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The Indirect Effects of Cheatgrass Invasion: Grasshopper Herbivory on Native Grasses Determined by Neighboring Cheatgrass

Julie Beckstead, Susan E. Meyer, and Carol K. Augsperger

Abstract—Invasion biology has focused on the direct effects of plant invasion and has generally overlooked indirect interactions. Here we link theories of invasion biology and herbivory to explore an indirect effect of one invading species on associational herbivory (the effect of neighboring plants on herbivory) of native species. We studied a Great Basin shadscale (*Atriplex confertifolia*)-bunchgrass community in western Utah, U.S.A. This community is dominated by native bunchgrasses, invaded by cheatgrass (*Bromus tectorum*), and home to large populations of grasshoppers (*Xanthippus corallipes* and *Melanoplus confusus*). Observations of associational herbivory provided support for the attractant-source hypothesis for one of two native species studied. *Elymus elymoides* experienced 43% greater cumulative herbivory of vegetative structures and produced 11X fewer reproductive structures in naturally high- compared to naturally low-density cheatgrass, thus demonstrating associational susceptibility. In contrast, *Poa secunda* showed no indication of associational herbivory; its amount of herbivory did not differ in high- compared to low-density cheatgrass patches. *Elymus elymoides* remained a viable food source when cheatgrass senesced, whereas *P. secunda* entered early summer dormancy. Through indirect effects, invading species may generate important shifts in herbivory on native species.

Introduction

The amount of herbivory a plant experiences depends not only on its own chemical and physical traits, but also on the characteristics of its neighbors (Root 1973; Atsatt and O'Dowd 1976). This concept of neighborhood effect, also known as associational herbivory, arose from observations that plants in natural polycultures suffer less herbivory than plants in agricultural or natural monocultures (Pimentel

1961). Associational herbivory has two contrasting outcomes: associational resistance, in which a focal plant species experiences less herbivory when grown in the presence of a neighbor (Tahvanainen and Root 1972; Root 1973; Bach 1980), and associational susceptibility, in which a focal plant experiences increased herbivory (Brown and Ewel 1987)—also called “associational damage” (Thomas 1986) and “shared-doom” (Wahl and Hay 1995).

The introduction of a “new” neighbor, such as an invasive plant species, can alter old and/or create new patterns of associational herbivory by affecting the herbivore's behavior and/or population density. The effect could occur directly as a new food source and/or indirectly by influencing the herbivore's ability to locate native plants. Associational herbivory theories have not been applied to the interactions of invasive species in natural systems; this study explores that connection.

Three alternative hypotheses regarding associational herbivory emerge from previous research (for review, see Huntly 1991). We incorporate invasive species into these hypotheses. Predicted outcomes for the native species depend on whether the herbivore is a generalist or a specialist, whether the invasive species also is utilized by the herbivore, and the relative feeding preference among plant species. If an invasive species experiences herbivory, it is predicted to come from a generalist that consumes native species of a similar phylogeny (Strong and others 1984; Mack 1996).

1. Repellent-plant hypothesis: If the invader acts as a repellent-plant to the herbivore (Root 1973; Atsatt and O'Dowd 1976) and indirectly affects the herbivore's behavior, then a native species located next to an invader will experience less herbivory than in its absence (associational resistance).
2. Attractant-sink hypothesis: If the invader acts as an attractant-sink (decoy) to the herbivore (Atsatt and O'Dowd 1976) and is directly utilized by the herbivore, then a native species located next to an invader will experience less herbivory than in its absence (associational resistance).
3. Attractant-source hypothesis: If the invader acts as an attractant-source to the herbivore (Wahl and Hay 1995) and is directly utilized by the herbivore, then a native species located next to an invader will experience greater herbivory than in its absence (associational susceptibility).

To determine which hypothesis is supported for an invasive species, we studied a cold desert shadscale (*Atriplex confertifolia* Wats.)-bunchgrass community in western Utah, U.S.A.

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This system has been invaded by cheatgrass (*Bromus tectorum* L.) and is home to large populations of grasshoppers, the primarily grass-feeding redshanked grasshopper (*Xanthippus corallipes* Haldeman) and the mixed-feeder (grasses and forbs) pasture grasshopper (*Melanoplus confusus* Scudder). Previous studies found that cheatgrass is a highly utilized food source within this system (Beckstead 2001). Given that the herbivores in this system are generalists and that cheatgrass is eaten by the herbivores, the repellent-plant hypothesis can be eliminated. However, this hypothesis may be applicable to other invaded systems in which herbivore specialists have a strong influence. To explore the remaining two hypotheses, we obtained data from naturally occurring patches of cheatgrass. At the study site, cheatgrass exists in a mosaic of low-, intermediate-, and high-density cheatgrass patches on a scale of <10 m (a distance that grasshoppers can traverse in minutes), intermixed with the native plant community (Beckstead 2001). Previous field experiments at the study site found that differential resource availability explains the observed variation in cheatgrass density, and variation in natural resistance to invasion by cheatgrass (Beckstead and Augspurger 2004). This spatial pattern of contrasting densities at this scale provides an opportunity to study the indirect effects of cheatgrass on native plant species through associational herbivory.

The primary objective of this study is to document whether associational herbivory is occurring for a natural system involving an invasive species. First, we investigated the associational herbivory hypotheses by comparing the amount of herbivory on two dominant native grasses surrounded by low vs. high densities of cheatgrass (range naturally available to grasshoppers). Secondarily, to interpret the associational herbivory results, we investigated feeding preferences of the grasshoppers among six common native species, including the two dominant grasses in the associational herbivory study, and developed a mechanistic explanation for the pattern based on tissue chemistry and phenology.

Materials and Methods

Study Sites and Study Species

The two study sites were located within the same valley in western Utah, U.S.A., on Bureau of Land Management land. Mean monthly temperature is 18.3 °C and mean annual precipitation is 176 mm (Stevens and others 1983). The observations addressing the associational herbivory hypotheses occurred at a cheatgrass "mosaic" site (4 ha; 14 km S of Dugway; 40°7'N, 112°40'W; 1,550 m elevation). Currently, the dominant native species are the shadscale shrub and two perennial bunchgrasses: sandberg bluegrass (*Poa secunda* Presl.) and squirreltail (*Elymus elymoides* Raf.). Experiments and data utilized to develop the predictive mechanism (i.e., grasshopper feeding preferences, tissue chemistry, and phenology) were conducted at a nearby site. Both study sites have been grazed by cattle, sheep, wild horses, and antelope (J. Beckstead, personal observation). Prior to data collection, the study sites were enclosed by a wire fence to exclude large grazing ungulates.

Cheatgrass, a winter annual of European origin (Mack 1981), is the most common and widespread invasive species at both study sites. In western Utah, its seeds usually

germinate in October and November in response to autumn rains (Beckstead and others 1995) and seeds ripen in June and July, usually before most native grass species.

Two common grasshopper herbivores of the community are *Xanthippus corallipes* and *Melanoplus confusus*. *Xanthippus corallipes* is a large grasshopper (female body length 35–41 mm; male body length 24–30 mm) that feeds exclusively on grasses and sedges (Pfadt 1994). It has a wide distribution in western North America, where it inhabits grassland and shrub-grass communities. *Melanoplus confusus* is a smaller grasshopper (female body length 23–24 mm; male body length 18–19 mm) that feeds on both grasses and forbs (Pfadt 1994). It is common in grassland habitats of the West and meadows and pastures of the Midwest and eastern United States. Both grasshopper species have an early season phenology: eggs hatch in late February–March; nymph stages progress quickly in April; adult size is attained in May; and egg-laying and death occur in June–July (Pfadt 1994).

Associational Herbivory Study

To investigate associational herbivory on native species in the presence of neighboring cheatgrass, we utilized naturally occurring low- and high-density cheatgrass patches interspersed among a native shadscale-bunchgrass community at the "mosaic" site. We arbitrarily set limits for the low- (<15% cover) and high- (>85% cover) density cheatgrass patches. In a mapped area (5,000 m²) within the study area, low-density patches covered 25% and were intermixed with high-density patches that covered 30% of area (data obtained from aerial photographs taken in 1999). Native species are found within the mosaic of cheatgrass density patches, most commonly *P. secunda* and *E. elymoides*. Frequencies for these two native species were obtained for 15 low- and 15 high-density cheatgrass patches in 1997. Frequency data were analyzed using Yates corrected chi-square test. The total percent plant cover was slightly lower in low- than in high-density cheatgrass patches (Beckstead 2001), although the two patch types had similar species richness (J. Beckstead, unpublished data on file at Gonzaga University).

Grasshoppers were quantified in early June 1999, when grasshoppers had achieved adult size. We randomly selected 12 low- and 12 high-density patches, each with two 30 x 30 cm plots, in which to quantify grasshopper densities. Then, in the early morning as the observer walked towards each plot within each patch, the number of grasshoppers jumping out was counted (modified USDA Animal and Plant Health Inspection Service (APHIS) method; Onsager and Henry 1977). Grasshopper densities were analyzed using a one-way analysis of variance (ANOVA) and a mixed model procedure (PROC MIXED) (SAS 1997) with subsampling; data met the normality assumption. Herbivory effects on cheatgrass in low- and high-density cheatgrass patches were measured in a concurrent study in many of the same cheatgrass patches assessed for grasshopper density (Beckstead and Augspurger 2004); results are summarized in the discussion.

The Mormon cricket (*Anabrus simplex* Haldeman), a shield-backed katydid and not a true cricket (Pfadt 1994), migrated to the site in 1998. To isolate the herbivore effects of resident grasshoppers from that of migrating Mormon crickets, we baited the study area with 3 L of carbaryl (active ingredient in Sevin™) wheatbran from March to June 1999. This

selective insecticidal bait differentially kills Mormon crickets but not grasshoppers (Quinn and others 1989; confirmed by counting carcasses following bait application).

In late June 1999, we measured cumulative grasshopper herbivory on two native grasses in low- and high-density patches of neighboring cheatgrass. The target species in this natural experiment were *E. elymoides* and *P. secunda*, the two most common native grass species. We randomly selected 17 low- and 17 high-density cheatgrass patches between 5–15 m wide within a 5,000 m² area at the study site. Within each patch, two individuals of each species were randomly selected for a total of 34 *E. elymoides* plants and 34 *P. secunda* plants. Given that plants in this desert system have a very short growing season, we chose to measure the herbivory only once at the end of the growing season. At the time of this cumulative herbivory measurement, cheatgrass was senescing, *E. elymoides* was at the seed-ripening stage, *P. secunda* had just gone dormant, and grasshoppers were nearing the end of their life cycle.

We measured the amount of herbivory on above-ground vegetative structures (leaves and stems combined) and reproductive structures (seed-bearing stems) of *E. elymoides* and *P. secunda*. For vegetative structures, the percent removed by herbivores (eaten) was determined by visually estimating the damage on the individual and placing each into one of five classes (0, 25, 50, 75, and 100% removed; similar to White and Whitham 2000). Although this estimation has its limitations, it is reasonably accurate, given the large measurement increments (25%).

We measured herbivory on reproductive structures for each plant by counting the number of stems supporting seeds that remained following herbivory. The number of grazed seed-bearing stems was not counted due to the difficulty of distinguishing grazed reproductive stems from the narrow, round grazed leaves for *P. secunda*. Assuming that plant size is the best predictor for seed-bearing stem production (i.e., number of stems present in the absence of herbivory), we measured plant basal diameter (plant width at ground level) to control for variation in reproduction due to plant size. Basal diameter is a good indicator of reproductive potential for bunchgrasses (S. Monsen, personal observation; and supported by significant correlations in these results).

We analyzed herbivory of vegetative structures (percent leaf/stem eaten) as a mixed model ANOVA and herbivory of reproductive structures (number of seed-bearing stems remaining) as a mixed model analysis of covariance (ANCOVA; PROC MIXED) (SAS 1997). This two-factor nested design with subsampling included fixed effects (patch, species nested within patch, and basal diameter as a covariate) and random effects (replication and subsampling). PROC MIXED is recommended for mixed models and is based on restricted maximum likelihood estimation (REML) of linear statistical models involving both fixed and random effects (for further discussion see Steel and others 1997). Assumptions of ANCOVA were met following model selection procedures recommended by Littell and others (1996). Differences between plant basal diameter for each species in low- and high-density patches were determined by a similar mixed model ANOVA (SAS 1997). Appropriate transformations were performed when needed to meet the assumption of normality. To compare differences between the two species within each patch type, we used the protected Fisher's LSD using the least square means (to account for the appropriate standard errors) (SAS Institute 1997).

Comparative Herbivory Experiment

To compare the amount of herbivory among common native species, we planted six species in an experimental array in a common garden and subjected them to the natural density of grasshoppers. The species were the five dominant perennial grasses and one forb found in this shadscale-bunchgrass community (table 1). Two of the grass species were *E. elymoides* and *P. secunda*, the target species for the associational herbivory study. To create the experimental arrays, seeds were collected from the study site when available; otherwise, they were obtained from desert communities with similar arid environments. Seeds were germinated and seedlings grown for 5 months in a greenhouse. In March 1997, one seedling of each species was transplanted 15 cm apart into each of six corners of nine adjacent hexagons in a 1.44-m² plot. Each plot was spaced 1 m apart and replicated 12 times. Prior to transplanting the seedlings, the pre-existing seed bank of

Table 1—Descriptive traits of six native plant species common in the shadscale-bunchgrass community and the invasive cheatgrass. Nomenclature is from Welsh and others (1987).

Species	Growth form	Flowering	Seed-ripening
<i>Elymus elymoides</i> Raf. Squirreltail	Perennial bunchgrass	June	July
<i>Elymus smithii</i> Gould Western wheatgrass	Perennial rhizomatous grass	June-July	July-Aug
<i>Stipa hymenoides</i> R. & S. Indian ricegrass	Perennial bunchgrass	June	July
<i>Poa secunda</i> Presl. Sandberg bluegrass	Perennial bunchgrass	May	June
<i>Stipa comata</i> Trin. & Rupr. Needle-and-thread	Perennial bunchgrass	June	July
<i>Sphaeralcea munroana</i> Gray Munroe globemallow	Perennial forb	July-Aug	Aug-Sept
<i>Bromus tectorum</i> L. Cheatgrass	Annual grass	May	June

cheatgrass was removed in 1996 by raking the litter and seeds off each plot and then watering in August 1996 to promote precocious germination of any remaining seeds (Beckstead and others 1995). At the time of measuring herbivory, the natural densities of *X. corallipes* and *M. confusus* were 15-20 grasshoppers per m² (J. Beckstead, personal observation). The arrays covered an area of 1,024 m² and were surrounded by cheatgrass densities of 11,834/m² ± 3,056 (mean ± SD; n = 17).

In June 1998, cumulative herbivory of the six native species was measured once during flowering, which occurred near the end of the grasshopper life cycle. We estimated the percent eaten (herbivory) for each species collectively within a plot using five classes (as described above). We analyzed species differences in percent eaten (herbivory) with analysis of variance (ANOVA; PROC GLM) (SAS 1997). The assumption of normality was met by a square root (y + 3/8) transformation. Multiple comparisons between the six native species were performed with Scheffe's test.

To assess the relationship between herbivory and nitrogen and silica content, plant tissue was collected in June 1999 from a natural community near the experimental site. Samples were taken from 15 individuals for each of the six native plant species at the flowering stage and at three developmental stages of cheatgrass (bolting, flowering, and seed-ripening). Above-ground tissues (leaves and stems, excluding inflorescences, except for cheatgrass) were dried at 60 °C for 48 hours, ground to a uniform powder, randomly combined into three or five samples (due to limited amount of tissue collected from each individual), and analyzed for total nitrogen content using the Association of Official Analytical Chemists (AOAC) semi-automated method (Horwitz 1980). Due to a limited amount of tissue, samples of *P. secunda*, *S. munroana*, and bolting and seed-ripening cheatgrass samples were analyzed for total nitrogen using the AOAC micro-Kjeldahl method (Horwitz 1980). Nitrogen content was expressed as total percent nitrogen. Percent silica content was analyzed using a muffle furnace for complete combustion followed by a hydrochloric acid extraction (Allen and others 1974).

Species differences in percent nitrogen and silica were analyzed with ANOVA by a general linear model procedure

(PROC GLM) (SAS 1997). Values for both traits were arcsine transformed to meet the assumption of normality. Multiple pairwise comparisons for the six native species were performed with protected Fisher's least significance difference (LSD) tests. Pairwise comparisons were also made for each of the six native species and the three developmental stages of cheatgrass.

Descriptive traits, such as plant growth form and phenology, were noted at the time of tissue collection and confirmed by species descriptions in Welsh and others (1987; table 1). This information was used for data interpretation.

Results

Associational Herbivory Study

The low-density patches and high-density patches differed in frequency for the two native grass species, *P. secunda* and *E. elymoides*, and the density of grasshoppers. Although *P. secunda* was found more frequently in the low-density patches than the high patches, *E. elymoides* did not differ in its frequency between the two patch types (table 2). Grasshopper densities were twice as high in the high-density than in the low-density cheatgrass patches (ANOVA, *F* = 14.74, *df* = 1, 11, *P* = 0.0028) (table 2).

Mean cumulative herbivory on vegetative (leaves and stems) and reproductive (seed-bearing stems) structures was greater in the high-density cheatgrass patches in comparison to the low-density patches (patch effect, ANOVA, *F* = 24.96, *df* = 1,16, *P* < 0.001 and ANCOVA, *F* = 61.10, *df* = 1, 16, *P* < 0.0001, respectively). However, the two native grasses differed in their response to the associational herbivory on both vegetative structures (species effect nested within patch, ANOVA, *F* = 100.51, *df* = 2,16, *P* < 0.0001) and reproductive structures (species effect nested within patch, ANCOVA, *F* = 80.50, *df* = 2,32, *P* < 0.0001). For *E. elymoides*, the mean percent eaten per individual (leaf/stem) was higher in high- (98.3%) than in low-density cheatgrass patches (55.2%; Fisher's LSD, *t* = 5.37, *P* < 0.0001) (fig. 1). The high herbivory in high-density patches resulted in a lower mean number of seed-bearing stems per individual in comparison to low-density cheatgrass patches: 1.4 vs. 15.7, respectively (Fisher's LSD, *t* = 10.56, *P* < 0.0001) (fig. 1).

Table 2—Native plant (frequency and basal diameter) and grasshopper (density) descriptive data for low- vs. high-density cheatgrass patches at the “mosaic” study site. Data are means ± 1 SD. Different small letters indicate differences between low- vs. high-density cheatgrass patches significant at *P* < 0.05 from Protected Fisher's LSD test following Analysis of Variance for basal diameter and grasshopper density and chi-square analysis for native plant frequency.

Cheatgrass patch	Native plants				Grasshoppers
	Frequency <i>E. elymoides</i>	Frequency <i>P. secunda</i>	Basal dia (cm) <i>E. elymoides</i>	Basal dia (cm) <i>P. secunda</i>	Density Number m ⁻²
	----- (n = 15) -----		----- (n = 34) -----		(n = 24)
Low density (≤ 15% cover)	27% ^a	100% ^a	14.2 ^a ± 3.8	8.2 ^a ± 1.9	11.6 ^b ± 8.0
High density (≥ 85% cover)	22% ^a	67% ^b	14.9 ^a ± 4.4	9.1 ^a ± 2.4	22.7 ^a ± 6.5

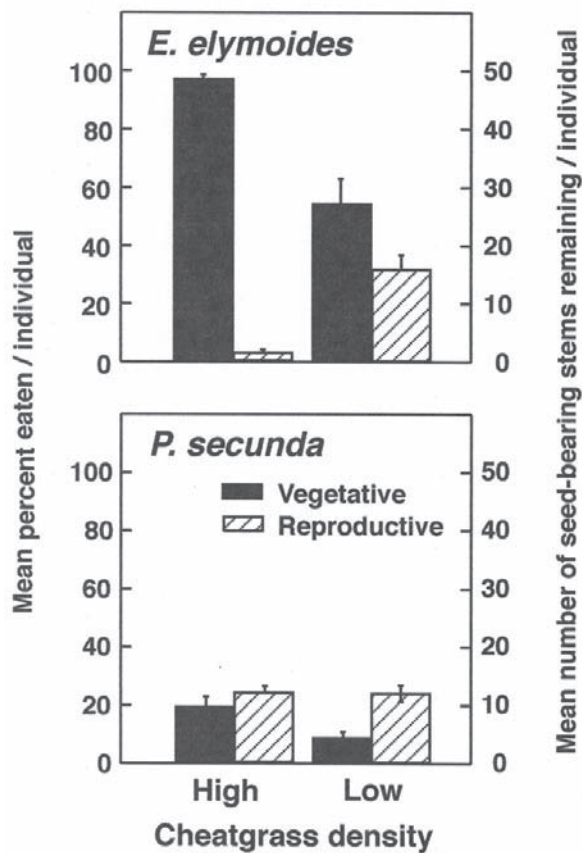


Figure 1—Cumulative herbivory on vegetative (left axis; mean % eaten/individual) and reproductive (right axis; mean number of seed-bearing stems remaining/individual) structures for *E. elymoides*, a highly preferred species, and *P. secunda*, a less-preferred species, in high- vs. low-density cheatgrass patches (means + 1 SE; n = 26 and n = 34, respectively).

E. elymoides experienced associational susceptibility when located in high-density cheatgrass patches as a result of the higher concentration of grasshoppers in high- compared to low-density patches. In contrast, for *P. secunda* neither herbivory on vegetative or reproductive structures differed between patch types (Fisher’s LSD, $t = 1.69, P = 0.10$ and $t = 0.54, P = 0.59$, respectively); thus there was no associational herbivory (fig. 1).

Plant basal diameter was a significant covariate for herbivory in the reproductive structures model (ANCOVA, $F = 47.00, df = 1, 67, P < 0.0001$). It was also significantly correlated with the number of seed-bearing stems for *E. elymoides* (Pearson’s $r = 0.31, P < 0.01$) and *P. secunda* (Pearson’s $r = 0.56, P < 0.0001$). The basal diameters of *E. elymoides* and *P. secunda* did not differ significantly between low- and high-density patches (ANOVA, $F = 1.44, df = 1, 16, P = 0.25$) (table 2), indicating that differences in number of seed-bearing stems could not be attributed to differences in plant size.

Comparative Herbivory Experiment

Cumulative herbivory varied significantly among the six native species (fig. 2; one-way ANOVA, $F = 69.29, df = 5, P < 0.0001$) and resulted in three distinct groups: (1) a highly preferred group (>70% plant cover removed; *E. elymoides*, *E. smithii*, and *S. hymenoides*), (2) a less-preferred group (<30% plant cover removed; *P. secunda* and *S. comata*), and (3) one unpalatable species (0% plant cover removed; *S. munroana*). Thus, the two target species for the associational herbivory study were categorized as a highly preferred species (*E. elymoides*) and a less-preferred species (*P. secunda*).

The six native species differed significantly in total percent nitrogen (one-way ANOVA, $F = 54.34, df = 5, P < 0.0001$) and silica content (one-way ANOVA, $F = 74.12, df = 5, P < 0.0001$). However, only total percent nitrogen was separable into three distinct groups that corresponded to the herbivore preference groups of the palatable species (table 3; fig. 2). The less-preferred species, *P. secunda* and *S. comata*, contained significantly lower nitrogen than two highly-preferred species, *E. elymoides* and *S. hymenoides*. *E. smithii*, one of three highly preferred species, did not differ from the less-preferred species. Although *S. munroana*, the only forb, had the highest total percent nitrogen, its leaves were not eaten. It did receive some damage from the grasshoppers, which congregated around the base of the plants and girdled some of the lower branches resulting in branch death.

Difference in total percent nitrogen between cheatgrass and the native species depended on the developmental stage of cheatgrass (one-way ANOVA, $F = 73.51, df = 8, P < 0.0001$) (table 3). Young cheatgrass plants at the bolting

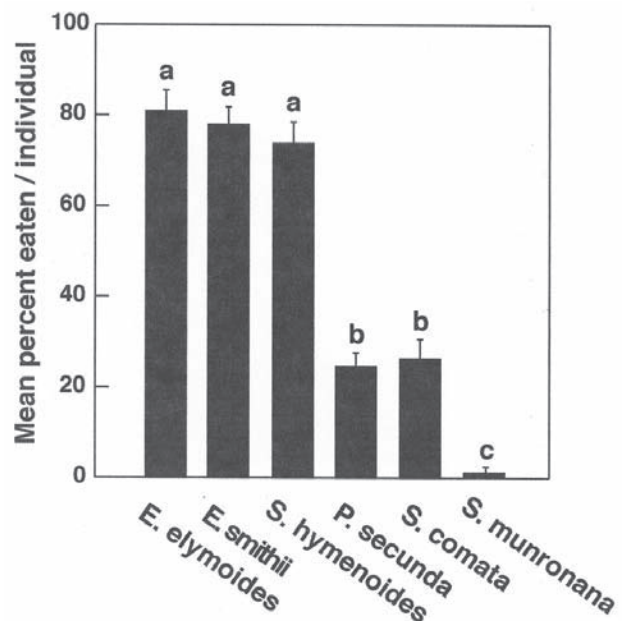


Figure 2—Amounts of grasshopper cumulative herbivory (mean % eaten/individual) on six native plant species grown in common garden plots (means + 1 SE; n = 12). Different small letters indicate significant differences between species ($P < 0.05$; Scheffe’s multiple comparison test).

Table 3—Total percent nitrogen and percent silica for plant tissue of six native species at their flowering stage and for cheatgrass at three developmental stages. Values are means (± 1 SE). Different small letters indicate significant differences among species at $P < 0.05$ from Protected Fisher's LSD test following Analysis of Variance. Asterisks indicate differences in percent nitrogen between selected species pairs (a given native species and a cheatgrass stage) significant at $P < 0.05$ from Protected Fisher's LSD test following analysis of variance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = nonsignificant).

Species	Percent nitrogen at cheatgrass developmental stages				
	% Nitrogen	% Silica	Bolting, n = 3 2.35 (0.04)	Flowering, n = 5 1.42 (0.07)	Seed-ripening, n = 3 0.37 (0.01)
<i>E. elymoides</i> , n = 5	1.64 ^{bc} (0.06)	4.54 ^a (0.20)	***	*	***
<i>E. smithii</i> , n = 5	1.49 ^{cd} (0.10)	2.71 ^b (0.03)	***	ns	***
<i>S. hymenoides</i> , n = 5	1.74 ^b (0.08)	1.76 ^e (0.10)	***	**	***
<i>P. secunda</i> , n = 3	1.29 ^d (0.11)	2.52 ^{bc} (0.25)	***	ns	***
<i>S. comata</i> , n = 5	1.40 ^d (0.04)	2.50 ^{cd} (0.16)	***	ns	***
<i>S. munroana</i> , n=3	3.26 ^a (0.13)	0.51 ^f (0.03)	***	***	***

stage contained significantly higher levels of nitrogen than the five palatable species. At its flowering stage, total percent nitrogen did not differ significantly from *E. smithii*, *P. secunda*, or *S. comata*. Both *E. elymoides* and *S. hymenoides* contained higher total percent nitrogen than flowering cheatgrass. By the seed-ripening stage, cheatgrass contained significantly lower levels of nitrogen in comparison to all native species.

Discussion

This study offers a unique example of an invasive species acting as an attractant-source resulting in associational susceptibility for a native species. Native *E. elymoides* experienced greater herbivory to both reproductive and vegetative structures in high- compared to low-density cheatgrass patches; thus demonstrating associational susceptibility. In contrast, native *P. secunda* showed no indication of associational herbivory; its amount of herbivory did not differ in low- compared to high-density cheatgrass patches. These contrasting associational herbivory patterns can be explained in part by the herbivores' feeding preference, which is driven, in turn, by the tissue chemistry and phenology of cheatgrass in relation to the two native species.

Associational Herbivory Study

First, we found that high-density cheatgrass patches attracted greater numbers of generalist grasshoppers than did low-density cheatgrass patches, presumably by providing a preferred feeding area. According to the resource concentration hypothesis (Root 1973), herbivores should accumulate where their food resources are most concentrated.

Supporting this, measurements taken concurrently with this study found that, in both low- and high-density cheatgrass patches, herbivory on cheatgrass was higher with greater cheatgrass biomass and density (Beckstead and Augspurger 2004). We propose that cheatgrass acts as an attractant-source by its influence on the grasshopper population density (a numerical response via immigration). Grasshopper densities were twice as high in high-density cheatgrass patches as they were in low-density patches. The high nitrogen levels found in bolting and flowering cheatgrass plants may attract and/or retain more grasshoppers in the high-density compared to the low-density cheatgrass patches. It is unknown whether cheatgrass densities may also influence grasshopper survival or how frequently these patterns occur across years. Future studies are necessary to decipher the mechanism(s) by which cheatgrass acts as an attractant-source and the thresholds of cheatgrass and grasshopper densities required for associational herbivory. Given the physical uniformity of the site, the magnitude of the effect we measured, and the relatively small spatial scale of low- vs. high-density cheatgrass patches (<10 m), it seems unlikely that grasshopper density and consequent differences in herbivory levels on associated native grasses were greatly influenced by factors other than cheatgrass density itself.

In this study using a natural range of cheatgrass densities, the attractant-source hypothesis was supported by *E. elymoides*, but not by *P. secunda*. Using a marine system, Wahl and Hay (1995) found that the strength of associational herbivory patterns varied with the relative preference of the omnivorous sea urchin for pairwise combinations of host seaweed and epibionts. It is possible that the relative preference in our plant-grasshopper system is a mechanism underlying our observed associational herbivory pattern.

A Mechanistic Explanation of Associational Herbivory

Among the five common grass species in the shadscale-bunchgrass community, the amount of herbivory corresponded to the total percent nitrogen and not percent silica. The only forb in the study, *S. munroana*, which had the highest level of nitrogen and was not consumed by grasshoppers, was the exception. The plant chemistry of forbs, in general, is distinct from that of grasses. The unpalatability of *S. munroana* could be due to some unmeasured secondary compound; Bernays and Chapman (1970) found that forbs lack a chemical substance necessary to induce biting by many grass-feeding grasshoppers. Among the five grass species, the highly preferred species, *E. elymoides*, *E. smithii*, and *S. hymenoides*, had higher nitrogen levels than less preferred species. High nitrogen or amino acid content has been associated with increases in grasshopper herbivory (for review see Chapman 1990). Although high silica content in grasses has been proposed to be an important deterrent for grasshopper herbivory (Joern 1979), no such pattern was found in this study. Water content (Lewis and Bernays 1985) and sucrose concentration (Bernays and Chapman 1978) are potentially important tissue traits affecting herbivory of grasses, but were not measured in this study.

In addition to explaining feeding preferences, we propose that phenology is also a key factor driving the contrasting associational herbivory patterns for the highly-preferred, *E. elymoides* (associational susceptibility) and the less-preferred, *P. secunda* (no associational herbivory). As noted in table 1, the early summer dormancy of *P. secunda* may allow it to escape herbivory temporarily; it becomes dormant before the grasshoppers reach adult size. Although this study did not include pairwise preference experiments between cheatgrass at different phenological stages and each of the native species, we did compare total percent nitrogen of cheatgrass at three developmental stages with nitrogen levels of native species at the flowering stage. Cheatgrass, an annual, undergoes these stages in a very short period of time (Young and others 1969) and each perennial native species at its flowering stage will encounter more than one cheatgrass stage. Based on these comparisons, we predict that: (1) young cheatgrass plants will be preferred over all native grasses, (2) *E. elymoides* and *S. hymenoides* will be preferred over flowering cheatgrass plants, and (3) all native grasses in the flowering stage will be preferred over cheatgrass at the seed-ripening stage. Direct feeding trials would be a means of testing these predictions.

Our findings for the associational herbivory study support our predictions of pairwise comparisons of cheatgrass with the common native species. The herbivore effects in this experiment were measured at seed production for the native grasses, such that the native species had experienced herbivory during all cheatgrass stages. *E. elymoides*, a predicted preferred food source over cheatgrass at two of three stages, had lower final reproductive output in high- compared with low-density cheatgrass patches (i.e., associational susceptibility). In contrast, *P. secunda* is predicted to be preferred over cheatgrass only during cheatgrass' seed-ripening stage; however, it escapes herbivory at this time through early summer dormancy (table 1). Associational susceptibility

appeared to result when grasshoppers shifted food preference to *E. elymoides*, driven by the early phenology of cheatgrass. White and Whitham (2000) found associational susceptibility resulted when a generalist herbivore reached outbreak proportions and consumed their preferred host; the herbivore then moved to nearby less-preferred hosts to complete their life cycle. In this study, cheatgrass was not completely eliminated by grasshoppers. Instead, it appears that cheatgrass became less preferred near the end of its life cycle.

This study indicates that indirect interactions between invasive and native species may have large consequences for native species success. The indirect effect of cheatgrass on native species via associational herbivory indicates the potential for a shift in species composition within the shadscale-bunchgrass community, specifically, a decrease in the *E. elymoides* population relative to no change for *P. secunda* populations. Although these shifts in species composition are possible, the long-term effects of associational herbivory and the frequency of these events on community composition are unknown.

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