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F. Leland Russell
Wichita State University, leland.russell@wichita.edu

Karen E. Rose
University of Sheffield

Svata M. Louda
University of Nebraska - Lincoln, slouda1@unl.edu

Seed availability and insect herbivory limit recruitment and adult density of native tall thistle

F. Leland Russell,[1,4] Karen E. Rose,[2] and Svata M. Louda[3]

[1]*Department of Biology, Wichita State University, Wichita, Kansas 67260 USA*
[2]*Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN United Kingdom*
[3]*School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588 USA*

Abstract. Understanding spatial and temporal variation in factors influencing plant regeneration is critical to predicting plant population growth. We experimentally evaluated seed limitation, insect herbivory, and their interaction in the regeneration and density of tall thistle (*Cirsium altissimum*) across a topographic ecosystem productivity gradient in tallgrass prairie over two years. On ridges and in valleys, we used a factorial experiment manipulating seed availability and insect herbivory to quantify effects of: seed input on seedling density, insect herbivory on juvenile density, and cumulative impacts of both seed input and herbivory on reproductive adult density. Seed addition increased seedling densities at three of five sites in 2006 and all five sites in 2007. Insect herbivory reduced seedling survival across all sites in both years, as well as rosette survival from the previous year's seedlings. In both years, insecticide treatment of seed addition plots led to greater adult tall thistle densities in the following year, reflecting the increase in juvenile thistle densities in the experimental year. Seedling survival was not density dependent. Our analytical projection model predicts a significant long-term increase in adult densities from seed input, with a greater increase under experimentally reduced insect herbivory. While plant community biomass and water stress varied significantly between ridges and valleys, the effects of seed addition and insect herbivory did not vary with gradient position. These results support conceptual models that predict seedling and adult densities of short-lived monocarpic perennial plants should be seed limited. Further, the experiment demonstrates that even at high juvenile plant densities, at which density dependence potentially could have overridden herbivore effects on plant survival, insect herbivory strongly affected juvenile thistle performance and adult densities of this native prairie species.

Key words: analytical approximation; Cirsium; *ecosystem productivity; insect herbivory; Nebraska, USA; population dynamics; seed limitation; tall thistle; tallgrass prairie.*

Introduction

Two defining goals in ecology are to identify the factors that limit population size and to predict how the strength of each factor varies in space and time. Plant population size may be limited by the availability of microsites that are sufficiently benign to allow recruitment to reproductive size classes (Harper 1977, Eriksson and Ehrlen 1992, Crawley 1997). Alternatively, plant populations may be seed limited (Harper 1977, Louda 1982, 1983, Eriksson and Ehrlen 1992, Fenner 1992, Louda and Potvin 1995, Crawley 1997), meaning that too few seeds are available to colonize all suitable microsites.

Understanding the role of seed availability in limiting plant population size is critical to evaluating herbivore impacts on plant populations (Louda 1982, 1983, Fenner 1992, Turnbull et al. 2000, Maron and Crone 2006). Herbivores that do not kill adult plants but

reduce lifetime seed production can reduce the size of seed-limited plant populations (e.g., Louda and Potvin 1995). By contrast, reductions in seed output will have little effect on the size of microsite-limited plant populations; increased numbers of seeds produced in the absence of herbivores are dispersed into inhospitable microsites (Turnbull et al. 2000). Thus, seed addition experiments can produce fundamental insights into plant population dynamics and the role of plant–animal interactions.

Plant ecologists have hypothesized that life history differences contribute to variation among species in the role of seed limitation (Andersen 1989, Crawley 1989, Louda and Potvin 1995, Maron and Gardner 2000). Populations of iterocarpic perennials and of species with persistent seed banks are expected to be most susceptible to microsite limitation. However, recent herbivore exclusion experiments challenge this paradigm, by demonstrating that greater seed input can increase population density even for iterocarpic perennials (Kelly and Dyer 2002, Miller et al. 2009) and species with long-lived seed banks (Maron and Simms 2001, Maron and

Kauffman 2006). By contrast, Louda and Potvin (1995) argued that population sizes of monocarpic perennial plants that lack a permanent seed bank should be closely tied to each year's reproduction. If microsites are available and seed input does not stimulate density-dependent mortality of seeds or juveniles, then cohort size is expected to be seed limited. However, few multisite, multiyear studies of monocarpic perennials have evaluated how often and at what rate added seed increases adult plant recruitment (Turnbull et al. 2000).

Plant community ecologists also have hypothesized that the role of seed limitation will vary with ecosystem productivity. In productive grasslands, light competition can limit safe microsites for adult plant recruitment to a number that is saturated by local seed input (Turnbull et al. 2000, Foster et al. 2004, Maron and Crone 2006). However, variation in abiotic resource levels, such as light, also can alter the amount of herbivore damage (Louda et al. 1987, Louda and Rodman 1996) and plant tolerance for damage (Maschinski and Whitham 1989, Wise and Abrahamson 2007). Greater herbivory or reduced tolerance in productive sites could limit suitable microsites for juvenile plant survival and eliminate a direct relationship between seed input and plant population size. Ecologists rarely have addressed how herbivore effects on plant performance vary with natural variation in abiotic resource levels (but see Louda and Rodman 1996).

In grasslands, seedling herbivory, by mollusks in Europe (Hanley et al. 1996, Pywell et al. 2007) and by small mammals in North America (Maron and Kauffman 2006), reduced recruitment to subsequent life stages. Insect herbivory on seedlings in North American grasslands has received little attention; however, recent work shows that it can reduce seedling survival and growth for both exotic (Suwa et al. 2010; J. O. Eckberg, S. M. Louda, and B. Tenhumberg, *unpublished manuscript*) and native (T. Suwa and S. M. Louda, *unpublished manuscript*) thistles. Even small amounts of tissue loss may strongly affect seedling performance because seedlings have few stored resources and limited ability to acquire resources for compensatory growth. When germination is seed limited and subsequent density dependence is weak, higher mortality rates or slower growth caused by insect herbivory at early stages could lead to fewer reproductive adults. To date, however, there are few direct tests of the role of insect herbivory in seedling regeneration and plant density.

We used a factorial experiment involving seed addition and insecticide application to quantify effects of seed limitation and insect herbivory on seedling recruitment by a native thistle, *Cirsium altissimum* (L.) Spreng, and to determine how these effects vary with position on topographic, ecosystem productivity gradients in tallgrass prairie in Nebraska, USA. We asked the following: (1) Do greater seed inputs increase seedling densities? (2) Does insect herbivory reduce survival and growth of juveniles recruited? (3) Do seed addition and insect herbivory have cumulative effects on the number of reproductive adults? (4) Do effects of seed input and insect herbivory vary in relation to ecosystem productivity (ridge vs. valley habitat)? The experimental results provide new data to predict the single and joint effects of seed availability and insect herbivory on juveniles in determining sizes and spatial distributions of adult plant populations.

Methods

Study species

Cirsium altissimum (tall thistle) is a native, monocarpic, short-lived perennial that occurs in moderately disturbed areas in grasslands of eastern North America (Great Plains Flora Association 1986). Our study sites in eastern Nebraska are near tall thistle's western range limit (Kaul et al. 2006), where it is the most common native thistle (Andersen and Louda 2008). In our region, large tall thistle rosettes begin producing a reproductive stalk (bolting) in May. Flower heads open in August through September, and seed maturation and dispersal begin in late August. Seedling germination occurs primarily in spring. For example, for seed sown in March–April 2007, 90.7% of seedlings observed in 2007 were found May–June and only 9.3% were initially found later, in October (F. L. Russell, K. E. Rose, and S. M. Louda, *unpublished data*).

The main insect herbivores observed on tall thistle seedlings and rosettes in our region were: grasshoppers and lepidopteran larvae, especially those of the painted lady butterfly *Vanessa cardui* L., which chew leaves; adult beetles, including *Systena hudsonias* Forster and the native weevil *Baris* nr. *subsimilis* Casey, which scrape epidermis and mesophyll tissue or chew holes in leaf blades and stems; and leafminers, which kill leaves by mining leaf midribs (Takahashi 2006).

Study sites

Our five southeastern Nebraska study sites included four Nebraska Game and Parks wildlife areas: Triple Creek (40.7° N, 96.4° W), Jack Sinn (41° N, 96.6° W), Twin Lakes (40.9° N, 96.9° W), and Divoky Acres (40.3° N, 97.2° W) and the University of Nebraska–Lincoln's Nine-Mile Prairie Research Preserve (40.9° N, 96.7° W). Each site had a clear local topographic gradient with tall thistles both on ridges and in valleys. The wildlife areas are prairie restorations from cropland (C. Lesiak, *personal communication*). Restoration began at Jack Sinn and Twin Lakes 15 and 30 years ago, respectively; neither has been burned since 1995. Hay is cut at Jack Sinn once every five years, most recently in 2003. Triple Creek and Divoky Acres were reseeded in 2000; neither has been burned or hayed. Nine-Mile Prairie has never been plowed but has been hayed; this site has been burned every 3–4 years since 1978, most recently in 2004 (D. Wedin, *personal communication*). Tall thistle densities varied greatly among sites and years (Table 1).

TABLE 1. Natural densities of tall thistle (*Cirsium altissimum*) juveniles (seedlings + rosettes) and bolting adults at each study site in southeastern Nebraska, USA, based upon counts in control plots in 2007 and 2008, and August–September 2008 standing-crop plant community biomass.

| Site | Position | Density (no. plants/m^2) | | | | Biomass (g/m^2) |
| | | 2007 | | 2008 | | |
		Juveniles	Bolters	Juveniles	Bolters	
Triple Creek	ridge	33.25 (9.03)	14.25 (3.2)	8 (3.01)	18.25 (3.99)	369.8 (67.0)
	valley	7 (1.73)	2.75 (1.3)	3.5 (1.2)	4.0 (1.03)	516.4 (85.7)
Jack Sinn	ridge	0.25 (0.25)	0	0.25 (0.25)	0.25 (0.25)	276.5 (44.2)
	valley	0.25 (0.25)	0.25 (0.25)	0.75 (0.4)	0	305.1 (35.8)
Nine-Mile	ridge	0	0	0	0	322.5 (30.6)
	valley	0.4 (0.28)	0	0.2 (0.2)	0	485.2 (83.2)
Twin Lakes	ridge	0	0	0.25 (0.25)	0	287.2 (20.1)
	valley	0.25 (0.25)	0	0.25 (0.25)	0	265.9 (8.9)
Divoky Acres	ridge	6.0 (1.97)	3.5 (1.36)	3.25 (1.28)	2.75 (1.38)	610.7 (42.4)
	valley	9.5 (4.71)	1.25 (0.79)	5.25 (2.77)	0.25 (0.25)	847.9 (93.0)

Notes: Values are given as means with SE in parentheses. Control plots from both the 2006 and 2007 experiments were used to estimate tall thistle densities. Densities are numbers of plants/m^2, so counts in each 50×50 cm plot were multiplied by 4 before calculating means and SEs.

Experimental design

We used a full factorial experiment that manipulated tall thistle seed input density and insect herbivory. The experiment was repeated in 2006 and 2007, and follow-up continued in 2008 until plots were destroyed. In February–April 2006 at each site, four blocks were randomly located on the ridge, and four were located in the valley. Each block contained 16 plots (50×50 cm), arranged in two rows of eight with 1.25 m between plots. Blocks were oriented perpendicular to the topographic gradient. In each block, half the plots from the upper row and half from the lower row were used each year; plots used in 2006 alternated with plots used in 2007. Therefore, in each year (2006 and 2007) each seed addition × insect herbivory treatment combination was replicated twice in each block. In each topographic position at each site, two blocks were randomly selected to receive seed addition in the upper row, and the remaining two blocks had seed addition in the lower row. Columns within blocks were randomly assigned to the herbivory treatment; the pattern was consistent for all blocks at a site.

The seed density treatment had two levels: 100 tall thistle seeds vs. no seeds added (control) per plot. Undamaged, filled seeds were extracted from flower heads collected at the site the previous autumn and stored outdoors. Tetrazolium tests of a random subset of seeds, removed before sowing, indicated >70% viability. We sprinkled seeds on plots from 20 cm height. In 2006, seeds were sown at Nine-Mile on 25 February, at Triple Creek on 30 March, and at Jack Sinn, Twin Lakes, and Divoky Acres on 15–16 April. In 2007, seeds were sown at Jack Sinn, Twin Lakes, and Triple Creek on 9–10 March and at Divoky Acres and Nine-Mile on 6–7 April. Date of sowing was determined according to when dissections of flower heads from each site were completed and seeds were available.

The herbivory treatment had two levels: insecticide-in-water spray (reduced herbivory) and water-only spray (control). The broad-spectrum, nonsystemic, synthetic pyrethroid insecticide Bifin I/T (the active ingredient is bifenthrin; Control Solutions, Pasadena, Texas, USA) was applied to designated 50×50 cm plots to reduce insect herbivory (15.9 mL Bifin I/T per liter water); an equal volume of water was applied to control plots. Plots were sprayed every 2–3 weeks from 1 May to 15 September each year. In greenhouse trials, no phytosimulatory or phytotoxic effects of bifenthrin were found (T. Suwa, J. Eckberg, and S. M. Louda, *unpublished data*).

Measurements

We censused recruitment and survival near the beginning and at the end of each growing season. In 2006, we counted seedlings per plot on 23–29 May and surviving juvenile rosettes plus new seedlings on 17–29 September. In 2007, we counted all tall thistles (seedlings, juvenile rosettes, and bolting adults) in all plots of both the 2006 and 2007 experiments on 17 May to 4 June and 27 September to 3 November. In 2008, we recounted all plots in May; some tagged plants from the 2006 cohort remained alive and had not yet bolted (Triple Creek, 11.2%; Jack Sinn, 83.3%; Twin Lakes, 77.8%; Divoky Acres, 31.2%; and Nine-Mile, 84.6%). The experiment ended when plots at Jack Sinn and Twin Lakes were destroyed by land management activities, such as disking and construction of firebreaks.

Plant size and herbivore damage were measured for a subset of marked seedlings on the dates we quantified recruitment and survival. In both years, we marked up to four seedlings per plot with a numbered tag, picking the seedling nearest the center of each quadrant of each 50×50 cm plot ($n = 4$ per plot); sample size was reduced when plots did not have a seedling in each quadrant. Initial numbers of tagged tall thistle seedlings were

(2006, 2007, respectively): Nine-Mile, 56, 53; Divoky, 155, 19; Jack Sinn, 21, 74; Triple Creek, 200, 91; Twin Lakes, 14, 26. To quantify plant size, in 2006 we measured the widest plant diameter and counted the number of green leaves on each marked plant. In 2007 and 2008, we also measured the root crown diameter of all marked plants. To quantify herbivory each year, we counted the numbers of green leaves that were damaged or severely damaged (>30% leaf area), as well as the total number of green leaves, including cotyledons. In addition to spring and fall censuses, we quantified mid-season herbivore damage 31 July to 8 August 2006 and 2–10 August 2007. Herbivore damage was expressed as the proportion of green leaves counted at the census date.

Soil moisture by volume on the ridge and in the valley at each site was measured on 14–17 July 2006 and 17–23 July 2007 (≥ 2 d after the last rain), using a time domain refractometer (TDR; Model 100, Spectrum Technologies, Plainfield, Illinois, USA), with 20-cm probes. Measurements were taken 1.5 m beyond each end of each experimental block. We measured soil moisture in late July because high temperatures and declining precipitation at this time of the growing season could produce drought stress (data *available online*).[5]

We measured drought stress for tall thistle rosettes on ridges and in valleys as predawn leaf water potentials (27 August and 1 September 2006; 31 August and 2 September 2007) at two sites, supplemented with midday leaf water potentials (8, 9, 16 September and 5 October 2007) at four sites, using a Scholander pressure chamber. Water potentials could not be measured at sites where all juveniles in the plots were censused (sites with low juvenile thistle density). Because water potential measurements require that a leaf be cut from the plant and placed in the pressure chamber, leaf removal would have compromised our measure of leaf number per plant and, possibly, affected plant performance.

Aboveground standing crop plant biomass on ridges and in valleys at each site was quantified 29–31 August and 19–20 September 2008. In August, living plant biomass was clipped at ground level in a 50×50 cm frame located 1 m west of the middle of each block. In September, two blocks in each topographic position at each site were randomly selected and living plant biomass within a 50×50 cm frame located 1 m east of the middle of the selected blocks was harvested. Biomass was dried at 60°C for 72 h before weighing.

Statistical methods

Linear and generalized linear models (GLMs) were fit to the data as appropriate using R version 2.8 (R Foundation for Statistical Computing, Vienna, Austria). Site was fit as a fixed effect, estimating a parameter for

each site, giving us conservative tests of significance associated with the slight loss of power (Bolker 2008). Sites were not randomly chosen, since we specifically wanted to test whether effects of seed input and insect herbivory depended upon ecosystem productivity (ridge vs. valley habitat). We tested the hypotheses that: (1) tall thistle population density increases less with seed addition in higher productivity valleys than on lower productivity ridges (Turnbull et al. 2000, Foster et al. 2004, Maron and Crone 2006); and (2) insect herbivore damage (Louda and Rodman 1996) and impacts on plant performance (Maschinski and Whitham 1989) are greater on ridges, where plants are more water stressed, than in valleys. Growth data were fitted using a linear regression that related size in year $t + 1$ to size in year t. Survival and flowering data were fitted using logistic regressions with binomial errors and a log link function (Metcalf et al. 2003). Depending on the form of the model (F or χ^2 tests), we assessed the significance of terms by calculating the change in deviance when the item was dropped from the maximal model which, in all cases, was: size $\times$ seed addition $\times$ insecticide $\times$ site $\times$ topography $\times$ seedling density in the year of emergence, where $\times$ indicates fitting a term and all its higher order interactions. In analyses of growth, survival, and flowering for May 2006 to May 2007 in the 2006 experiment, "size" was initial rosette diameter. In comparable analyses for May 2007 to May 2008 in both the 2006 and 2007 experiments, "size" was initial root crown diameter. For the 2006 experiment, growth between 2006 and 2007 was estimated using difference in rosette diameter; growth between 2007 and 2008 was estimated using change in root crown diameter, a more precise measure. Size was (natural) log transformed throughout.

The efficacy of the insecticide treatment was tested using a GLM of leaf damage (number of leaves with any damage divided by the number of undamaged leaves per plant) in August of each year, using binomial errors and a log link function. Response variables that were counts were modeled using GLMs with Poisson errors and a log link function. If a Poisson model showed signs of overdispersion, a GLM with negative binomial errors was fitted instead.

We tested the potential cumulative effects of seed addition and insecticide treatment indirectly in two ways, because disturbances ended the experiment before these could be evaluated directly. First, we looked at the effects of seed addition in early 2006 on the number of rosettes at the end of the 2006 growing season (September). This estimate of population density was the most precise available. A suspected second episode of germination occurred just before the May 2007 census at Nine-Mile and Jack Sinn; so, using the May 2007 or 2008 census numbers would have overestimated rosette abundance. Further, data from Divoky and Triple Creek could not be used since plots at these sites contained large numbers of unmarked rosettes, the age
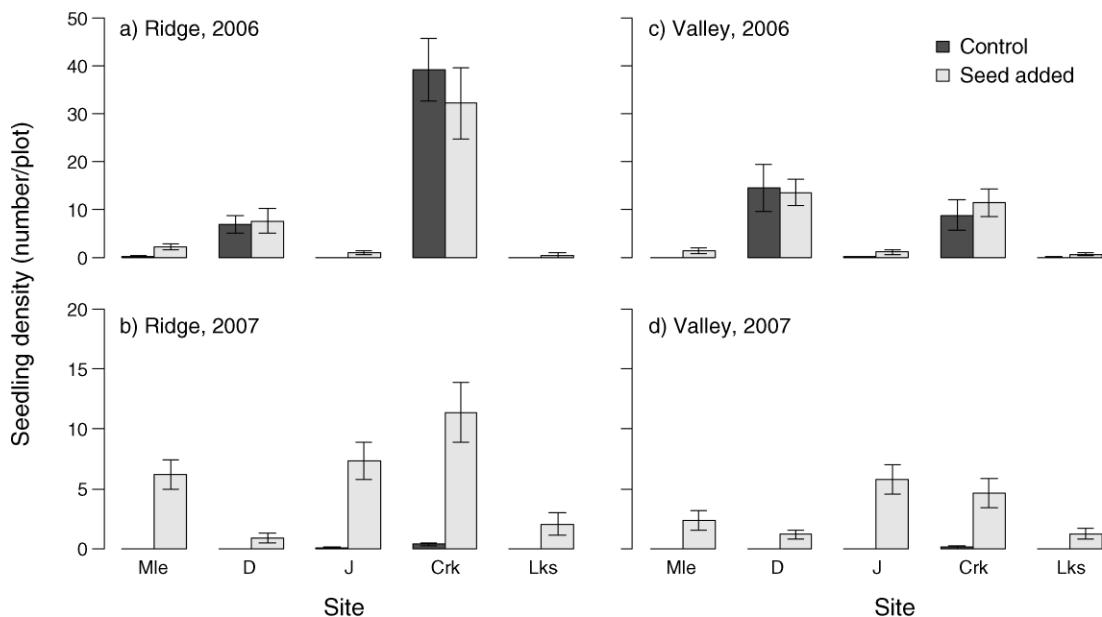
FIG. 1. The effect of seed addition (+100 seeds per 50 × 50 cm plot) on seedling density per plot (mean ± SE) in May 2006 (for seeds sown in 2006) and May 2007 (for seeds sown in 2007) for tall thistle (*Cirsium altissimum*) in plots in southeastern Nebraska, USA. There was a significant year × addition interaction with a larger response in 2007 than in 2006. Site abbreviations are: Mle, Nine-Mile Prairie; D, Divoky Acres; J, Jack Sinn; Crk, Triple Creek; Lks, Twin Lakes.

of which was not known with certainty. Second, we estimated the future number of adults using an analytical approximation (see *Results*).

RESULTS

Topographic and site differences in soil moisture and productivity

While variation in soil moisture along topographic gradients was more complex than a straightforward contrast between valleys and ridges, point estimates of differences in productivity and water stress were in the direction predicted (Appendices A and B). Valleys were moister than ridges at three sites and equal at one (site × topography: $F_{4, 165} = 8.25$, $P < 0.001$). Leaf water potentials were significantly more negative (greater drought stress) on ridges compared to in valleys ($F_{1, 161} = 49.89$, $P = 0.023$; Appendices A and B). Valleys had significantly more biomass in general than ridges ($F_{1, 54} = 9.12$, $P = 0.004$; Table 1). Twin Lakes was the exception, with greater biomass and soil moisture content on ridges than in valleys (Appendix A).

Insecticide treatment effect

Herbivore damage, as the proportion of leaves with damage per plant in August, differed statistically between topographic positions in 2006, with higher damage on the ridge (ridge, 0.69 ± 0.03; valley, 0.61 ± 0.07 (mean ± SE), $\chi^2 = 3.96$, df = 1, 242, $P = 0.05$; Appendix C), but not in 2007, although the pattern was the same (ridge, 0.37 ± 0.04; valley, 0.33 ± 0.05). Insecticide treatment effects did not differ with topographic position in either year (Appendix C). However,

one-year-old plants from the 2006 experiment (August 2007) had greater herbivore damage in the valleys than on the ridges (ridge, 0.49 ± 0.04; valley, 0.59 ± 0.05; $\chi^2 = 4.73$, df = 1, 125, $P = 0.034$). Because of a significant site × treatment × topography interaction, however, no consistent overall difference in herbivory emerged between ridges and valleys. Therefore, we combined topographic positions in our comparison of damage levels between sites and spray treatments. This had the added advantage of maintaining biologically meaningful sample sizes; because of high ambient seedling mortality, sites with naturally low population densities (e.g., Twin Lakes, Nine-Mile) had few (1–5) individuals still alive in the second year.

For marked experimental plants in the 2006 experiment, insecticide treatment significantly reduced the proportion of leaves damaged at the end of both the first (2006, $\chi^2 = 4.16$, df = 1, 238, $P = 0.04$) and the second (2007, $\chi^2 = 25.83$, df = 1, 125, $P < 0.001$) growing seasons (Appendices C and D). In the 2007 experiment, insecticide treatment significantly reduced damage at the end of the first season (2007) at two sites, but across all five sites a similar trend did not reach statistical significance ($\chi^2 = 2.55$, df = 1, 47, $P = 0.11$; Appendices C and D).

Effect of seed input on seedling densities

Overall, seed addition led to significantly more seedlings recruited into the population relative to the controls, especially in 2007 (Fig. 1). The main effect of seed addition was significant ($\chi^2 = 941.1$, df = 1, 674, $P < 0.001$). The number of seedlings emerging in May
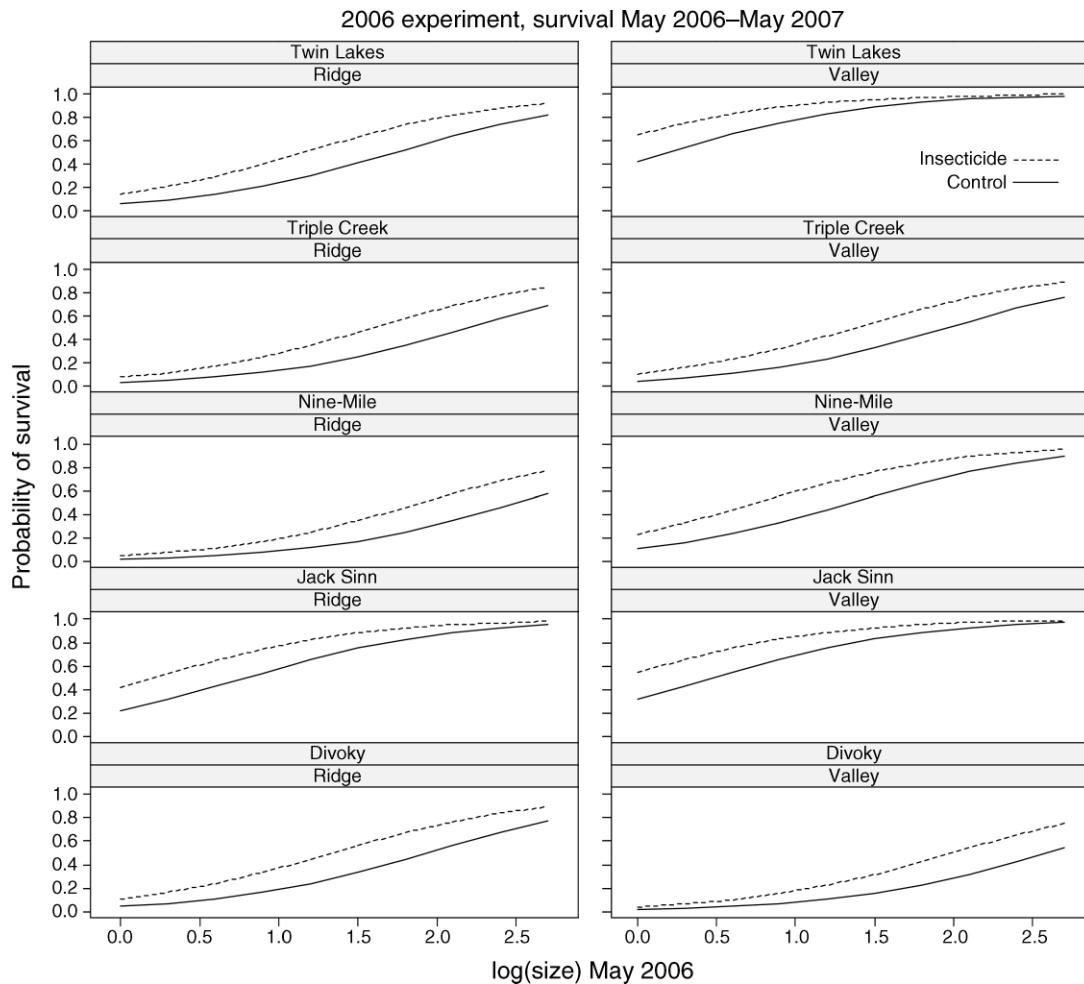
2006 experiment, survival May 2006–May 2007

Fig. 2. The size-related survival from May 2006 to May 2007 of marked tall thistle seedlings in the 2006 experiment, showing significant effects of seedling size ($P < 0.0001$), insecticide treatment ($P < 0.0001$), site ($P < 0.001$), and the site × topographic position interaction ($P < 0.001$).

each year also varied significantly among sites ($\chi^2 = 299.6$, df = 4, 674, $P < 0.001$), topographic positions ($\chi^2 = 42.4$, df = 1, 674, $P < 0.001$), and years ($\chi^2 = 624.1$, df = 1, 674, $P < 0.001$). There was a significant year × seed addition treatment interaction, confirming that the response to addition was greater in 2007 than 2006 ($\chi^2 = 7.24$, df =1, 670, $P = 0.01$; Fig. 1). The insecticide treatment did not affect initial seedling density, early (May) in the year of seed sowing ($\chi^2 = 2.07$, df = 1, 671, $P = 0.15$). Although ridges in general supported more seedlings than did valleys, the response to seed addition was of a statistically similar magnitude for both topographic positions; and the interaction between topographic position and seed addition treatment was not significant ($\chi^2 = 1.30$, df = 1, 665, $P = 0.25$). To confirm that seed addition had a biologically significant effect in 2006, we also analyzed that year separately. Seed addition did significantly increase the number of seedlings in 2006 (main effect of seed addition, $\chi^2 = 27.00$, df = 1, 346, $P < 0.001$), even though the

magnitude of that effect varied widely among sites (site × seed addition interaction, $\chi^2 = 48.38$, df = 1, 350, $P < 0.001$; Fig. 1).

Early demography: first-year survival and growth

We examined effects of herbivory and topography on the early demography of the marked subset of plants. For the 2006 experiment, seedling survival over the first year (May 2006 to May 2007) was greater for insecticide-treated plants than for control plants ($\chi^2 = 15.96$, df = 4, 404, $P < 0.0001$; Fig. 2), and it increased with plant size in May 2006 ($\chi^2 = 32.23$, df = 1, 409, $P < 0.0001$; Appendix E). Initial seedling density did not affect survival (Fig. 3a, Appendix E). Despite a significant site effect ($\chi^2 = 31.23$, df = 4, 408, $P < 0.001$) and a topography × site interaction ($\chi^2 = 17.73$, df = 4, 402, $P = 0.001$), the overall survival rate was the same for valleys (0.42 ± 0.04) and ridges (0.46 ± 0.03). Of 446 seedlings that were tagged in May 2006, 182 (41%) were alive in May 2007 and 48 (11%) reproduced
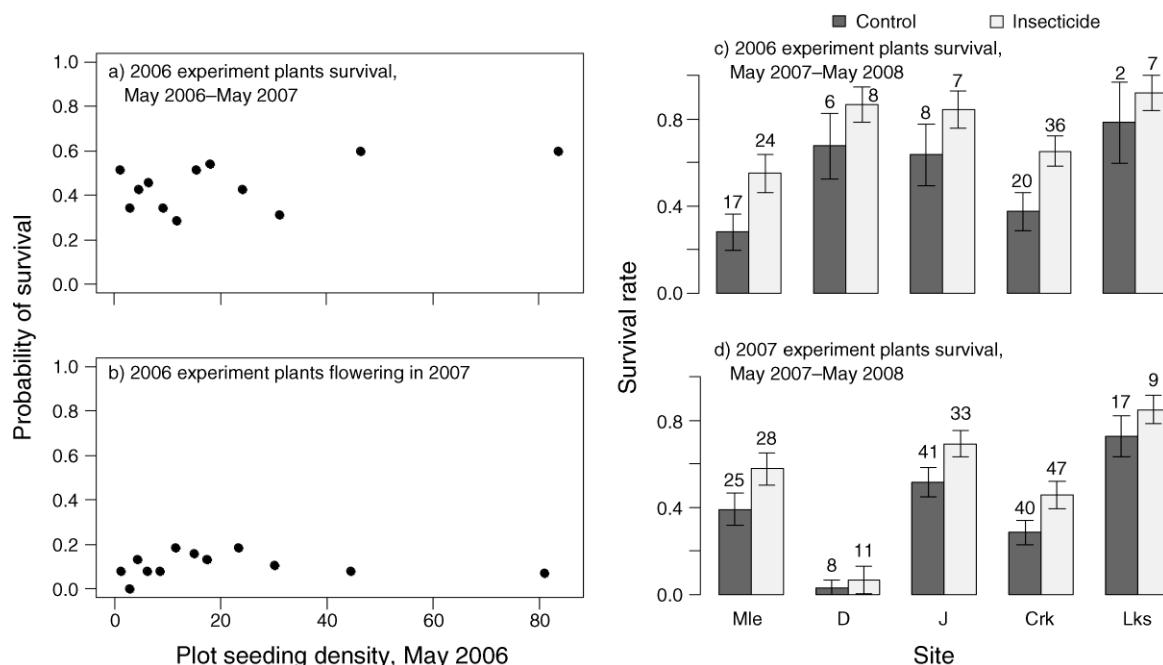
FIG. 3. (a) Tall thistle seedling survival from May 2006 to May 2007 and (b) flowering in the first post-seedling year (2007 for the 2006 cohort) were independent of May 2006 seedling density. Survival from May 2007 to May 2008 (mean ± SE) was significantly increased by insecticide, for both (c) one-year-old juveniles from the 2006 experiment and (d) for seedlings from the 2007 experiment. Numbers associated with bars in panels (c) and (d) are sample sizes. Site abbreviations are: Mle, Nine-Mile Prairie; D, Divoky Acres; J, Jack Sinn; Crk, Triple Creek; Lks, Twin Lakes.

at the end of their first post-seedling year as one-year-olds. For the 135 plants that survived until May 2007 and did not reproduce in 2007, 79 (58%) were alive in May 2008 and 47 (35%) reproduced as two-year-olds. Site destruction precluded further quantification of subsequent survival and reproduction.

For all sites and seedling densities, insecticide-treated plants grew ~4% faster than control plants ($F_{1, 166} = 5.39$, $P = 0.02$; Appendix E). Further, seedling growth in the first year (May 2006 to May 2007) increased with initial seedling size ($F_{1, 172} = 51.52$, $P < 0.0001$) and varied among sites ($F_{4, 170} = 4.193$, $P = 0.003$; Appendix E). At Twin Lakes, the site with lowest vegetation biomass (Table 1), plants grew much less than at the other sites. Growth was significantly faster in valleys than on ridges ($F_{1, 116} = 4.63$, $P = 0.03$), but the absolute difference was ~2% (Appendix E). Plot seeding density in May did not affect growth rate ($F_{1, 165} = 0.08$, $P = 0.77$).

Survival from May 2007 to May 2008 of the one-year-old juveniles from the 2006 experiment that neither died nor flowered in 2007 varied significantly between sites ($\chi^2 = 1.77$, df = 4, 134, $P = 0.019$), and it was 36% higher with the insecticide treatment ($\chi^2 = 8.88$, df = 1,130, $P = 0.003$; Fig. 3c). Plant size in May 2007 did not affect subsequent survival. However, the size of these plants the following year (May 2008) increased with plant size in May 2007 ($F_{1,73} = 44.8$, $P < 0.0001$). Growth varied among sites ($F_{4,71} = 5.86$, $P = 0.004$) and was ~10% faster in valleys than on ridges ($F_{1,67} = 5.61$, $P = 0.012$).

For the 2007 seed addition experiment, we quantified the demography of marked plants from May 2007 to May 2008. Early seedling size (May 2007) had no effect on survival; survival instead varied among sites ($\chi^2 = 40.79$, df = 4, 260, $P < 0.001$). Survival did not differ between ridges and valleys, nor did it vary with the initial (May) density of seedlings in the plot (both $P > 0.25$). There was, however, a substantial effect of insecticide treatment. Seedlings in control plots had up to 35% lower survival than did seedlings in insecticide plots ($\chi^2 = 7.67$, df = 1, 254, $P = 0.01$; Fig. 3d). First-year growth of the 2007 experiment seedlings was significantly influenced by early (May 2007) size ($F_{1, 106} = 10.03$, $P = 0.002$) and, again, it varied among sites ($F_{4, 110} = 27.59$, $P < 0.0001$). There were no significant effects of topographic position, initial seedling density, or insecticide on seedling growth (all $P > 0.25$). Of the seedlings that emerged in May 2007, 48% survived until May 2008; only 6% of those reproduced at the end of their first year as one-year-olds.

Probability of flowering

For the marked subset of plants, probability of flowering at ages 1 or 2 was an increasing function of individual size in both experiments and both years (2006 experiment plants flowering in 2007 [age 1] and in 2008 [age 2], both $P < 0.001$; 2007 experiment plants flowering in 2008 [age 1], $\chi^2 = 4.27$, df = 1, 225, $P = 0.04$). Root crown diameter in the spring of the year of

TABLE 2. Site mean flowering probabilities (p_f) and sample sizes (of both flowering and nonflowering tall thistle [*Cirsium altissimum*] plants) in relation to topographic position and insecticide treatment for the subset of marked plants in both the 2006 and 2007 seed addition experiments.

Site and treatment	2006 experiment								2007 experiment			
	2007 (age 1)				2008 (age 2)				2008 (age 1)			
	Ridge		Valley		Ridge		Valley		Ridge		Valley	
	p_f	n	p_f	n	p_f	n	p_f	n	p_f	n	p_f	n
Triple Creek												
Control	0.09	56	0.14	42	0.29	14	0.67	6	0.13	23	0.14	29
Insecticide	0.27	64	0.25	32	0.31	26	0.80	10	0.18	17	0.33	18
Divoky												
Control	0.17	30	0.02	44	0.22	9	0.13	8	0.00	3	0.00	2
Insecticide	0.15	40	0.00	51	0.31	13	0.09	11	0.00	5	0.00	9
Nine-Mile												
Control	0.00	20	0.00	10	⋯	0	0.20	1	0.00	16	0.00	18
Insecticide	0.00	16	0.00	6	⋯	0	0.25	1	0.00	9	0.00	10
Jack Sinn												
Control	0.00	4	0.00	7	0.50	2	0.00	4	0.00	22	0.00	16
Insecticide	0.00	4	0.00	6	0.00	30	0.20	5	0.00	19	0.00	17
Twin Lakes												
Control	0.00	1	0.00	4	⋯	0	0.00	2	0.00	9	0.00	4
Insecticide	0.00	3	0.00	6	0.00	1	0.33	6	0.00	8	0.00	5

bolting was 8.74 ± 0.43 mm on ridges and 7.38 ± 0.49 mm in valleys for plants bolting at age 1. For tall thistles bolting at age 2, spring root crown diameter was 9.75 ± 1.01 mm on ridges and 12.63 ± 1.05 mm in valleys.

The number of 2006 experiment plants reproducing in 2007 as one-year-olds was highest at Triple Creek, followed closely by Divoky Acres, and it was very low at the other three sites (Table 2). At the two sites with many reproductive individuals, flowering probability was higher on ridges (Table 2), resulting in a significant topography × site interaction ($\chi^2 = 11.42$, df = 1, 120, $P = 0.01$). Initial flowering probability was 75% higher on average for insecticide-treated plants (mean = 0.14) than for control plants (mean = 0.08), although this effect was statistically marginal ($\chi^2 = 3.43$, df = 1, 434, $P = 0.064$).

Although flowering probability decreased significantly as the initial plot seedling density in May 2006 increased ($\chi^2 = 6.78$, df = 1, 434, $P = 0.009$), this relationship was driven by two plots at Triple Creek with unusually high numbers of seedlings (129 and 91 seedlings per plot). When these two outlier plots were excluded, site and seedling density in May no longer contributed significantly to explaining variation in flowering probability (Appendix E).

The number of 2006 seedlings reproducing in 2008 as two-year-olds reflected the numbers of juvenile plants in 2007 (Table 2), and flowering probability showed the same pattern of variation across sites and topographic positions as in 2007. The main effects of site and topography were not significant (both $P > 0.10$); however, a significant site × topography interaction occurred ($\chi^2 = 21.37$, df = 1, 125, $P < 0.001$). Insecticide treatment did not alter flowering probability for 2006

plants as two-year-olds in 2008 (mean rates of flowering as two-year-olds, control, 0.25; insecticide, 0.30; $\chi^2 = 0.43$, df = 1, 116, $P = 0.43$).

Few 2007 experiment plants reproduced as one-year-olds in 2008, and they were restricted to Triple Creek (Table 2). Apart from size, only site affected the probability of flowering that year. There was no significant effect of topography or insecticide (Appendix E).

Herbivory and flowering plant density

For the complete sample (all marked and unmarked plants in experimental plots), we found that insecticide application increased the number of reproductive plants per plot in the next year (Table 3), as well as increasing the flowering probability of tagged plants. For the 2006 experiment, the number of reproductive adults per plot (one-year-olds) in 2007 in the control plots was 0.41 ± 0.10 and in the insecticide treatment was 0.72 ± 0.14; and for subsequently flowering two-year-olds in 2008 the number of reproductive adults per plot in the control plots was 0.52 ± 0.12 and in the insecticide treatments was 1.1 ± 0.22 (significantly higher in insecticide-treated plots than in control plots; likelihood ratio tests of negative binomial GLM for "treatment" term for plants flowering in 2007, LR = 4.02, df = 1, $P = 0.045$; for plants flowering in 2008, LR = 12.01, df = 1, $P < 0.0001$; Table 3). For the 2007 experiment, insecticide treatment again significantly increased the number of flowering plants per plot in 2008 (control, 0.69 ± 0.14; insecticide, 1.2 ± 0.22; LR = 8.42, df = 1, $P = 0.004$; Table 3).

In both experiments, ridges had significantly more reproductive plants than valleys (LR test for treatment

TABLE 3. The total number of flowering tall thistle (*Cirsium altissimum*) plants per site in relation to topographic position and insecticide treatment for the larger sample of all tall thistle plants in experimental plots in both the 2006 and 2007 seed addition experiments.

| Site and treatment | 2006 experiment | | | | 2007 experiment | |
| | 2007 (age 1) | | 2008 (age 2) | | 2008 (age 1) | |
	Ridge	Valley	Ridge	Valley	Ridge	Valley
Triple Creek						
Control	39	11	52	24	79	21
Insecticide	78	23	120	22	118	32
Divoky						
Control	15	7	5	6	7	2
Insecticide	19	5	24	14	13	14
Nine-Mile						
Control	0	0	0	3	0	0
Insecticide	0	1	1	5	0	1
Jack Sinn						
Control	0	1	2	0	0	1
Insecticide	1	0	2	1	0	0
Twin Lakes						
Control	0	0	0	0	0	0
Insecticide	0	0	0	2	0	1

term for all three years, $P < 0.02$; Table 3). Further, there were significant differences in the numbers of plants reproducing among sites (LR test for site term for all three years, $P < 0.001$; Table 3). Triple Creek, followed by Divoky Acres, consistently had the most reproductive plants, in both ridges and valleys.

Cumulative effects of treatments on the number of reproductive adults

The potential cumulative effects of seed addition and insecticide treatment, tested indirectly in two ways because disturbances prevented a direct test, showed that the effect of seed addition was significant. First, the number of rosettes at the end of the 2006 growing season (September) with vs. without seed addition, were: Nine-Mile, 14 vs. 1; Jack Sinn, 35 vs. 3; Twin Lakes, 31 vs. 1. Using this conservative estimate of rosette abundance, seed addition would lead to significantly more adult plants (LR = 34.16, df = 1, 188, $P < 0.001$).

Second, comparable results emerged when we estimated the future number of adults using an analytical projection model. Given the simple monocarpic life history of tall thistle, we know the number of juvenile rosettes equals the potential number of reproductive individuals in future years. However, this number likely overestimates future reproductive effort, as it does not take subsequent mortality and reproductive delay into account. We can evaluate the future number of plants, taking survival and reproductive delay into consideration, by showing that, if

$$n_{t+1} = (1 - p(f_T))p(s_T)n_t$$

or in general

$$n_{t+k} = [(1 - p(f_T))p(s_T)]^k n_t \qquad (1)$$

then the number of reproductive plants from n_0 to infinity is

$$
\begin{aligned}
F_T^{\text{TOT}} &= \sum_{i=0}^{\infty} p(f_T)n_t = \sum_{i=0}^{\infty} p(f_T)[(1 - p(f_T))p(s_T)]^i n_0 \\
&= p(f_T)n_0 \sum_{i=0}^{\infty}[1 - p(f_T)p(s_T)]^i \\
&= \frac{p(f_T)n_0}{1 - [1 - p(f_T)]p(s_T)}
\end{aligned} \qquad (2)
$$

where n_0 is the initial number of juvenile rosettes per plot (September 2006) and $p(s_T)$ and $p(f_T)$ are the mean survival and flowering rates, estimated the from the second (2007 to 2008) transition for 2006 experimental plants, where the subscript T indicates the experiment treatment (control or insecticide). These rates were: $p(s_T) = 0.43$, 0.68 and $p(f_T) = 0.25$, 0.30 for control and insecticide plants, respectively.

Using these survival and flowering rates and the counts of rosettes above, Eq. 2 shows that, taking survival and reproductive delay into account, the highly significant effect of seed addition on the number of established rosettes translates into significantly more adults ($\chi^2 = 43.87$, df = 1, 8, $P < 0.001$; Fig. 4); further, that effect of seed addition was mediated by the impact of insect herbivores on the individual survival and flowering rates. Predicted numbers of adults in control plots that were not protected from the negative demographic impact of herbivory were significantly lower ($\chi^2 = 4.36$, df = 1, 8, $P = 0.036$) than insecticide-treated plots, as a consequence of their lower probabilities of survival and flowering.

Thus, this simple projection model demonstrates that seed addition is expected to lead to significantly more
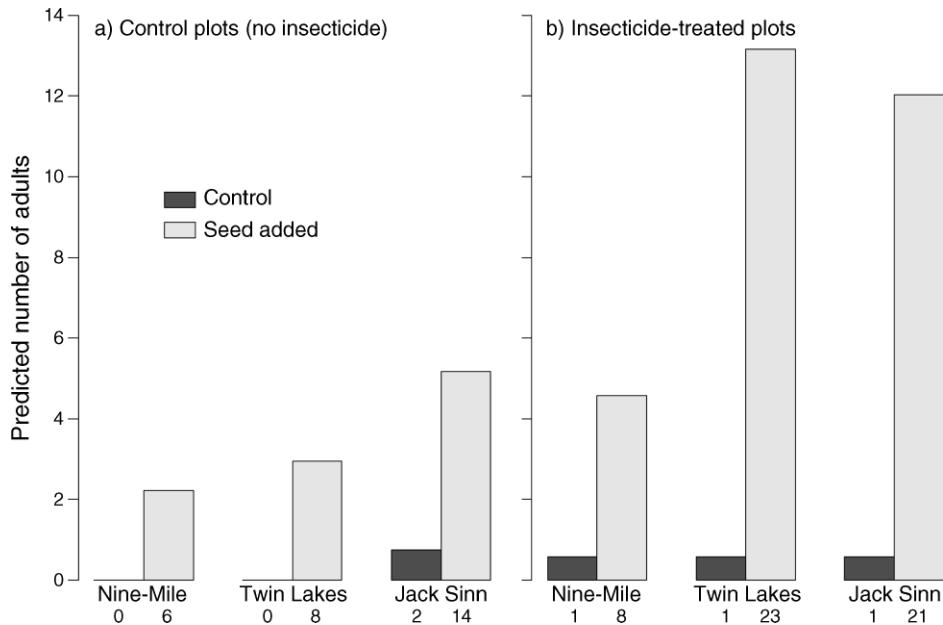
FIG. 4. Effects of seed addition and insecticide treatment on the predicted cumulative number of tall thistle adults at three sites. Bars show the number of rosettes at each site that were present in September 2006 and predicted to transition to adulthood for: (a) control or (b) insecticide plots. Predicted numbers of adults are based on: survival and reproductive rates estimated from the experimental data (Eq. 2), which differ for control and insecticide-treated plants, and on the number of rosettes in control and seed addition plots at each site in September 2006. Values beneath the site names are rosette counts in September 2006. Using this very conservative estimate of adult population size, there is evidence that seed addition translated into increased numbers of adults and that the demographic effects of insect herbivory translate into smaller adult population sizes.

adults in the population (LR = 74.34, df = 1, 188, $P <$ 0.0001), but that the demographic impact of insect herbivores will determine the extent of seed limitation. Given that the only varying rate in Eq. 2 is the per plot number of plants, n_0, the same result would be found by using the number of one-year-old juvenile rosettes to project the cumulative number of adults for the 2007 experiment (based on comparing control and seed addition plots in Fig. 1b, d). Thus, both methods show a strong, positive cumulative effect of seed addition that is significantly enhanced by insect herbivore reduction.

DISCUSSION

The size of a plant cohort at adulthood is limited by a series of environmental filters that act from the time of seed production by the parental generation through juvenile life stages (Harper 1977, Crawley 1997). Our results provide evidence that seed availability, as influenced by insect herbivory, commonly limits tall thistle (*Cirsium altissimum*) cohort sizes and determines adult plant densities in western tallgrass prairie of the central Great Plains, USA. Effects of these environmental filters on tall thistle cohorts were independent of topographic variation in tallgrass ecosystem productivity.

Seed limitation in tall thistle populations

For added seed input to increase cohort size at adulthood, more seed must increase seedling densities and compensatory density-dependent mortality must be

weak. Since site was a fixed effect, our results are specific to these particular sites. Nonetheless, the patterns in our results are illuminating. At three sites in 2006 and at all sites in 2007, seed addition increased tall thistle seedling densities, demonstrating that germination microsites were not limiting at these sites. At Divoky Acres and Triple Creek in 2006, where seedling densities were high and unaffected by added seed, between-year variation in seed limitation must result from variation in the density of the natural seed rain. Hospitable microsites were abundant in both years, as evidenced by high seedling densities both overall and in 2007 in plots where we added seeds. Greater adult tall thistle densities at Divoky Acres and Triple Creek than at the other sites (Table 1) suggest that seed production at these sites may saturate safe microsites, as in 2006. Sparse natural seed rain in 2007 likely reflects large, temporal variation in adult density (Table 1) or in pre-dispersal seed predation (Louda 1998, Louda and Rand 2002). Increases in tall thistle seedling densities after seed addition support models that predict a tight link between seed production and the next year's seedling densities for plants that lack a long-lived seed bank (Crawley 1989, Louda and Potvin 1995).

Three results presented here combine to provide strong evidence that adult tall thistle densities often are seed limited. First, tall thistle juvenile survival was not density dependent, even at the high seedling densities produced by adding 400 seeds/m². Without density-

dependent reductions in survival over the range of seedling densities observed in the field and in the experiment, greater seedling densities will produce greater adult densities.

Second, densities of one-year-old tall thistle juveniles (in 2007 for the 2006 cohort) remained much greater in seed addition plots than in control plots, indicating a clear relationship of subsequent higher densities of juvenile rosettes to seed input.

Third, the analytical approximation showed that, given observed juvenile survival rates, higher juvenile rosette densities will translate into greater adult densities (Fig. 4). Further, in years with less insect herbivory on juvenile plants (such as in 2007 vs. 2006), the increase in adult thistle recruitment, resulting from greater seed input, will be much larger (Fig. 4).

These results add new experimental evidence to the small, but growing list of studies (reviewed by Maron and Crone 2006) that show adult cohort size of short-lived, monocarpic perennial plants, including three other *Cirsium* species (Louda and Potvin 1995, Maron et al. 2002, Rose et al. 2005; J. O. Eckberg, S. M. Louda, and B. Tenhumberg, *unpublished manuscript*) often is limited by seed availability.

Insect herbivory and tall thistle juvenile demography

Whether insect herbivores limit sizes of plant populations has been controversial (Louda 1982, Crawley 1989, Louda and Potvin 1995, Kelly and Dyer 2002, Munzbergova 2005, Maron and Crone 2006, Steets et al. 2007). Insects often are assumed to remove too little plant tissue to reduce survival of established plants (Crawley 1989). Thus, hypothesized mechanisms for insect herbivore limitation of plant population growth typically include reducing seed production in seed-limited populations or killing seedlings (e.g., Louda 1982, 1983, Louda and Potvin 1995, Kelly and Dyer 2002, Maron et al. 2002; J. O. Eckberg, S. M. Louda, and B. Tenhumberg, *unpublished manuscript*). The generality of insect herbivore effects on the transition rate to post-seedling life stages, however, has been questioned because, especially at high seed or seedling densities, juvenile plants killed by herbivores might otherwise die due to negative density-dependent survival (Edwards and Crawley 1999).

Our results suggest a need to revise this conceptual framework. First, insect herbivory did reduce tall thistle seedling survival into their second growing season for both cohorts across a geographically widespread array of sites that included sites with high seedling densities. Second, insects reduced survival of second-year, established tall thistle rosettes (Fig. 3c). This result was striking because established rosettes have substantial root systems that could store or gather resources for a compensatory response. Third, our projection model indicates that higher juvenile thistle survival rates with reduced insect herbivory will translate into larger cohort size at adulthood. Importantly, our study, like most field studies using insecticide, provides a very conservative estimate of insect herbivore effects on plant performance; the insecticide did not eliminate foliage damage, but only reduced it ~20% in most sites and years.

Reducing insect herbivory on seedlings and juveniles increased the subsequent density of reproductive tall thistle in the next year in both our 2006 and 2007 experiments, similar to results for the rare thistle, *Cirsium pitcheri*, in Michigan (Bevill et al. 1999). Increases in adult densities at Triple Creek and Divoky Acres were especially large (Table 1b), mirroring the higher seedling recruitment rates at these sites. Further, these sites had the fastest juvenile thistle growth rates (Appendix F), so the threshold size for flowering (Metcalf et al. 2003) was achieved more quickly. These sites also had higher densities of naturally occurring juvenile rosettes in plots (Table 1), potentially driving the strong response in adult density to insecticide application. Greater density of bolters after insecticide application at Triple Creek and Divoky Acres may reflect increased survival and flowering of naturally occurring juveniles, as well as the marked subset of experimental seedlings. However, it is clear that insect herbivory strongly affects tall thistle population dynamics at juvenile life stages and reduces densities of adult plants.

Because we applied insecticide to entire plots rather than spraying only juvenile thistles within plots, tall thistle performance may have been enhanced by indirect mechanisms, such as effects of insecticide on tall thistle interactions with competing plants and/or the microbial community in a plot. However, for at least three reasons, we think that enhanced performance of tall thistle juveniles in insecticide plots resulted primarily from the direct effects of reduced insect damage. First, we demonstrated that the insecticide reduced folivory on tall thistle. Second, if insect herbivory on tall thistle's competitors was reduced, then we would expect tall thistle, an early-to-mid-successional species, to suffer more intense competition and, thus, to show reduced, not enhanced, performance where insecticide was applied. Third, although tall thistle performance could have been enhanced if the insecticide harmed tall thistle's competitors, we observed no evidence of insecticide phytotoxicity, such as dry, crinkled leaves that only occurred in insecticide plots, when we collected data in experimental plots or applied insecticide. Thus, the results are most consistent with the inference that herbivory has significant direct effects on tall thistle regeneration and dynamics.

Seed limitation and insect herbivory in relation to the productivity gradient

The importance of seed limitation and insect herbivory at juvenile life stages to tall thistle cohort dynamics was independent of topography, despite significant differences in plant community biomass and water stress between ridges and valleys. These results contradict the prediction for mesic grasslands, like tallgrass prairie:

that low light penetration in high-productivity sites will cause seed addition to affect plant densities less in high-productivity than in low-productivity sites (Foster et al. 2004). Here the effect of tall thistle seed addition did not vary with topographic differences in ecosystem productivity at any thistle life stage: seedling, rosette, or, based on the projection model, flowering adult. When plant performance did differ between ridges and valleys, growth was faster in the more heavily vegetated valleys. This outcome is consistent with expectations for juvenile plant dynamics in drier grasslands, where shade reduces water stress (Wilsey and Polley 2003). Because our study sites were at the xeric (western) range limit of tall thistle, plants may better tolerate the lower light levels in productive valleys than the lower, late-summer water potentials on ridges.

Abiotic resource availability can influence herbivore impacts on plant populations by affecting the amount of herbivore damage (Louda 1982, 1983, Louda et al. 1987, Louda and Rodman 1996, Miller et al. 2009) or host plants' tolerance of damage (Maschinski and Whitham 1989, Wise and Abrahamson 2007). However, here the amount of insect damage to juvenile tall thistles did not vary strongly or consistently with position on a physical productivity gradient. Further, similar insect herbivore impacts on juvenile tall thistles on ridges and in valleys suggest that tall thistle tolerance for this relatively constant level of damage did not vary with ecosystem productivity, even though faster rosette growth in valleys indicated more benign conditions there. Although it is intuitive that plant tolerance for damage should increase with abiotic resource availability, tolerance and resource levels may be unrelated if the resource that limits plant performance in the low-resource habitat is not the resource whose acquisition is primarily affected by the herbivory (Wise and Abrahamson 2007). Similar juvenile tall thistle compensatory responses along our topographic productivity gradients may occur because folivory is likely to primarily affect light acquisition, whereas we found greater drought stress for rosettes on ridges, along with faster rosette growth in valleys, suggesting that soil resources limited rosette performance on ridges.

Understanding the combined effects of seed limitation, insect herbivory, and compensatory density-dependent mortality for juvenile plants is critical to predicting the role of herbivory in limiting plant population size. Our results strongly suggest that seed limitation of tall thistle cohort size is widespread, and other work shows that seed is limited by floral herbivory (Louda 1998, Louda and Rand 2002). However, temporal variation in the role of seed availability may be greater in earlier succession sites, where thistle populations are denser, than in mid-successional tallgrass prairies, where established tall thistle populations are characteristic, but relatively sparse (Andersen and Louda 2008). We found that aboveground insect herbivory on seedlings and rosettes consistently reduced juvenile and initial adult tall thistle population densities and these reductions were projected to translate over the long term into lower adult densities. In western tallgrass prairie, compensatory density-dependent mortality did not erase the limiting effects of seed availability, plus insect herbivory at juvenile life stages, on tall thistle population dynamics.

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APPENDIX A

Site mean soil moisture and predawn and midday leaf water potentials (*Ecological Archives* E091-214-A1).

APPENDIX B

ANOVA results for measures of site soil moisture and productivity (*Ecological Archives* E091-214-A2).

APPENDIX C

ANOVA results for leaf damage by insect herbivores (*Ecological Archives* E091-214-A3).

APPENDIX D

The proportion of leaves with any amount of herbivore damage for control and insecticide-treated plants (*Ecological Archives* E091-214-A4).

APPENDIX E

ANOVA results for demographic models (survival, growth, and flowering) for a subset of marked plants (*Ecological Archives* E091-214-A5).

APPENDIX F

Seedling growth between May 2006 and May 2007 for plants in the 2006 seed addition experiment (*Ecological Archives* E091-214-A6).