

Efficacy of prescribed grazing depends on timing intensity and frequency

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Summary

1. Exotic weeds and woody plants have invaded many grasslands, and prescribed grazing is one management technique used to combat these plants. Prescribed grazing entails introducing livestock such as sheep or goats that eat unwanted plants. It sometimes has desirable effects, but inconsistencies among study results discourage widespread use. Detailed studies that manipulate grazing timings, intensities and frequencies may explain inconsistencies among previous studies and identify effective weed control strategies.

2. We studied *Euphorbia esula*, an invasive forb avoided by cattle but eaten by sheep. We used simulated grazing (clipping) to estimate *E. esula* and resident plant responses to cattle and sheep grazing protocols.

3. Depending on timing, intensity and frequency, simulated grazing either: (i) did not dramatically affect the invader and/or resident species, (ii) increased the invader and decreased resident species or (iii) decreased the invader and increased resident species. These disparate results illustrate that successful prescribed grazing entails more than simply introducing animals that eat unwanted plants.

4. Our most promising finding was that removing small quantities of invader and resident species' biomass at early growth stages reduced the invader and increased resident species over time. Defoliating more intensively at later growth stages often gave the opposite response. Forage availability is lowest in spring, so a given landmass can be prescription grazed with fewer animals (or in less time) in spring compared with later in the year.

5. *Synthesis and applications.* Our study illustrates that responses to prescribed grazing depend heavily on the specifics of the grazing regime. Our results show that some grazing strategies have the potential to exacerbate weed problems, while other strategies help to control the invader and restore desired species. In the case of *E. esula*, very light prescribed grazing can be beneficial when conducted early in the growing season.

Key-words: *Euphorbia esula*, herbivore defence, invasive species, leafy spurge, rangeland, sheep, simulated grazing, targeted grazing

Introduction

Prescribed grazing seeks to suppress invasive plants and encroaching woody plants in grasslands by manipulating the timing, intensity and frequency of grazing and by stocking animal species based on dietary preferences (DiTomaso 2000; Wheeler *et al.* 2007). For example, goats are browsers, so they are sometimes stocked on grasslands invaded by pines and junipers (Campbell *et al.* 2007), and sheep eat forbs, so they are sometimes stocked on exotic forb-invaded grasslands (Popay & Field 1996).

Prescribed grazing has received some attention in recent decades, but studies have been limited in scope because of the logistical difficulties involved in manipulating large numbers of animals. Studies are often restricted to only one prescribed grazing treatment (e.g. Johnson & Peake 1960; Olson & Wallander 2001; Sheley, Jacobs & Martin 2004), and even the largest studies have had three or fewer treatments (e.g. Lym, Sedivec & Kirby 1997; Bruijn & Bork 2006; Seefeldt, Taylor & Van Vleet 2007). If plant community dynamics vary widely depending on the timing, intensity and frequency of grazing, then studies that evaluate larger numbers of grazing treatments will be needed to identify optimal prescribed grazing strategies.

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Our study used simulated grazing (clipping) to overcome limitations associated with using animals. This technique provides a means for evaluating large numbers of 'grazing' treatments without prohibitive labour or expense. Also, simulated grazing allowed us to measure both 'grazed' and 'not-grazed' biomass, so we were able to estimate total annual biomass production.

Our specific objective was to identify prescribed grazing strategies that restore resident species and reduce populations of *Euphorbia esula*; a clonal exotic invasive perennial forb infesting ~1.5 million hectares in the western United States (Duncan *et al.* 2004). We simulated both sheep and cattle grazing. Cattle are the predominant grazer of U.S. grasslands, and they tend to not eat *E. esula*. By contrast, sheep and goats often eat considerable quantities of *E. esula*. Sheep and goat grazing has appreciably reduced *E. esula* populations in some studies (Johnson & Peake 1960; Lym *et al.* 1997) but not in others (Lacey & Sheley 1996; Olson & Wallander 1998; Seefeldt *et al.* 2007), and these inconsistent findings make it difficult for managers to decide about stocking sheep and goats. Our aim was to unify past *E. esula* grazing research by studying a large number of grazing treatments. We observed sheep grazing *E. esula* under typical field conditions and then instituted simulated grazing treatments that mimicked our observations. We also instituted a supplemental irrigation treatment to measure the influence of inter-annual variation on grazing responses.

In addition to providing practical guidance, we aimed to gauge the importance of manipulating grazing timings, intensities and frequencies in prescribed grazing studies.

Materials and methods

Data on *E. esula* herbivory by sheep at a site near Terry, Montana (46°43'6"N, 105°21'0"W) were used to design simulated grazing treatments for three other sites. Data were collected in 2005 at *E. esula* pre-flowering (April), flowering (May) and seed production (June) immediately after sheep grazing was discontinued. Prior to flowering, sheep completely defoliated almost 100% of stems. At flowering and seed production, sheep partially defoliated between 80% and 100% of stems (based on 10 randomly placed 1000-cm² frames). We sampled 100 grazed stems and 100 not-grazed stems randomly at flowering and seed production to estimate the percentage of stem height removed. We regressed basal stem diameter on stem height (flowering: $R^2 = 0.47$; seed-producing: $R^2 = 0.67$) to estimate how tall grazed stems would have been had they not been grazed. Based on this protocol, we concluded that sheep reduced stem heights by $20 \pm 8\%$ at flowering and $30 \pm 10\%$ at seed production.

STUDY SITES

Our three study sites were in south-east Montana, and each site had a long history of cattle grazing. We fenced the sites to exclude livestock grazing over the course of our study.

Site 1

Site 1 was located 16 km south of Locate, Montana (46°16'38"N, 105°08'56"W). Pre-treatment *E. esula* ranged between 50 and 100 stems m⁻². Grasses present at the site were *Pascopyrum smithii*, *Poa pratensis* and *Bouteloua gracilis*. Forbs included *Taraxacum officinale*,

Lactuca serriola, *Lactuca tatarica*, *Medicago sativa* and *Tragopogon dubius* and made up less than 7% of the site's biomass.

Site 2

Site 2 was located 50 km south-east of Fallon, Montana (46°41'49"N, 104°39'48"W). Pre-treatment *E. esula* ranged between 10 and 20 stems m⁻². The only grass in evidence was *Bromus inermis*, and the forbs *L. tatarica*, *M. sativa*, *Melilotus officinalis*, *Melilotus albus*, *T. dubius*, *T. officinale* and *Vicia americana* made up less than 8% of the site's biomass.

Site 3

Site 3 was located 8 km west of Miles City, Montana (46°20'50"N, 105°59'11"W). Pre-treatment *E. esula* ranged between 150 and 300 stems m⁻². Grasses present at the site included *Bromus japonicus*, *Bromus tectorum* and *P. smithii*. Forbs (*Glycyrrhiza lepidota*, *Lepidium densiflorum*, *T. dubius*, *T. officinale*) made up less than 2% of the site's biomass.

EXPERIMENTAL DESIGN

Euphorbia esula pre-flowering, flowering, seed production and pre-flowering + seed production defoliation treatments were applied from 2005 to 2007 (Fig. 1). Corresponding to our sheep grazing observations, we defoliated 80% or 100% of stems, and we also had treatments that defoliated no stems in order to simulate cattle grazing. In addition to varying percentages of stems defoliated, we also varied the defoliation height in accordance with our sheep grazing data. *Euphorbia esula* stems were defoliated to ground level at pre-flowering, whereas only the top 20% and 30% of stems were removed at flowering and seed-production respectively.

We also defoliated the other forbs and grasses across a range of levels corresponding to no, light and heavy grazing. (Hereafter, we refer to the forbs and grasses as 'resident species', although several of the species are not native to the United States) Resident plant defoliation

P L 100	P L 100	P H 100	P H 100	F L 0	F L 0	F H 0
F H 0	F L 80	F H 80	F H 80	F L 100	F H 100	F H 100
S L 80	S H 80	S H 80	S L 100	S H 100	S H 100	P/S L 80
P/S H 80	P/S H 80	P/S L 100	P/S H 100	P/S H 100	N	N

Fig. 1. One of two blocks of the simulated grazing experiments conducted at sites 1 and 2. Each box represents a treatment that was randomly assigned to plots. Plants were either not defoliated (N), or were defoliated at the pre-flowering (P), flowering (F), seed-producing (S), or pre-flowering and seed-producing (P/S) stages of *Euphorbia esula* growth. Either 0% (0), 80% (80) or 100% (100) of *E. esula* stems were defoliated. Approximately 50% of resident plant biomass was removed from lightly defoliated plots (L), whereas resident plants in heavily defoliated plots (H) were defoliated at 2 cm above the soil surface. Dots indicate plots that were irrigated with 54 mm in May and 61 mm in June.

treatments were: (i) no defoliation; (ii) remove 50% of biomass by defoliating at a fixed height (hereafter 'light defoliation'); and (iii) defoliate plants at 2 cm above soil level (hereafter 'heavy defoliation') (Fig. 1).

We applied a supplemental water treatment to assess the effects of growing season precipitation. Irrigated plots received the 30-year monthly average precipitation for May (54 mm) in May, and likewise the average precipitation for June (61 mm) in June (Fig. 1). Plots were irrigated with a handheld sprinkler with half the water being added early in the month and the remainder mid-month.

Site 1 and 2 experiments were arranged in a randomized block design with two replicates. Plot dimensions were 1.25 × 1.25 m, but only the inner 1.0 m² was measured to obviate edge effects. We used an electric string trimmer to remove the top ~30% of flowering stems in a large (~10 m) plot buffer area around plots to limit unrealistic *E. esula* seed influxes into grazed plots. This step may have been unnecessary because very few *E. esula* seeds germinate, survive and contribute appreciably to biomass production within mature *E. esula* stands (Bowes & Thomas 1978).

Site 3 had much higher *E. esula* densities than sites 1 and 2. In 2006 and 2007, we applied a subset of the defoliation treatments to site 3; (i) a not-defoliated control; (ii) defoliation of all *E. esula* stems combined with the light resident plant defoliation treatment; and (iii) defoliation of all *E. esula* stems combined with the heavy resident plant defoliation treatment. Growth stages at times of defoliation were as described for sites 1 and 2, as were *E. esula* defoliation heights, plot dimensions and the plot border protocol. Plots were arranged in a thrice-replicated split-plot design with defoliation timing as the whole-plot factor and defoliation treatments as sub-plot factors (3 replicates × 4 growth stages × 3 defoliation treatments = 36 plots).

DATA COLLECTION

We gathered pre-treatment data to control for differences among plots. At sites 1 and 2, we clipped all plants to soil level in late summer 2004 when plants were dormant. At site 3, we measured *E. esula* stem lengths around peak standing crop in 2005 and clipped all resident plants to ground level in two randomly placed 0.1-m² frames. The pre-treatment samples were sorted into current-year resident forb, grass and *E. esula* components. All biomass samples were weighed after drying for 48 h at 60 °C.

We needed to measure biomass removed from plots through simulated grazing as well as biomass remaining in plots in order to estimate annual production per plot. Measuring removed biomass was straightforward: we retained, dried and weighed it. We developed regressions that predicted stem weights from heights and applied these regressions to stem material remaining in plots at peak standing crop to estimate not-removed *E. esula* biomass. Regression data came from 100 stems gathered outside the plots at each site. We defoliated half the stems, which allowed us to develop separate regressions for defoliated and not-defoliated stems. The regression equations were fairly precise ($R^2 = 0.64\text{--}0.89$), except for one ($R^2 = 0.16$). We concluded the low R^2 resulted from a lack of stem height variation at site 3, and the mean square error indicates the regression predicts plant weights fairly accurately. In 2005 and 2006, we estimated not-defoliated biomass of resident plants by clipping to soil level in small randomly placed frames (300 cm² in 2005, 800 cm² in 2006). In the final year (2007), we clipped all plants to ground level around peak standing crop. Therefore, our final-year production estimates are likely the most accurate because they did not rely on regressions or subsampling. However, extracting current-year biomass from the large 2007

biomass samples was impractical, so we used regression to predict percent current-year growth from ocular estimates ($R^2 = 0.95$, $n = 30$).

ANALYSIS

We analysed the site 1 and 2 data jointly, but site 3 was analysed separately due to differences in experimental design, the sequence of study years and because the dominant grasses were annuals as opposed to perennials. Several candidate models were fit to the data, and in part, we relied on posterior predictive checks to select models (Gelman *et al.* 2004). Specifically, we simulated 20 replicate data sets by sampling the posterior distribution of model parameters and inserting deviates into the models. We then searched for systematic differences between simulated and observed data. Systematic differences indicated when important parameter(s) were missing from the models. We also relied on other considerations in selecting models, and we discuss these in the course of presenting our results. The model we ultimately used for the site 1 and 2 data was:

$$\ln(y_{jl}) \sim N(\mu + s_i + t_{ij} + w_{ijk} + \beta_{ij}q_l + d_{jm} + r_n + p_l, \sigma_j^2) \quad \text{eqn 1}$$

where the response (y_{jl}) is biomass production of the plant/plant group being modelled (i.e. *E. esula* or resident plants) in plot l during year j . Other terms describe a mean (μ) and effects of site i (s_i), year j at site i (t_{ij}), water treatment k , during year j , at site i (w_{ijk}), pre-treatment biomass of the plant/plant group being modelled in plot l during year j at site i ($\beta_{ij}q_l$), defoliation treatment m during year j (d_{jm}), block n (r_n) and plot l (p_l), with the (p_l) being modelled as random effects. To simplify model interpretation, pre-treatment data were standardized to mean 0, standard deviation 1. We assumed the measurement error variance (σ^2) varied by year because our measurement protocol varied by year. We also fit models containing terms for residual temporal covariances (Pourahmadi & Daniels 2002), but these terms did not appreciably change estimates of treatment responses, so we fixed them at zero. The site 3 models were the same as the site 1 and 2 models, except that whole-plot factors were included to account for the split-plot design, and these were modelled as random effects.

We fit the models in a Bayesian way. We assigned non-informative prior distributions to the parameters, and the regression coefficients and random effects means were assigned uniform priors. Priors for the random error variances were $p(\sigma^2) \propto \frac{1}{\sigma^2}$, and priors for random effects variances were proportional to 1.0. All marginal posterior distributions were in closed form with the variances being scaled inverse chi-square, and other parameters being normally distributed. Thus we used a Gibbs sampler constructed in FORTRAN to simulate the joint posterior distributions (Intel Corporation 2003). We assessed convergence by comparing within- and between-chain variances of 10 parallel Markov chains via the potential scale reduction factor described by Gelman & Rubin (1992). Chains of length 5000 with the first half discarded as burnin were sufficient to obtain convergence (i.e. potential scale reduction factors < 1.1). Inferences were based on 50% and 95% Bayesian credible intervals, which are analogous to confidence intervals but with a simpler interpretation (Berry & Lindgren 1996). For example, there is simply a 0.5 probability that a parameter falls within the 50% credible interval.

Results

Equation 1 assumes treatments had the same effects at sites 1 and 2. A posterior predictive check helped justify this

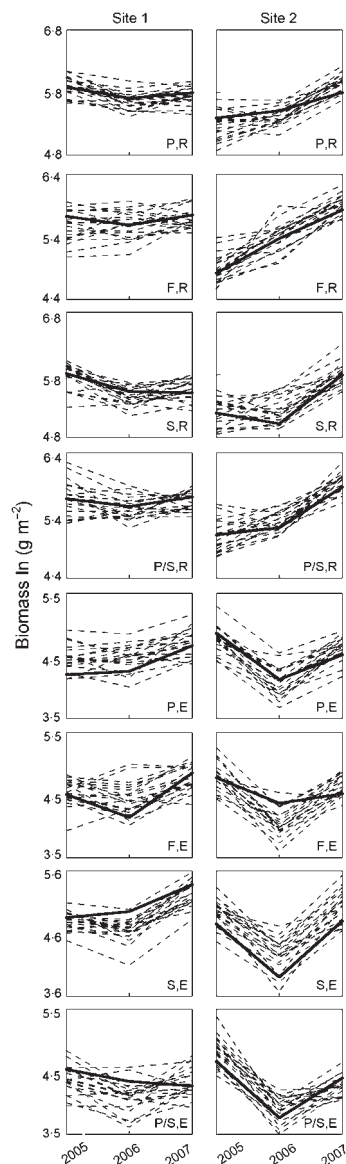


Fig. 2. Observed (dark lines) and simulated (dotted lines) biomass profiles for resident plants (R) and *Euphorbia esula* (E). Dark profiles depict average resident plant and *E. esula* biomass production in field plots defoliated at the pre-flowering (P), flowering (F), seed-producing (S), or pre-flowering and seed-producing (P/S) stages of *E. esula* growth. Resident plant defoliation removed 50% of resident plant biomass, and *E. esula* defoliation mimicked sheep grazing. The lack of systematic differences between observed and simulated profiles indicates the observed data are plausible under the model.

assumption. If treatment effects varied appreciably by site, simulated profiles from eqn 1 would systematically over-predict observed profiles from one site and under-predict profiles from the other site, and there is little evidence for these inaccurate predictions (Fig. 2). Figure 2 presents data on plots subjected to light resident plant defoliation, but a predictive check for heavy defoliations gave similar results (data not shown).

Raw means and credible intervals suggested not-grazed controls yielded similarly to plots receiving simulated cattle

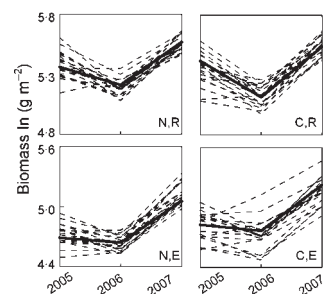


Fig. 3. Observed (dark lines) and simulated (dotted lines) biomass profiles for resident plants (R) and *Euphorbia esula* (E). All profiles are for treatments that did not defoliate *E. esula*. Profiles depict average biomass production when 50% of resident plant biomass was removed at *E. esula* flowering (C), or biomass production with no defoliation (N). The overlap between observed and simulated profiles indicates the observed data are plausible under the model.

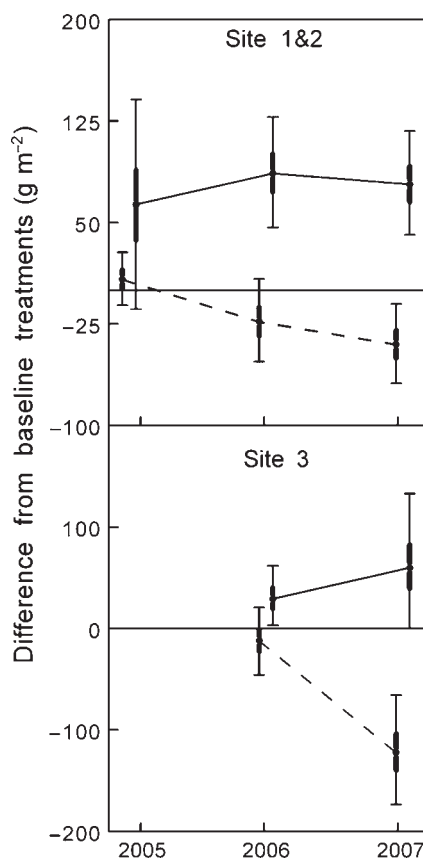


Fig. 4. Responses of *Euphorbia esula* (dotted lines) and resident plants (solid lines) to simulated grazing in eastern Montana. Defoliation occurred prior to *E. esula* flowering. Thick and thin bars represent 50% and 95% Bayesian credible intervals respectively. Unlike Figs 5–7, this figure has only two panels because light and heavy defoliation treatments were combined. The cattle-grazing treatment (resident plants lightly defoliated, *E. esula* not defoliated) yielded similarly to the not-grazed treatment, and these treatments combined served as a baseline treatment (i.e. the zero line).

grazing (i.e. resident plants lightly defoliated, *E. esula* not defoliated). Therefore, we did predictive checking, which justified combining these two treatments (Fig. 3). Together, we used the

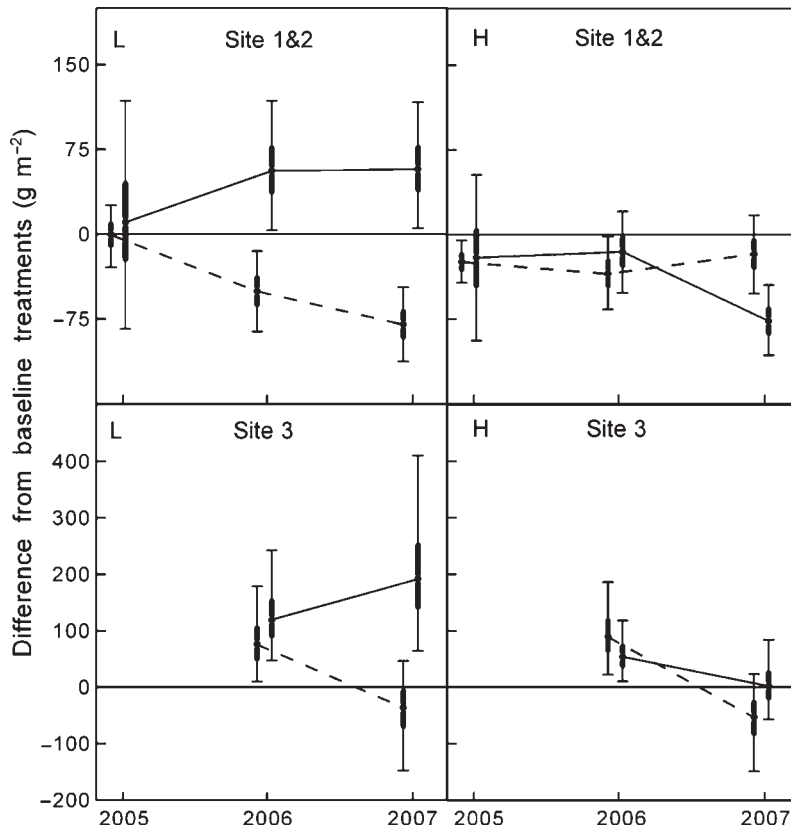


Fig. 5. Responses of *Euphorbia esula* (dotted lines) and resident plants (solid lines) to simulated grazing in eastern Montana. Defoliation occurred prior to *E. esula* flowering and again during *E. esula* seed production. Thick and thin bars represent 50% and 95% Bayesian credible intervals respectively. The cattle-grazing treatment (resident plants lightly defoliated, *E. esula* not defoliated) yielded similarly to the not-grazed treatment, and these treatments combined served as a baseline treatment (i.e. the zero line). In light defoliation plots (L), 50% of resident plant biomass was removed, and in heavy defoliation plots (H) resident plants were defoliated 2 cm above soil level.

Table 1. Percentage [mean (SD)] plant biomass removed at three *Euphorbia esula* growth stages (pre-flower, flower and seed-producing) averaged across three study sites in mixed-grass communities in the northern great plains. For example, if a plot produced 100 g in a given year and 10 g was removed at pre-flowering, then 10% was removed from the plot

Defoliation timings	<i>E. esula</i>			Resident plants					
	2005	2006	2007	Light defoliation			Heavy defoliation		
	2005	2006	2007	2005	2006	2007	2005	2006	2007
Pre-flower	10 (4)	8 (12)	11 (5)	13 (6)	9 (5)	6 (3)	20 (7)	14 (5)	14 (4)
Flower	14 (5)	12 (16)	9 (5)	30 (11)	36 (20)	17 (7)	35 (14)	57 (14)	46 (16)
Seed-producing	41 (10)	39 (14)	22 (6)	41 (12)	43 (9)	37 (21)	83 (7)	87 (5)	78 (10)

cattle grazing treatment and not-grazed control as a basis for comparison (Figs 4–7). The cattle grazing treatment mimicked prevalent U.S. grazing practices, so potential sheep grazing strategies were compared with this baseline.

Parameters describing the main effects of supplemental watering were marginally positive. Parameters describing water \times defoliation interactions had credible intervals nearly centred on zero, and a predictive check suggested water \times defoliation interaction terms were unnecessary (data not shown). This suggests our defoliation responses are robust to changes in growing season precipitation. However, precipitation was above the 30-year average every year, and water \times defoliation interactions might have been important had it been drier.

Credible intervals for treatments defoliating 80% vs. 100% of *E. esula* stems were very similar, and a predictive check (data not shown) further justified combining these treatments.

Measurement error probably prevented us from distinguishing subtle differences between 80% and 100% defoliations. We also combined the treatments that defoliated resident plants at the pre-flower timing. The similar amount of resident plant biomass removed in the treatments helped justify the decision (Table 1), as did the close correspondence between observed and simulated profiles (Fig. 2, first and fifth rows).

On a percentage basis, pre-flower treatments tended to defoliate resident plants more heavily than *E. esula* (Table 1). Nevertheless, pre-flower defoliations consistently increased resident plants and decreased the invader over time (Fig. 4). Compared with defoliating at the pre-flower stage only, defoliating at seed production in addition to pre-flower gave less consistently favourable results (Fig. 5). Specifically, defoliating twice a year sometimes caused resident plants to decrease in abundance in comparison with the baseline treatment (Fig. 5, right-hand side).

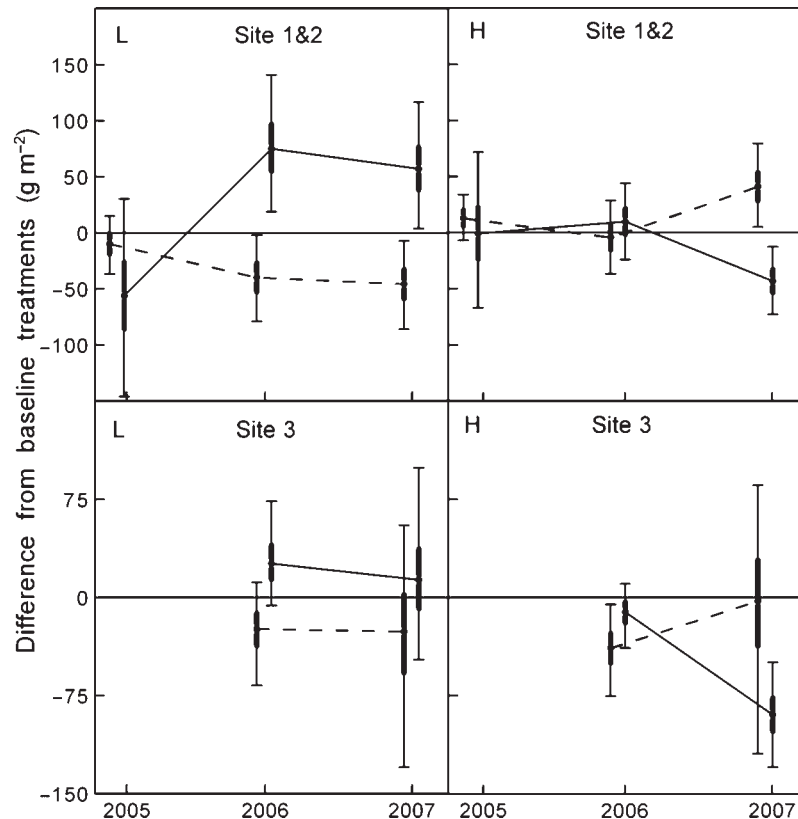


Fig. 6. Responses of *Euphorbia esula* (dotted lines) and resident plants (solid lines) to simulated grazing in eastern Montana. Defoliation occurred during *E. esula* flowering. Thick and thin bars represent 50% and 95% Bayesian credible intervals respectively. The cattle-grazing treatment (resident plants lightly defoliated, *E. esula* not defoliated) yielded similarly to the not-grazed treatment, and these treatments combined served as a baseline treatment (i.e. the zero line). In light defoliation plots (L), 50% of resident plant biomass was removed, and in heavy defoliation plots (H) resident plants were defoliated 2 cm above soil level.

Pre-flower and light flowering defoliations tended to have similar effects (Figs 4 and 6) although the flowering treatment at site 3 is one possible exception: the wide credible intervals that overlap zero indicate our data are inconclusive with regard to this treatment (Fig. 6).

Heavy defoliations at flowering had a negative impact on resident plants and increased *E. esula* over time at two or maybe all three sites (Figs. 6). Heavy defoliation at seed production was also generally harmful to resident plants but the effects on *E. esula* were inconclusive (Figs 5 and 7). On a percentage basis, heavy defoliations at flowering and seed-production removed much more resident plant than *E. esula* biomass (Table 1). Thus it is perhaps unsurprising that these defoliation treatments tended to reduce resident plants over time (Figs 5–7) while sometimes increasing the invader (Fig. 6).

The only light defoliation that conclusively reduced the number of resident plants was the seed-production defoliation treatment at site 3 (Fig. 7). Annual grasses predominated at site 3, and simulated grazing may have limited annual grass seed production and recruitment.

Discussion

The pre-flower treatments that defoliated both *E. esula* and resident plants closely mimicked spring sheep grazing. These treatments tended to reduce the invader and increase resident species over time (Fig. 4). Defoliating more intensively when *E. esula* was flowering and producing seeds sometimes had a

similar effect and sometimes increased the invader at the expense of resident species (Figs 5–7, Table 1). These results are consistent with an appreciable body of *E. esula* grazing research. Specifically, three studies reported gradual reductions in *E. esula* abundance when much of the sheep/goat grazing targeted vegetative stems (Johnson & Peake 1960; Lym *et al.* 1997; Jacobs, Sheley & Borkowski 2006), and three other studies reported no significant effect of sheep grazing when much of the grazing targeted flowering and seed-producing stems (Lacey & Sheley 1996; Olson & Wallander 1998; Seefeldt *et al.* 2007). In addition to the *E. esula* growth stage, numerous other factors varied among the previous studies (e.g. plant community, precipitation), so the previous studies do not pinpoint vegetative plants as susceptible to defoliation. Instead, grazing of seed-producing plants is usually advocated because of its (ostensibly) greater impact on *E. esula* seed production. Our study was well suited to compare the timing of grazing because it held other factors constant. In identifying optimal prescribed grazing strategies for other weeds, it is likely important to manipulate timings and intensities of grazing within the same study.

Unlike our study, another simulated grazing found no statistically significant difference between pre-flower and seed-producing *E. esula* defoliations, and compared with pre-flower defoliations, flowering defoliations provided better control (Kirby *et al.* 1997a). Kirby *et al.* (1997a) reported *E. esula* yields of 204 ± 35 (control), 157 ± 18 (vegetative), 38 ± 10 (flowering) and 95 ± 16 (seed-producing) g m^{-2} for the last

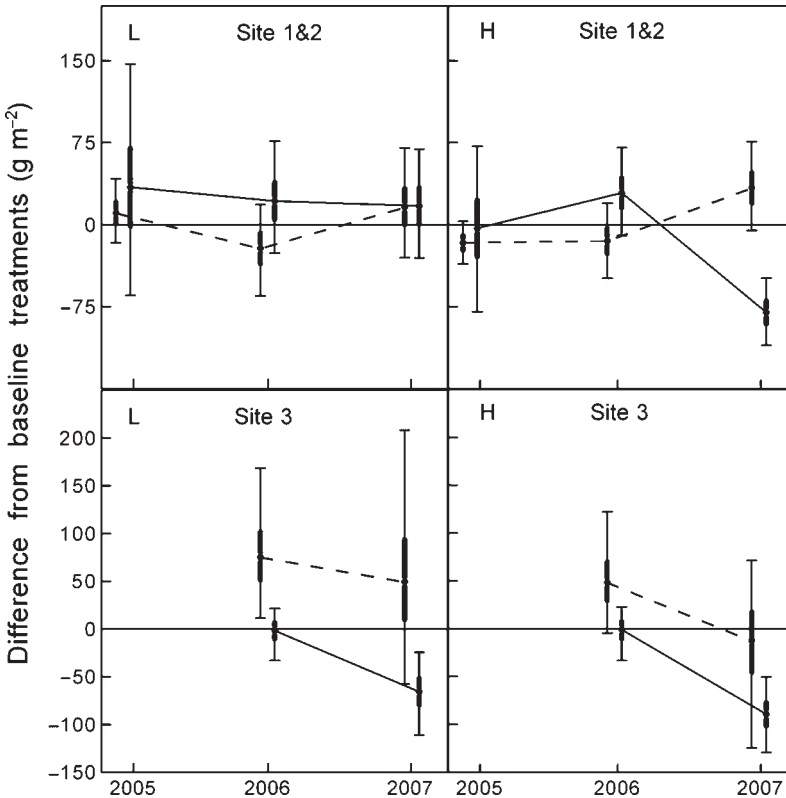


Fig. 7. Responses of *Euphorbia esula* (dotted lines) and resident plants (solid lines) to simulated grazing in eastern Montana. Defoliation occurred during *E. esula* seed production. Thick and thin bars represent 50% and 95% Bayesian credible intervals respectively. The cattle-grazing treatment (resident plants lightly defoliated, *E. esula* not defoliated) yielded similarly to the not-grazed treatment, and these treatments combined served as a baseline treatment (i.e. the zero line). In light defoliation plots (L), 50% of resident plant biomass was removed, and in heavy defoliation plots (H) resident plants were defoliated 2 cm above soil level.

year of their 5-year study. Also in contrast with our study, Kirby *et al.* (1997a) found that resident plant yields were not statistically different regardless of whether *E. esula* was defoliated when vegetative, flowering or producing seeds. A major difference between the studies is that Kirby *et al.* (1997a) did not defoliate resident plants. Herbivory tends to be more deleterious in highly competitive environments (Tiffin 2002), so had Kirby *et al.* (1997a) defoliated the resident plants and thereby changed their production/competitive ability, then *E. esula* probably would have responded differently. Studies that defoliate resident plants in addition to weeds are more representative of typical prescribed grazing situations.

Prescribed sheep grazing in spring partially controls *E. esula* while favouring resident species. It would be desirable to identify effective spring grazing strategies for other invasive weeds, because a given landmass can be grazed in less time and/or with fewer animals in spring when biomass per unit area is low. This is particularly important in the United States where sheep and goat populations are in continued decline (NASS 2008).

The energetic costs of herbivore defence may explain why *E. esula* is most susceptible to spring defoliation (Gershenson 1994; Stamp 2003). Defoliating *E. esula* induces production/translocation of tannins and perhaps other carbon-based compounds that deter feeding (Roberts & Olson 1999). When *E. esula* is grazed only once a year, this investment in defence could have negative fitness consequences because it will not prevent further feeding and it may reduce plant growth. If *E. esula* produces tannins for the entire growing season following defoliation, then the costs of defence will be highest follow-

ing spring defoliation because tannins will be produced for longer time periods.

Herbivore defence may also explain why *E. esula* fitness declined only after multiple years of defoliation. *Euphorbia esula* stores large reserves of non-structural carbohydrates in its extensive root system (Lym & Messersmith 1987; Gesch, Palmquist & Anderson 2007). When defoliated only 1 year, *E. esula* may use stored carbohydrates to maintain both tannin production and growth. But as annual defoliations deplete carbon reserves (Johnson & Peake 1960; Lym *et al.* 1997), allocation to defence may restrict allocation to growth. Of course, even if energetic costs of herbivore defence are negligible, gradual carbon depletion may explain why multiple years of defoliation are required to reduce *E. esula*.

In our study the resident plants were primarily grasses, for which silica uptake is an important herbivore defence response (Vicari & Bazely 1993). As with the production of tannins, there are energetic costs to silica uptake (Ma *et al.* 2006), but the costs may be lower than synthesizing tannins (Massey, Roland-Ennos & Hartley 2007). Inducing both invaders and resident plants to defend may ultimately benefit resident plants, particularly if the invader experiences higher defence costs.

Like *E. esula*, several other species are susceptible to defoliation at early growth stages (Marquis 1992; Garcia & Ehrlen 2002; Gustafson 2004; Knight 2005). Conversely, several other species are more susceptible to defoliation at later growth stages (Escarre, Lepart & Sentuck 1996; Valderrabana & Torrano 2000; Ramula 2008). These disparate responses illustrate the risks inherent in generalizing our results to other invasive

weeds. In designing prescribed grazing management strategies for any given invader, it will be important to determine how the invader and its neighbours respond to a range of grazing protocols. Simulated grazing provides an efficient method to compare grazing timings, intensities and frequencies (Lindgren, Johan & Jon 2007; Schutzenhofer & Knight 2007). However, several authors have pointed out that simulated grazing is somewhat artificial in that it omits grazing influences such as trampling and deposition of urine and saliva (Escarre *et al.* 1996; Schutzenhofer & Knight 2007). Nonetheless, our study and that of Lehtila & Boalt (2004) demonstrate that simulated and natural herbivory can induce similar plant growth responses. We believe prescribed grazing strategies will be more reliable when natural grazing studies corroborate results from simulated grazing.

Semi-arid grasslands are expansive ecosystems that generate relatively low revenues per unit area. Therefore, the typical grassland manager cannot afford to invest extensive resources in large-scale weed management. Instead, managers seek inexpensive strategies capable of minimizing invaders and their impacts. Compared with other strategies, such as herbicide application and seeding, prescribed grazing can be inexpensive, and our study shows that even very light prescribed grazing with sheep can reduce weeds and increase desired species. We believe that with careful study and use, prescribed grazing could become a powerful tool for restoring degraded plant communities.

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