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Assessing Invasiveness of Exotic Weeds outside their Current Invasive Range

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When exotic species invade a region, it becomes important to assess their invasiveness in adjacent uninvaded regions to determine if weed prevention measures are needed. Leafy spurge and knapweed species are absent from the vast majority of eastern Montana, but the region is surrounded by regions heavily invaded by these species. To assess invasiveness of leafy spurge and Russian and spotted knapweed in common eastern Montana grassland sites, I introduced these species to three sites as seeds (120 live seeds plot^{-1}) and seedlings (6 plot^{-1}). I assessed how common grazing regimes influenced invasiveness by imposing cattle, sheep, mixed grazing (i.e., cattle plus sheep), and grazing exclusion treatments for 7 yr. Invader survival did not appear to differ greatly among sheep, cattle, and mixed grazing treatments, but excluding grazing lowered probabilities that plots maintained invaders for the entire study period at two of three sites. At these same sites, grazing exclusion increased growth rates of those invaders that did survive, at least in the case of leafy spurge. Regardless of grazing treatment or site, however, large proportions of plots did not maintain invaders through the end of the study period. At one heavy clay site, only one small leafy spurge plant persisted through the end of the study. In the seventh study year, the plots with the most leafy spurge and Russian knapweed produced 222 and 112 stems, respectively, and the stems remained mostly confined to the 2- by 2-m plots. These findings suggest that, barring intense disturbance, leafy spurge and spotted and Russian knapweed might be incapable of invading some grasslands of eastern Montana, particularly upland sites with high clay content. Any upland sites in the region these species are capable of invading will likely be invaded only very slowly.

Nomenclature: Leafy spurge, *Euphorbia esula* L.; Russian knapweed, *Acroptilon repens* (L.) DC.; Spotted knapweed, *Centaurea stoebe* L.

Key words: Cattle, grazing, invader, invasion, invasive, population dynamics, sheep.

Large regions often remain relatively free of exotic species long after adjacent, seemingly ecologically similar regions have become heavily invaded (Davies and Johnson 2011). When and where this occurs, management decisions hinge on how capable the invaders are of spreading from the invaded to uninvaded regions. U.S. grasslands provide prime examples of such partially invaded ecosystems. It is estimated that spotted knapweed (*Centaurea stroebe* L.), leafy spurge (*Euphorbia esula* L.), downy brome (*Bromus tectorum* L.), and thirteen other prevalent exotic weeds have invaded roughly 20% of the 263 million ha (156 million ac) of grasslands existing in the country (Duncan et al. 2004). If these common invaders are capable of spreading into large tracts of as yet uninvaded grasslands, then weed prevention efforts will be critical, because invasions by these species cause considerable economic and ecological damage (DiTomaso 2000; Rinella and Luschei 2007). Currently, the ability of the common invaders to spread beyond the grasslands they have already invaded is uncertain, so the extent to which land managers should prioritize preventing seed dispersal (e.g., Wace 1977), searching for and eradicating newly colonizing invader populations (e.g., Goodwin et al. 2012; Lonsdale and Lane 1994), and other weed prevention measures is not entirely clear.

It might be that the prevalent grassland invaders are well-adapted to U.S. grasslands as a whole, similar to what was found in a study of Scandinavian grasslands (Eriksson et al. 2006). If so, most or all uninvaded grasslands could gradually be invaded by one or more of the common invaders once sufficiently large introductions of seeds or other propagules occur (Clark 2007; Eriksson and Ehrlen 1992). An entirely different possibility, however, is that the uninvaded grasslands already routinely receive large

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Management Implications

Important management decisions hinge on how capable invasive plants are of spreading from invaded to uninvaded regions. I evaluated the invasiveness of leafy spurge and spotted and Russian knapweed in eastern Montana, a largely weed-free region surrounded by regions supporting large infestations of these invaders. Despite being introduced from large numbers of seeds and seedlings, the invaders failed to survive the 6-yr study period at one of three study sites, suggesting that the species cannot invade the many areas of eastern Montana that resemble that study site, particularly upland sites with high clay content. Extinction rates were high at the other two sites as well, but invaders did persist and grow modestly in some plots at these sites. Six yr after introduction, all invaders remained mostly confined to the 2- by 2-m plots where they were planted. This suggests that any invasions by the focal species in eastern Montana will likely proceed slowly, and careful scouting of any given uninvaded area once every several years should be sufficient to detect and efficiently eradicate newly colonizing populations. Finally, the study had grazing exclusion, sheep, cattle, and mixed grazing (cattle plus sheep) treatments. Compared to the grazing treatments, grazing exclusion decreased the number of plots that maintained invaders for the entire study period. Conversely, grazing exclusion increased invader biomass production in those plots that did maintain invaders for the entire study period, at least in the case of leafy spurge. Collectively, these results suggest grazing exclusion alone is unlikely to prevent invasions indefinitely. These results are consistent with research showing sheep grazing can be used to constrain spotted knapweed and leafy spurge abundances.

influxes of propagules, but they nevertheless remain uninvaded because they do not meet the common invaders' niche requirements. A number of the most problematic invaders of U.S. grasslands were introduced over a century ago (Sheley and Petroff 1999). Additionally, invasive weeds tend to be prolific seed producers (Mason et al. 2008) and their seeds are often transported long distances by vehicles, equipment, and animals (Hogan and Phillips 2011; Von der Lippe and Kowarik 2007). Together, these realities suggest that seeds of common invaders have been widely dispersed into grasslands for long periods but some grasslands have been able to repel invasions by these species. A small number of species-introduction experiments support the notion that some plant communities are inherently resistant to invasion (D'Antonio 1993; Lambrinos 2002; Vilà et al. 2008).

My overall goal in this study was to assess the ability of common, widely distributed exotic weeds to invade grasslands outside their current invasive range. My first specific objective was to test the ability of three invasive forbs, leafy spurge, spotted knapweed and Russian knapweed [*Acroptilon repens* (L.) DC.], to invade common grasslands of eastern Montana. This region is largely devoid of these invaders (Goodwin et al. 2012), except for small ($< \sim$0.01 ha), sparsely distributed patches along disturbed roadsides and a small number of larger populations ($\sim$ 20 ha) occurring in riparian corridors. These populations occur on far less than 1% of the land in the region, and it is unclear if the places where they occur represent rare, anomalous patches of habitat capable of supporting the invaders due to atypical environmental conditions and disturbance regimes or if the invaders are capable of spreading throughout a wide range of habitats in the region. It might be that any additional spread will remain confined to the types of roadside and riparian habitats where the invaders currently exist. Whereas this type of spread would cause negative impacts, the impacts would be much more severe if the invaders proved capable of invading the upland sites that comprise the overwhelming majority of the land area in the region. It is unknown if leafy spurge and knapweed species are invasive in typical upland habitats in the region.

The low abundance of knapweeds and leafy spurge in eastern Montana contrasts sharply with the neighboring regions of North Dakota, which is extensively invaded by leafy spurge, and western Montana, which is extensively invaded by spotted knapweed and leafy spurge and is invaded to a lesser extent by Russian knapweed. The proximity of these heavily invaded regions to eastern Montana, combined with concerns over the small, scattered invader populations that currently occur in eastern Montana, has motivated government-funded programs focused on preventing the invaders from spreading into eastern Montana (Goodwin et al. 2012). These programs have developed in the absence of information about the ability of the common invaders to invade the typical eastern Montana grasslands that make up the overwhelming majority of the region. There are important ecological and environmental differences between eastern Montana and the areas where the knapweeds and leafy spurge have proven highly invasive, and this should raise questions about the ability of these species to invade eastern Montana. Eastern Montana is considerably more arid than western Montana, most of North Dakota, and other regions heavily invaded by the knapweeds and leafy spurge (NOAA 2012). Also, compared to invaded areas of western Montana (Ortega and Pearson 2011; Rice et al. 1997), eastern Montana (Heitschmidt et al. 2005) supports far lower abundances of native forbs. It could be that, similar to many native forbs, invasive forbs such as the knapweeds and leafy spurge are poorly adapted to eastern Montana.

My second specific objective was to compare grazing exclusion and sheep (*Ovis aries*), cattle (*Bos primigenius*), and mixed grazing (cattle plus sheep) treatments to determine how they varied in terms of invader defoliation and effects on invasion dynamics. It is important to consider grazing management in evaluating the susceptibility of grasslands to invasion because herbivory is known to influence invasion dynamics (Eschtruth and Battles

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2009; Lambrinos 2002; Levine et al. 2004). Cattle and sheep are dominant herbivores of eastern Montana grasslands. Cattle generally consume only small proportions of the available leafy spurge biomass when grazing grasslands heavily invaded by this species (Kronberg 1993; Landgraf et al. 1984; Lym and Kirby 1987), whereas sheep tend to consume considerably greater quantities (Kronberg and Walker 1999; Seefeldt et al. 2007; Walker et al. 1994). Sheep grazing has reduced well-established leafy spurge and spotted knapweed populations in some studies (Jacobs et al. 2006; Rinella and Hileman 2009; Seefeldt et al. 2007; Sheley et al. 2004), and this suggests it might be possible to use sheep grazing to prevent forb invaders from colonizing uninvaded sites.

Materials and Methods

Study Sites. This study took place at three upland sites on the 22,260-ha Fort Keogh Livestock and Range Research Station in eastern Montana. Distances between sites ranged from 10 to 16 km (6.2 to 9.9 mi). The sites had a long history of cattle grazing with conservative stocking rates selected to remove ~50% of the plant biomass produced on an annual basis. Soils at Site 1 were Marvan-Vanda silty clays, and dominant plant species were western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], and Japanese brome (*Bromus japonicus* Thumb. ex Murr.). Soils at Site 2 were Eapa loams, and dominant plant species were western wheatgrass, blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], and threadleaf sedge (*Carex filifolia* Nutt.). Soils at Site 3 were Havre loams, and dominant plant species were western wheatgrass and needle-and-thread.

Experimental Protocol. Seeds of each of the three study invaders were collected at a different site in western Montana (near Bozeman, MT) in August 2004 and stored in a cold storage room at −7 C. Individual seedlings were established in 2.5-cm-diam by 12-cm-deep (1.0- by 4.7-in) pots containing commercial potting mix (Sunshine Mix #1; Sun Gro Horticulture, Inc., 15831 NE 8th Street, No. 100, Bellevue, WA 98008) in a greenhouse in January 2005. In March 2005, four 0.25-ha pastures were established at each site with one of these pastures grazed by sheep, one by cattle, one by sheep and cattle, and one not grazed. Within each pasture, each invader species (spotted knapweed, Russian knapweed, leafy spurge) was randomly assigned to a block of four 2- by 2-m (6.6- by 6.6-ft) plots (Figure 1). Within each block of four plots, two plots were randomly chosen to receive invader seed additions and the other two plots received invader seedling additions. In seedling addition plots, six seedlings per plot were planted with even spacing into intact resident vegetation in late March 2005 when Russian and spotted knapweed averaged five and eight true leaves per plant, respectively, and when leafy spurge averaged two stems per plant that averaged 4.9 cm in length. Within each of 12 evenly spaced 18-cm-diam microplots within each seed addition plot, 10 germinable seeds per microplot (germinability assessed with germination test) were evenly spread on the soil surface under the resident vegetation.

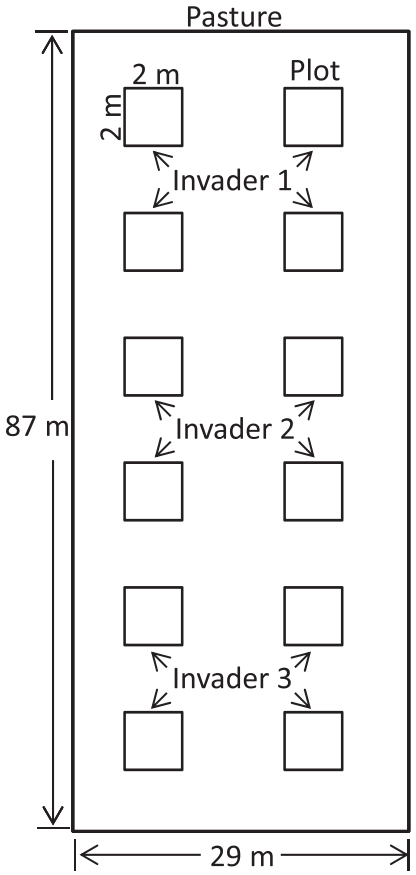


Figure 1. Arrangement of 12 plots in one of 12 pastures (three sites, four pastures per site) used to study the ability of spotted knapweed, Russian knapweed, and leafy spurge to invade eastern Montana grasslands. A different invader species was randomly assigned to the bottom, middle, and top group of four plots. Within each group of four plots, two plots were randomly chosen to receive invader seed additions and the other two plots received invader seedling additions.

Cattle and sheep grazing occurred at Site 1, then 2, then 3, once per year beginning around June 10 when plants were actively growing. Within any given year, the grazing period was the same for all pastures within a site, and grazing was discontinued when ocular estimates suggested 40% of noninvader biomass had been removed. This generally required between 4 and 7 d of grazing per site. All sites were grazed from 2005 to 2011, except for Site 1

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which was not grazed beyond 2009 because only one small invader plant remained living. At each site, one pasture was grazed by four heifers, one by 24 ewes, one by 12 ewes and two heifers, and one not grazed. The ratio of six ewes per heifer was based on differences in body weight and was chosen to encourage similar levels of resident species biomass removal across grazing treatments.

Data Collection. Data on invader and resident species abundances were gathered from all pastures immediately before grazing and again from grazed pastures immediately following grazing each year from 2005 to 2011. Within each plot, lengths of all invader stems were measured, and lengths of all leaves were measured for spotted and Russian knapweed rosettes. Resident species biomass was clipped to ground level from 20 areas measuring 20 by 50 cm. These clipping areas were randomly placed throughout each pasture, with the exception that they did not occur in invader plots. The biomass was dried at 60 C (140 F) for 48 h and weighed.

To estimate invader biomass nondestructively, additional length data were gathered from leaves of 45 Russian and spotted knapweed rosettes and 200 Russian and spotted knapweed and leafy spurge stems growing in small, isolated riparian populations in eastern Montana. In addition to measuring lengths of these plants, I harvested and weighed them using the methods described in the previous paragraph, which allowed me to develop allometric relationships for estimating biomass from length data.

Analysis. Five allometric relationships (one for stems of each species and two for rosette leaves of the knapweed species) were developed for converting invader stem and leaf length measurements to estimated biomass values. These relationships were developed by regressing the natural log of biomass on lengths. After back-transforming, the regression models accurately predicted mean biomass from lengths, but coefficients of variation for the regressions ranged between 0.3 and 0.74, illustrating considerable weight variation among stems and leaves of a given length. All data analyses involving estimated biomass values were repeated using the length data, and the two analyses gave similar results, so I concluded uncertainty in the regression models did not greatly influence conclusions.

The goal of the statistical analysis was to estimate the magnitude of the treatment effects. Therefore, instead of using ANOVA to test whether or not various treatment combinations differed statistically, I calculated confidence intervals to quantify the magnitude of the treatment effects (Rinella and James 2010). The following regression model was used to estimate the proportion of invader biomass grazed from plot i (y_i):

$$g(y_i) \sim N\left(\beta_0 + \beta_{1,j(i)} + \beta_{2,k(i)} + \beta_{3,l(i)} + \beta_{4,m(i)}, \sigma\right) \quad [1]$$

where $N(,)$ is the normal distribution with the first argument, before the comma, being the mean and the second argument, after the comma, being the standard deviation, and $g(y) = \log(y/(1 - y))$ is the logit transformation for proportional data. Indicator functions $j(i)$, $k(i)$, $l(i)$, and $m(i)$ indicate features of observation i. Specifically, the proportion of biomass of invader species $j(i)$ removed by grazing treatment $k(i)$ at site $l(i)$ in year $m(i)$ is given by y_i. This proportion was calculated by subtracting from 1.0 the ratio of post- to pregraze biomass totals. The biomass totals were calculated by summing biomass values from the four plots planted to a species in a pasture. Year effects (i.e., β_4) were modeled as random effects and all other parameters were fixed. More complicated models with two- and three-way interactions gave results similar to Equation 1.

A model nearly identical to Equation 1 was used to estimate the ratio of removed to total resident species biomass. With this model, however, the ratio of post- to pregraze biomass was estimated from the 20 frames clipped from each grazed pasture pre- and postgrazing.

The following logistic regression model, called the probit model (Albert and Chib 1993), was used to estimate probabilities plots supported invaders through the end of the 6-yr study period at Sites 2 and 3:

$$\Pr(y_i = 1) = \Phi(\alpha_0 + \alpha_{1,j(i)} + \alpha_{2,k(i)} + \alpha_{3,l(i)} + \alpha_{4,m(i)}). \quad [2]$$

Site 1 data were not analyzed with this model because only one small plant survived through the fifth growing season of the study at this site. With only one surviving plant, it would not be possible to use the model to estimate effects of invader species, introduction method (i.e., seed vs. seedling), and grazing for Site 1. Therefore, instead of using Equation 2 to model survival at Site 1, I estimated a confidence interval on the probability that plots maintained invaders irrespective of treatment for Site 1. With Equation 2, $y_i = 1$ if invaders remained living in plot i at the end of the study period, 0 otherwise, and $\Phi(\,)$ denotes the normal distribution function with the one argument being the mean and the standard deviation being 1.0. With Equation 2, the indicator functions $j(i)$, $k(i)$, $l(i)$, and $m(i)$ denote effects of invader species, introduction method (seed vs. seedling), pasture, and grazing (not grazed vs. grazed), respectively, in plot i. Grazing treatments were grouped together for analysis because, according to Bayesian posterior predictive P-values (Gelman et al. 2004), separate sheep (P = 0.26), cattle (P = 0.39), and mixed grazing (i.e., cattle plus sheep) (P = 0.22) parameters were not needed for the model to fit the data. A site term was also not needed (P = 0.43), nor were several interaction terms that were tested. The pasture effects (α_3) were modeled as random, and all other parameters were modeled as fixed. In using Equation 2 to estimate treatment effects on survival probabilities, and

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in using regression to estimate treatment effects on invader biomass production in the final study year (see next paragraph), I assumed the two plots that received the same invader species and introduction treatment within the same pasture represented independent replicates. The purpose of the pasture indicator variables (i.e., α_3) was to better meet this assumption. The assumption that replicate treatments within the same grazing pasture represent independent replicates is very common in grazing research because of the labor and expense of replicating grazing treatments (e.g., Bates 2005; Schmidt et al. 2012; Stohlgren et al. 1999).

To assess invader biomass per plot in the final study year, I used a regression model to estimate pregrazing invader biomass in the final study year, conditional on plots maintaining invaders at that time. This entailed using the common approach of deleting all zero values from the dataset and fitting the model to the remaining data (e.g., Gelman and Hill 2007), which rendered several of the more complicated candidate models unidentifiable. The model I fit had terms for site, invader species, and grazing vs. no grazing. The model also had a pasture random effect to reduce residual correlation among plots in the same pasture. FORTRAN programs were written to estimate parameters of all models of this study (Intel Corporation 2010).

Results and Discussion

Grazing of Resident Species. Estimates of resident species biomass removed by grazing treatments were similar whether or not models had site by grazing treatment and year by grazing treatment interactions. This indicated that differences among grazing treatments were fairly consistent across study sites and years, so estimated proportions of grazed to total biomass are reported as averages across sites and years (Figure 2). The cattle grazing point estimate for resident vegetation was −0.75 (Figure 2). Applying the inverse logit transformation to this estimate suggests that $32\% = 100 \times (e^{-0.75} / (1 + e^{-0.75}))$ of resident species biomass was removed by the cattle grazing treatment. Corresponding estimates for sheep and mixed grazing treatments are 41 and 35%, respectively. Collectively, these values suggest the three grazing treatments removed fairly similar quantities of resident species biomass.

Grazing of Invaders. As with resident species biomass, estimates of grazed invader biomass are reported as averages across sites and years because site by grazing treatment and year by grazing treatment interactions did not greatly affect estimates (Figure 2). The sheep and mixed grazing treatments appeared to remove similar percentages of invader biomass (Figure 2). Averaged across sites and years, point estimates suggest sheep and mixed grazing treatments removed 82, 85, and 69% of leafy spurge, Russian knapweed, and spotted knapweed biomass, respectively (Figure 2). Corresponding estimates for cattle grazing are lower: 58, 62, and 39%, respectively (Figure 2). There is > 0.99 probability that sheep and mixed grazing removed more biomass of each invader species than cattle grazing, even though the cattle confidence intervals (CIs) overlap the sheep and mixed grazing CIs appreciably (Figure 2). This is so because Figure 2 reports CIs on marginal distributions, not distributions of one grazing treatment conditional on another grazing treatment. The lower estimates for spotted knapweed than the other invaders are likely a result of animals avoiding the fibrous stems of this species (Olson and Wallander 2001).

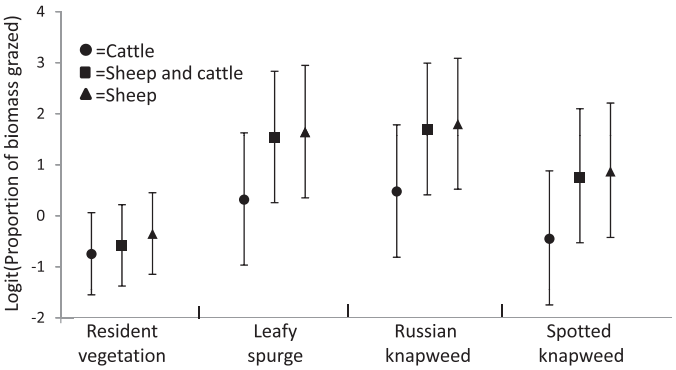


Figure 2. Point estimates (symbols) and 95% confidence intervals (CI) (bars) estimating biomass of resident species and three invasive forbs removed by sheep grazing, cattle grazing, or mixed grazing by sheep and cattle in eastern Montana. The estimates represent (logit-transformed) ratios of grazed to total biomass averaged over the three sites and seven growing seasons of the study. The inverse logit function transforms values from the figure to percentages. For example, the cattle grazing point estimate of −0.75 suggests that cattle removed $32\% = 100 \times (e^{-0.75} / (1 + e^{-0.75}))$ of resident species' biomass.

Invader Persistence. At Site 1, initial invader establishment was low (Figure 3), and only one small leafy spurge plant remained living by the fifth growing season. Consequently, grazing treatments and data collection were discontinued at Site 1. The probability that plots supported invaders through the fifth study year at Site 1 was 0.0208 ± 0.0206 (95% CI). Compared to Site 1, survival probabilities were considerably greater for Sites 2 and 3 (Figures 3, 4). The lower survival probabilities of site 1 could owe to soil compaction at that site resulting from its much higher clay content (Haan et al. 2012) or to the large differences in resident species compositions that existed between the sites.

Survival probabilities were greater for grazed than not-grazed plots ($P = 0.97$) (Figure 4). Similarly, other studies have found that grazing increases native forb colonization (Perez-Camacho and Rebollo 2009; Rinella et al. 2009). It

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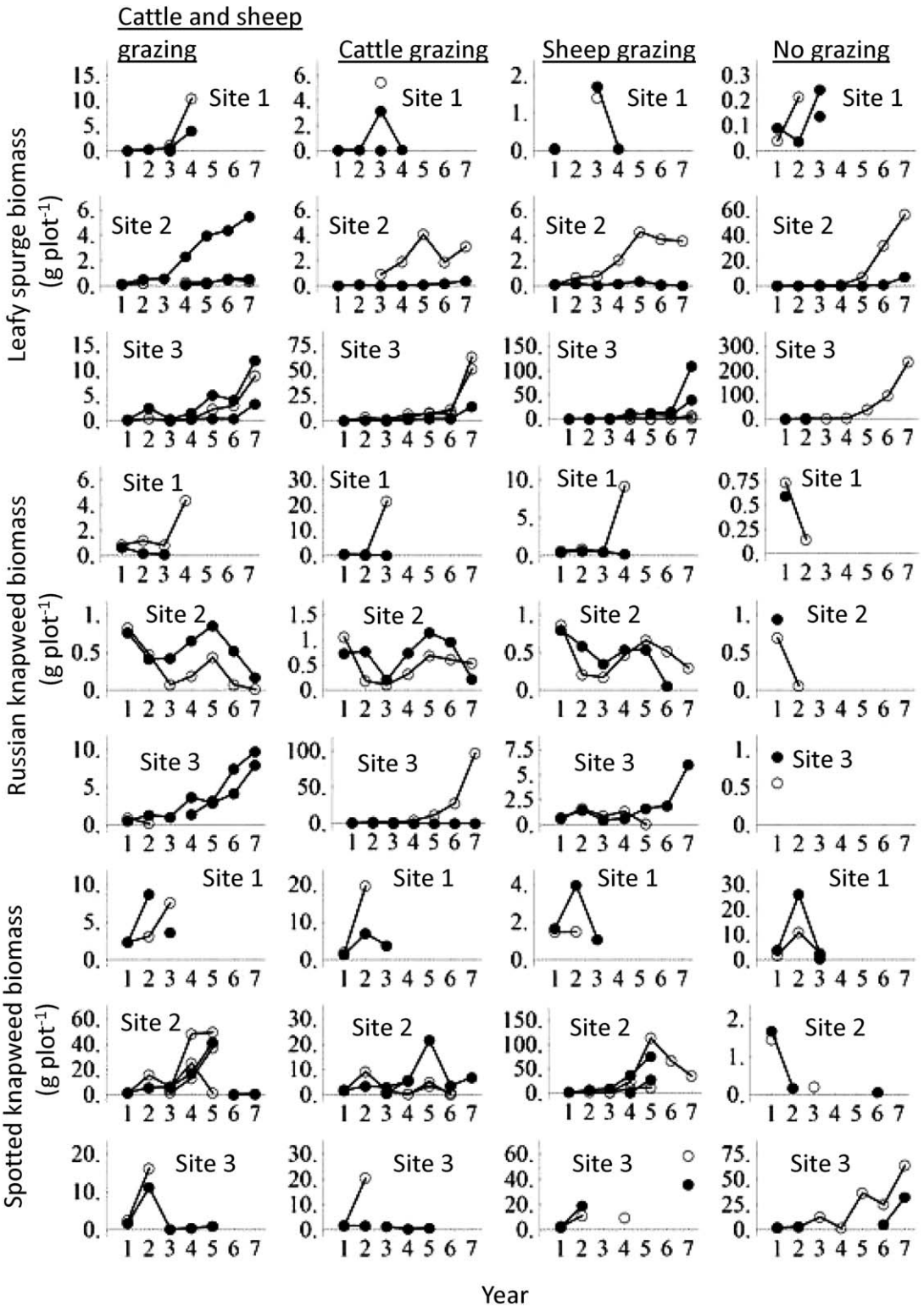


Figure 3. Biomass per population (i.e., plot) of three experimentally introduced invasive forbs in eastern Montana. Reported biomass values are from measurements taken prior to yearly grazing treatments. Invader populations were initiated from seed (hollow symbols) and seedlings (filled symbols). Biomass values for four field plots are graphed within each panel (two seed plots plus two seedling plots), but zero biomass values are omitted.

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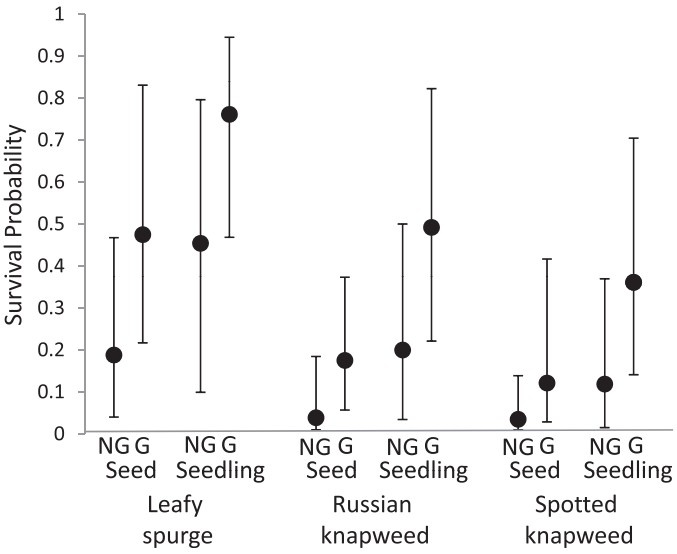


Figure 4. Point estimates (dots) and 95% confidence intervals (CI) (bars) estimating probabilities that grazed (G) and not grazed (NG) plots maintained invasive forb populations seven growing seasons after introduction. The study had sheep, cattle, and mixed grazing treatments, but model selection procedures indicated these three treatments could be combined into one grazing treatment for analysis. Populations were introduced from seed and seedlings. Data from Site 1 were not analyzed due to low plant survival.

appears that grazing can decrease the size and/or number of propagule introductions required for invaders to colonize eastern Montana grasslands.

Survival probabilities were greater for plots receiving six seedlings than 120 seeds ($P = 0.99$) (Figure 4), but whether introduced as seeds or seedlings, each species persisted for at least a few years at each site (Figure 3). These findings are consistent with some studies reporting invaders established from seed sown into mature stands of resident vegetation (D'Antonio 1993; Eriksson et al. 2006), although other studies have reported invaders failing to establish from seed (Eriksson and Ehrlen 1992; Meyer and Schmid 1999).

Regardless of invader species, site, and grazing treatment, invaders failed to persist in large numbers of plots when introduced from numerous seeds, which aids in overcoming safe site limitations (Oesterheld and Sala 1990), and when introduced as seedlings, which overcomes barriers to plant population establishment in grasslands (Figures 3, 4) (James et al. 2011). This provides evidence that, without large propagule introductions, the study invaders have low probabilities of colonizing grassland sites in eastern Montana. Propagule limitation and the chance events that act against small populations (i.e., demographic stochasticity) likely serve as critical deterrents to invader colonization in the region (Simberloff 2009; Snyder 2003).

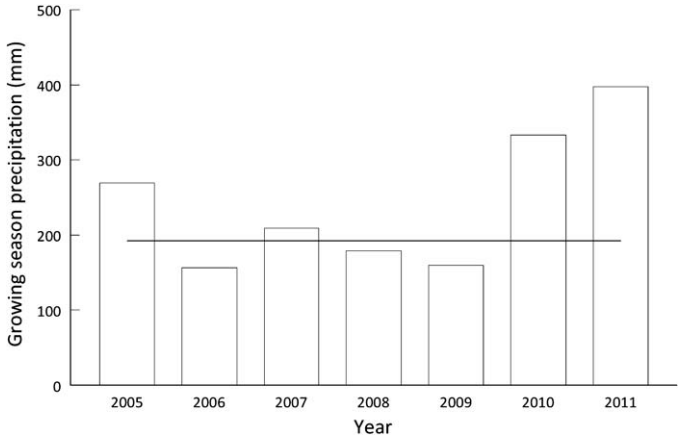


Figure 5. Total precipitation between April 1 and June 30 for each study year (bars) and averaged over the years 1877 to 2011 (horizontal line).

It might be that the study invaders are not capable of persisting in some eastern Montana grasslands, even when they do successfully colonize. The study invaders colonized Site 1, but appeared incapable of persisting there (Figure 3). This provides evidence the study invaders are incapable of invading Site 1 and many similarly high-clay sites in the region. The invaders also colonized Sites 2 and 3, but extinctions continued occurring throughout the study period at these sites (Figure 3). This leaves open the possibility that some or all the invaders that survived to the end of the study might have gradually become extinct if the study had been continued for a longer time period.

Invader Growth. Invader abundances at Sites 2 and 3 increased modestly in some plots over the study period both in terms of biomass (Figure 3) and stem and/or plant numbers. In the final study year, the plots with the most leafy spurge at Sites 2 and 3 produced 78 stems of mean length 29 cm and 222 stems of mean length 32 cm, respectively. The plots with the most Russian knapweed produced 112 stems of mean height 23 cm, and the plots with the most spotted knapweed had 6 and 12 flowering plants at Sites 2 and 3, respectively. The invaders remained mostly confined to the 2- by 2-m plots, although they had spread a few meters outside plot boundaries in some plots by the end of the study. The most rapid increases in invader biomass tended to occur during the last two study years (Figure 3). These increases might have reflected the increasingly rapid phase of exponential population growth (Cousens and Mortimer 1995) or a release from water limitation in the last two exceptionally wet years of the study (Figure 5).

Although grazing increased invader survival (Figure 4), it decreased leafy spurge biomass per plot ($P > 0.99$) (Figure 6). This finding might be at least partially explained by the greater defoliation of leafy spurge

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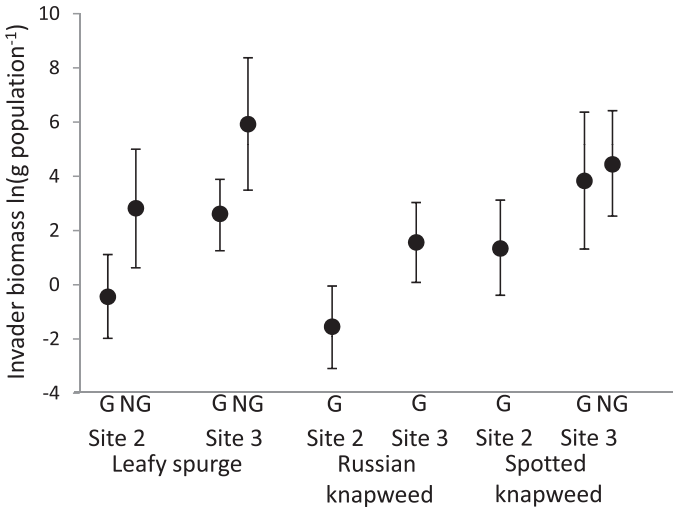


Figure 6. Point estimates (dots) and 95% confidence intervals (CI) (bars) estimating biomass of populations of three invasive forbs in the seventh growing season after they were experimentally introduced. The study had a not-grazed treatment (NG) and three grazing treatments (i.e., sheep, cattle, mixed grazing) that were combined for analysis (G). Data from Site 1 were not analyzed due to low plant survival. Because a number of populations became extinct, it was not possible to estimate mean biomass of not-grazed populations of Russian knapweed at Sites 2 and 3 and spotted knapweed at Site 2.

compared to resident species (Figure 2). The finding that grazing increased colonization but decreased growth is consistent with a meta-analysis reporting that herbivory usually does not outright prevent invasions but sometimes constrains invader abundances (Levine et al. 2004). The finding is also consistent with studies reporting that sheep grazing can reduce well-established populations of leafy spurge and spotted knapweed (Jacobs et al. 2006; Rinella and Hileman 2009; Seefeldt et al. 2007; Sheley et al. 2004).

Prior to this study, exceedingly little was known about the invasion dynamics of knapweeds and leafy spurge in eastern Montana. Thus a variety of experimental outcomes were considered possible prior to conducting this study, including the possibility that all introduced invaders would quickly become extinct and the possibility the invaders would spread so rapidly the study would have to be cut short to prevent large infestations from developing. Another possibility was that the invaders would spread rapidly under some grazing treatments but remain small or consistently become extinct under others. This study helped narrow the range of invasion dynamics to be expected of common invasive forbs in eastern Montana. Despite being introduced from large numbers of propagules, the invaders failed to persist at Site 1 (except for one small plant), and survival probabilities tended to be low to moderate at Sites 2 and 3 as well (Figure 4). Invader abundances remained low six growing seasons after introduction. These findings suggest leafy spurge and spotted and Russian knapweed are unlikely to establish unless large numbers of propagules are introduced at one time or small numbers of propagules are established on numerous occasions. Where these species do establish, they might or might not prove invasive, and where they prove invasive, their invasions will likely proceed only slowly. It is important to note, however, that grasslands of this study were not subject to recent, heavy disturbance such as overgrazing or wildfire. The invaders might have had greater survival and growth rates in the presence of disturbance (Davis et al. 2000; Lodge 1993). Finally, because propagules of the species derived from only three sites, it remains possible that the species might have had somewhat different survival and growth rates if different biotypes had been investigated (Crawford and Whitney 2010; Lachmuth et al. 2010).

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