PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

# No interaction between competition and herbivory in limiting introduced *Cirsium vulgare* rosette growth and reproduction

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**Abstract** Both competition and herbivory have been shown to reduce plant survival, growth, and reproduction. Much less is known about whether competition and herbivory interact in determining plant performance, especially for introduced, weedy plant species in the invaded habitat. We simultaneously evaluated both the main and interactive effects of plant neighbors and insect herbivory on rosette growth and seed reproduction in the year of flowering for *Cirsium vulgare* (bull thistle, spear thistle), an introduced Eurasian species, in tallgrass prairie in 2 years. Effects of insect herbivory were strong and consistent in both years, causing reduced plant growth and seed production, whereas the effects of competition with established vegetation were weak. The amount of herbivore damage inflicted on rosettes did not depend on the presence of neighbor plants. We also found no interaction between competition and herbivory on key parameters of plant growth and fitness. The results of this study contradict the hypothesis that competitive context interacts with insect herbivory in limiting the invasiveness of this introduced thistle. Further, the results provide additional, experimental evidence that high levels of herbivory on established rosettes by native insects exert significant biotic resistance to the invasiveness of *C. vulgare* in western tallgrass prairie.

## Introduction

Competition from neighboring plants and tissue loss to herbivores are challenges that plants face in most ecosystems (Harper 1977; Crawley 1983; Gurevitch et al. 2000; Hämback and Beckerman 2003). Competition for limited resources, such as nutrients, water and light, often reduces plant performance (Tilman 1982; Goldberg and Novoplansky 1997). Tissue loss to herbivores also can reduce plant survival, growth, or reproduction and decrease plant population density (Louda 1982; Crawley 1983; Louda and Potvin 1995; Maron and Vila 2001; Levine et al. 2004; Maron and Crone 2006). However, much less is known about the potential interactive effects of competition and herbivory on plant performance, especially for introduced plants.

Three mutually exclusive hypotheses for the joint effects of competition and herbivory have been proposed. Competition and herbivory might influence plant fitness: (1) independently (Rees and Brown 1992; Reader and Bonser 1998; Hämback and Beckerman 2003), (2) synergistically (McEvoy et al. 1993; Meiners and Handel 2000), or (3)

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antagonistically (Parmesan 2000; Haag et al. 2004). If the effects of herbivory and competition are independent, then their combined effect on plant performance is predicted by multiplying their individual effects (See Fowler and Rausher 1985; Rees and Brown 1992). If the effects of herbivory and competition are synergistic, then their net negative effect on performance should be greater than the product of their individual effects (i.e., competition exacerbates the negative fitness effects of herbivory, or vice versa). Synergistic interaction effects could result directly, if a resource allocation trade-off occurs between competitive ability and herbivore defense or tolerance (Harper 1977; Herms and Mattson 1992), or indirectly, if neighbors increase herbivore damage to a host plant (also known as associational susceptibility) (Parker and Root 1981). If the effects of herbivory and competition are antagonistic, then their joint effect on plant performance should be less than the product of their individual effects. Antagonistic interactions could result if neighbors hide a plant from its herbivores, reducing the magnitude of herbivory (also known as associational resistance) (Tahvanainen and Root 1972); or, it could result if herbivores feed preferentially on the neighbor plants reducing their competitive effect on the focal plant (Hamilton et al. 1998; Haag et al. 2004). Since competition and herbivory are widespread, understanding whether and how they interact to limit plant reproduction is of general importance in predicting population dynamics in basic and applied contexts.

Large effects of competition or herbivory or both on performance and population growth of native plant species motivate the question of how these interactions affect invasiveness of introduced species. A recent meta-analysis (Levine et al. 2004) found that biotic interactions, including both competition and herbivory by native species, often limit invasive species' success in recipient communities. Simultaneous augmentation of neighbor plant competition and insect herbivory has been prescribed as a strategy for controlling introduced weedy plants (e.g., Harris 1981). Nevertheless, most empirical studies have focused on the individual effects of either competition or herbivory in limiting introduced species, not the occurrence and nature of their interactive effects.

In this study, we examined the individual and combined effects of ambient levels of plant competition and herbivory by native insects on *Cirsium vulgare* (Savi) Tenore (bull thistle, spear thistle), an introduced Eurasian species (Gleason and Cronquist 1991) in the western tallgrass prairie region of Nebraska in the central Great Plains, USA. This thistle is listed as a noxious, invasive weed, both worldwide (Julien and Griffiths 1998) and in many parts of the USA, including two states bordering Nebraska, Colorado and Iowa (USDA 2009). However, although *C. vulgare* has been collected in Nebraska for >100 years

(Kaul et al. 2006), it occurs only at very low densities across the Nebraska tallgrass prairie region (Andersen and Louda 2008), and it is not listed as a noxious weed (Nebraska Department of Agriculture 2009). Louda and Rand (2002) quantified high levels of floral herbivory and hypothesized that such herbivory by native insects limited *C. vulgare* invasiveness in this region. A recent matrix model supports the strong demographic effect of this floral herbivory on *C. vulgare* (Tenhumberg et al. 2008). However, no study has measured the effect of competition, or the interaction between competition and insect herbivory, on the growth and flowering of *C. vulgare* rosettes in this region.

Here, we experimentally tested the hypothesis that competition from established vegetation and native insect herbivory interact to reduce *C. vulgare* rosette growth and reproduction, contributing to this species' low densities in our region. Specifically, we quantified the relative importance of direct and indirect effects of neighboring plants and of ambient levels of insect herbivory on the growth and seed production of the monocarpic rosettes of *C. vulgare* in their reproductive year. We expected that competition would decrease *C. vulgare* growth and reproduction, and that high competition environments would increase the negative effect of herbivory. The first prediction was based on the frequent association between introduced weedy plants and disturbances (Grime 1988). The second prediction was based on the observation that *C. vulgare* generally grows in successional habitats where grasses are dominant and may provide strong competition that could reduce the plant's ability to defend against or tolerate herbivory. Thus, we predicted that a synergistic interaction between competition and herbivory reduces fitness of *C. vulgare* flowering plants in tallgrass prairie.

## Materials and methods

### Natural history

*Cirsium vulgare,* a short-lived, monocarpic perennial plant (Klinkhamer et al. 1988), is generally found in road sides, old fields, or overgrazed pastures in tallgrass prairie. In our region, flowering and seed production occur from late July through September (Kaul et al. 2006). The probability of flowering increases with rosette size, and flowering plants often form multiple stems, in response to damage to the rosette meristem (personal observation).

Over 190 morphospecies of insects, 97% of which are native species, feed on *C. vulgare* in eastern Nebraska (Takahashi 2006). Damage to developing flower shoots was caused mainly by larvae of three indigenous insects: the artichoke plume moth, *Platyptilia carduidactyla* (Riley) (Pterophoridae), the weevil *Baris* nr. *subsimilis*

Casey (Curculionidae), and the fly *Paracantha culta* (Wiedemann) (Tephritidae). Damage to flower heads was caused primarily by these three insects, plus two native moths, *Lobesia carduana* (Busck) (Tortricidae) and *Homoeosoma eremophasma* complex (formerly *H. stypticellum*) (Pyralidae), and a native midge, *Dasineura* sp. (Cecidomyiidae) (Takahashi 2006).

## Study sites

Experiments were completed in 2006 and 2007 in Lancaster County, Nebraska, at three sites in 2006 and, because one site was lost, at two of the sites in 2007. The sites were: Pioneers Park Nature Center (40°46′34.74″N, 96°46′43.30″W; 360 m elevation), University of Nebraska Challenge Course (40°51′31.03″N, 96°48′43.59″W; 385 m), and Straight Water Wildlife Management Area (40°52′5.55″N, 97°13′23.39″W; 475 m). In 2007, plots at the Challenge Course were flooded and destroyed by heavy rain (13–14 June).

The sites were typical of disturbed tallgrass prairie where *C. vulgare* occurs in eastern Nebraska, with successional vegetation characterized by mixtures of native and introduced plants. The Pioneers Park site was a formerly overgrazed pasture where prairie restoration began in 1999 (B. Seth, personal communication). The dominant species were two native grasses, *Schizachyrium scoparium* (Michx.) Nash and *Andropogon gerardii* Vitman, the introduced grass *Bromus inermis* Leyss; and, one native forb, *Conyza canadensis* (L.) Cronquist. The Challenge Course site was a formerly farmed, successional field with *C. vulgare* in disturbed areas around a pond. The dominant species were two native grasses, *Phalaris arundinacea* L. and *Poa pratensis* L., the introduced grass *B. inermis,* the native forb *Helianthus annuus* L. and the introduced forb *Lactuca serriola* L. The Straight Water site was a fallow hillside pasture. The dominant species were three grasses, including two native species, *Hordeum jubatum* L. and *Elymus canadensis* L., and the introduced *Bromus arvense* L, and three forbs, including two native species, *Physalis virginiana* Mill. and *Ambrosia trifida* L., and the introduced *Taraxacum officinale* F. H. Wigg.

## Experimental design and treatments

In order to quantify interaction effects in the critical flowering year, we manipulated both competition from in situ neighboring vegetation and insect herbivory for large juveniles (rosette diameter >15 cm) that were likely to flower (bolt). Treatments in each year were randomly assigned to these focal juveniles. Different rosettes were used in 2006 and in 2007 because rosettes die after flowering.

## Competition treatments

We manipulated plant competition within a plot (1.2 m × 1.2 m) around each experimental rosette. Plots were randomly assigned to high (ambient) or low (reduced) competition treatments. Vegetation cover before experimental manipulation was recorded per plot by point sampling (8–12 May 2006, 15–16 May 2007). Competition treatments were established 17–22 May in both years. In low competition plots, neighboring vegetation was reduced to 20–25% of initial cover. To do this, we clipped the vegetation at ground level and painted the clipped vegetation with a non-selective herbicide, Roundup (2% glyphosate in water; Monsanto, St. Louis, Mo.) in 12 randomly selected 30-cm × 30-cm subplots of the 16 available per 1.2-m × 1.2-m plot; the remaining subplots (25%) were not manipulated. Low competition was maintained by periodic re-clipping throughout the growing season. In high competition plots, the neighboring vegetation around each focal *C. vulgare* plant was not altered (65–90% vegetation cover). Sample size for each competition treatment (ambient, low) by year (2006 and 2007) was: 20 and 20 at Pioneers Park, 28 and 20 at Straight Water and 26 (2006 only) at Challenge Course; thus, total sample size was 148 in 2006 and 80 in 2007. Unequal sample sizes between sites and years reflected the availability of large *C. vulgare* rosettes.

## Insect herbivory treatments

To reduce herbivory, we sprayed the focal *C. vulgare* rosette in half of the plots in each competition treatment with insecticide in water; the other half were used as control plots and sprayed with an equivalent amount of water. Plots within each competition treatment at a site were randomly assigned to receive insecticide or water. Rosettes were sprayed every 20 days from 13 May–15 September each year, except in August when a 15-day interval was used because insect floral herbivores were common. We used the insecticide Talstar One (7.9% synthetic pyrethroid bifenthrin; FMC Professional Solutions, Philadelphia, Pa.) at the recommended rate of 0.06% in water solution. This insecticide does not contain nitrogen (MSDA ref. no. 82657-04-3-116), and it does not break down easily with rain once it has bonded to the plant surface (EXTOXNET 1995). In a parallel greenhouse experiment ($n = 20$ replicates per spray treatment), the insecticide did not affect *C. vulgare* survival or growth from seed over 4 months (survival, $Z = 1.082$, $P = 0.279$: vegetative biomass, $F_1 = 3.33$, $P = 0.076$; root biomass, $F_1 = 0.058$, $P = 0.811$; T. Suwa, J. Eckberg and S. M. Louda, unpublished data).

Measurements

We measured rosette diameter, number of leaves, and total number of flower heads by stage (Suwa 2008) on 14–16 August 2006 and 18–21 August 2007, as well as final plant biomass post-senescence in September. The number of flower heads matured included all heads that exerted any florets. For plants with ≤2 flowering stems, we counted leaves and flower heads on each stem. On larger plants (from three to 16 flowering stems), we made our counts on the odd-numbered stems, and multiplied to convert to number per plant. As plants senesced, they were harvested, dried at 65°C for 7 days, and weighed to quantify total aboveground biomass.

Seed production was quantified by collecting a sample of mature flower heads. Each week we bagged the ten most mature (post-anthesis) flower heads on each plant with fine mesh fabric (15 August–15 September 2006, 15 August–12 October 2007). Bags prevented seed dispersal, but allowed seeds to mature before flower heads were harvested. From the bagged heads, we haphazardly selected a sub-sample from each experimental plant to dissect to count seed. To make the seed counts proportional to the reproductive effort on each date, the size of the sub-sample was proportional to the number of mature flower heads on a plant on that date (up to 5 heads per plant per date). The average number of filled seeds per mature head was multiplied by the number of mature heads in August to estimate seeds per plant. Following previous studies, we assumed that the filled seeds, determined visually and by pinching, were viable.

Herbivory was quantified by plant part. For leaves, we recorded the number that had any evidence of insect feeding, excluding senescing leaves, and the number that were heavily damaged (>30% leaf area missing or damaged, estimated visually). For stems, we recorded presence and type of insect feeding; type referred to external damage (e.g., scraping), internal damage (e.g., stem mines or insect frass), or no insect damage. For flower heads, we recorded any evidence of insect feeding (Suwa 2008).

Statistical analyses

To evaluate the effectiveness of the insecticide treatment and the effect of competition ($C$) on the amount of herbivore damage ($H$; $C \times H$ interaction), we analyzed the arcsine-square-root-transformed proportions of leaves, stems, and flower heads damaged per plant in separate analyses of covariance (ANCOVA). The proportion of flower heads damaged was defined as the proportion of all heads initiated, calculated as the sum of all inflorescence shoots, flower head buds and mature heads with evidence of herbivory, divided by the total number of shoots, buds, and mature heads. In these analyses, and all subsequent

ANCOVAs and multivariate analysis of covariance (MANCOVA), we treated competition, herbivory and year as fixed factors, site as a random factor, and we used initial mean rosette diameter (square-root transformed) as the covariate. We report only main factors and two-way interaction terms since none of the higher order interaction terms were statistically significant ($P > 0.05$). Eleven experimental rosettes did not bolt in 2007 at Pioneers Park and, so, were excluded from the analyses. Further, rosettes that bolted, but died prior to August measurement ($n = 12$ in 2006, $n = 19$ in 2007) were excluded in analyses of insecticide efficacy (final $n$: 72 insecticide, 61 control in 2006; 32 insecticide, 18 control in 2007). All analyses were conducted using Proc GLM and Proc MIXED in SAS (version 9.1.3, SAS Institute 2007).

To evaluate treatment effects on plant growth, we used a three-way MANCOVA. The dependent variables were: mean rosette diameter, number of leaves per plant in August, and end-of-season aboveground vegetative biomass. Number of leaves and final biomass were natural-log transformed to meet MANCOVA assumptions. We used Pillai's trace test statistic, because it is the most robust to small violations of the sphericity assumption (Norusis 2006). When the MANCOVA model was significant, we used separate ANCOVA tests to examine the effects of herbivory, competition, and site on individual response variables.

To evaluate treatment effects on seed production, we proceeded in two steps. First, because some bolting plants died without setting seed, we tested for a treatment effect on whether bolting experimental *C. vulgare* plants produced any seed or not. Plants were unsuccessful in setting seed, because either: (1) they did not bolt at all (2007: $n = 3$ control; $n = 8$ insecticide); or (2) they bolted but died before maturing any flower heads (2007: $n = 11$ control; $n = 0$ insecticide); or (3) their few flower heads produced no seeds (2006: $n = 15$ control, $n = 0$ insecticide; 2007: $n = 7$ control, $n = 0$ insecticide). We analyzed this binomial response variable using logistic ANCOVA (Proc GENMOD, version 9.1.3, SAS Institute 2007).

Second, for plants that produced seed, we used separate ANCOVA tests to evaluate the effect of herbivory and competition on two key components of seed fitness per plant (natural-log transformed counts): total number of flower heads matured, and total number of seeds produced.

## Results

### Effectiveness of insecticide treatment on herbivory

Overall, insecticide reduced herbivory, as planned (Fig. 1). Insecticide treatment significantly lowered both the proportion of leaves damaged (by 68% in 2006, and by 81% in

**Fig. 1** Levels of insect herbivory on established *Cirsium vulgare* rosettes in each year in relation to treatment, measured as mean (SE) proportions of leaves, flower heads, and stems with evidence of insect feeding in August, by treatment combination in the 2 years: 2006 (**a–d**), and 2007 (**e–h**). *Black bar* = water-only treatment (ambient herbivory) and *white bar* = insecticide treatment (reduced herbivory). The two treatment levels of competition were high (ambient vegetation cover: 65–90%) and low (reduced to 20–25% of initial cover). *Different letters* above bars within each year indicate that treatment combinations differed statistically (*P* < 0.05; Tukey post hoc test). *Numbers* inside each bar are sample size for each treatment combination
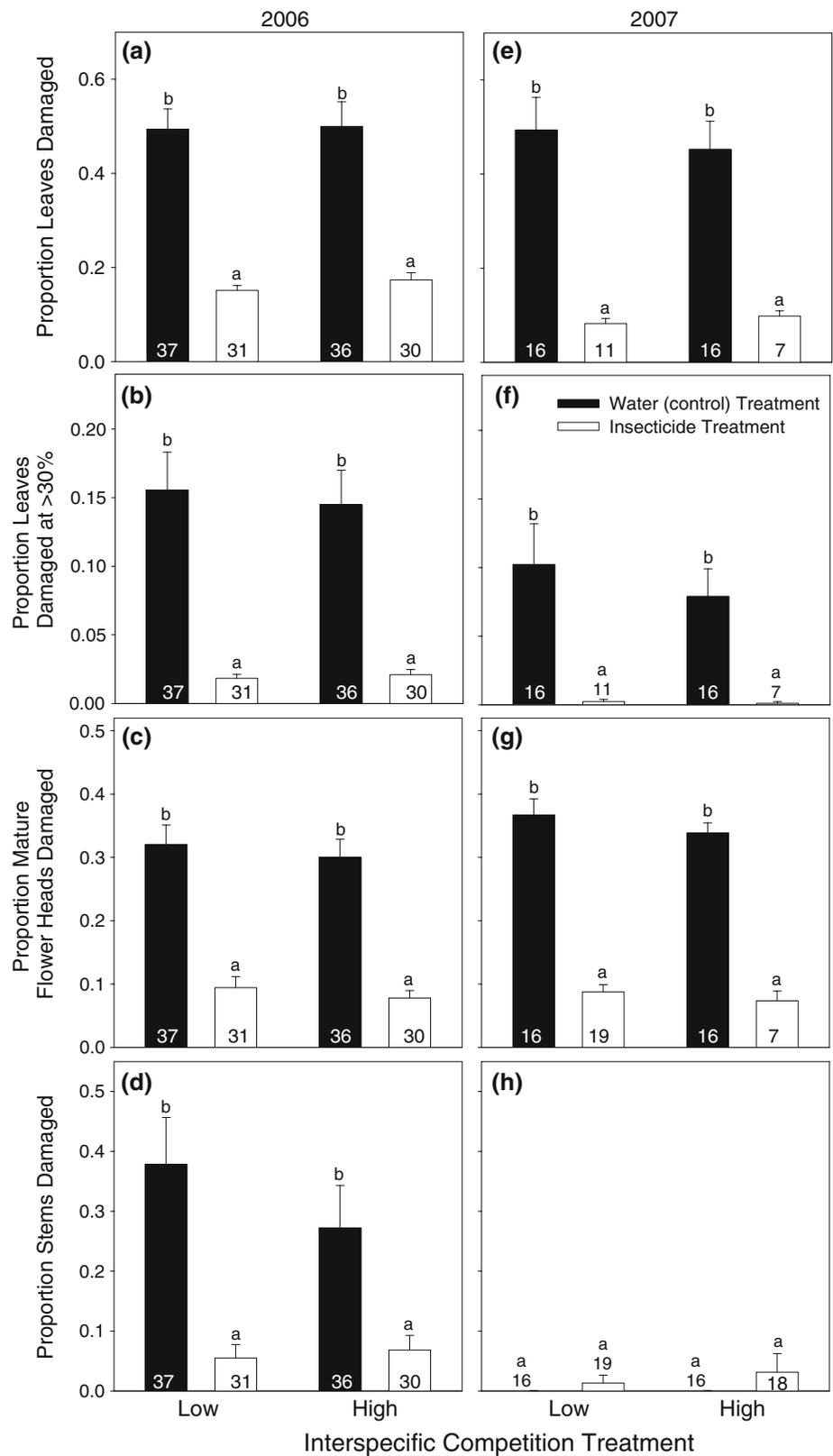


2007) and the proportion of total flower heads damaged (by 73% in 2006, and by 78% in 2007; Table 1, *P* < 0.001). Insecticide significantly reduced the proportion of stems damaged in 2006 ($F_1 = 28.655$, *P* < 0.001), but not in 2007 (*P* = 0.723), when evidence of stem damage was rare even on control plants.

**Table 1** Analysis of covariance (ANCOVA) of herbivore damage on established rosettes of *Cirsium vulgare* in the experimental manipulation of insect herbivory (*H*) and vegetation competition (*C*) in August in 2 years (*Y*) (2006, 2007)

| Factor[a] | Proportion leaves damaged | | Proportion leaves damaged at >30% | | Proportion flower heads damaged | |
|---|---|---|---|---|---|---|
| | df | F | df | F | df | F |
| H | 1,176 | 209.11*** | 1,176 | 183.23*** | 1,176 | 189.83*** |
| C | 1,176 | 0.37 | 1,176 | 0.24 | 1,176 | 1.49 |
| Y | 1,176 | 0.26 | 1,176 | 3.80 | 1,176 | 1.46 |
| ID | 1,176 | 6.82** | 1,176 | 7.87** | 1,176 | 4.27* |
| Site | $\chi^2 = 17.7$*** | | $\chi^2 = 8.3$** | | $\chi^2 = 0.2$ | |

Measures of *H* were the proportions of: leaves damaged, leaves damaged at >30% leaf area, and total flower heads damaged

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Site was treated as a random factor, and initial rosette diameter (*ID*) was used as the covariate. Random factors were examined using likelihood ratio tests, which approximately follow a $\chi^2$ distribution with 1 *df*

**Table 2** Multivariate analysis of covariance (MANCOVA) for three measures of plant size[a], followed by ANCOVA of individual plant size parameters, for *C. vulgare* rosettes in the experimental manipulation of H and C in 2 years (2006, 2007). For other abbreviations, see Table 1

| Factor[b] | MANCOVA | | | Final rosette diameter (August) | | Total number of leaves (August) | | Final vegetative biomass | |
|---|---|---|---|---|---|---|---|---|---|
| | Pillai | df | F | df | F | df | F | df | F |
| H | 0.07 | 3, 162 | 4.17** | 1,171 | 0.02 | 1,177 | 0.02 | 1,194 | 5.87* |
| C | 0.04 | 3, 162 | 1.96 | 1,171 | 0.33 | 1,177 | <0.001 | 1,194 | 5.23* |
| Y | 0.06 | 3, 162 | 3.19* | 1,171 | 5.46* | 1,177 | 2.90 | 1,194 | 0.71 |
| ID | 0.37 | 3, 162 | 31.08*** | 1,171 | 71.63*** | 1,177 | 56.57*** | 1,194 | 94.38*** |
| H × C | 0.01 | 3, 162 | 0.68 | 1,171 | 2.60 | 1,177 | 1.93 | 1,194 | 0.01 |
| H × Y | 0.09 | 3, 162 | 5.40** | 1,171 | 0.26 | 1,177 | 10.33** | 1,194 | 7.62** |
| H × ID | 0.07 | 3, 162 | 4.22** | 1,171 | 1.24 | 1,177 | 1.53 | 1,194 | 1.20 |
| C × Y | 0.02 | 3, 162 | 1.08 | 1,171 | 1.01 | 1,177 | 0.09 | 1,194 | 0.36 |
| C × ID | 0.04 | 3, 162 | 2.32 | 1,171 | 0.12 | 1,177 | 0.14 | 1,194 | 3.45 |
| Y × ID | 0.04 | 3, 162 | 2.44 | 1,171 | 4.70* | 1,177 | 2.26 | 1,194 | 0.34 |
| Site | 0.18 | 6, 326 | 5.53*** | $\chi^2 = 21.8$*** | | $\chi^2 = 22.1$*** | | $\chi^2 = 12.3$*** | |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] The three plant size variables analyzed with MANCOVA were: rosette diameter, leaves per plant, and final vegetative biomass in August or in the subsequent end-of-season harvest

[b] Site was treated as a random factor, and *ID* was used as a covariate. Random factors were examined using likelihood ratio tests, which approximately follows a $\chi^2$ distribution with 1 *df*

## Effect of herbivory and competitive context on plant growth

Insect herbivory significantly reduced overall plant growth in both years (Table 2). There were small, but consistently negative effects on each of the three component measures of growth (Fig. 2). The strength of the herbivore effect was greater in 2007 than in 2006 for both number of leaves and final vegetative biomass (Fig. 2). Ambient levels of plant competition did not significantly reduce overall plant growth (MANCOVA; Table 2). However, ANCOVA revealed that final vegetative biomass decreased significantly under the high (ambient) competition (Table 2). There was also a trend toward lower numbers of leaves (29%) under high competition in 2006 (Fig. 2b), but not in

2007 (Fig. 2e). The lack of a significant competitive effect on growth was consistent between years and herbivory treatments (Table 2).

## Effects of herbivory on flowering and seed production

We found a consistent effect of cumulative insect herbivory on seed reproduction, reflecting both a trend toward decreased probability of flowering plus a highly significant decrease in both the number of flower heads matured and the number of seeds filled per *C. vulgare* plant (Fig. 3). First, for all rosettes that initiated bolting, insecticide treatment increased the proportion that succeeded in producing at least some seed, both in 2006 and in 2007 ($\chi^2 = 48.57$, $P < 0.001$; Fig. 3a, d). For insecticide-treated

Fig. 2 Plant size response of established *C. vulgare* rosettes to treatment in each year, measured as end of season mean (SE): rosette diameter (cm), number of leaves, and vegetative biomass (g) by treatment combination in the 2 years: 2006 (**a–c**), and 2007 (**b–f**). *Black bar* = water-only treatment (ambient herbivory) and *white bar* = insecticide treatment (reduced herbivory). The two treatment levels of competition were high (ambient vegetation cover: 65–90%) and low (cover reduced to 20–25% of initial cover). *Different letters* above bars within each year indicate that treatment combinations differed statistically ($P < 0.05$, Tukey post hoc test). *Numbers* inside each bar are sample size for each treatment combination
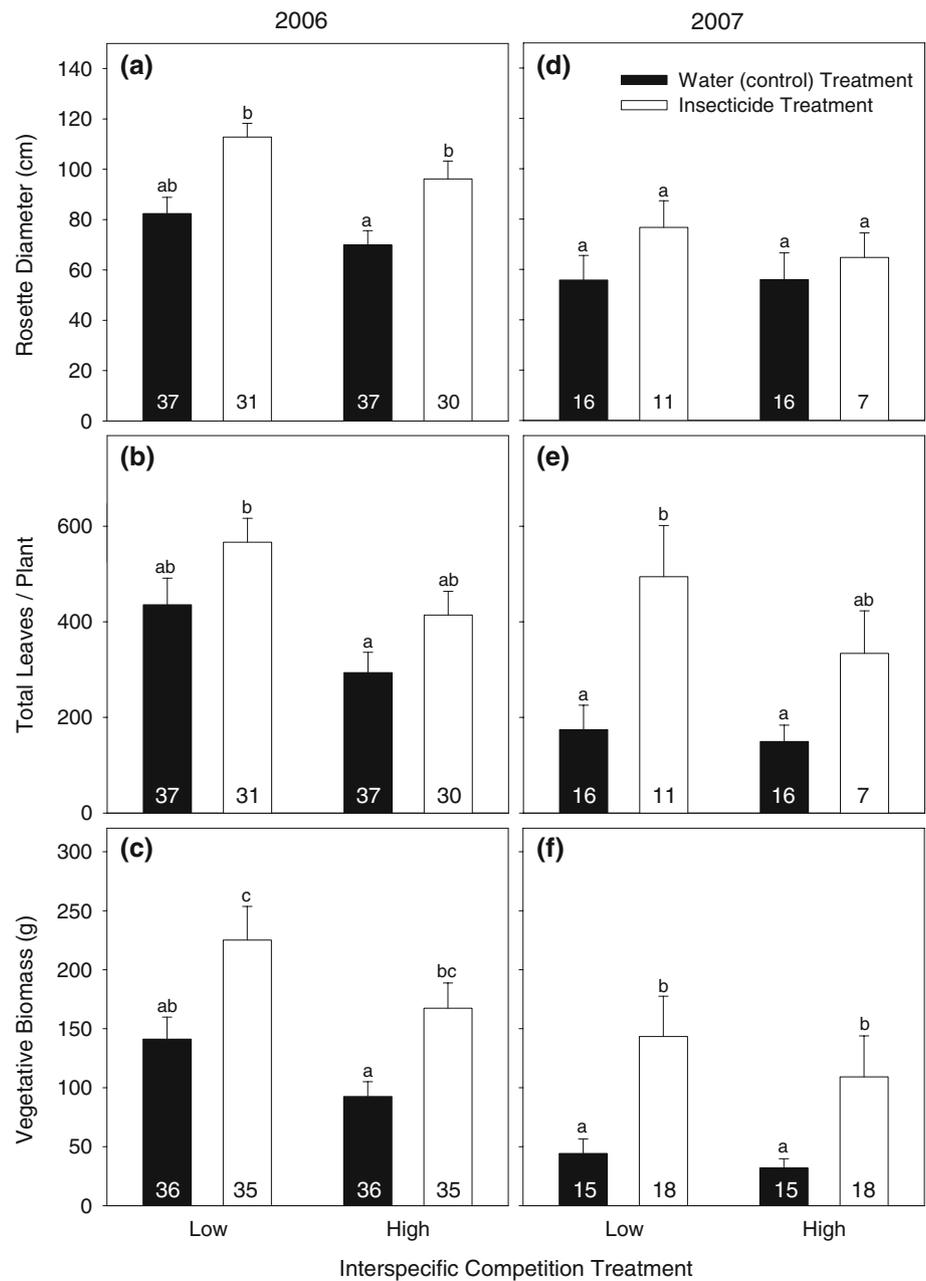


plants, 100% produced some seeds in both years, whereas, for control plants 80% produced some seed in 2006, but only 43% did in 2007 (Fig. 3). Thus, herbivory decreased the probability of flowering.

Second, herbivory significantly reduced the number of flower heads matured by plants that produced any flower heads ($n = 133$ in 2006, $n = 47$ in 2007; Table 3). The magnitude of the herbivore impact was greater in 2007 than in 2006 (Fig. 3b, e). In the 2007 experiment, insecticide-treated plants produced 390% more flower heads than did control plants, whereas in the 2006 experiment

insecticide-treated plants produced 140% more mature flower heads per plant than did the control plants (Fig. 3b, e). So, herbivory decreased the number of flower heads maturing per plant.

Third, herbivory also significantly reduced the number of filled seeds matured per plant by plants that produced any flower heads (Table 3). The reduction on average was 50% in 2006 and 83% in 2007 (Fig. 3c, f). In sum, herbivory significantly reduced the probability of flowering, the number of flower heads that matured, and the number of filled seeds per *C. vulgare* plant.

**Fig. 3** Reproductive response of established *C. vulgare* rosettes to treatment in each year, measured as proportion of focal rosettes setting any seed (mean, SE), total number of flower heads and filled (viable) seeds by treatment combination in 2006 (**a**–**c**) and in 2007 (**d**–**f**). *Black bar* = water-only treatment (ambient herbivory) and *white bar* = insecticide treatment (reduced herbivory). The two treatment levels of competition were high (ambient vegetation cover: 65–90%) and low (cover reduced to 20–25% of initial cover). To be conservative, rosettes that did not bolt were not included in the analysis for the proportion of rosettes producing any seeds (**a**, **d**). Also, rosettes that bolted but died before setting seeds were not included in the analysis of the total number of heads flowering (**b**, **e**) and seeds (**c**, **f**); these rosettes either bolted, but died before developing heads (2007, *n* = 11 control, *n* = 0 insecticide) or, bolted, produced heads, but no seeds (2006, *n* = 15 control, *n* = 0 insecticide; 2007, *n* = 7 control, *n* = 0 insecticide). *Different letters* above bars within each year indicate that treatment combinations differed statistically (*P* < 0.05, Tukey post hoc test). *Numbers* inside each bar indicate sample size for each treatment combination
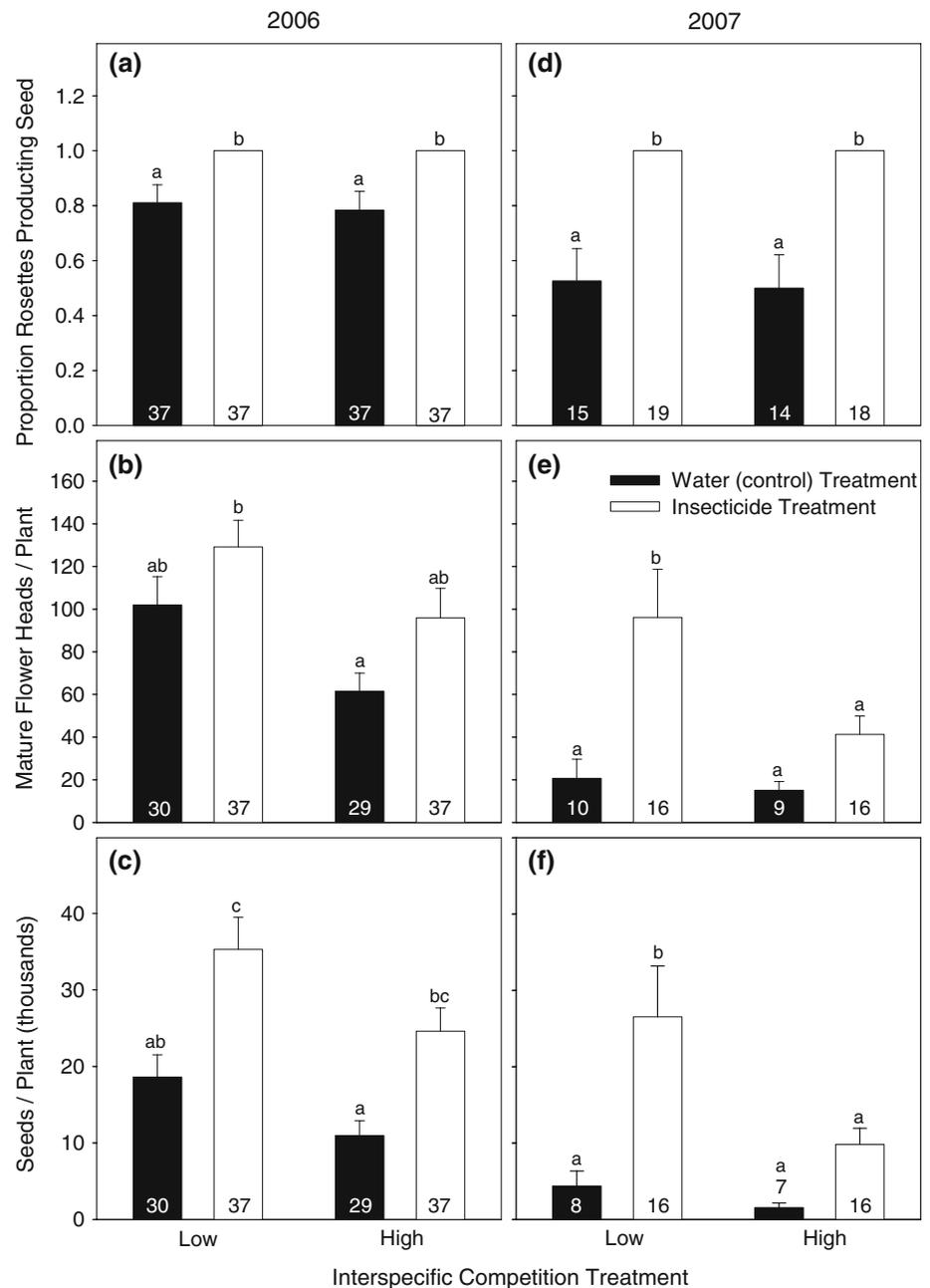


## Effects of competitive context on flowering and seed production

Reducing cover of neighboring plants did not significantly affect any measured reproductive parameter in either year for the plants that produced seed. However, plants in the low competition treatment, with reduced vegetation cover, trended toward a higher total number of flower heads (45 and 112% in 2006 and 2007, respectively; Fig. 3b, e) and higher number of undamaged, filled seeds (49 and 166% in 2006 and 2007, respectively; Fig. 3c, f). Both high

variation in reproductive effort among plants and the smaller sample size in 2007 likely contributed to the lack of statistical significance of these observed trends.

## Interaction of competition and herbivory

The amount of cover of neighbor plants, ambient (65–90%) versus reduced (20–25% of ambient), did not affect the proportion of *C. vulgare* leaves or flower heads damaged in either year (Fig. 1). Further, there was no interaction between competition and herbivory for any estimate of

**Table 3** ANCOVA of plant reproductive responses[a] by *C. vulgare* in the experimental manipulation of H and C for 2 years (2006, 2007). For abbreviations, see Table 1

| Factor[b] | Total mature flower heads | | Total seeds per plant | |
|---|---|---|---|---|
| | df | F | df | F |
| H | 1,170 | 7.80** | 1,166 | 10.09** |
| C | 1,170 | 0.11 | 1,166 | 0.01 |
| Y | 1,170 | 0.50 | 1,166 | 0.03 |
| ID | 1,170 | 62.18*** | 1,166 | 33.87*** |
| H × C | 1,170 | 2.39 | 1,166 | 0.37 |
| H × Y | 1,170 | 15.03*** | 1,166 | 12.95*** |
| H × ID | 1,170 | 2.11 | 1,166 | 2.43 |
| C × Y | 1,170 | 0.23 | 1,166 | 0.29 |
| C × ID | 1,170 | 0.33 | 1,166 | 0.23 |
| Y × ID | 1,170 | <0.001 | 1,166 | 0.43 |
| Site | $\chi^2 = 2.7$ | | $\chi^2 = 4.9*$ | |

\* $P < 0.05$, \*\* $P < 0.01$, \*\*\* $P < 0.001$

[a] The plant reproductive traits measured in the final, reproductive year were: total number of mature flower heads and total number of seeds per plant

[b] H, C and year (Y) were treated as fixed factors; and, site was treated as a random factor. Random factors were examined using likelihood ratio tests, which approximately follows a $\chi^2$ distribution with 1 *df*. Rosette diameter in May (ID) was used as the covariate. The analyses were conservative since all the bolting rosettes that failed to mature any seed were excluded; the excluded rosettes were those that bolted, but died prior to developing flower heads in 2007 ($n = 11$ control, $n = 0$ insecticide) or, produced some flower heads but no seeds in 2006 ($n = 15$ control, $n = 0$ insecticide) and in 2007 ($n = 7$ control, $n = 0$ insecticide)

damage measured (Table 1). Thus, these experiments provide no evidence of any effect of competitive context on the magnitude of insect herbivory on *C. vulgare*.

We also found no evidence of a significant interaction between competition and insect herbivory for any of the parameters of either plant growth or seed reproduction by *C. vulgare* in two years (Tables 1, 2, 3). Thus, the data show that insect herbivory did not influence the competitive effect of the ambient level of vegetation; and, vegetation cover did not alter the high impact of insect herbivory observed on *C. vulgare* rosettes in their final, flowering year.

## Discussion

Insect herbivory had strong, negative impacts on growth and seed reproduction of *C. vulgare* rosettes in their ultimate, flowering year in the tallgrass prairie region of Nebraska. In contrast, competition had little or no effect. Further, we found no evidence of any interaction between competition and herbivory on either plant performance or

plant vulnerability to insect herbivory. These data require that we reject the hypothesis that there was a synergistic interaction between competition and herbivory in suppressing growth and seed production of *C. vulgare* in its new, western tallgrass prairie environment. Instead, the results provide strong support for the hypothesis that herbivory by native insects directly contributed significant biotic resistance to invasiveness by *C. vulgare* in this region, as suggested (Louda and Rand 2002; Tenhumberg et al. 2008).

### Effects of competition context

Effects of competition by neighboring plants on growth and seed production by *C. vulgare* rosettes in their final, flowering year were small, at most (Figs. 2, 3). While ambient levels of competition reduced final vegetative biomass (Table 2), trends toward lower numbers of flower heads and seeds (Fig. 3) with competition were not statistically significant (Table 3). This result was surprising, since *C. vulgare* is a known invasive weedy plant that occurs primarily in disturbed habitats (low competition). Further, neighboring grasses often suppress performance of rosette-forming plants (Wilson 1993; Eskelinen 2008), including *Cirsium* species (Jongejans et al. 2006). In fact, Jongejans et al. (2006) hypothesized that competitive effects are especially strong on short-lived, rosette-forming species, such as *C. vulgare*. However, the data here do not support this hypothesis.

At least three hypotheses may explain the weak effect of competition on *C. vulgare* flowering rosettes. First, larger rosettes may have a size escape from the strongest effects of competition from neighboring vegetation. Competitive effects may be imposed primarily on earlier life stages, such as seedlings (Suwa 2008). Second, because *C. vulgare* generally occurs in disturbed habitats, low vegetation density may decrease the importance of competition in *C. vulgare* performance. Light competition, which can strongly suppress performance of rosette-forming plants in particular (Wilson 1993), is hypothesized to be low at relatively early successional sites, increasing as succession proceeds (Kosola and Gross 1999). However, the relatively high cover of ambient vegetation at our sites, averaging 65–90%, makes this hypothesis an unlikely explanation for our results. Third, specific competitive interactions may be more important than general levels of cover. Since our experimental design manipulated ambient levels of vegetation cover, this hypothesis could not be evaluated using the data here. A subsequent test of the competition effect, perhaps with the tallgrass prairie dominant grasses, specifically *A. gerardii, Sorghastrum nutans,* and *P, virgata*), could be used to evaluate the effects of individual, highly competitive species. Overall, across 2 years in three sites,

we found little evidence of competitive suppression of *C. vulgare* performance at the flowering stage.

### Effects of insect herbivory

Herbivory by native insects had an overall strong, negative effect on all measures of plant growth and reproduction (Figs. 2, 3). This outcome is consistent with mounting evidence documenting significant effects of insect herbivory on parameters of fitness of both native and introduced thistle species (Louda et al. 1990; Louda and Potvin 1995; Jackson 1998; Maron et al. 2002; Rose et al. 2005; Eckberg 2008; Suwa 2008).

Our experimental data support the hypothesis that the invasiveness of *C. vulgare* in the tallgrass prairie region of eastern Nebraska is significantly limited by insect herbivory (Louda and Rand 2002). Although *C. vulgare* is sparse in eastern Nebraska (Andersen and Louda 2008), it is highly invasive in other regions of the USA (USDA 2009), as well as in Australia (Medd 1981) and New Zealand (Johnson 1982). In eastern Nebraska, *C. vulgare* is a host plant for many indigenous insect herbivore species (Takahashi et al. 2009); and, we found that feeding by these insects on *C. vulgare* significantly reduced both growth (Fig. 2) and seed matured (Fig. 3) in its final, flowering year. Contrary to the classic assumption that competition from native plants provides strongest resistance to invasion by introduced weeds, a recent meta-analysis (Levine et al. 2004) found that herbivory by native insects can be as important as competition in resisting invasion by introduced plants. In fact, our results suggest that native insect herbivory is the primary mechanism of biotic resistance limiting *C. vulgare* invasion in the western tallgrass prairie in Nebraska.

The large effect of insect herbivores on *C. vulgare* in eastern Nebraska likely results from the richness and abundance of thistle-feeding insects on *Cirsium altissimum* (Takahashi et al. 2009), the most common native thistle in western tallgrass prairie (Louda and Rand 2002; Kaul et al. 2006). Both richness and abundance of thistle specialist and generalist insect herbivores on *C. vulgare* were comparable to the native *C. altissimum* (Takahashi et al. 2009). The phenological synchrony of *C. vulgare* with *C. altissimum* has been hypothesized to facilitate herbivore transfer (Jackson 1998; Louda and Rand 2002; Andersen and Louda 2008). Overall, the data here provide strong experimental evidence of the magnitude and influence of native insect herbivores in limiting adult growth and lifetime reproductive success of *C. vulgare*. Thus, the evidence provides crucial experimental support for the biotic resistance hypothesis to explain the low abundance of this introduced Eurasian weed in western tallgrass prairie.

### Interaction of competition and herbivory

We found no clear evidence of an interaction, either synergistic or antagonistic, between competition and herbivory on any measures of *C. vulgare* growth or reproduction. Four hypotheses could explain the lack of an interaction between competition and herbivory in *C. vulgare* performance. First, there may be no trade-off in resource allocation for growth versus defense or tolerance of herbivory for *C. vulgare* in its final, flowering year, in contrast to other studies (e.g., Simms 1992; Strauss and Agrawal 1999; Hochwender et al. 2000; Stowe et al. 2000). If rosettes in their flowering year have large amounts of stored nutrients in their taproots, then allocation of resources to both growth and defense or tolerance may be possible.

Second, the intensity of competition from the ambient vegetation may not have been high enough to require a trade-off to growth versus defense or tolerance. Competition from ambient levels of cover may have been too low to impose competition; however, recorded cover was relatively high (65–90%). Alternately, specific species required to impose significant competition may have been absent. Further research is necessary to evaluate these alternatives.

Third, the insecticide treatment, by being concentrated only on the focal experimental plant rather than on the entire plot, could have increased herbivory on the neighbor plants by shared generalist herbivores, weakening the competitive effect on the focal rosette (Haag et al. 2004). We did not measure herbivory on the neighboring plants in our plots; however, we found that neighboring plants did not reduce herbivory on the focal plant (Table 1), suggesting neighbors did not lure herbivores off of our focal experimental plant. Given this observation, such masked indirect effects are unlikely to alter the interpretation of this study.

Fourth, any interaction between competition and herbivory may occur at an earlier life stage, when plants have few stored resources. Synergistic interaction effects between competition and herbivory could arise if neighboring plants reduce a plant's tolerance for tissue loss to herbivores (Hämback and Beckerman 2003). Small plants with few stored resources could be dependent on resource acquisition to compensate for herbivory and, hence, be especially vulnerable to resource pre-emption by neighbors. Further study of this hypothesis is merited.

In conclusion, we found that insect herbivory strongly and consistently reduced growth and reproduction of *C. vulgare* rosettes in their final, flowering year, while the effect of competitive context was weak. The combined effects of competition and herbivory were independent, with no clear evidence for synergistic or antagonistic interactions between these two factors. The results provide

important experimental support for the hypothesis that high levels of herbivory on the introduced *C. vulgare* by native insects exert significant resistance to invasiveness by *C. vulgare* in western tallgrass prairie.

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