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## Geology and Topography Effects on Exotic Plant Distribution in a Semi-arid Mima Mound Prairie in Eastern Washington

### Abstract

Native prairie plant communities are among the most endangered habitats due to extensive agricultural use and exotic species invasion. Understanding how species composition, particularly of exotic species, varies with environment is essential for management and preservation of these communities. In semi-arid prairies, plant establishment is often heterogeneous across the landscape and depends on the patchy availability of resources across environmental gradients. We studied how soil geologic substrate, topography, and grazing history relate to patterns of native and exotic plant distribution in a semi-arid Mima mound prairie in eastern Washington. We analyzed the relationship between native and exotic species richness and abundance on 61 Mima mounds in a prairie underlain by two types of soil geologic substrate (glacial alluvium and basalt) where half of each had been grazed recently. We found that exotic species richness and cover were lowest and native species cover was highest on mounds underlain by basalt bedrock that had experienced recent grazing; on sites underlain by glacial alluvium there was little difference between more and less recently grazed mounds. Moreover, we found that exotic abundance was greatest at the top of Mima mounds compared to the sides; the opposite was true for native species. Our findings indicate that geologic substrate and grazing history may interact to determine plant distribution in semi-arid prairie communities. This study demonstrates that land managers aiming to restore native plant communities need to consider the synergistic effects of multiple environmental factors in order to focus restoration funding and effort.

**Keywords:** aspect; channeled scablands; grazing; Mima mound; plant invasion

### Introduction

Undisturbed prairies have become rare in the last century due to agricultural conversion and exotic species invasion, and re-establishment of native vegetation in these ecosystems is at the forefront of restoration ecology. It is estimated that less than 1% of original prairies remain in eastern Washington, and conservation groups are working to conserve native prairie plant communities (Donovan et al. 2009). In semi-arid prairies, establishment of plants, including exotics, is heterogeneous across the landscape and depends highly on the patchy availability of resources in the environment (Vinton and Burke 1995). Understanding how native and exotic (i.e., non-native) species composition varies with environment is essential for management of exotic species and re-establishment of native plant communities. Environmental factors, such as soil

geologic substrate, aspect, and grazing, contribute to the structure of the plant community and need to be studied before appropriate techniques for habitat restoration can be initiated (Holmes and Richardson 1999).

Soil characteristics like porosity, moisture availability, and mineral content vary with geologic substrate type and climate. Eastern Washington has two distinct and common geologic substrates: basalt and alluvium (Bretz 1969, Waite 1980, Baker 2009). Alluvium may allow for increased moisture availability to plants since it has greater pore space compared to basalt (Searcy et al. 2003). Especially in arid and semi-arid regions, soil moisture is associated with higher plant cover, diversity, and invasibility (Harrington 1991, Boeken and Shachak 1994). Given the dry summer conditions in semi-arid eastern Washington, increased moisture availability may influence plant species composition and exotic species invasion.

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One of the unique geologic features in the channeled scablands of eastern Washington is the presence of Mima mounds. These hemispherical mounds consist of deep, fine-grained topsoil surrounded by an intermound area. Prairies that are patterned with Mima mounds have been documented in several locations in the United States (Del Moral and Deardorff 1976, Nelson 1997, Horwath and Johnson 2006, Seifert et al. 2009), and in Africa (Cox 1985, Moore and Picker 1991, Esler and Cowling 1995). In eastern Washington, where much of the prairie habitat has been converted to cropland (Donovan et al. 2009), remaining prairie often contains Mima mounds, likely due to the difficulty of using farm equipment on uneven terrain. Eastern Washington Mima mounds are underlain by either basalt bedrock or alluvial substrates. When the mounds are underlain by basalt bedrock substrate, the soil of the intermound area is much more shallow (less than 5 cm) than the soil on the mounds (about 1 m), resulting in sharp moisture gradients when the shallow soil dries out in mid-to late spring (Boeken and Shachak 1994). This results in very distinct plant communities on the mound and intermound areas. The mounds underlain by alluvial substrate tend to be smaller and appear less distinct from the surrounding intermound habitat. Also, given that alluvial substrates have greater potential for moisture retention than basalt bedrock, it is possible that the mounds overlying alluvial substrates provide plants with greater access to soil resources than mounds underlain by basalt.

Topography also influences soil moisture and plant distributions. Aspect, a topographic characteristic describing the direction that a slope faces, affects solar radiation with greater light, heat, and moisture loss on slopes facing the equator (Olivero and Hix 1998, Searcy et al. 2003). On Mima mounds in eastern Washington, south facing sides of mounds experience higher levels of solar radiation and are, therefore, likely to be hotter and drier than north facing sides.

Soil depth is another topographic factor influencing plants (Boeken and Shachak 1994); all else being equal, deeper soil stays moist for longer than shallower soil, and the more soil plants have for rooting, the better access to nutrients and moisture. In general, the greater soil depth at the

tops of Mima mounds likely helps maintain soil moisture for longer than the sides of mounds or intermound areas.

Disturbance, the removal of plant biomass or other perturbation of the natural system also affects plant communities (Armesto and Pickett 1985). In most of the semi-arid regions of the western United States, one of the most common forms of anthropogenic disturbance is livestock grazing, which has been practiced for the past century (Fleischner 1994). The documented ecological costs of livestock grazing include a reduction in species richness, decrease in density of individual native species, and change in overall community structure (D'Antonio and Vitousek 1992, Fleischner 1994, Safford and Harrison 2001, Manier and Hobbs 2007). Many exotic species are able to flourish in lands grazed by cattle, partly because they are unpalatable (Kufeld 1973) and cattle prefer to graze on leafy native species or are fed a supplemental diet. Reduction in total plant biomass creates gaps that exotic species can easily occupy (Harrington 1991, Chambers et al. 2007). Cattle also accelerate nitrogen cycling, a limited resource in semi-arid prairies, through inputs of manure and urine (Li et al. 2010). Cattle may release exotic species from natural stress in semi-arid prairies, enabling them to outcompete natives (Marty et al. 2005).

Invasion theory suggests that invading plants depend on resource availability to gain a foothold; thus we might expect more exotic species in habitats with high levels of resources and disturbance, which removes established plants, making the resources available to invaders (Davis et al. 2000). This would suggest that the tops of cattle-grazed Mima mounds, which likely have relatively high levels of soil resources compared to the surrounding habitat (extremely shallow soil over bedrock) would favor invading exotic species. In addition, it would suggest that Mima mounds located over glacial alluvium would have greater resources and thus more invaders than the mounds over basalt bedrock, since alluvium has greater moisture retaining ability.

The goal of this study was to determine which environmental factors (geologic substrate, grazing history, and aspect) are related to native and exotic plant species richness and abundance in

eastern Washington Mima mound prairies. This is the only study, to our knowledge, that has examined the influence of these factors in Mima mound prairies. Specifically, we tested the following hypotheses: 1) exotic plant species are more abundant (as measured by species richness and percent cover) on mounds that are underlain by alluvial gravel and were recently grazed; 2) native plant species, like exotic plants, will have higher abundance (cover and richness) in areas likely to have more soil moisture (alluvial underlain mounds), but unlike exotics will be less abundant on recently grazed mounds; 3) species composition of mounds will be related to underlying substrate and grazing history, and certain individual species will be more important than others as indicators of different plant communities; 4) aspect on mounds will influence species composition, with higher richness and cover of native and exotic species at the tops and north-facing sides of mounds.

## Methods

### Site Description

This study was conducted in the southeast corner of Turnbull National Wildlife Refuge (hereafter Turnbull; Figure 1). Turnbull includes 6,475 ha

of channeled scablands located near Cheney, WA, USA (47° 24'N; 117° 31'W). Both basalt and glacial alluvium underlie Mima mounds at Turnbull. In the basalt area, mounds average 1.2 m tall, 19 m long, and 13.5 m wide, whereas in the alluvial area they are much smaller, measuring on average 0.3 m tall, 8.7 m long, and 6.8 m wide. In our study site, each substrate type also has two cattle grazing histories. The Stubblefield tract of Turnbull has been grazed within the past 35 years (hereafter, grazed), while the Public Use Area tract was grazed over 35 years ago (hereafter, ungrazed). In both tracts, 26 to 38 cattle per 100 ha grazed from late fall until early spring. Because portions of both the alluvial and basalt areas varied in grazing, we incorporated grazing as part of the study design.

### Experimental Design

We established 81 1-m<sup>2</sup> plots on the tops and sides of 61 Mima mounds at Turnbull during the summer of 2009. Our experimental design included three factors: grazing (grazed or ungrazed), soil geologic substrate (alluvium or basalt), and aspect (north side, south side, and top of mound). There are four distinct treatment areas at Turnbull (Figure 1), including grazed alluvial, ungrazed alluvial,

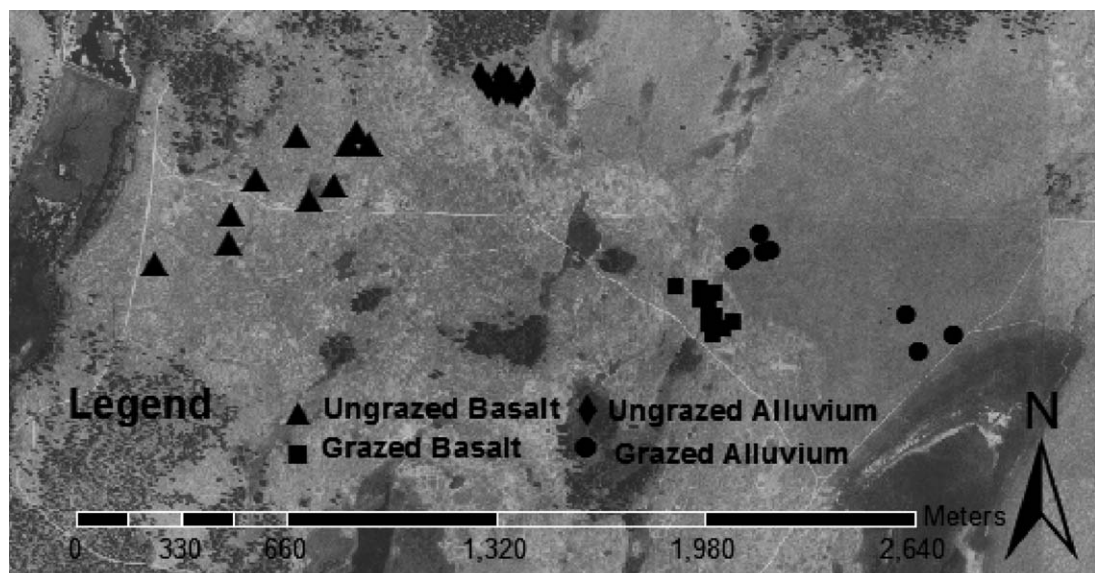


Figure 1. Study site located at Turnbull National Wildlife Refuge, 5 miles to the southeast of Cheney, WA, USA. Symbols represent the locations of all Mima mounds used in this study.

grazed basalt, and ungrazed basalt. One quadrat was placed at the top of 61 mounds to answer questions related to substrate and grazing. In addition to the top-of-mound quadrats, 10 mounds also have one quadrat on the north-facing side and one quadrat on the south-facing side to answer questions about aspect. Thus, 10 mounds have 3 quadrats each (top, north, and south side) and 51 mounds have one quadrat each (top only), totaling 61 mounds and 81 quadrats. In each treatment area we sampled 10 mounds except the larger grazed alluvial area where we sampled 31 mounds. Aspect was analyzed independently of the other factors in the study; for aspect we focused on the 10 ungrazed basalt mounds because these were large enough to establish distinct plots on different aspects. Data gathered from the 10 plots at the top of ungrazed basalt mounds was therefore analyzed twice: once when examining effects of grazing history and geologic substrate, and again when separately analyzing the effects of aspect.

#### Data Collection

Within each plot we recorded vascular plant species composition and percent cover, which was estimated using a modified Braun-Blanquet (1932) cover class system (Kent and Coker 1992). The cover classes included: trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, and 95-100%. For analysis, cover classes were converted to their midpoints, with 0.1% given for trace. Cover classes allow for greater consistency, efficiency, and repeatability, and because these plots will be resampled over many years as part of a separate study, consistency and repeatability among different field crews sampling at different times will be essential.

Botanical nomenclature follows Hitchcock and Cronquist (1973) and, if necessary, was updated according to the Integrated Taxonomic Information System (ITIS) (<http://www.itis.gov>; retrieved 19 September 2009). The survey began in mid June, 2009 and ended in mid August, 2009, so by the end of the survey some plants had senesced. Species cover was partially influenced by degree of senescence; cover declines as senescence progresses. To minimize the effect of phenol-

ogy on our results, we randomized the sampling times across all treatments to ensure that no one treatment was unduly influenced by phenology. Species richness values were not greatly affected by phenology because most species were readily identifiable even after senescence.

#### Data Analysis

To test for patterns of native and exotic species richness and cover (measured as the midpoint of each cover class for species in each plot, as described above) related to geologic substrate and grazing history, we used a two-way analysis of variance (ANOVA) followed by a post-hoc Student's *t*-test ( $\alpha = 0.05$ ) (JMP 8, Cary, NC, USA). To examine patterns in overall species composition, we used non-metric multidimensional scaling (NMDS, PcOrd V5.0, MjM Software, Gleneden Beach, OR, USA), a nonparametric ordination technique for the 61 plots at tops of mounds. We used median percent values for each cover class as our dependent variable in NMDS analysis. We used relative Sorenson similarity as the distance measure in the NMDS. The data were run 50 times using 250 iterations for up to 6 axes starting with a randomly generated configuration and stability criteria of 0.0005. Results reported are based on a three dimensional solution (fewest number of axes needed to achieve low stress) with Varimax rotation to maximize the variation explained by each axis. Dufrêne and Legendre's (1997, cited in McCune and Grace 2002) indicator species analysis was used to identify the species most associated with each treatment group. Monte Carlo permutations (4,999) were used to test the significance of each species' highest indicator value; significant indicators ( $p < 0.05$ ) are reported here. To determine if aspect was related to patterns of exotic and native species richness or cover, we used a one-way ANOVA comparing the top, north, and south facing sides of the 30 basalt-underlain plots where all three were sampled.

#### Results

A total of 56 species were recorded in this study, of which 13 were exotic (Table 1). Geologic substrate and grazing history had significant interactions

TABLE 1. Species list of all vascular plants recorded in the plots during summer 2009 at Turnbull National Wildlife Refuge Mima mound prairie.

Species name
<i>Achillea millefolium</i> L.
<i>Agoseris grandiflora</i> (Nutt.) Greene
<i>Agoseris heterophylla</i> (Nutt.) Greene
<i>Allium columbianum</i> (Ownbey & Mingrone) P. Peterson Annable & Rieseberg
<i>Amsinckia menziesii</i> (Lehm.) A. Nels. & J.F. Macbr.
<i>Antennaria</i> sp.
<i>Apera interrupta</i> (L.) Beauv.
Asteraceae spp.
<i>Blepharipappus scaber</i> Hook.
<i>Bromus arenarius</i>
<i>Bromus commutatus</i> Schrad.
<i>Bromus commutatus</i> Schrad. var. <i>apricorum</i> Simonkai
<i>Bromus japonicus</i> Thunb. ex Murr.
<i>Bromus secalinus</i> L.
<i>Bromus tectorum</i> L.
<i>Buglossoides arvensis</i> (L.) I.M. Johnston
<i>Centaurea solstitialis</i> L.
<i>Cerastium nutans</i> Raf.
<i>Clarkia pulchella</i> Pursh
<i>Collomia linearis</i> Nutt.
<i>Collinsia parviflora</i> Lindl.
<i>Delphinium nuttallianum</i> Pritz. ex Walp.
<i>Descurainia incana</i> (Bernh. ex Fisch. & C.A. Mey.) Dorn
Dicot sp.
<i>Draba verna</i> L.
<i>Epilobium brachycarpum</i> K. Presl
<i>Eriogonum heracleoides</i> Nutt. var. <i>angustifolium</i> (Nutt.) Torr. & Gray
<i>Festuca idahoensis</i> Elmer
<i>Fritillaria pudica</i> (Pursh) Spreng.
<i>Gaillardia aristata</i> Pursh
<i>Galium aparine</i> L.
<i>Hordeum jubatum</i> L.
<i>Lactuca serriola</i> L.
<i>Lagophylla ramosissima</i> Nutt.
<i>Linaria dalmatica</i> (L.) P. Mill.
<i>Lithophragma parviflorum</i> (Hook.) Nutt. ex Torr. & Gray
<i>Lithospermum ruderale</i> Dougl. ex Lehm.
<i>Lomatium ambiguum</i> (Nutt.) Coult. & Rose
<i>Lomatium triternatum</i> (Pursh) Coult. & Rose
<i>Lotus unifoliolatus</i> (Hook.) Benth.
<i>Lupinus sericeus</i> Pursh ssp. <i>sericeus</i>
<i>Madia gracilis</i> (Sm.) Keck & J. Clausen ex Applegate
<i>Medicago lupulina</i> L.
<i>Myosotis stricta</i> Link ex Roemer & J.A. Schultes
<i>Phlox gracilis</i> (Hook.) Greene ssp. <i>gracilis</i>
<i>Poa bulbosa</i> L.
<i>Poa nemoralis</i> L. ssp. <i>interior</i> (Rydb.) W.A. Weber
<i>Polemonium micranthum</i> Benth.
<i>Polygonum douglasii</i> Greene
<i>Potentilla argentea</i> L.
<i>Pseudoroegneria spicata</i> (Pursh) A. Löve
<i>Sisymbrium altissimum</i> L.
<i>Tragopogon dubius</i> Scop.
<i>Ventenata dubia</i> (Leers) Coss. & Durieu
<i>Veronica</i> spp.
<i>Vicia cracca</i> L.

TABLE 2. Results from analysis of variance (ANOVA) in the grazing x substrate study and the aspect study. \* Denotes significance at  $P < 0.05$ .

Treatment	Statistic	Exotic		Native		Total	
		richness	cover	richness	cover	richness	cover
grazing	<i>F</i>	3.10	1.50	0.22	1.30	1.04	0.21
	<i>P</i>	0.003*	0.13	0.83	0.19	0.30	0.83
substrate	<i>F</i>	0.23	0.07	3.19	0.71	5.55	0.46
	<i>P</i>	0.81	0.94	0.002*	0.48	0.002*	0.64
grazing x substrate	<i>F</i>	6.24	3.08	3.84	2.01	3.64	0.20
	<i>P</i>	<0.001*	0.03*	0.01*	0.04*	0.02*	0.50
aspect	<i>F</i>	11.18	9.11	4.44	1.19	0.42	13.39
	<i>P</i>	<0.001*	<0.001*	0.02*	0.32	0.66	<0.001*

with exotic species richness per  $m^2$  ( $F = 6.24$ ,  $P < 0.001$ , Table 2) and cover ( $F = 3.08$ ,  $P = 0.03$ , Figure 2). On mounds underlain by basalt, exotic

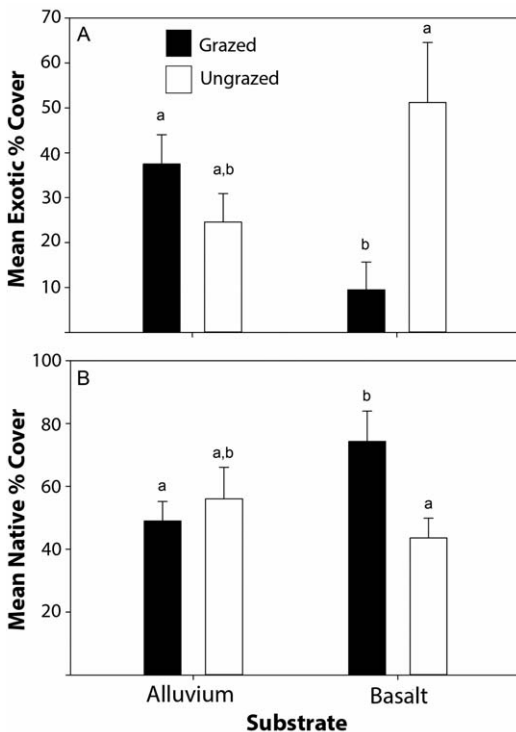


Figure 2. The effect of grazing history on mean exotic species percent cover (A) and mean native species percent cover (B) in sites with either alluvium or basalt bedrock. The effect of grazing depends on the soil geologic substrate for both exotics ( $p = 0.006$ ) and natives (0.04). Percent cover recorded is the median percent in one of 9 cover classes described in the text. Bars indicate SE and letters denote treatment differences based on post-hoc Student's *t*-test ( $p < 0.05$ ). For grazed mounds underlain with alluvium  $n = 31$  and for all other treatments  $n = 10$ .

richness was nearly twice as great on ungrazed mounds compared to grazed mounds, and exotic cover was over 5 times greater (Table 3). This effect did not carry over to mounds underlain by alluvium, where there was no difference in exotic cover or richness between grazed and ungrazed mounds.

Geologic substrate and grazing history also had significant interactions with patterns of native species richness ( $F = 3.84$ ,  $P = 0.01$ ), with alluvial mounds having 30% higher native species richness than basalt mounds ( $F = 3.19$ ,  $P = 0.002$ ). Native species cover also differed with grazing history depending on geologic substrate ( $F = 2.01$ ,  $P = 0.042$ , Figure 2). Like exotic cover, native cover did not differ between grazed and ungrazed mounds underlain by alluvium. However, on mounds underlain by basalt, there was 71% greater native cover on grazed mounds than ungrazed mounds.

Total species richness followed the same pattern as native (due to there being relatively more native species); total richness was 22% greater ( $F = 5.55$ ,  $P = 0.002$ ) on mounds underlain by alluvium compared to those underlain by basalt, and the effect of substrate interacted with grazing ( $F = 3.64$ ,  $P = 0.02$ ). Total species cover did not differ among treatments ( $F = 0.20$ ,  $P = 0.50$ ).

Species composition of plant communities on alluvial and basalt underlain mounds overlapped, as shown by ordination analysis (stress = 14.48, final stability = 0.00001; Figure 3). The ordination shows clear separation of grazed and ungrazed plots on the basalt mounds, but not on the alluvial mounds (Figure 3). Indicator species

TABLE 3. Mean (standard deviation) values for data collected in the grazing x substrate study (a) and the aspect study (b). The grazing x substrate study examined the interaction between historical grazing regime and soil substrate type on plant communities. The aspect study compared plant communities on the top, north-facing side, and south-facing side of mounds. Mima mounds in the grazing x substrate study are have either not been grazed for >35 y (ungrazed) or grazed within the last 15 y (grazed) and are underlain by either basalt or alluvial parent material. Mima mounds in the aspect study are all ungrazed and underlain by basalt. Mean cover values for each treatment are calculated using median percentages of cover classes, which included trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, and 95-100%.

Treatment	Exotic		Native		Total	
	richness	cover	richness	cover	richness	cover
<i>a) Grazing x Substrate</i>						
ungrazed basalt	5 (2)	51.2 (42.2)	8 (3)	43.6 (19.8)	13 (4)	94.8 (37.9)
grazed basalt	3 (1)	9.5 (19.5)	9 (2)	74.3 (30.4)	12 (3)	83.8 (36.2)
ungrazed alluvium	4 (2)	24.6 (20.6)	12 (2)	56.0 (31.8)	16 (1)	80.6 (37.4)
grazed alluvium	4 (1)	37.5 (36.4)	10 (4)	48.9 (34.6)	14 (3)	86.4 (47.9)
<i>b) Aspect</i>						
top	5 (2)	51.2 (42.2)	8 (3)	43.6 (19.8)	13 (4)	94.8 (37.9)
north	3 (1)	5.2 (8.8)	10 (2)	31.5 (19.3)	13 (2)	36.7 (19.1)
south	3 (1)	9.6 (16.3)	11 (3)	34.2 (15.6)	14 (3)	43.8 (21.1)

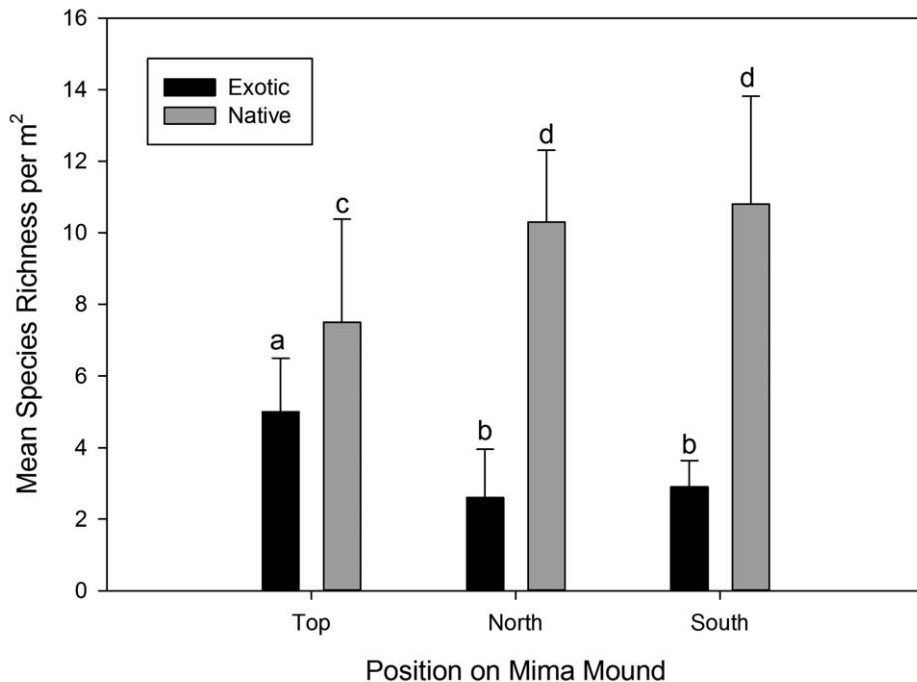


Figure 3. Mean exotic ( $p < 0.001$ ) and native ( $p = 0.02$ ) species richness per  $m^2$  on different sides of Mima mounds that are underlain by basalt and have not been grazed for at least 35 years ( $n = 10$ ). Bars indicate SE and letters denote treatment differences based on post-hoc Student's  $t$ -test ( $p < 0.05$ ).

analysis showed that grazed alluvial mounds were indicated by *Ventenata dubia*, an invasive annual grass that was also common throughout the inter-

mound areas of both alluvial and basalt mounds. Ungrazed alluvial mounds were indicated by two native annual forbs (*Phlox gracilis* and *Agoseris*



TABLE 4. Results of indicator species analysis. Only species with Monte Carlo p-values < 0.05 are shown. Relative abundance is average abundance of a given species in a given group of plots over the average abundance of that species in all plots.

Group	Indicator Species	Indicator Value	Frequency	Relative Abundance	P
GA <sup>a</sup>	<i>Ventenata dubia</i>	53	94%	56%	0.0120
UA <sup>b</sup>	<i>Phlox gracilis</i>	47	100%	47%	0.0108
UA	<i>Lomatium triternatum</i>	47	50%	93%	0.0018
UA	<i>Agoseris heterophylla</i>	24	30%	79%	0.0490
GB <sup>c</sup>	<i>Polygonum douglasii</i>	76	90%	84%	0.0008
GB	<i>Clarkia pulchella</i>	64	70%	91%	0.0006
GB	<i>Madia gracilis</i>	53	90%	58%	0.0162
UB <sup>d</sup>	<i>Vicia cracca</i>	83	100%	83%	0.0002
UB	<i>Galium aparine</i>	68	70%	97%	0.0002
UB	<i>Lactuca serriola</i>	49	90%	55%	0.0290
UB	<i>Bromus tectorum</i>	47	90%	52%	0.0090
UB	<i>Lomatium ambiguum</i>	38	40%	94%	0.0046

<sup>a</sup>GA = grazed alluvium

<sup>b</sup>UA = ungrazed alluvium

<sup>c</sup>GB = grazed basalt

<sup>d</sup>UB = ungrazed basalt

*heterophylla*) as well as a native perennial forb (*Lomatium triternatum*). Grazed basalt mounds were indicated by three native annual forbs (*Polygonum douglasii*, *Clarkia pulchella*, and *Madia gracilis*). Ungrazed basalt mounds were indicated by three invasive species (perennial forb *Vicia cracca*, annual grass *Bromus tectorum*, annual forb *Lactuca serriola*), and two native species (perennial *Lomatium ambiguum* and annual *Galium aparine*; results summarized in Table 4). The prevalence of invasive and native indicator species is consistent with the patterns of native and exotic species richness and cover in the four treatments.

The tops of ungrazed basalt mounds had greater exotic richness per m<sup>2</sup> than native richness ( $F = 11.18, P < 0.001$ , Figure 4). Exotic cover on the

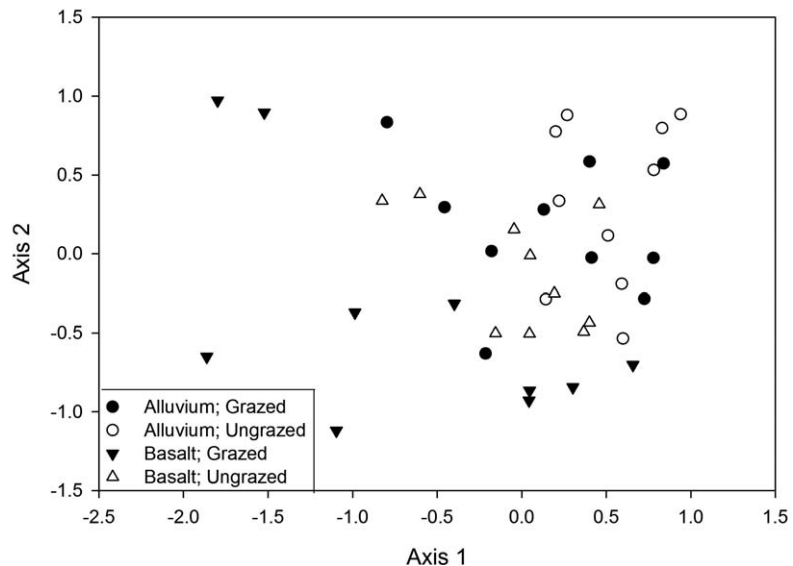


Figure 4. Ordination of community similarity in grazed alluvial (GA), ungrazed alluvial (UA), grazed basalt (GB) and ungrazed basalt (UB) treatments based on non-metric multidimensional scaling (NMDS). The NMDS plot illustrates similarity in species composition among plots based on median percent values for each cover class. Grazed represents plots grazed <35 years ago, while ungrazed represents plots grazed >35 years ago. Each symbol represents the plant community in a 1m<sup>2</sup> plot on the top of a Mima mound.

tops of mounds was 10 times greater than on the north side and 5 times greater than on the south side ( $F = 9.11, P < 0.001$ ; Figure 4). Aspect had the opposite relationship with native species richness, which was less on the top of the mounds ( $F = 4.44, P = 0.02$ , Figure 4) than either the north

or the south-facing sides. Native cover ( $F = 1.19$ ,  $P = 0.32$ ) and total species richness ( $F = 0.42$ ,  $P = 0.66$ ) did not vary with aspect. Total species cover was greatest at the tops of the mounds ( $F = 13.39$ ,  $P < 0.001$ ).

## Discussion

A key finding of our study was that geologic substrate and grazing interacted to affect native and exotic species distribution, which we did not expect. Contrary to our predictions, grazed basalt mounds actually had lower exotic richness and cover and higher native species cover than ungrazed basalt mounds, while alluvial mounds showed no differences related to grazing. There are several possible explanations for this pattern. Because of their height, basalt mounds might be avoided by grazing cattle, creating a refuge habitat, which is known to be important for shaping plant communities in semiarid environments (Milchunas and Noy-Meir 2002). However, given that mounds tended to have more lush plant cover than the bedrock intermounds, we suspect that grazers did use the mounds.

It is possible that grazing on the basalt mounds may have helped native species by reducing the dominance of competitive exotic plant species, as Collins et al. (1998) observed in tallgrass prairie at Konza Prairie Long-Term Ecological Research site in northeastern Kansas, United States. Targeted grazing is sometimes employed as a means to control exotics and improve cover of native plant species (Brock 1988, Popay and Field 1996, Germano et al. 1991). But why wouldn't grazing have a similar effect on the alluvial mounds? In a similar study, Gelbard and Harrison (2003) also found an interaction between substrate and grazing, with more exotic species on ungrazed non-serpentine (i.e., fertile) and grazed serpentine (i.e., less fertile) soils. Sites with high soil fertility may experience higher productivity and greater competition, which grazing helps to mitigate. Therefore, there would be fewer exotics on grazed, fertile sites. But there does not appear to be a difference in fertility (at least soil nitrogen) among grazed alluvial and ungrazed basalt mounds (Reyncke 2012). Still,

Reyncke (2012) did not sample soil fertility extensively or across all treatments, which we would recommend.

Abundant native annual species in certain areas may out compete exotic plants (Pantone et al. 1989), which would account for the lower abundance of exotics on ungrazed alluvial and grazed basalt mounds. These areas both had native annual plants as indicator species, which is calculated based on cover and frequency. If natives are competitive against invasive annual grasses, seeding annual species such as *Phlox gracilis*, *Madia gracilis*, and *Clarkia pulchella* could be useful for restoration of this highly invaded habitat, rather than only seeding slow-establishing perennial bunchgrasses, as is typically done (Cox and Anderson 2004).

Contrary to expectation, mound species composition overlapped among the treatments, except for grazed basalt mounds, which stood out from the others with relatively more native species. It is unclear why these mounds were different from the rest as they were adjacent to the grazed alluvial mounds, and both grazed and ungrazed basalt mounds had similar levels of human disturbance (e.g., proximity to roads) other than grazing.

There could be differences among the four treatment areas besides substrate and grazing that were not fully measured by this study. While it would have been ideal to replicate this study in several other prairies (Hurlbert 1984), this was not possible, due to the rarity of prairies not used for agriculture in eastern Washington. Other Mima mound reserves in the area (e.g., Puget Sound Mima prairie) do not have similar geologic substrate types or grazing histories.

In addition to grazing and substrate, we found that aspect influenced species composition on mounds. Exotic species cover was greatest and native species richness was lowest at the tops of mounds, as expected. Boeken and Shachak (1994) also found high cover of exotic species on man-made mounds in a semiarid prairie and attributed their result to the mounds trapping wind-blown seeds of exotic grasses. The high cover of exotics on mounds tops may also be attributed to soil

moisture; we suspect that the relatively deeper soils at the top of mounds retain more moisture, enabling highly productive exotic species to be more competitive than native plants on tops of mounds (Humphrey and Schupp 2004).

Our hypothesis that north-facing sides of mounds would have more exotic species was not supported. All sides of the mounds, regardless of direction, have lower soil depth than the tops of mounds and are probably steep enough for moisture to run off and be less available than on top. The activity of burrowing animals could also be mitigating competition through increased disturbance on the tops of the mounds (Eldridge and Whitford 2009). The supply of resources made available through burrowing could tip competition in favor of the exotics, thus enabling them to out-compete native species at the top of mounds.

To minimize cost and effort, we recommend that land managers carefully consider how multiple environmental gradients synergistically influence plant distributions in order to select the best invasive control techniques for a particular site. As an example of environmental synergism, we have shown here that geologic substrate and grazing history interact to influence the distribution of exotic and native plant species. Additionally, our study demonstrates that in a Mima mound prairie, exotics are concentrated on the tops of mounds,

while the sides naturally maintain native plant communities. Therefore, exotic plant removal techniques (e.g., herbicide, manual removal, bio-control insects) could be focused on the tops of mounds to reduce cost and prevent overkill of native species. Finally, we recommend that the seeding of native annual species as competitors against invasive annual grasses be further studied. Restoring native prairies is a monumental challenge and understanding how species composition varies within microhabitats will be crucial to the restoration of Mima mound prairies.

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### Literature Cited

- Armesto, J. J., and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant communities- impact on species richness and abundance. *Ecology* 66:230-240.
- Baker, V. R. 2009. The channeled scabland: a retrospective. *Annual Review of Earth and Planetary Sciences* 37:393-411.
- Boeken, B., and M. Shachak. 1994. Desert plant-communities in human-made patches – implications for management. *Ecological Applications* 4:702-716.
- Bretz, J. H. 1969. The Lake Missoula Floods and the Channeled Scabland. *Journal of Geology* 77:505-543.
- Braun-Blanquet, J. 1932. *Plant sociology. The Study of Plant Communities*. McGraw-Hill Book Company, Inc. New York and London.
- Brock, J. 1988. Livestock: biological control in brush/weed management programs. *Rangelands* 10:32-34.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invisable by *Bromus tectorum*? *Ecological Monographs* 77:117-145.
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280:745-747.
- Cox, G. W. 1985. Mima mound microtopography and vegetation pattern in Kenyan savannas. *Journal of Tropical Ecology* 1:23-36.
- Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Rangeland Ecology & Management* 57:203-210.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88:528-534.

- Del Moral, R., and D. C. Deardorff. 1976. Vegetation of the Mima mounds, Washington State. *Ecology* 57:520-530.
- Donovan, S. M., C. Looney, T. Hanson, Y. S. de Leon, J. D. Wulforst, S. D. Eigenbrode, M. Jennings, J. Johnson-Maynard, and N. A. B. Perez. 2009. Reconciling social and biological needs in an endangered ecosystem: the Palouse as a model for bioregional planning. *Ecology and Society* 14:9.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Eldridge, D. J., and W. G. Whitford. 2009. Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem. *Journal of Arid Environments* 73:66-73.
- Esler, K. J., and R. M. Cowling. 1995. The comparison of selected life-history characteristics of mesembryanthema species occurring on and off mima-like mounds (heuweltjies) in semiarid southern Africa. *Vegetatio* 116:41-50.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629-644.
- Gelbard, J. L., and S. Harrison. 2003. Roadless habitats as refuges for native grasslands: Interactions with soil, aspect, and grazing. *Ecological Applications* 13:404-415.
- Germano, D. J., G. B. Rathbun, and L. R. Saslaw. 1991. Managing exotic grasses and conserving declining species. *Wildlife Society Bulletin* 29:551-559.
- Harrington, G. N. 1991. Effects of soil-moisture on shrub seedling survival in a semiarid grassland. *Ecology* 72:1138-1149.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, Washington.
- Holmes, P. M., and D. M. Richardson. 1999. Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African fynbos. *Restoration Ecology* 7:215-230.
- Horwath, J. L., and D. L. Johnson. 2006. Mima-type mounds in southwest Missouri: Expressions of point-centered and locally thickened biomantles. *Geomorphology* 77:308-319.
- Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405-422.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- JMP, Version 8. SAS Institute Inc., Cary, NC, 1989-2007.
- Kent, M., and P. Coker. 1992. *Vegetation Description and Analysis: A Practical Approach*. CRC Press, Ann Arbor, Michigan.
- Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. *Journal of Range Management* 26:106-113.
- Li, C. L., X. Y. Hao, W. D. Willms, M. L. Zhao, and G. D. Han. 2010. Effect of long-term cattle grazing on seasonal nitrogen and phosphorus concentrations in range forage species in the fescue grassland of southwestern Alberta. *Journal of Plant Nutrition and Soil Science* 173:946-951.
- Manier, D. J., and N. T. Hobbs. 2007. Large herbivores in sagebrush-steppe ecosystems: livestock and wild ungulates influence structure and function. *Oecologia* 152:739-750.
- Marty, J. T., S. K. Collinge, and K. J. Rice. 2005. Responses of a remnant California native bunchgrass population to grazing, burning and climatic variation. *Plant Ecology* 181:101-112.
- McCune, B., and Grace, J. B. 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, OR.
- Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99:113-130.
- Moore, J. M., and M. D. Picker. 1991. Heuweltjies (earth mounds) in the Clanwilliam district, Cape-Province, South-Africa—4000-year-old termite nests. *Oecologia* 86:424-432.
- Nelson, R. E. 1997. Implications of subfossil Coleoptera for the evolution of mima mounds of southwestern Puget Lowland, Washington. *Quaternary Research* 47:356-358.
- Olivero, A. M., and D. M. Hix. 1998. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. *Plant Ecology* 139:177-187.
- Pantone, D. J., W. A. Williams, and A. R. Maggenti. 1989. An alternative approach for evaluating the efficacy of potential biocontrol agents of weeds. 2. Path analysis. *Weed Science* 37:778-783.
- Popay, I., and R. Field. 1996. Grazing animals as weed control agents. *Weed Technology* 10:217-231.
- Reynecke, B. K. 2012. Plant community restoration on Mima mounds at Turnbull National Wildlife Refuge, WA. M.S. Thesis, Eastern Washington University, Cheney.
- Safford, H. D., and S. P. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications* 11:1112-1122.
- Searcy, K. B., B. F. Wilson, and J. H. Fownes. 2003. Influence of bedrock and aspect on soils and plant distribution in the Holyoke Range, Massachusetts. *Journal of the Torrey Botanical Society* 130:158-169.
- Seifert, C. L., R. T. Cox, S. L. Forman, T. L. Foti, T. A. Wasklewicz, and A. T. McColgan. 2009. Relict nebkhas (pimple mounds) record prolonged late

Holocene drought in the forested region of south-central United States. *Quaternary Research* 71:329-339.

Vinton, M. A., and I. C. Burke. 1995. Interactions between individual plant-species and soil nutrient status in shortgrass steppe. *Ecology* 76:1116-1133.

Waite, R. B. 1980. About forty late-glacial Lake Missoula jökulhlaups through southern Washington. *Journal of Geology* 88:653-679.

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