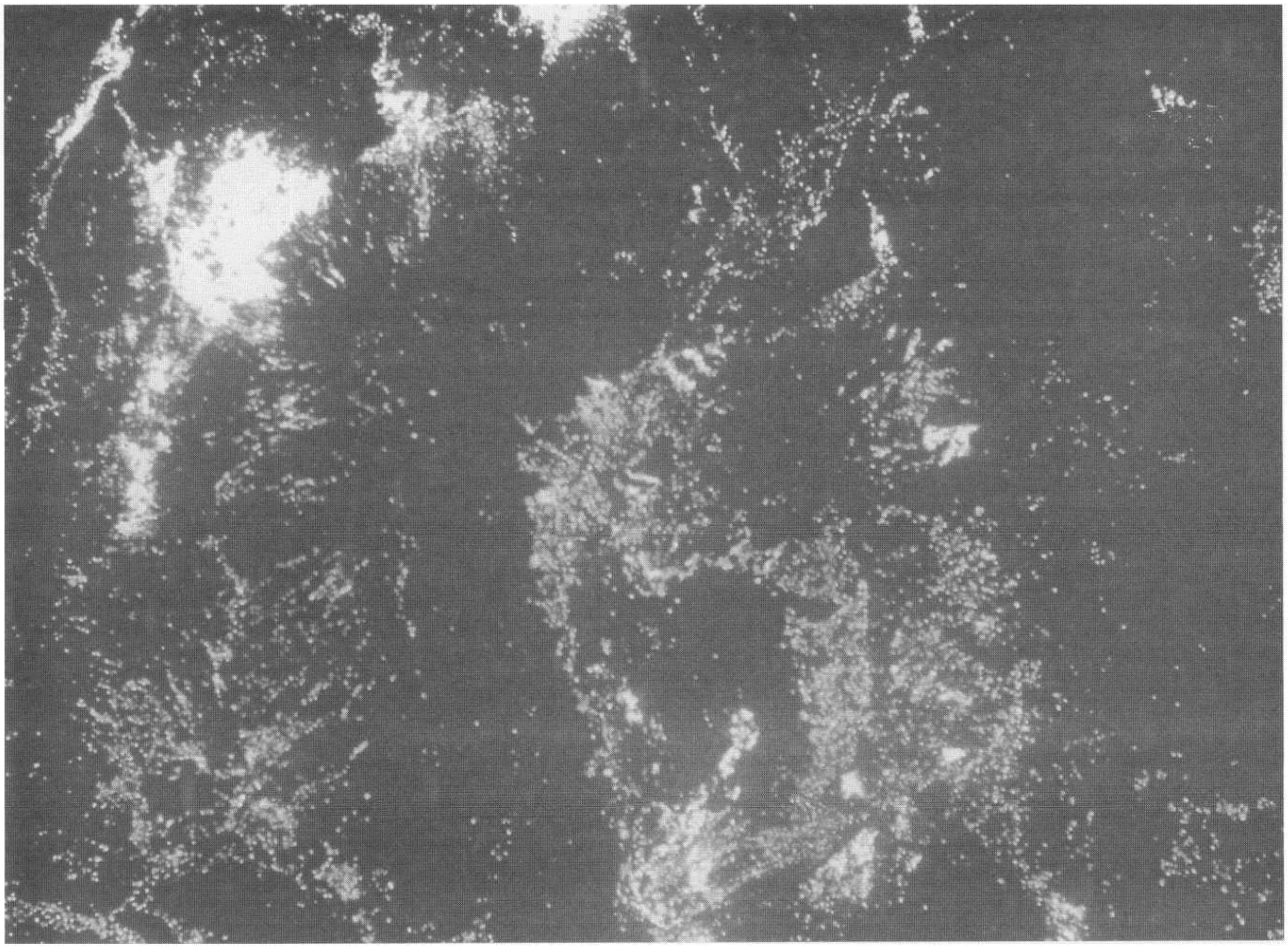

Fig. 6. + 3σ Euclidean distance. One large swath of apparent change extends southward from the left-most lava bed.

detect and express the scales and patterns of change in rangeland ecosystems. In this study we compared methods of change detection and stratification using Landsat MSS imagery and GIS. We conclude that these methods can identify successfully the spatial patterns of extreme rangeland vegetation change and emerging risks.

Drought and heavy grazing by cattle have apparently initiated the redistribution of water, organic nitrogen, and other soil resources, causing these grasslands to change to a patchy mesquite-shrub desert. These findings underscore the inertia of change once set in, but more importantly they demonstrate we have the technology to monitor these changes. The computer-assisted change-detection techniques demonstrated herein thus appear to provide managers with tools to guide future rangeland sustainability.

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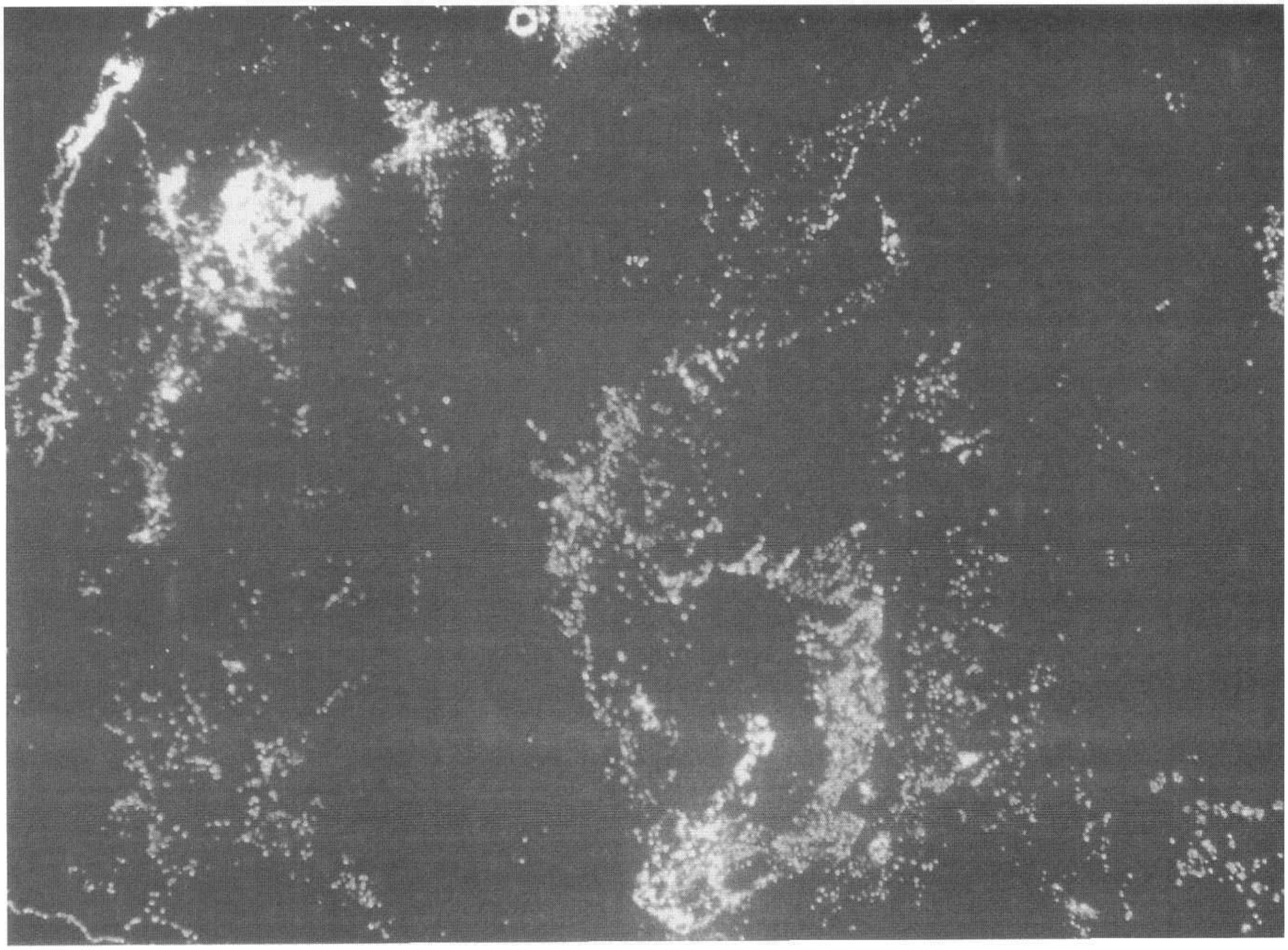

Fig. 7. +3σ SPC2. The pattern of change appears more fragmented in the southernmost portion of the Jornada Basin. Areas around the White Sands National Monument also show significant vegetation change, while the Monument interior shows little or no change.

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Classifying ecological types and evaluating site degradation

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Abstract

An analytical method for classifying ecological types was developed and tested for mountain meadows in central Nevada. Six ecological types were identified by plot sampling of vegetation and soil-site variables. Two-way indicator species analysis and canonical correspondence analysis were used to identify ecological types and to compare the discriminating abilities of different ecosystem components. Each ecological type was a characteristic combination of landform, soil, and vegetation. Changes in vegetation and soil conditions were assessed along a gradient of degradation within one ecological type—the dry graminoid/Cryoboroll/trough drainageway type. Direct gradient analysis was used to display changes in plant composition and indicators of site degradation. Plant and soil indicators of degradation were basal cover of vegetation, standing crop production of 3 key grass species, rates of infiltration, and soil compaction. Three states of range degradation were identified along the gradient. The grass-dominated state was the most desirable in terms of forage production, basal cover of vegetation and infiltration, while the grass/forb/shrub state represented the most degraded and least productive state.

Key Words: canonical correspondence analysis, discriminant analysis, infiltration, range condition, range site, riparian

Resumen

Un método analítico para la clasificación de tipos ecologicos fué desarrollado y evaluado para las áreas abiertas de bosques en la región central de Nevada. Se identificaron 6 tipos ecológicos mediante el muestreo de parcelas de vegetación y variables de suelo-sitio. Se utilizaron análisis de correspondencia canónica y de 2 entradas para las especies indicadoras con el fin de identificar los tipos ecológicos y para comparar las habilidades discriminatorias de los diferentes componentes de los ecosistemas. Cada tipo ecológico fué caracterizado mediante una combinación de forma del paisaje, suelo, y vegetación. Los cambios en la vegetación y las condiciones del suelo fueron evaluadas a lo largo de un gradiente de degradación dentro de un tipo ecológico—el graminoide seco/Cryoboroll/drenaje tipo cóncavo. El análisis de gradiente directo fue usado para mostrar cambios en la composición de plantas y en los indicadores de degradación de sitio. Los indicadores de degradación de plantas y suelo fueron cobertura basal de vegetación, producción de follaje de 3 especies claves de zacates, grados de infiltración, y compactación del suelo. Tres niveles de degradación de sitios fueron identificados a lo largo del gradiente. El área dominada por zacates fue la más deseable en términos de productividad de forraje, cobertura basal de vegetación e infiltración, mientras que el area con zacate/hierbas/arbustos represento la mayor degradación y menor productividad.

Classification of landtypes and condition of those landtypes has long been a topic in resource management (Dyksterhuis 1949, 1958, Joyce 1993). Classification of landtypes into ecological types is an attempt to understand spatial variation across the landscape (Pamo et a. 1991). Condition of a site attempts to measure temporal variation in 1 ecological type. Changes in range condition usually are assessed from measurements of the type and quantity of vegetation. However, according to Wilson and Tupper (1982), range condition should also be based on soil stability as soil degradation is the most serious manifestation of a decline in range condition. The relationship between site degradation and vegetation change needs study if range scientists are to understand and quantify ecosystem effects associated with range degradation.

Soil and vegetation indicators of degradation are likely to be site specific, and therefore apply to specific ecological types. For the purposes of this study, the term ecological type (USDA-FS 1991) is synonymous with ecological site and range site. It is important that a classification of ecological types be developed before range condition is assessed so that the productive capabilities of a site are known (West et al. 1994). Bosch and Kellner (1991) emphasized the importance of understanding the process of rangeland degradation before assessing the condition of any area.

Several authors (Laycock 1991, Tausch et al. 1993, Westoby et al. 1989) have proposed that rangeland dynamics be described by a set of discrete "states' of vegetation on a site and a set of "transitions" between states. Westoby et al. (1989) indicated that management criteria should be used in selecting and defining the

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states that occur in a given situation. Although management of rangelands and the assessment of condition has been ongoing for many years in central Nevada, few studies have been undertaken to assess changes in vegetation composition associated with site degradation of mountain meadows. The objectives of this study were to: 1) define a classification of ecological types for mountain meadows in central Nevada; 2) to identify indicators of community deterioration and the different degradation states within the dry graminoid/Cryoboroll/trough drainageway ecological type; and 3) outline possible states and transitions between states within the dry graminoid/Cryoboroll/trough drainageway ecological type.

Study Area and Methods

Study Area

This study was conducted in the Shoshone, Toiyabe, Toquima, and Monitor mountain ranges of the Toiyabe National Forest in central Nevada. Field work was conducted from about June 1 to September 15 each year from 1990 through 1993. The study area lies in the center of the Great Basin physiographic province. The elevation of the study sites ranged from 2,030 to 3,200 m. Stream courses in the study area are narrow and often incised. Important graminoid species in meadows were: Nebraska sedge (*Carex nebrascensis* Dewey), Aquatic sedge (*Carex aquatilis* Wahlenb.), tufted hairgrass (*Deschampsia cespitosa* [L.] Beauv.), Nevada bluegrass (*Poa secunda* ssp. *juncifolia* Scribner R. Soreng), Kentucky bluegrass (*Poa pratensis* ssp. *pratensis* L.), Douglas sedge (*Carex douglasii* Boott., slender wheatgrass (*Elymus trachycaulus* [Link] Malte.), mat muhly (*Muhlenbergia richardsonis* [Trin.] Rydb.), and baltic rush (*Juncus balticus* Willd.). Important shrub species were: basin big sagebrush (*Artemisia tridentata* ssp. *tridentata* Nutt.) and rabbitbrush (*Chrysothamnus* spp.). Plant nomenclature follows Hickman (1993). Riparian communities occurred on 4 dominant landform types: floodplains, springs, trough drainageways, and stream terraces.

The semi-arid climate is characterized by cold winters and warm summers with most precipitation occurring as winter snow. The average temperature ranges from –4°C in January to 20°C in July, with a yearly mean of 12°C. Average annual precipitation is 31 cm at the townsite of Austin, Nev. (Sakamoto, 1973).

Sampling Design

Ecological Type Classification: One-hundred ten plots were selected for study that represented a range of meadow plant communities, parent material, landforms, soil taxa, and elevations occurring within the study area. Vegetation, soil, and landform characteristics were homogeneous within plots. Due to the narrowness of riparian zones in the study area, sample plots were typically 10 to 20 m in width, and 20 to 50 m in length. Plots were sampled for canopy cover of plant species along 3 parallel 20-m transects. Direction of the initial transect and distance between transects were random within the boundaries of each plot. Canopy cover was estimated by cover classes in 6 ($0.25 m^2$) quadrats systematically placed at 3-m intervals along each transect. This gave a total of 18 cover quadrats for the 3 transects which met a sampling objective where the standard error of the mean divided by the mean was less than 0.15 for more important (abundant) species. More abundant species was defined as the 3 species having the greatest foliar cover on a plot. Ten cover classes were used in estimating cover for individual species (Jensen et al. 1993). Canopy cover of individual species was estimated as a mean percentage by averaging over the 3 transects for each plot. Points on a quadrat frame were used to record basal cover of vegetation and soil cover on each of the 3 vegetation transects. Quadrat frames were placed at 1-m intervals along each transect and 10 points were recorded at each frame. A total of 200 points per transect were used for a total of 600 hundred points per plot. The number of points intersecting basal vegetation and soil were converted to a percentage by dividing the number of points intersecting each category by the total number of points.

At each plot, soils were described to at least 1 meter depth and classified to family level (Soil Survey Staff 1975, 1992). Soil texture and coarse fragment data were estimated in the field for each soil horizon to provide estimates of drainage and soil hydraulic conductivity. In addition, size and sorting of material was analyzed by plotting grain size distribution curves from sieve analysis of surface horizons. This allowed for a comparison of the similarity of soil texture and grain sizes among and within ecological types formed in fluvial deposits. Soil hydraulic conductivity varies with both grain size and sorting of soil material. Hazen (1911) developed a durable empirical equation to relate hydraulic conductivity to the D_{10} grain size (Bowles 1979, Freeze and Cherry 1979). The D_{10} grain size was determined from the grain size distribution curves for each plot. The D_{10} size is the particle size (microns) of the finest 10% of the earth material. Particular attention was paid to soil moisture status by depth, redoximorphic features, and temperature because these factors have been described as important in characterizing ecosystems (Jenny 1980, Vepraskas 1992). Sites sampled in the month of June were revisited in July so that soil temperature and moisture depths for those plots reflected mid-season readings.

Site Degradation: Twenty-two sites from the 110 plots were selected for study that were within the dry graminoid/Cryoboroll/trough drainageway ecological type. Sites with different grazing histories were sampled–ranging from sites that had received heavy, season long grazing, to sites which had a history of light, short duration grazing. One site, which had a history of light to moderate use by livestock, was selected as a reference site. This site, which was considered to be relatively nondegraded, provided a point of reference during the analysis phase of the study. All plots were on slopes of 1 to 6%. Plots were sampled for canopy cover of plant species and basal cover of vegetation as described above. At each plot, soils were described to at least 1 meter depth and classified to family level (Soil Survey Staff 1975, 1992). Depth and abundance of roots was recorded (Soil Survey Staff 1975). Weaver (1919) emphasized the importance of rooting depth in the assessment of condition. Branson et al. (1981) reported on the relationship of condition to kinds of roots (tap-root vs. fibrous roots) and infiltration. Particular attention was paid to the size (very fine, fine, medium, and coarse) and abundance classes (few, common, and many) of roots by depth. In addition, the shape and grade of soil structure was recorded by depth (Soil Survey Staff 1975). Soil structure has 5 shapes: platy, prismatic, columnar, blocky, and granular and 3 grades: weak, moderate, and strong. The grade of platy soil structure was recorded in one of 3 classes; 1 = weak, 2 = moderate; and 3 = strong.

Vegetation was clipped at the height of standing crop on sites that had not been grazed that year to determine standing crop accumulation. Clipping was done between 4 and 21 July 1994. Vegetation was clipped to a height of 1 cm in 10 randomly placed 0.25 m^2 quadrats on each plot. Samples were dried and standing crop production (kg/ha) was calculated for each plot by key forage species (Nevada bluegrass, slender wheatgrass, and mat muhly) and by total standing crop biomass (graminoids, forbs, and shrubs).

Three double cylinder infiltration tests (Cook and Stubbendieck 1986) were run on each plot. Infiltration is influenced by soil hydraulic conductivity and water content (Pullan 1990, Reynolds and Elrick 1990). Hydraulic conductivity varies by both size and sorting of material as well as the continuity of soil macro and micro pores. Edwards et al. (1992) reported that flow paths within the soil were related to infiltration while bulk density was not. To attain uniform antecedent soil water content, all plots were prewet with 5 liters of water and drained overnight. Tests consisted of 5 refill readings at 5 minute intervals over 30 minutes in order to attain a steady state infiltration measurement. In Nevada rangeland plant communities, Blackburn (1975) obtained steady state values within 30 minutes with a ponded test.

Statistical Analysis

Site Classification: Two-way indicator species analysis (TWINSPAN) (Hill 1979) was used to classify the 110 study plots into discrete plant community groups. This analysis was based on the presence or absence of plant species on a plot. Because TWINSPAN classification is based on ordination, it produces a vegetation classification that reflects dominant gradients in the data. In the case of riparian vegetation, this is often a gradient that reflects soil moisture. Recent studies have indicated that the order in which stands are input into the analysis can affect classification results (Tausch et al. 1995). Thus, stand order was rerandomized for each of 5 separate TWINSPAN runs to determine plant community groups consistently present through all analyses.

Multivariate discriminant analysis was then used on the groups derived from TWINSPAN classification to determine which groups were different in soil and landform characteristics (Greig-Smith 1983, Ludwig and Reynolds 1988). At each division in the classification, a minimal set of soil and landform variables that best explained the classification was identified using the option of forward selection of variables in the discriminant tests. Groups that were not different in soil and landform features were aggregated into ecological types. This approach is similar to that described by Fincher and Smith (1993) for classifying ecological types of hardwood stands in Vermont. Soil-site variables used in this analysis were: parent material, elevation, slope, aspect, landform type, soil taxon, grain size, depth to saturation, depth to mottles, depth to coarse fragments (> 20% gravel and/or cobble), and soil temperature. Prior to analysis, the environmental variables were checked for normality and found to have Poisson distributions. These variables were normalized using a square root transformation.

In classifying ecological types, it is useful to subject the soil and landscape data to ordination analysis to determine the dominant environmental gradients in the data. We did this by performing canonical correspondence analysis (CCA) (ter Braak 1987a). The CCA is a direct gradient analysis program which relates species data directly to a set of environmental data (ter Braak 1987b). The CCA scores for the first 3 axes for each plot were used as input to cluster analysis. Multiple discriminant analysis then was used on the groups derived from cluster analysis to determine which groups were different in soil and landscape characteristics. By performing both TWINSPAN and CCA analyses on the data, important environmental variables having the most influence on vegetation patterns were determined.

Site Degradation: Direct gradient analysis in the form of canonical correspondence analysis (CCA) (ter Braak 1987a) was used to determine a gradient of degradation within the dry graminoid/Cryoboroll ecological type. Environmental features used as indicators of degradation were: 1) standing crop production of 3 key grass species (Nevada bluegrass, slender wheatgrass, and mat muhly); 2) percent basal cover of all vegetation; 3) rate of infiltration (ml/5 min); and 4) the degree of compaction as indicated by the occurrence and grade of platy soil structure. The CCA allows major elements in the distribution patterns of different locations to be compared and related to environmental information (Jongman et al 1987, Palmer 1993). This approach does not assume a climax condition, but produces classes and orders of locations that define a gradient according to known site factors, plant species composition, and soil conditions (Beeskow et al. 1995). The CCA produces a plot of both sites and environmental factors in the same ordination space. In this way, the relationship of individual plots to the environmental variables was shown. The position of the reference plot along the gradient served as a check to determine if the reference site was actually in a relatively nondegraded condition as shown by the measured plant and environmental variables.

Three classes of sites, or states, were derived from the CCA ordination of sites within the dry graminoid/Cryoboroll/trough drainageway ecological type. Analysis of variance and Fisher's L.S.D. were used to determine significant differences in the environmental variables among states. The Student's "t" test was used to determine differences in rooting depths and D_{10} grain sizes among states.

Results and Discussion

Ecological Type Classification

TWINSPAN classification of the 110 riparian meadow sites followed by discriminant analysis using soil-site characteristics delineated 6 basic clusters (site types) (Fig. 1) depicted as a dendrogram. At each division in the dendrogram, a minimal set of variables that best explained the classification is shown. The names of each of the 6 ecological types represent the dominant vegetation on the site at the nondegraded state, followed by the dominant soil suborder, and finally the dominant landform of the type. These results were compared with the groups obtained from clustering of canonical correspondence analysis (CCA) scores followed by discriminant analysis of site characteristics. Eight plots were classified differently using the CCA technique. The plots which were classified differently belonged to 3 site types; types 1, 2, and 3. This was probably due to the fact that these types shared some common species and were separated by subtle soil moisture characteristcs. Yet, these types also displayed significant differences in plant species composition and soil moisture (Table 1).

Examination of depths to soil mottling and depths to soil satu-

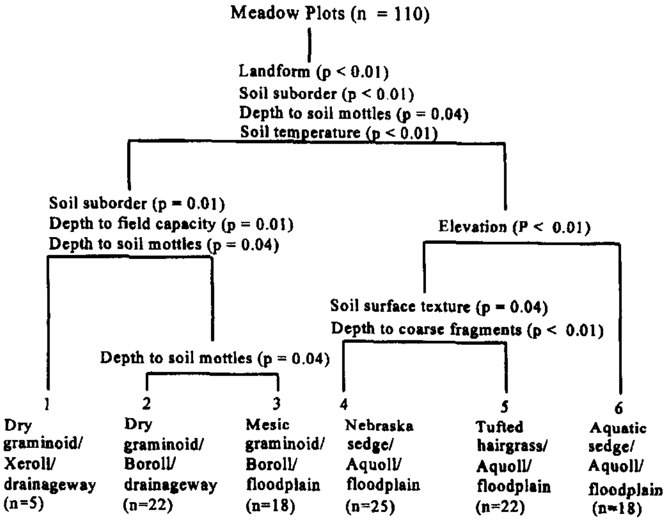


Fig. 1 Classification of 110 meadow plots into 6 ecological types based on discriminating soil and landform characteristics.

ration in Table 1 shows a clear moisture gradient from the drier ecological types (1, 2, and 3) to the wetter types (4, 5, and 6). Douglas sedge, Nevada bluegrass, and mat muhly were associated with deeper depths to soil saturation and soil mottling (Table 1). Nebraska sedge, tufted hairgrass, and aquatic sedge were associated with shallower depths to soil saturation and mottling.

Variables associated with landscape position and substrate—soil suborder, depth to soil mottling, elevation and depth to coarse fragments—were the most highly correlated factors with both species and sample distribution. Each ecological type was a characteristic combination of ecosystem components (physiography, landform, vegetation, and soil).

The results from the ecological classification of sites increases our understanding of how these sites relate to landscape position and substrate. Soils occurring on drainageways with deeper depths to soil mottles typical of Types 1, 2, and 3 occur in the drier meadows. The affinity of dry graminoid species for these sites indicates that these soils are not saturated within the rooting zone during the growing season. Soils occurring on floodplains (Types 4, 5) and at springs along faultlines (Type 6) have shallower depths to soil mottles and saturation. The affinity of sedges for these sites indicates soils that are saturated for at least a part of the growing season. Results of the soil sieve analysis indicated that Types 4 and 5 differed significantly (t-test, P=0.04) in D_{10} grain size, and therefore in soil permeability, and texture (Table 1).

A number of studies have been developed that use multivariate analysis to identify patterns in species distributions and associations among soil, vegetation, and physiographic variables (Pregitzer and Barnes 1982, Barnes et al. 1982). Other studies (Daubenmire 1976, Jimerson 1990, Pfister and Arno 1980) have used vegetation as a key integrative component in site evaluation that can be used to qualify response to climatic, physiographic, and soil factors. Smith (1993, 1995) used TWINSPAN classification and CCA for determining ecological types in northern hardwood stands in central Vermont. In that study, only undisturbed stands were used in the analysis process. That approach is useful because the classification is not complicated by analyzing seral gradients concurrently with ecological type classification. An important part of any landtype classification is further testing of the classification to determine the integrity and robustness of the ecological classes. In our study, we are in the process of collecting additional data and conducting analyses on the independent data set as a means of verifying the classification system.

Table 1. Summary of selected physiographic, soil, vegetation variables (mean±SD) for the 6 riparian ecological types.

Soil-site and vegetation characteristics	Ecological types[1]					
	1 n=5	2 n=22	3 n=18	4 n=25	5 n=22	6 n=18
Depth to saturation, cm	>100	>100	94±28	28±21	41±31	15±13
Soil temperature at 50cm[2]	11±3	10±3	10±2	7±4	8±4	7±3
Depth to mottles, cm	90±17	80±29	57±33	36±34	35±33	34±22
Slope, degrees	4±3	6±6	6±4	6±4	8±5	6±3
Aspect	All	All	All	All	All	All
Elevation, meters	2360±144	2560±389	2507±312	2416±190	2743±321	3091±180
Depth to 20% coarse fragments, cm	85±26	73±32	86±28	67±33	22±26	51±37
Soil texture (D_{10} size)[3]	41±12	49±28	43±19	42±12	65±30	66±16
Landform	Drainageway	Drainageway	Floodplain	Floodplain	Floodplain	Spring
Soil Suborder	Xeroll	Boroll	Boroll	Aquoll	Aquoll	Aquoll
Constancy, percent						
Douglas sedge	100	68	55	16	9	20
Nevada bluegrass	38	86	61	29	13	0
Mat muhly	36	54	38	12	13	0
Nebraska sedge	0	0	55	75	36	6
Kentucky bluegrass	1	22	72	70	59	20
Baltic rush	8	81	88	79	34	66
Tufted hairgrass	0	0	5	45	63	53
Aquatic sedge	0	0	0	2	0	93

[1] 1=Dry graminoid/Xeroll/trough drainway; 2=Dry graminoid/Cryoboroll/trough drainway; 3=Mesic graminoid/Boroll/floodplain; 4=Nebraska sedge/Aquoll/floodplain; 5=Tufted hairgrass/Aquoll/floodplain; 6=Aquatic sedge/Cryaquoll/floodplain.
[2] Degrees Celsius
[3] microns

Site Degradation

The canonical corresponence analysis (CCA) ordination of sites within the dry graminoid/Cryoboroll/trough drainageway ecological type is shown in Fig. 2. Axis 1 represents the relative position of the samples along a gradient of community composition and environmental features. Axis 1 was primarily a gradient of basal cover of vegetation, standing crop biomass production of 3 key grasses, and soil compaction as indicated by the distinctness of soil plate structure. The ordination of sites along the y-axis separated sites differing mainly in the rate of infiltration. For the environmental variables, the arrows point in the direction of increasing value (ter Braak 1987b). From the plot, the relationship of the variables to each other becomes apparent. For example, the amount of basal cover of vegetation points in the opposite direction from soil compaction, and therefore these 2 variables are negatively correlated. The length of an arrow is a measure of how much the species distributions differ along that environmental variable. Important environmental variables have longer arrows than less important environmental variables (ter Braak 1987b). Autocorrelation among variables was checked using the Variance Inflation Factor (VIF) in the statistical package CANOCO (ter Braak 1987b).

The reference site position along the degradation gradient is shown in Fig. 2. This site was considered to be relatively nondegraded and was characterized by graminoid dominance, a high basal cover of vegetation, low soil cover, high standing crop biomass, and relatively high rates of infiltration (Table 2). Sites in the same portion of the gradient were considered to be relatively nondegraded (State I) (Table 2). Changes in composition and abundance of forage species were observed along the main gradient, apparently reflecting vegetation response to a gradient of degradation. With an increase in degradation, a decrease of perennial grasses and an increase in forb species occurred. The 3 dominant species in the grass meadows, the cool-season bunchgrasses, Nevada bluegrass and slender wheatgrass, classified as highly palatable, and the rhizomatous species mat muhly, considered palatable, were considered decreasers under light to moderate degradation. These grass species accounted for most of the standing crop production and a majority of the forage production (Table 2). On more degraded sites, forbs such as iris (*Iris missouriensis* Nutt.) and yarrow (*Achillea millefolium* L.) were more abundant (State II) (Table 2). At this stage, scattered shrubs were evident. Basin big sagebrush, a dominant shrub in low areas along drainageways in fine textured soils occurs on these sites at State III. Rabbitbrush, an aggressive colonizer of disturbed sites, also occurs at State III. The low palatability of these shrubs probably has been important in the establishment of these shrubs.

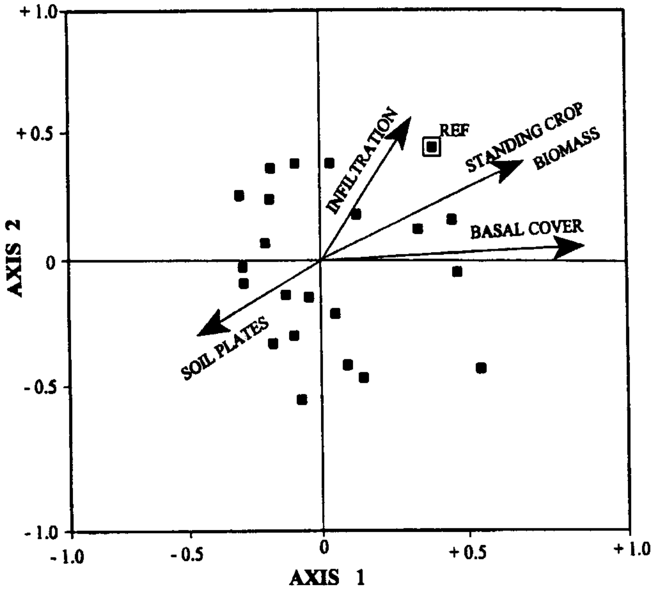


Fig. 2. Canonical correspondence analysis of sites within the dry graminoid ecological type. The 4 indicator variables for site degradation are shown by arrows. Each arrow points in the direction of increasing value for a variable. Axis 1 was primarily a gradient of standing crop biomass of 3 key grass species and basal cover of vegetation with these variables increasing in value to the right side of the diagram. The distinctness of soil plate structure increased to the left on axis 1. Axis 2 was primarily a gradient of infiltration rate. The reference site (REF) was an example of a nondegraded site.

Table 2. Average values (±SD) for important soil and vegetation variables in each of the 3 states identified in the dry graminoid/Cryoboroll/trough drainageway ecological type in central Nevada. Data for States I, II, and III represent the right, center, and left portions of the x-axis of Fig. 2, respectively.

Soil and vegetation characteristics	State I Grass n=4	State II Grass/forb n=8	State III Grass/forb/shrub n=10
Key species biomass[1]	2694±944^{a}	1472±306^{a}	1111±361^{b}
Total standing crop[2]	2829±1216^{a}	1678±553^{b}	1564±313^{b}
Basal area cover (%)	34±5^{a}	15±4^{b}	9±5^{b}
Soil cover (%)	7±2^{a}	12±7^{b}	16±8^{b}
Infiltration rate[3]	1219±373^{a}	721±527^{ab}	465±214^{b}
Frequency of plates (%)[4]	0	45	73
Mean foliar cover, percent			
Nevada bluegrass	39	10	7
Slender wheatgrass	2	19	4
Mat Muhly	17	11	6
Iris	0	12	27
Yarrow	1	3	6
Basin Big Sagebrush	0	1	6
Rabbitbrush	0	1	4

Means in the same row followed by the same lowercase superscripts (a,b) are not significantly different at $P<0.05$, Fisher's L.S.D. test

[1] Standing crop biomasss of 3 key grass species (kg/ha): Nevada bluegrass, slender wheatgrass, and mat muhly

[2] Standing crop biomass of all species combined (kg/ha)

[3] Infiltration rate (ml/5 min)

[4] Frequency of occurrence of moderate to strong plate structure

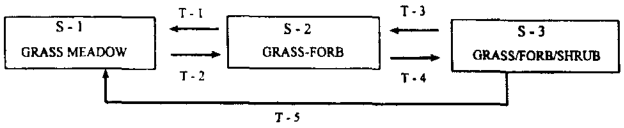
Average rooting depths were not different between States I (45 cm) and II (46 cm) (t-test, P=0.89). Rooting depths were shallower in State III (22 cm) as compared with State II, however, this difference was not significant (t-test, P=0.07). The shallow rooting depths in State III may be due to soil compaction. Rooting depths in State III generally occurred at the depth at which moderate plate structure was observed. The depths of subsoil plates in our study generally agree with depths reported elsewhere for soil compaction in grazed area (Lull 1959) as well as soil mechanics theory (Terzaghi 1943, Bowles 1979, Das 1994).

Tongway and Hindley (1995) have developed a method for assessing soil condition in Australia. Their methods are for use on arid shrublands and tropical grasslands. Important indicators used in their study were vegetation basal cover, soil cover, litter cover, cryptogram cover, and erosion features. Tongway and Hindley (1995) state that a soil in good condition is able to absorb and store rainfall, store and cycle nutrients, provide appropriate habitat for growth of plants, and resist erosion.

Beeskow et al. (1995) used gradient analysis to study soil degradation for grasslands of Patagonia, Argentina. They reported on changes in the vegetation and soil surface along a grazing intensity gradient and documented 3 stages of range deterioration from a grass steppe to shrub steppe. Blackburn (1975) studied the relationship of soil infiltration and erosion as measured by sediment production on 28 different sagebrush plant communities in central and eastern Nevada. He reported that for sagebrush sites, higher erosion was associated with lowered rates of infiltration and poor soil aggregate structure. We did not measure erosion in our study, however, there were significant differences in rates of infiltration between States I, II, and III (Table 2). These differences occurred without significant differences in soil textures among states. Sieve analyses of soils indicated that grain size distributions were similar among States I, II, and III, therefore, hydraulic conductivity and rates of infiltration should be similar among these groups. However, in States II and III, soil compaction was associated with lower rates of infiltration apparently reflecting changes in infiltration along a gradient of site degradation. Spaeth et al. (1996) reported that the use of plant species biomass improved infiltration prediction. In our study, rates of infiltration increased as biomass on the site increased (Table 2).

States and Transitions

Cover data were categorized into 3 groups (Fig. 3), using the results from canonical correspondence analysis (CCA) (Table 2). Each group represented a plant physiognomy that was identifiable in the field. These physiognomic classifications may be viewed as stable states of the state and transition concept of Westoby et al. (1989) (Fig. 3). Transitions between states can occur following changes in soil moisture due to changes in water table or to management practices. Since soil moisture and water table levels were approximately the same for all sites within this ecological type, these factors were considered not as important as management practices in causing the vegetation and site degradation we observed. Classifying ecological types, as was done in this study, allows for the environment and productive capabilities to be held relatively constant while studying changes in condition.



DOMINANT PLANT SPECIES

Nevada bluegrass	Slender wheatgrass	Nevada bluegrass
Slender wheatgrass	Iris	Iris
Mat muhly	Yarrow	Basin big sagebrush

DOMINANT VEGETATION AND SOIL CONDITIONS

High basal cover	Moderate basal cover	Low basal cover
High forage production	Moderate production	Low production
High infiltration	Moderate to low infiltration	Moderate to low infiltration

Transitions

T - 1: Reduced grazing pressure. Improved soil conditions.
T - 2: Reduced herbaceous vigor by heavy grazing and/or lowered water table. Soil degradation.
T - 3: Fire or other shrub control technique. Improved soil conditions.
T - 4: Continued heavy grazing pressure and/or drop in water table. Soil degradation.
T - 5: Fire or other shrub control technique. Improvement in hydrologic conditions.

Fig. 3. State (S) and transition (T) diagram for the dry graminoid/Cryoboroll/trough drainway ecological type.

Site degradation, in the form of increased soil cover and an increase in the frequency of soil compaction, reduces perennial herbaceous vigor, reduces rates of infiltration, and appears to be a precursor for an increase in forb and shrub abundance in these graminoid meadows (transition 1). The 2 endpoints of the gradient were characterized by grasses with no shrub cover (State I) or a mixture of grasses, forbs, and shrubs (State III). The intermediate state represents a transition state with a mix of graminoids and forbs.

Some mountain big sagebrush and rabbitbrush seedlings were found in bare areas in State II. In contrast, no young plants were found in the graminoid-dominated sites. The increase in soil cover (Table 2) could explain the difference in shrub establishment between States I and II, and may be a principle factor in transition 3 (Fig. 3). Shrub control techniques as well as changes in livestock grazing might be used to encourage transition 5, the change from the grass/forb/shrub state (III) to the grass-dominated state (I). Currently it is not known what management options including grazing strategies would promote transition 2, the change from the grass/forb to the grass-dominated meadow state Although the different states (Fig. 3) might represent a successional pathway with grass-dominated meadows being the climax condition, it is not known whether the grass/forb/shrub state will change to a grass-dominated state following a decrease in the stocking rate or grazing exclusion. Management options such as brush control, reseeding, and other reclamation practices may be necessary if a rapid return to graminoid dominance is desired.

Conclusions

We were able to classify 6 meadow ecological types using a combination of classification by TWINSPAN analysis followed by discriminant analysis tests using site information. Ordination of plots using canonical correspondence analysis (CCA) of soil and landform data gave similar results. The 2 methods revealed distinct relationships between vegetation, landform, and soil factors in the study area. Variables associated with landscape position and substrate were the most highly correlated factors with both species distribution and sample distribution.

Direct gradient analysis in the form of CCA was used to determine a gradient of degradation within the dry graminoid/Cryoboroll/trough drainageway ecological type in central Nevada. Basal area cover of vegetation, production of 3 key grass species, and rates of infiltration were used as quantitative measures of the extent of ecosystem degradation. In this type, the main vegetation change associated with a gradient of degradation was the transformation of a grass-dominated into a grass/forb/shrub state. The grass/forb state represented a transition state represented a transition state between these 2 extremes. The invasion of forbs with low forage value into the graminoid meadow systems has decreased forage production. The invasion of shrubs, primarily basin big sagebrush and rabbitbrush, also has decreased forage production. Grass-dominated communities represented the most desirable state in terms of forage production, basal cover of vegetation and infiltration, while the grass/forb/shrub communities represented the least productive and most degraded state.

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COMMENT: Big sagebrush pro versus con

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Key Words: ***Artemisia tridentata*, nutritive value, forage value**

As a self-proclaimed defender of big sagebrush (*Artemisia tridentata* Nutt.), I am compelled to comment on the article by Ngugi et al. (1995) published in the *Journal of Range Management.*

My comments center on 2 points: bias in the literature review and the methods used to conduct the experiment.

In my opinion their use of the literature was biased. For example, they stated: "However, the nutritive value of most sagebrush species, including mountain big sagebrush, is still uncertain because of deleterious effects of substances in sagebrush on digestibility (Johnson et al. 1976)." A puzzling statement because the Johnson et al. (1976) study had nothing to do with digestibility. Their concerns were, and I quote from their highlight: "Big sagebrush (*Artemisia tridentata*) fed to sheep by stomach pump to study its abortifacient properties during the 2nd trimester of pregnancy produced no reproductive difficulties. However, big sagebrush was lethal when 3/4 lb was fed by this method daily for 1, 2, or 3 days. Sagebrush fed 1/4 lb daily and slowly increased to 3/4 lb daily was not toxic." The Johnson et al. (1976) study illustrates the problems that can be encountered when domestic sheep are force-fed ground big sagebrush tissues without a proper adjustment period.

It takes 16 to 20 weeks for sage grouse chicks—an animal that co-evolved with and is a true obligate to big sagebrush—to reach the fall season big sagebrush diet level (66% to 95%) of adults (Braun et al. 1977, Klebenow and Gray 1968, Leach and Hensley 1954, Patterson 1952, Peterson 1970, Rasmussen and Griner 1938, Wallestad et al. 1975). Big sagebrush makes up about 15% of the diet of 10-week-old sage grouse chicks (Braun et al. 1977, Klebenow and Gray 1968, Patterson 1952, Peterson 1970, Rasmussen and Griner 1938). If it takes 16 to 20 weeks for sage grouse to adjust to big sagebrush, why do humans think they can force adjustments on a caged animal—such as sheep that did not co-evolve with big sagebrush—in a few days (Daniel et al. 1993, Holechek et al. 1989, Laycock 1978)?

Another statement by Ngugi et al. (1995) appears biased: "However, the relationship between in vivo digestibility and in vitro digestibility for big sagebrush needs additional study. Of the 13 forages subjected to both in vivo and in vitro digestibility trials for mule deer by Urness et al. (1977), big sagebrush was the only forage for which in vitro digestibility (62%) exceeded in vivo digestibility (54%)" (p. 489). The authors would like the readers to infer that somehow in vitro digestion makes big sagebrush look better than it really is. What they quoted is true. What they did not point out was that the Smith et al. (1966) study, also cited by them, showed just the opposite—40% in vitro digestion versus 55% in vivo digestion.

Another point, if the in vivo digestibilities of the 13 forage samples of the Urness et al. (1977) study were arranged in an array from highest to lowest, big sagebrush would be—**fifth.** Filaree (*Erodium cicutarium* (L.) L'Her., **spring** whole plant, 67%), curl-leaf mahogany (*Cercocarpus ledifolius* Nutt. ex Torr. & Gray, **winter** twigs and leaves, 64%), mesquite (*Prosopis juliflora* Torr., **fruit** 60%), and desert ceanothus (*Ceanothus greggii* Gray, **leaves** 55%) are the 4 forage samples out of 13 that exceeded in vivo digestion of big sagebrush **winter** leaves and stems. Big sagebrush exceeded 8 of 13 forage samples. So, 54% in vivo dry matter digestion of sagebrush winter leaves and stems is good compared to other forages.

In addition, it could be possible that the in vivo techniques used by Ngugi et al. (1995) underestimated the value of big sagebrush as a forage plant.

Again, Ngugi et al. (1995) stated: "Big sagebrush also contains highly lignified, indigestible cell walls, surrounding a large and relatively digestible fraction of cell solubles (Kufeld et al. 1981)" (p. 489). The content of big sagebrush lignin in Kufeld et al. (1981) was 12% compared to 24% in Gamble oak (*Quercus gambelii* Nutt.). Lignin content of other forages that exceed big sagebrush are: 13% timothy hay (*Phleum pratense* L.) sun cured very mature; 14% smooth brome hay (*Bromus inermis* Leyss.) mature; 15% crested wheatgrass (*Agropyron desertorum* (L.) Gartn.) early bloom; 17% bluestem wheatgrass (*A. smithii* Rydb.) forage very mature; 21% snowberry (*Symphoricarpos* spp.); 13% shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.) dormant; and 13% red clover (*Trifolium pratense* Steb. & Sch.) hay (National Research Council 1958, 1964). Are there forages that contain less than 12% lignin? Absolutely! So what's the point? The point is those who dislike big sagebrush will point out the weaknesses and those who like big sagebrush the strengths. Who is right? Both are!

Yes, big sagebrush tissues contain substances that have anticellulolytic properties, but they also have large, highly digestible amounts of cellular content. Several studies have demonstrated the loss of essential or volatile oils from ingesta of a number of animals (Cluff et al. 1982, Foley et al. 1987, Narjisse 1981, Welch et al. 1989, White et al. 1982). Yet, Ngugi et al. (1995) have totally ignored these mitigating factors. Hobbs et al. (1986)—cited by Ngugi et al. (1995)—suggested another mitigating factor. Van Soest (1994) states: "Some plants high in essential oils—for example, sagebrush (*Artemisia*)—are known to possess anticellulolytic principles, but browsing ruminants can adapt

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and detoxify these compounds."

In addition to bias in their literature review, I believe that the methods and materials used to conduct the experiment were biased against big sagebrush. These methods and materials were the use of big sagebrush leaves (p. 487), grinding of the sagebrush tissues (p. 487), and use of mature grass (p. 478).

Leaves contain higher levels of essential or volatile oils than leaves and stems, or stems alone. Feeding leaves alone would expose the consuming animal to a greater concentration of essential or volatile oils than a mixture of leaves and stems. Domestic sheep I have watched feeding on big sagebrush consumed both leaves and stems, just as do native shrubland animals such as pronghorn antelope (*Antilocapra americana*), mule deer (*Odocoileus hemionus hemionus*), etc. Wintering sage grouse (*Centrocercus urophasianus*) is the only animal I know of whose diet consists of nearly 100% big sagebrush leaves (Patterson 1952). Ironically, this occurs at a time (winter) when they are gaining weight (Patterson 1952, Beck and Braun 1978). Of course, sage grouse are not ruminants but do depend on microbes in their cecum for digestion of cellulose (Leopold 1953).

Grinding of big sagebrush tissues releases greater amounts of essential or volatile oils faster than normal bite sizes. This release could intensify the adverse effects of essential or volatile oils beyond the real world. Smith et al. (1966), however, when they ground sagebrush tissues for their in vivo digestion trials, reported: "The addition of sagebrush by mechanical means in Trial 3 did not result in lowered digestibility values, indicating that lambs utilized sagebrush quite satisfactorily as one-half of their diet." So, we have 2 in vivo digestion studies—Ngugi et al. (1995), and Smith et al. (1966)—that ground sagebrush tissues but came to opposite conclusions. Who's right? The answer is as variable as populations of mountain big sagebrush, as variable as the feeding experiences of the test animals, and as variable as the manners/conditions in which the materials were prepared and handled by the experimenters.

A final point: The objective of the Ngugi et al. (1995) study was to determine the effects of big sagebrush on grass digestion. Question: How much mature grass do wintering animals of western shrublands such as mule deer, pronghorn antelope, sage grouse, pygmy rabbits (*Brachylagus idahoensis*), etc. consume? Not much (Wallmo 1981, Smith and Beale 1980, Patterson 1952, Green and Flinders 1980).

To answer the question posed by Bastian et al. (1995) in their title, "How much sagebrush is too much," depends on if you are grazing livestock on western shrublands or one of many organisms such as sage grouse that depend on big sagebrush for their very existence.

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J. Range Manage.
50:324–325

Rebuttal for comment: Big sagebrush pro vs con

F.C. HINDS

I am writing in response to comments made by Bruce L. Welch regarding a paper published in the *Journal of Range Management* titled "Mountain big sagebrush browse decreases dry matter intake digestibility, and nutritive quality of sheep diets" by Ngugi, et. al. 1995. Vol. 48, Number 6 pages 487–497. Dr. Welch expresses 2 concerns: 1) bias in the literature review and 2) the methods used to conduct the research.

Regarding the first concern, to suggest the review of literature was biased is affectation. However, to say the review of literature was incomplete is no doubt Dr. Welch's feeling. I would challenge any author, Dr. Welch included, when writing for a scientific journal, except a review article, to compose a review of literature, with the space restraints imposed by policy, totally satisfactory to all readers. I too find manuscripts lacking references I would prefer to see cited but I wasn't the reviewer of the manuscript prior to publication. Finally, I can assure Dr. Welch there was no bias in selecting the literature to be cited and regret we did not include references he feels are important.

Most of Dr. Welch's concerns relate to the procedures used in conducting the research such as 1) animal adaptation to sagebrush, 2) the agreement or lack of agreement between in vivo and in vitro results, 3) the relative amount of lignin in plants, 4) the loss of volatiles during prehension, mastication and possibly other as yet unknown physiological process, 5) the use of leaves in the research, 6) the grinding of leaves prior to feeding and 7) the use of mature grass hay as a basal diet. I will discuss each of the foregoing and in some cases refer the reader to the manuscript where a rational has been discussed.

1) There is no question mammals adapt to changes in diet and, as in the ruminant, changes in diet generally require a change in the microbial population in the digestive tract. The lambs used were born and reared to weaning on a sagebrush-short grass range and might, although doubtful, have consumed sagebrush. We had a limited supply of sagebrush leaves and twig tips and, unfortunately, were not able to provide the lambs with an extended adaptation period. This was a considered decision taking into account the length of the feeding period, the levels of sagebrush to be fed, the number of lambs and how long an adaptation period could be needed. Yes, our decision was to shorten the adaptation period, a decision we at the time wished we didn't need to make but did. Since that time a study (unpublished at this time) using in vitro procedures and administering sagebrush leaves via rumen cannula for 32 consecutive days was conducted. Also, research on the amount of essential oil from 2 sources of big sagebrush necessary to influence an in vitro formentation was conducted.

2) The relationship between in vivo and in vitro results using similar substrates and inoculum can be rather varied. However, the data from our in vivo study suggested a strong influence of sagebrush on dry matter digestibility of the diet fed lambs. Thus, we chose to move to in vitro studies to evaluate the influence of sagebrush per se and the extracted essential oils on dry matter disappearance. Initial studies, using from 0–30% of the substrate dry matter as sagebrush, did not produce a depression in in vitro dry matter disappearance. Thus the statement by Ngugi et al. (1995). "However, the relationship between in vivo digestibility and in vitro digestibility for big sagebrush needs additional study." Subsequent research using extracted oil demonstrated oil added to in vitro systems equivalent to that found if 60% of the substrate dry matter were sagebrush was necessary to cause a depression in microbial activity measured as gas production. Why levels of sagebrush in in vitro systems don't produce results similar to the same levels in vivo raises many questions, a few of which Dr. Welch mentions.

The "adaptation" study previously mentioned produced results similar to the other in vitro study—no apparent influence of 32 days of adaptation on the ability of inoculum to influence in vitro dry matter disappearance. This in retrospect should not be surprising considering the results of the in vitro research using various levels of added oils.

3) Dr. Welch is concerned about the mention of sagebrush having "highly lignified, indigestible cell walls...". This is merely a matter of reference since leaves from many plants (alfalfa, clovers, and many forbes) contain relatively little lignin. Mentioning lignin in sagebrush was not, as implied by Dr. Welch, an attempt to denigrate sagebrush but was simply a statement of what we and others have found.

4) The loss of volatiles during prehension, mastication and other physiological processes is a very interesting and important area of research we discussed in detail. We have considered many possible modes for this to occur but, unfortiantely, it is hard to explain our in vivo results using several of the mitigating adaptive adjustments suggested by Dr. Welch. We, in our research, had no evidence of adaptation. This is not to say some species have, through time developed adaptive mechanisms that allow them to consume sagebrush with little or no negative impact.

5) The use of leaves and twig tips in our research was simply a matter of being able to obtain this material readily and further it was felt this was a reasonable representation of what sheep would consume, especially during periods when snow cover prevented exposure to most other forms of vegetation.

6) As mentioned in the paper, sagebrush was ground while frozen in a pre-chilled wiley mill to make it difficult for sheep to be highly selective when receiving a ground hay basal diet. The procedure used to grind the sagebrush is commonly used to reduce particle size of fresh material containing volatile compounds (a good example is silage). Again, this is not to say some small amount of the volatiles are not lost. Some volatiles, albeit small amounts, may be lost but the extracted oil used in our research and estimates of amounts found in our sagebrush were obtained from samples ground while frozen.

7) Lastly, Dr. Welch expressed concern over the use of "mature grass" as the basic diet in our research. He asks "How much

mature grass do wintering animals of western rangelands such as mule deer, pronghorn antelope, sage grouse, pygmy rabbits, etc. consume?" First, Dr. Welch may have lost sight of the fact we were studying sheep. Our concern is what happens when snow covers most vegetation other than sagebrush and sheep move from consuming cured-in-the-stand grass to sagebrush to meet their daily dietary needs. At least in Wyoming this is not uncommon. Secondly, we were not proposing our research should in any way be applicable to non-domestic rangeland mammals, although Dr. Ngugi, in the review of literature in his dissertation, does address estimates of intakes of sagebrush by season of the year for several species of wildlife.

Finally, I believe as scientists we must be objective in our approach to solving problems and answering questions. On several occasions my colleagues and I are referred to as being biased and on more than one occasion, through innuendo, we are implied to be opponents of big sagebrush and "attack" sagebrush. On the other hand the commentator states "As a self-proclaimed defender of big sagebrush....". My colleagues and I in no way intended our work as an attack on sagebrush nor does it represent a bias on our part. I guess in the final analysis the comments represent one person's opinions and hopeful the reader will take the manuscript for what it is—a report of research results several scientists felt should be shared with others. (Although there are several errors in the comments the one that is most confusing to the unsuspecting readers is where I presume Dr. Welch meant Ngugi et al. (1995) but said Nagagi et al. (1995).

J. Range Manage.
50:326–328

Viewpoint: The importance of range science to federal grazing policy

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Abstract

The value of science to policy design is questioned by many, including political scientists. Critics view scientific expertise as subject to monopolization by an elite technocracy; a process with antidemocratic consequences. Science has been influential in the development of federal grazing policy by creating the Clementsian paradigm, by affecting the policy agenda, and by defining terms of discussion. Science has been less influential in the implementation of grazing policy. In contrast with many policy issues, science is important to sound grazing policy, because western rangelands are isolated from the thought process of the general public by geographic, demographic, and temporal features. In America, good policy is that which solves important problems and fosters democracy. Democratic forums in which grazing policies are born are enlightened by the disciplined competency of science. More than any other form of knowing, science represents concentrated, devoted study of a topic. Range science should provide the basis of public information and opinion that is converted, via the political process, into federal grazing policy.

Key Words: expertise, history, technocracy

In the policy arena, science is a two-edged sword. It can help to slice through the pluralism that has long reduced public policy to the perpetual "muddling through" that Lindblom aptly described (1959) and documented periodically since (1979, 1988). Scientific management has been extolled at least since the Progressive movement that ushered in the 20th century (Knott and Miller 1987). Science has transcended its application to management, however, and has carved out a large niche in public policy itself (Quade 1982, Brewer and deLeon 1983). At its worst, science can excise much of the public participation by which democracy is served (Dryzek 1990).

Once widely viewed as a panacea for policy problems, the scientific perspective is increasingly viewed as the problem itself, creating a communication gap between the policy arena and the public, and a dependence of policy makers on technical expertise rather than public preference (Fischer 1990). The German sociologist, Max Weber, predicted as much while observing the Progressive buildup a century ago, and even foresaw a subservience of politicians to scientists (Weber 1978). Of the dependence of policy makers on technical experts, Barnes and Edge (1982:233) said, "It is hard to exaggerate the practical importance of this problem. It pervades whole areas of policy... the list is endless." If that were strictly true, then grazing policy would be included. My viewpoint addresses 2 questions: 1) In the arena of federal grazing policy, how well entrenched is range science? 2) Is the scientific perspective helpful or harmful in the design of grazing policy?

To answer the first question, I will employ a scheme recently developed by Schneider and Ingram (in press). Schneider and Ingram envisioned the amount of scientific influence on policy design to fall along a spectrum from "no influence" to "complete control of all phases of design".

The second question is impossible to answer without specifying the evaluation criteria. American public policy should solve problems in an efficient manner while fostering democracy (Ingram and Smith 1993). (Democracy is "...a means of selecting policy makers and of organizing government to ensure that policy represents and responds to the public's preferences [Lineberry 1980:33].") A phenomenon, the scientific perspective in this case, should be defined as "helpful" in the formulation and implementation of policy when it contributes to both of these ends, or at least to one without hindering the other. In other words, the impact of range science on grazing policy will not be evaluated from a purely scientific perspective, because such an evaluation would be guilty of begging the question. Heeding the civic-minded exhortations of Ingram and Smith (1993), the merits of range science will be evaluated in more holistic terms.

Historical Overview of Range Science

Arthur W. Sampson (1923) wrote the first range management textbook, and established the Clementsian view of plant succession as the ecological paradigm of the range management profession. In this view (Clements 1916), vegetation is seen in terms of community stability, with disturbance (e.g., grazing) causing an interruption in a community's succession to its naturally stabilized, or "climax", state. When Dyksterhuis (1949) published a paper detailing the use of the climax concept in evaluating the condition and trend of rangelands, it "resulted in the institutionalization of the concept as national policy for dealing with rangeland resources" (Johnson and Mayeux 1992:323). Although Clementsian succession may have been abandoned by increasing numbers of plant ecologists during the post Dust Bowl decades, "All major inventory and classification methods in use today are

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modifications of that basic [Clementsian] concept" (National Research Council 1994:61).

The Clementsian paradigm was early and frequently challenged by plant ecologists, beginning with the individualistic concept of plant associations (Gleason 1926). Criticisms center around the lack of evidence for ecosystem stability, the evidence for "natural" plant invasions, and stochastic processes in the organization of plant communities (Johnson and Mayeux 1992). Due to the policy implications, the argument has intensified in recent years. The Clementsian paradigm encourages range reformists to rail against the conversion of plant communities by overgrazing, while critics argue that nature would do the same thing, if on a different time scale.

The Influence of Range Science in Grazing Policy

The amount of influence that range science has held over grazing policy is a bit paradoxical. Apparently regardless of which theory is in vogue, range scientist Herman Mayeux believes that,"The accepted theory of vegetation dynamics and ecosystem function strongly influences public policy and law in essentially all matters concerning our environment, and the efficacy of such policy and law depends on whether or not the theory is a [sic] fundamentally sound" (Johnson and Mayeux 1992; 323). Yet, political scientists have usually attributed the design of grazing policy to pluralistic politics (e.g., Foss 1960, Clarke and McCool 1996), and forest and range policy specialists Cubbage et al. (1993) consider the Bureau of Land Management (BLM) to be a textbook example of agency capture.

Perhaps these observers are considering different portions of the aforementioned policy influence spectrum, rather than the entire spectrum. In preparing their manuscript, Schneider and Ingram (in press) scored the amount of influence that science has on a policy as 2 if it contributes to the formulation of policy alternatives, 4 if it modifies policy specifications during implementation, 6 if it provides the underlying rationale for policy design and implementation, 8 if it defines the issues and related terminology, and 10 if it completely controls the policy arena.

Under this scheme, range science should be given credit for about 5 or 6 total points. This is not quite the same as saying that the position of range science on the spectrum is 5 or 6.[1] Considering the elements separately, surely range science gets 2 points for contributing to the formulation of policy alternatives, and for providing underlying rationale (especially the Clementsian paradigm) for policy design and implementation. Range science has to some extent defined the issues (e.g., value of native vs. exotic species), too. On the other hand, due to agency capture, it has not been historically dominant in the implementation of policy on BLM lands, and has been quite powerless in the political contests of the policy arena (Foss 1960, Cawley 1993).

By comparison, scientific expertise has been credited with far more influence in other natural resource policy arenas. Perhaps the best example is endangered species policy. The Endangered Species Act of 1973 (16 U.S.C. 1531-1544) has been called "...one of the most sweeping pieces of prohibitive policy to be enacted..." (Yaffee 1982:13), and wildlife scientists are clearly responsible for much of its origins, rationale, and implementation. By some accounts, the scientific expertise involved in endangered species management would score a 10 in the Schneider and Ingram system; Mann and Plummer (1995:220) thought the Endangered Species Act "...ended up turning... wildlife biologists into ecological mandarins, deciding the fate of resentful communities."

Even in policy arenas where scientific expertise is thought to be exceedingly powerful, however, critics are wary of moving too far in the other direction. They tend to acknowledge that expertise is required for sound decision making, and that purely politicized policies are no better than technocratically derived ones. Thus, continuing their discussion on the role of wildlife biologists in endangered species policy formulation, Mann and Plummer (1995:229) added, "...[Noah's] ark is not big enough, and no one is better equipped to decide which species, communities, and ecosystems are more necessary than others and how best to protect them."

Worth of a Scientific Perspective to Grazing Policy Design

Fischer (1990), Willard (1990), and Schneider and Ingram (in press), have outlined in generic terms the problems caused by a deference to scientific expertise in the design of policy. These problems include an unhealthy cessation of policy dialogue in the public sphere, potential for fallacious *argumentum ad verecundiam* (appeal to authority), public cynicism, and an undemocratic dependence of policy makers on technical expertise rather than public preference. As the above discussion suggests, however, and as Schneider and Ingram (in press) emphasize, each policy arena must be assessed within its socio-political context. Grazing policy stands out immediately for several reasons.

First, federal grazing policy is concerned with the activities on the public rangelands of 11 western states, while federal policy makers are accountable to a constituency with a majority residing in the East. Second, ranching is a rural occupation, while the overwhelming majority of citizens are urbanites. Third, the effects of grazing are to be measured in terms of ecological and geological time, while human society tends to operate on circadian, or, at the longest, corporate time. Each of these distinctions point to a greater-than-average importance of sound range science in policy design.

Recall that science is useful to policy when it solves problems in an efficient manner, as long as it does not hinder democracy. I propose 2 components to problem-solving capability on the western range; experience and education. It is highly unlikely that an easterner, or even a western urbanite, will have any range experience, and practically all citizens are isolated from the type of decision making that applies to geological time. The general public's problem-solving potential, then, is contingent upon education. Good candidates for providing that education are those that study the topic full time and are relatively accessible; i.e., range scientists and natural resource scientists in general.

Given that range science contributes to problem-solving capacity in the design of policy, does it then pass the test of promoting (or at least failing to hinder) democracy? A major criticism of technocracy is that it does not (Dryzek 1990, Fischer 1990). In the case of federal grazing policy, however, the same factors that

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[1] Schneider and Ingram recognized the difficulty of portraying scientific influence along a spectrum. They have replaced it with a table in which each element of influence is considered separately (A. Schneider, Arizona State Univ., pers. comm., 12 July 1996), as I have done.

enhance the worth of range science for problem solving do likewise for democracy.

Eastern and urban citizens are not eliminated from discursive democracy by range scientists. Policy makers, rather, have set the tone for the level of public participation in grazing policy debates. In a string of legislation that began with the National Environmental Policy Act (42 U.S.C. 4341-4347) and stretched to the Federal Land Policy and Management Act of 1976 (43 U.S.C. 1701-1784), Congress was explicit that there be planning efforts for the management of public natural resources, and that these efforts would formally incorporate public participation. For that reason, the Stockmen Advisory Boards that were created by the Taylor Grazing Act of 1934 (48 Stat. 1275) and were comprised entirely of ranchers, have been replaced by interdisciplinary committees that include interested citizens. In addition, BLM management plans are subject to public review periods which include the assembling of public hearings by the BLM. Congress has not been entirely unsuccessful in fostering democracy with these policy revisions.

What role does range science play in these public forums? As Fischer (1990) pessimistically points out, the scientific nature of a topic dissuades many citizens from entering the discourse. These citizens may feel inhibited by the intellectual and authoritative nature of such proceedings. What Fischer neglects to mention, however, is that citizens who do participate ask difficult, intelligent questions, and experts are often the only ones capable of postulating an answer. The loss of citizen participation caused by a scientific presence in the public forum is countered by the tendency of scientific expertise to turn a potentially incoherent argument into a more informed debate.

Conclusion

The role of science in policy design has been critically reviewed in recent times by political scientists, who focus on the pitfalls to democracy caused by the authority of expertise. Sometimes these criticisms neglect the other aspects of sound policy, but as Schneider and Ingram (in press) point out, good policy not only fosters democracy but solves important problems.

In the case of federal grazing policy, it appears that science has been relatively influential by creating the Clementsian paradigm, affecting the agenda, and defining terms, and less influential in terms of implementation. Range science should be credited with but a subset of this influence, however. Plant ecologists, wildlife biologists, foresters, and other natural resource scientists have contributed a large proportion of "range" science.

Science is a valuable component of sound grazing policy, because western rangelands are isolated from the thought process of the general citizenry by powerful geographic, demographic, and temporal features. The "ideal speech situation" of liberal democracy includes not only unconstrained discourse, but competency also (Habermas 1970). Some argue that science may not be the best form of knowing, in terms of policy formulation. More than any other form, however, science represents concentrated, devoted study of a topic. It is therefore the logical candidate to inform that considerable portion of the public that is interested in federal grazing policy.

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Book Reviews

Rhymes of a Rexall Wrangler. By Dick Hart. 1996. Bend Press, 3017 Kashiwa St., Torrance, California. Individual copies may be obtained by writing to the author at 7132 Cordova Drive, Cheyenne, Wyoming. 49 p. US$8.95 paper. ISBN 0-9643598-1-2.

I've never known quite how to take cowboy poets. Most of the hard-working cowboys and ranchers I've known are too tired at the end of the day to read something as intricate as poetry, let alone write it. And my impression is that most cowboy poets are alike—disguised artistic hams sporting big cowboy hats, lots of mustache wax, more than a trace of Western elitism, and polysyllabic enunciation especially in their ability to stretch the word *cowboy* into 6 syllables. But in opening Dick Hart's new book, one reads that he was born and raised in Iowa, sees no photographic trace of a cowboy hat, and realizes that his brush, although impressive, doesn't need much mustache wax. But wax poetic he does anyway in *Rhymes of a Rexall Wrangler*, a creative and entertaining collection of past and recent verse and prose drawing on Hart's creative talents as a range scientist, philosopher, dramatic artist, and poet.

Each of over 20 poems and 2 short pieces of prose is preceded by a brief, interesting introduction providing the reader with sufficient background to fully appreciate what follows. The works address diverse subjects, and include range science-oriented ones such as *Holism and Hydrology*, and *Herbage Meter Blues*. Those with low capacity for such jargonized meter may better appreciate *Buck and Pal*, and *The Ballad of 1-4-0*. Every flashlight farmer or rancher should relate to *The Most Expensive Cowboy in Wyoming*, and *Iceland is a Nice Land* and *Identity Crisis* are short, simple, and certainly worth mention. Of the 2 pieces of prose, *Ancestors* seems to provide a major unifying theme, especially when it is considered within the collective context of the biographical information, the author's introduction, and all of the book's other poetry and prose.

Attractive in format, *Rhymes of a Rexall Wrangler* features the artwork of the late Robert E. Jenkins on the front and back covers, and throughout the book. The style of the artwork varies somewhat, but the quality of some of the works, including the colored works on the front and rear covers, is excellent. These works effectively complement Hart's writings. In fact, the whole book has a sort of synergy about it in that all of its creative and slightly offbeat elements—the title, the biographical information, the author's leisurely introduction and background pieces, the poetry, the prose, the artwork—all curiously come together to give the book honest charm and first-book energy. Any sequel would be taxed to do as well.

Like any book, a book of cowboy poetry may be judged on many accounts, but it should, after all, be at least clever, entertaining, relevant, honest, and not excessively self-serving. *Rhymes of a Rexall Wrangler* succeeds in all these respects, but Hart's folksy honesty, and the book's relevance to a wide audience including range/ranch professionals, certainly help make his clever words more effective. The result is a collection of ultimately greater message and authenticity than those of some of his traditionally-accoutered poetic colleagues.

In fact, at a higher level, the real poetry of *Rhymes of a Rexall Wrangler* may be as a story of a man who knows where he's from, who he is, and who came to the Western Range to find a creative career or 2, a family life, a way of life, a home. Wyoming got not only a distinguished scientist/philosopher, but an artistic writer and cowboy poet as well. Now, if we could just figure a way to get some of the less well-versed, waxed-mustached, hams of the hat squad back to Iowa, so that they too might find a home, among all that corn.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

Dryland Forestry: Planning and Management. By Peter F. Ffolliott, Kenneth N. Brooks, Hans M. Gregersen, and Allen L. Lundgren. 1995. John Wiley & Sons, New York. 453 p. US$99.95 cloth. ISBN 0-471-54800-6.

Challenges of tree-growing in arid regions have been described as some of the most difficult facing world agriculture. Salinity, wind, cold and especially heat can badly compound dryness. Natural or planted in origin, sparsely wooded lands occupy the tougher environments of the U.S. Southwest, Latin America, interior Australia and Africa. Site remoteness or torridity hinder the relatively low number of investigators and extensionists tackling the challenge. They must try to grasp and augment a multilingual, partly "grey" literature lacking the size or cohesion of temperate-zone silviculture's.

This book is an authoritative, long-needed consolidation of this diffuse knowledge into an attractive volume. *Dryland Forestry* is at once undergraduate text, training manual and unique reference. The authors consider their title subject a discipline-cluster comprised of numerous indispensable fields. Range management is among them, mainly because such lands are readily penetrated by cattle, sheep, swine, and goats. Livestock often profoundly influence woody plant survival, productivity, and form. However, they and their tenders can play complementary roles in the diverse mix of realizable human benefits. And in many locales, arid-zone forestry is effectively *shrub* culture for fuel, charcoal, fodder, fruits, and other locally-used products. It might also be *community* (read village or ranching) as opposed to commercial forestry.

The book's list of Contents spans 12 pages in 5 parts. This reflects the authors' ambitious mission and their desire to be both comprehensive and informed in an intercontinental, multidisciplinary treatment of these lands. They have wisely emphasized breadth of coverage, at least touching on over 350 topics. Nonetheless, under Part IV are found special, in-depth expositions of agroforestry, rehabilitation of salt-afflicted landscapes, windbreaks and much more. The varied Literature Cited sections after each chapter will let the focused reader go further into subjects of concern.

Rich in context, the book is really a general, never oversimplistic primer on arid-land bioresources and watersheds. The authors are systems-oriented, long-term collaborators with decades of collective experience in utilization, hydrology, development planning, and economics. Ffolliott has pioneered in understanding and promotion of the vast semiarid woodlands of Arizona and adjacent Mexico. However, no undue favoritism is shown that area, whose circumstances are unique yet generally illustrative of firewood or other depletion crises. The writing is uniformly clear and undaunting. Typesetting, graphics, and binding bespeak top-notch editorial and production backing. Not quite a "handbook" in the lookup sense, *Dryland Forestry* has few tabular entries or standard values (e.g. site quality curves). Appendix 2 simply presents common tree species suited to particular adverse growing conditions. Not much in a quantitative vein is found throughout the book, but there are revealing data on yields under different input/protection scenarios. Tables, graphs, and boxed examples nicely support the text.

Dryland Forestry doesn't presume to advance a summary research agenda, but the authors note that a tremendous amount remains to be learned and usefully applied. Instead, they conclude with a discussion of extension's role in thoughtful forestry and in making rural people participatory stakeholders in durable projects. Much on the technical side is eased when pastoralists embrace the permanent values of trees to their livelihoods.—*Nicholas S. Van Pelt*, Salt Lake City, Utah.

Proceedings of the 1997 Juniper Symposium. Texas Agricultural Experiment Station, Technical Report 97-1. Texas Agricultural Experiment Station, Box 918, Sonora, Texas 76950-0918. US$10.00 paper.

Ashe juniper (*Juniperus ashei*) and redberry juniper (*Juniperus pinchotii*) are 2 species common to the Edwards Plateau and Rolling Plains of Texas. They are widely considered to be the most important species of brush affecting agriculture in these areas. Because of their tendency to dominate rangeland ecosystems, land managers are faced with the need to control or better manage them on areas that are suitable for the production of cattle, sheep, goats, and wildlife.

The 1997 Juniper Symposium updates and expands information presented in a 1994 symposium and ties together the history, ecology, taxonomy, physiology, control, and societal effects of juniper into one publication. The 23 articles, divided among 8 chapters present a well organized look at how juniper affects Texas rangeland. Most articles are well documented for those interested in additional reading.

Chapter one, *Environmental and Land Use Changes: A Long Term Perspective* examines vegetative and land use changes that have generally occurred during the last 300 years in Texas. Two maps show the current range of Ashe and redberry juniper in Texas and the text has a good discussion of factors that have contributed to the increase in woody vegetation in the Edwards Plateau and Rolling Plains of Texas.

Chapter 2, *Environmental and Economic Tradeoffs* considers the changes in vegetation more from an economic standpoint and discusses how land use practices affect and are affected by current economic conditions. It also considers the effects land use practices have on off-ranch consumers such as downstream users of water. More and more the practices used by landowners are having far reaching effects and these need to be taken into consideration when making management decisions.

Chapter 3, *Biology, Ecology and Ecophysiology of Juniper* contains 4 articles. Topics include seed rain, seed dispersal, germination rates and viability, leaf area, transpiration and photosynthetic rates, carbon gain, growth forms, effects of browsing and the interaction of juniper with herbaceous plants. Very good background information is provided.

Chapter 4, *Holistic Perspective, Rangeland Hydrology and Wildlife Considerations* presents an alternative view of the historical distribution of juniper in Texas, explores the effects of juniper removal on rangeland hydrology and discusses the endangered species act, wildlife and their use of juniper, and compromises that must be made between wildlife and livestock production.

Chapter 5, *Juniper Control and Management* is the largest section, containing 7 articles. This is understandable since much of the past and present research on juniper in Texas has been directed towards juniper control. Chemical and mechanical treatments, fire, and browsing by herbivores are discussed. The age of complete plant eradication is past and this chapter reflects the attitude that effective control can be cost effective and a complement to other activities on the land.

I found Chapter 6, *The Economics of Juniper Control* the most difficult to follow, although this may simply be a reflection of my knowledge of economics. The 2 articles were technical, and although presented useful information, were not very reader friendly. This is unfortunate since these days good juniper management is dependent upon good financial management.

Articles in Chapter 7, *Interactions Between Grazing, Fire, Weather and Juniper* explore the possibility of selective breeding to develop animals better able to deal with the toxic elements in juniper. Also, the basic biochemistry of juniper is covered. Management practices which have shown to be effective in juniper control and the interaction of these practices with prescribed fire under different scenarios are discussed. The final paper in this chapter points out the long-term effects of grazing, fire, and weather on juniper. The articles in this chapter affirm that there is clearly a cause and effect relationship when it comes to juniper management and it is important to consider the many possible directions a practice may take the ecosystem.

The final chapter, *Commercial Uses and Policy Issues and Options* is an upbeat ending to the book. The management of juniper does have a positive side. There are commercial products from the plant and these products have the potential to be turned into a profit by the land manager. Also, it is made clear that management of juniper goes way beyond the bounds of the land itself. Land managers must consider downstream water users, urban populations and endangered species when planning management practices.

Whether you are planning a large scale control operation, thinning a small cedar break or are just interested in how juniper affects the animals that eat it, this book may provide the information you need. For the most part well written and easy to understand, it provides a wealth of information for anyone interested in juniper management and ecology.—*Nick Garza*, Texas Agricultural Experiment Station, Sonora, Texas.

The Ecology of Woodland Creation. Edited by Richard Ferris-Kaan. 1995. John Wiley & Sons Ltd., Chichester, West Sussex, England. 244 p. US$75.00 hardbound. ISBN 0-471-95484-5.

The establishment of woodland plant communities on lands where such vegetation has not existed and the re-establishment of historic woodlands is of great interest to many. *The Ecology of Woodland Creation* is a compilation of papers which were originally presented at the British Ecological Society's Forest Ecology Group Symposium *Ecological Aspects of the Creation of New Broadleaved Woodland* as well as some additional material. The emphasis in this book is on the re-establishment of native woodland in Britain with some limited attention paid to activities in the eastern United States. While workers outside Britain might be disinclined to review *The Ecology of Woodland Creation*, they would do so at a loss, for the book presents a plethora of ideas worthy of consideration in many 'reclamation' efforts.

Editor Ferris-Kaan has arranged the papers into 14 chapters presented in a logical order. Beginning with a chapter entitled *To What Extent Can We Recreate Woodland*, the text moves through discussions on planning new woodlands for specific purposes and needs, woodlands in the landscape, plant distribution and the design of woodlands, and vegetation classification as a tool to further woodland creation. Following this background or introductory material, 2 chapters address soils and soil biota. A chapter regarding establishment of woodland by seeding or planting (of seedlings or cuttings) discusses and evaluates these 2 approaches to afforestation and reforestation. *Introduction of Plants and Manipulation of Field Layer Vegetation* presents results of experimentation and large scale establishment trials. Four chapters discuss animal populations and their functions in woodland creation. In the concluding paper, Ferris-Kaan integrates the material presented in the preceding papers in a practical sequence of activity involved in creating new woodland.

Of considerable value is that the papers presented do not focus solely upon techniques (e.g. dig a small hole...) but rather, as the title suggests, emphasize the ecological aspects of establishment of trees and associated vegetation in efforts to create woodlands. Techniques, however, are not ignored, but rather placed in an appropriate context. Indeed, the author of one of the papers recounts a 17th Century recommendation which would certainly be of interest to those working in California's Integrated Hardwood Program:

> *Sow acrones, ye owners that timber do love*
> *So hay and rie with them, the better to prove*
> *If cattle or coney may enter the crop*
> *Young oak is in danger of losing his top (!)*

The findings of experimentation and experience presented are useful in reclamation and restoration planning efforts. As a reclamation planner and practitioner I found *The Ecology of Woodland Creation* to be an interesting and useful book. Indeed, some of the concepts presented have found their way into a recent revision of the reclamation plan for a minesite in Washington! However, as most of us who work directly with natural systems have learned, we should always keep in mind the opening sentence of J.W. Spencer's paper, that "Any habitat creation project, but especially any woodland habitat creation project, is destined to mature in ways unforeseen by its planners."—*Jeff S. White*, Battle Mountain Gold Company, Oroville, Washington.