

Linaria dalmatica invades south-facing slopes and less grazed areas in grazing-tolerant mixed-grass prairie

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Abstract Identifying environments where invasive plants are most invasive is key to understanding causes of invasion and developing effective management strategies. In mixed-grass prairie, invasive plants are often successful in relatively wet, nitrogen-rich areas, and areas protected from grazing. Dalmatian toadflax, a common invader of mixed-grass prairie, can also be favored by high water and nitrogen availability, but is thought to be relatively unpalatable to cattle, and therefore favored by grazing. We used spatially-

adjusted model selection techniques to quantify relationships between toadflax cover (measured using very high-resolution aerial imagery), and relative snow deposition (estimated with a blowing snow model), slope, aspect, soil texture, and grazing intensity (estimated by proximity to water tanks). Toadflax was common throughout the 400 ha study site, occurring in 742 of 1,861 images. Toadflax cover was high on steeper slopes, particularly those with southern aspects. These two topographic variables were more effective in explaining toadflax distribution than modeled snow deposition, suggesting that factors other than snow deposition cause toadflax invasion on south-facing slopes. Toadflax cover was also high in areas further from water tanks, indicating that grazing may inhibit toadflax invasion. More broadly, this result suggests that grazing can reduce invasion of even relatively unpalatable species in ecosystems with long evolutionary histories of grazing.

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Introduction

The mixed-grass prairie is the largest remaining grassland in North America. Although it is dominated by native species, large areas have also been invaded

by introduced species (Larson et al. 2001). Invasibility of mixed-grass prairie depends on both environmental variables and land use practices. At a landscape scale, invasive species richness and abundance tends to be highest in riparian areas, in species-rich plant communities, and along roadways, perhaps due to high water and nitrogen availability in such areas (Larson et al. 2001; Stohlgren et al. 1998; 1999a). Livestock grazing is the primary land use throughout the mixed-grass prairie. Although grazing can facilitate invasion in many ecosystems (Mack 1981; Sala et al. 1986; Hobbs 2001; Brooks et al. 2006), in mixed-grass prairie it has been found to have little effect on the richness of introduced species (Stohlgren et al. 1999b), and to inhibit invasion by several palatable introduced perennial grasses (Murphy and Grant 2005; Stacy et al. 2005; Vaness and Wilson 2007). This resistance to invasion in the presence of grazing may stem from the long evolutionary history of grazing in mixed-grass prairie (Milchunas et al. 1988; 1992; Stohlgren et al. 1999b; Lyman and Wolverton 2002).

In this study, we examined relationships between the spatial distribution of Dalmatian toadflax (*Linaria dalmatica* (L.) P. Mill. ssp. *Dalmatica*; henceforth “toadflax”) in mixed-grass prairie, and environmental variables thought to influence its invasion. Toadflax is a widespread invasive forb in western North America, including much of the mixed-grass prairie. It has been declared noxious in 12 western US states, and can reduce forage availability (Robocker 1974), livestock carrying capacity, and the land value of rangeland (Lacey and Olsen 1991).

Observations of toadflax suggest that it tends to invade disturbed areas, open rocky sites, well-drained, coarse-textured soils, and sloped areas, particularly those with a southern aspect (Alex 1962; Robocker 1974; Vujnovic and Wein 1996; Lajeunesse 1999; Rew et al. 2005). Experimental studies in mixed-grass prairie have found toadflax to be favored by both low species richness and high nitrogen availability (Maron and Marler 2008; Blumenthal 2009). Effects of water addition have been mixed. Spring water addition had little effect on toadflax invasion of experimental two-year-old mixed-grass prairie plant communities in western Montana (Maron and Marler 2008). In contrast, increased snowfall was critical to toadflax invasion of relatively undisturbed mixed-grass prairie in southeastern Wyoming (Blumenthal et al. 2008;

Blumenthal 2009). At the same study site, we have observed dense toadflax infestations on slopes with southern aspects. We hypothesize that such infestations might be associated with areas of high snow accumulation that develop as northwest winter winds blow snow onto southeast-facing slopes (Liston et al. 2007).

Although forage quality of toadflax is sufficient to meet livestock requirements (Frost et al. 2008), its stems and leaves contain bitter-tasting iridoid glycosides, and a potentially toxic quinazoline alkaloid (Groger and Johne 1965; Mahmoudian et al. 2002; Jamieson and Bowers 2010). Iridoid glycoside concentrations are highest early in the season, when relatively high forage quality would otherwise make toadflax most palatable (Frost et al. 2008, Jamieson and Bowers 2010). Observations that cattle tend to avoid toadflax also suggest that it is relatively unpalatable (Harris and Carter 1971; Lajeunesse 1999; Brown 2005). Consequently, grazing is thought to facilitate toadflax invasion (Brown 2005). In accord with this suggestion, we have rarely observed grazed toadflax at our study site. In contrast with this suggestion, however, we have observed dense toadflax infestations within cattle exclosures. It is therefore difficult to predict how grazing influences toadflax in mixed-grass prairie. Does grazing favor toadflax because cattle avoid it, or inhibit toadflax because native mixed-grass prairie species are well adapted to grazing?

Our objective was to quantitatively assess the relationship between toadflax distribution and environmental and management factors that might influence mixed-grass prairie invasibility. Specifically, we examined relationships between toadflax cover (estimated from very high-resolution aerial images) and snow accumulation (modeled with a blowing snow model), slope, aspect, soil texture, and cattle grazing intensity (estimated by proximity to water sources). We used spatially-adjusted model selection analysis (Hoeting et al. 2006) to identify the set of environmental factors that most parsimoniously explained toadflax abundance.

Materials and methods

To identify environmental correlates of toadflax invasion, we measured toadflax cover at 1,861 evenly-spaced locations within a 400 ha area of

native mixed-grass prairie using very high-resolution aerial imagery (Blumenthal et al. 2007). We then linked toadflax cover data with environmental data using the geographic information system, ArcGIS 9 (ESRI 2007), and used spatial linear models to determine the combination of variables that best explained toadflax cover.

Study site

The study site was located at the High Plains Grasslands Research Station, Cheyenne, Wyoming, at the southwestern edge of the northern mixed-grass prairie. This part of the mixed-grass prairie is relatively dry, with a long-term (130 year) average annual precipitation of 381 mm, and a peak in May. Precipitation during the year preceding sampling (July 2002–June 2003) was 340 mm. Measurements were made between late July and early August 2003 within five annually grazed (June through mid-October) pastures (Fig. 1). Throughout the site, vegetation was dominated by C3 grasses, primarily western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) and needle-and-thread (*Hesperostipa comata* Trin & Rupr.), and the C4 grass blue grama (*Bouteloua gracilis* (H.B.K.) Lab. Ex Steud). Primary soil series were Ascalon and Altvan sandy loams (Stevenson et al. 1984). The pastures were grazed for

at least 28 years prior to this study, and were grazed at either 6.29 ha per cow-calf pair (approximately 40% removal of above-ground net primary productivity) or 5.14 ha per cow-calf pair (60% removal) season-long stocking rates during the 8 years immediately preceding sampling.

Measurements of toadflax cover

We measured toadflax cover using aerial imagery with approximately 2 mm GSD (ground sample distance, a measure of resolution). The area represented in each image was approximately 8.5×5.7 m, varying slightly due to variation in airplane flight altitude. Details of image acquisition and analysis are described in Blumenthal et al. (2007). Briefly, images were taken from a piloted fixed-wing aircraft flown at 72 km h^{-1} ground speed, 100 m above ground, mounted with an 11.1-mega-pixel camera equipped with a 300 mm lens. An aerial survey system (Track'Air, Oldenzaal, The Netherlands) allowed the pilot to follow a predetermined flight plan (Didger II, Golden Software, Golden, CO, USA), and automatically triggered the camera to capture images at specified GPS (global positioning system) coordinates 70 m apart on east–west flight-lines spaced 30 m apart north to south. Resultant image resolution was sufficient for trained observers

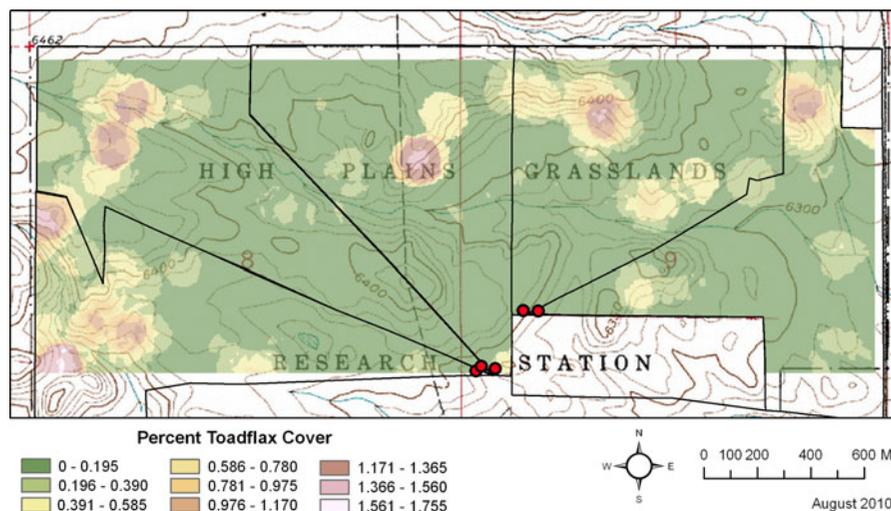


Fig. 1 Kriged map of toadflax cover superimposed on a topographic map with locations of fences (solid lines), and water tanks (filled circles). Kriging interpolates between values from measured locations to provide predicted values for non-

measured locations. Raw data, not Kriged estimates, were used in model selection analysis. Map was created in ArcGIS 9 using ordinary kriging tools with a semivariogram model, a cell size of 5 m, and a search radius of 12 points

to reliably identify and measure individual toadflax plants (Blumenthal et al. 2007).

We estimated toadflax cover within each image visually. Images were displayed at 66 or 100% magnification in Photoshop Elements (Adobe Systems Inc., San Jose, CA). To increase the accuracy of visual estimates, a 1-pixel-thick digital grid was superimposed over each image, dividing the image into 1,350 squares similar in size to sections of toadflax plants. We then estimated the number of squares that could be fully covered by toadflax in each image, and converted square number to percent cover. Tests of this technique confirmed accuracy: image-based cover estimates explained 94% of the variation in ground-based biomass collections (Blumenthal et al. 2007). This study was limited to good-quality images in relatively-undisturbed rangeland. Occasional poor-quality images, and images containing roads, fences and water tanks, were excluded.

Collection of environmental data

Slope and aspect were derived from a digital elevation model (DEM) for the study site (USGS 1993). The calculated slope represents the maximum rate of change between each DEM grid cell and its neighbors. For example, a grid cell with a lower slope value equals flatter terrain. Aspect can be thought of as the compass direction a hill faces, and is identified as the steepest downslope direction from each cell to its neighbors. The soils layer was added by scanning a detailed soil survey map for the site (Stevenson et al. 1984). We then used the percent sand of the soil type at each survey location to represent soil texture while limiting the number of variables in our statistical models (Burnham and Anderson 2002).

Grazing intensity was approximated by the straight-line distance between a sampling location and the water tank within the same pasture. The area surrounding water sources, known as the piosphere, is characterized by sharply decreasing grazing intensity with increasing distance from the water source, and has been used to study effects of grazing on a wide range of processes, including invasion (Andrew 1988; Brooks et al. 2006). Grazing intensity decreases with distance from water both because animals spend more time close to water sources, and because the area

available for grazing typically increases with distance from water sources (Andrew 1988), as was the case in this study (Fig. 1).

Relative snow accumulation and erosion were modeled using SnowModel (Liston and Elder 2006a; Liston et al. 2008), a spatially-distributed snow-evolution modeling system designed for application in all landscapes, climates, and conditions where snow occurs. It is an aggregation of three sub-models: (1) EnBal (Liston 1995; Liston et al. 2000) calculates surface energy exchanges and snowmelt, (2) Snow-Pack (Liston and Hall 1995) simulates snow depth and water-equivalent evolution, and (3) SnowTran-3D (Liston and Sturm 1998; Liston et al. 2007) accounts for snow redistribution by wind. Simulated processes included accumulation from snow precipitation, blowing-snow redistribution and sublimation, snow-density evolution, and snowpack ripening and melt. SnowModel inputs were spatially-distributed fields of topography, vegetation type, and meteorological conditions.

Meteorological forcings required by SnowModel were provided by MicroMet (Liston and Elder 2006b), a quasi-physically-based, high-resolution, meteorological distribution model. MicroMet is a data assimilation and interpolation model that utilizes meteorological station datasets and/or gridded atmospheric model or analyses datasets. At each time step, MicroMet generates spatial distributions of air temperature, relative humidity, wind speed, wind direction, incoming solar radiation, incoming longwave radiation, surface pressure, and precipitation, and makes them accessible to SnowModel.

For the simulations presented herein, vegetation type was uniformly grassland. SnowModel was provided with 50 cm of snow over the entire (5.8-km by 5.5-km) domain on a 5-m grid. The model was then supplied with 15 m s^{-1} winds from the west-northwest (280°), the daily average maximum wind speed and dominant wind direction from November through March. The resulting snow-depth distribution was divided by the original 50 cm snow depth. This yielded a snow accumulation and erosion index, where values above unity represent accumulation, and lower values indicate erosion. Resulting patterns displayed a loss of snow from northwest-facing slopes and accumulation of snow on southeast-facing slopes.

Statistical analysis

We examined the effectiveness of different environmental variables for explaining toadflax invasion using model selection, based on the Akaike Information Criterion (AIC). This approach takes into account both the degree to which particular models explain variation in the data, and the complexity of these models (Burnham and Anderson 2002). To yield robust results, model selection requires a limited set of a priori models (Table 1), which defines the range of possible results. We chose these models to provide comparisons among different types of environmental variables: topographic variables (slope and aspect), resource variables (snow and soil type), and a single management variable (grazing intensity). We then compared models containing each variable on its own, models containing both topographic variables or both resource variables, models containing multiple types of variables (topographic

and resource, topographic and management, resource and management), and models containing all variables (the global model). We also included an identical set of models with interactions. Because the global model with interactions is a composite of all other models it includes all interactions present in those models rather than all possible interactions.

An additional complication in datasets like ours, where survey points are separated by relatively short distances, is that data points cannot be considered to be independent of one another, due to the likelihood of spatial autocorrelation. Consequently, novel methods are required to calculate AIC values while accounting for spatial autocorrelation. We followed the methods of Hoeting et al. (2006), which use a Matern autocorrelation function in association with AIC analysis. This approach uses maximum likelihood to simultaneously estimate fixed effect parameters and the random effect of spatial autocorrelation of toadflax cover. This approach is a more conservative approach than the

Table 1 A-priori models included in AIC analyses

Model description	Model variables
Single factor models	
Slope	Sl
Aspect	A
Snow	Sn
Percent sand	Sa
Grazing intensity	G
Multiple-factor models	
Global model	Sl, A, Sn, Sa, G
Topographic variables	Sl, A
Resource variables	Sn, Sa
Topographic and resource variables	Sl, A, Sn, Sa
Topographic and grazing variables	Sl, A, G
Resource and grazing variables	Sn, Sa, G
Multiple-factor models with interactions	
Global model and all interactions in sub-models	Sl, A, Sn, Sa, G, and all interactions listed below
Topographic variables and interactions	Sl, A, Sl·A
Resource variables and interactions	Sn, Sa, Sn·Sa
Topographic and resource variables and interactions	Sl, A, Sn, Sa, Sl·A, Sl·Sn, Sl·Sa, A·Sn, A·Sa, Sn·Sa, Sl·A·Sn, Sl·A·Sa, Sl·Sn·Sa, A·Sn·Sa, Sl·A·Sn·Sa
Topographic and grazing variables and interactions	Sl, A, G, Sl·A, Sl·G, A·G, Sl·A·G
Resource and grazing variables and interactions	Sn, Sa, G, Sl·Sa, Sl·G, Sa·G, Sl·Sa·G

use of restricted maximum likelihood (REML) methods that estimate fixed effect parameters first, and then adjust the estimates for modeled autocorrelation between residuals. This is particularly true when explanatory variables are themselves likely to be spatially autocorrelated, as is the case with this dataset. The correlation function uses two parameters θ_1 and θ_2 , which determine the range and “steepness” of the spatial autocorrelation. All analyses were conducted in R with the software package provided by Hoeting et al. (2006; Ecological Archives A016-007-S1). Percent cover by toadflax was $\ln(X + 0.01)$ -transformed prior to analysis. To ensure that the models considered fit the data reasonably well, a precondition of meaningful model selection (Burnham and Anderson 2002), we compared AIC values of our selected best models to those of two null models, one containing the intercept alone, and the second containing both the intercept and the spatial information. We also calculated R^2 values for all models using methods provided by Nagelkerke (1991), with the intercept-only model as the null model.

Results

Toadflax was common at the study site, occurring in 742 (40%) of the 1,861 images examined. At the scale of individual images (48.5 m²), however, toadflax was not a dominant species. Where toadflax was present, its cover was generally less than 1% (642 images), and at most 8.7%. Based on AIC analyses, the three top models (with at least 10% of the Akaike weight of the

best model; Table 2), were substantially better at explaining toadflax distribution than either the intercept-only or the intercept-plus-spatial-information null models, indicating that the models we considered explained sufficient variation to be meaningful.

The best model for explaining toadflax cover contained slope, aspect and their interaction (Table 2). Sloped areas were common in the dataset, with 25% of sites having slopes of 4% or more, but slopes were generally moderate, with less than 1% of sites having slopes exceeding 10%. Toadflax cover was greater on steeper slopes and south-facing slopes (Figs. 1, 2). The model containing slope and aspect but not their interaction was not among the top models (Table 2), suggesting that this interaction is also an important predictor of toadflax cover. Not surprisingly, aspect influenced toadflax cover more strongly in sloped areas than relatively flat areas.

The second-best model for explaining toadflax cover contained grazing intensity in addition to slope, aspect, and all interactions among these variables (Table 2). This model had only slightly lower support than the best model, with an evidence ratio (the ratio of the two models' Akaike weights) of 1.6 (Table 2). Toadflax cover was lower, on average, close to water tanks (Figs. 1, 2). Distance from water tanks ranged from 26 m to 2,026 m, with long distances being more common than short distances, due to pasture shape (Fig. 1). Neither slope nor aspect varied with distance from water. The second-best model had substantially higher support than the same model without interactions, the third-best model (evidence ratio of 3.9; Table 2), suggesting that interactions between slope,

Table 2 Model selection statistics for the models that best explained toadflax cover and the two intercept-only models

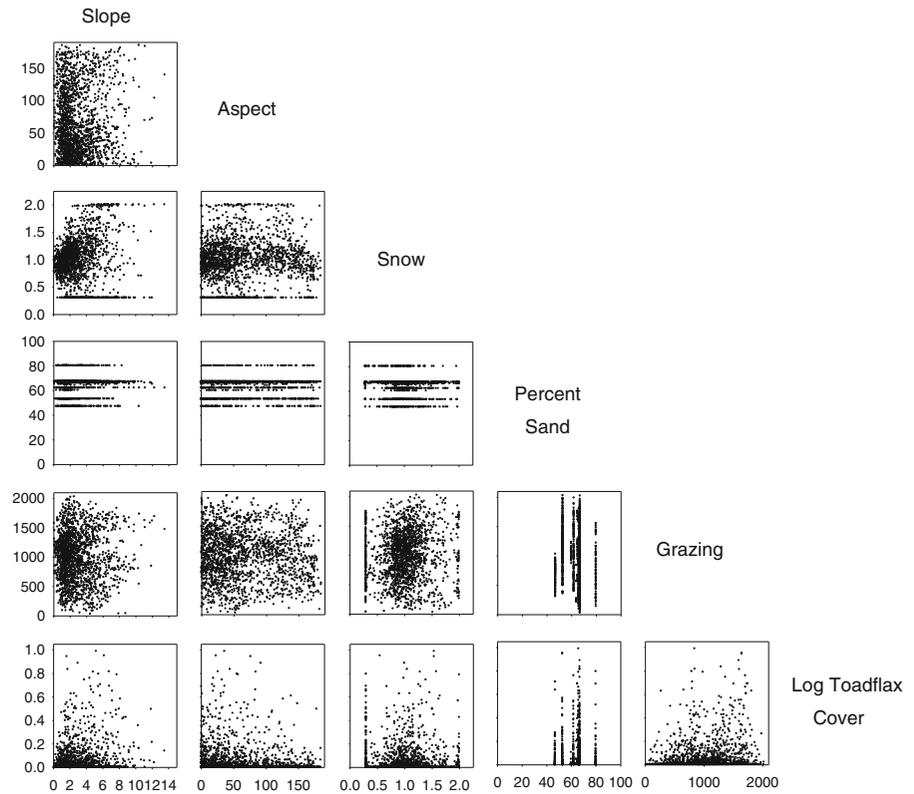
Model description [†]	K	Log (L)	AIC _c	Δ AIC _c	w_i^*	R^2	θ_1	θ_2
Slope (Sl), Aspect (A), Sl·A	6	−1,692	3,399	0	0.53	0.22	297.77	0.043
Sl, A, Grazing intensity (G), Sl·A, Sl·G, G·A, Sl·A·G	10	−1,689	3,400	0.96	0.33	0.22	125.08	0.045
Sl, A, G	6	−1,694	3,402	3.64	0.085	0.21	113.69	0.049
Intercept	3	−1,730	3,468	70	–	–	215.05	0.059
Intercept, no spatial structure	1	−1,883	3,704	305	–	–	–	–

For a given model, K is the number of parameters, including the intercept and θ_1 and θ_2 from the correlation structure, L is the maximum likelihood, AIC_c is the Akaike Information Criterion adjusted for small sample size, and Δ AIC_c is the difference in AIC_c between that model and the best model. R^2 is calculated from L , using the intercept-only model as the null model (Nagelkerke 1991)

* Models are presented in order of decreasing Akaike weights (w_i), which describe the probability that a given model is the best model, given the data and set of a priori models

[†] Only models with at least 10% of the Akaike weight of the best model are presented

Fig. 2 Scatterplot matrix of environmental variables and toadflax cover. Aspect is defined as the distance in degrees from true South. Snow ranges from 25 to 200% of ambient snowfall. Grazing intensity is defined as the distance in meters from artificial water sources used by cattle



aspect and grazing were also important determinants of toadflax cover. These interactions indicated that the presence of southeast-facing slopes increased toadflax cover less in areas close to water tanks than in areas far from water tanks.

Toadflax cover was significantly spatially autocorrelated in all models. Autocorrelation was weaker, at a given distance, in models with grazing intensity than in models without grazing intensity (Fig. 3, Table 2). This likely reflects the strong autocorrelation in grazing intensity, which decreased linearly with distance from water tanks. Including spatial autocorrelation in the model structure likely reduced the influence of grazing intensity on model fit, making our analysis of grazing effects on toadflax cover quite conservative.

There was considerable variation in both soil texture and modeled snow deposition. Soils ranged from 47 to 80% sand. Relative snow depths ranged from 30 to 200% of initial snow depth. Nevertheless, percent sand and snow deposition were not present in any of the best models, suggesting that they were relatively unimportant to toadflax invasion at this site.

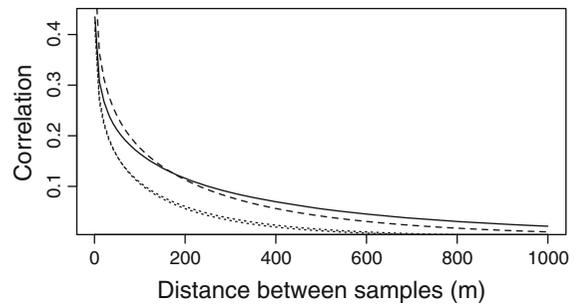


Fig. 3 Estimated correlation between observations as a function of distance between samples. *Solid line*: estimates from the best-fit model, which does not include grazing intensity. *Dashed line*: estimates from the intercept-only model. *Dotted lines*: estimates from the second and third best-fit models, which do include grazing intensity

Discussion

Forty percent of survey locations contained toadflax, indicating that it can tolerate a broad array of environmental conditions at this study site. It was rarely abundant, however, suggesting that relatively undisturbed mixed-grass prairie provides substantial biotic resistance to toadflax invasion.

Of the environmental factors we examined, toadflax cover depended most strongly on the topographic variables, being higher on steeper and south-facing slopes. Our results show that this is a general pattern at the study site. Given previous observations of toadflax on slopes, and south-facing slopes in particular (Robocker 1974; Rew et al. 2005), this pattern may also be consistent across sites.

The hypothesis that toadflax occurs on southeast-facing slopes because of high snow deposition was not supported by our results, however. The snow model we employed was based on slope and aspect. The key difference between these closely-related variables was in direction. Based on dominant northwest winter winds, the snow model predicted that snow would accumulate preferentially on southeast-facing slopes. Because toadflax cover was highest on south-facing, rather than southeast-facing slopes, slope and aspect were more effective explanatory factors than snow. It is possible that the snow model is inaccurate if, for example, the average wind direction we used doesn't reflect the wind directions associated with large snowstorms, but we have little evidence for this. Observations that toadflax invades south-facing slopes in other areas (Robocker 1974), which are likely to have other wind directions, suggests that factors other than snow deposition, such as temperature, may be driving the relationship between topography and toadflax cover.

Toadflax cover was also higher in areas with lower grazing intensity, as estimated by proximity to water sources. This pattern is in accord with our observation of dense toadflax populations within grazing exclosures, but not with observations that toadflax is avoided by cattle (Harris and Carter 1971), nor with suggestions that grazing may contribute to its invasion (Lajeunesse 1999). It also contrasts sharply with studies showing that invasion increases with (Tueller and Platou 1991; Landsberg et al. 2003; Brooks et al. 2006; Todd 2006), or is unaffected by (McClaran and Anable 1992), proximity to livestock water sources in other ecosystems.

These apparent contradictions may stem from differences in the long-term history of grazing among ecosystems, and resulting differences in the adaptation of native species to grazing (Mack and Thompson 1982, Milchunas et al. 1988). The mixed-grass prairie differs from much of toadflax's North American range in that it was historically heavily grazed by

bison (Lyman and Wolverton 2002). In such systems, grazing can favor short-statured, competitive native species (Milchunas et al. 1988; Milchunas and Lauenroth 1993), and reduce invasion. For example, a long-term history of grazing reduced annual forb invasion of shortgrass steppe even in plots not grazed during the study, suggesting that grazing influenced invasion indirectly through changes in the native plant community, rather than directly through defoliation of invasive species (Milchunas et al. 1992). Similarly, negative relationships between grazing intensity and toadflax cover in this study may be indirect, mediated by positive relationships between grazing and competitive mixed-grass prairie species. At this site, heavier grazing tends to increase the proportion of warm-season grasses relative to cool-season grasses and forbs, decrease litter, decrease nitrogen mineralization, and reduce the size of plant interspaces (Ingram et al. 2008; Derner and Whitman 2009). Such changes may inhibit the establishment or competitive ability of toadflax. Thus it is possible that grazing inhibits toadflax invasion in the western Great Plains, where it favors dominant, competitive perennial grasses, but facilitates toadflax invasion in ecosystems such as sagebrush steppe, where it can inhibit dominant, competitive perennial grasses (Mack and Thompson 1982; Milchunas et al. 1988).

Although reports in the literature and our own observations suggest that toadflax is not frequently eaten by cattle, we cannot rule out the possibility that consumption by cattle influenced toadflax distribution. For example, large herbivores are more likely to consume relatively unpalatable species when they are rare (Augustine and McNaughton 1998), which could have contributed to the pattern observed here. It is also important to note that while slope, aspect and grazing were clearly the most important factors in explaining toadflax cover in our dataset, they explained a relatively small portion of the variation in toadflax cover (Table 2). This is not surprising, given that many processes influencing toadflax distribution, such as dispersal and recruitment, involve considerable stochasticity. However, it suggests that factors not considered in this study, such as soil disturbance (Robocker 1974) or plant species richness (Maron and Marler 2008), may also influence toadflax invasion in mixed-grass prairie. Furthermore, while snow deposition and soil texture were not important in determining toadflax cover in this

study, previous experimental work demonstrated that nitrogen and water availability strongly influence toadflax invasion at this study site (Blumenthal et al. 2008, Blumenthal 2009). It may be that more precise measures of resource availability would be more strongly correlated with toadflax cover.

In this study, toadflax preferentially invaded south-facing slopes with relatively little grazing pressure. These patterns can help predict locations of current and future toadflax infestations. They also suggest that, in mixed-grass prairie, and perhaps other Great Plains grasslands, grazing can be used to inhibit toadflax invasion. It is important, however, to identify the mechanism underlying this pattern. If grazing inhibits toadflax through long-term effects on plant communities but livestock avoid toadflax once it has invaded, grazing may be more useful in preventing invasion than in controlling existing infestations. More broadly, these results show that in grazing-adapted systems, grazing can reduce invasion of even relatively unpalatable species. This finding reinforces the idea that grazing can be important in maintaining biotic resistance where it is an endogenous disturbance (Margalef 1968; Milchunas et al. 1988; Hobbs and Huenneke 1992; Milchunas et al. 1992).

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