

Comparison of damage to native and exotic tallgrass prairie plants by natural enemies

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Abstract We surveyed the prevalence and amount of leaf damage related to herbivory and pathogens on 12 pairs of exotic (invasive and noninvasive) and ecologically similar native plant species in tallgrass prairie to examine whether patterns of damage match predictions from the enemy release hypothesis. We also assessed whether natural enemy impacts differed in response to key environmental factors in tallgrass prairie by surveying the prevalence of rust on the dominant C₄ grass, *Andropogon gerardii*, and its congeneric invasive exotic C₄ grass, *A. bladhii*, in response to fire and nitrogen fertilization treatments. Overall, we found that the native species sustain 56.4% more overall leaf damage and 83.6% more herbivore-related leaf damage when compared to the exotic species. Moreover, we found that the invasive exotic species sustained less damage from enemies relative to their corresponding native species than the

noninvasive exotic species. Finally, we found that burning and nitrogen fertilization both significantly increased the prevalence of rust fungi in the native grass, while rust fungi rarely occurred on the exotic grass. These results indicate that reduced damage from enemies may in part explain the successful naturalization of exotic species and the spread of invasive exotic species in tallgrass prairie.

Keywords Enemy release hypothesis · Grassland · Invasiveness · Leaf damage · Rust fungi

Introduction

Biological invasions are considered a significant component of global change (Mooney and Drake 1987; Sala et al. 2000; Vitousek et al. 1997) and are recognized to be an ecological and economic problem of growing severity. The threat to biodiversity due to deliberately or unintentionally introduced invasive alien species is second only to that of habitat destruction (Gandon 1998; Mack et al. 2000; Wilcove et al. 1998). However, the mechanisms of successful establishment and dispersal of exotic species in novel environments remain poorly understood (Kolar and Lodge 2001).

The enemy release hypothesis (Elton 1958; Keane and Crawley 2002) is one of the most compelling explanations for the successful establishment and spread of exotic species. It states that the release of a

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plant population from control by herbivores and other natural enemies in areas of introduction contributes to its ability to successfully establish and invade (Elton 1958; Keane and Crawley 2002). Recent comparative studies suggest that a wide range of exotic species sustain less diverse assemblages and lower numbers of herbivores and pathogens in introduced areas as compared to their native habitats (Callaway et al. 2004; DeWalt et al. 2004; Mitchell and Power 2003; Poulin and Mouillot 2003; Wolfe 2002). Although comparisons of this kind provide the first step to testing the enemy release hypothesis, they do not provide a complete understanding, because a lower diversity or abundance of enemies does not necessarily translate to less damage, and consequently higher competitive ability of exotic (Agrawal and Kotanen 2003; Maron and Vila 2001; Schierenbeck et al. 1994).

Thus, a necessary next step beyond quantifying enemy diversity or abundance is to compare the impact from natural enemies (e.g., herbivores and pathogens) on exotic species and their co-occurring native species in the introduced community (Agrawal and Kotanen 2003; Schierenbeck et al. 1994). Few studies have taken this step, and for those that have, the results vary among individual species (Bellingham 1998; Colautti et al. 2004; DeWalt et al. 2004; Goergen and Daehler 2001; Gross et al. 2001; Schierenbeck et al. 1994; Siemann and Rogers 2003). Even for the few multiple species studies, the results were not consistent (Agrawal and Kotanen 2003; Agrawal et al. 2005; Carpenter and Cappuccino 2005). Furthermore, confusion could arise from the fact that the difference in enemy impact might be explained by the systematic variation of physiological and morphological traits between native and exotic species (Agrawal and Kotanen 2003; Agrawal et al. 2005; Rejmanek and Richardson 1996) rather than the origin of species per se. Therefore, we conducted the current study in which we compare multiple, co-occurring exotic and native species pairs with similar physiological and morphological traits to provide a unique and more general insight into this question.

The primary objective of this study was to examine whether the prevalence of and damage caused by natural enemies (herbivores and pathogens) differs between exotic plant species and their co-occurring native competitors in tallgrass prairie, and whether any differences in prevalence are related to the degree of invasiveness of the exotic plant species. We chose

the tallgrass prairie as our study system because it contains a suite of exotic plant species (some invasive) that are closely related to a number of native plants. The native plants represent both the dominant C_4 grass species in tallgrass prairie (*Andropogon gerardii*), as well as a number of subordinate C_3 grass and forb species that contribute to community diversity. They are commonly attacked by a wide range of natural enemies, including vertebrate herbivores, insects and microbial diseases (Branson et al. 2006; Garrett et al. 2004; Kaufman et al. 1998; Mitchell et al. 2002; Stoner and Joern 2004).

Variability in environmental resources may interact with natural enemies and affect invasibility through mediating growth-defense allocation of plants (Herms and Mattson 1992), determining community diversity (Dietz et al. 2004), and further altering natural enemies' density (Mitchell et al. 2002). However, the way in which natural enemy pressure on invasive and native plants varies with environmental conditions has rarely been tested (Dietz et al. 2004). Thus, a second objective of this study was to examine whether natural enemy impacts, with focus on the native, dominant C_4 grass, *A. gerardii*, and its invasive congener, *A. bladhii*, differed in their response to fire and nitrogen availability. Fire is an important disturbance in tallgrass prairie that alters resource availability, plant community structure, and affects patterns of invasion (Collins and Steinauer 1998; Collins and Wallace 1990; Knapp et al. 1998; Smith and Knapp 1999, 2001a). Nitrogen is a key limiting resource in this system (Blair et al. 1998).

To address our objectives, we used two approaches. First, in order to gain a general understanding of the prevalence of natural enemies on native and exotic species in tallgrass prairie, we conducted a field survey to compare the presence of natural enemies on and the leaf damage for multiple sympatric or ecologically similar native and exotic species pairs representing key functional groups. A previous study showed that these closely related sympatric species pairs do not have generalizable differences in physiological or morphological traits related to resource utilization and carbon gain (Smith and Knapp 2001b). By using these pairs, we kept growth form and life history strategies of the paired studied species as similar as possible. Second, to explore whether fire and nitrogen availability affect the infection rates of a common type of natural enemy, rust fungi, on the

dominant C₄ grass in tallgrass prairie, we examined the prevalence of and leaf damage caused by rust fungi on *A. gerardii* and its invasive competitor *A. bladhii* in long-term (>15 year) experimental plots subjected to fire and nitrogen fertilization treatments.

Materials and methods

Study site

This study was conducted at the Konza Prairie Biological Station (KPBS), a 3487-ha tallgrass prairie preserve located in the Flint Hills region of north-eastern Kansas (39°05'N, 96°35'W). KPBS has a mid-continental climate (Hayden 1998). The vegetation at Konza Prairie includes ~576 vascular plant species, while the nonnative plant species ($n = 96$) account for 16.7% of the total flora (Towne 2002). The majority of Konza Prairie is dominated by native prairie species, especially warm-season (C₄) grass species, including big bluestem (*A. gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*A. scoparium*), and switchgrass (*Panicum virgatum*). A number of subdominant warm and cool-season (C₃)

grasses, forbs, and woody species are distributed within the matrix of grasses (Knapp et al. 1998).

KPBS is composed of 60 watershed units (average size ~60 ha) (Knapp et al. 1998). The watersheds are managed with different burning and grazing treatments. Replicate watersheds are burned at 1, 2, 4, 10, and 20 year intervals. The comparative study of damage from natural enemies was conducted in five ungrazed watersheds: one unburned until 2000 (R1B) but now burned annually in the spring, one annually burned in summer (SuB), one annually burned in winter (WA), one burned every 10 years (10B), and one left unburned (20B) (Table 1).

To assess the effect of fire, mowing and fertilization on the tallgrass prairie, the Belowground Plot Experiment was established in 1986 in a lowland unplowed prairie site (see Rice et al. 1998 for details). The experiment is set up as a split-split plot design with burning (annually burned or unburned) as the whole plot treatment, mowing (annually mowed or unmowed) as the subplot treatment, and fertilizer (10 g m⁻² N only, 1 g m⁻² P only, N and P, or no fertilizer) as the sub-subplot treatment for a total of 16 treatment combinations. Each treatment combination is replicated four times for a total of 64 12 × 12 m

Table 1 Study sites and number of individual plants sampled for the seven native (N) and exotic (E) species pairs

Functional group	Pair no.	Species pairs	Study site	Sample size
C ₄ biennial forbs	1	<i>Lactuca serriola</i> (E)	10B, R1B	66
	1	<i>Lactuca ludoviciana</i> (N)	10B, R1B	107
	2	<i>Tragopogon dubius</i> (E)	10B, R1B	55
	2	<i>Lactuca ludoviciana</i> (N)	10B, R1B	107
Legumes	3	<i>Melilotus officinalis</i> (E)	WA	50
	3	<i>Psoralea tenuiflora</i> (N)	WA	50
	4	<i>Coronilla varia</i> (E)	10B, 20B	59
	4	<i>Psoralea tenuiflora</i> (N)	WA	50
	5	<i>Lespedeza cuneata</i> (E)	SuB	32
C ₃ grasses	5	<i>Lespedeza capitata</i> (N)	SuB	32
	6	<i>Bromus inermis</i> (E)	10B	50
C ₄ grasses	6	<i>Elymus canadensis</i> (N)	10B	50
	7	<i>Andropogon bladhii</i> (E)	LTEP	262
	7	<i>Andropogon gerardii</i> (N)	LTEP	254

Note that *L. ludoviciana* comprised the native counterpart for *T. dubius* as well as *L. serriola*, and *P. tenuiflora* comprised the native counterpart for *C. varia* and *M. officinalis*, because they were the most ecologically similar. 10B = 10-year burn interval watershed. R1B = 20-year burn interval through 2000, now annually burned watershed. WA = winter (Feb; annually) burned watershed. SuB = summer (Aug; every other year) burned watershed. 20B = 20-year burn interval (unburned) watershed. LTEP = long-term experimental plots. Nomenclature follows the Great Plains Flora Association (1986)

experimental plots, which are arrayed in two adjacent sets of blocks. For the current study, we used a subset of eight plots to examine the effects of fire and nitrogen availability on the prevalence and damage by a natural enemy, rust fungi, on the dominant C₄ grass, *A. gerardii*, and the invasive C₄ grass, *A. bladhii*. Specifically, we focused on the following subset of treatments for our surveys (all annually mowed except for the year of the survey; $n = 2$ plots/trt): burned and N fertilized (BN), burned and unfertilized (BC), unburned and N fertilized (UN), and control (unburned and unfertilized, UC).

Study species

In addition to *A. gerardii* and *A. bladhii*, we selected an additional six pairs, each consisting of congeneric or ecologically similar (i.e., similar growth form and life history) native ($n = 5$) and exotic ($n = 7$) plant species representing the three most common plant families (Asteraceae, Fabaceae, and Poaceae) and four functional groups (C₃ biennial forbs, legumes, C₃ grasses, and C₄ grasses) found at KPBS (Table 1). Four of the seven exotic species (*Lactuca serriola*, *Tragopogon dubius*, *Melilotus officinalis*, and *Bromus inermis*), which are all native to Europe or Eurasia, were categorized as noninvasive species, because their abundance has not increased significantly on KPBS over the past two decades (Smith and Knapp 1999). The other three exotic species (*Lespedeza cuneata*, *Coronilla varia*, and *A. bladhii*) were considered invasive, because they are aggressively invading several tallgrass prairie sites on KPBS. *L. cuneata* was introduced from East Asia in the 1930s for erosion control and soil improvement, wildlife food and cover. It is listed as a noxious weed in Kansas because of its resistance to drought, tolerance of low soil fertility and production of residues containing phenolic compounds, which may be allelopathic. These traits are thought to be important in influencing its ability to dramatically reduce native diversity in tallgrass prairie (Kalburtji and Mosjidis 1992; Langdale and Giddens 1967). *C. varia* was introduced from Europe and was widely cultivated as a ground cover and for erosion control in the US since the 1950s. In some areas, it completely dominates pastures and abandoned fields (Heim 1990; invasive.org 2003). *A. bladhii* was introduced from Russia to the southern and central

Great Plains in 1919 as an alternative forage crop to the southern and central Great Plains and is thought to be invasive because of its resistance to drought and grazing and prolific seed production (Christiansen and Svejcar 1987; Svejcar and Christiansen 1987).

Sampling methods

For each species pair, individuals were sampled without regard to plant size or condition in 2004 from co-occurring populations in the same watershed, except for the *T. dubius* and *Lactuca* spp. pairs. For these pairs, a census in adjacent watersheds was conducted, because adequate populations of the two species did not occur in the same area. All sampling was conducted during the flowering season (June or August) of each species, except for *Lespedeza* spp., which were sampled early in June, prior to flowering. Sample sizes and sites for each species are summarized in Table 1.

For *Lespedeza* spp., each visible individual was sampled and collected for biomass measurement in late June. For the more widespread species, systematic or random sampling was applied. Specifically, *M. officinalis* and *P. tenuiflora* individuals were systematically sampled on the intersections of fifty 2 × 1 m grids within large, intermixed populations (total area: 18 × 5 m) in late June; *C. varia* individuals were selected in three relatively large, discrete populations at the same time by randomly throwing a hoop with a marker to the population and choosing the individual closest to the marker. Each of the C₃ grasses (*E. canadensis* and *B. inermis*) was sampled systematically on the intersections of 2 × 1 m grids within a mixed population (total area: 10 × 10 m) in mid-June.

For the C₄ grasses, *A. gerardii* and *A. bladhii* individuals were sampled by randomly throwing a hoop with a marker to the population and choosing the individual closest to the marker. The samples were from mixed populations in the long-term experimental plots in mid-August, when prevalence of rust fungi tends to be high (S. P. Dendy and K. A. Garrett, unpubl. data). To improve estimates, each plot was sampled three times over a 6-day period. One replicate each of the treatments (BN, BC, UN, and UC) were sampled on the first, third, and fifth day; and the remaining replicates were sampled on the second, fourth, and sixth day. Within a day,

sample sizes for each plot were the same. In addition, the percentage aerial cover of each C_4 grass was estimated visually in four 1×1 m subplots, randomly located within each plot. Abundance was estimated by averaging relative cover of each species in the four subplots.

Enemy prevalence and damage measurements

The natural enemies that were assessed in this study include insect herbivores and pathogens, such as those causing rust and powdery mildew and other foliar lesions. Large vertebrate herbivores (bison or cattle) were not assessed because this study was conducted in ungrazed sites. We used two measures to estimate the overall damage from natural enemies and unknown abiotic stresses for each individual plant surveyed: (1) the percentage loss of green leaf area (GLA), i.e., the proportion of what would have been the whole leaf area that was either missing, dry, nongreen or covered by pathogens, estimated using nearby intact leaves of the same size as a standard, and (2) the percentage of missing leaf area (MLA), i.e., the proportion of a whole intact leaf area apparently lost due to herbivory or abiotic stress. The GLA reduction ($1 - \%GLA$) and MLA were visually estimated for each leaf on an individual by placing the GLA or MLA into the following categories: less than 5%, 5–25%, 26–50%, 51–75%, and 76–99%. Mean GLA reduction and MLA were calculated by taking the midpoints of each of the four categories and averaging them for each individual plant. For each species, we recorded the number of individuals sampled and the total number of leaves on each individual. Note that this sampling method was useful for detecting within-leaf damage, but not larger scales of damage that might result in the loss of multiple leaves or stems. This method also will not necessarily provide information about systemic infections by pathogens such as viruses (Garrett et al. 2004).

To analyze whether the degree of invasiveness affected the amount of damage that a particular species experienced relative to its native counterpart, we calculated the relative GLA reduction for each exotic species (G) using the following formula:

$$G = (G_n - G_e) / G_n$$

where G_n is the percentage of GLA reduction averaged for all individuals sampled for each native

species; and G_e represents the percentage of GLA reduction for each individual sampled for each exotic species. We excluded *A. gerardii* and *A. bladhii* individuals sampled from the nitrogen fertilized plots from these calculations, because other species pairs sampled were not subjected to N fertilization.

To differentiate the sources of leaf damage, we counted the number of leaves on each individual with visible damage from different types of herbivore feeding. Though insects causing damage were not generally present when plants were sampled, we defined several distinct types of damage (Roy et al. 2004): “Marginal damage”, minor damage with small chewing marks to the leaf margin (<0.5 cm into the leaf; or in the case of grasses, <25% of the width of the leaf); “chewing damage”, damage with chewing marks extending into the center of the leaf; “shot-hole damage”, a circular hole (diameter = 0.3–0.5 cm) in the leaf; “leaf miner damage”, feeding between the upper and lower epidermis; “skeletonization”, the removal of the leaf tissue between the intact veins; “leaf roller damage”, a portion of a single leaf rolled or folded over and secured in place with an arthropod-derived substance; and “leaf tying damage”, two or more leaves attached together by an arthropod-derived substance.

To evaluate visible damage, first, we calculated the percentage of leaves with all types of insect damage, including rolling, tying, marginal damage, chewing and shot hole, skeletonization and leaf mining damage. Second, we calculated the frequency of individuals and leaves that were infected by pathogens, including rust fungi, other fungi causing leaf spots, and bacterial pathogens. Occurrence of rust was identified by aecia in June on *M. officinalis*, *P. tenuiflora*, and *E. canadensis*, and by visible urediniospores or teliospores in August on *Andropogon* spp.

To survey the occurrence of rust fungi on individuals of the two *Andropogon* spp. in the experimental plots, we identified each plant as having rust infection or not. The proportion of infected individuals for each species in each plot was calculated as rust incidence (hereafter referred to as prevalence).

Finally, to examine whether the damage level from enemies was correlated with plant performance, we collected the above-ground tissue of each plant immediately after sampling, and weighed them after drying at 60°C for 48 h. Then we used individual

plant biomass as an indicator of plant performance, and examined the correlation between plant biomass and natural enemy damage.

Statistical analyses

All statistical analyses were conducted using MINITAB 14.2 or SAS[®] V9.0. The percentage of GLA and MLA were arcsine square root transformed to meet the assumption of equal variances. *T*-tests were used to compare the transformed GLA and MLA for each of the seven pairs of exotic and native species. *T*-tests were also used to compare all types of the insect attack prevalence on native and exotic species pairs. For the seven independent *t*-tests, significance levels were set at $P \leq 0.007$ (0.05/7) after Bonferroni correction. Significance levels for other tests were set at $P \leq 0.05$.

A one-way ANOVA was performed to compare the damage from enemies indicated by MLA and the reduction of GLA between native and exotic species groups. A *t*-test was used to compare the damage between noninvasive and invasive species using the relative damage metric (G). Simple linear regressions were applied to assess the relationships between damage and plant biomass in three analyses: within species, within exotic and native groups, and over all individuals.

To investigate the treatment effects of burning, fertilization and the interaction of burning and fertilization on rust infection on *Andropogon* spp., the arcsine square root transformed rust prevalence data (the proportion of infected plants) and relative abundance for each species in each plot were subjected to an ANOVA using the mixed model procedure in SAS v9.0 software (SAS Institute, Inc.) to account for the nested experimental design. Fire, nitrogen fertilization, species, and the interaction of nitrogen fertilization and species were considered fixed effects when examining rust prevalence, while the interaction of block and fire, and the interaction of block and nitrogen within fire were considered the random effects. Fire, nitrogen fertilization, species, and the interaction of fire and species were considered fixed effects when examining plant relative abundance, while the block within the interaction of fire and nitrogen fertilization was considered the random effect. Simple linear regression was applied

to assess the relationship between the relative abundance of *Andropogon* spp. within each plot and the average rust fungal prevalence on *Andropogon* spp.

Results

Pattern of damage

When grouped into exotic species and native species, weighting each individual species equally, the five native species sustained overall 56.4% higher damage from natural enemies and/or abiotic stress than the seven exotic species (GLA reduction: native 17.2%; exotic 11.0%, $F_{1,10} = 8.25$, $P = 0.017$). Also, the native species sustained 83.6% more MLA than the exotic species (MLA: native 11.8%; exotic 6.4%, $F_{1,10} = 5.08$, $P = 0.048$), which indicates that the native species as a whole were attacked more by herbivores or experienced more abiotic stress or leaf area loss than the exotic species. For five of the seven native-exotic pairs, native species sustained greater total damage (GLA reduction) and greater loss of leaf area (MLA; Figs. 1 and 2) than their exotic counterparts. Two exceptions to this were the pairs of C₃ biennial forbs, *L. serriola* and *L. ludoviciana* ($T = -1.79$, $df = 167$, $P = 0.038$), and C₃ grasses, *B. inermis* and *E. canadensis* ($T = 1.87$, $df = 90$, $P = 0.065$), which did not show any significant difference in damage. Overall, there was no clear relationship between GLA reduction and the plant performance as estimated by total aboveground biomass at time of flowering (except for *Lespedeza* spp.; for all seven exotic species, $R^2 = 0.001$; $F = 0.37$; $P = 0.544$. For all five native species, $R^2 = 0.012$; $F = 4.42$; $P = 0.036$). Furthermore, we found that the invasive species had 55.3% less relative GLA reduction (indicating the reduced green leaf area damage relative to their native counterparts) than the noninvasive species (noninvasive 0.230 vs. invasive 0.514; $T = 1.39$, $df = 4$, $P = 0.12$; Fig. 3).

Natural enemy prevalence

We found that most insect damage, including rolling, tying, marginal, skeletonization, and mining, occurred more frequently on native species than on their exotic counterparts, while only chewing and

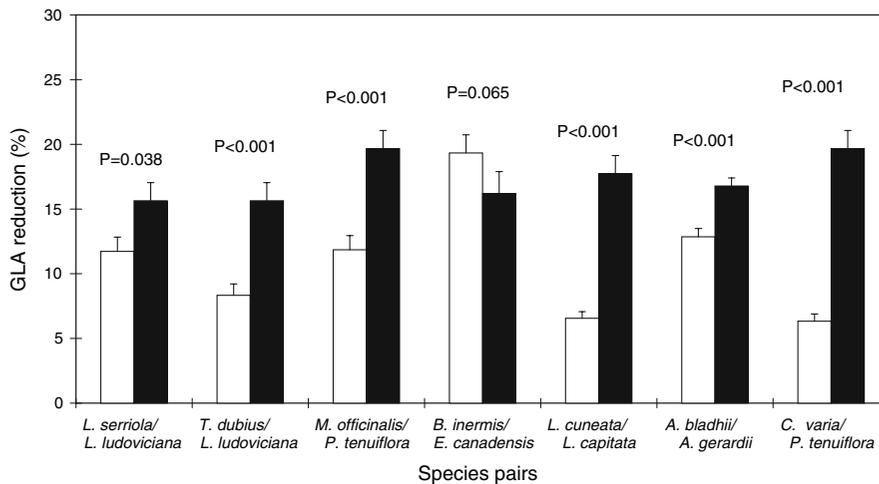


Fig. 1 Comparison of the reduction of total percent (%) green leaf area ((1 – %GLA); mean per individual) for exotic (*white bars*) and native (*black bars*) species pairs in tallgrass prairie. The first four pairs of bars are noninvasive species and

corresponding native species; the last three pairs of bars are invasive species and corresponding native species. Data are means across all individuals sampled for a species, and error bars indicate ±1SE of the mean

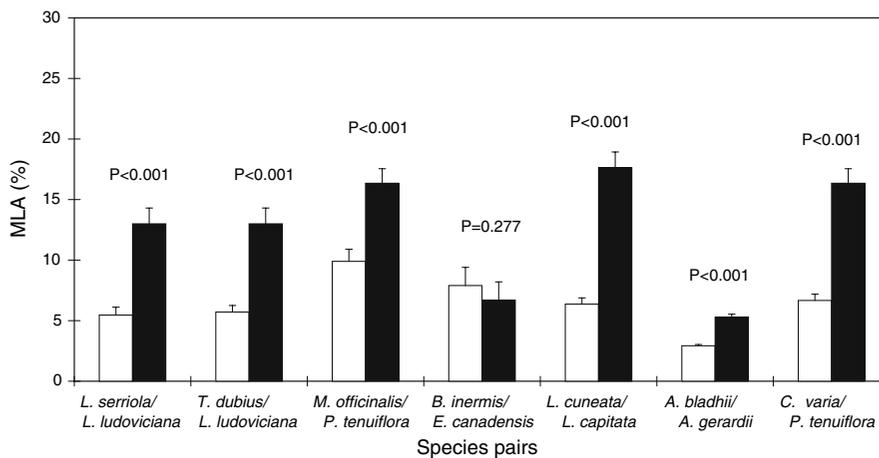


Fig. 2 Comparison of total % missing leaf area (MLA; mean per individual), which includes damage resulting from herbivory and/or abiotic stress, between exotic (*white bars*) and native (*black bars*) species pairs in tallgrass prairie. The first four pairs of bars are noninvasive species and corresponding native

species; last three pairs of bars are invasive species and corresponding native species. Data are means across all individuals sampled for a species, and error bars indicate ±1SE of the mean

shot-hole damage occurred more on exotics than native species (Table 2). Overall, the results suggest that native species suffered more damage from insect enemies than exotic species, in agreement with observed patterns for GLA reduction and MLA.

For all species that were infected by pathogens, the native species had higher infection frequencies (Table 3). For example, *P. tenuiflora* had a higher pathogen infection frequency than *M. officinalis*

(62.0% vs. 40.0%, $z_{98} = 2.26$, $P = 0.024$) or *C. varia* (62.0% vs. 40.7%, $z_{107} = 2.27$, $P = 0.023$). In total, 54% of *P. tenuiflora* individuals were infected by the lesion-causing fungus *Phyllosticta psoraleae*, while 38.0% of *M. officinalis* individuals were infected by bacterial pathogens and 40.7% of *C. varia* individuals were infected by the fungus *Cercospora rautensis* ($z_{98} = 2.05$, $P = 0.041$; $z_{107} = 1.61$, $P = 0.107$). For *E. canadensis*, 14.0% of individuals were infected by

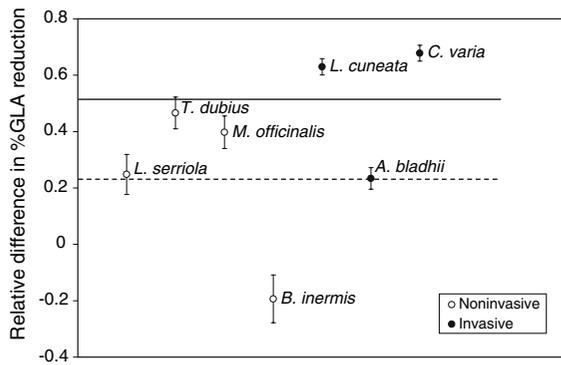


Fig. 3 Relative difference in leaf damage (GLA reduction; $1 - \%GLA$) for the noninvasive and invasive exotic species. For each exotic individual the relative difference in GLA reduction was calculated as: (average $\%GLA$ reduction of the corresponding native species $- \%GLA$ reduction of each exotic individual)/average $\%GLA$ reduction of the corresponding native species. Thus a larger relative difference in $\%GLA$ reduction indicates greater damage to the native vs. exotic species. For each exotic species, data are calculated as means across all individual plants sampled for a species and represented by dark dots (invasive species) and white dots (noninvasive species). Error bars indicate $\pm 1SE$ of the mean. The solid line represents the average relative damage for the invasive exotic species (Mean = 0.514; $N = 3$); the dashed line represents the average relative damage for the noninvasive exotic species (Mean = 0.230; $N = 4$)

rust fungi while no *B. inermis* individuals were infected by rust fungi ($z_{98} = 2.85$, $P = 0.004$). Finally, significantly more *A. gerardii* individuals were infected by the rust fungi, *Puccinia andropogonis*, than were *A. bladhii* individuals (23.2% vs. 0.8%, $z_{514} = 8.31$, $P < 0.001$).

Effect of fire and fertilization on rust prevalence

Rust infection on the native C_4 grass, *A. gerardii*, and exotic species, *A. bladhii*, was differentially impacted by the fire and fertilization treatments. Overall, more than one-fifth of all *A. gerardii* individuals surveyed were infected by rust fungi. In contrast, only a small percentage of *A. bladhii* individuals were infected by rust fungi, and those individuals were found only in the combined treatment of burning and nitrogen fertilization (Fig. 4). Burning significantly increased the prevalence of rust on both species ($F_{\text{burning}} = 44.36$, $df = 1, 2$, $P = 0.022$), while nitrogen fertilization enhanced the rust prevalence only on *A. gerardii* ($F_{\text{nitrogen} \times \text{species}} = 7.17$, $df = 1, 6$, $P = 0.037$;

$T = -3.75$, $df = 6$, $P_{A. gerardii} = 0.0095$; $T = -0.52$, $df = 6$, $P_{A. bladhii} = 0.624$) (Fig. 4). Burning considerably increased *A. bladhii*'s abundance ($T = 6.61$, $df = 50$, $P < 0.0001$), while it had no significant effect on *A. gerardii*'s abundance ($T = -0.50$, $df = 50$, $P = 0.621$). In the burned plots, *A. bladhii* was much more abundant than *A. gerardii* ($T = -5.75$, $df = 50$, $P < 0.001$), while in the unburned plots, *A. gerardii* was much more abundant than *A. bladhii* ($T = 2.96$, $df = 50$, $P = 0.005$). Fertilization had no significant effect on both species' abundance. Overall, there was only a weak positive correlation between plant abundance and rust prevalence for *A. gerardii* ($R^2 = 0.51$, $F_{1,6} = 6.28$, $P = 0.046$; Fig. 4). Thus, the relative abundance of either species did not appear to be driving the observed patterns of rust prevalence.

Discussion

A major goal of research on biological invasion has been to understand whether exotic species are less vulnerable than native species to natural enemies in the invaded region—a central prediction of the enemy release hypothesis. However, there is considerable debate as to the extent to which natural enemies influence the invasibility of communities (Agrawal and Kotanen 2003; Agrawal et al. 2005; Colautti et al. 2004; Eppinga et al. 2006; Keane and Crawley 2002; Lau and Strauss 2005; Maron and Vila 2001; Parker et al. 2006). In the present study, we measured the leaf-level damage of native and exotic plant pairs caused by either invertebrate herbivory, pathogens or unknown abiotic stresses, which could be related to impacts on photosynthesis and metabolism, and found that native species tended to have greater damage and higher prevalence of natural enemies than their congeneric or ecologically equivalent exotic counterparts (Figs. 1 and 2). The exotic C_3 forb *L. serriola* and the C_3 grass *B. inermis* were the only exceptions to this pattern. Although *B. inermis* did not show significantly lower impact from natural enemies, the remarkably low incidence of rust fungi when compared to *E. canadensis* (Table 3), suggests lower damage from enemies. Thus, the patterns of natural enemies we observed provides support for the enemy release hypothesis.

The measures of within-leaf damage that we used in this study could lead to underestimation of the

Table 2 Insect damage prevalence on seven native (N) and exotic (E) species pairs in tallgrass prairie

Functional group	Pair no.	Species pair	N individuals	N leaves	Insect damage							N individuals with insects
					Rolling	Tying	Marginal	Che-wing	Shot-hole	Skeletonization	Mining	
C ₃ biennial forbs	1	<i>Lactuca scariola</i> (E)	66	592	0.6*	0.0	0.4	12.7***	3.4	0.3	0.5	16
	1	<i>Lactuca ludoviciana</i> (N)	107	639	3.0*	1.1	0.1	0.0***	2.1	1.0	0.0	27
	2	<i>Tragopogon dubius</i> (E)	55	3553	0.2**	0.0**	0.7	0.0	0.2	0.1	0.5	21
Legumes:	2	<i>Lactuca ludoviciana</i> (N)	107	639	3.0**	1.1**	0.1	0.0	2.1	1.0	0.0	27
	3	<i>Melilotus officinalis</i> (E)	50	1604	0.2	0.1	18.8***	0.0	1.6	2.6***	0.1*	4
	3	<i>Psoralea tenuiflora</i> (N)	50	1896	0.1	0.0	57.8***	0.0	1.8	0.3***	1.0*	1
	4	<i>Coronilla varia</i> (E)	59	1167	0.0	0.2	34.6***	5.2***	7.0*	0.0*	0.5	2
C ₃ grasses	4	<i>Psoralea tenuiflora</i> (N)	50	1896	0.1	0.0	57.8***	0.0***	1.8*	0.3***	1.0	1
	5	<i>Lespedeza cuneata</i> (E)	32	4365	0.0	0.1	21.2***	0.0	0.6***	0.7***	0.1*	4
	5	<i>Lespedeza capitata</i> (N)	32	1250	0.0	0.0	74.9***	0.0	5.8***	3.6***	1.3*	6
	6	<i>Bromus inermis</i> (E)	50	447	0.0	0.3	0.0	80.4***	0.7	0.4	0.0*	1
	6	<i>Elymus canadensis</i> (N)	50	293	0.0	0.0	0.0	29.7***	0.0	0.5	1.8*	1
C ₄ grasses	7	<i>Andropogon bladhii</i> (E)	262	2214	0.0	0.0	0.0	0.1	0.5**	0.0	0.0	8
	7	<i>Andropogon gerardii</i> (N)	254	1471	1.0	0.0	0.0	0.4	0.0**	0.0	0.0	12

Insect damage data are the mean proportion of leaves of each individual sampled categorized by type of damage (rolling, tying, marginal, che wing, shot-hole, skeletonization, and mining). Asterisks indicate statistically significant differences for a particular species pair between native and exotic species, and those that are underlined indicate exotic species with insect damage prevalence greater than their native counterpart. All comparisons were based on either 2-proportion tests (adapted *t*-tests for two binomial proportions) or 2-sample *t*-tests on transformed data

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Table 3 Pathogen incidence (number of individuals or leaves infected) of seven native (N) and exotic (E) species pairs in tallgrass prairie

Functional group	Pair no.	Species pair	N individual	N leaf	% Individuals with pathogens	% Individuals with rust	% Individuals with spot lesions	Mean of % leaves infected by rust on individual	Mean of % leaves with spots on individual
C ₃ biennial forbs	1	<i>Lactuca serriola</i> (E)	66	592	0.0	0.0	0.0	0.0	0.0
	1	<i>Lactuca ludoviciana</i> (N)	107	639	0.0	0.0	0.0	0.0	0.0
	2	<i>Tragopogon dubius</i> (E)	55	3553	0.0	0.0	0.0	0.0	0.0
Legumes	2	<i>Lactuca ludoviciana</i> (N)	107	639	0.0	0.0	0.0	0.0	0.0
	3	<i>Melilotus officinalis</i> (E)	50	1604	40.0**	2.0**	38.0*	0.2**	9.9
	3	<i>Psoralea tenuiflora</i> (N)	50	1896	62.0**	22.0**	54.0*	3.1**	7.7
	4	<i>Coronilla varia</i> (E)	59	1167	40.7**	0.0***	40.7	0.0***	4.2
	4	<i>Psoralea tenuiflora</i> (N)	50	1896	62.0**	22.0***	54.0	3.1***	7.7
C ₃ grasses	5	<i>Lespedeza cuneata</i> (E)	32	4365	0.0	0.0	0.0	0.0	0.0
	5	<i>Lespedeza capitata</i> (N)	32	1250	0.0	0.0	0.0	0.0	0.0
	6	<i>Bromus inermis</i> (E)	50	447	0.0**	0.0**	0.0	0.0***	0.0
C ₄ grasses	6	<i>Elymus canadensis</i> (N)	50	293	14.0**	14.0**	0.0	6.9***	0.0
	7	<i>Andropogon bladhii</i> (E)	262	2214	0.8***	0.8***	0.0	0.1***	0.0
	7	<i>Andropogon gerardii</i> (N)	254	1471	23.2***	23.2***	0.0	9.7***	0.0

Asterisks indicate statistically significant differences between species in a pair. All comparisons represent 2-proportion test (an adapted *t*-test for two binomial proportions) or 2-sample *t*-tests on transformed data

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

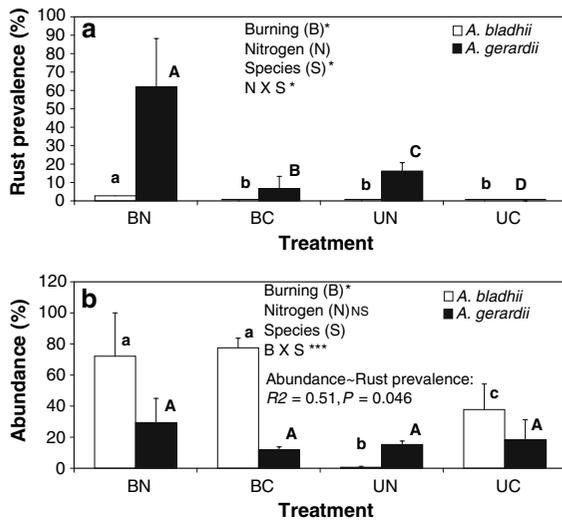


Fig. 4 (a) Proportion of individuals infected with rust (rust prevalence) on *A. gerardii* and *A. bladhii* in long-term experimental plots subjected to different fire and fertilization treatments. BN = burned and with nitrogen fertilization, BC = burned and control (without fertilization), UN = unburned and with nitrogen fertilization, UC = unburned and control (without fertilization). (b) Relative abundance of *A. gerardii* and *A. bladhii*, calculated by averaging the relative cover of each species in four subplots within each experimental plot. Bars represent the mean of two replicate plots. Error bars indicate ± 1 SE of the mean. Different letters indicate significant difference ($P \leq 0.05$) between treatments. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; NS indicates $P > 0.10$

damage caused by herbivores, since it does not detect the removal of whole leaves or plants. Our study methods did not allow us to evaluate leaf or plant mortality resulting from pathogens or insect damage. However, we believe comparisons within species pairs still provide useful relative measures of damage because (i) the whole samplings were conducted in ungrazed watersheds, where the lethal herbivory from herbivores is not common (Joern 2005; Kaufman et al. 1998) and (ii) the potential underestimation likely applies to both exotic and native species though perhaps not to the same extent. Higher levels of within-leaf damage are likely to be strongly correlated with higher probabilities of leaf loss.

Our results of lower leaf damage on exotic species are consistent with recent studies of leaf damage in Canadian old field forbs (Agrawal et al. 2005) and European open forest woody plants (Dietz et al. 2004), but not with the results of Agrawal and Kotanen (2003). Specific community structures (Dietz et al. 2004) and species traits (Agrawal et al. 2005)

may interfere with the pressure from natural enemies, and explain the discrepancy in results. The overall pattern of lower prevalence or damage on exotic species observed in our study could potentially contribute to the successful invasion of these nonnative species in tallgrass prairie, while a previous study of the same species pairs revealed that these exotic species and their native counterparts did not differ significantly in morphological and physiological traits (Smith and Knapp 2001b).

The relationship between the degree of invasiveness and the damage from enemies has been noted before (Mitchell and Power 2003), but has rarely been studied (Colautti et al. 2004). It is worth pointing out that the relative leaf damage due to either herbivory, fungal pathogens, or abiotic stress was consistently lower (though not significantly) in the three invasive species—*L. cuneata*, *C. varia* and *A. bladhii*—when compared to the noninvasive exotic species examined in this study (Fig. 3). This pattern suggests that the degree of natural enemy impact may play a role in determining whether an exotic species will become invasive or remain noninvasive over time. However, it is important to consider how damage by herbivores impacts population dynamics and fitness over time, and the link between the two certainly requires further study.

We found that the native species had higher prevalence of damage associated with insects (i.e., mining, rolling, etc.) and incidence of pathogens than their exotic counterparts. The higher prevalence of different types of insect damage on the natives is in line with the patterns of greater leaf damage and missing leaf area observed. When considering fungal pathogens, rust incidence on the dominant native C_4 grass, *A. gerardii*, was 30-fold higher than on the invasive C_4 grass, *A. bladhii*, though *A. gerardii* also tends to have higher levels of rust infection than the other three most common C_4 grasses at KPBS (Garrett and Dendy, unpubl. data). Previous studies have revealed fewer microbial diseases reported for plants in their naturalized range compared to their native range (Mitchell and Power 2003). In our study, it is likely that the lower prevalence of insect or fungal pathogens in the exotic species could provide an advantage to establishment of exotic plant species in the tallgrass prairie, compared to the native legumes, C_3 and C_4 grasses with a higher frequency of insect damage types and incidence of fungal infection.

Enemy release, disturbance, and resource availability may interact and contribute to plant invasion simultaneously (Beckstead and Augspurger 2004; Blumenthal 2006). It has been proposed that increased resources availability from disturbance or eutrophication may increase the release of exotic species from enemies, and thus increase the advantage for exotic over native species (Blumenthal 2006). Following this argument, the species with stronger regulation by enemies in their native ranges would benefit more from enemy release in the introduced ranges; the species adapting to high resource availability are generally those that may be more strongly regulated by enemies because of a low investment in defense and high nutritional value; high resource availability would select for these species, resulting in a greater advantage from enemy release for exotic over native species (Blumenthal 2006). Fire and nitrogen fertilization are two important environmental factors in tallgrass prairie and are both known to increase resource availability, but their effect on disease varies from one system to another (Bockus et al. 1983; Ehrenreich and Aikman 1963; Gibson 1989; Hardison 1976; Hulbert 1988). We examined how fungal pathogen incidence on *A. gerardii* and its invasive counterpart, *A. bladhii*, responded to these two factors (Fig. 4) and found the similar trends as Blumenthal (2006). Fire and nitrogen addition both increased the incidence of fungal pathogens on the native tallgrass *A. gerardii* while the exotic grass appeared generally free of infection.

In tallgrass prairie, nitrogen fertilization enhances C_4 abundance and productivity, and also appears to increase infection by rust fungi. In our study, the high prevalence of rust fungi on *A. gerardii* with fire and fertilization may be related to the increased abundance of the C_4 grass with those treatments, although the correlation was weak, suggesting that other factors may be important as well in influencing fungal infection. In contrast, high abundance of *A. bladhii* was not related to high prevalence of the rust fungi, even though *A. bladhii* has a similar plant architecture and phenology to *A. gerardii*, which probably creates similar microenvironments for pathogens (McIntosh et al. 1995). It is not clear whether high prevalence of rust fungi reduces the fitness of *A. gerardii* individuals and further regulates their abundance. The rust coverage on leaves likely reduces photosynthesis efficiency and potentially impacts both vegetative and reproductive growth.

Although our current study showed a weak relationship between plants' aboveground biomass and green leaf damage, a study of fungus exclusion in tallgrass prairie dominated by *A. gerardii* indicated that fungi significantly reduced plants' root production and leaf longevity (Mitchell 2003). Furthermore, rust is most prevalent on *A. gerardii* later in the growing season, which may mitigate the impact on plant fitness. Nonetheless, the patterns of the rust fungal infection that we observed suggests enemy release for the exotic species *A. bladhii* when compared to the native species *A. gerardii* under the higher resource availability associated with burning and N fertilization. This may contribute to the invasiveness of *A. bladhii*; however, the potential mechanisms underlying these patterns require further examination.

Overall, results from our study provide support for the enemy release hypothesis. The most significant result in this article is that a diverse array of exotic flowering plants in tallgrass prairie appeared to experience lower prevalence of and damage by natural enemies (insect and pathogens), when compared with their native counterparts. Moreover, invasive exotic species sustained lower levels of damage (i.e., higher green leaf tissue (GLA)) relative to their native counterparts) when compared to the noninvasive exotic species, which suggests that natural enemies could play an important role in determining invasiveness. However, to elucidate the mechanisms underlying these patterns and their relevance for plant population dynamics and fitness, further studies are needed.

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