Targeted Grazing of White Locoweed: Short-Term Effects of Herbivory Regime on Vegetation and Sheep

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Abstract

White locoweed (*Oxytropis sericea* Nuttall) and nontarget vegetation response to 2 yr of targeted grazing by sheep, one treatment of picloram plus 2, 4-D (HER) or no treatment (CON) were compared. Serum of sheep that grazed locoweed intermittently (IGZ, 5 d on locoweed followed by 3 d off locoweed) vs. counterparts that grazed locoweed continuously for 24 d (CGZ) was also examined. Alkaloid toxicity was inferred by serum levels of thyroxine (T4), triiodothyronine (T3), alkaline phosphatase (ALKP), aspartate aminotransferase (AST), and swainsonine, as well as behavior and body weight gains. Three sites were used in a randomized complete block design. IGZ, CGZ, and HER treatments reduced locoweed density ($P < 0.01$), canopy cover ($P < 0.01$), number of flower stalks (IGZ: $P = 0.02$, CGZ and HER: $P = 0.01$), and plant size ($P < 0.01$). White locoweed seed density in the soil seed bank was not reduced with grazing, and nontarget vegetation was mostly unaffected by treatments. Grass canopy cover increased in grazed and herbicide plots throughout the study (IGZ: $P = 0.03$, CGZ and HER: $P < 0.01$). Percentage bare ground was unchanged (IGZ: $P = 0.46$, CGZ: $P = 0.44$) in grazed plots but decreased ($P = 0.03$) in HER plots. After 24 d, ewes in the IGZ treatment had lower levels of serum ALKP ($P < 0.01$) and AST ($P = 0.02$) and marginally lower swainsonine levels ($P < 0.07$) than CGZ ewes that tended to exhibit lower serum T3 ($P < 0.07$) and similar serum T4 ($P = 0.25$) levels. Time spent feeding on locoweed tended to differ ($P = 0.06$) between treatments. Body weight gain was the same ($P = 0.19$) regardless of treatment. IGZ of locoweed-infested rangeland with sheep may be a viable short-term means of reducing locoweed density without detrimentally affecting animal health.

Key Words: biological control, prescribed grazing, seed bank, swainsonine, toxic plants

INTRODUCTION

Targeted grazing (TG), defined as the "application of a specific kind of livestock at a determined season, duration, and intensity to accomplish vegetation or landscape goals" (Launchbaugh and Walker 2006), has been used successfully to control a wide variety of invasive plants. Diffuse (*Centaurea diffusa* Lam.), Russian (*Acroptilon repens* [L.] DC.), and spotted (*Centaurea stoebe* L.) knapweed, kudzu (*Pueraria montana* [Lour.] Merr.), musk thistle (*Carduus nutans* L.), yellow starthistle (*Centaurea solstitialis* L.), blackberry (*Rubus* spp.), juniper (*Juniperus* spp.), and cheatgrass (*Bromus tectorum* L.) are a few examples (Wilson et al. 2006). Sheep (*Ovis aries*) are often the livestock species used in TG programs, particularly if the target plants are forbs, as their rumen to body volume ratio make forbs their most preferred

plant functional group (Demment 1982; Hanley 1982). Sheep have been used successfully to decrease larkspur (*Delphinium barbeyi* [Huth] Huth), an alkaloid-synthesizing forb, for a season because they are more resistant to its toxins than cattle (Olsen 1978). By grazing sheep prior to cattle in larkspur-infested (*D. glaucescens* Wats) pastures, subsequent larkspur use by cows was reduced by 43–93% (Ralphs and Olsen 1992).

White locoweed (*Oxytropis sericea* Nuttall) is a common alkaloid-synthesizing toxic rangeland legume that is responsible for substantial economic losses to the livestock industry in western North America (Nielsen 1978; Torell et al. 2000). Relatively little is known about the efficacy of biological methods to suppress locoweed compared with more traditional chemical control techniques (McDaniel et al. 2007). The effectiveness of TG or severe defoliation in killing or decreasing vigor of locoweed plants is unknown. Most research has investigated methods to prevent locoweed grazing by livestock because it contains swainsonine, an indolizidine alkaloid (Molyneux and James 1982; Molyneux et al. 1999) that has negative effects on reproduction (James et al. 1967; James and Van Kampen 1971; McIlwraith and James 1982; Panter and James 1989; Ralphs et al. 1994b; Ortiz et al. 1997), weight gains (Stegelmeier et al. 1999a; Ralphs et al. 2000), and behavior (Panter et al. 1999; Pfister et al. 2006a, 2006b) of all classes of livestock (Molyneux et al. 1985; Stegelmeier et al. 2007).

Although sheep are susceptible to alkaloid intoxication if ingestion of white locoweed occurs continuously for 30 d at levels as low as 3% of their diet (James et al. 1967; Stegelmeier et al. 1995, 1999a, 2007), little is known about how animals are affected by intermittent grazing of locoweed-infested pastures. When sheep consume levels of swainsonine known to cause lesions, the distribution and extent of lesions do not increase with a higher toxin dose, suggesting that there is a threshold response to swainsonine ingestion (Stegelmeier et al. 1999a). Rapid recovery of animals receiving high concentrations of swainsonine for short periods of time has been reported (Stegelmeier et al. 1998, 2004). Furthermore, there is anecdotal evidence (James et al. 1986) as well as research results that suggest that an intermittent grazing regime may provide a way of preventing intoxication associated with white locoweed ingestion (Pfister et al. 1996; Stegelmeier et al. 1999b; Obeidat et al. 2005; Ashley et al. 2006). Because swainsonine exhibits rapid blood clearance rates, intermittent grazing of white locoweed may be an effective means of controlling this undesired plant while avoiding the intoxication of grazers.

The main objective of this study was to evaluate the influence of 2 yr of TG by sheep on the survival and reproductive vigor of white locoweed plants. The efficacy of TG was assessed by comparing it to a proven chemical control method (positive control) and to untreated, infested rangeland (negative control). The hypotheses tested were that 1) TG with sheep for two consecutive years would reduce locoweed abundance (including seed bank abundance of locoweed seeds) and that its efficacy would be intermediate compared to untreated and chemically treated rangeland, 2) abundance of grasses and other forbs would not be negatively affected by the TG prescription, and 3) intermittent and continuous TG for two consecutive years would affect locoweed abundance similarly. A secondary objective of this study was to evaluate the influence of intermittent TG prescriptions of white locoweed on serum constituents, grazing behavior, and body weight gains of sheep. The hypotheses tested were that sheep grazing locoweed-infested plots intermittently would have 1) lower serum swainsonine concentrations, 2) lower serum alkaline phosphatase [ALKP] and aspartate aminotransferase [AST] levels, 3) higher serum triiodothyronine [T3] and thyroxine [T4] levels, 4) similar foraging behavior, and 5) similar body-weight gains as sheep that grazed locoweed-infested plots continuously.

METHODS

Study Sites
The study was conducted on three ranches in Union County, New Mexico, during May and June 2009 and 2010. Sites were selected for their similar white locoweed densities and equidistance from water (< 0.4 km). Mean annual, spring, and summer precipitation for this area are 408, 114, and 239 mm respectively, based on approximately 12 yr of records from the National Weather Service Cooperative Observation station in Capulin, New Mexico (lat 36°44′N, long 103°59′W) ([NOAA] National Oceanic and Aeronautic Administration 2010). Spring (January through May) precipitation was 81 mm (dry)

and 212 mm (wet) for 2009 and 2010, respectively, while summer (June through September) precipitation was 242 mm (average) and 167 mm (dry) for each of the two study years, respectively. The 2 yr following the study were also dry with mean annual precipitation of 345 mm (2011) and 267 mm (2012).

The first site was located on Archuleta Ranch, 1.48 km southwest of Des Moines, New Mexico (lat 36°45′12.43″N, long 103°51′00.99″W) at an elevation of 2062 m above sea level. It had a moderate slope with northern exposure and the soils consisted of cobbly loam and cobbly clay loam with basalt rock outcroppings. Basalt fragments occupy 5–35% of the surface and soil at this site ([USDA, NRCS] United States Department of Agriculture, Natural Resource Conservation Service 2007). Dominant grasses included blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve), sideoats grama (*B. curtipendula* [Michx.] Torr.), and hairy grama (*B. hirsuta* Lag.). Forbs consisted of white locoweed, globemallow (*Sphaeralcea* spp.), and dalea (*Dalea* spp.), with white locoweed being the most frequent. Fringed sagewort (*Artemisia frigida* Willd), skunkbush sumac (*Rhus trilobata* Nutt.), yucca (*Yucca* spp.), one-seed juniper (*Juniperus monosperma* [Engelm.] Sarg.), and pinyon pine (*Pinus edulis* Engelm.) were common woody plants, while plains pricklypear (*Opuntia polyacantha* Haw.) was the predominant cactus.

The second site was located on Mondragon Ranch, 2.18 km northwest of Des Moines, New Mexico (lat 36°46′21.18″N, long 103°51′32.13″W) at an elevation of 2 042 m above sea level. This area of open grassland had loam, clay loam, and gravelly loam soils. Dominant grasses were blue grama, galleta (*Pleuraphis jamesii* Torr.), tobosa (*P. mutica* Buckley), buffalograss (*Buchloe dactyloides* [Nutt.] J.T. Columbus), sideoats grama, sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), and western wheatgrass. Here too the most prevalent forb was white locoweed. Other forbs included globemallow and sunflower (*Helianthus annuus* L.). Shrubs were rare, although winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit) and groundsel (*Senecio* spp.) were present.

The third site was at the base of Capulin Volcano (lat 36°45′22.87″N, long 103°58′24.47″W), 2.34 km northeast of Capulin, New Mexico, at an elevation of 2 099 m above sea level. Blue grama, western wheatgrass, bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), sideoats grama, perennial threeawn (*Aristida* spp.), and buffalograss were common grasses. Again the dominant forb was white locoweed, with western ragweed (*Ambrosia psilostachya* DC.), dotted gayfeather (*Liatris punctata* Hook.), prairie coneflower (*Ratibida columnifera* [Nutt.] Woot. & Standl.), sunflower, and globemallow also present. The only shrub present in the study plots was fringed sagewort, although skunkbush sumac, one-seed juniper, and pinyon pine were nearby.

Experimental Protocol
At each of the three sites four 200 m² plots (10 m × 20 m) with similar density of locoweed plants were established and randomly assigned to one of the following treatments: 1) control with no treatment [CON]; 2) herbicide as a positive control [HER]; 3) grazed for 5 d by ewes exposed to locoweed

Table 1. Date × treatment comparisons of locoweed (*Oxytropis sericea*) responses to two seasons of intermittent or continuous grazing with sheep (IGZ or CGZ), one application of Grazon® P+D (HER), or no treatment (CON) at three sites in northern New Mexico. Option pdiff was used on a subset of preplanned comparisons. Values are least square means.

	Variable[2]							
	Locoweed density[3] (plants·m⁻²)				Locoweed canopy[4] cover (%)			
Date[1]	CON	IGZ	CGZ	HER	CON	IGZ	CGZ	HER
Pregrazing 2009	1.17a d	1.45a d	1.56a d	1.59a d	4.39a d	4.56a d	5.48a d	5.66a d
Fall 2009	0.98	1.05	1.38	0.10	2.46	0.61	0.79	0.39
Pregrazing 2010	0.86	1.04	1.27	0.32	3.46	3.46	3.51	0.39
Fall 2010	0.78a d	0.44b d	0.69b d	0.32b d	2.63a d	0.09b e	0.39b e	0.75b de
Spring 2013	0.01c d	0.03c d	0.08c d	0.01b d	—	—	—	—

[1]Pregrazing measurements were taken in June, and fall measurements were taken in September in both years.

[2]Means with different letters in columns (abc) indicate detectable differences ($P < 0.05$) by treatment between pregrazing in 2009, fall 2010, and spring 2013 (density); means with different letters in rows (def) indicate detectable differences ($P < 0.05$) between treatments within dates.

[3]Locoweed density SEM: pregrazing 2009=0.06; fall 2009=0.14; pregrazing 2010=0.12; fall 2010=0.06; spring 2013=0.01.

[4]Locoweed canopy cover SEM: pregrazing 2009=0.18; fall 2009=0.27; pregrazing 2010=0.44; fall 2010=0.33.

[5]Flowering stalks SEM: pregrazing 2009=0.14; fall 2009=0.16; pregrazing 2010=0.18; fall 2010=0.08.

[6]Plant size SEM: pregrazing 2009=4.79; fall 2009=7.09; pregrazing 2010=9.09; fall 2010=7.43.

[7]Locoweed biomass SEM: pregrazing 2009=1.96; fall 2009=0.17; pregrazing 2010 1.27; fall 2010=0.35.

plots continuously [CGZ]; and 4) grazed for 5 d by ewes exposed to locoweed intermittently [IGZ]. One additional plot was used to analyze the effectiveness of a new herbicide although those results are not reported here. Two additional 200 m² plots, one locoweed free (assigned to IGZ ewes) and another locoweed infested (assigned to CGZ ewes), were grazed for 3 d at each site to achieve the intermittent and continuous grazing treatments. All locoweed-infested plots had initial mean locoweed densities ranging between 1.17 to 1.59 plants·m⁻², and each plot received the same treatment in both years. Plot size was selected to a) ensure that initial locoweed densities would be similar across plots at each site and b) represent dense locoweed patches commonly found in our study area. The swainsonine level of *Oxytropis* plants at our research sites has been described in detail and is usually below 0.1% (Gardner et al. 2001; Ralphs et al. 2002; Martin 2008). Grazed plots received the same treatment in 2009 and 2010, whereas herbicide treatment was applied once at the beginning of the study in 2009.

The New Mexico State University Institutional Animal Care and Use Committee approved the experimental protocol. Twelve mature western white-faced ewes, raised at the Corona Range and Livestock Research Center in central New Mexico with a mean weight of 56.28 kg ± 1.36 SE, were used in 2009. All ewes were presumed open, but two lambed during the study. In 2010, 12 different western white-faced open ewes weighing 61.58 kg ± 4.18 SE were obtained from the New Mexico State University Campus Farm. Ewes were adapted to the vegetation and weather conditions for a minimum of 6 d prior to grazing trials and were randomly assigned to intermittent or continuous grazing treatment. Adaptation included exposure to locoweed-infested range for all ewes, regardless of treatment group.

All ewes grazed at each site for 8 d. The six ewes in the intermittent grazing treatment grazed locoweed plots for 5 d (treatment plots) and locoweed-free plots during the following 3 d at each site. Conversely, the six sheep in the continuous grazing treatment were exposed to locoweed in both the 5- and

3-d plots for a total of 24 consecutive days. A 5-d or shorter locoweed dosing has been shown not to induce permanent negative neuronal effects in animals (Stegelmeier et al. 2004). Based on the 20-h half-life of swainsonine clearance from blood serum (Stegelmeier et al. 1998), a 3-d withdrawal period between locoweed grazing periods was deemed sufficient to allow ewes to recover. Pfister et al. (1996) found that sheep fed locoweed for 28 d resolved brain lesions but did not recover behaviorally, so an overall study duration of 24 d was chosen to limit the length of locoweed exposure of sheep in continuously grazed treatment.

Electric net fencing (Kencove Supplies, Blairsville, PA) was used to contain the sheep inside plots. In 2009 forage availability in the plots provided a mean allocation of 505 g ± 89 SE of DM·ewe⁻¹·d⁻¹, an amount estimated to be approximately 50% of a ewe's daily forage demand for a target intake of 1.8% body weight·d⁻¹ DM basis. In 2010, mean animal forage allowance was 495 g ± 143 SE of DM·ewe⁻¹·d⁻¹, which was approximately 45% of daily forage demand for the same target intake as in 2009. Alfalfa (*Medicago sativa* L.) hay was weighed and fed in the evening following behavior observations, to bring daily intake up to 1.8% of body weight on a DM basis. Alfalfa hay supplementation was selected since James and Van Kampen (1974) found no decreases in intoxication of ewes fed a diet of 81% alfalfa and 19% locoweed. Hay was typically fed in tubs on the last 2 d in the 5-d plots, as grazing intensity increased with time. Mean forage utilization in both IGZ and CGZ plots for 2009 and 2010 was 81% ± 1 SE and 78 % ± 9 SE, respectively. To induce high levels of utilization we applied a stocking rate of 0.30 acres/AUM over 5 d, approximately an order of magnitude higher than stocking rates of 2–3 acres/AUM (USDA, NRCS 2007) recommended for continuously grazed rangeland of the area in excellent condition.

The herbicide, Grazon® P + D (picloram [4-amino-3, 5, 6-trichloro-pyridinecarboxylic acid] plus 2, 4-D [{2, 4-dichlorophenoxy} acetic acid]) was sprayed at a rate of 0.12 kg·a.e.·ha⁻¹ in HER plots. Herbicide was applied using a

	Variable[2]										
Flowering stalks[5] (no./plant)				Plant size[6] (cm²)				Locoweed biomass[7] (g·m⁻²)			
CON	IGZ	CGZ	HER	CON	IGZ	CGZ	HER	CON	IGZ	CGZ	HER
3.10a d	3.52a d	4.03a d	4.15a d	83.24a d	91.89a d	114.61ad	116.60ad	2.83a e	1.63a e	5.78a de	16.57a d
1.23	0.05	0.17	0.30	59.80	55.22	30.08	19.38	1.73	1.47	0.38	1.43
1.56	0.80	0.39	0.10	93.86	76.89	72.52	20.83	10.35	6.90	3.87	0.00
0.58a d	0.00b e	0.00b e	0.01b e	64.33a d	7.74b e	15.41bde	17.35bde	2.50a d	0.25a d	0.00a d	0.00b d
—	—	—	—	—	—	—	—	—	—	—	—

five-nozzle boom sprayer with CO_2 cartridge delivering $200 \cdot L \cdot ha^{-1}$ in June 2009. White locoweed was in the late-flowering stage at all sites when sprayed. Weather on the days that herbicides were applied averaged ambient air temperature of $22°C \pm 2$ SEM, soil temperature of $20°C \pm 1$ SEM, relative humidity of $21\% \pm 3$ SEM, and wind speed of $3 \, m \cdot sec^{-1} \pm 0.3$ SEM. Herbicide-treated plots were fenced until the following fall to prevent cattle from grazing the dead locoweed plants immediately after treatment per producers' request. Cattle grazing of plots following herbicide treatment and TG were at moderate stocking rates.

Canopy cover of white locoweed, perennial grasses, forbs, and litter in addition to bare ground cover were recorded in all plots using point intercept taken every 10 cm on four 20-m permanent transects per plot. Locoweed density was also recorded on the same transect using a 1-m² quadrat, centered at each odd meter mark on the transect tape (40 frames per plot). Number of plants (plants $\cdot m^{-2}$) and plant vigor attributes were recorded in each frame. Any aboveground or crown material greater than or equal to 1 cm² was counted as a plant. Vigor attributes included longest canopy diameter and its perpendicular and number of flowering heads. The area of an ellipse was used to calculate plant canopy area (cm²) and is hereafter referred to as plant size. Herbaceous biomass samples (g $\cdot m^{-2}$) were collected by clipping eight 0.25-m² quadrats (50 cm × 50 cm) at ground level in each plot. Samples were dried at 60°C for 72 h, sorted into grass, white locoweed, other, and weighed. In both years (2009 and 2010), plant data were collected prior to treatment in May and June, immediately after treatment in late June, and again at the end of the growing season in September. Herbicide plots were not measured immediately after treatment, due to the expected lag time (1 mo from treatment) in plant response. One additional locoweed density measurement was taken in all plots in spring 2013 to make inferences regarding the longer-term impact of treatments.

Thirty-six soil samples were collected at each site during fall 2010. Two soil cores (7.5 cm × 3 cm deep soil auger as in Ralphs and Cronin 1987) were collected from each of 12 1-m² frames placed along fixed 20-m transects (in the same locations previously used to determine locoweed density) in CON, IGZ, and HER experiment plots at each site. Locoweed plant density was used as the criterion to select the location of soil sample frame placement. Thus, frames with highest ($n=6$) and lowest ($n=6$) initial locoweed density in each of the three experiment plots at each site were sampled. Soil samples ($n=108$) were

manually crushed and screened in the lab, and locoweed seeds were separated from rock, soil, root material, and organic matter using both a 1-mm and 0.5-mm mesh screen soil sieve. Seeds recovered from each soil sample were counted and classified into presumed recent (brown) or older (black) seed crops.

In addition to soil samples, dry sheep fecal pellets were also collected during the fall of 2010 from grazed plots. Seed removal from feces began with a 4-h soak in cold water prior to washing. Fecal pellets were washed using two mesh screen sieves (2 and 1 mm) to recover white locoweed seeds. Fecal pellets were rinsed with running water and rubbed lightly to break up the sample. The material recovered from the sieve was dried at 37°C for 24 h and then placed in cold storage in preparation for seed retrieval (Olson et al. 1997).

All white locoweed seeds were tested in the laboratory for germinability using an Intellus Environmental Controller, where temperature regulation and lighting can be controlled and monitored. Prior to germination, locoweed seeds were surface sterilized by immersion in 70% ethanol for 1 min, followed by 10% bleach solution for 2 min and rinsed in sterile deionized water for 5 min. Seeds were then placed on sterile paper towels to dry prior to mechanical scarification, which consisted of gently rubbing seeds between two pieces of sterile fine-grit sand paper (Delaney et al. 2011). After the scarification process, seeds were placed in petri dishes lined with water-moistened Whatman filter paper and placed in the germination chamber for 6 wk at 7°C for 10 h and 13°C for 14 h to simulate spring day and night soil temperatures (Ziemkiewicz and Cronin 1981).

Sheep response variables measured included blood serum constituents, behavior, and weight. Blood samples were collected from all animals via jugular venipuncture prior to locoweed grazing and upon completion of 5-d and 3-d grazing periods at each site. Blood samples were allowed to clot at room temperature for 30 min and then centrifuged at $1\,700 \times g$ for 20 min. Serum was decanted into polypropylene tubes and stored at −10°C until subsequent analysis. Analyses included assays to detect levels of swainsonine, ALKP, AST, T3, and T4. All blood analyses were conducted on a subset of 16 ewes (4 ewes $\cdot$ treatment$^{-1} \cdot$ year^{-1}) consisting of the top four locoweed eaters in each treatment except in the IGZ treatment in 2009 where two pregnant ewes, which ranked first and fourth in frequency of locoweed grazing observations, were replaced by lower-ranking open peers. Pregnancy has been found to alter

Table 2. Date × treatment comparisons of nontarget vegetation responses to two seasons of intermittent or continuous grazing with sheep (IGZ or CGZ), one application of Grazon P+D (HER), or no treatment (control) at three sites in northern New Mexico. Option pdiff was used on a subset of preplanned comparisons. Values are least square means.

	Variable[2]							
	grass biomass[3] (g·m⁻²)				Grass canopy cover[4] (%)			
Date[1]	CON	IGZ	CGZ	HER	CON	IGZ	CGZ	HER
Pregrazing 2009	90.46a d	85.26a d	95.76a d	109.20a d	73.60a d	71.58b d	69.60b d	70.79b d
Fall 2009	84.52	49.84	61.44	110.60	78.55	79.91	80.75	81.89
Pregrazing 2010	115.71	80.75	90.20	143.20	72.89	71.62	70.35	80.83
Fall 2010	85.48a d	45.22a e	44.78b e	93.02a d	76.01a e	78.20a de	79.56a de	84.60a d

[1]Pregrazing measurements were taken in June, and fall measurements were taken in September in both years.
[2]Means with different letters in columns (abc) indicate detectable differences ($P < 0.05$) by treatment between pregrazing in 2009 and fall 2010; means with different letters in rows (def) indicate detectable differences ($P < 0.05$) between treatments within dates.
[3]Grass biomass SEM: pregrazing 2009=2.97; fall 2009=7.75; pregrazing 2010=8.09; fall 2010=7.43.
[4]Grass canopy cover SEM: pregrazing 2009=0.48; fall 2009=0.40; pregrazing 2010=1.36; fall 2010=1.05.
[5]Forb canopy cover SEM: pregrazing 2009=0.35; fall 2009=0.61; pregrazing 2010=0.57; fall 2010=0.94.
[6]Bare ground SEM: pregrazing 2009=0.49; fall 2009=0.67; pregrazing 2010=0.72; fall 2010=0.98.

serum ALKP, AST (Hallford and Gaylean 1982), T3, and T4 (Glinoer et al. 1990; Glinoer 1999) levels, and it was therefore judged reasonable to use pregnancy as the criterion for exclusion in this treatment group. Although pregnancy is unlikely to alter serum swainsonine concentration; blood samples from the same subset of ewes described above were analyzed to maintain consistency. Swainsonine analyses were conducted at the USDA ARS Poisonous Plant Lab in Logan, Utah, following a protocol developed by Stegelmeier et al. (1998). Levels of ALKP and AST were determined at the New Mexico Department Agriculture Veterinary Diagnostic Lab in Albuquerque, New Mexico, and T3 and T4 analyses were conducted in the Endocrinology Laboratory of the Department of Animal and Range Sciences at New Mexico State University using protocols developed by Wells et al. (2003) and Richards et al. (1999) for T3 and T4 analyses, respectively.

Sheep foraging behavior data were recorded every 2 min using instantaneous scan sampling for all ewes for 1 h by two observers during the morning and evening grazing sessions, in the 5-d plots at each site. The afternoon of the fifth day was not recorded because blood was drawn and the animals were moved to the next site during this time. A total of 810 behavior observations were recorded for each ewe. Activities recorded were grazing locoweed, grazing other, ruminating, walking, lying, drinking, and other. If an animal was seen both walking and grazing, the feeding activity was recorded. Only time grazing locoweed is reported here and is expressed as the percentage of total feeding observations.

Body weight was measured prior to and at the completion of the grazing trials in both years. Animals were fasted from feed for 24 h prior to each weighing event. The same four ewes for each treatment in each year were used for the blood, behavior, and body weight analysis.

Statistical Analyses

The experimental design used was a randomized complete block with plot as the experimental unit and site as the blocking factor. The effect of site, date, treatment, and the interaction of treatment and date on all vegetation response variables listed below were analyzed with a repeated measures mixed model using version 9.1 of SAS (SAS 2006). Response variables considered were white locoweed density (plants·m⁻²), white locoweed cover (%), number of white locoweed flowering heads, white locoweed plant canopy size (cm²), white locoweed biomass (g·m⁻²), grass biomass (g·m⁻²), grass cover (%), forb cover (%), and bare ground (%). A subset (initial and final) of selected date by treatment comparisons of interest were conducted for each response variable using least square means. Covariance structures were tested for each variable and residual plots were examined to detect outliers and violations of analysis of variance (ANOVA) assumptions. Differences were declared statistically significant at $P \leq 0.05$. Treatment by date interactions with $P \leq 0.10$ were further examined.

Two-way contingency analysis was conducted to determine association between experiment treatments and a) black (presumed old) vs. brown (presumed new) seed counts, b) total seed counts, and c) germination rates. A χ^2 test was used to determine whether association was statistically detectable. All analyses were conducted in SAS 9.1 using the FREQ procedure, and tests with $P \leq 0.01$ were declared significant.

Blood serum constituent data were analyzed using a randomized complete block experimental design with year as the blocking factor and individual ewes nested within year as the experimental unit. All statistical analyses were conducted using the subset of 16 ewes (4 ewes·treatment⁻¹·yr⁻¹) mentioned above. The effect of treatment, date (blood sampled on days 1, 5, 8, 13, 16, 21, and 24 of the experiment), year, and the interaction of treatment×date on the levels of blood metabolites were analyzed as repeated measures using PROC MIXED in SAS 9.1. A first order autoregressive covariance structure was used, and residual plots were examined to detect outliers and violations of ANOVA assumptions.

The model used to analyze ewe feeding behavior determined the effect of treatment, period (days 1–8, 9–16, or 17–24), year, and the interaction of treatment×period on the frequency of locoweed grazing using a repeated measures mixed model with individual ewes nested within year as the experimental unit. The same covariance structure and diagnostic tests as those described above were used in this analysis.

Table 2. Extended.

Variable[2]							
Forb canopy cover[5] (%)				Bare ground[6] (%)			
CON	IGZ	CGZ	HER	CON	IGZ	CGZ	HER
6.36b d	5.39a d	5.09a d	5.75a d	5.00a d	8.46a d	8.07a d	6.93a d
6.71	3.55	2.81	6.93	2.19	6.58	6.18	2.50
7.85	7.02	6.75	4.03	2.32	7.02	6.67	2.81
11.67a d	7.01a de	3.73a e	7.85a de	0.96a e	6.75a d	6.27a de	1.84b de

Finally, the effects of treatment and year on body-weight gains were analyzed with a mixed model using individual ewes nested within year as the experimental unit and initial body-weight as a covariate. A compound symmetry covariance structure was used and residual plots were again examined to detect violations of ANOVA assumptions. Differences were declared statistically significant at $P \leq 0.05$ for blood serum constituents, feeding behavior, and body weights.

RESULTS

Effects of Targeted Grazing and Herbicide on White Locoweed

There was no detectable effect of the experiment site (block) on any of the locoweed response variables considered except for locoweed canopy cover ($P < 0.01$: Table 1) which responded differently at the Archuleta site (1). Treatment by date interactions (detailed below) were detected for locoweed density ($P < 0.01$), cover ($P = 0.10$), and plant size ($P = 0.04$).

Locoweed density was similar in all plots prior to treatment in June 2009 (Table 1) and decreased by the end of the experiment for IGZ ($P < 0.01$), CGZ ($P < 0.01$), and HER-treated ($P < 0.01$) plots, but remained the same in CON plots ($P = 0.17$). Density was lower in spring 2013 compared to fall 2010 in CON ($P < 0.01$), IGZ ($P = 0.03$), and CGZ ($P < 0.01$), but not in HER ($P = 0.09$). All plots had similar density in spring 2013 (Table 1). Mean canopy area of locoweed plants (plant size) did not differ across plots at the beginning of the experiment in 2009 and decreased in IGZ ($P < 0.01$), CGZ ($P < 0.01$), and HER ($P < 0.01$) but not in CON plots ($P = 0.38$) by fall 2010 (Table 1). IGZ plots had smaller plants than those in CON plots at the end of the study ($P = 0.05$, Table 1).

Locoweed canopy cover dynamics resembled that of density; all plots had similar cover prior to treatment in June 2009 followed by a decrease in cover in response to IGZ ($P < 0.01$), CGZ ($P < 0.01$), and HER ($P < 0.01$) treatments but not to CON ($P = 0.10$), by the end of the experiment (Table 1). In fall 2010, locoweed cover was lower in IGZ and CGZ than CON plots ($P = 0.02$, and $P = 0.03$, respectively) but was the same in CON vs. HER plots ($P = 0.07$), which had intermediate levels of locoweed cover (Table 1). Locoweed cover in HER plots in fall 2010 was not different from that of the IGZ- and CGZ-treated plots ($P = 0.51$ and 0.73, respectively).

Mean number of flower stalks on locoweed plants in CON, IGZ, CGZ, and HER plots did not differ in June 2009, prior to applying treatments. As with other response variables, the mean number of flower stalks per plant in CON plots did not change during the experiment ($P = 0.09$) but decreased in IGZ ($P = 0.02$), CGZ ($P = 0.01$), and HER ($P = 0.01$) plots from June 2009 to fall 2010 (Table 1). By the end of the study, number of flower stalks on locoweed plants in IGZ, CGZ, and HER-treated plots were similar to each other and lower than on plants in the CON plots ($P = 0.03$, $P = 0.03$, and $P = 0.03$, respectively; Table 1).

Locoweed biomass differed among plots at the onset of the experiment. HER plots had greater locoweed biomass than CON ($P = 0.03$) and IGZ ($P = 0.02$) plots in June 2009 and were the only treatment plots that showed a decrease in locoweed biomass by the end of the study in fall 2010 ($P < 0.01$; Table 1).

Effects of Targeted Grazing and Herbicide on Nontarget Vegetation and Bare Ground

Grass biomass ($P = 0.04$), grass cover ($P < 0.01$), and forb cover ($P = 0.02$) responded differently at different sites. Of the nontarget vegetation variables, forb cover was the only one to exhibit a marginal treatment by date interaction ($P = 0.10$).

Grass biomass was similar in all plots at the beginning of the study (Table 2) and remained similar over time in CON ($P = 0.83$), IGZ ($P = 0.09$), and HER-treated ($P = 0.49$) plots. Grass biomass in CGZ plots decreased ($P = 0.04$) from June 2009 to fall 2010, but CGZ- and IGZ-treated plots were similar ($P = 0.98$) in fall 2010. Grass biomass was lower in both grazing treatment plots than in CON and HER plots in fall 2010 (Table 2). Conversely, grass canopy cover in IGZ ($P = 0.03$), CGZ ($P < 0.01$), and HER-treated ($P < 0.01$) plots increased from June 2009 to fall 2010, and by the end of the study the HER plots had higher grass canopy cover ($P = 0.03$) than CON, while all other treatments were similar (Table 2). Again, all plots were similar (Table 2) to each other in grass cover prior to treatment and CON plots remained constant over time ($P = 0.41$).

Forb canopy cover was similar among plots prior to treatment (Table 2), but in contrast to the other variables, forb cover in IGZ ($P = 0.45$), CGZ ($P = 0.53$), and HER-treated ($P = 0.33$) plots was similar from beginning to end, but increased in CON plots ($P = 0.02$) through time. CON plots had higher ($P = 0.01$) forb canopy cover than CGZ plots in fall 2010, but the CGZ plots did not differ from IGZ ($P = 0.27$) or HER ($P = 0.17$) plots (Table 2).

Table 3. A) Number of black (presumed old), brown (presumed recent) and total white locoweed (*Oxytropis sericea*) seeds recovered from soil cores of experiment plots that received either no treatment (control), targeted grazing with sheep, or herbicide application. Germination rates for seeds in each treatment group are also shown. B) Number and germination rates of white locoweed seeds recovered from the soil seed bank from all sites and treatments and digested locoweed seeds recovered from sheep fecal pellets. C) Results of contingency analysis determining whether treatments and a) proportion of black vs. brown seeds recovered, b) total number of seeds recovered, and c) seed germination rates were associated.

| | Seed count (no. seeds) | | | | | |
	Black	Brown	Total	Germination rate (%)	χ^2	P
A						
Control	23	9	32	87.50		
Targeted grazing	47	23	70	88.57		
Herbicide	19	41	60	76.67		
B						
Soil seed bank			162	83.95		
Digested seeds			23	0.00		
C						
a. Black and brown seed count vs. treatment					21.05	< 0.01
b. Total seed count vs. treatment					14.37	< 0.01
c. Germination rate vs. treatment					3.77	0.15

All plots had similar percentages of bare ground at the beginning of the study (Table 2), and HER plots were the only treatment that showed a decrease ($P=0.03$) in this variable by the end of the study. CON ($P=0.09$), IGZ ($P=0.46$), and CGZ-treated ($P=0.44$) plots all showed a decrease, in percentage bare ground as well, but differences in this case were not statistically detectable (Table 2). By fall 2010, CON plots, which began with the lowest percent of bare ground, continued to exhibit the lowest levels of this variable; conversely, IGZ plots had the highest levels of bare ground cover at both the beginning and end of the study. IGZ plots had more bare ground than the CON ($P=0.04$) but were similar to CGZ ($P=0.86$) and HER ($P=0.08$) plots in fall 2010.

Effects of Targeted Grazing and Herbicide on Locoweed Seed Density and Germinability

We found an association ($P < 0.01$) between the proportion of black vs. brown seeds and experimental treatments (Table 3). Herbicide-treated plots had more than double the proportion (68%) of brown seeds compared to control (28%) and grazed (32%) plots (Table 3). Experimental treatments were also associated with total number of locoweed seeds recovered ($P < 0.01$). Soil cores from plots treated with targeted grazing or herbicide had roughly twice the number of white locoweed seeds compared with control plots (Table 3). We found no association between white locoweed germination rates and experimental treatments ($P=0.15$; Table 3). Overall germination rate for seeds retrieved from the soil seed bank was 83.95%, whereas germination of digested seeds recovered from sheep fecal pellets was nil (Table 3).

Blood Constituents

Sampling date affected most blood metabolites (SWA: $P=0.14$; ALKP: $P < 0.01$; AST: $P < 0.01$: T3: $P < 0.01$; T4: $P < 0.01$) reflecting both temporal variation in metabolite levels and a tendency for treatments to diverge as time progressed (Fig. 1).

Initially, sheep in both treatments had similar values for all blood constituents (ALKP: $P=0.98$, AST: $P=0.82$, T3: $P=1$, T4: $P=0.64$, SWA: $P=1$). By the end of the 24-d period in each year, sheep that grazed locoweed intermittently had lower levels of serum ALKP ($P < 0.01$), AST ($P=0.04$), and marginally lower ($P=0.07$) swainsonine levels than sheep that grazed locoweed continuously (Table 4). Furthermore, levels of T3 were marginally depressed ($P=0.07$) in CGZ ewes versus their IGZ counterparts by day 24 (Table 4).

Grazing Behavior

Ewes that grazed locoweed intermittently were observed feeding on locoweed less often than ewes that grazed locoweed continuously for 24 d, although these differences were only marginal (Table 4: $P=0.06$). However, ewes in both treatment groups tended to increase their locoweed consumption over time.

Body-Weight Gains

Although body-weight gains in both treatments were similar ($P=0.19$), ewes that grazed locoweed intermittently gained almost twice as much body weight as ewes in the CGZ group (Table 4). When body weight gains of the eight ewes in 2009 were considered alone, ewes in the IGZ group gained more weight (7.41 kg $\pm$ 1.88 SEM, $P=0.04$) than their CGZ counterparts (1.32 kg $\pm$ 1.88 SEM).

DISCUSSION

Vegetation and Soil Seed Bank

The reduction in locoweed density, canopy cover, number of flower stalks, and plant size as a result of TG supported our first hypothesis that TG with sheep for two consecutive years would temporarily decrease locoweed abundance. Furthermore, locoweed responses to TG were in some cases better than predicted when compared to untreated and chemically treated
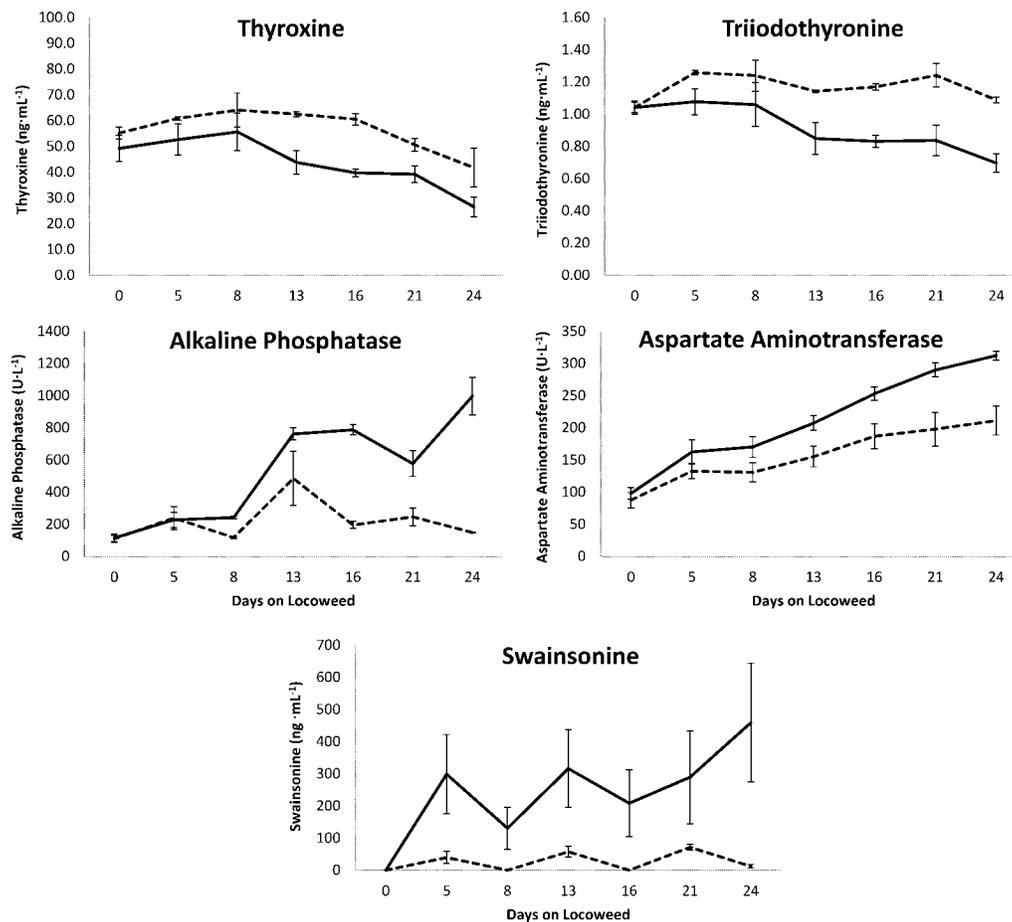
Figure 1. Mean serum concentration of thyroxine (T3), triiodothyronine (T4), alkaline phosphatase (ALKP), aspartate aminotransferase (AST), and swainsonine in ewes assigned to the intermittent (IGZ, dashed line) and continuous (CGZ, solid line) locoweed (*Oxytropis sericea*) targeted grazing treatments. Means for 2009 and 2010 grazing seasons are shown. Bars indicate standard error of means.

rangeland. Grazed and chemically treated plots performed in a similar manner by exhibiting similarly low values of locoweed canopy cover, number of flower stalks, and plant size. TG involved actual removal of most of the aerial plant parts (often including crowns and superficial roots) while the herbicide

killed plants but left dead standing biomass intact. This may be an important difference as the toxicity of senesced white locoweed is unknown and complete removal of plant parts maybe the only safe way, when utilizing infested rangeland, to prevent grazing and subsequent intoxication.

Table 4. Least square means of blood constituents at day 24 and overall means for grazing behavior and body-weight gains of sheep that grazed locoweed (*Oxytropis sericea*) intermittently (IGZ) or continuously (CGZ) for 24 d.

	Treatment[1,2,3]			
Variable	Intermittent	Continuous	SE	P
Swainsonine (ng · mL^{-1})	11.80	459.14	228.83	0.07
Alkaline phosphatase (ALKP, U · L^{-1})	148.75	995.87	189.51	< 0.01
Aspartate aminotranferase (AST, U · L^{-1})	211.12	312.25	44.47	0.04
Triiodothyronine (T3, ng · mL^{-1})	1.09	0.70	0.19	0.07
Thyroxine (T4, ng · mL^{-1})	41.71	26.49	12.70	0.25
Locoweed grazing frequency (%)	1.95	4.99	1.56	0.06
Initial weights (kg)[4]	58.74	53.18	—	0.25
Weight gains (kg)	6.21	3.42	1.98	0.19

[1]Treatments diverged through time (day by treatment interaction); therefore means for last day (day 24) are shown.

[2]Prelocoweed exposure values for SWA: IGZ < 0.01; CGZ < 0.01, ALKP: IGZ=109.38; CGZ=114.38, AST: IGZ=87.62; CGZ=97.87, T3: IGZ=1.04; CGZ=1.04, T4: IGZ=55.14; CGZ=49.14. Preexposure levels of all blood constituents measured were similar between treatments (P > 0.05).

[3]Normal value ranges: ALKP < 161 U · L^{-1}; AST < 93 U · L^{-1} (Stegelmeier et al. 1999a); T3=0.75–2.4 ng · mL^{-1} (Obeidat et al. 2005, Camacho et al. 2012); T4=50–85 ng · mL^{-1} (Richards et al. 1999; Camacho et al. 2012). Normal values can vary based on analytical method, and type, age, and physiological state of the animal.

[4]Values shown are actual means and P values for the covariate.

Our results differ from those reported by Ralphs et al. (2002) who found that clipping white locoweed plants for four consecutive years did not reduce leaf length (~ plant size in this study) or increase mortality (i.e., decrease density). This apparent inconsistency may be due to known differences in plant responses to clipping vs. grazing (Weir and Torell 1959; Taylor et al. 1960; Peterson et al. 1994) and in this case differences in the severity of defoliation. In a comparison of continuous grazing, rotational grazing, and repeated clipping on Kura clover (*Trifolium ambiguum* M. Bieb.), Peterson et al. (1994) found that stand density, total nonstructural carbohydrates, and total below-ground mass all decreased with grazing but not with clipping. The authors speculated that this may have been due to the low stubble height left in the grazed plots. Clipping rarely disturbs the root crowns of target plants, whereas sheep in this study severely damaged root crowns and often uprooted entire plants even when other forage was abundant. James et al. (1968) observed similar behaviors and reported that sheep dug below the soil surface to eat the succulent locoweed crowns and roots. The apparent discrepancy between locoweed canopy cover and biomass results was most likely due to the large difference in sampling intensity used to estimate each of these plant attributes. Since biomass estimates involved destructive sampling (clipping), the intensity with which this attribute was measured was intentionally low. Areawise, biomass samples totaled 1% of each plot while density samples totaled 20%. The apparent increase in locoweed biomass measured in the second season could have also been caused by a very wet spring that occurred in that year.

Our grazing results, however, do support the findings of Ralphs et al. (2002) regarding a reduction in the number of flower stalks induced by clipping. Wyka (1999) also observed that clipping treatments suppressed growth of new inflorescences of *O. sericea* in an alpine meadow at high elevation. The decrease in number of flower stalks observed in our study was likely not related to normal end of season senescence since numbers in the control plots remained unchanged, while treated plots exhibited a detectable decrease. Two years of drought following our experiment appeared to erase all short-term treatment effects. Locoweed populations naturally decrease during dry years (Ralphs et al. 2002, 2003); however, the effects of targeted grazing and herbicide application on postdrought population recovery are unknown.

Soil cores from control plots yielded the lowest number of locoweed seeds. We speculate that levels of seed predation by invertebrates during our study may have been highest in control plots where seed pods were allowed to complete their cycle undisturbed. Although monitoring of this phenomenon was beyond the scope of our study, heavy infestation by insect larvae were observed at one of our study sites. Recovery of a few seeds from sheep fecal pellets suggests that a degree of granivory by sheep occurred in our study. Although the number of digested seeds was too small to derive statistically valid conclusions regarding their germination rates, our results suggest that the likelihood of locoweed seed dispersal by sheep is possibly very limited. Lacey et al. (1992) reported that sheep ingestion reduced germinability and viability of leafy spurge seeds, an observation that supports our limited results. Herbicide-treated plots had twice the density of new locoweed seeds compared to targeted grazing plots, suggesting that in the

absence of seed predation by invertebrates, TG may be a more effective means of controlling long-term population cycles.

The overall effects of targeted grazing with sheep on white locoweed observed in this experiment are analogous to results obtained in studies investigating effects of similar herbivory regimes on other forb species. For example, Ralphs et al. (1991) reported decreases of 14–73% of flowering heads, and 0–89% of stalks with leaves on waxy larkspur plants (another alkaloid-synthesizing forb) following sheep grazing. In the first 2 yr of that study, stem heights were reduced an average of 14 cm (Ralphs and Olson 1992). In another study, a high-intensity low-frequency system using cattle decreased density, height, and number of flowering stems of Canada thistle (*Cirsium arvense* [L.] Scop) (De Bruijn and Bork 2006). Plots in that study were grazed at comparable utilization levels (72%) and for similar grazing periods of 3.0–4.1 d to those used in our experiment. De Bruijn and Bork's (2006) treatment was so effective that the bud stage was only reached by three Canada thistle plants in the high-intensity low-frequency plots in the entire 3-yr study. Lacey and Shelley (1996) also reported that stem densities were reduced and stems tended to be shorter and produce fewer flowers on leafy spurge (*Euphorbia esula* L.) plots following sheep grazing.

Grass cover increased following both grazing treatments supporting our second hypothesis. The increase in grass canopy cover observed may have been due to increased tillering by blue grama following defoliation (Eneboe et al. 2002) supported by the increased rate of nutrient cycling due to the urine and feces deposition from sheep in grazed plots (Hobbs 1996 and references therein). Forb cover in the grazed plots was more similar to the herbicide treatment than the control possibly due to the limited ability of dicotyledonous plants to recover following grazing (Archer and Tieszen 1986). Although grass canopy cover increased after treatment, grass biomass remained the same or decreased in grazed plots. Utilization in TG plots was approximately 80% in both years, and although blue grama recovers well after severe defoliation, western wheatgrass (which was abundant at all sites) does not recover as quickly since most of its tillers are produced before mid-July (Hart et al. 1993). Grass biomass in the grazed plots may have also been affected by subsequent grazing by wildlife and cattle, which prefer the succulent regrowth of previously grazed patches (Laca 2008; Goodman, unpublished data). The amount of bare ground was not affected by the TG treatments and remained unchanged throughout the 2 yr of the study, a trend which mirrored the CON plots. Bare ground decreased in the HER-treated plots, most likely due to an apparent pulse of grass growth that occurred after herbicide application from decreased competition with locoweed for nutrients (Mueggler 1972) and/or exclusion of cattle and antelope grazing during the first growing season after treatment (June–September 2009). Collectively, grass canopy cover, forb canopy cover, and bare ground results support our second hypothesis that the grazing treatments would not negatively affect nontarget vegetation.

Our third hypothesis, that intermittent and continuous TG would affect locoweed similarly, was supported by our results since no detectable difference in white locoweed responses were found between IGZ and CGZ. Selectivity may have been different for the first couple days of the experiment in each year,

but as grazing pressure increased choices became more limited. Sheep in both grazing treatments exhibited grazing behavior analogous to that reported by Ralphs et al. (1994a) who found that as grazing pressure increased because of lack of available forage, white locoweed consumption increased in the diets of cattle not predisposed to consume locoweed.

Sheep Serum, Behavior, and Weight Gains

Serum swainsonine has been used as an indicator of locoweed intoxication (Stegelmeier et al. 1995, 1999a; Taylor et al. 2000; Whittet et al. 2002), although its concentration can drop below detectable levels within days of poisoning, depending on the dose administered (Ashley et al. 2006). This is most likely due to its short half-life of 18 to 20 h (Stegelmeier et al. 1998, 1999a). Differences between treatments, in this study, may have been even greater than shown as it is likely that serum swainsonine levels dropped in both intermittent and continuous groups particularly at the third site, when ewes typically began eating locoweed earlier and consumed most of the locoweed during the first day of the 5- and 3-d periods. This would have given swainsonine more than double the time of its half-life to clear from the serum before blood was drawn, rendering it less detectable. Nevertheless, significantly lower swainsonine levels were detected in ewes in the IGZ treatment, supporting the hypothesis that sheep grazing locoweed intermittently have lower serum swainsonine concentrations than sheep allowed to graze locoweed continuously.

Serum ALKP has been found to increase in sheep and cattle consuming locoweed (Pulsipher et al. 1994; Taylor et al. 2000), a response that occurs as early as 24 h after a single locoweed gavage (Taylor and Strickland 2002). Serum levels of AST and ALKP may be not only the earliest but also the most sensitive indicators of swainsonine-induced α-mannosidase inhibition, since swainsonine doses as low as 0.05 and 0.10 mg·kg^{-1} can alter these serum constituents (Stegelmeier et al. 1999a). Increases outside of normal ranges were found in AST and ALKP levels in sheep dosed with only 0.05 mg·kg^{-1} for 15 d, and AST increased within the first 3 d of the animals receiving locoweed through gavage. Furthermore, these increases were seen before swainsonine was detected in the serum, while body-weight gains were still unaffected, and only minimal histological changes had occurred (Stegelmeier et al. 1999a). Serum ALKP is generally used as an index of diseased liver or bone tissue. Cellular vacuolization of the hepatocytic cells of the liver (Van Kampen and James 1969; Bachman et al. 1992; Pulsipher et al. 1994) or altered glycoprotein processing (Obeidat et al. 2005) are likely the cause of increases of ALKP with increased locoweed consumption. Increased serum AST may be caused by vacuolization of neural, hepatic, or renal tissue (Obeidat et al. 2005). Because ALKP and AST concentrations are altered by cell damage, levels remain elevated for some time. ALKP has been reported to remain high for 7 d and above normal for 14 d, following the termination of subacute locoweed exposure (Bachman et al. 1992; Pulsipher et al. 1994; Taylor et al. 2000). This suggests ewes grazing locoweed intermittently were most likely receiving low doses of swainsonine since even after a spike in ALKP following 5 d of grazing locoweed, ALKP levels dropped back down following 3 d of grazing locoweed free plots. These results support our hypothesis that ewes grazing

locoweed plots, intermittently, would have lower serum ALKP and AST levels than ewes grazing locoweed continuously.

Serum T3 and T4 levels are usually depressed by locoweed consumption (Pulsipher et al. 1994; Ortiz et al. 1997; Richards et al. 1999). This effect is most likely caused by either an increase in catabolism of the hormones or by follicular cell destruction in the thyroid (Pulsipher et al. 1994). As described above, swainsonine interrupts the enzyme α-mannosidase function by preventing it from trimming sugar molecules from glycoproteins for digestion. This in turn causes oligosaccharides and glycoproteins to build up in the cell and eventually cause vacuolation, or accumulation of vacuoles (Molyneux 1999). The storage form of and precursor to the thyroid hormone, thyroglobulin, is a glycoprotein (Kaneko 1997), which may also be a reason for depressed T3 and T4 levels. Follicular cell destruction may decrease thyroid hormone levels because thyroglobulin is converted to T3 and T4 by using lysosomal proteases of the thyroid follicular cells. Serum T3 and T4 levels have been found to decrease within 7 d of initiating locoweed feeding (Ortiz et al. 1997; Richards et al. 1999; Obeidat et al. 2005) and were not different than the control 7 d after the completion of locoweed feeding (Ortiz et al. 1997). This would explain why T3 and T4 levels did not decrease for either treatment until after 8 d of locoweed grazing. These data support the hypothesis that ewes grazing locoweed-infested plots, intermittently, would have higher T3 and T4 levels than ewes grazing locoweed continuously.

Ewes that grazed locoweed intermittently exhibited a tendency to graze locoweed less frequently than their CGZ counterparts contradicting our prediction that both groups would exhibit similar grazing behaviors. All ewes avoided locoweed during the first days of the study and tended to spend more time feeding on locoweed as the trial progressed. This was most likely due to increasing reduction in available forage choices, although alfalfa was supplemented to maintain intake at 1.8% body weight. Hay supplementation may have altered behavior in the last 2 d of grazing at each site; however, previous studies have shown that alfalfa did not decrease intoxication of sheep that received a diet composed of 81% alfalfa hay (James and Van Kampen 1974). Locoweed consumption by intoxicated animals tends to increase with time until animal behavior is altered because of neurological damage (Pritchard et al. 1990; Ralphs et al. 1996) so increased consumption in this study is likely due to increasing levels of toxicosis although no clinical symptoms of neurological alterations were observed in ewes of either treatment. The fact that ewes in the CGZ group showed a tendency to spend more time feeding on locoweed could point to their advancing state of intoxication, although these differences were not reflected in the vegetation responses as no detectable differences were found in locoweed response variables to IGZ and CGZ.

Our last hypothesis predicted that ewe body-weight would not differ between treatments because ewes did not graze locoweed for more than the 30-d threshold (Stegelmeier et al. 1999a) needed for clinical intoxication or histological lesions to develop and consequently cause body weight to decrease. We expected to see no difference in body-weight gains between treatments based on the fact that previous studies had found that such differences were not seen until 35 d after the initiation of locoweed consumption at levels of 7%, 14%, and 21% of

diet (Ortiz et al. 1997). Differences between years in ewe body-weight gains are likely due to differences in foraging experience as 2010 ewes were pen raised. Despite this, our results suggest that there is a potential for intermittent TG of locoweed to be associated with greater body-weight gains than prescriptions that involve continuous TG of this noxious plant.

IMPLICATIONS

TG with sheep may be an effective tool to reduce small patches of locoweed, although additional research and practical experience is needed to assess its long-term effects on locoweed populations and nontarget vegetation. Large-scale application of this grazing method is not recommended due to the high-utilization levels needed to negatively impact locoweed plants. Even if TG only promoted a short-term decrease of white locoweed patches, it could allow producers to graze infested ranges, following TG with sheep, and to expect reduced levels of intoxication in cattle. Decreased livestock losses, reduction in herbicide and fencing costs may also have positive economic implications. Our study suggests that intermittent exposure of sheep to locoweed-infested rangeland appears to prevent significant cell damage induced by swainsonine ingestion. However, because our study lacked a satisfactory level of animal replication, implications of these results are mostly restricted to our research sites in northeastern New Mexico. The on-and-off grazing regime used in this study may be a way to safely graze locoweed-infested ranges although additional research with independent replications is needed to confirm these results.

ACKNOWLEDGMENTS

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