

VARIATION IN DEMOGRAPHY AND EFFECT OF INSECT HERBIVORY
ON PLATTE THISTLE (*CIRSIUM CANESCENS*) BETWEEN
BIOGEOGRAPHIC RANGE CENTER AND RANGE EDGE

A Thesis by

Mason R. Taylor

Bachelor of Science Degree, Wayland Baptist University, 2017

Submitted to the Department of Biology
and the faculty of the Graduate School of
Wichita State University
in partial fulfillment of
the requirements for the degree of
Master of Science

December 2020

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RANGE EDGE

The following faculty members have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science with a major in Biological Sciences.

Leland Russell, Committee Chair

Greg Houseman, Committee Member

Andrew Swindle, Committee Member

ABSTRACT

Insect herbivory can reduce plant fitness, but the strength of these effects varies greatly in space and time. The Abundant Center Hypothesis (ACH) states that species will encounter more stressful abiotic conditions at the edge of their biogeographic range and that the species' abundance and performance will decline from range center to edge. Lower plant densities and more stressful conditions at the range edge may affect specialist herbivore attack rates and plant compensatory ability. Platte thistle (*Cirsium canescens*) is a monocarpic species whose range is centered in the Nebraska Sand Hills and reaches its western limit in central Colorado. This study addressed 1) How do key Platte thistle demographic rates differ between range edge and center? and 2) How do insect herbivore effects on Platte thistle fecundity and recruitment differ between range edge and center? I addressed these questions by monitoring of juvenile thistles and using insect exclusion experiments on adult Platte thistles. Survival of large juvenile thistles was higher in the range center, and probability of transitioning to reproduction in small juvenile thistles was significantly higher at the range edge, seeming to support the predictions of the ACH. The reduction in seed production and seedling recruitment caused by insect herbivory was not significantly different between range center and edge, but seed production and seedling recruitment overall were significantly higher at the range edge, defying predictions of the ACH. Better reproductive performance at the range edge may be result from different levels of pollination success, whereas differences in juvenile thistle demography may reflect greater abiotic stress at the range edge. My findings seem to support a growing sentiment in ecology that the ACH is too simple to be able to accurately predict the patterns of plant reproductive success and demography at species biogeographic range edges.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Leland Russell, for his incredible patience, encouragement, and insight. I would like to thank my committee members, Greg Houseman and Andrew Swindle, for agreeing to be part of my committee and providing helpful recommendations in improving my study. I could not have accomplished this study without the help of the State of Colorado, United States Forest Service, Bureau of Land Management, Annie Vohs, Tara Flanagan, and Greg Wright. A special thank you goes out to Svata Louda, whose experience and guidance has proven invaluable in my work.

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INTRODUCTION

Understanding factors that limit individual fitness and population growth is a defining goal of both evolutionary ecology and population ecology. Further, understanding variation in effects of these limiting factors at landscape and geographic scales is central to explaining species' habitat and geographical distributions. Accumulating evidence suggests that insect herbivory can strongly reduce plant fitness (Bigger and Marvier 1998, Maron et al. 2014) and limit plant populations (Maron and Kauffman 2006, Tenhumberg et al. 2015), but the magnitudes of these effects are highly variable at a range of spatial scales. Plant vigor (Hilbert et al. 1981, Maschinski and Whitham 1989, Wise and Abrahamson 2007), potentially reflecting underlying resource availability, and plant density (Root 1973, Hambaeck and Englund 2005) within populations are key explanatory variables in conceptual models for spatial variation in herbivore effects. Understanding biogeographic variation in fitness- and population-limiting factors is becoming increasingly important as global climate change progresses, shifting species range limits in the process (Rehm et al. 2015).

The magnitude of herbivores' effects on plant fitness reflects the amount of tissue that herbivores damage upon plants and the ability of the plant to compensate in reproductive output for that damage. Variation in abiotic resource availability to plants and variation in host plant density frequently are hypothesized to drive spatial heterogeneity in the amount of tissue herbivores damage on plants. The Plant Vigor Hypothesis (Price 1991), stating that more vigorous plants are likely to experience herbivory, and Plant Stress Hypothesis (White 1984), stating that stressed plants are more likely to experience herbivory, exemplify the effect of abiotic conditions on variation in herbivory. According to the Plant Vigor Hypothesis, more

vigorous plants suffer greater herbivore damage because their rapidly growing tissues are more difficult to defend and contain more concentrated nutrients (nitrogen and phosphorus) usable by herbivores (Price 1991). According to the Plant Stress Hypothesis, more stressed plants may produce fewer defensive secondary compounds (Louda et al. 1987, Joern and Mole 2005). Biotic factors such as density of con-specific neighbors (Root 1973, Underwood and Halpern 2012) may also affect the levels of herbivory suffered by plants. According to the Resource Concentration Hypothesis (Root 1973), dense populations of a plant species will display disproportionately high densities of specialist insect herbivores, whereas sparse plant populations will display lower densities of specialist herbivores. This difference in insect herbivore densities is likely the result of having a smaller resource base for the specialist herbivores to feed upon, resulting in lower insect reproductive success, as well as a decrease in immigration and increase in emigration from less dense host plant patches (Karieva 1985, Matter 1997).

Abiotic resource availability is central to foundational conceptual models for variation in plant abilities to compensate for herbivore damage, meaning recoup reproductive output lost to herbivory. For example, Maschinski and Whitham (1989) found that seed production in *Ipomopsis arizonica* could respond either positively or negatively to vertebrate herbivory depending on soil water and nitrogen availability and the intensity of competition from neighboring plants. Maschinski and Whitham (1989)'s Compensatory Continuum Model suggests that plants compensate best for herbivory under high resource conditions. By contrast, Hilbert et al. (1981) performed a modeling study that demonstrated that in some cases a plant's compensatory ability will be greatest under low resource, high stress conditions. Hilbert et al.'s (1981) Growth Rate Model suggested that plants growing under low resource conditions may better compensate because 1) they have unused physiological capacity for growth while under

high resource conditions plants are already growing at their maximum and 2) it is easier to match the fitness of their undamaged, slow-growing neighbors. Hawkes and Sullivan (2001) conducted a meta-analysis to evaluate empirical support for the conflicting Compensatory Continuum Hypothesis (Maschinski and Whitham 1989) and Growth Rate Model (Hilbert et al. 1981). They found that monocots that grow from a basal meristem compensated more after herbivory in high resource environments, whereas herbaceous and woody dicots compensated more in low resource environments.

At a biogeographic scale, the Abundant Center Hypothesis (ACH) predicts systematic variation in the stressful vs. benign nature of abiotic conditions and, consequently, in population densities from the center of a species range to its range edge. The ACH states that a species will be more abundant toward the center of its biogeographic distribution, and scarcer toward the range edge (Brown 1984). Differences in the frequency and density of a species' populations between range center vs. edge are predicted because the ACH anticipates that reproductive success and overall fitness will decrease toward the range edge. In turn, lower fitness in range edge populations is hypothesized based on predicted changes in abiotic factors that create an environment less suitable for the species near the range edge. If true, such systematic variation in abiotic stress experienced by a species and in abundance could drive differences in herbivore-plant interactions in range center vs. range edge positions.

While ACH predictions concerning frequency and density of a species' populations at the range center vs. edge are tested frequently, fewer studies have quantified range center – range edge variation in demographic rates and fitness (Hengeveld and Haeck 1982, Sagarin and Gaines 2002, Sexton et al. 2009, Abeli et al. 2014). In their review, Sexton et al. (2009) demonstrated

that survival and recruitment rates, in particular, rarely have been compared between range center and range edge populations. Quantifying biogeographic variation in plant vital rates and fitness is more challenging than quantifying static measures of population structure because it requires monitoring through time, often in populations that are very distant from one another. To overcome the difficulty of collecting detailed demographic data in distant populations, some studies have substituted sampling along a species elevational range for sampling across biogeographic range. For example, Angert (2006) collected demographic data from populations along the elevational ranges of two monkey flower species (*Mimulus cardinalis* and *M. lewisii*) near Yosemite National Park in California. The two closely related species provided conflicting results concerning ACH predictions. Survival and fecundity of *M. lewisii* were higher in the range center, whereas the opposite was true for *M. cardinalis*. While substituting elevation ranges for biogeographic ranges may increase the logistical feasibility of comparisons, it is at the cost of limiting the sample to a small portion of the geographic species range.

Only a handful of studies exist that examine variation in plant-animal interactions from the center of a plant species range to the edge of its range (Louda 1982, Garcia et al. 2000, Alexander et al. 2007, Garcia et al. 2010). Should the assumptions of the ACH prove true, in that species populations become less frequent and less dense near the range edge, the amount of damage imposed on plants by their specialist herbivores may decrease from range center to edge. One of the few studies to compare damage to plants by specialist natural enemies between central and peripheral portions of a plant species range supports this hypothesis. Alexander et al. (2007) found that levels of infestation by a smut fungus (*Anthracoidea blanda*) and a rust fungus (*Puccinia caricina*) and intensity of pre-dispersal seed predation by chalcid wasps in peripheral populations of *Carex blanda* in eastern to central Kansas were lower than in central populations

in Missouri. This was thought to be due to a lack of adequate dispersal ability of pathogens and seed predators. While this elegant study quantified damage by natural enemies, it did not address range center – range edge variation in effect of these natural enemies on plant performance.

Conceptual models, such as the Compensatory Continuum Hypothesis and the Growth Rate Model, that postulate a key role for plant vigor, in determining compensatory ability for herbivore damage provide a basis for predicting variation in plant compensatory ability between populations at the species range center vs. range edge. Dicots are likely to more fully compensate for tissue loss when experiencing herbivory in low soil resource, high competition environments (Hawkes and Sullivan 2001), consistent with the Growth Rate Model. The ACH predicts that the edge of a species' range will possess more stressful abiotic conditions, thus increasing the likelihood that plant compensatory ability will improve toward the range edge. Therefore, evidence presented by Alexander et al. (2007) and Hawkes and Sullivan (2001) may suggest that herbivores should have less impact on plant performance, including fitness, at the range edge than near the range center.

Few studies have quantified variation in herbivore effect on plant performance across a substantial portion of a plant species biogeographic range. However, Louda (1982) examined the impact of pre-dispersal seed predation on seed production and seedling recruitment in populations of a temperate shrub, *Haplopappus squarrosus*, throughout the species range in southern California using insect exclusion experiments. The effect of herbivory in reducing seed production steadily increased heading inland, whereas herbivores' effect on seedling recruitment decreased heading inland. These opposite trends in herbivores' effects on fecundity and recruitment likely occurred because the inland habitat had fewer microsites in which seeds could

successfully germinate, therefore disconnecting reductions in seed production from seedling recruitment. The effects of insect herbivory were not consistently higher or lower near the range edge than near the range center, rather the relationship was unimodal with the highest effect at one edge and the weakest effect at the other edge.

Here I address Platte thistle (*Cirsium canescens*) demography and herbivore-plant interactions at the species' range edge and I quantitatively compare my results to previously published experiments from the species' range center. My specific questions concerning Platte thistle demography and herbivore-plant interactions at the range edge are 1) Do insect herbivory on adult Platte thistles and elevation affect lifetime seed production? 2) Does the effect of insect herbivory on lifetime seed production vary with elevation? 3) Do insect herbivory on adult Platte thistles and elevation affect seed to seedling transition rates? 4) Does the effect of insect herbivory on the seed-seedling transition vary with elevation? and 5) Do Platte thistle survival, growth rates, and flowering probability vary with elevation?

The range center – range edge comparison arises by comparing my data from the range edge with population parameters available in published literature for the range center. The experiments in my research parallel experiments performed near the range center of *C. canescens* in the Nebraska Sand Hills (Louda et al. 1990, Louda and Potvin 1995). My specific questions concerning the comparison of Platte thistle demography and herbivore-plant interactions between the range center and edge are 1) How does the effect of insect herbivory on Platte thistle lifetime seed production differ between populations from the range center and range edge? 2) How does the effect of insect herbivory on the adult plant-seedling transition of Platte thistle differ between

populations from the range center and range edge? and 3) How does juvenile Platte thistle survival, growth, and transition to bolting differ between range center to range edge?

MATERIALS AND METHODS

Study Species

Platte thistle (*Cirsium canescens*) is a monocarpic plant species whose biogeographic range is centered in the Nebraska Sand Hills and stretches from its western range limit in south central Colorado and eastern Wyoming to its eastern range limit in southern South Dakota and central Nebraska (McMinn et al. 2016). Platte thistles grow as juvenile rosettes for approximately 1-5 years before producing a reproductive stalk with typically 3-20 flower heads and flowering, after which the plant dies. Platte thistle exhibits determinate flowering. Flowering in the range center typically begins in early to mid-May and finishes by the end of June (Louda 1998), whereas flowering at the range edge begins in late-May and finishes in mid-July (M. Taylor Pers Obs).

Platte thistle is attacked by native insect herbivores that target its relatively large, resource-rich flower heads. These insects include species that oviposit on flower heads then the larvae inflict damage, and one species whose adults attack flower heads. The ovipositing species include two fly species, *Paracantha culta* and *Terellia occidentalis* (formerly *Orellia occidentalis*), and a moth species, *Homeosoma stypticellum*. The adult insect herbivore species is a scarab beetle, *Euphoria inda* (Louda 1998, Personal Observation). These insect herbivore attacks may decrease seed production and seedling recruitment.

Over a large portion of its range, Platte thistle is attacked by an invasive weevil, *Rhinocyllus conicus*, that reproduces and feeds on thistle inflorescences. This Eurasian weevil was introduced as biological control for Musk thistle (*Carduus nutans*) but has since migrated to Platte thistle and many other native North American *Cirsium* species (Gassman and Louda 2001). Attack by *R. conicus* has severely reduced Platte thistle reproductive success in the portions of the range that it has invaded (Rose et al 2005).

Louda et al. (1990), Louda and Potvin (1995) and Rose et al. (2005) quantified the negative effects of insect herbivory on lifetime seed production in Platte thistle populations in the Nebraska Sand Hills. These studies demonstrate that, near the center of the species range, insect herbivory reduces seed production and population growth rate. Previous biogeographic research on *C. canescens* has shown that populations occur less frequently at the range edge, although densities of plants within populations are not significantly different between range center and range edge (McMinn et al. 2016). In addition, McMinn et al. (2016) showed that populations at the western range edge were less genetically diverse than those in the range center, although eastern edge populations were not.

Study Sites

I conducted my research at the range edge of Platte thistle in the Upper Arkansas River Valley in Chaffee County, CO. This region contains the only Platte thistle populations that have not been invaded by *R. conicus* (S Louda Pers Comm.). For Chaffee County, the county-level 30 year (1981-2010) average temperature in the warmest month, July, is 17.5 °C, and the 30-year average temperature of the coldest month, January, is -5.2 °C. The county-level 30 year mean annual precipitation is 30.5 cm (High Plains Regional Climate Center). The vegetation of the

upper Arkansas River Valley is primarily a mixture of montane grassland and coniferous forest. This area contains populations of *Cirsium canescens* at the southwestern edge of the species geographic distribution (McMinn et al. 2016). Five study sites were established along an elevational gradient ranging from 2435-2776 m (Table 1). These five sites were used in all three growing seasons of this study (2017-2019). A sixth lower elevation study site at 2348 m was added for 2019.

Project 1: Effect of Insect Herbivory on Seed Production

The first project quantified effects of herbivory by insects that attack plant reproductive structures on Platte thistle lifetime seed production. As a monocarpic plant, Platte thistles attempt reproduction (bolt) only once. In May 2017 and May 2018, I selected 12 adult plants at each of the five sites, and in 2019 I selected 20 adult plants at each of the five sites. Plants were chosen if they were not ‘multiples’ (multiple rosettes originating from one root) and did not exhibit severe damage such as severed stems. At each site, levels of the insect exclusion treatment were assigned randomly to each plant. From 2017-2018, 7 plants were treated with insecticide biweekly, 3 plants were treated with water biweekly (water-controls), and 2 plants were left untreated (unmanipulated-controls). In 2019, the sample size was increased so that 10 plants were treated with insecticide biweekly, 5 plants were treated with water biweekly, and 5 plants were left untreated. The insecticide Orthene (Ortho) was used at the start of 2017 because this insecticide was used in Louda et al. (1990). However, at my study sites Orthene was ineffective in reducing insect damage and I replaced it with Bifen IT (Control Solutions Inc.) in June 2017. Bifen IT was applied after diluting 1:10 in water. In May 2018, I tried reducing insect herbivory on Platte thistle by spraying Tanglefoot (The Tanglefoot Company) on developing flower heads,

but this killed the flower heads. Therefore, I reverted to applying only Bifen IT in June 2018 and thereafter. For insecticide-treated plants, insecticide was applied to the entire plant via hand pumped sprayers. However, florets of flowering plants were not sprayed to avoid discouraging pollinators. Similarly, I did not spray water on florets on water-control plants.

For each experimental plant, I quantified its root crown diameter, height, number of flowering heads, number of damaged flowering heads, number of large ($\geq 12\text{mm}$) and small ($< 12\text{mm}$) non-flowering heads, and number of large and small damaged heads. I collected more detailed data on specific flower heads on each plant. To identify specific flower heads, I used a numbering system based on flower head position that has been used in previous studies of *Cirsium* species (S. Louda pers. comm., Adhikari and Russell 2014). The apical flower head of each thistle is labeled as the 100 head. Terminal heads on lateral branches are labeled as 200, 300, etc. in increasing order down the stem. Axillary flower heads, which emerge from branches off of lateral branches, are assigned head numbers such as 310, 320, etc. depending on the number of the terminal head on the lateral branch of origin. In my project, I collected data on the 100, 300, 310, 500, and 700 heads regarding head developmental stage, head diameter, level of damage, and number of *Rhinocyllus conicus* eggs present (if any) on the head. The developmental stages of heads and damage scores are as shown in Table 2 and Table 3. These measurements were performed in the first weeks of June (early Platte thistle flowering), July (start of seed dispersal), and August (late seed dispersal).

To quantify reproduction, Organza fabric bags were placed over post-anthesis flower heads on each plant, and each head was collected after dispersal had begun. Flower heads were checked approximately once per week. The heads were dissected to quantify total seed initiated,

viable seed production, and internal insect damage to the flower head. Because I could not bag and collect every head on every plant before it dispersed, I estimated viable seed production per plant by multiplying the mean viable seed production per head by the total number of flowered heads per plant as counted in the August census.

Before I began analyzing insect herbivores' effects on seed production, I first evaluated whether water-control plants and unmanipulated-control plants could be pooled into a single 'control' treatment level. Because we were concerned that adding water might enhance plant performance, we compared unmanipulated-control plants and water-control plants for two dependent variables that we expected to reflect plant vigor. To do this, I ran two models using my combined data from Projects 1 and 2 targeting plant height and total number of flowered heads per plant as dependent variables. The models were a linear mixed model for plant height and a Poisson generalized linear mixed model for number of flower heads produced per plant. For both models, my independent variables were treatment (water and untreated control), plant size (root crown diameter), and year, all being fixed effects, and site, which is a random effect. I found that there was no significant effect of treatment on plant height (LRT = 0.011, $p = 0.916$) or total number of flower heads ($z = 0.343$, $p = 0.732$). Therefore, I combined the water and untreated control plants into one treatment level in all subsequent analyses.

I then evaluated the efficacy of my insecticide treatment, meaning whether insecticide application reduced insect damage, by running a binomial generalized linear mixed model with the same fixed and random effects as the model described above, but with all two-way interaction effects. The dependent variable was the proportion of heads damaged by insects per plant. Throughout my analyses, to explore two-way interaction effects, I examined the effect of

one of the independent variables in each level of the other independent variable. For example, if I encountered a significant interaction between X and Y then I examined the effect of X in each level of Y. I found a significant interaction effect of treatment and year (LRT = 32.093, $p < 0.001$), and therefore analyzed the effect of my insecticide treatment in each year. I found that my insecticide treatment had no significant effect in 2017 but significantly decreased the proportion of heads damaged by insects in 2018 (LRT = 33.938, $p < 0.001$) and 2019 (LRT = 111.238, $p < 0.001$) (Figure 1).

For my analysis of insect herbivores' effects on seed production, I first used generalized linear mixed models in which the independent variables were insecticide treatment (insecticide and control), elevation, and plant size (root crown diameter), all of which are fixed effects, and site, which is a random effect. I included two-way interaction effects between each of my fixed effects. My dependent variables were proportion of flower heads damaged per plant, viable seed production per plant, number of flower heads that flowered per plant and number of viable seeds per flower head for those heads that I dissected. If two-way interaction effects were not significant then I dropped them from the model and examined the main effects only.

Project 2: Effects of Insect Herbivory on Seedling Recruitment

The second project quantified effects of insect herbivory on the adult to seedling and seed to seedling transitions of *C. canescens*. In the 2017 and 2018 growing seasons, I selected 12 adult plants at each site, and in 2019 I selected 20 adult plants at each of the five sites. Plants were chosen in the same manner as with Project 1, with the exception that Project 2 plants could not have any other bolting plants within a 4 m radius to reduce potential overlap in seed dispersal between plants. In the few cases where this distance requirement could not be met, bolting plants

within the 4 m radius were removed. Each plant was marked with an aluminum tag and galvanized metal stake. In the Nebraska Sand Hills, Louda and Potvin (1995) showed an approximately exponential decline in Platte thistle seedlings with increasing distance from the maternal plant over the first 3 m. Approximately 90% of seedlings within 3 m of the maternal plant established within 2 m of the parent (Louda and Potvin 1995).

The selected bolting plants at each site were randomly assigned to experimental treatments. In 2017 and 2018, 7 plants were sprayed with insecticide biweekly, 3 plants were sprayed with water biweekly, and 2 plants were left untreated as a control. In 2019, the sample sizes were increased to 10 insecticide plants, 5 water plants, and 5 untreated control plants. Insecticide application and field measurements were conducted as described in Project 1.

For each flower head that flowered, I non-destructively estimated the percentage of seeds produced that were viable. I placed an Organza fabric bag over each head post-anthesis to prevent seed dispersal. As the flower head began to disperse into the bag, I removed the dispersing seeds, grasping the pappus, and visually estimated the percentage of seeds that appeared to be viable. Viable seeds are a dark caramel or slightly tan color with rounded sides. Seeds then were re-inserted into the head to allow natural dispersal.

Seedling emergence around the previous year's marked bolting plants was measured May-August 2018, 2019 and 2020. I found the carcasses of the previous year's plants, each marked with a galvanized metal stake, after which I walked a 2 m radius around each plant and counted any seedlings. Seedlings were identified by the presence of cotyledons and/or entire, rounded leaf margins. The data gathered on any successful seedlings were rosette diameter, number of leaves, longest leaf, and presence of cotyledons.

In the analysis for Project 2, the plant – seedling transition rate was the number of seedlings within a 2 m radius. To quantify the seed – seedling transition rate, I estimated seed production per plant based on relationships derived from Project 1 regarding how plant size, represented by root crown diameter as in Rose et al. (2005), is related to viable seed production in undamaged plants. I then multiplied these predicted levels of seed production for undamaged plants by the mean percentage of viable seeds across all flower heads on that plant from my flower head surveys. The seed – seedling transition rate was calculated as the number of seedlings around each plant divided by the number of predicted viable seeds produced per plant.

For my analysis of the plant – seedling transition, I ran a negative binomial generalized linear mixed model in which my fixed effects were plant size, insecticide treatment, year, and elevation, with their two-way interaction effects, and site as a random effect. My dependent variable was the number of seedlings established around each maternal plant in the first year after bolting. For my analysis of the seed – seedling transition, I ran a binomial generalized linear mixed model in which my fixed and random effects were the same as in the previous model, but with my dependent variable was the number of seedlings in year $t + 1$ divided by the predicted number of seeds per plant.

Project 3: Stage Specific Survival and Growth of Juvenile Platte Thistles

The third project quantified growth, survival, and transition to bolting of juvenile *C. canescens*. For this project, I used the same five sites as in Projects 1 and 2 for 2017-2020 but added a sixth site for 2019-2020. To ensure sampling across the size range of juvenile plants, at each site I sampled 10 rosettes in each of the following size classes: Very Small-1-3 leaves; Small-4-6 leaves; Large-7-9 leaves; Very Large- ≥ 10 leaves. This resulted in 40 juveniles

sampled per site per year. I sampled juvenile thistles adjacent to the areas used for Projects 1 and 2 to quantify the performance of juvenile plants within the same population as the adult plants in my study. Within these areas, I selected the first 10 plants of each size class that I found, unless the plant was heavily damaged or in danger of imminent death. This was done to maximize the possibility of being able to track the same plant across multiple growing seasons. Each plant selected was marked with a numbered aluminum tag and mapped.

Initial data were collected on each tagged plant in early June 2017, with ‘end-of-season’ measurements taken in mid-August. These data included rosette diameter, longest leaf length, number of leaves, presence of cotyledons, and whether the plant consisted of multiple rosettes. All plants were then re-measured at the start of the next year’s (2018) growing season in June. Any plants that died or transitioned to reproductive adults were recorded. These plants were replaced by newly selected rosettes in order to maintain a sample size of 10 rosettes in each size class. These new plants were then measured, tagged and followed in the same manner as their forebearers. This process was carried out in both June and August-September of each year through 2020, capturing three annual transitions for the tagged plants.

In the analysis for Project 3, my independent variables were elevation, year, and initial plant size, all fixed effects, and site and plant ID as random effects. My models also included all two-way interaction effects. My dependent variables were proportional change in plant size, whether the plant survived (Yes / No), and whether the plant bolted (Yes / No). Proportional change in plant size for each plant during each annual transition was calculated by dividing the difference of root crown diameter in year $t + 1$ and year t by the root crown diameter in year t .

For my analysis of proportional change in plant size, I used a mixed linear model. For analyses of both survival and bolting, I used binomial generalized linear mixed models.

Characterization of Study Sites

To better understand the elevational gradient of study sites, I quantified Platte thistle flowering phenology at each site 2017-2019 and, in 2019 and 2020, I estimated plant community net primary productivity at the five sites used in all years, but not at Flanagan's. Phenology surveys involved measuring root crown diameter, plant height, and diameter of flower heads on each Project 1 and Project 2 plant in the second week of June, after which the date of first flowering (first date of at least one head at stage 4 (Table 2)) was recorded for each plant. If a plant had started to flower before the second week of June, the date on which flowering was noticed was recorded for that plant. Plants were checked for flowering weekly.

Plant community biomass was collected August 4-9, 2019 and August 2-5, 2020. This harvest date was chosen to be late in the growing season and was logistically feasible with other data collection. At sites with cattle, plant biomass was harvested within cattle exclosures that had been present throughout the growing season. In 2019 biomass was harvested in three cattle exclosures at each site and in 2020 biomass was harvested in two exclosures per site. Three 50 cm x 50 cm plots were harvested within each cattle exclosure resulting in 9 plots harvested per site in 2019 and 6 plots harvested per site in 2020. All living, aboveground herbaceous growth and within-season woody growth was removed in 50 cm X 50 cm plots and placed in a paper bag. Biomass samples were dried for three days at 60°C and weighed.

I analyzed whether there was an effect of elevation and/or site on 1) Platte thistle flowering phenology and 2) plant community biomass using linear mixed models. For my analysis of flowering phenology, my dependent variable was the date of first flowering by each tagged plant, represented by number of days into the year (e.g. a date of first flowering of June 10 was recorded as 162 days since January 1), my independent variables were site (fixed), elevation (fixed) and year (fixed), as well as their two-way interaction. For my analysis regarding plant community biomass, my dependent variable was biomass per 50 cm X 50 cm plots and my independent variables were the same as in the analysis of flowering phenology, except for including 'block', meaning cattle enclosure, as a random effect.

Analysis Strategy for Range Center – Range Edge Comparisons

My comparison of range center vs. range edge Platte thistle demography and insect herbivore interactions uses results from previous experiments conducted in the species range center (Louda et al. 1990, Louda and Potvin 1995) and analyses of long-term observational data (Rose et al. 2005). Louda et al. (1990) and Louda and Potvin (1995) conducted insect exclusion experiments in Arthur Co. NE in the southwestern portion of the Nebraska Sand Hills, during 1984 and 1985. Rose et al. (2005) constructed integral projection models to examine effects of insect herbivory on *C. canescens* population growth and in doing so developed relationships describing the size-dependency of key demographic rates, such as growth, survival, transition to bolting and seed production. The authors used demographic census data on all Platte thistle life-stages that were collected in permanent plots over 11 years from 1990-2002. Data in Louda et al. (1990) and Louda and Potvin (1995) were collected before invasion of their study site by *R. conicus* in 1993. Data from Rose et al. (2005) include both pre- and post-invasion conditions.

For all three projects, comparisons of range edge data, with range center parameters, were made by calculating 95% confidence intervals around range edge and range center parameters estimates (e.g. means, regression slopes, differences between treatment means) and predicted values. Significant differences were assessed based on lack of overlap in the confidence intervals around parameters or predicted values from the different range positions.

For my range center vs. range edge comparisons, I pooled my range edge data across all years and sites. Similarly, Rose et al. (2005) pooled data across years. I pooled 'range edge' data across sites because 1) site was not a factor in analyses for the range center (all Nebraska data were collected at a single site) and 2) the distances between my range edge sites were very small compared to the distance between range center and range edge. Using the data that I collected at the range edge, I fit a linear mixed model for growth. For probability of survival and probability of bolting, I used generalized linear mixed models. Each model had a fixed independent variable of natural log (root crown diameter) in year t . The mixed models included plant ID as a random independent variable because individual plants could be followed for multiple years. My models had dependent variables of the natural log (root crown diameter) in year $t + 1$, survival (Yes/No), transition to bolting (Yes/No) and mean number of viable seeds produced per plant. For probability of survival and probability of bolting, these were binomial error distributions. For seed production, the error distribution was negative binomial. From these models, I extracted parameter values and standard errors in the same manner as described in Rose et al. (2005). For seed production, I compared treatment means and the confidence intervals around those means.

Often it was difficult to interpret the biological meaning of differences in model parameters between range center vs. range edge size-based demographic rates. Therefore, I

compared predicted values between range center vs. range edge size-based demographic rates. I generated confidence limits for predicted values for size-based Platte thistle demographic rates between range center and range edge by randomly sampling 1000 parameter values (e.g. slope and intercept for growth)) for both the range center and range edge from normal distributions that had the mean of the parameter value and a standard deviation equal to the standard error of the parameter value from the statistical models that I fit or that were in Rose et al. (2005). These 1000 randomly sampled parameter values were then inserted into the relevant size-based models to generate a range of predicted size-based relationships. I evaluated the predicted values from these size-based relationships at three evenly spaced points within the size range of Platte thistles from the range center and the range edge. 95% confidence limits were determined by using the 25th smallest value and the 975th smallest value among the 1000 predicted values as the upper and lower confidence limits.

To compare the magnitude of effect of insects on 1) the number of viable seeds produced per plant and 2) the plant – seedling transition rate between the range center and range edge, I calculated 95% confidence intervals around the mean decrease in seed production between insecticide-treated and control plants and around the mean difference in number of seedlings established between insecticide-treated and control plants at both range center and range edge. To do this, I first calculated the differences between insecticide and control means at both range locations. I then calculated the standard error of the difference in means by taking the square root of the sum of the standard errors of the two treatment groups (Zar 2010). I then calculated 95% confidence intervals from those standard errors of differences between means.

RESULTS

Within-region comparisons: Platte thistle demography and interactions at the range edge

Characterization of Productivity and Phenology at Study Sites

Estimates of net primary productivity (NPP) in 2019 ranged from 106 g/m² at Forman's to 174 g/m² at Brown's Creek, and in 2020 they ranged from 38 g/m² at Lost Creek to 84 g/m² at Brown's Creek. Mean NPP was significantly affected by both site (LRT = 9.968, $p = 0.019$) and year, with mean NPP being higher in 2019 ($t = -8.081$, $p < 0.001$). There was no significant effect of elevation. Post-hoc analysis showed mean NPP, averaged across years, was only marginally significantly different ($t = 2.825$, $p = 0.073$) between two sites, Brown's Creek and Forman's (Table 4).

Mean first date of flowering at a site varied from day 168 (June 17) at Centerville to day 175 (June 24) at Forest 300. Among years, mean first date of flowering varied from day 166 (June 14) in 2018 to day 179 (June 28) in 2019. I found that mean date of first flowering was significantly affected by both site (LRT = 14.315, $p = 0.006$) and year (LRT = 35.319, $p < 0.001$). Post-hoc pairwise comparisons of sites revealed a significant difference between Centerville and Forest 300 (z ratio = -3.311, $p = 0.008$), and marginally significant differences between Centerville – Lost Creek (z ratio = -2.606, $p = 0.068$) and Centerville – Forman's (z ratio = -2.615, $p = 0.061$) (Table 4). Post-hoc pairwise comparisons of years revealed significant differences between 2017 – 2019 (z ratio = -5.363, $p < 0.001$) and 2018 – 2019 (z ratio = -7.573, $p < 0.001$). 2017 and 2018 did not differ in mean date of first flowering.

Projects 1 and 2: Herbivore damage at the range edge

For analyzing natural levels of insect damage to Platte thistle flower heads at the species' range edge, I considered only bolting plants that were not treated with insecticide. I found a significant effect of year on mean proportion of heads damaged by insects for untreated plants (LRT = 24.253, $p < 0.001$), but no significant effect of either plant size or elevation. I also found a significant effect of year on damage by any herbivore, insect or mammal, (LRT = 22.401, $p < 0.001$), with no significant effect of either plant size or elevation. Mean proportion of heads damaged by insects per plant at the range edge varied from 0.42 in 2017 to 0.67 in 2019. Post-hoc comparisons showed damage in 2017 and 2018 did not significantly differ, but 2019 showed significantly higher levels of insect damage than both previous years ($p < 0.001$, Figure 1). Mean proportion of heads damaged by any herbivore per plant at the range edge showed the same pattern, with 2017 and 2018 not significantly differing and 2019 having significantly greater damage ($p < 0.001$, Figure 1).

Project 1: Effect of insect herbivory on seed production at the range edge

When examining mean number of viable seeds produced per flower head for all years combined, I found no significant effect of treatment, year, or elevation, and a marginally significant positive effect of plant size ($z = 1.657$, $p = 0.098$). I then analyzed the mean viable seeds produced per head in 2019 only in the same manner, as this was the year that the insecticide treatment was effective. I found a significant positive effect of plant size ($z = 2.037$, $p = 0.042$). Further, in 2019 insecticide-treated plants produced significantly more viable seeds per head than did control plants ($z = 1.978$, $p = 0.048$, Figure 2). Viable seed production per head was 24.7% greater in insecticide plants than in control plants in 2019.

I found that the mean number of heads per plant that flowered (reached stage 4) for all years combined was only marginally significantly affected by treatment ($z = 1.717$, $p = 0.086$), with insecticide plants having more heads that flowered. There was a significant plant size X year interaction effect ($z = 3.331$, $p < 0.001$). I also found a significant negative effect of elevation ($z = 2.229$, $p = 0.026$). Investigating the plant size X year interaction, I found a significant positive effect of plant size on the number of heads that flowered per plant for both 2018 ($z = 3.586$, $p < 0.001$) and 2019 ($z = 6.690$, $p < 0.001$), but no effect of size in 2017. Analysis of the number of heads per plant that flowered from 2019 only showed a significant negative effect of elevation ($z = -2.323$, $p = 0.02$), with no significant effect of treatment.

I found that the mean number of viable seeds produced per plant for all years combined was not affected by treatment. However, I found a significant positive effect of plant size ($z = 6.774$, $p < 0.001$) and a marginally negative effect of elevation ($z = -1.649$, $p = 0.099$). I then analyzed the viable seeds produced per plant for 2019, again because this was the most effective year of insecticide treatment, and found a significant positive effect of plant size ($z = 4.777$, $p < 0.001$) and a significant effect of treatment ($z = 2.116$, $p = 0.034$). Viable seed production per plant was 23.8% greater in insecticide plants than in control plants in 2019.

Project 2: Effect of insect herbivory on seedling recruitment at the range edge

I found that the mean number of seedlings established per plant in the first year after bolting was significantly affected by the interaction effect of plant size and treatment (LRT = 10.536, $p = 0.001$) and by year, with significantly more seedlings in both 2018 ($z = 4.645$, $p < 0.001$) and 2019 ($z = 2.938$, $p = 0.003$) than in 2017. Mean number of seedlings per plant in year $t + 1$ ranged from 0.09 seedlings for insecticide plants in 2017 to 10.32 seedlings for insecticide

plants in 2018. The plant size X treatment interaction effect arose because there was no effect of plant size on the adult-seedling transition for insecticide plants, but there was a significant positive effect of plant size ($LRT = 14.771$, $p < 0.001$) for control plants. There was no significant effect of elevation. As with Project 1, I analyzed 2019 alone. I found no significant effect of plant size, treatment, or elevation.

Mean number of seedlings per seed ranged from 0.0001 seedlings per seed for 2017 control plants to 0.065 seedlings per seed for 2018 insecticide plants (Figure 3). I found that the mean number of seedlings per seed was significantly affected by the interaction of plant size and treatment ($z = -3.31$, $p < 0.001$), as well as by year. The seed-seedling transition rate was greater for 2018 bolters ($z = 2.69$, $p = 0.007$). To address the plant size X treatment interaction, I analyzed the effect of size in each level of the insecticide treatment. For insecticide plants, I found a significant negative effect of plant size ($z = -6.06$, $p < 0.001$). For control plants, I found no significant effect of plant size. I analyzed 2019 alone and found a significant negative effect of plant size ($z = -2.59$, $p = 0.010$) and no effect of either treatment or elevation.

Project 3: Growth, survival, and transition to bolting of rosettes at the range edge

Initial plant size, specifically root crown diameter, had a significant effect ($t = -4.707$, $p < 0.001$) on proportional growth. As initial plant size increased, the annual proportional rate of change in root crown diameter decreased (Figure 4). There was also a significant interaction effect of year and elevation ($p = 0.021$). For 2017-2018, elevation had a marginally significant positive effect ($t = 1.448$, $p = 0.075$) on growth. However, there was no effect of elevation on proportional growth rate of Platte thistle rosettes in any other annual transition.

I found that rosettes' probability of survival was significantly affected by the interaction effect between initial plant size and year ($p < 0.001$). For both 2017-2018 and 2019-2020, size had a significant positive effect ($p < 0.001$) on probability of survival (Figure 5). However, size did not affect survival probability in 2018-2019. Elevation did not affect survival probability in any year.

I found that rosettes' probability of bolting was significantly affected by the interaction effects between both size and year ($p < 0.001$) and year and elevation ($p = 0.014$). Initial plant size had a significant positive effect on bolting probability in 2017-2018 ($p = 0.001$) and 2019-2020 ($p = 0.004$), but there was no effect of plant size on bolting probability in 2018-2019 (Figure 6). The interaction effect of year and elevation arose because of a marginally significant positive effect ($p = 0.095$) of elevation in 2019-2020, but in no other year.

Comparisons between the Platte thistle populations at the range edge vs. the range center

Project 1: Effect of insect herbivory on seed production at range center vs. edge

Based upon lack of overlap in confidence limits, I found that mean viable seed production per plant was significantly higher overall at the range edge than the range center for both plants exposed to ambient insect herbivory and for plants treated with insecticide (Figure 7). As examples of the magnitude of these differences, the minimum and maximum mean viable seed production per plant values at the range edge were 220 seeds for insecticide plants in 2018 and 957 seeds for insecticide plants in 2019. By comparison, for the range center population these minimum and maximum values for mean viable seed production per plant were 32 seeds for control plants and 105 seeds for insecticide plants.

In determining the impact of insect damage, I used only range edge results from 2019, as this was the year in which my insecticide treatment was most effective. I found no evidence that insect herbivores' effect in reducing the number of viable seeds produced per plant differed between the range center vs. edge; 95% confidence limits for the mean reductions in number of viable seed produced per plant overlapped (Figure 7). However, the proportional reduction in seed production in control plants as compared to insecticide-treated plants appeared to be larger at the range center, 69.5% at the range center and 23.8% at the range edge, but I could not statistically compare these percentages.

Project 2: Effect of insect herbivory on plant to seedling transition at range center vs. edge

Based upon lack of overlap in confidence limits, I found that control plants in the range center in Nebraska produced significantly fewer seedlings than plants of either treatment (control or insecticide) at the range edge. By contrast, I found no significant difference in the mean number of seedlings per plant between range center insecticide plants and plants of either treatment level at the range edge (Figure 8). Based on overlapping confidence limits, I also found no significant difference in the magnitude of the reduction in number of seedlings per plant caused by insect herbivory between range center and range edge (Figure 8).

Project 3: Juvenile Platte thistle growth, survival, and transition to bolting at range center vs. edge

I found no evidence that growth rates of juvenile Platte thistles differed between the range center and the range edge. Specifically, 95% confidence limits for predicted plant root

crown diameter in year t+1 overlapped between the range center and range edge across the entire range of root crown diameters in year t (Figure 9).

The probability of juvenile survival was significantly different between the range center and the range edge for larger rosettes; 95% confidence intervals around mean predicted probabilities of survival do not overlap for large rosettes but do overlap for small and medium-sized rosettes (Figure 10). Large rosettes at the range center have a significantly higher probability of survival than large rosettes at the range edge.

The probability of transitioning to bolting was significantly different between range center and range edge for small plants; 95% confidence intervals around mean probability of bolting do not overlap for small rosettes but do overlap for medium-sized and large rosettes (Figure 11). Small rosettes at the range edge have a significantly higher probability of transitioning to bolting than small rosettes at the range center.

DISCUSSION

Effects of insect herbivory on *Platte thistle* seed production and recruitment at the range edge

Insect herbivory on plant reproductive structures can greatly reduce viable seed production, especially in Asteraceae species (Louda 1982, Kelley and Dyer 2002, Adhikari and Russell 2014). In my study, I was most successful at manipulating insect herbivory in 2019 and this was also the year in which insect herbivory on flower heads was most intense. In 2019, I found that insects significantly reduced both the number of viable seeds produced per flower head and the number of viable seeds produced per plant. The reduction of viable seeds per plant

seems to be directly tied to the reduction in viable seeds per head, as insect damage did not significantly affect the number of flower heads that reached anthesis per plant. The failure of insect herbivory to reduce the number of flower heads that flowered per plant in 2019 may reflect compensatory flowering of later-developing terminal and axillary flower heads when more apical heads are damaged by insects (Adhikari and Russell 2014, West and Louda 2018). Similarly, West and Louda (2018) found that simulated insect damage to the apical flower head actually increased the number of flower heads that matured per plant and the number of heads that produced undamaged viable seeds, if insect damage to heads other than the apical head was reduced experimentally.

The smaller number of viable seeds per flower head on plants exposed to insect herbivory in 2019 could have arisen through several mechanisms. Lower mean seeds per head on control plants may occur because 1) insects destroyed seeds in heads that flowered or 2) insects prevented early developing heads from flowering and then compensatory flowering occurred by later, smaller flower heads. When thistles increase production of axillary or lower terminal heads in response to severe damage in higher, earlier blooming heads, these flower heads are often smaller and have fewer ovules than earlier-developing flower heads (Adhikari and Russell 2014). In my range edge populations, the reduction in mean seeds per head likely is more tied to the seed damage inflicted by insect herbivores within heads that flowered than it is by a shift to smaller compensatory heads. First, my pre-dispersal, visual inspections of seed in Project 2 revealed significantly higher proportions of viable seeds per head in insecticide plants in both 2018 and 2019, consistent with insects directly destroying seeds in heads that flowered. Second, insect herbivory in most flower heads would rarely lead to abortion of the head itself, even in cases of heavier insect damage such as complete chewing of the receptacle base by a *Euphoria*

inda scarab. As heads were less likely to abort from insect damage, there was less chance for compensatory head production.

Although my visual inspections of flower heads in Project 2 revealed significantly higher proportions of viable seeds per head in insecticide plants, seedlings from insecticide plants were only significantly more numerous in the 2018-2019 transition. This is likely due to the 2018-2019 transition having much more precipitation than either the 2017-2018 or 2019-2020 transition. Lastly, the negative effect of plant size on the seed to seedling transition rate may suggest microsite limitation at the range edge. If there are a limited number of microsites where seedling germination can occur, and larger plants produce more viable seed than smaller plants then the seed-seedling transition will decrease with increasing plant size. In comparison, Platte thistles in the range center are strongly seed limited (Louda and Potvin 1995, Rand et al. 2020).

Platte thistle rosette demography at the range edge

The significant interaction effects of initial plant size and year on survival and transition to bolting of juvenile thistles are consistent with the large climatological variation, especially in precipitation, that occurred during this study. Specifically, 2018 and 2020 were notably dry, as were the 2017-2018 and 2019-2020 transitions (Table 5). Such environmental stressors could possibly outweigh the expected positive effects of plant size on probability of survival and transition to bolting. The natural tendency of larger rosettes to have higher survival probabilities may be less likely to matter when conditions are abnormally poor. The nullification of the effect of plant size on bolting in the transition from 2018-2019 results from the higher rate of bolting for smaller plants in that transition. Attempting reproduction, despite small size and low

reproductive output, may be adaptive under adverse conditions because chances of surviving to reproduce at a larger size in future years are quite low (Metcalf et al. 2003).

It is somewhat surprising that I found no strong significant effect of elevation on demography for any yearly transitions except 2019-2020. The marginal effect of elevation in 2019-2020 could possibly be accredited to the addition of a sixth, lower elevation site in 2019, increasing the elevational gradient by almost 90 m. Despite this, my elevational gradient was likely still too narrow to capture a strong elevational effect. Angert (2006) used an elevational gradient spanning 1920 m and found a much stronger effect of elevation on demography of two *Mimulus* species in the Sierra Nevada Mountains of California. It is also possible that I did not observe an elevational effect because I did not capture the extreme highest and lowest elevations at which Platte thistles occur in the upper Arkansas River valley. Elevational effects may only become pronounced near the edges of the species elevational distribution. I chose not to use higher elevation thistle populations for my study because they had already been invaded by *R. conicus*. I chose not to use the lowest occurrence of Platte thistle because there were too few thistles for my experiments.

Comparison of Platte thistle demographic rates between the range center and range edge

The ACH predicts that range edge populations of a species will experience more harsh abiotic conditions and, hence, have poorer performance than range center populations (Brown 1984). Comparisons of Platte thistle demographic rates between range center and range edge populations were in some cases consistent with this prediction and in other cases were contrary.

Sexton et al. (2009) found particularly few studies that compare survival and recruitment between range center and range edge. For Platte thistle rosettes, patterns of survival partially support the predictions of the ACH. According to the ACH, one could expect lower survival rates at the range edge. However, probability of survival of juvenile Platte thistles only significantly differed for larger plants, with larger plants at the range edge being less likely to survive than larger plants at the range center. The absence of differences in survival rates between range center and range edge for small rosettes could be attributed to generally high mortality for younger, smaller thistles. In other words, because small rosettes already have quite high mortality rates in the range center there is not much opportunity for further increase in their mortality rates at the range edge.

The pattern of small rosettes bolting at a higher rate at the range edge than in the range center is consistent with the ACH when this difference is considered in the context of life-history evolution theory. At the range center, the likelihood of bolting for smaller plants is nonexistent. This rarity could be the result of an evolutionarily stable strategy in which plants will ‘choose’ to bolt when prospects of bolting outweigh the costs of delaying reproduction an additional season (Metcalf et al. 2003, Simmons and Johnston 2003). This strategy could explain the increased probability of bolting at the range edge, as the ACH predicts that plants at the range edge are likely to experience more stress, which increase the probability that plants that wait to reproduce may die before reproducing. This explanation for higher rates of bolting among small rosettes at the range edge is consistent with lower survival rates among large plants that I observed at the range edge. It is also worth noting that smaller plants were especially likely bolt in 2018, which was the driest year of my experiment.

Comparisons of Platte thistle fecundity between range center and range edge populations appear to contradict predictions of the ACH; specifically, I found viable seed production to be much higher at the range edge than in the range center. First, I considered methodological explanations for this difference. Differences in estimated viable seeds per plant between Louda et al. (1990) and my study could result from difficulties I had in capturing all heads on a plant before they dispersed, especially with larger plants. As my estimates of viable seed production hinged on the mean seeds per head and the total number of heads per plant, it is possible that oversampling of the earlier, more productive heads could inflate plant fecundity estimates. To address this possibility, I performed the range center – range edge comparison a second time using only range edge plants which I dissected more than half of flower heads. Fecundity estimates for such plants would be less subject to over-estimation. Further, this is a conservative approach because it tends to exclude the largest range edge plants for which capturing their many flower heads was most difficult. However, even with this conservative data set seed production was significantly greater in range edge populations.

A second methodological explanation for the higher fecundity of Platte thistle at the range edge could be a difference assessing viability of seeds between the range center study and my range edge study. Such a difference could lead to either overestimation or underestimation of the number of viable seeds per head in dissections. However, there are two reasons for me to believe that my estimates are accurate. First, I was taught to dissect thistle heads and identify viable seeds by the lead author of the experiments from the range center to best align our identifications. Second, in an experiment I conducted at the range edge that is not included in my thesis, I sowed 160 plots with 100 seeds per plot and saw successful germination rates greater than 50 seedlings per plot in some plots. Such high germination rates under field conditions leads

me to believe that my recognition of viable seeds is reasonably accurate. Therefore, I feel confident that viable seed production at the range edge is greater than in the range center.

One possible biological, rather than methodological, explanation for lower viable seed production in the range center could be lower rates of successful pollination in range center populations. This hypothesis is suggested by the low proportion of initiated flowers that produced viable seeds in the range center (Louda et al. 1990), which could arise from decreased pollination success. By contrast, in dissection of flower heads from the range edge, unpollinated ovules appeared to be uncommon. Low pollination success in the range center may be the result of higher levels of competition for pollinators. Platte thistle in the range center coexists with wavyleaf thistle (*Cirsium undulatum*), whereas Platte thistle populations at my range edge study sites exist without any other thistles that would directly compete for pollinators. Competition from flowering plants of a closely related species with similar flowering characteristics has been shown to change the behavior of floral-visiting insects of the target species (Russell and Louda 2005).

Studies that have compared seed production between range center and range edge populations of plant species have often, but not always, found lower seed production at the range edge. Jump and Woodward (2003) showed seed production of two *Cirsium* species, *C. acaule* and *C. heterophyllum*, in the United Kingdom was lower at the range edge than the range center, supporting predictions of the ACH. The most important difference that may explain their different results would be that their study species reproduce both clonally and with seeds. The multiple reproductive options available to these *Cirsium* species could explain the lessening of seed production toward the range edge. Angert (2006) studied two *Mimulus* species, *M. lewisii*

and *M. cardinalis*, across their elevational ranges and found that *M. lewisii* had lower fecundity at its range edge, whereas *M. cardinalis* had higher fecundity at its range edge. Fecundity of *M. lewisii* suffered at its range edge due to fewer fruits maturing per plant and a two-fold reduction in seeds per fruit, with the reduction in seeds being attributed to either physiological limits or pollen limitation. Fecundity of *M. cardinalis* had lower fecundity in its range center because plants were smaller, with far fewer flower heads to mature fruit.

Comparison of insect herbivore effects between range center vs. range edge

According to the predictions of the ACH, Resource Concentration Hypothesis, and Compensatory Continuum Hypothesis, populations at the range edge should be expected to experience less herbivore impact than denser and resource-rich range center populations. However, these predictions did not hold true in my range edge Platte thistle populations. This could be explained by Platte thistle range edge populations having comparable densities to range center populations (McMinn et al. 2016) and by overall fecundity in range edge populations being high enough to overcome any increased susceptibility to damage from resource stress. It is also possible that my ability to make robust comparisons between range center and range edge insect herbivore effects was greatly limited by the difficulties in successfully excluding insect herbivores in two of the three years of my experimental manipulation.

Addressing potential confounding of space and time

A primary concern with my comparisons of Platte thistle demography and insect herbivore interactions between range center and range edge is the possible confounding of spatial variation (range position) and temporal change between when Louda and colleagues collected

data in the range center and my study at the range edge. Long-term directional, environmental changes could lead to either over-estimation or under-estimation of differences between range center and range edge populations.

In particular, climate change in the roughly 35 years between when the range center studies were conducted, and my range edge study could confound the comparison between range positions. However, comparing precipitation and temperature in both range center and range edge during both time periods that the studies were conducted gives some comfort (Table 5). In the years since the range center studies, the difference in precipitation between range center and range edge study sites has widened, with the range center becoming moister and range edge becoming drier. For example, the difference in mean precipitation between center and edge in 1984 – 1986 was 14.02 cm/year and the difference in 2017 – 2020 was 33.09 cm/year. My comparisons between the range center in 1984 – 1986 and range edge in 2017 – 2020 then fall somewhere in the middle with a difference of 22.96 cm/year. Therefore, to the extent that water availability may drive demographic differences between the range center and the species southwestern range edge, my results are likely to provide an intermediate estimate of these differences associated with range position.

The progression of invasion by *R. conicus* over roughly 35 years could also create difficulties in making accurate comparisons between the range center studies and my range edge study. However, I have reason to believe that I have adequately controlled for this possibility. First, *R. conicus* should have no effect on juvenile thistles, as they are flower head specialists. Second, my sites were chosen because they were either not yet invaded or had low levels of *R. conicus* usage.

Conclusions

My findings at the range edge in Colorado show large fluctuations in both climatic conditions and Platte thistle performance across the years of my study. In particular, seedling recruitment, juvenile survival, and juvenile transition to bolting were strongly variable among years. The effects of insect herbivory were also variable among years, though it is difficult to know that annual variation was not caused by difficulties in insect exclusion. The significant effect of treatment on viable seed production in 2019 suggests that insects may commonly have negative effects on Platte thistle reproductive success, though further successful insect exclusion would be necessary to ensure such a pattern. The general lack of effect of elevation at the range edge may show either that elevational gradients need to be larger to have a pronounced effect, or that other environmental factors far outweigh any effect of elevation.

My comparisons of Platte thistle demography and effects of insect herbivory between range edge and range center populations seem to support a growing sentiment in ecology that the ACH is too simple to accurately predict the patterns of plant reproductive success and demography at species biogeographic range edges. While more stressful abiotic conditions seem to play an important role in affecting demographic rates and effects of insect herbivory, there remains a great deal of complex biotic interactions that have yet to be examined.

Future research directions could include investigation of plant size differences and pollination competition at both range center and range edge. Given the large year-to-year variation in climatic conditions and plant performance that I observed at the range edge, a long-term study would also be appropriate to address the hypothesis that species experience greater temporal variation in demography and interactions at their range edge (Sexton et al. 2009).

Lastly, long-term studies would benefit from being performed in a species' range center and range edge concurrently to capture climatic shifts in both range center and range edge.

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REFERENCES

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APPENDIX

Table 1: Description of locations and land usages at upper Arkansas River valley (Chaffee County CO) study sites.

Site Name	Latitude	Longitude	Elevation(m)	Ownership	Land Use	Years Used
Flanagan's	38°39'17"N	106°5'7"W	2348	Private	Ungrazed	2019-2020
Centerville	38°40'55.85"N	106°5'13.94"W	2435	Private	Grazing	2017-2020
Brown's Creek	38°41'39.46"N	106°7'15.03"W	2502	BLM	Grazing	2017-2020
Lost Creek	38°45'29.85"N	106°9'26.14"W	2577	State of Colorado	Grazing	2017-2020
Forman's	38°53'56.68"N	106°12'22.75"W	2665	BLM	Roadside (ungrazed)	2017-2020
Forest 300	38°49'32.08"N	105°59'40.30"W	2776	USFS	Grazing, Recreation	2017-2020

Table 2. Explanation of scores assigned to Platte thistle flower heads to represent specific stages in development.

Stage	Meaning
1	Small head; Head diameter < 12mm
2	Large head; Head diameter ≥ 12mm
3	Head producing few florets, but not complete flowering
4	Head in full flower, beginning after a full ring of florets has emerged around entire circumference of head
5	Head post-anthesis
6	Head fully dispersed

Table 3: Explanation of damage scores assigned to Platte thistle flower heads. Percentages represent the proportion of each flower head receptacle base that is estimated to be damaged.

Damage Score	Meaning
1	Damage suspected; 0-20%
2	Slight damage; 20-40%
3	Moderate damage; 40-60%
4	Significant damage; 60-80%
5	Extreme damage; 80-100%
6	Special score-Hole present in head

Table 4: Characterization of biotic conditions at upper Arkansas River valley (Chaffee County CO) study sites. Biomass was collected in 2019 and 2020. Flowering phenology was tracked from 2017-2019. Letters in parentheses correspond to p-values less than 0.1.

Site Name	Mean net primary productivity (g/m ²)	Mean first date of flowering (# of days since Jan 1))
Centerville	104.18 (AB)	168 (a)
Brown's Creek	138.04 (A)	170 (ab)
Lost Creek	99.82 (AB)	174 (bc)
Forman's	82.26 (B)	174 (bc)
Forest 300	121.18 (AB)	175 (bc)

Table 5. Precipitation and mean annual temperature for each calendar year during which experiments were conducted at the range center in Nebraska (Louda et al. 1990) and at the range edge in Colorado (the current study). Data in Louda et al. 1990 from the range center were collected 1983-1986. Data in Taylor (2020) from the range edge were collected 2017-2020. Climate data were obtained from High Plains Regional Climate Center. *2020 data are from Jan. 1 – Sept. 30.

Year	Range Center Precipitation (cm/year)	Range Edge Precipitation (cm/year)	Range Center Temperature (°C)	Range Edge Temperature (°C)
1984	36.45	31.27	8.5	6.1
1985	44.96	25.43	7.5	6.4
1986	47.32	29.97	9.7	6.7
2017	48.11	26.47	10.0	8.4
2018	69.04	15.47	8.8	8.1
2019	55.19	26.67	8.3	6.4
2020 *	39.80	11.18	11.6	9.2

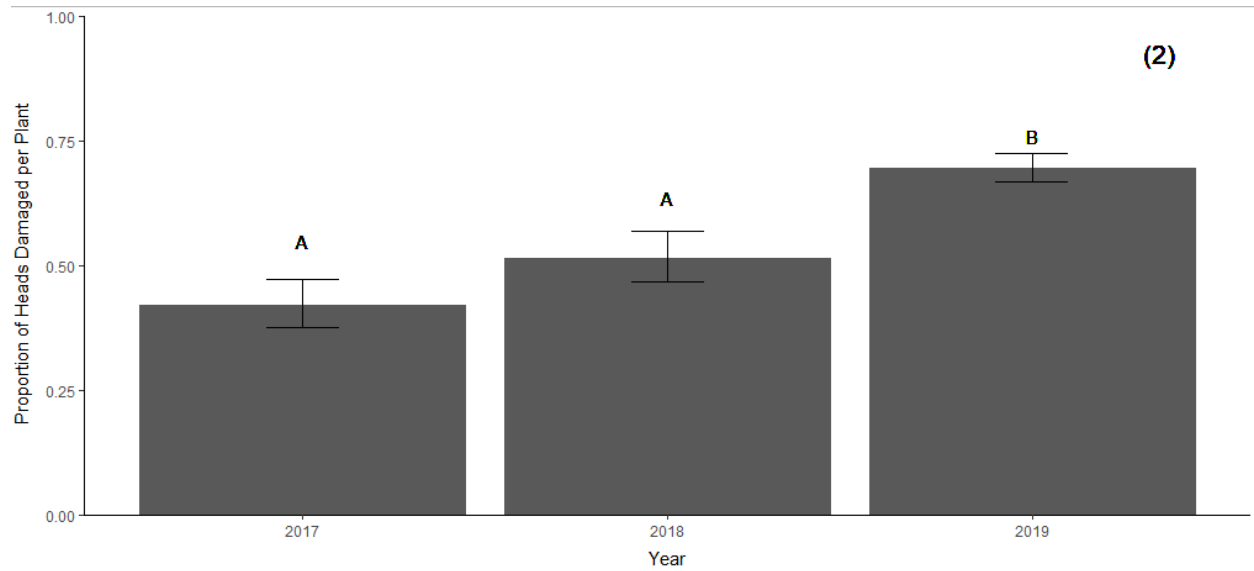
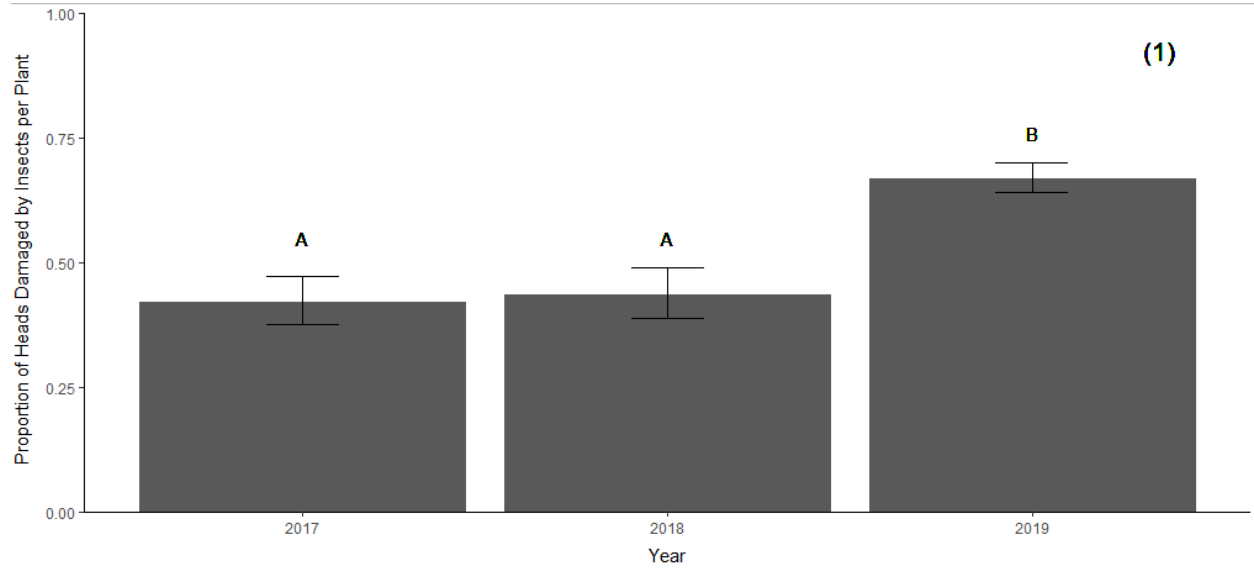


Figure 1. Mean proportion of heads damaged per plant for untreated adult Platte thistle at species range edge in Colorado from 2017-2019. Figure 1.1 represents damage from insects, and Figure 1.2 represents damage from any herbivore. Error bars represent standard error.

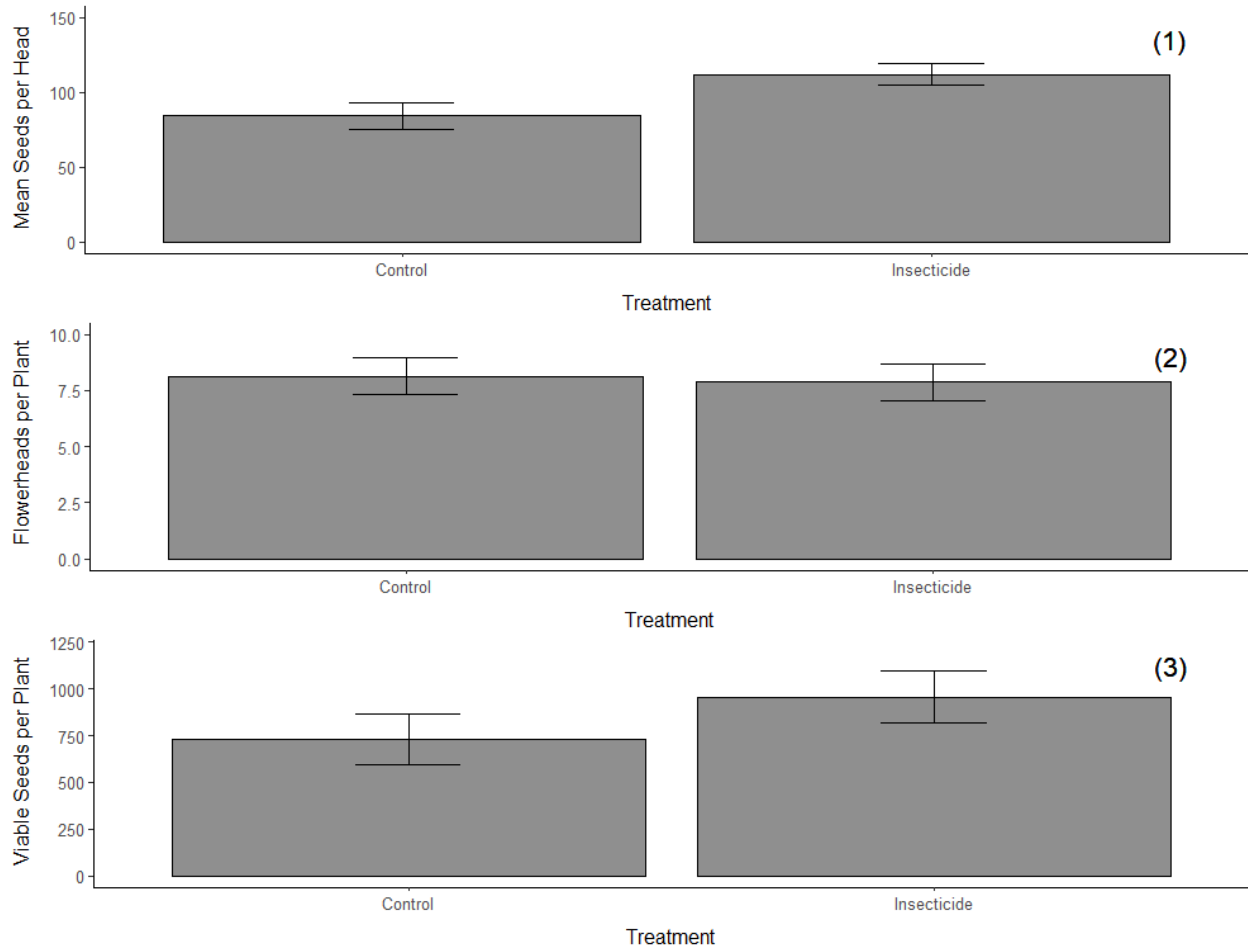


Figure 2. Mean number of viable seeds per head (1), mean number of heads that flowered per plant (2), and mean number of viable seeds per plant (3) for control and insecticide-treated Platte thistles in 2019. 2019 was the one year in which the insecticide was effective in reducing damage and no flower heads were damaged by the application of Tanglefoot. Error bars represent standard error.

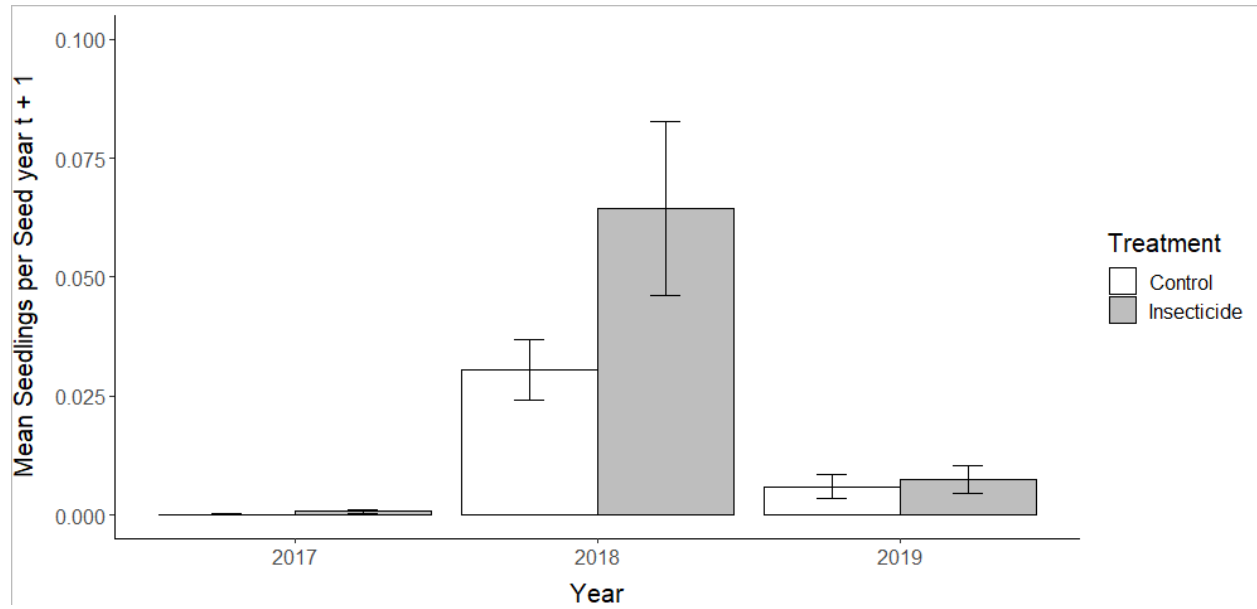


Figure 3. Mean number of seedlings per seed in the first year after bolting at the range edge in Colorado for both insecticide treatments for 2017-2019. Error bars represent 95% standard error.

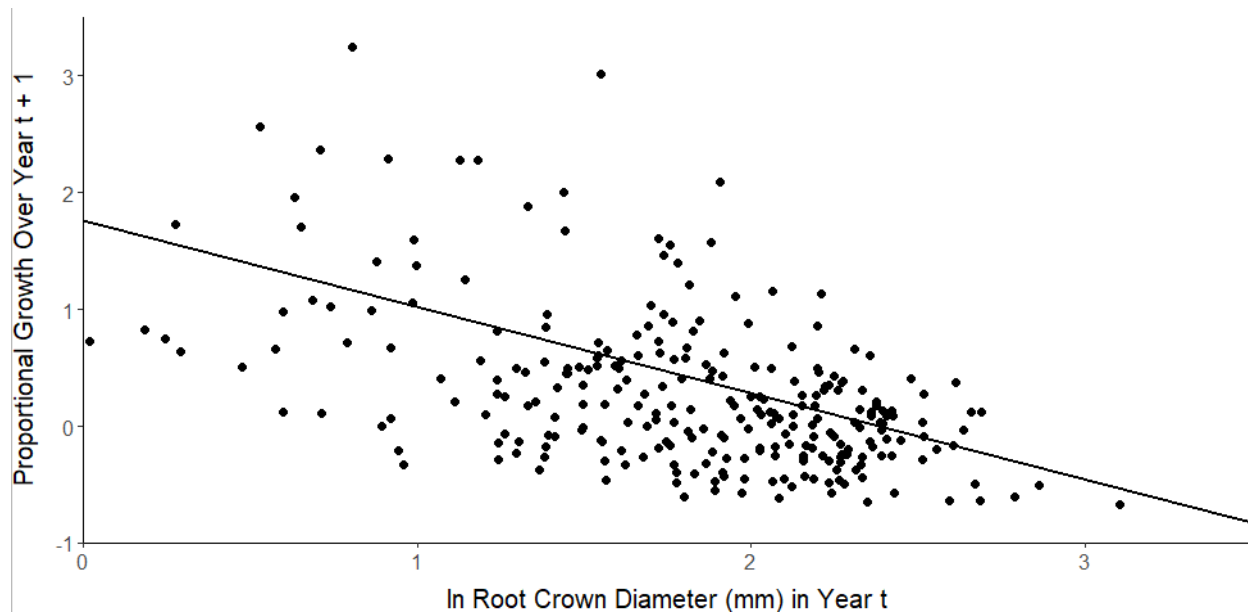


Figure 4. Proportional growth of juvenile Platte thistles at the range edge in Colorado. Shown as proportional growth over year $t + 1$ based on plant size in year t . Proportional growth was calculated by dividing the difference in root crown diameter in year $t + 1$ and year t by the root crown in year t .

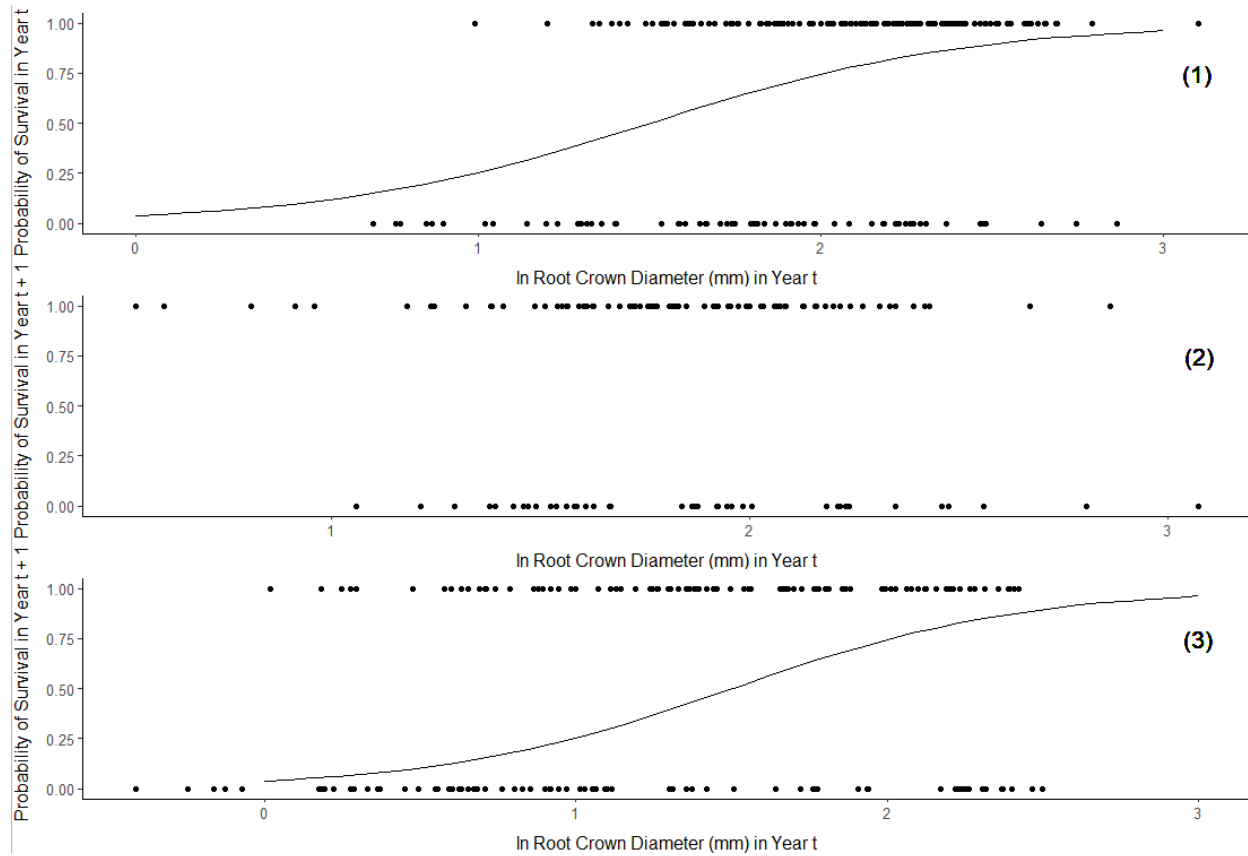


Figure 5. Probability of survival in year $t + 1$ at the range edge in Colorado for 2017 (5.1), 2018 (5.2), and 2019 (5.3). Shown as probability of survival in year $t + 1$ based on plant size in year t . Points represent survival data (0 = Did Not Survive, 1 = Survived). Curves represent significant relationships.

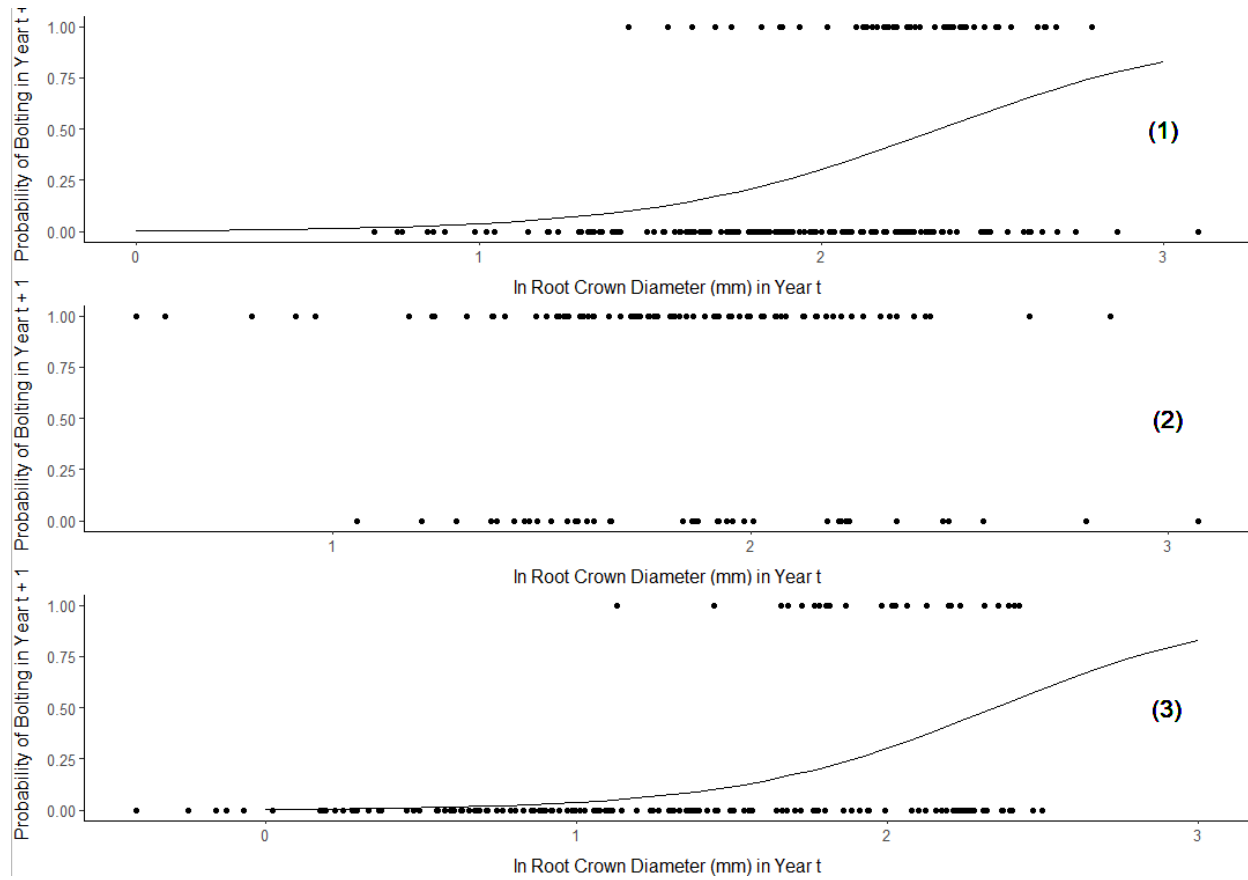


Figure 6. Probability of bolting in year $t + 1$ at the range edge in Colorado for 2017 (5.1), 2018 (5.2), and 2019 (5.3). Shown as probability of bolting in year $t + 1$ based on plant size in year t . Points represent bolting data (0 = Did Not Bolt, 1 = Bolted). Curves represent significant relationships.

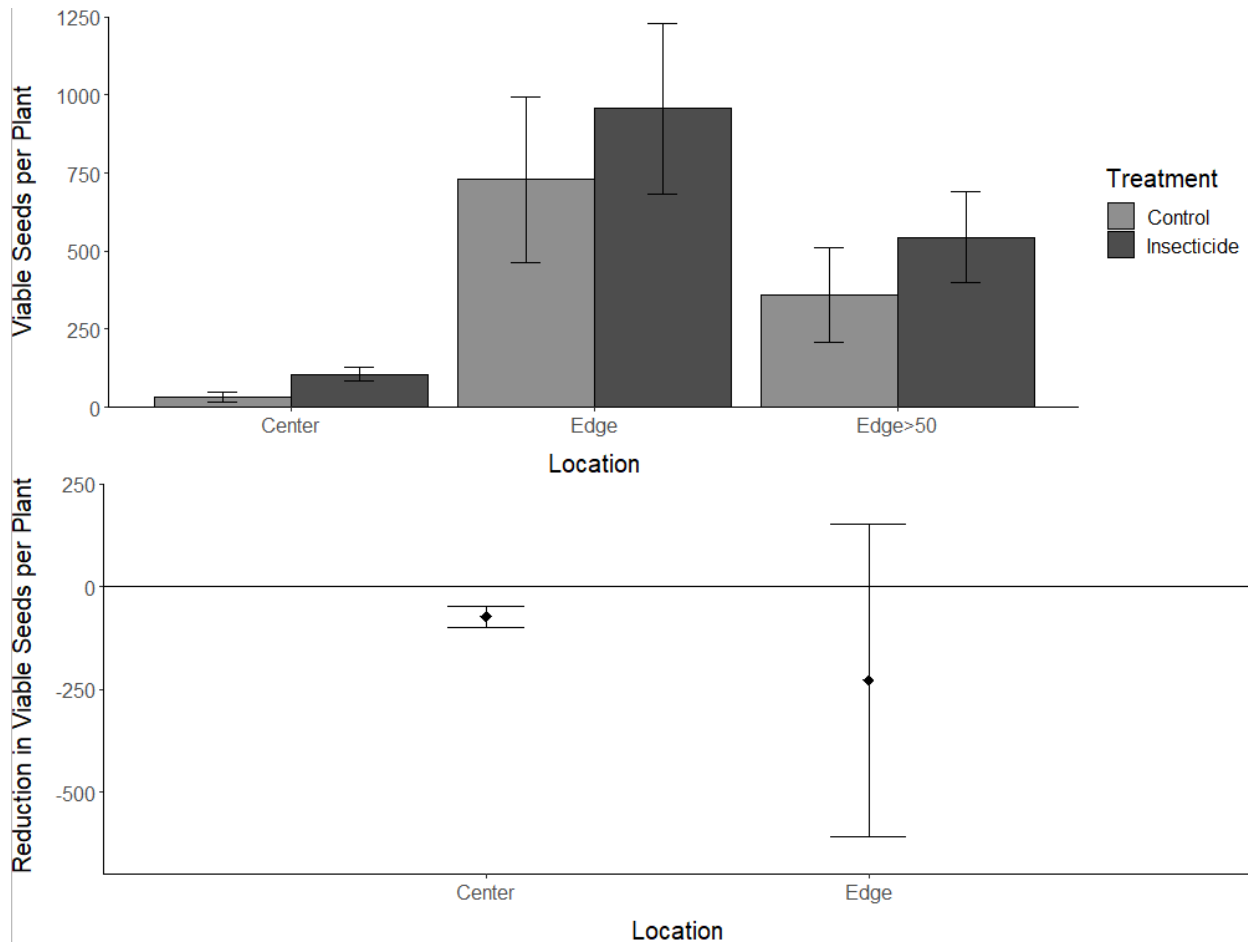


Figure 7. Mean viable seeds produced per plant for each treatment at both range center in Nebraska and range edge in Colorado (3.1) and reduction in mean viable seeds from insect damage (3.2). Range edge means are from 2019, as it was the year in which my insecticide treatment was effective, and no heads were lost to Tanglefoot ‘Edge’ group represents data collected from all plants at range edge, and ‘Edge>50’ group represents plants for which more than half of flowered heads were successfully collected and dissected. Error bars represent 95% confidence intervals.

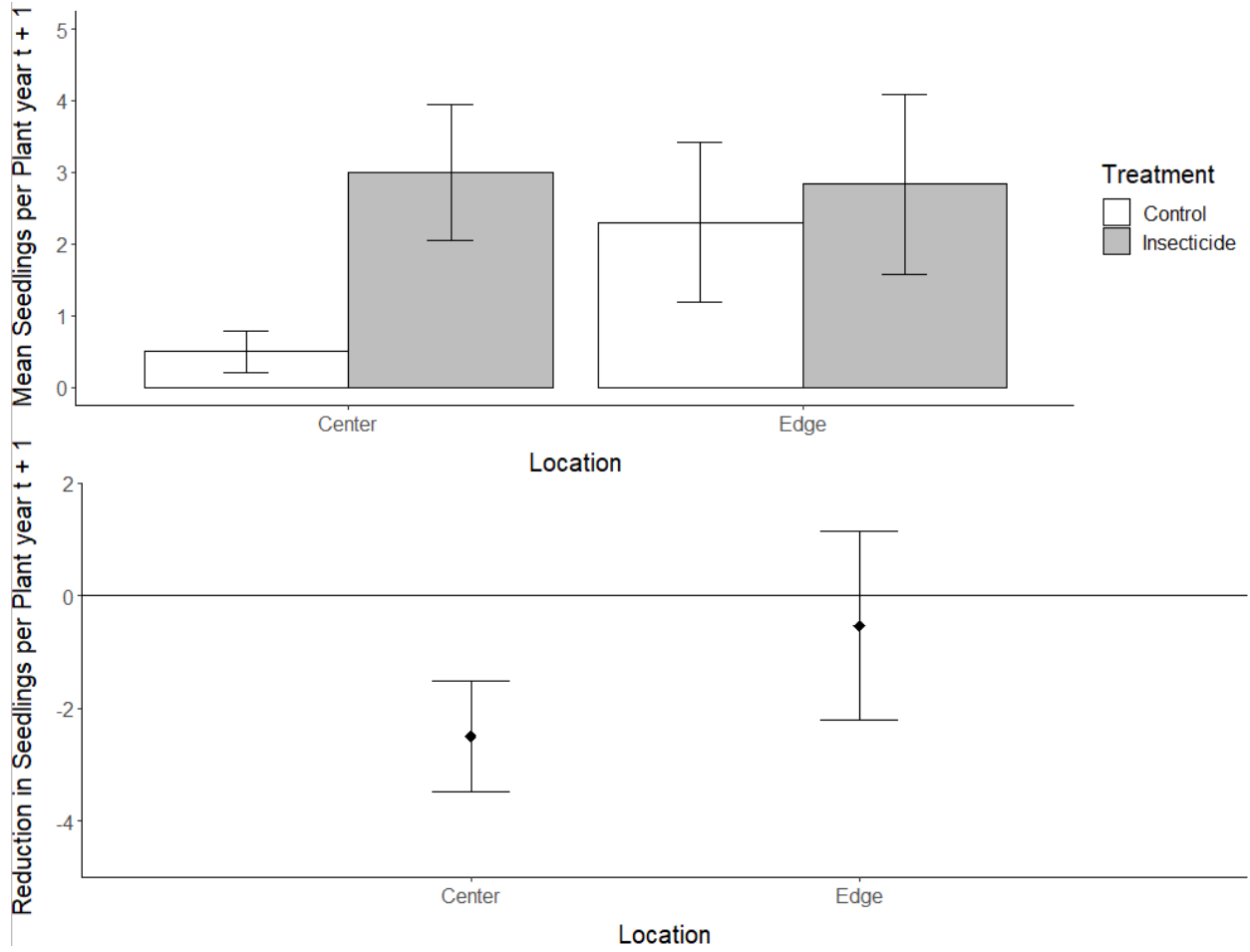


Figure 8. Mean number of seedlings per plant in year $t + 1$ at range center in Nebraska and range edge in Colorado in 2019 for both insecticide treatments. Error bars represent 95% confidence intervals

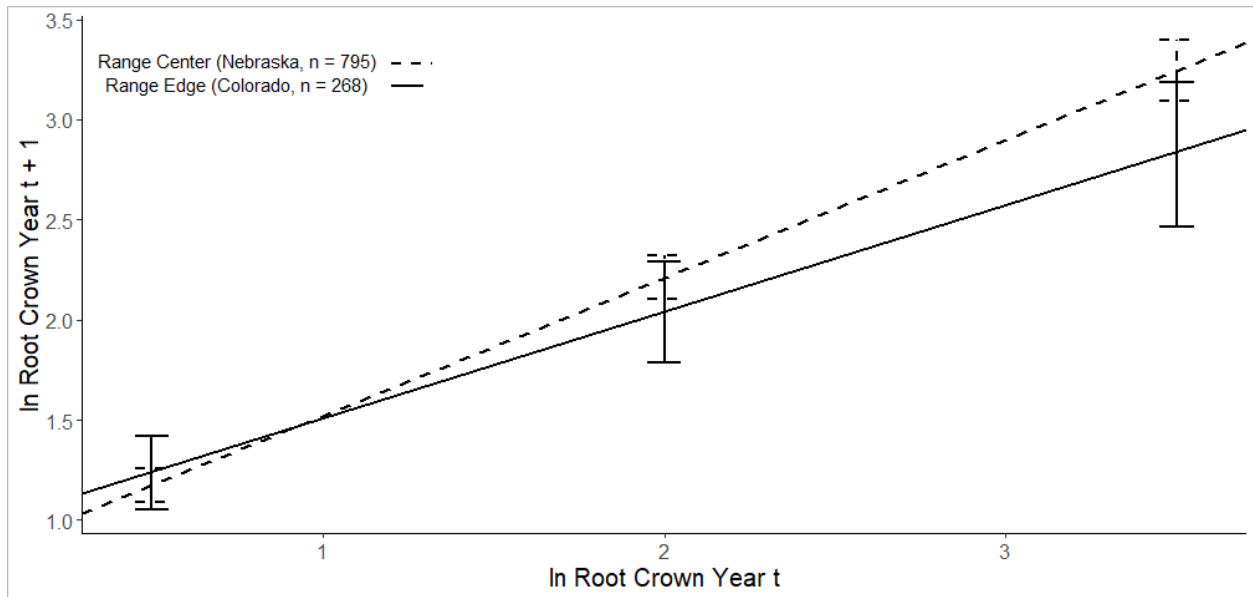


Figure 9. Growth of juvenile Platte thistles at the species range center in Nebraska (dotted line) and range edge in Colorado (solid line). Growth is shown as natural log of root crown diameter (mm) in year $t + 1$ based on size in year t . Error bars represent 95% confidence intervals.

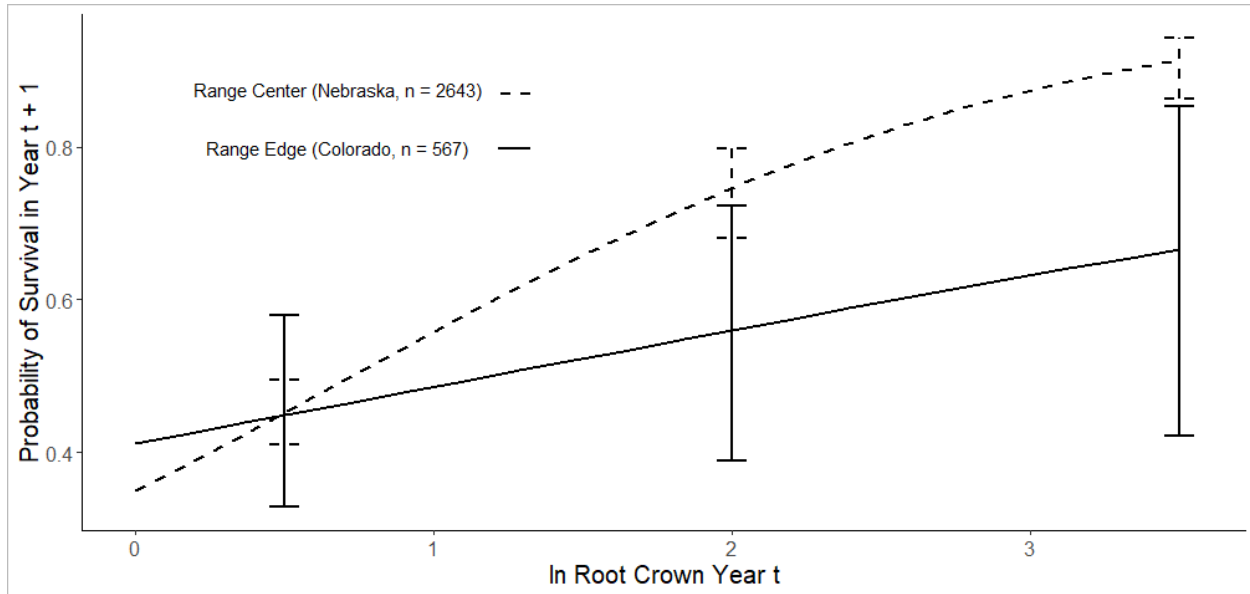


Figure 10. Probability of survival of juvenile Platte thistles in year $t + 1$ based on size (natural log of root crown diameter in mm) in year t at the species range center in Nebraska (dotted line) and range edge in Colorado (solid line). Error bars represent 95% confidence intervals.

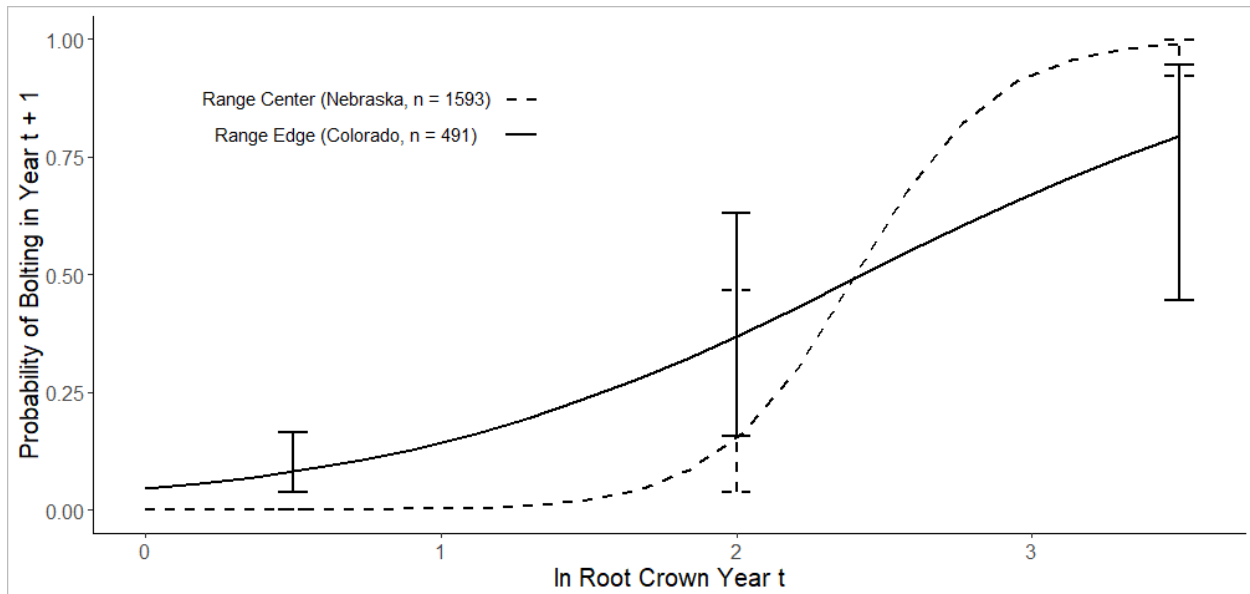


Figure 11. Probability of transitioning to bolting of juvenile Platte thistles in year $t + 1$ based on size (natural log of root crown diameter in mm) in year t at the species range center in Nebraska (dotted line) and range edge in Colorado (solid line). Error bars represent 95% confidence intervals.