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Integral projection model of insect herbivore effects on *Cirsium altissimum* populations along productivity gradients

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Abstract. Prediction of the role of native insect herbivores in the population growth and spatial distribution of native plants within the environment remains limited. We developed an integral projection model (IPM) to explore the effect of native insect herbivores on the population dynamics and distribution of the native plant *Cirsium altissimum* (tall thistle), in two different productivity zones in tallgrass prairie in Nebraska USA. Model parameters were extracted from two field experiments: a seed addition experiment that demonstrated seed limitation by insect herbivores on adult recruitment and an insect herbivory exclusion experiment that demonstrated significant herbivore impacts on both rosette performance and adult fecundity. Zones differed in elevation, soil moisture and biomass. Using our model, we asked: (1) does insect herbivory reduce plant population growth rate (λ), (2) does the effect on (λ) differ between productivity zones, (3) does it primarily operate by limiting growth or fecundity and (4) is there evidence for density dependence in mediating impact on (λ)? We found that insect herbivory suppressed tall thistle population growth rate, but the magnitude of this effect did not vary with ecosystem productivity. Insect herbivores' effect on λ arose primarily through suppression of fecundity. We found no evidence of negative density dependence counteracting seed limitation effects of insect herbivory on tall thistle population growth. The similar magnitudes of these effects in different productivity zones eliminate variation in ecosystem productivity as a majority condition in determining insect herbivores' impact in shaping local distribution of this native plant. Overall, the results show that native insect herbivores suppress population growth of this native plant, mediated through seed limitation that functionally determines adult density, without differences related to ecosystem productivity.

Key words: density dependence; insect herbivore; integral projection model; pre-dispersal seed predators; productivity gradient; seed limitation; thistle.

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INTRODUCTION

Determining and predicting the factors that limit the growth of populations is a defining goal of population ecology. Evidence exists that native insect herbivores can limit plant key demographic parameters and, so, population growth (Louda

1982, 1983, Crawley 1989, Louda and Potvin 1995, Kelly and Dyer 2002, Maron et al. 2002, Rose et al. 2005, Miller et al. 2009). For natural enemies like herbivores to limit plant populations, they must reduce plant lifetime fitness, either by significantly reducing survival or seed production. Because plants show strong com-

pensatory ability under some conditions, insect herbivores are considered to have weak effects on plant lifetime seed production (Crawley 1989). Especially for perennial plants, having multiple growing seasons for a compensatory response may minimize the impact of herbivore attack. However, in an increasing number of cases insect exclusion experiments demonstrate strong effects of many insect herbivore guilds in limiting lifetime seed production, including by: folivores (Rausher and Feeny 1980), floral herbivores (“pre-dispersal seed predators”) (Louda 1982, 1983, Louda and Potvin 1995, Kelly and Dyer 2002, Maron et al. 2002), and even root-feeders (Maron 1998). Quantifying the population consequences of insect herbivory requires evaluation of both more interactions and more factors potentially driving variation in interaction intensities.

Potential contributing factors are many and diverse. Several studies demonstrate the role of spatial variation in the magnitude of insect herbivory in determining plant abundances along environmental gradients or between adjacent habitats (Parker and Root 1981, Louda 1982, 1983, Louda et al. 1987a, Louda and Rodman 1996, Miller et al. 2009). Additionally, more subtle effects occur (Maron 1998), such as the smoothing of a species’ distribution along a gradient where resource concentrations predict greater heterogeneity in local population densities. Few experiments have addressed spatial variation in insect herbivore impacts on the host plant population distribution (Louda 1982, 1983, Louda et al. 1987a, Louda and Potvin 1995, Louda and Rodman 1996, Maron et al. 2002, Maron and Kauffman 2006, Miller et al. 2009), but all demonstrate insect herbivory can sometimes be significant in determining population spatial structure.

Circumstantial evidence suggests that such insect herbivore effects on plant population spatial structure may be widespread. First, significant spatial variation in the amount of damage characterizes many insect herbivore-host plant interactions (Parker and Root 1981, Louda 1982, 1983, Louda et al. 1987a, b, c, Louda and Rodman 1996, Rand 2002). Second, abiotic resource availability varies across a range of spatial scales in ecosystems and often mediates plants’ abilities to tolerate tissue loss (Maschinski

and Whitham 1989, Wise and Abrahamson 2005, Knochel and Seastedt 2010). Third, the extent to which plant population sizes are limited by the availability of seed can vary greatly in space (reviewed in Turnbull et al. 2000, Maron and Crone 2006). Factors driving such variation require further experimental evaluation.

Ecosystem productivity is often used as an organizing axis in conceptual models for spatial variation in herbivore impact upon plants (Oksanen et al. 1981, van de Koppel et al. 1996). Variation in productivity likely influences all of the above mechanisms creating spatial variation in insect herbivore abundances and, so, effects on plant populations. For example, variation in abiotic resource availability along productivity gradients can affect plant tissue quality for insect herbivores (Louda et al. 1987a, Crutsinger et al. 2008), and it can drive large differences in plant compensatory ability (Maschinski and Whitham 1989, Wise and Abrahamson 2005). In montane meadows of Colorado USA, Knochel and Seastedt (2010) showed that attack rate of the flowerhead-feeding weevil *Larinus minutus* on the invasive weed, *Centaurea stoebe*, was increased by clipping neighboring vegetation, thereby reducing resource competition, and that tolerance for *L. minutus* damage was least where soil nitrogen was experimentally reduced. Further, bare ground exposure is emerging as a powerful predictor for where and when plant populations will be seed-limited (Turnbull et al. 2000, Maron and Crone 2006); and, bare ground exposure is often correlated with ecosystem productivity. More generally, Shea et al. 2005 demonstrate that plant community context, including competitive environment related to ecosystem productivity, can alter elasticities associated with life-stage transitions impacted by specific insect herbivores and, hence, can lead to large spatial variability in the insect herbivores’ impacts on plant population growth rates. Thus, we hypothesize that ecosystem productivity gradients provide an informative context for understanding spatial variation in insect herbivore effects on plant populations.

Another condition potentially contributing to the variation in the effects of insect herbivores on host plant populations may be existence of density-dependent processes, such as microsite-limitation of safe-sites for recruitment to adult

life-stage (Harper 1977); such processes may prevent any lasting increase in population size even when insect herbivore effects on seed production are reduced. Experimental evidence is accumulating, however, that seed limitation of plant population size may actually be typical for a diverse group of plants varying in life-history (Eriksson and Ehrlén 1992, Turnbull et al. 2000). Still, the cumulative evidence to evaluate the arguments for and against the effects of insect herbivores on population growth of their host plants is sparse; studies that use experimentally determined parameters quantifying herbivory by native insects to develop predictive models of the demographic consequences of interaction for plant population growth are rare (see, e.g., Maron and Kauffman 2006, Miller et al. 2009).

We used two years of data from a seed addition experiment and three years of data from an insect herbivore reduction experiment to develop an integral projection model to examine variation in insect herbivore effects on population growth of a native, monocarpic thistle, tall thistle (*Cirsium altissimum*), in two different ecosystem productivity zones in the tallgrass prairie region of eastern Nebraska USA. Detailed analysis of the seed addition experiment results showed (Russell et al. 2010): significant variation in demographic parameters between sites, significantly increased demographic rates for juvenile thistles when insect herbivory was reduced with insecticide, and long-term seed limitation of tall thistle adult densities at most sites. Thus, in this study, we focused here on how the difference in λ with and without herbivory varied in magnitude across the gradient.

We asked four questions: (1) Does insect herbivory, by all of the aboveground feeding guilds combined, reduce the asymptotic growth rate of tall thistle populations? (2) Does the presence or magnitude of insect herbivore effects on population growth rate differ between lower productivity zones (ridges) and higher productivity zones (valleys) along local topographic gradients? (3) Do herbivore impacts on population growth largely result from the effect of insect herbivory on tall thistle growth or on fecundity? (4) Is there evidence of density dependence in population growth rates countering the effects of increased seed with decreased herbivory? The results provide new evidence to understand and

predict the still under-explored conditions under which native insect herbivores affect plant population dynamics and spatial structure.

METHODS

Study system

The biology of *Cirsium altissimum* (tall thistle) is described in Russell et al. (2010). Tall thistle is a native, monocarpic, short-lived perennial species that occurs in moderately disturbed areas in grasslands and woodlands of eastern North America (Great Plains Flora Association 1986). Our study sites in eastern Nebraska are near the western range limit of both tallgrass prairie and tall thistle (Kaul et al. 2006). Tall thistle is the most common native thistle in these grasslands (Andersen and Louda 2008). In our region, juveniles (rosettes) take one to four or more years to reach reproductive size (F. L. Russell, unpublished data). In their flowering year, they begin producing a reproductive stalk (bolting) in May, and flower heads open and mature in August through September. Seed dispersal begins about three weeks after flowering. Flowering is fatal, as with other monocarpic species. Seed germination and seedling establishment occur primarily in the following spring, after over-wintering as seed.

Takahashi (2006) quantified the main insect folivores of tall thistle rosettes and adults in this region. The main foliage feeders observed were: grasshoppers and lepidopteran larvae, especially those of the Painted Lady butterfly *Vanessa cardui* L., which chewed leaves; adult beetles, including *Systema hudsonias* Forster and *Baris* nr. *subsimilis* Casey, which scraped epidermis and mesophyll tissue or chewed holes in stems and leaf blades; and, leafminers, which mined leaf midribs, often killing the leaf. The main insect floral herbivores were: the artichoke plume moth *Platyptilia carduidactyla* Riley, which mined floral meristem tissues of the new branches, and two internal flower head-feeders: the tephritid fly *Paracantha culta* Weidemann, and the pyralid moth *Homoeosoma eremophasma* Goodson and Neunzig. All are typical, native, thistle-feeding genera.

Field methods

Study sites.—The parameters needed were extracted primarily from two experiments con-

ducted at five eastern Nebraska tallgrass prairie sites (Divoky Acres, Jack Sinn, Triple Creek, Twin Lakes, Nine-mile Prairie (see Russell et al. 2010 for detailed site descriptions)). We attempted to estimate productivity differences at each site \times topography combination by quantifying soil moisture content, drought stress and biomass. Soil moisture by volume on the ridge and in the valley at each site was measured on July 14–17, 2006 and July 17–23, 2007 (>2 d after the last rain), using a Time Domain Reflectometer (TDR; Model 100, Spectrum Technologies, Plainfield, IL), 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 (Ken Dewey, Applied Climate Sciences, University of Nebraska-Lincoln, www.lincolnweather.org)).

Aboveground standing crop plant biomass on ridges and in valleys at each site was quantified August 29–31 and September 19–20, 2008. In August, living plant biomass was clipped at ground level in a 50 cm \times 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 cm \times 50 cm frame located 1 m east of the middle of the selected blocks was harvested. Biomass was dried at 60°C for 72 hours before weighing. We predicted that ridge habitats would be drier and support less biomass than valley habitats in the same study site. From here on we refer to “productivity zones” (ridges = “low” productivity, valleys = “high” productivity) to reflect topographic differences in biomass and soil moisture, as well as elevation (the statistical significance of these differences is described in the Results section).

Experimental design.—In the first experiment, which was initiated in two years (2006, 2007), we used a factorial design to quantify variation in seed limitation of tall thistle seedling establishment and insect herbivores’ effects on seedling growth and survival along the gradients (see Russell et al., 2010). The experiment involved three treatments: seed addition (100 seeds added vs. no seeds added in 50 cm \times 50 cm plots), insect herbivory reduction (non-systemic insecticide

[bifenthrin] vs. water-only spray), and productivity zone (low vs. high) defined by topographic position. All tall thistle plants per plot in both years were counted by life-stage in spring and in fall from initiation (2006 or 2007) to May 2009 at all sites that remained undisturbed. In addition, survival, growth and herbivory were recorded on up to four marked seedlings per plot.

In the second experiment, we quantified the effect of insect herbivores on survival and growth of naturally-occurring, established tall thistle rosettes and on fecundity of tall thistle adults. We applied three insect herbivory treatments to naturally-established tall thistle individuals (juvenile rosettes, bolting adults) in both productivity zones (low vs. high). The treatments were: insecticide (bifenthrin)-in-water spray, water-only spray control, and unsprayed total control. The experiment was initiated in 2005 at two of the sites: Nine-mile and Triple Creek, and expanded in 2006 and 2007 to all five study sites (site descriptions, locations, and management in Russell et al. 2010).

In low and high productivity zones corresponding to ridge and valley topographies at each study site, at 5 m intervals along a transect we tagged the nearest tall thistle individual as an experimental plant; the only constraint was that tagged plants had to be >2 m apart to reduce any insecticide drift effects. Rosettes and adults were sampled along separate transects. Different plants were tagged in each year. In 2005, we extended transects until we tagged 100 rosettes and 50 adults in each topography at each site. In 2006 and 2007, we extended transects until we tagged 40 rosettes and 20 adults in each zone, except in sparse tall thistle populations (two sites) or where we encountered the property boundary or ran out of the ridge or valley habitat. Sample sizes for rosettes across all sites combined were (low, high productivity zone): 183, 195 in 2005; 183, 159 in 2006; and 133, 101 in 2007. For bolting plants (adults), sample sizes across all sites combined (low, high productivity zone) were: 74, 85 in 2006; and 70, 75 in 2007. We do not report 2005 data since some flower heads were collected after seed dispersal had started.

We used a size-stratified randomization to assign plants to levels within the insect herbivory treatment. Specifically, for productivity zone at each site, we ordered rosettes and, separately

adults, according to initial root crown diameter and within pairs of plants that were closest in size one plant was randomly assigned to receive insecticide and the other remain as a control. Subsequently, each “control” plant was randomly assigned to “water-only spray control” or “no-spray control.” Plants in the insecticide-in-water (reduced insect herbivory) treatment were sprayed at 2–3 week intervals with the non-systemic insecticide Bifin I/T using a dilution rate of 15.9 ml Bifin I/T per liter water. “Water control” plants were sprayed with an equal volume of water. Plants were sprayed from late June through the end of the growing season in early October. To avoid harming pollinators, individual flower heads were not sprayed while that flower head had colored florets.

To quantify insect folivory on rosettes and adult plants, we counted the number of green leaves per plant, the number of green leaves that had any evidence of folivore damage, and the number of green leaves that were damaged over >30% of their surface area each June and October. To quantify insect damage to adult reproductive tissues in the field, we counted lateral branches and lateral branches with mined apical meristems as well as flower heads initiated and flower heads that showed external evidence of insect damage per plant. These data were recorded in June and in September/October, at year-end, when the first post-anthesis flower head on a plant was collected (2006) or bagged to prevent seed dispersal (2007). We did not systematically sample insects from the tall thistles on ridges vs. in valleys, so we do not have estimates of the relative densities of individual herbivore species in the different topographic/productivity positions. Nevertheless, qualitative observations of the insect herbivores present suggested that the common flower head feeding, meristem mining and folivore insect species were the same in both positions. Further, although the amount of damage to plants differed somewhat between topographic positions, there were no forms of tissue damage (e.g., edge-chewing of leaves vs. leaf mid-rib mining vs. scraping of holes through leaves) that were unique to a particular topographic/productivity position.

To quantify rosette and adult size, root crown and rosette diameters were measured in June and October. In the field, to quantify reproductive

effort and success of adults, we counted both the number of flower heads initiated and the number of flower heads that flowered (exserted colored florets) per plant. Each of the five sites was visited 1–2 times per week to collect or bag flower heads. Heads that flowered were collected for dissection, except when flower heads had substantially dispersed their seeds between visits to the site. In 2006, post-anthesis flower heads (florets dried) that were near seed dispersal, evidenced by a change in shape from flask- to U-shaped, were collected (80.2% of flowering heads collected: 293 of 365 heads from 92 plants of 112 with flowering heads). In 2007, post-anthesis flower heads were covered in an organza fabric bag and collected when seed dispersal into the bag began (48.2% of flowering heads collected: 234 of 485 heads from 70 plants of 92 with flowering heads). We dissected the collected heads and scored internal damage by insect herbivores and counted undamaged, filled seeds. These seeds had high viability rates (>75%) in tetrazolium tests (F. L. Russell, unpublished data).

One parameter not available from these experiments was over-winter seed loss. We estimated this mortality from the literature. Published estimates varied widely (between 0–100% seed loss) across many factors, including the plant species, habitat, and trophic level of the seed predator (e.g., Table 6.2 in Crawley 1992). Many estimates were based on very short-term (e.g., 1 wk) observations. However, longer-term loss (over 150 d) of seeds to predators for *Cirsium vulgare* (Savi) Ten., a tall thistle congener, was 60% in the dune system in Holland (de Jong and Klinkhamer 1986). Seed loss of *Carlina vulgaris* Linnaeus, another European grassland thistle, to post-dispersal seed predators was estimated to be between 83–90% (Greig-Smith and Sagar 1981). Further, nearly all grass seed set out in dishes in Oklahoma tallgrass prairie (99%) was lost to predators (Haught and Myster 2008). Based on these studies, we set over-winter seed loss at 70%, an intermediate value, making seed survival, p_{ssr} equal 0.30.

Analysis of variation in herbivory by treatment and topographic type

Did our insecticide application reduce damage to plants? For seedlings, our seed addition experiment showed 20% reduction in the pro-

portion of leaves damaged with insecticide application (Russell et al. 2010). For individual juvenile rosettes and bolting adults, we used results from the insecticide experiment to evaluate the efficacy of insect exclusion and to quantify differences in insect damage between productivity zones (Appendix A). Seasonal cumulative effect of insecticide treatment was represented by treatment vs. control levels of damage to plants in October each year. Damage to vegetative structures was estimated as (number of damaged leaves/number of undamaged leaves per plant). Reproductive damage was estimated as both (1) (number of flower heads damaged/number of undamaged flower heads produced), and (2) (number of primary branch meristems mined/number of primary branches unmined). Damage measures were analyzed using GLMs with a log link function and binomial errors. The explanatory variables for each model were: insecticide treatment (insecticide/control), productivity zone (low/high) and individual size (root crown diameter (mm) natural log transformed). Statistical models were implemented in R version 2.8.0 (R Development Core Team 2008).

Integral projection model

We used an integral projection model (IPM: Easterling et al. 2000, Rose et al. 2005, Ellner and Rees 2006) to evaluate if, and how effects of insect herbivory on individuals translate to effects on tall thistle population dynamics. The IPM is an integro-difference equation that predicts population growth in discrete time by integrating demographic contributions across all plant sizes. These models consist of continuous functions that describe size-dependent survival, growth, and fecundity. Full details of the model and its underlying functions are in Appendix B. We fit all IPM functions to the natural logarithm of plant size. IPM construction and analysis were conducted in R Version 2.8.0. (R Development Core Team 2008). For each site, we used AIC-based model selection methods (Burnham and Anderson 2002) to determine if the shapes of the survival and growth functions differed between herbivory treatments, productivity zones, or both. Models that are either a poor fit to the data or are parameter-heavy have higher values for AIC; and, ΔAIC , the difference in AIC between models, indicates the statistical merit

of competing models. Model fitting details are in Appendix B. We pooled data for the three inter-annual transitions (two for fecundity) to represent a single t to $t + 1$ time step, as in other studies where multiple years of demographic data are available but insufficient to fit a stochastic IPM (e.g., Easterling et al. 2000, Rose et al. 2005, Ellner and Rees 2006, Kolb et al. 2007, Miller et al. 2009). However, we did analyze the demographic response for each site separately, since we had evidence of large between-site variation in the demographic rates (Russell et al. 2010). Furthermore, this allowed us to explore the relationship between site mean density of tall thistles and λ , across sites, at a later stage.

Demographic consequences of herbivory and its effect on growth vs. fecundity

Following Miller et al. (2009), we calculated the total demographic effect of insect herbivory as the difference in λ between the insecticide and control treatments ($\Delta\lambda_{ij} = \lambda_{Iij} - \lambda_{Cij}$), for each site i and productivity zone j . We also partitioned this difference between effects on plant growth versus effects on fecundity by calculating λ when either the fecundity function ($f(y, x)$) or the growth function ($g(y, x)$) in the insecticide kernel was replaced with the corresponding function from the control treatment. This generated expected population growth rates for each site i and zone j , if the effects of herbivory were restricted either to plant growth (λ_{Gij}) or to plant fecundity (λ_{Fij}). The differences between each of these values and the control value $\Delta\lambda_{ij}$ represent, for each site and zone, the independent demographic effect of herbivory that reduces growth, $\Delta\lambda_{Gij}$, and of herbivory that reduces fecundity $\Delta\lambda_{Fij}$. Any remainder in the total demographic effect, once these independent effects are accounted for, represents the joint, synergistic effect ($\Delta\lambda_{Xij}$) of insects simultaneously reducing plant growth and fecundity. These relationships can be summarized as:

$$\Delta\lambda_{ij} = \lambda_{Iij} - \lambda_{Cij}$$

$$\Delta\lambda_{Gij} = \lambda_{Iij} - \lambda_{Gij}$$

$$\Delta\lambda_{Fij} = \lambda_{Iij} - \lambda_{Fij}$$

$$\Delta\lambda_{Xij} = \Delta\lambda_{ij} - (\Delta\lambda_{Gij} + \Delta\lambda_{Fij}).$$

Table 1. Site mean soil moisture (% by volume) and biomass (g/m²) of ambient vegetation (SE) by site and topographic position.

Site	Position	Soil moisture (%)				Biomass (g/m ²)	
		2006		2007		2008	
		Mean	SE	Mean	SE	Mean	SE
Nine Mile	Ridge	9.2	0.5	19.6	1.4	332.5	30.6
	Valley	9.1	0.4	22.3	1.2	485.2	83.2
Triple Creek	Ridge	13.1	1.4	8.8	0.5	369.8	67.0
	Valley	18.7	2.2	13.8	2.0	516.4	85.7
Divoky	Ridge	28.2	4.0	15.1	0.6	610.7	42.4
	Valley	25.3	1.3	16.4	1.5	847.9	93.0
Jack Sinn	Ridge	29.6	2.4	31.8	2.9	276.5	44.2
	Valley	35.7	3.0	43.9	1.4	305.1	35.8
Twin Lakes	Ridge	33.3	3.7	31.4	1.4	287.2	20.1
	Valley	25.5	2.4	27.5	1.7	265.9	8.9

RESULTS

Topographic and site differences in soil moisture and productivity

Whilst variation in soil moisture between topographic positions was more complex than a straightforward contrast between valleys and ridges (Table 1), differences in moisture and biomass were in the direction expected and the main effect of topography significantly explained variation in biomass (Table 2). Valleys were moister than ridges at three sites and equal at one (such that the site \times topography interaction was highly significant), in addition valleys supported significantly more biomass per m² in general than did ridges (Table 2). In exception to this, the Twin Lakes site had greater biomass and higher soil moisture content on ridges than in valleys, in contrast to the other four sites (Table 1).

Variation in insect herbivore damage by site

Detailed results for variation in insect herbivore damage are presented in Appendix A. To summarize, insecticide reduced field estimates of damage by folivores, meristem miners and flower head feeders by about 20–30%. For each of these guilds, models that included insecticide treatment as an explanatory variable fit significantly better than models that did not include insecticide application. Productivity zone significantly contributed to explaining variation in damage by the flower head guild and the meristem-mining guild. These results support our use of insecticide treatment as an explanatory factor in the IPMs developed below.

Observed population densities

Our five study sites varied widely in their apparent population dynamics (Table 3). Both Triple Creek and Divoky Acres supported very high densities of tall thistle in 2006, these had decreased more than fourfold by 2007, and then remained constant. In contrast, the three other sites (Jack Sinn, Twin Lakes and Triple Creek) supported very low densities of tall thistles throughout the study period. There was no clear association between productivity zone and tall thistle density; at Triple Creek the highest density was in the low productivity zone whilst the opposite was the case at Divoky (Table 3). At the three remaining sites, no obvious difference between zones in tall thistle density was apparent.

Table 2. ANOVA results for measures of site soil moisture and productivity: soil moisture, in response to variation in site (1:5), year (2006, 2007) and topography (ridge, valley); and biomass, measured in 2008, in response to variation between sites (1:5) and topography (ridge, valley).

Effect	df	F	p
Soil moisture (%)			
Site	4, 175	10.55	<0.0001
Year	1, 175	2.73	0.10
Topography	1, 175	2.66	0.10
Site \times Topography	4, 165	8.25	<0.001
Site \times Year	4, 165	23.53	<0.0001
Biomass (g/m ²)			
Site	4, 49	19.51	<0.0001
Topography	1, 49	8.68	0.005
Site \times Topography	4, 49	1.61	0.19

Table 3. Mean (SE) natural densities per m² of tall thistle (*Cirsium altissimum*) at the five study sites based upon counts in control (no seed addition, no insecticide) plots in May 2006–2009. In 2006, the first year of the study, we only had counts of juveniles (seedlings + rosettes). For 2007–2009 we counted juveniles and flowering adults (destruction of plots due to land management actions at Jack Sinn and Twin Lakes prevented their being sampled in 2009).

Site	Zone	Statistic	2006	2007		2008		2009	
			Juveniles	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
Triple Creek	Low	Mean	153.0	33.25	14.25	8.0	18.25	0.5	0.0
		SE	37.72	9.03	3.2	3.01	3.99		
	High	Mean	47.0	7.0	2.75	3.5	4.0	0.0	0.0
		SE	21.8	1.73	1.3	1.2	1.03		
Divoky Acres	Low	Mean	19.0	6.0	3.5	3.25	2.75	1.0	0.0
		SE	9.0	1.97	1.36	1.28	1.38		
	High	Mean	56.6	9.5	1.25	5.25	0.25	0.5	0.0
		SE	35.8	4.71	0.79	2.77	0.25		
Jack Sinn	Low	Mean	0.0	0.25	0.0	0.25	0.25
		SE	0.0	0.25	0.0	0.25	0.25		
	High	Mean	0.5	0.25	0.25	0.75	0.0
		SE	0.5	0.25	0.25	0.4	0.0		
Nine Mile	Low	Mean	0.33	0.0	0.0	0.0	0.0	0.0	0.0
		SE	1.33						
	High	Mean	0.0	0.4	0.0	0.2	0.0	0.0	0.0
		SE	0.0	0.275		0.2	0.0		
Twin Lakes	Low	Mean	0.0	0.0	0.0	0.25	0.0
		SE	0.0			0.25	0.0		
	High	Mean	0.0	0.25	0.0	0.25	0.0
		SE	0.0	0.25		0.25	0.0		

Demographic functions in relation to productivity zone and insecticide treatment by site

The size-related survival function $p_s(x)$ varied between zones and treatments, except for one site (Jack Sinn) (Table 4). For four of the five sites, the best model included productivity zone- and insecticide treatment-specific parameters (Table 4). For Jack Sinn, the best model was the one with average effects for both zone and treatment; however, this model was not statistically distinguishable ($\Delta\text{AIC} < 2$) from the full model with both treatment and zone varying. Given these results, as an initial approximation, we parameterized the IPM with the fully varying model for all five sites. Zone and treatment specific size-related survival functions are plotted in Russell et al. (2010). The treatment- and zone-specific survival parameters used to parameterize the IPM kernel for each site are in Table 5.

The growth function, $g(x, y)$, varied somewhat between zones and treatments. For three of the five sites, the GLM with treatment- and zone-specific parameters was substantially better than models with parameters held constant across zones and treatments (Table 4). Growth was significantly faster in the high productivity zone

than in the low productivity zone, although the absolute difference was small (data plotted, averaged across all sites, in Russell et al. 2010). The candidate GLM that best fit the data for Divoky had varying zone and constant treatment parameters, whilst for Twin Lakes constant zone and varying treatment parameters provided the best fit. Again, since the magnitude of the difference between the candidate models was small among the sites ($\Delta\text{AIC} < 2$), we fit the fully varying model to the data for all five sites (parameter values in Table 5).

For four out of five sites, the size-related flowering function was substantially improved by allowing the insecticide treatment and zone parameters to vary, compared to models with common intercepts (Table 4). For the remaining site (Jack Sinn), the GLM model with a single common intercept was best supported by the data (Table 4). The lack of significant treatment or zone effects at Jack Sinn could be explained in part as a sample size effect as very few reproductive individuals were observed at this site throughout the study (<2 per site/zone/year: Russell et al. 2010).

Finally, the fecundity function, $f_n(x)$, was

Table 4. Candidate models of tall thistle demographic functions (survival, growth, and flowering) with results of model fitting AIC values. Individual probabilities of survival and flowering, and growth rate, were modelled in response to variation in: site, productivity zone (low, high) and insecticide treatment (insecticide, control). Demographic rates were analysed for each site independently, given evidence of strong between site differences. The model that best explains data for each rate at each site is bolded.

Model	Twin Lakes	Divoky	Jack Sinn	Nine Mile	Triple Creek
Survival					
Logit(survival) = $b \times size_t$	142.2	127.0	184.6	306.2	407.6
Logit(survival) = $a_i + b \times size_t$	135.3	124.4	186.6	301.8	399.6
Logit(survival) = $a_j + b \times size_t$	130.6	118.8	184.7	302.6	389.9
Logit(survival) = $a_{ij} + b \times size_t$	122.9	116.2	186.5	298.2	381.6
Growth					
Size _{t+1} = $b \times size_t$	-121.8	-109.2	-92.6	-408.4	-219.1
Size _{t+1} = $a_i + b \times size_t$	-124.6	-107.3	-95.2	-432.0	-229.2
Size _{t+1} = $a_j + b \times size_t$	-119.8	-112.7	-96.7	-428.7	-220.8
Size _{t+1} = $a_{ij} + b \times size_t$	-122.6	-110.8	-98.3	-455.9	-231.0
Flowering					
Logit(flowering) = $b \times size_t$	130.8	158.9	171.2	423.0	424.2
Logit(flowering) = $a_i + b \times size_t$	123.9	158.7	172.1	403.8	414.1
Logit(flowering) = $a_j + b \times size_t$	127.7	151.6	173.1	408.6	406.3
Logit(flowering) = $a_{ij} + b \times size_t$	120.6	151.5	174.0	388.9	395.8

Notes: Subscripts i and j represent productivity zone (low, high) and insecticide spray treatment (insecticide, control).

positively related to individual size (LR statistic = 4.03, $p = 0.045$). In addition, insecticide treatment had a highly significant effect, increasing realized fecundity dramatically (Fig. 1). For example, an insecticide-treated individual with the mean log size (2.40) produced on average almost five times more seed (197 seeds) than a control plant of the same size (44 seeds). The model with the lowest

AIC included size and separate intercepts for insecticide treatments (AIC = 1713.45). Although mean seed production (SE) was higher in the high productivity zone, 286.4 (161.9), than in the low productivity zone, 174.1 (36.8), this difference was not statistically significant ($\Delta AIC < 2$). Thus, we used the most parsimonious model, the one with size- and treatment-specific effects,

Table 5. Treatment (C = control, I = insecticide treated) and zone (Low = low productivity, High = high productivity) specific intercepts underlying the survival and growth functions in the IPM kernel by site. The intercept represents the mean value for each level; so, direct comparison can be made between coefficients for different sites, zones, and treatments. Thus, for example, the more negative an intercept is, the lower the rate is for that particular site/zone/treatment combination. Probability of seed establishment, p_E , was calculated as the mean per plot of (number of seedlings [seed added treatment] – number of seedlings [control treatment]) / number of seed added per plot [100], for both zones in each site (see Methods for details). The size-related seed production function did not vary between sites, parameter values can be found in Fig. 1.

Site	Survival intercept				Growth intercept				p_E			
	Low		High		Low		High		Low		High	
	C	C	I	I	C	C	I	I	Mean	SE	Mean	SE
Triple Creek	-2.12	-1.00	-1.32	-0.21	1.50	1.65	1.78	1.93	0.11	0.024	0.05	0.013
Jack Sinn	-0.39	-0.85	-0.22	-0.68	0.92	1.18	1.14	1.40	0.07	0.015	0.06	0.012
Nine Mile	0.17	0.89	0.92	1.65	1.67	1.94	1.95	2.22	0.06	0.012	0.02	0.008
Divoky	1.23	-0.35	2.27	0.69	1.70	1.43	1.74	1.47	0.01	0.004	0.01	0.003
Twin Lakes	3.72	1.93	5.19	3.39	1.32	1.29	1.55	1.53	0.02	0.004	0.01	0.005

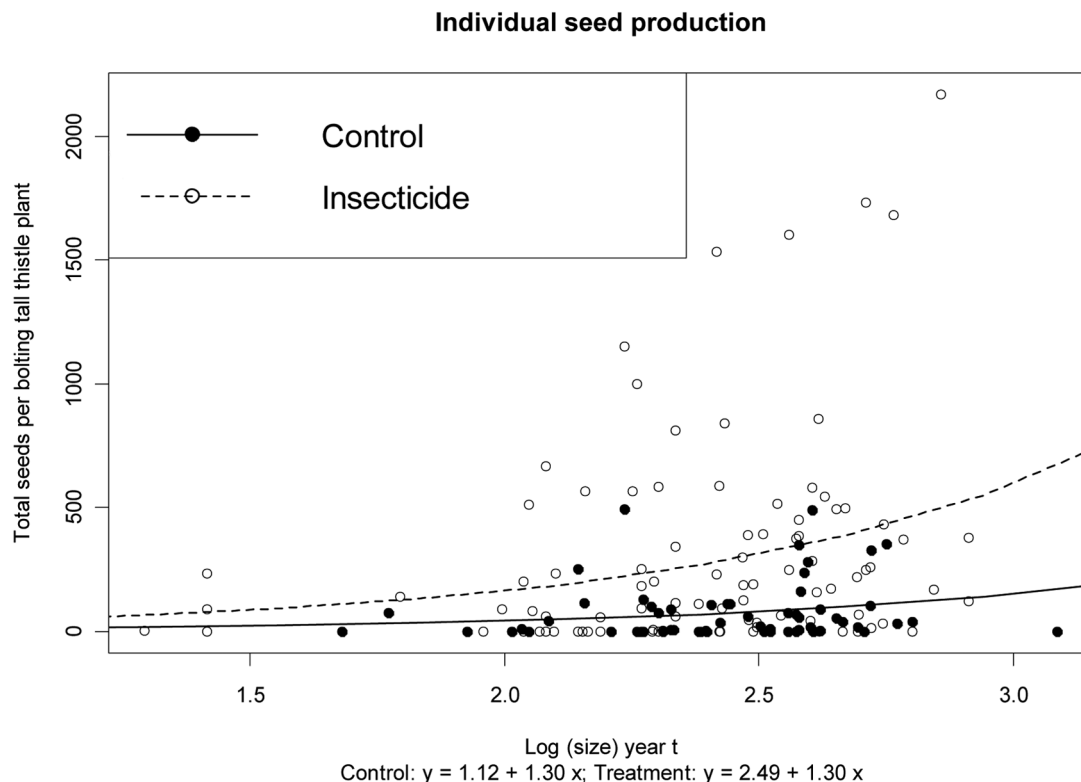


Fig. 1. Size-dependent fecundity in *Cirsium altissimum* (tall thistle) showing the effects of insecticide treatment (control, insecticide applied) on individual seed production. Fecundity was estimated for a sample of plants whose heads were collected and dissected (see Methods). Productivity zone did not significantly enter the GLM of fecundity (details in text).

to parameterize the fecundity function for all five sites, i.e., the fecundity function in the IPM did not vary between sites (Table 5).

Spatial variation in seedling establishment

Seed establishment probabilities for each site, p_E , were estimated from our seed addition experiment (Russell et al. 2010). The site means (SE) ranged from 0.01 (0.004) at Divoky to 0.11 (0.024) at Triple Creek (Table 5). At all sites except Nine Mile, establishment rates were 2–5× greater in the low productivity zone than in high productivity zone (Table 5). Seed probability of establishment p_E varied significantly between sites ($F_{4,158} = 11.24$, $p < 0.0001$) and between productivity zones ($F_{1,155} = 9.82$, $p = 0.002$).

Herbivory treatment and productivity zone effects on population dynamics

Using the experimentally-derived demograph-

ic functions (above) to construct an IPM kernel, with and without herbivory, for each productivity zone at each site, we calculated asymptotic population growth rates (λ) for each site × zone × treatment combination (Table 6). Although site population growth rates for treatment control plots varied, they were generally consistent with thistle densities observed at each site over the study (Table 3). The positive effect on λ of reducing insect damage was obvious. The difference between treatments ($\Delta\lambda$) was >0 at every site, ranging from 0.3 (Twin Lakes, Low zone) to 1.2 (at both Divoky and Triple Creek, High zone; Table 6). These results demonstrate that insect herbivory substantially decreased population growth rate at all sites.

Productivity zone effects on λ varied between sites (Table 6). At two sites (Twin Lakes, Divoky), λ was slightly higher in the low productivity zone than the high one. At one site (Jack Sinn), λ

Table 6. Density independent asymptotic rates of population growth (λ) in relation to productivity zone (low/high) and insecticide treatment (insect herbivores present/excluded by insecticide), for each study site; $\Delta\lambda$ measures the difference in λ between levels of the insecticide treatment at each productivity zone.

Site	Zone	λ Insects present	λ Insects excluded	$\Delta\lambda$
Twin Lakes	Low	0.8	1.1	0.3
	High	0.5	1.0	0.5
Divoky	Low	0.9	2.9	1.1
	High	0.8	2.0	1.2
Jack Sinn	Low	1.0	1.8	0.8
	High	1.1	2.0	0.9
Nine Mile	Low	1.1	1.6	0.5
	High	1.6	2.1	0.5
Triple Creek	Low	1.2	2.2	1.0
	High	2.2	3.4	1.2

was roughly equivalent in both zones; and at two sites (Nine Mile, Triple Creek), λ was higher in the high productivity zone than in the low one. In an ANOVA with λ as the response variable and treatment (2 levels) and zone (2 levels) as independent variables, spray treatment effects were highly significant ($F_{1,16} = 9.24$, $p = 0.008$) in explaining differences in λ . In contrast, productivity did not significantly explain differences in estimates of λ ($F_{1,16} = 1.30$, $p = 0.27$). Also, the zone \times treatment interaction was not significant ($F_{1,16} = 0.05$, $p = 0.82$), despite the fact that $\Delta\lambda$ was around 20% larger in the high productivity zone than the low productivity zone at three of the five sites (Table 6).

Partitioning the reduction in λ due to insect herbivory into effects on growth (λ_G) or on fecundity (λ_F), or on both jointly ($\Delta\lambda_X$), for sites and zones showed that the difference in λ between treatment and control plants was driven primarily by the effects of insects on fecundity (Fig. 2a, b). This result was consistent across sites and zones (Fig. 2a, b). Although reductions in growth λ_G were small, they were about twice as important in the low productivity zone as in the high productivity zone at each site. The joint reduction in growth and fecundity by herbivory ($\Delta\lambda_X$) was much less important than the reduction of growth (λ_G) or of fecundity (λ_F) separately. However, large synergistic effects occurred at two sites: Triple Creek (both zones: Fig. 2a, b) and Twin Lakes (High zone only: Fig. 2b), and a

very small synergism occurred at Jack Sinn (both zones: Fig. 2a, b). Finally, site-by-site, the joint impact on both growth and fecundity by insect herbivores ($\Delta\lambda_X$) appears to have been more important in the high productivity zone than in the low productivity zone.

Evaluation of density dependence of population growth rate

We found no relationship between λ and site mean population density in either productivity zone (Fig. 2c, d), with density measured as all juveniles (seedlings + rosettes) in 2007 and 2008. In both zones, the site with highest λ (Triple Creek) was the site with the highest thistle densities (Fig. 2c, d). Thus, the data provide no evidence of density dependence underlying the estimates of λ .

DISCUSSION

To limit plant populations, insect herbivory must reduce lifetime seed production (maternal fitness) and the resulting lower seed input must not alleviate density-dependent performance. Insect herbivory had a strong, negative influence on lifetime seed production of the monocarpic, perennial tall thistle, *Cirsium altissimum* (Fig. 1). We found no evidence of negative density dependence (Fig. 2c, d), so these effects on seed production translated directly into significant decreases in asymptotic population growth rate at all five sites, with $\Delta\lambda$ varying from 0.3 to 1.2 (Table 6). We conclude that insect herbivory is limiting tall thistle population growth in the western tallgrass prairie region in the central Great Plains. These results add to a growing, but still short, list of studies that provide evidence for the limitation of plant populations by insect herbivory (e.g., Louda 1982, 1983, Louda and Potvin 1995, Fagan and Bishop 2000, Kelly and Dyer 2002, Maron et al. 2002, Rose et al. 2005, Miller et al. 2009).

Effect of insect herbivory on seed production and maternal fitness

Above-ground insect herbivory greatly reduced tall thistle (*C. altissimum*) maternal fitness, quantified as λ , as observed for congeners Platte thistle (*Cirsium canescens*) in sand prairie (Louda and Potvin 1995, Rose et al. 2005) and cobweb

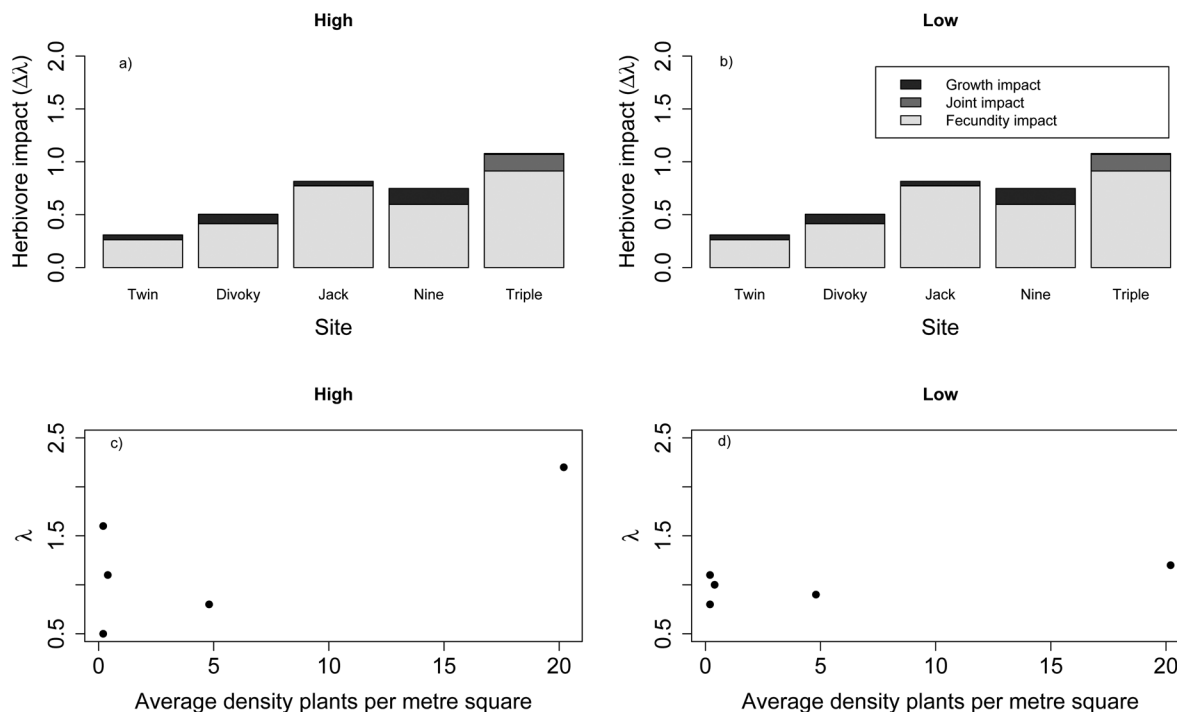


Fig. 2. The relative effect on λ of insect herbivore impacts on growth and fecundity, for plants growing in (a) High (valleys) and (b) Low productivity (ridge) zones at each site. The change in λ is partitioned into the independent effects of insect herbivores on plant growth $\Delta\lambda_G$ and fecundity $\Delta\lambda_F$, and the joint synergistic effect $\Delta\lambda_X$ on both growth and fecundity. See text for more details. We tested for density dependent effects on population growth rate in the (c) High and (d) Low productivity zones by plotting site estimates of λ against site mean (average of 2007 and 2008) density of juvenile plants. Juvenile plant densities are in Table 3.

thistle (*C. occidentale*) in coastal dunes in California (Maron et al. 2002). All of the fitness components that we measured were reduced, however herbivore effects on the size-fecundity relationship were primarily responsible for decreased λ . The importance of insect herbivore-mediated changes in tall thistle fecundity to reducing lifetime seed output is consistent with findings from sensitivity analyses of matrix models for short-lived monocarpic herbs, which often show high sensitivity to changes in fecundity (Franco and Silvertown 2004).

Why were insect herbivores so effective at reducing tall thistle seed production? Asteraceae species often experience intense insect herbivory on flower heads (Louda 1982, 1983, Maron et al. 2002, Amsberry and Maron 2006), and we observed high rates of damage to both flower heads and meristems, consistent with earlier data (Louda 1998, Louda and Rand 2002). Further,

herbivore impacts on plant performance can be determined by whether the timing of damage allows a compensatory response (Maschinski and Whitham 1989). Tall thistle's late flowering phenology, with flower head initiation in late June and maturation of seeds September–October, may limit the opportunity to mature additional flower heads in response to herbivory before autumn frosts. Further, the late season phenology of damage by larvae of a prominent flower head feeder, *Homoeosoma eremophasma*, which feed on multiple, post-anthesis flower heads, also may contribute to preventing fully compensatory seed production.

At one site (Triple Creek), values of λ predicted by the integral projection model were larger than expected, based on our observations of declining tall thistle densities in control plots of the seed addition experiment 2006–2009 (Russell et al. 2010). Possibly, sowing tall thistle seeds in late

February–early April, rather than when seeds naturally disperse in September–November, led to over-estimation of winter seed survival and, hence, the seed-to-seedling transition rate. However, we corrected for this by multiplying our empirical seed-to-seedling transition rate by 0.3, an estimate based upon published rates of post-dispersal seed predation for closely-related species and grasslands (see Methods). At most sites and topographic positions, this correction produced estimates of population growth that closely matched observed changes in densities. Triple Creek differed from our other study sites, however; as the most eastern site, it was embedded in a more forested landscape and it was the most recently restored from agriculture. Either its distinctive landscape context or its strong agricultural legacy may have influenced the post-dispersal seed predator population and, in turn, produced higher seed-to-seedling transition rates for which our correction was too conservative.

Density dependence in effect of insect herbivory on population growth rate

In plant populations, negative density dependent processes are often important, operating at any life-stage or at multiple life-stages (Fowler et al. 2006, Ramula and Buckley 2009). If negative density dependence is sufficiently strong, then increased seed production with reduced insect herbivory will not translate to increased population growth rate and size. Two lines of evidence, however, suggest that at our study sites negative density dependence is not strong enough to eliminate effects of insect herbivores on tall thistle population growth. First, at all five study sites in 2007, and at all sites except Divoky Acres and Triple Creek in 2006, thistle seedling densities were shown to be seed-limited (Russell et al. 2010). Because seedling densities did not influence juvenile survival, growth, or time until flowering, rates of adult recruitment also were seed-limited (Russell et al. 2010). Yet, this seed addition experiment did not address the possibility of negative density dependence in tall thistle fecundity directly. However, both the strong, positive relationships observed between size and lifetime seed production for many monocarpic plants (Metcalf et al. 2003), including for tall thistle (see Results), and the absence of

any density effects on tall thistle growth, reduce the likelihood of strong negative density dependence acting on seed production.

Second, in this study we were able to quantify the relationship between tall thistle density and λ across sites. Maron and Crone (2006) concluded that almost no studies of plant-herbivore interactions had tested for density dependence. We hope that our study goes some way to demonstrating how this can be done. An even better route would have been to include additional levels in the seed addition treatment (currently two levels; 100 seed added/no seed added). This would have allowed us to parameterize more exactly the relationship between seed density and number of recruits per plot and therefore test for density dependent recruitment.

Variation in herbivore impact along ecosystem productivity gradients

Few studies have examined the relationship between the magnitude of insect herbivory effects on plant population growth and ecosystem productivity, in spite of the central role of ecosystem productivity in influential conceptual models of herbivore-plant interactions (Oksanen et al. 1981, Coley et al. 1985, van de Koppel et al. 1996). For cobweb thistle (*C. occidentale*), Maron et al. (2002) found little difference in the impact of flower head-feeding insects on recruitment of 1 year-old juveniles between later-successional (relatively high cover) and young (lower cover) coastal dunes. In this case, insect herbivory greatly reduced recruitment in both habitats. The similarity in population response between habitats arose because, while insect damage was greater in the more productive older dunes, the increase in seed was countered by greater microsite-limitation in the older dunes than in the younger dunes. Also, a study of insect herbivory on the iterocarpic perennial cactus, *Opuntia imbricata*, across three sites on elevational gradients ranging over 120 m in the Chihuahuan desert (Miller et al. 2009), showed much larger differences among topographic productivity zones in insect herbivores' impacts on population growth than we found here. Insect impacts on *O. imbricata* population growth rates were greatest at low elevation sites with intermediate plant cover and were non-existent at high elevation sites with the least plant cover, and insect

herbivore damage also varied among productivity zones (Miller et al. 2009). Our results contrast with these studies. We found that insect herbivores had similar effects on tall thistle in both high and low productivity zones; neither the intensity of most forms of herbivory nor the degree of seed limitation differed significantly between low (ridge) and high (valley) productivity zones.

Our finding of little relationship between ecosystem productivity and insect herbivore impact on tall thistle populations may have occurred because differences in productivity were small. The elevation differences between high and low productivity zones in our study were relatively small (mean 10.91 m, range: 6.4 m at Divoky Acres to 19.5 m at Nine-mile Prairie), reflecting the rolling to flat landscape of the tallgrass prairie region. The differences in productivity between ridges and valleys (29% greater plant community standing crop biomass in valleys) may not have been large enough to generate strongly divergent effects of insect herbivores on tall thistle populations, although it affected several plant performance variables. Since the sizes of topographic gradients used in our study are typical of our region, we do not think the productivity differences underestimate the variation in ecosystem productivity of local sites within the tallgrass prairie. Instead, the results likely reflect an ecological reality, dictated by the narrow elevational range and variable thistle densities observed in tallgrass prairie. In future experiments of this type, adding quantitative estimates of plant community standing crop biomass or cover as in this study will help calibrate differences and patterns. Such data can be used to begin to establish predictions concerning the sizes of productivity differences between habitats that are required to influence insect herbivore impacts on plant populations.

The dominant role of insect herbivores' effects on fecundity in driving their overall effect on tall thistle population growth was consistent in both the valley higher productivity zone and the ridge lower productivity zone. Although the importance of the different vital rates to plant population growth should change along successional gradients (Franco and Silvertown 2004), often represented by gradients in biomass, we found that the differences in standing crop

biomass within our sites did not shift from a strong fecundity influence to a strong growth influence. One likely explanation underlying this finding is that no significant change in the degree of seed limitation of tall thistle population size occurred along the gradient. Therefore, the results suggest that for monocarpic perennial species, like tall thistle, the insect herbivore effects on fecundity will drive the significant effect of herbivory on host plant population growth rate over a biologically relevant range of productivity conditions.

Our tall thistle populations occurred near the western, xeric limit of the species' geographic range, which raises the question of whether the impact of insect herbivores on tall thistle population dynamics would be different in more central portions of the range. How herbivore impacts on host plant populations differ across a plant's geographic range appears to have been addressed rarely, if at all. The fact that the easternmost of our study sites, Triple Creek, differed from the four more westerly sites its tall thistle population dynamics at least suggests that proximity to the range limit might be an intriguing explanatory variable in insect herbivore-host plant interactions. Based on the resource concentration hypothesis (Root 1973), if host plant populations are less dense near range limits then one might expect weaker impacts of specialist insect herbivores near the range edge. However, often species' populations do not appear to be less dense near range limits than in the center (Sagarin and Gaines 2006). While ecosystem productivity did not significantly explain variation in insect herbivore-tall thistle interactions along small productivity gradients within sites, the large variation in productivity from east to west across tall thistle's range might drive geographical variation in the impact of insects on tall thistle population dynamics. Whether productivity- or resource-based conceptual models for variation in insect herbivore damage to plants, in plant compensatory ability and in seed limitation of plant population sizes scale up to explain variation in plant-herbivore interactions at geographical scales is an open question.

Conclusions

Moving forward, further research on hypoth-

eses to explain variation in where, when and how insect herbivores do or do not limit populations of their host plants is essential. Our results support prior conceptual models that argue populations of short-lived monocarpic perennial plants are vulnerable to being strongly impacted by insect herbivores, but reject the ecosystem productivity hypothesis for mediation of the within site intensity of insect herbivore impact on population growth rate. Further studies are needed to provide sufficient data for quantitative prediction of the magnitude of between-habitat productivity differences required to generate differing outcomes of insect herbivore impacts on host plant population growth. One step toward this goal is quantifying differences in standing crop biomass or cover along gradients in all studies examining the relationship between productivity and herbivore impact on host plant populations.

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APPENDIX A

INSECTICIDE AND PRODUCTIVITY ZONE EFFECTS ON HERBIVORE DAMAGE TO TALL THISTLE

We used results from the insecticide experiment to quantify differences in insect damage between productivity zones and to evaluate the efficacy of insect exclusion.

Insect foliage herbivory did not differ significantly between zones. The proportion of leaves damaged per rosette in the insecticide treatment averaged (SE) 0.41 (0.02) in the high productivity zone (valleys) vs. 0.40 (0.02) in the low productivity zone (ridges), whereas in the control treatment foliage herbivory averaged 0.58 (0.02) on plants in the high productivity zone vs. 0.54 (0.02) on those in the low productivity zone. In contrast, insecticide treatment significantly reduced levels of vegetative damage, by about 25–30%, in both zones (Table A1). From the candidate GLMs of foliage damage, the model with only insecticide treatment-specific effects provided the best fit to the data.

Insect mining damage to developing floral branches destroyed the first flower head buds and stopped development of those branches. The patterns of damage to the lateral branches by meristem-mining insects varied substantially between productivity zones. A higher proportion of lateral branches (mean (SE)) were mined in the high productivity zone (high productivity zone controls: 0.43 (0.05), compared to the low productivity zone controls: 0.29 (0.05). The candidate model with treatment and zone specific parameters had the lowest AIC (519.8, Table A1) and was borderline distinguishable from the model with only treatment-specific parameters (Δ AIC = 1.99, Table A1). Levels of

mining also were higher for the control treatment plants, compared to insecticide treatment plants (treatment mean (SE): high productivity zone: 0.22 (0.04) vs. low productivity zone: 0.19 (0.04)). Thus, from the candidate GLMs, the model including zone- and treatment-specific parameters provided best fit (Table A1).

Finally, the proportion of flowering heads with externally apparent damage in the field, among all flower heads initiated, averaged (SE) higher for control treatment plants (high productivity zone: 0.36 (0.06), and low productivity zone: 0.38 (0.06)) than for insecticide treated plants (High: 0.21 (0.04), and Low: 0.23 (0.04)). From the candidate GLMs of this field estimate of flower head damage, the model with both treatment- and zone-specific parameters provided a better fit than did the models with only treatment or only zone effects (Table A1).

Table A1. Candidate models of damage to structures of *C. altissimum* by insect herbivores with the results of model fitting. Insect damage to leaves, flowering branches that were mined, and externally apparent damage to flower heads (field estimates) were modelled in relation to variation in: Zone (low/high productivity positions on local gradient) and Treatment (insecticide/control spray). The model that best explains damage is highlighted in bold. AIC was used to contrast and select models.

Model	AIC		
	Leaves	Flower heads	Flowering branches
Treatment	2288.8	522.1	521.7
Zone	2334.0	540.1	537.0
Treatment + zone	2290.6	514.1	519.8

Notes: AIC (Akaike's Information Criterion, Δ) allows comparison between models; lower values of AIC reveal the best model (boldface). Models with that differ by $\Delta < 2$ are equivalent, by $\Delta = 4$ –7 are clearly distinguishable, and by $\Delta > 10$ are definitely different (B. Bolker, personal communication).

APPENDIX B

DEFINITION AND PARAMETERIZATION OF THE INTEGRAL PROJECTION MODEL

The tall thistle IPM describes change in population size (n) over annual time steps ($\Delta t = 1$ yr from May–May). The full model takes the form:

$$n(y, t + 1) = \int_{\Omega} K(y, x) n(x, t) dx \quad (\text{B.1})$$

where Ω is the range of all possible sizes and $K(y, x)$ is the projection kernel describing all possible transitions from size x to size y . We measured root crown diameter for a subset of seedlings in 2007, and found that their size distribution did not overlap that of older plants. A preliminary IPM incorporating this seedling size data underestimated the density of small plants, suggesting that a particular size class was missing and that a discrete cotyledon (seedling) stage was needed in the model. Thus, the number of plants in the cotyledon (seedling) stage in year $t + 1$ is given by

$$C(t + 1) = p_{ss} p_E \int_{\Omega} p_f(x) f_s(x) p_s(x) n(x, t) dx \quad (\text{B.2})$$

where p_E is the probability that a seed becomes a seedling and p_{ss} is the survival rate of seeds in the soil (constant, estimated at 0.3). The term to the right of the integral sign is total seed production, the product of three functions: the probabilities of survival, $p_s(x)$ and flowering, $p_f(x)$ and the expected seed production, $f_s(x)$, by an individual of size x .

The distribution of established plant sizes is given by:

$$n(y, t + 1) = C(t) p_{sc} f_{sd}(y) + \int_{\Omega} p(y, x) n(x, t) dx \quad (\text{B.3})$$

which comprises two parts: plants that establish from seedlings (first term) and established plants that survive and grow (second term). Also, p_{sc} is the probability that a plant at the seedling stage becomes an established rosette, and $f_{sd}(y)$ is the distribution of recruit sizes.

The survival-growth component, $p(y, x)$ can be

broken down such that:

$$p(y, x) = p_s(x)(1 - p_f(x))g(y, x) \quad (\text{B.4})$$

where $g(y, x)$ is the probability of an individual of size x growing to size y ; and $g(y, x)$ follows a Gaussian density function with mean $\hat{u}_g = a_g + b_g x$. The probability of flowering $p_f(x)$ enters the survival-growth function because flowering is fatal for tall thistle.

Eqs. B.2, B.3, and B.4 form the IPM “kernel”, a surface that describes the frequency of all demographic possibilities over a single time step. Since this kernel dictates the population dynamics, we aimed to determine whether insect herbivory, productivity, and their interaction influenced its shape.

MODEL PARAMETERIZATION

We pooled data for the three inter-annual transitions (two for fecundity) to represent a single t to $t + 1$ time step, as in other studies where multiple years of demographic data are available but insufficient to fit a stochastic IPM (e.g., Easterling et al. 2000, Rose et al. 2005, Ellner and Rees 2006, Kolb et al. 2007). However, we did analyze the demographic response for each site separately, since we had evidence of large between-site variation in the demographic rates (Russell et al. 2010). We fit all IPM functions to the natural logarithm of plant size. IPM construction and analysis were conducted in R Version 2.8.0. (R Development Core Team 2008). For each site, we used AIC-based model selection methods (Burnham and Anderson 2002) to determine if the shapes of the survival and growth functions differed between herbivory treatments, productivity zones, or both. Models that are either a poor fit to the data or are parameter-heavy have higher values for AIC; and ΔAIC , the difference in AIC between models, indicates the statistical merit of competing models.

This parameterization process yielded five IPM kernels that were specific to each site and could vary by all zone + treatment combinations. We discretized each kernel into matrices (200×200) and calculated the asymptotic population growth rate, λ_{ij} , as the dominant eigenvalue of each

corresponding matrix (where i represents herbivory treatment [+ or –] effects and j represents topographically defined productivity zones [ridge or valley] effects).

PARAMETERIZATION OF THE IPM

First for survival, $p_s(x)$, we fit a logistic regression model to binomial data (survived/died) for each site. We compared the fit of a model with productivity-, treatment-, or productivity + treatment-specific parameters, to that of a “null” model with a common slope and intercepts. Then, for the logistic model of flowering probability $p_f(x)$, we followed the same protocol. As for survival, individual flowering (flowered, not flowered) and growth data were modeled separately for each site. To parameterize the growth function $g(y, x)$, we compared the fit of a null linear model of size (year t) against size (year $t + 1$) with constant parameters to models with productivity-, treatment-, or productivity + treatment-specific parameters.

Using data from flower head dissections, we estimate average seed production per head that flowered as: (total developed, undamaged seeds per plant/total heads dissected per plant). Total seed production per individual plant was estimated as: (average seed per head that flowered) \times (total flower heads that flowered per plant). To parameterize the fecundity function $f_s(x)$, we used a negative binomial model to describe size-specific total seed production, and we

compared the fit of a null model with average parameters to models with productivity-, or treatment-, or productivity + treatment-specific parameters. In this case, there were insufficient data to parameterize a fecundity function for each site separately (for example, there were data for 14 plants at Twin Lakes). So, although there was evidence to suggest that fecundity varied between sites, we fit a common fecundity function to all five sites.

We estimated the density-independent probability of establishment (p_E) for each plot as

$$p_E = \frac{n_{100} - n_0}{100}$$

where n_{100} = the total number of seedlings in each seed addition plot (100 seed added) and n_0 = the total number of seedlings established in the corresponding control plot (zero seed added). We used counts of seedlings in May 2007 for the 2007 seed addition experiment, as these were counted with 100% certainty by observing plants with cotyledons still present. This gave 16 estimates of p_E for each site \times zone combination. The distribution of seedling size for each site \times zone combination was determined from the mean and variance of tagged seedlings measured in our seed addition plots in May 2007 [$\ln(\text{seedling size}) \sim N(-2.1, 0.29)$]. Finally, we estimated p_{sc} the average seedling-juvenile transition rate for each site \times zone combination as: number of juveniles (June)/number of seedlings (May).