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HERBIVORY AFFECTS PATTERNS OF PLANT REPRODUCTIVE EFFORT AND SEED PRODUCTION

by

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Insect herbivory can have a major influence on plant reproduction, and potentially drive selection for strategies that reduce or resist herbivore effects. I used a combination of field experiments and ecological modeling to examine how modifications in the patterns and timing of reproductive investment might ameliorate the consequences of herbivore damage for plant reproduction. I performed experiments to examine how changes in reproductive effort after apical damage and reduction of insect herbivory affected seed production in two thistles native to Nebraska. I then used field data to parameterize a life history model predicting the resource allocation among buds and size and timing of flowering that would optimize fitness under a continual risk of herbivory.

In monocarpic *Cirsium canescens*, insect herbivores had a severe impact on plant seed production. Plants did modify reproductive effort in response to apical damage. High seed production from a large apical head, as well as increased flowering and seed production with apical damage from later flower heads, played a role in improving seed production. However, changes in flowering and investment patterns were insufficient to compensate for high insect damage; plants had lower seed set under ambient herbivory. We found similar effects in the iterocarpic *Cirsium undulatum*, although plant responses were not consistent between years. The combination of these two experiments allowed us to quantify the influence of plant reproductive response on the consequences of insect damage, and how it varies between plants with different life history strategies.

To better understand how the risk of insect herbivory might shape optimal plant allocation patterns, I constructed a stochastic dynamic programming model (SDP) to examine the optimal allocation between flower heads through time, and the size and time at which buds should flower to maximize fitness. The model predicts optimal allocation patterns should vary with survival risk, and plants should favor strategies that reduce the duration of risk. Both the model and experiments demonstrate the pressure insect herbivores can exert over plant reproductive strategies, and broaden our understanding of how ecological interactions can affect influence basic life history decisions.

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Chapter 1.

Variation in cumulative insect floral herbivory affects expression of plant tolerance

Abstract. Insect floral herbivory can dramatically reduce plant reproductive success. Thus, plants should have evolved mechanisms that minimize the effect of insect herbivores, particularly in monocarpic species that must maximize fitness in a single flowering year. Tolerance is one such mechanism; however, few experiments to date evaluate underlying mechanisms of plant tolerance under natural conditions. We compared plant seed production by the monocarpic *Cirsium canescens* (Platte thistle) in control (undamaged) plants versus plants with damage imposed upon the apical, flower head. We hypothesized that *C. canescens* would tolerate damage to its large, early, apical flower head by increasing reproductive effort in subsequent flower heads, compensating for potential fitness loss under herbivore pressure during its final, fatal, flowering season. In addition, we examined the consequences of each damage treatment in plants with versus without experimentally reduced subsequent floral herbivory. We found that plants under ambient herbivory (unprotected subsequent heads) undercompensated for the loss of apical seed production; total plant seed set was lower when the large apical flower head was damaged. However, when insect herbivory was reduced on the later flower heads, significant compensation for apical seed loss occurred. The compensation reflected greater seed maturation by later flower heads, rather than greater subsequent flower head production, indicating that the total number of flower heads was constrained. These results provide the first analysis of plant mechanisms that reduce the effects of insect floral herbivores on *C. canescens*, a well-studied species in which the local abundance and population dynamics are strongly influenced by insect herbivory. Further, the study highlights the importance of considering how variation in the intensity of biological interactions can determine the success of plant tolerance strategies to maximize individual plant fitness.

Keywords: apical dominance, Cirsium, herbivory, insect herbivory, plant population, plant reproductive biology, plant tolerance, plant-insect interaction, thistle

INTRODUCTION

Insect floral herbivory represents a major challenge to fitness for many monocarpic plants. Destruction of developing inflorescences and seeds, sometimes called predispersal seed predation, affects many species (Janzen 1971, Harper 1977, Crawley 1992). Floral consumption often dramatically reduces plant reproductive success (Louda 1982, Hendrix 1988, Crawley 1992, Karban and Strauss 1993, Louda and Potvin 1995, Crawley 1997, Krupnick et al. 1999, McCall and Irwin 2006), and can significantly lower plant population growth rate (Tenhumberg et al 2008) and, thus, plant population density (Louda 1983, Louda and Potvin 1995, Kolb et al. 2007, Jongejans et al. 2008). Whereas iterocarpic plants have multiple reproductive bouts in which to increase fitness in the presence of high, but variable, floral herbivore pressure, monocarpic species must maximize reproductive fitness in their single flowering season. Therefore, where monocarpic plants are consistently exposed to intense floral herbivory, plant responses that increase tolerance for within-season reproductive losses to herbivores would be expected to provide an important contribution to plant fitness (Järemo and Palmqvist 2001).

Compensatory reproductive effort has been proposed as an important tolerance mechanism to ensure reproductive success despite substantial herbivory (Strauss and Agrawal 1999, Huhta et al. 2000, Lehtilä 2000). Compensatory reproductive response to floral herbivory has been observed and demonstrated in some species (Whigham and Chapa 1999, Hawkes and Sullivan 2001, Klimešová et al. 2007). However, the ecological dynamics, magnitudes of response, and fitness consequences of reproductive compensation as a tolerance mechanism for floral herbivory under field conditions remain largely unexplored (Hendrix 1988, Tiffin 2000, Valladares et al. 2007).

Plant resistance to herbivory, involving minimization of damage by enhanced defenses, has received extensive study (e.g., Ehrlich and Raven 1964, Agrawal 2005, Boege et al. 2007, Heil 2008). Plant tolerance to herbivory, involving minimization of the consequences of herbivore damage on plant growth or reproduction (e.g., Pilson 2000, Tiffin 2000, Pilson and Decker 2002, Wise et al. 2008), has received much less attention (Stransky 1984, Stowe et al. 2000, Banta et al. 2010). Further, previous research on tolerance has focused primarily on compensation for foliar losses, especially to ungulate grazing (e.g., McNaughton, 1983, Tuomi et al. 1994), and on evolutionary aspects of the reproductive response to herbivory, such as flowering pattern (Lloyd 1980, Lovett Doust and Lovett Doust 1988), optimal resource allocation to reproduction (Miller et al 2008), sex allocation (Brunet 1996, Sanchez-Lafuente 2007), and suites of traits that give rise to tolerance (Pilson and Decker 2002, Östergård et al. 2007, Wise et al. 2008). Few experimental field studies to date have evaluated the degree to which changes in the within plant distribution of flowering and seed production occur in response to insect floral herbivory or the extent to which such responses succeed in compensating for herbivory losses within natural plant populations (Trumble et al. 1993, Huhta et al. 2000).

Herbivory tolerance due apical damage has been perceived as arising from a quantitative response in branch number or in flower head number, i.e., more branching or more flower head buds activated or developed when apical dominance is broken (Aarssen 1995). However, more experimental evaluation of this expectation is needed under natural conditions, to provide information on: components of the plant flowering response; consequences for fitness following damage to the initial apical flower head; and the relative contribution of apical dominance and subsequent flowering to tolerance.

The aim of our experiment was to develop a better mechanistic understanding of plant tolerance to herbivory and quantify the benefit of plant tolerance with respect to the fitness of monocarpic plants under field conditions. As a case study, we manipulated apical damage and subsequent floral herbivory to quantify the response in flowering and successful fruit by *Cirsium canescens* Nutt. (Platte thistle), a well-studied, monocarpic, native plant characteristic of sand prairie in the Great Plains (Kaul et al. 2007). Prior experimental evidence has shown that intense insect floral herbivory significantly reduces average plant fitness and population density, and lowers the population growth rate of *C. canescens* (Lamp and McCarty 1981, Louda et al. 1990, Louda and Potvin 1995, Rose et al. 2005). Therefore, we would expect to find modifications in plant growth and allocation that increase individual plant fitness might provide some degree of insect herbivory tolerance.

We evaluated this prediction by quantifying patterns in plant response to experimentally-imposed early-season insect herbivory on the largest flower head, the initial apical head, compared to controls. In addition, each apical treatment was divided into plants with versus and without experimental reduction of herbivory on the subsequent, later flowering heads. Previous work showed that herbivory on the apical flower head is often severe, but highly variable in occurrence (Louda and Potvin 1995); also, the proportion of individuals within a season that have aborted apical flower heads due to insect damage can be as high as 50% (Lamp 1980). Similarly, herbivory on subsequent heads is severe, but highly variable among individuals (Lamp 1980, Louda and Potvin 1995). When the apical flower head of *C. canescens* escapes herbivory, it contributes substantially to plant fitness by producing more seeds than do later flower heads (Louda and Potvin 1995). Since apical dominance leads to unequal partitioning of resources (Cline 1991, Obeso 2002), loss of this particular flower head could have disproportionate consequences for plant fitness.

Based on plant allocation theory, we expected damage to the apical head to lead to significant increases in the number of subsequent, lower-positioned flower heads that develop and reach anthesis, compensating or potentially overcompensating for early apical head seed losses (Tuomi et al. 1994, Aarssen 1995, Banta et al. 2010). Reproductive structures represent high priority resource sinks, and loss of apical dominance allows activation of dormant buds (Cline 1991, Obeso 2002). Therefore, increase in branching or in subsequent flower head development after release from apical dominance is expected to aid in plant tolerance for herbivory (Cline 1991, Marquis 1996, Strauss and Agrawal 1999, Obeso 2002).

We also expected that a reduction of herbivory on subsequent flower heads, simulating the observed variation in insect damage among individuals, would show the plant's capacity for compensatory response under field conditions (Figure 1.1A). Seed production in *C. canescens* is not resource limited (Louda and Potvin 1995). Thus, we reasoned that when herbivory on subsequent flower heads was reduced, relatively more later, lower positioned, sub-apical flower heads (Figure 1.1B) would develop through flowering and set seed than would develop under higher average (ambient) levels of herbivory. If so, then the flowering response would demonstrate the extent of tolerance via plant compensatory response to apical flower head damage (Figure 1.1A). Thus, the overall aim of the experiment was to evaluate the magnitude and ecological dynamics of potential compensatory reproductive effort as a tolerance mechanism for floral herbivory.

Thus, we asked three questions: 1) Does the outcome of apical damage interact with variation in subsequent insect floral herbivory to affect total seed reproduction by *C. canescens*?; 2) What changes occur in plant structural investment (i.e., numbers of flower buds or branches) or in plant reproductive effort (i.e., numbers of flowering heads or seeds matured), and are these response patterns similar under different levels of herbivory?; and, 3) Is the within plant distribution of subsequent flowering effort and seed production altered after apical damage, and do differences in the level of floral herbivory on the subsequent, later-flowering heads affect the realized plant fitness outcome? The experimental results demonstrate complex variation in the ecological tolerance response.

METHODS

Study System

Cirsium canescens (Platte thistle) is a short-lived, monocarpic perennial that is native to sand and gravel soils of the upper Great Plains and southern Rocky Mountains (Kaul et al. 2007). This taprooted, monocarpic plant grows as a rosette for two – eight years prior to its reproductive year (Louda and Potvin 1995). As a flowering adult, *C. canescens* produces large flower heads with cream-colored flowers, opening from mid- to late-May through late-June; reproduction is solely by seed (Lamp 1980, Kaul et al. 2007). Flowering is determinate and begins with the initial, terminal, apical flower head (capitulum); the undamaged apical flower is usually the largest flower head produced

(Louda and Potvin 1995). Over the season, subsequent flower heads (capitula) develop basipetally, flowering sequentially from the terminal apical head down the stem or down each branch below the apical head.

The five native floral- and seed-feeding herbivores at our site were: two tephritid flies (*Paracantha culta* Wiedemann, *Orellia occidentale* Snow), two pyralid moths (*Pyrausta subsequalis* Gn., *Homoeosoma eremophasma* Neunzig [complex]), and a weevil (*Baris* nr. *subsimilis* Walker) (Lamp 1980, Louda and Potvin 1995). In addition, the Eurasian flower head weevil (*Rhinocyllus conicus* Frölich) invaded the floral-feeding guild in 1993 (Louda et al. 1997, Louda 1998). The feeding damage (Lamp and McCarty 1981) and the population level impacts (Louda et al. 1990, Louda and Potvin 1995, Rose et al. 2005, Russell and Louda 2005) of floral herbivory by these six floral herbivores have been documented. However, no analysis to date has experimentally evaluated plant flowering responses and their role as potential tolerance mechanisms for the extensive, but variable ambient floral herbivory documented in this system.

Study Site

The study was done at six sand prairie sites in Arthur County, western Nebraska, in the upper Great Plains, USA. Three sites were within Arapaho Prairie Preserve, a 1,200 ha reserve owned by The Nature Conservancy and managed for research by the University of Nebraska Cedar Point Biological Station. Management since 1977 has involved the exclusion of cattle grazing, plus hay mowing in successive quarters on a four-year rotation (Keeler et al. 1980, Louda and Potvin 1995). Three additional sites were in private ranchlands surrounding Arapaho Prairie; these are managed for sustained long term cattle productivity (Delwin Wilson, personal communication).

Experimental Protocol

We did two experiments (2007, 2008), and used the same protocol for each year's flowering cohort. The experimental design involved manipulating both apical head damage [AD] (damaged: "Apical Damage" [D]; versus not damaged, protected with insecticide: "No Apical Damage"[N]), and subsequent floral herbivory [H] on the later, lower, non-apical flower heads (insecticide-in-water = "Reduced Herbivory" [R] versus water-only control = "Ambient Herbivory" [A]) in a 2 x 2 factorial experiment with a completely randomized design (Figure 1A). We therefore had four treatment groups: 1) apical damage with reduced subsequent herbivory on lower heads (AD_D x H_R); 2) apical damage with ambient subsequent herbivory on lower heads (AD_D x H_A); 3) undamaged, protected apical head with reduced subsequent herbivory on lower heads (AD_N x H_R), and 4) undamaged, protected apical head with ambient subsequent herbivory on lower heads (AD_N x H_A).

In early season each year at each site, we selected and marked plants that were initiating an apical flower head bud within the center of the rosette (5 - 10 May 2007, 26 April - 10 May 2008); new plants had to be chosen each year because flowering is fatal. In 2007, we had 15 replicates of each of the four treatments (total n = 60 plants). In 2008, we increased the number of replicates to 35 for each of the four treatments (total n = 140 plants). Each replicate block consisted of four plants, matched by initial plant and apical flower head size to control for any effect of variation in early season size on treatment response. Initial plant size was measured as a combination of rosette diameter (cm), apical bud diameter (mid, mm), and total number of flower head buds initiated. We assigned the four treatment combinations randomly within each replicate block.

The apical head damage treatment simulated flower bud damage observed in the field that severely slows or stops apical flower head development, often causing the flower head to abort (unpublished data); up to 50% of flowering individuals a season suffer this damage in the field (Lamp 1980). We imposed apical flower head damage on the two plants randomly assigned to the apical head damage treatment within each replicate. To impose damage in 2007, we collected and caged three early thistle-feeding insects onto the flower head in 1 mm-mesh bags for 1 wk. (one native moth larva, *P. subsequalis* plus two adult native weevils, *B. subsimilis*), after drilling a small hole into the lower part of each flower head to facilitate moth larval entry. At the end of the week, we removed the bag. If the damage imposed did not appear to be comparable to that which impeded flower head development naturally, we further damaged the head using a razor blade to partially sever vascular transport from the stem to the flower head. In 2008, early insect abundances were low; thus, we set up both five replicates using insects, as in 2007, and an additional 30 replicates using only the mechanical damage (drilled hole + partial girdling), as in 2007. The effects of the two techniques of apical head damage (insect + mechanical damage vs. mechanical damage only) did not differ significantly in their effect on seed production (mixed effects GLM with plant as a random effect: seed set per head, $p = 0.77$; seed set per plant, $p = 0.69$). Thus, we present the combined data here. Plants in the apical damage treatment differed in the severity of damage realized. However, plant response did not differ qualitatively between plants with more versus less severe apical damage; plants with relatively less severe damage actually had a slightly greater response (Appendix 1.1). Apical heads assigned to the undamaged treatment were treated with insecticide (see below) to prevent apical damage.

The second treatment compared reduction of subsequent floral herbivory (H_R, reduced herbivory) to controls (H_A, ambient herbivory), simulating the variation observed in later insect herbivory during the season (Louda and Potvin 1995, unpublished data). On one apically damaged plant and one apically undamaged plant per replicate, we reduced subsequent floral herbivory by spraying all non-apical flower heads individually with insecticide-in-water. The other two plants (one apically damaged, one apically undamaged) received water-only spray as a control. In 2007, we used the insecticide Acephate (Isotox^R, Chevron Corp), applied every 7 – 10 d in a 1% solution. In 2008, in an effort to increase insecticide effectiveness, we used the insecticide bifenthrin (FMC Corporation Pty Ltd.), applied every 14 d in a 0.06% solution. The insecticide treatment each year was only partially effective, reducing floral herbivory on the later, lower flower heads by 28 - 30% (see Results).

Data Collection

After quantifying initial plant and flower head sizes when replicate blocks were created and the treatments imposed (8 - 10 May 2007; 11 - 13 May 2008), we measured the magnitude and distribution of reproductive effort every 2 wk in 2007 (to 31 July), and every 4 wk in 2008 (1 - 3 June, 1 - 3 July, 29 July – 2 Aug). On each sampling date for each plant, we recorded flower head diameters (mm) of terminal flower heads on all branches and counted the total number of smaller, subtending flower heads on each branch (Figure 1.1B). We also recorded plant height (cm), rosette diameter (average of two perpendicular diameters, cm), total number of branches per plant (> 1 cm long), and total number of flower heads initiated per plant. These data allowed us to incorporate the effects of plant size on treatment response in the statistical analyses (below).

As flower heads and branches senesced, we collected each flower head that matured (exerted at least one floret) for dissection. For each mature flower head collected, we recorded: mass (g); diameter (mm); number of developed, undamaged seeds; and amount of insect damage to the inflorescence receptacle, florets, and developing seeds. To quantify amount of internal damage by insects, we divided each flower head into four sections, and assigned a damage score to each quarter; this damage score was based on the percent area of the receptacle, florets and seeds in a quarter that were damaged: 0 = 0 - 1%; 1 = 1.1 - 10%; 2 = 10.1- 30%; 3 = 30.1 - 50%; 4 = 50.1 - 75%; and, 5 = 75.1 - 100%. The total damage score for the flower head was calculated as the average of the four individual quarter scores. For analysis, this mean score was converted to a proportion represented by the mid-point of its damage interval (e.g., score 1 = 0.005, score 2 = 0.15, etc.), providing a conservative estimate of mean damage per flower head.

Data Analysis

Plants were significantly larger in 2007 than in 2008 (both initial and final size estimates: Appendix 1.2); most parameters of plant performance and reproduction differed significantly between years (below). Thus, we first analyzed the interaction between treatment and year; we found no significant qualitative differences in the effects of treatment between years ($p > 0.10$ for all treatment x year interactions). Further, treatment effect on plant seed number did not differ significantly between the two annual experiments (ANCOVA, number of branches as a covariate for plant size, $p = 0.69$). So, to maximize our sample size for the analysis of treatment response, we combined the data from both years and incorporated year either as a random effect or as a covariate depending on the analysis.

All analyses were performed in R (R Core Development Team 2011). To ensure that initial size differences among treatments did not affect treatment outcomes, we first analyzed initial measurements (5 - 10 May 2007, 26 April - 10 May 2008) for number of flower heads per plant, mean rosette diameter, and apical head diameter, as a composite dependent variable representing plant size, using MANOVA with Pillai's trace test statistic. Although initial plant size parameters were significantly larger in 2007 compared to 2008 ($p \leq 0.001$; Appendix 1.2), no significant differences in initial size occurred among the four treatments within year (treatment x year: $p > 0.10$ for all variables).

To examine the effect of insecticide treatment on the amount of insect damage to flower heads, the mean internal damage per flower head proportion was arcsine-transformed prior to analysis to improve normality. Transformed proportions were evaluated in a mixed effects model, with year and plant as random effects.

To evaluate treatment effects on plant structural investment, we performed a MANOVA with year as a covariate. We analyzed final measurements of plant height, rosette diameter, number of branches, and number of flower heads per plant as a composite dependent variable representing final differences in plant structural investment.

To determine treatment effects on plant reproductive effort, we performed a second MANOVA with year as a covariate. We included both total number of flowering heads and number of flower heads that produced seeds (matured) in a composite dependent variable in that MANOVA. Both variables were included into the measure of reproductive effort since many heads that matured (exerted flowers) were heavily damaged and did not succeed in producing any viable seeds (see below).

When significant treatment effects or interactions occurred in the MANOVA, we subsequently examined each of the significant dependent variables included, using separate ANOVAs to determine which plant characters contributed to the differences observed among treatments. When ANOVAs were significant, we examined: (1) effect of apical damage within each herbivory treatment (H_A: Apical Damage versus No Apical Damage; H_R: Apical Damage versus No Apical Damage), and (2) the overall effect of subsequent herbivory (H: Ambient versus Reduced). These contrasts were designed to evaluate the evidence as tolerance for floral losses. First, did plants compensate for loss of the large apical head and, if so, under ambient as well as reduced herbivory? Second, among apically damaged plants, was seed production by plants under ambient herbivory equivalent to that found under reduced herbivory?

Under the high levels of ambient floral herbivory, we found that many flower heads produced few or zero undamaged seeds, resulting in a strongly left-biased distribution. Therefore, to analyze seed production by treatment, we used maximum likelihood to determine the most appropriate distribution for analysis of plant seed production; for the generalized linear model to evaluate plant seed production by treatment, the best fit was a negative binomial distribution (function glm.nb). When an interaction was significant in the overall ANOVA, we evaluated the effect of herbivory, and the effect of apical damage within insecticide treatment, with separate models (as above). We found a significant effect of year on plant seed production ($p < 0.010$), so year was included in the analysis as a covariate.

We analyzed seed set per flower head by head position on a plant (Figure 1.1B) and by treatment, with plant and year as random variables, in a linear mixed effects model (lme function), in order to evaluate how treatments influenced distribution of seed production within plants. Prior to analysis, number of undamaged, filled ("good") seeds per head was square root-transformed to approximate normality.

To examine the relative amount of seed production among treatments, we also calculated an estimate of expected (potential) seed production per flower head based on flower head size. To do so, we used published regressions for the number of undamaged filled seeds expected in relation to flower head size (Louda and Potvin 1995). To estimate the proportion of potential seed production realized, we divided observed seed count per head by the seed production potential expected per head, in order to assess whether a plant displayed tolerance after apical damage by compensatory seed production, under reduced and ambient herbivory. Both estimated whole plant seed production potential, and the percent realized good seeds per plant, were analyzed with generalized linear models followed by separate subsequent analyses of effects of herbivory and of apical damage within herbivory treatment, as above. Potential and realized seed production per flower head by treatment and by flower head position were analyzed with linear mixed effects models, with year and plant included as random effects. Proportions were square root-transformed before analysis.

For simplicity, relevant p-values for all analyses are reported in the Results, and full statistical tables are presented in the appendices (Appendix 1.3 and 1.4).

RESULTS

Initial size and floral herbivore damage levels

Initial size. Plant size initially did not vary among treatments (MANOVA: p_H = 0.67; p_{AD}= 0.59, Appendix 1.3B*i*.). Rosette diameters ranged between 28 - 31 cm, and apical bud diameters ranged from 21 - 24 cm. Each plant had 3 - 4 flower head buds at the start of each experiment. Also, no interaction occurred between apical damage treatment and herbivory treatment (MANOVA: $p_{H\,x\,AD}$= 0.21). Because initial conditions among treatments were comparable, final plant differences represent treatment responses.

Levels of Flower Head Damage. Variation in the level of damage we succeeded in imposing to the apical flower head did not influence the level of internal insect feeding on later, lower flower heads (Table 1.1A*i*, Appendix 1.3A). The average damage score per non-apical head did not differ significantly between apical damage treatments within each herbivory treatment (p_{AD} = 0.64). As is typical, the insecticide treatment did not eliminate floral herbivory, but only decreased it, in this case, by 28 - 30% (Table 1.1A). The insecticide did significantly reduce insect damage to later flowering heads ($p_H <$ 0.01). With ambient herbivory (water-only spray), later heads averaged 72% and 78% internal insect damage for plants with and without experimental apical damage, respectively. However, with reduced herbivory (insecticide spray), later heads averaged 48% internal insect damage both with and without experimental apical damage (Table 1.1A). Additionally, individual plants varied widely in the amount of subsequent flower head damage they experienced; variation was higher in the reduced herbivory treatment (Fig. 1.2A) than in the ambient herbivory treatment (Fig. 1.2B). Overall, we found no evidence that apical damage altered floral herbivory to later flowering heads.

Effects of apical damage and subsequent insect herbivory on total plant seed production

The outcome of apical damage for the plant was altered (Fig. 1.3), and total plant seed production was significantly increased (Table 1.1A), by reducing subsequent herbivory. Apical damage and herbivory on later, non-apical, heads interacted to influence the total number of undamaged ("good") seeds produced by a plant ($p_{AD \times H} = 0.042$); the interaction also influenced estimated potential seed production and the degree to which seed production potential was realized (Table 1.1A*ii*, Appendix 1.4B: potential seed production $p_{AD \times H} = 0.023$, realized seed production $p_{AD \times H} = 0.021$).

Apical damage increased the number of undamaged seed successfully produced per plant under reduced subsequent herbivory, but decreased the number produced under ambient herbivory (Fig. 1.3A). Apical damage alone, however, did not significantly alter average plant seed production ($p_{H:R} = 0.20$, $p_{H:A} = 0.07$; Appendix 1.4A). Thus, compensation for apical head damaged occurred, but only when subsequent herbivory was lower.

Similar patterns occurred in the proportion of estimated potential seed that was actually realized per plant (Table 1.1A*ii*, Fig. 1.3B). No significant difference in estimated seed potential occurred between apical damage treatments ($p_{H:R} = 0.15$, $p_{H:A} = 0.05$, Table 1.1A*ii*); however, under ambient herbivory, the proportion of potential seed production realized decreased with apical damage, whereas under reduced herbivory it increased (Table 1.1A*ii*, Appendix 1.4B). This decrease in potential seed production under ambient herbivory, in addition to the direct seed losses under ambient herbivory, led to a significantly lower realized plant seed production with apical damage ($p_{H:A} =$

0.03, Fig. 1.3, Appendix 1.4B). However, under reduced herbivory there was no difference in potential seed production realized with apical damage ($p_{H:\,R} = 0.32$).

Therefore, apical damage did influence the pattern of seed production, but the consequences of apical damage depended on subsequent herbivory. Although strong compensation for apical damage occurred within the reduced herbivory treatment, plants within the ambient (higher) herbivory treatment had a decrease in seed production with apical damage, under-compensating for the damage to the initial large flower head. Regardless of apical damage condition, seed production by plants under higher ambient herbivory did not equal that of plants under reduced herbivory (Table 1.1). Therefore, even with apical damage, plants under-compensated for floral herbivory overall.

Effects on plant structure and subsequent reproductive investment

Neither apical damage nor insect herbivory treatments significantly affected final plant size (structural investment, Table 1.1B) or reproductive investment (Table 1.1C) directly (MANOVA: $p_{H} = 0.17$; $p_{AD} = 0.22$; $p_{H\,x\,AD} = 0.32$; Appendix 1.3B*ii*). However, the treatments interacted in their effect on plant reproductive investment, which was quantified as the combination of number of flower heads matured and number of matured flower heads that produced any undamaged seeds ($p_{H\,x\,AD} = 0.04$, Table 1.1C; Appendix 1.3B). Specifically, the number of flower heads matured (reached anthesis) was higher with apical damage only when herbivory on subsequent heads was reduced ($p_{H\,x\,AD} =$ 0.03, Table 1.1C, Appendix 1.3C). This increase reflected more mature flower heads on plants in the apical damage plus reduced herbivory treatment ($p_{H:\,R} = 0.049$). Apical damage made no difference in number of mature flower heads with ambient levels of subsequent herbivory ($p_{H:\,A} = 0.229$, Appendix 1.3C). Finally, the number of mature flower heads that actually produced any undamaged seeds was highest for plants in the apical damage plus reduced subsequent herbivory treatment ($p_{H\ x\ AD} = 0.01$; Table 1.1C; Appendix 1.3C); no increase was realized in mature seed-producing heads in the apical damage plus ambient subsequent herbivory treatment ($p = 0.696$).

Therefore, apical damage did not influence plant structural investment regardless of insect herbivory treatment on later heads. However, apical damage led to an increase in reproductive investment realized by plants with reduced levels of subsequent herbivory that was not observed for plants with ambient subsequent herbivory.

Influence of floral herbivory and apical damage on within-plant seed distribution

Floral herbivory affected the degree to which non-apical flower heads contributed to plant fitness and exerted a major, negative influence on total seed production and realized reproductive effort. Specifically, when floral herbivory on subsequent, non-apical heads was reduced, apical damage increased the potential seed production of those flower heads (Table 1.1A), strongly increasing the contributions made by lower positioned flower heads ($p_{AD\ x\ Position} = 0.040$). As a result, both potential seed production and realized seed production per non-apical head increased when later floral herbivory was reduced (Fig. 1.4, $p_{AD\ x\ H} = 0.008$; Appendix 1.4), with greater realized seed contribution per lower positioned flower head (Fig. 1.5A, $p_{realized\ seed} = 0.022$, $p_{potential\ \ seed} = 0.021$; Appendix 1.4).

No such pattern was seen, however, under ambient (higher) herbivory on subsequent non-apical heads. Position alone explained both the potential and realized seed per non-apical head; higher positioned heads contributed the majority of the successful seed production (Fig. 1.5B, $p_{realized\ seed:\ position} = <0.01$, $p_{seeds\ per\ head:\ position} = 0.001$).

Therefore, apical damage altered the distribution of seed contribution within a plant, but subsequent herbivory affected the degree to which the alteration in distribution resulted in actual realized changes in seed contribution overall and by head position. Apical damage increased the contribution of lower heads to total plant seed production only under reduced subsequent herbivory conditions. As a result, plants with both apical damage and reduced herbivory had a similar, and even somewhat greater, overall realized seed set compared to plants without apical damage plus insecticide treatment.

DISCUSSION

Plants experiencing ambient (high) levels of herbivory on later, non-apical heads were unable to fully tolerate floral herbivory through the breaking of apical dominance. Plants with untreated later flower heads did not produce as many seeds as plants with insecticide-treated later heads, regardless of apical damage treatment. This result is consistent with earlier studies of *C. canescens* that found that ambient levels of insect floral herbivory had severe consequences for average realized seed production (Louda and Potvin 1995, Rose et al. 2005). These earlier studies, however, did not explore the plant's potential tolerance for floral herbivory, especially under varying levels of herbivory over the season. In this study, plants were able to fully compensate, and even slightly over-compensate, for early loss of the apical head through increases in reproductive effort and seed production by the later flower heads under some conditions, specifically when herbivory on subsequent, non-apical heads was lower. This result demonstrates the role of apical dominance as a contributor to plant seed reproductive fitness in the field.

Apical damage under reduced subsequent herbivory increased the number of flower heads that matured, and it also increased the relative seed contribution from later, lower-positioned flower heads. This finding is consistent with previous studies suggesting the release of lower, later buds by apical damage can provide a mechanism to compensate for fitness losses to herbivory (e.g., Nilsson et al. 1996, Huhta et al. 2000, Juenger and Bergelson 2000, Pilson and Decker 2002). Thus, we found that both apical damage, and variation in the level of herbivory on non-apical flower heads, affected the amount of successful seed production realized as well as its distribution within a plant.

Life history theory leads to the expectation that a monocarpic plant, like *C. canescens,* should have high compensatory ability to optimize lifetime reproductive fitness in the presence of herbivory (Huhta et al. 2000). Also, the expectation is that the plant should withhold some resources from reproduction to enable compensation when herbivory is high (Vail 1992). Apical dominance suppresses axillary meristems, and the existence of this dormant bud reserve is fundamental to compensation via this tolerance mechanism (Tuomi et al 1994, Aarssen 1995, Nilsson et al 1996). Optimality models favoring plant tolerance, or even over-compensation, in response to apical damage to date (i.e., McNaughton 1983, Tuomi 1994) have focused mainly on ungulate grazing, where herbivory is predictable, though often infrequent, and where the dormant bud bank can remain largely unavailable to herbivores. However, these models likely over-estimate the possibility of tolerance via compensation for the more variable, repeated herbivory imposed by insects (Stowe et al. 2000).

This field test directly examined this question, by evaluating the potential for tolerance through the breaking of apical dominance in a species where floral herbivory often causes severe seed reproductive losses. In this case, apical damage did result in relatively higher potential and realized seed production under the condition of reduced subsequent herbivory such as is observed in the field for some individuals (Louda and Potvin 1995, unpublished data). Under the mean levels of ambient herbivory, however, later flower heads were not able to produce sufficient seed to compensate for herbivore damage to the apical head, compared to the performance of reduced herbivory plants, even though the apical damage occurred early in the growing season. In this intensive study of *C. canescens*, we found that compensatory ability, while present, was suppressed on average by the generally high ambient level of insect herbivory during the growing season. This result suggests that, given that herbivory varies among individuals, strong apical dominance as a tolerance strategy for insect floral herbivory has the potential to provide important increases in fitness for some individuals in the population (Louda and Potvin 1995). However, this tolerance mechanism will not in general provide the average plant with a way of compensating and performing as well as the individual plant that escapes by occurring in a local environment with low herbivory.

Our results show that *C. canescens* plants had the potential to tolerate loss of the apical head, but that the consequences of apical head loss were greater on average for plants under ambient herbivory. Plants under ambient levels of floral herbivory realized significantly lower seed production when their apical head was damaged. The contribution of the apical head to total seed production for *C. canescens* presumably mitigates both the potential fitness costs associated with inhibition of later flower heads due to apical dominance (e.g., Aassen 1995, Irwin and Aarssen 1996) and the persistent floral herbivory reported (Louda and Potvin 1995, Fig. 1.5), at least for some individuals. In contrast, the observation that apical damage led to higher seed set under reduced herbivory supports the suggestion of a potential cost of apical dominance in the absence of herbivory (Aarssen 1995). However, because apical dominance did not significantly increase plant seed set even with reduced herbivory, and because herbivory pressure appears high on average, it seems unlikely that a cost of apical dominance would be realized under typical field conditions for this species.

Classic bet-hedging theory predicts that plants should maintain an alternative resource allocation strategy in an uncertain herbivory environment (Crawley 1997). Further, flowering strategies that allocate compensatory responses flexibly through time should increase reproductive success under conditions of repeated herbivory (Loeb 1986, Tuomi et al. 1994, Lehtilä 2000). In this *Cirsium* species, apical dominance resulted in priority investment in the apical flower head, which can produce ≥ 30% of total plant seed production if it is undamaged (Louda and Potvin 1995, Figure 1.5). Since the most common and one of the earliest native floral feeders on *C. canescens*, the tephritid fly *Paracantha culta,* oviposits preferentially on small flower heads (10 – 15 mm diameter) (Lamp and McCarty 1982), high investment in this early season flower head may confer a potential “size escape” (i.e., Vail 1992) from adapted floral herbivores.

Impairment of apical dominance by herbivore damage, however, resulted in more heads flowering and in more seed contributed from those lower-positioned flower heads, at least with reduced subsequent herbivory. However, under mean levels of ambient herbivory, the later, lower flower head positions on the average plant were less likely to realize seed set. Nevertheless, because of the basipetal nature of flowering in this species, we hypothesize that continued investment in lower positioned heads will be useful for some individuals, e.g., those that attract less subsequent herbivory, for partitioning reproductive effort through time, increasing the flowering period, and providing a partial escape from herbivores. This hypothesis is suggested by previous studies. For instance, later flower heads produced by clones of *Erigeron glaucus* had a higher probability of escaping herbivory by specialist tephritid flies (English-Loeb and Karban 1992). Also, flexible allocation to later-developing umbels by *Sanicula arctopoides* led to compensation under ambient levels of floral herbivory (Lowenburg 1994). Further, extended flowering time led to greater compensation capacity in *Helianthus annus* (Pilson and Decker 2002). Finally, models with gradual activation of dormant buds over time show decreases in the overall consequences of repeated herbivory in monocarpic species (Lehtilä 2000). Plant tolerance often occurs via a combination of different traits, each of which contributes to compensation and helps minimize impacts on plant fitness (Wise et al. 2005). In *C. canescens*, both the disproportionate apical investment, and the sustained bud release that arose after loss of strong apical dominance, provided potential plant tolerance, particularly under lowered levels of ambient herbivory.

The compensatory potential of *C. canescens* in response to damage to the apical flower head observed was not realized on average under ambient levels of floral herbivory in this study. We attribute this finding to the high incidence and high average level of damage per flower head under ambient herbivory in both years, consistent with previous studies (Louda and Potvin 1995, Rose et al. 2005). While more flower heads succeeded in flowering and producing seed in the apical damage treatment, seed production by the lower, later heads undercompensated, both for apical flower head loss and for whole plant seed production.

Because the lack of complete compensation was due to the insect herbivore environment, rather than obvious inherent constraints on the plants' ability to compensate, we argue that the compensatory capacity of *C. canescens* should be sufficient to fully compensate for apical loss for some individuals, maintaining their plant fitness. First, individuals vary in the probability of apical damage, and of subsequent damage, as well as the degree to which they compensate for damage (Strauss and Agrawal 1999, Juenger and Bergelsen 2002, Strauss and Agrawal 1999, Juenger and Bergelson 2000). Our analysis focused on the overall mean responses across individuals in order to understand the interactions. However, the variance in magnitude of floral herbivory is typically high among *C. canescens* plants (Fig. 1.2; Louda and Potvin 1995, Rose et al. 2005, Fornoni 2011). Thus, identifying the traits and conditions that lead to lower levels of herbivory among individuals in the population, and so confer higher fitness to them, has the potential of further elucidating mechanisms that are obscured by the usual emphasis on measuring treatment means (Pilson and Decker 2002, Wise et al. 2005).

Second, the effectiveness of response to herbivory for any plant will depend upon the interaction between the plant and its environment. The ability of plants to respond to herbivory, and the range of damage levels at which tolerance works, is expected to vary with environmental context (Maschinski and Whitham 1989, Huhta et al. 2003, Wise and Abrahamson 2007, Brody et al. 2007, Banta 2010). Plant resource condition, herbivore numbers, behavior and feeding intensity, and timing of damage have all been found or suggested to be factors controlling the degree of plant tolerance (Maschinski and Whitham 1989, Trumble et al. 1993, Honkanen and Haukioja 1998, Stowe et al. 2000, Hawkes and Sullivan 2001, Wise and Abrahamson 2007). For instance, we controlled for effects of plant size by matching plants into replicates by early season size, and there were no early season differences in size among treatments. However, we observed a trend for plants with reduced floral herbivory to be taller at the end of the season on average than plants with ambient floral herbivory. Such a resulting size difference could reflect an additional effect of resource limitation on tolerance capacity under high herbivory (see Wise and Abrahamson 2007, Gonzáles et al. 2008). Also, experimental logistics led to use of plants in areas with relatively high average patch density for this sparse native thistle (unpublished data). If herbivory is higher on plants in dense patches (e.g., Root 1973, Ehrlén 1996), then we predict more isolated individuals would be likely to encounter lower relative herbivore loads and, thus, have a greater probability of realizing the demonstrated potential for compensation.

Third, if the magnitude of herbivore damage effect is contingent upon the timing or synchrony with plant flowering phenology (Loeb and Karban 1992, Honkanen and Haukioja 1998, Russell and Louda 2004, 2005), then plants that distribute reproductive effort over longer time periods will reduce the probability of damage to at least a subset of flower heads. Therefore, further research aimed toward quantifying and predicting the circumstances under which the demonstrated compensatory potential is realized would be useful.

In summary, the results of this study demonstrate the magnitude and dynamics of potential reproductive compensatory response to floral herbivory on both the apical and later-flowering heads of a monocarpic plant. The study, thus, furthers our understanding of tolerance mechanisms and their operation under field conditions in increasing the chance of persistence of such characteristic, sparse prairie species.

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Table 1.1. End-of-season plant performance measures. Values are means (± S. E.) for each variable measured by treatment over two years for experimentally reduced (H_R) vs. ambient (H_A) subsequent herbivory on plants without (D_{ND}) versus with (D_D) experimental apical damage. (*) represents a significant main effect, and (^) indicates a significant treatment interaction. Letters indicate treatment differences for each significant variable (see Methods).

	Herbivory Reduced (H_R)		**Herbivory Ambient (H_A)**	
	D_{ND}	**D_D**	**D_{ND}**	**D_D**
A. Effects of Insect Damage				
i. Per Non-Apical Head				
% Flower Head Damage*	48.1(±2.6)^{a}	48.4(±2.9)^{a}	78.5(±2.5)^{b}	72.9(±4.3)^{b}
Potential Seeds per Head	141.1(±4.8)	156.1(±4.4)	157.0(±3.9)	151.1(±4.6)
Seeds Matured per Head	69.6(±7.5)^{a}	99.0(±6.8)^{a}	30.7(±5.3)^{b}	31.5(±6.5)^{b}
ii. Whole Plant				
Potential Seeds per Plant	562.7(±55.1)	721.8(±99.4)	604.6(±64.6)	446.4(±46.2)
Seeds Matured per Plant^	355.9(±49.0)^{a}	477.8(±81.8)^{a}	186.3(±29.6)^{b}	112.0(±27.9)^{b}
B. Plant Structural Investment				
Plant Height (cm)	53.3(±2.0)	53.9(±2.1)	50.6(±1.7)	47.5(±1.9)
Rosette Diameter (cm)	32.2(±1.6)	34.6(±1.7)	34.0(±1.6)	30.6(±1.4)
# Branches	5.2(±0.9)	6.6(±0.6)	5.9(±1.0)	5.4(±0.4)
# Buds per Plant	9.6(±0.9)	12.6(±1.4)	10.4(±1.8)	10.2(±0.8)
C. Plant Reproductive Investment (excluding Apical) ^				
# Mature Flower Heads^	2.9(±0.4)^{ab}	4.2(±0.6)^{b}	2.8(±0.4)^{a}	2.3(±0.3)^{a}
# Flowered with Seed^	1.9(±0.3)^{a}	3.5(±0.5)^{b}	1.5(±0.2)^{a}	1.3(±0.2)^{a}

Figure Legends

FIG. 1.1. Experimental predictions and explanation of thistle structure. (A) Prediction for the consequences of apical damage and reduced subsequent floral herbivory for *C. canescens* in the field. We expected greatest seed production from plants with apical head protected and subsequent herbivory reduced, and the least seed production from plants with both apical damage and ambient subsequent herbivory. (B) Diagram of the main thistle flower head structure, with positions numbered starting with the apical flower head successively down the stem for later emerging branches and flower heads.

FIG. 1.2. Average damage score per flower head for individual plants. The distribution (range and 95% CI) of average insect damage score per non-apical flower head for each individual plant in the herbivory treatments on later (non-apical) flowering heads: (A) reduced herbivory, and (B) ambient herbivory. Plants are presented in a random order within treatment. Damage scores (see Methods) were based on the proportion of receptacle base damaged by insects averaged over all later heads per plant. Overall, individuals in the reduced herbivory treatment experienced lower average herbivore damage on the treated heads.

FIG. 1.3. *Cirsium canescens* whole plant seed production (mean, SE): (A) number per plant and (B) proportion of seed production potential realized per plant by herbivory treatment: reduced herbivory (black, solid line) and ambient herbivory (gray, dashed line). Reducing insect herbivory on subsequent (non-apical) heads significantly increased whole plant seed production overall, and apical damage lead to a significant

increase in seed production. Percent realized seed set was quantified by dividing actual matured seed counts from field data by estimated potential seed production based on flower head sizes (See Methods). Potential seed set was estimated using data from Louda and Potvin (1995).

FIG. 1.4. *Cirsium canescens* seed production per flower head. Mean (SE) number (A) and percent (B) estimated seed set realized, per flower head, by treatment. Reducing insects increased seed set overall and showed that apical damage could increase realized seed production per head when herbivory was lowered, providing a mechanism for the whole plant response (Figure 1.3). Percent realized seed set was quantified by dividing actual matured seed counts from field data by estimated potential seed production based on flower head sizes (See Methods). Potential seed set was estimated using data from Louda and Potvin (1995).

FIG. 1.5. *Cirsium canescens* seed contribution per flower head position. Average percent of whole plant seed production contributed by each flower head position with: (A) experimentally reduced herbivory, and (B) ambient herbivory. Values indicate mean (SE) of the percent of the total undamaged seeds per flower head position for no apical damage (black bars) and experimental apical damage (gray bars) treatments. Notation: “b” heads are those below the branch terminal flower heads; “up” refers to positions below the 9th branch (numbered 10 - 13 in this study); and, “0” indicates positions where heads flowered, but did not produce undamaged, viable, seeds. Under reduced subsequent herbivory, lower-positioned flower heads made a greater contribution to

realized total seed in plants with apical damage compared to plants without apical damage. However, under mean levels of ambient subsequent herbivory, no increase in seed contribution by lower-positioned heads was observed in plants with apical head damage.

FIGURE 1.1

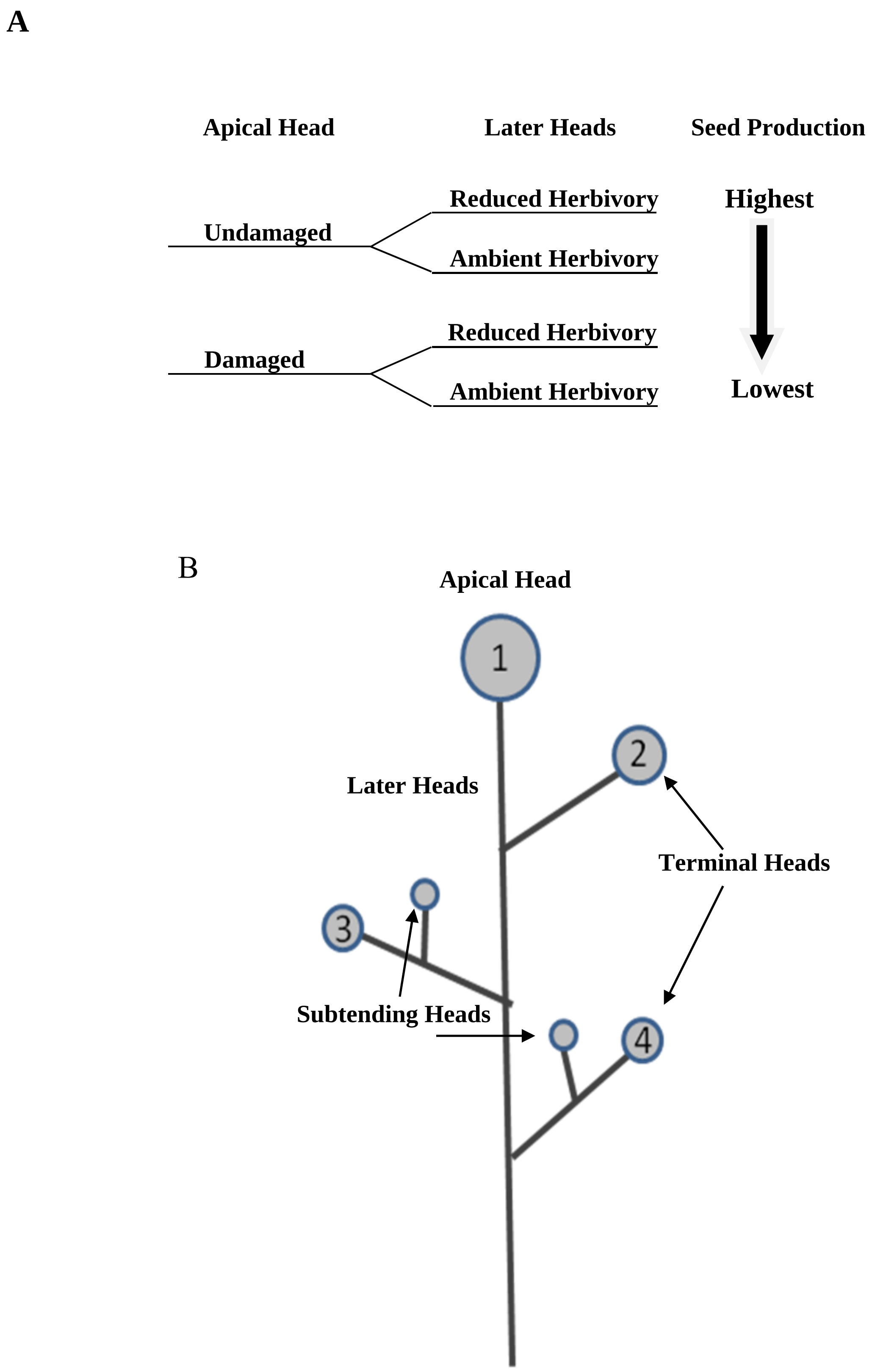
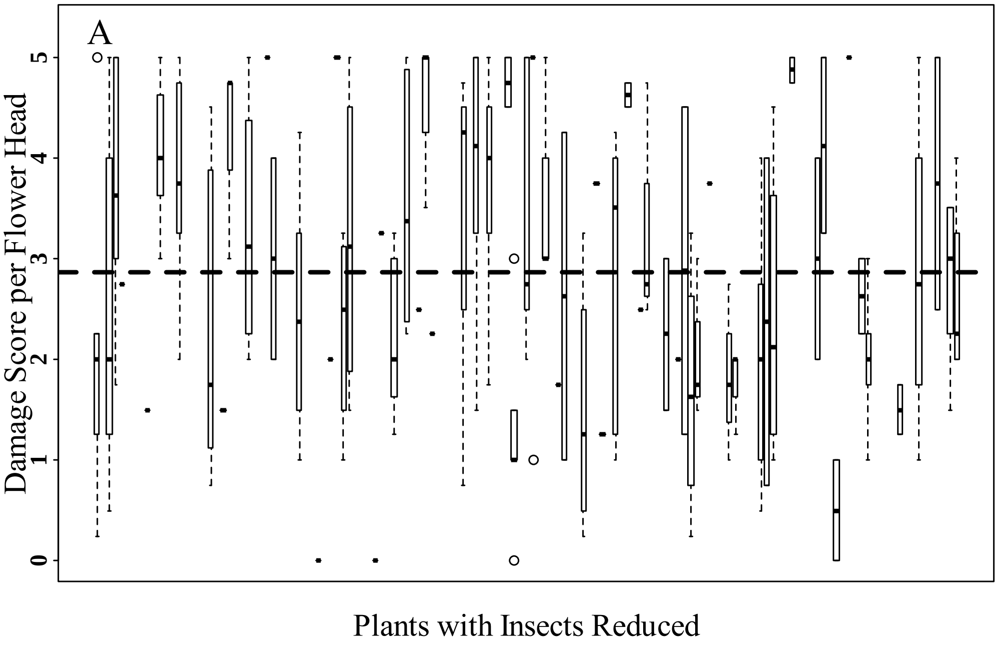

A
Apical Head
Later Heads
Seed Production
Undamaged
Reduced Herbivory
Ambient Herbivory
Damaged
Reduced Herbivory
Ambient Herbivory
Highest
Lowest
B
Apical Head
1
2
Later Heads
Terminal Heads
3
Subtending Heads
4

FIGURE 1.2.


A
Damage Score per Flower Head
0
1
2
3
4
5
Plants with Insects Reduced

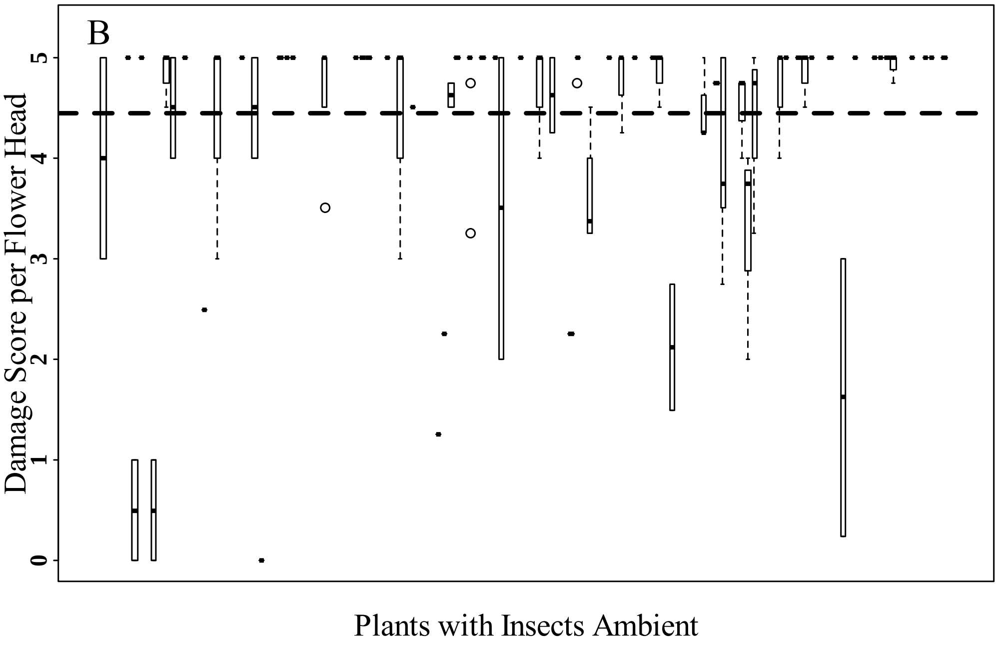

B
Damage Score per Flower Head
0
1
2
3
4
5
Plants with Insects Ambient

FIGURE 1.3.

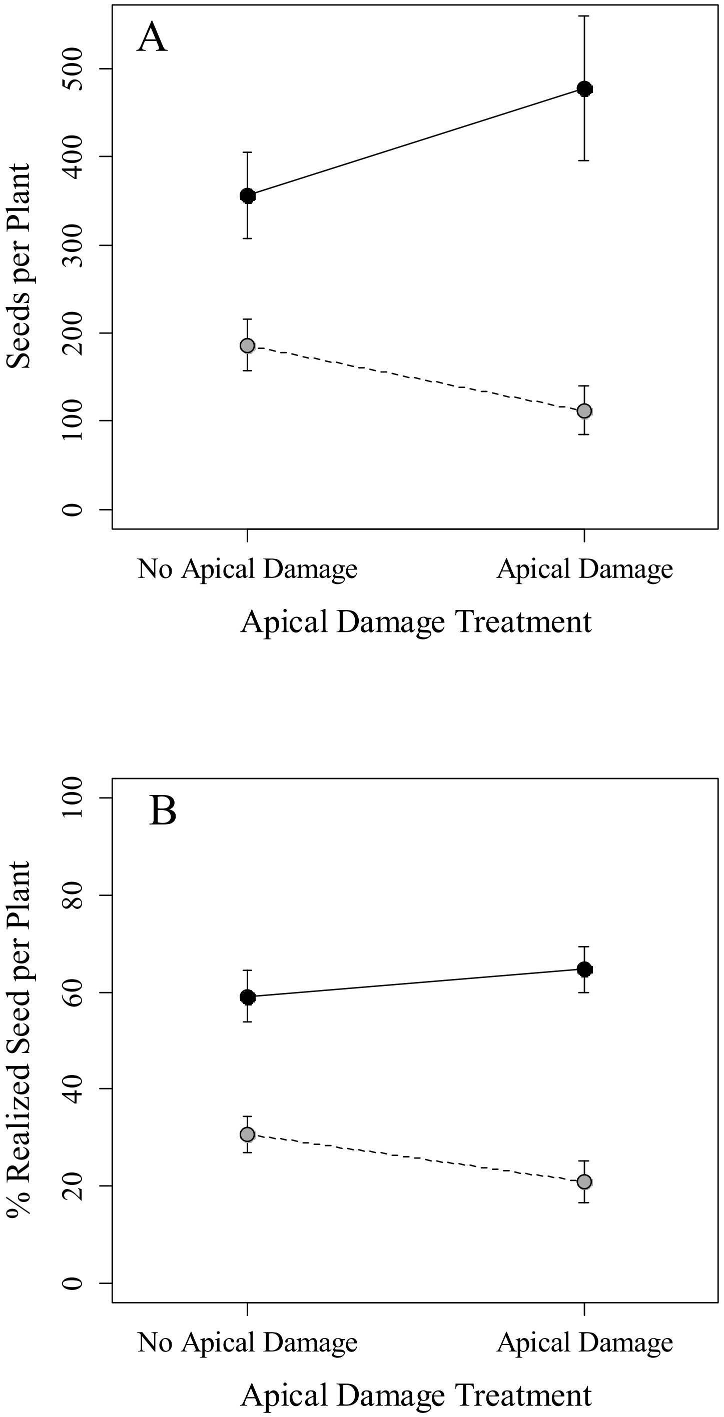

A
Seeds per Plant
0
100
200
300
400
500
No Apical Damage
Apical Damage
Apical Damage Treatment
B
% Realized Seed per Plant
0
20
40
60
80
100
No Apical Damage
Apical Damage
Apical Damage Treatment

FIGURE 1.4.

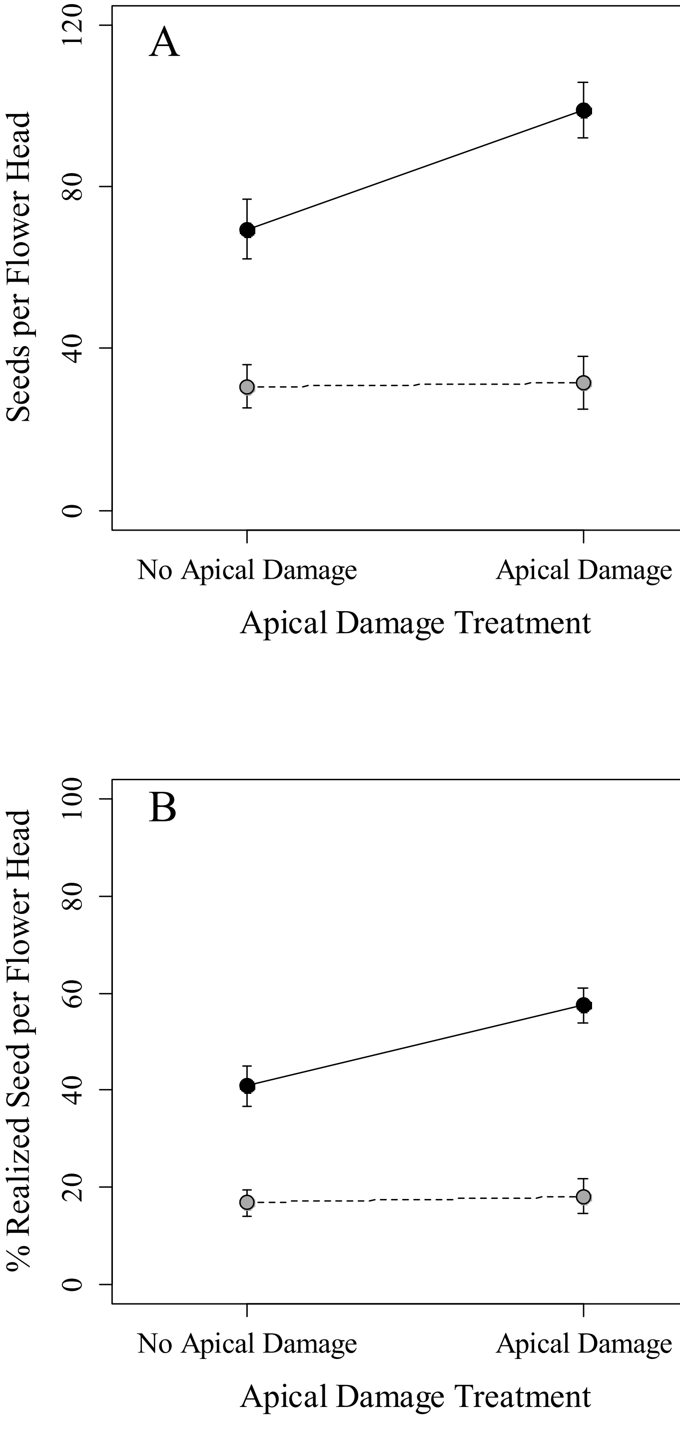
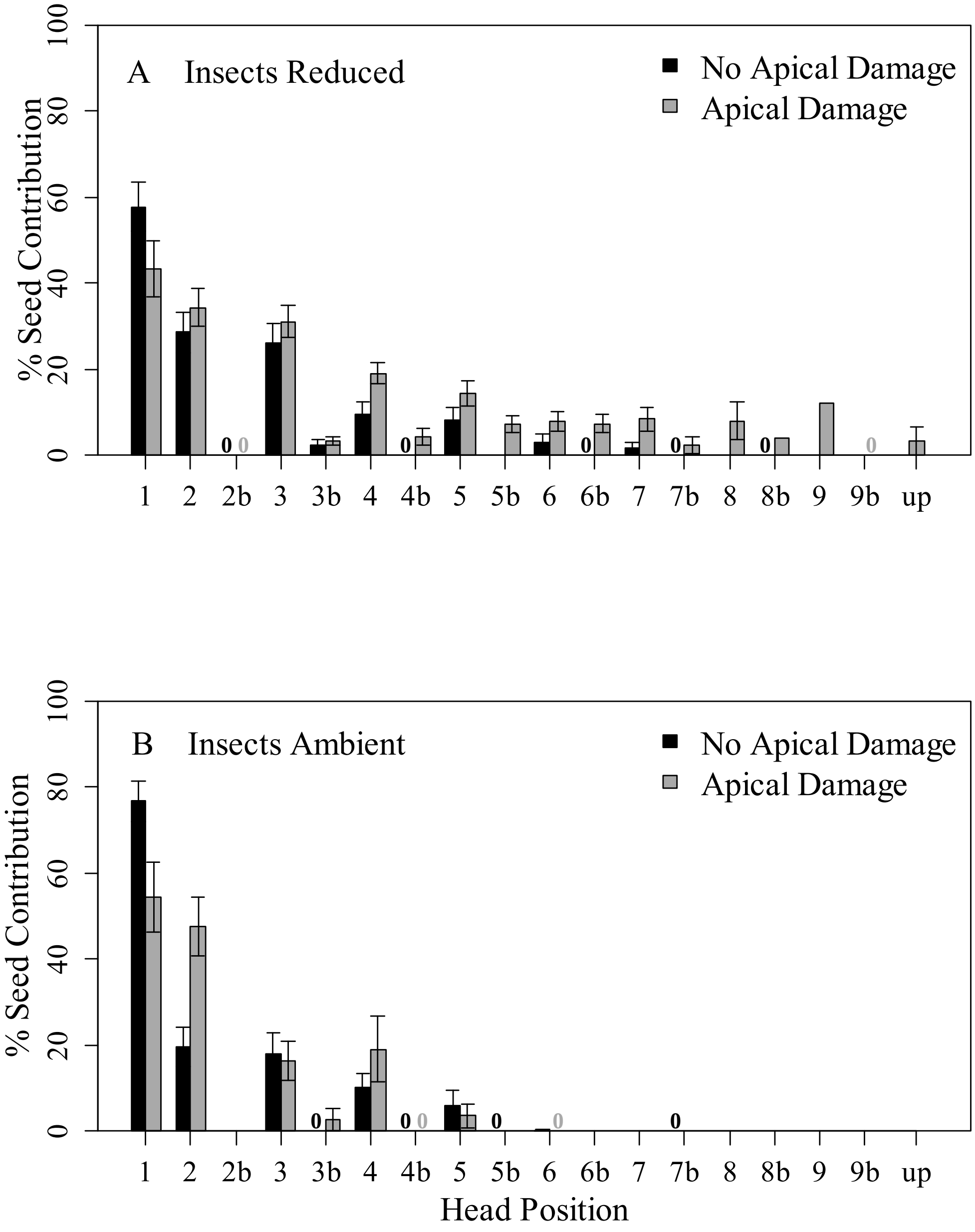

A
Seeds per Flower Head
0
40
80
120
No Apical Damage
Apical Damage
Apical Damage Treatment
B
% Realized Seed per Flower Head
0
20
40
60
80
100
No Apical Damage
Apical Damage
Apical Damage Treatment

FIGURE 1.5.


A Insects Reduced
B Insects Ambient
■ No Apical Damage
▨ Apical Damage
% Seed Contribution
0
20
40
60
80
100
1
2
2b
3
3b
4
4b
5
5b
6
6b
7
7b
8
8b
9
9b
up
Head Position
0

Appendix 1.1

The apical damage treatment varied in its effectiveness in simulating the severe damage observed in the field (Figure A1.1:1). Any damage that affects apical regions can result in release of the axillary buds (Cline 1991). Plants vary in the strength of their response to apical damage, and the sensitivity of buds to apical inhibition is an important aspect of tolerance capacity (Tuomi et al. 1994, Nilsson et al. 1996). Therefore, we examined the effects of different levels of experimental apical damage. In the treatment with no experimental damage imposed, we expected large numbers of filled, undamaged seeds in the apical head, but we found that some apical flower heads were damaged and developed 0 or only a few (< 100) seeds (Figure A1.1:1A). Alternately, in the treatment with experimental damaged imposed, we expected few filled seeds in the apical flower head, but we found that some apical flower heads produced large numbers of seeds ($\geq$150 seeds). Consequently, we analyzed treatment effects for plants that had low apical damage (< 100 seeds), as intended for the undamaged apical treatment, versus those that had high apical damage ($\geq$150 seeds), as intended for the damaged apical treatment (Figure A1.1:2A). In this contrast, three key results emerge. First, plants with low damage to the apical flower head produced as many, but not more, seeds in later flower heads on average as plants with high apical damage, under reduced herbivory. Second, under ambient subsequent herbivory conditions, the plants with low damage to the apical head produced more seeds per later, lower flower head than did plants with high damage to the apical head. Third, the pattern of response to high versus low levels of apical damage was similar per flower head, but stronger when examined as the proportion of the potential number of seeds that were actually realized (Figure A1.1:2B). Thus, we found evidence of compensatory ability for the early loss of the apical seeds, but unexpectedly the average contribution by later heads was greater on plants with low damage, rather than high damage, to the apical flower head.

Figure Legends

FIG. A1.1:1. Seeds per apical flower head in the apical damage treatment. The frequency distribution of filled, undamaged seeds per apical flower demonstrates the variation in severity in the apical damage treatment and, so, the effectiveness of the imposed treatment.

FIG. A1.1:2. Seeds per lightly damage versus heavily damaged apical head. (A) Number of filled, undamaged seeds per non-apical flower head by treatment on plants with either low damage (>150 seeds produced) or high damage (< 100 seeds produced) to the apical flower head as intended in the apical damage treatment (n = 5 per category); (B) Percent of realized potential seed production per flower head for non-apical heads on plants with either low damage or high damage to the apical flower head, with potential seed production by flower head size estimated with regression from Louda and Potvin (1995).

FIGURE A1.1:1.

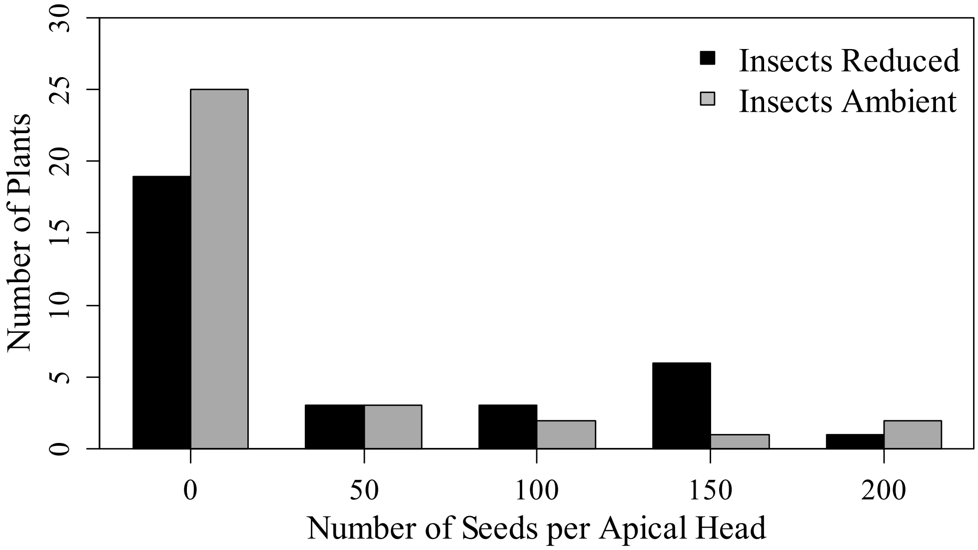
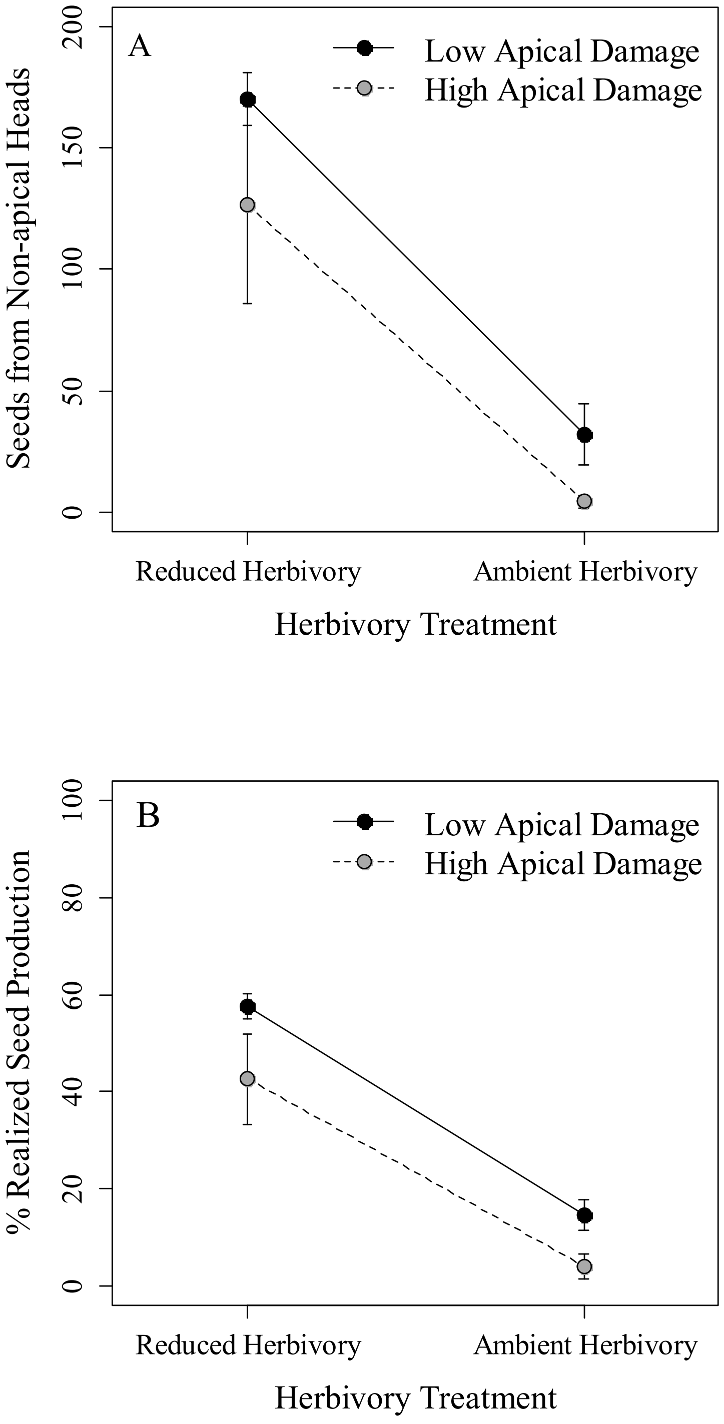

■ Insects Reduced
▨ Insects Ambient
Number of Plants
0
5
10
15
20
25
30
0
50
100
150
200
Number of Seeds per Apical Head

FIGURE A1.1:2.


A
Low Apical Damage
High Apical Damage
Seeds from Non-apical Heads
0
50
100
150
200
Reduced Herbivory
Ambient Herbivory
Herbivory Treatment
B
Low Apical Damage
High Apical Damage
% Realized Seed Production
0
20
40
60
80
100
Reduced Herbivory
Ambient Herbivory
Herbivory Treatment

Appendix 1.2.

Table A1.2:1. Initial size parameters for experimental *Cirsium canescens* plants by subsequent treatment manipulating both damage to the initial (apical) flower head and insect feeding on subsequently produced flower heads during the season (2007, 2008) at Arapaho Prairie, NE. Values presented represent the mean; standard errors of the mean are in parentheses.

		Herbivory Reduced (H_R)		**Herbivory Ambient (H_A)**	
Variable	Year*	D_{ND}	D_D	D_{ND}	D_D
Rosette Diameter					
	2007	33.2 (±2.0)^{a}	37.3 (±2.6)^{a}	37.5 (±2.0)^{a}	32.7 (±1.3)^{a}
	2008	29.6 (±2.2)^{b}	26.9 (±1.6)^{b}	27.2 (±1.7)^{b}	25.3 (±1.4)^{b}
	Overall	31.1 (±1.5)	31.1 (±1.7)	31.9 (±1.6)	28.4 (±1.1)
Apical Bud Diameter					
	2007	29.9 (±1.6)^{a}	31.4 (±1.9)^{a}	33.2 (±2.2)^{a}	29.6 (±1.6)^{a}
	2008	17.4 (±1.7)^{b}	17.5 (±1.6)^{b}	16.4 (±1.5)^{b}	15.5 (±1.3)^{b}
	Overall	22.8 (±1.6)	23.2 (±1.7)	24.0 (±1.9)	21.5 (±1.6)
Number of Buds					
	2007	3.9 (±0.5)^{a}	5.4 (±1.0)^{a}	5.6 (±0.9)^{a}	4.5 (±0.4)^{a}
	2008	2.8 (±0.5)^{b}	3.0 (±0.5)^{b}	2.9 (±0.5)^{b}	2.3 (±0.3)^{b}
	Overall	3.2 (±0.4)	4.0 (±0.5)	4.1 (±0.5)	3.2 (±0.3)
N	2007	15	13	15	14
	2008	35	32	33	33

Appendix 1.3.

Analyses of treatment effects on initial and end-of-season plant characters. Bolded values indicate significant effects reported in the Results. (A) Insect damage per flower head by treatment; (B) MANOVA tables for initial and end-of-season plant characters. Dependent variables included in (*i.*) are: average rosette diameter; apical bud diameter; and number of flower buds. Dependent variables included in (*ii.*) are: plant height, average rosette diameter, number of flower buds, and number of branches. Dependent variables in (*iii.*) are: number of flowered heads and number of heads with matured seeds. We used Pillai's trace test statistic. (C1 & 2) Separate ANOVA tables and subsequent ANOVAs for each of the dependent variables included as measures of plant reproductive investment. Dependent variables are: (*i.*) number of flowered heads, and (*ii.*) number of heads with matured seeds.

(A) Treatment effects on insect damage per *C. canescens* flower head (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
Intercept	0.468	0.0478	279	9.801	<0.001*
Apical Damage (*D*: N)	0.031	0.0664	127	0.464	0.644
Herbivory (*H:* A)	**0.409**	**0.0699**	**127**	**5.857**	**<0.001***
D x *H*	-0.007	0.0966	127	-0.075	0.940

(B) Treatment effects on plant characters (MANOVA)

Source	Pillai's	Approx. F	num Df	dens DF	Pr(>F)
(i.) Initial Measurements					
Apical Damage (*D*)	0.015	0.637	3	125	0.593
Herbivory (*H*)	0.012	0.522	3	125	0.668
Year	0.546	50.209	3	125	<0.001*
D x *H*	0.032	1.415	3	125	0.242
(ii.) Plant Structural Investment					
Apical Damage (*D*)	0.044	1.449	4	126	0.222
Herbivory (*H*)	0.0488	1.615	4	126	0.175
Year	0.167	6.33	4	126	<0.001*
D x *H*	0.037	1.193	4	126	0.317
(iii.) Plant Reproductive Investment					
Apical Damage (*D*)	0.078	5.419	2	128	<0.001*
Herbivory (*H*)	0.1075	7.704	2	128	<0.001*
Year	0.104	7.394	2	128	<0.001*
D* x *H	**0.049**	**3.324**	**2**	**128**	**0.039***

(C) Separate treatment effects on measures of reproductive investment (ANOVA)

C1

Source	Sum Sq	Df	F value	Pr(>F)
(i.) Number of Heads Flowered				
Apical Damage (*D*)	5.82	1	0.9813	0.324
Herbivory (*H*)	28.69	1	4.8413	0.0296*
Year	11.95	1	2.0171	0.158
D* x *H	**30.18**	**1**	**5.0937**	**0.0257***
Residuals	764.44	129		
(ii.) Number of Heads Flowered with Seeds				
Apical Damage (*D*)	18.62	1	4.9973	0.0271*
Herbivory (*H*)	45.87	1	12.3131	0.00062*
Year	4.17	1	1.1207	0.292
D* x *H	**24.73**	**1**	**6.6392**	**0.0111***
Residuals	480.53	129		

C2

Source	Sum Sq	Df	F value	Pr(>F)
(i.) Number of Heads Flowered				
Reduced Herbivory				
Apical Damage (*D*)	**32.79**	**1**	**4.0043**	**0.04956***
Year	36.7	1	4.4817	0.03809*
Residuals	532.29	65		
Ambient Herbivory				
Apical Damage (*D*)	4.829	1	1.4764	0.2289
Year	1.364	1	0.4171	0.5207
Residuals	206.046	63		
(ii.) Number of Heads Flowered with Seeds				
Reduced Herbivory				
Apical Damage (*D*)	**44.35**	**1**	**7.7925**	**0.006881***
Year	0.8	1	0.1402	0.709313
Residuals	369.91	65		
Ambient Herbivory				
Apical Damage (*D*)	0.244	1	0.1539	0.696151
Year	14.305	1	9.0398	0.003791*
Residuals	99.695	63		

Appendix 1.4.

Analyses of treatment effects on estimated seed production potential and realized seed production. Bolded values indicate significant effects reported in the Results. (A) Total seed production per plant; (B1-3) MANOVA table for analysis of potential and realized seed production per plant; (C) Separate ANOVA tables for potential and realized seed production per plant; (D) MANOVA table for analysis of seed production potential and realized seed production per flower head; (E) Separate ANOVA tables for seed production potential and realized seed production per flower head; (F) Results of the analysis of seed production by head position.

(A) Total seed production per plant (GLM, negative bionomial distribution)

Source	Estimate	Std. Error	z-value	P(>|z|)	Null df	Residual df
Good Seeds per Plant						
Intercept	6.4205	0.2481	25.882	<0.001*	133	129
Apical Damage (*D*: N)	-0.2893	0.2927	-0.989	0.320		
Herbivory (*H*: A)	-1.5756	0.3032	-5.197	<0.001*		
Year (2008)	-0.3756	0.2109	-1.781	0.075		
D* x *H	**0.8435**	**0.4166**	**2.025**	**0.043***		
Reduced Herbivory						
Intercept	6.1691	0.220	27.612	<0.001*	67	66
Apical Damage (*D*: N)	-0.296	0.233	-1.270	0.204		
Year	0.135	0.238	0.566	0.571		
Ambient Herbivory						
Intercept	5.054	0.315	16.054	<0.001*	65	64
Apical Damage (*D*: N)	0.615	0.345	1.786	0.074		
Year	-0.856	0.347	-2.468	0.014*		

(B) Treatment effects on seed production potential and realized seed production per plant (GLM and subsequent ANOVAs)

B1

Source	Sum Sq	Df	F value	Pr(>F)
(i.) Potential Seeds per Plant				
Apical Damage (*D*)	3.5	1	0.0619	0.8039
Herbivory (*H*)	124.9	1	2.2095	0.13953
D* x *H	**297.7**	**1**	**5.266**	**0.02332***
Residuals	7518.2	133		
(ii.) Realized Seeds per Plant				
Apical Damage (*D*)	0.0559	1	0.8492	0.358
Herbivory (*H*)	3.362	1	51.081	<0.001*
D* x *H	**0.357**	**1**	**5.4281**	**0.0213***
Residuals	8.754	133		

B2

Source	Estimate	Std. Error	t-value	P(>|t|)	Null df	Residual df
(i.) Potential Seeds per Plant						
Intercept	741.18	81.56	9.087	<0.001	136	132
Apical Damage (*D*: N)	-158.68	95.65	-1.659	0.0995		
Herbivory (*H*: A)	-275.96	98.92	-2.79	0.0061*		
Year (2008)	-32.65	69.15	-0.472	0.6376		
D* x *H	**316.31**	**136.54**	**2.317**	**0.0221***		
Reduced Herbivory						
Intercept	721.8	80.42	8.975	<0.001	69	68
Apical Damage (*D*: N)	-159.06	109.15	-1.457	0.150		
Ambient Herbivory						
Intercept	446.43	56.89	7.848	<0.001	66	65
Apical Damage (*D*: N)	158.18	79.86	1.981	0.0519		

B3

Source	Estimate	Std. Error	t-value	P(>|t|)	Null df	Residual df
(ii.) Percent Realized Seed Potential per Plant						
Intercept	0.81047	0.05238	15.472	<0.001*	136	132
Apical Damage (*D*: N)	-0.05936	0.06143	-0.966	0.3356		
Herbivory (*H*: A)	-0.42199	0.06353	-6.643	<0.001*		
Year (2008)	-0.05495	0.04441	-1.237	0.2182		
D* x *H	**0.20313**	**0.08769**	**2.316**	**0.0221***		
Reduced Herbivory						
Intercept	0.77784	0.04382	17.75	<0.001*	69	68
Apical Damage (*D*: N)	-0.06	0.05948	-1.009	0.317		
Ambient Herbivory						
Intercept	0.35684	0.04618	7.727	<0.001*	66	65
Apical Damage (*D*: N)	**0.1447**	**0.06483**	**2.232**	**0.0291***		

(C) Mature seeds produced per flower head by head position (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
(i.) Good Seeds by Head Position					
Intercept	11.5803	0.999	275	11.597	<0.001*
Apical Damage (*D*: N)	-0.1101	1.492	127	-0.0738	0.941
Herbivory (*H:* A)	**-5.0540**	**1.849**	**127**	**-2.734**	**0.0072***
Head Position (*Pos*)	-0.00812	0.002022	275	-4.0163	0.0001*
D x *H*	1.523	2.4704	127	0.617	0.537
D* x *Pos	**-0.00931**	**0.00347**	**275**	**-2.679**	**0.0078***
H x *Pos*	-0.00301	0.005109	275	-0.590	0.556
D x *H* x *Pos*	0.00553	0.00665	275	0.832	0.4063
(ii.) Insecticide					
Intercept	11.633	1.0742	171	10.82976	<0.001*
Apical Damage (*D*: N)	-0.241	1.612	64	-0.1498	0.881
Head Position (*Pos*)	-0.00808	0.00223	171	-3.62909	0.0004*
D* x *Pos	**-0.00889**	**0.00382**	**171**	**-2.32725**	**0.0211***
(iii.) Ambient Herbivory					
Intercept	6.772	1.286	103	5.267	<0.001*
Apical Damage (*D*: N)	1.425	1.637	63	0.8706	0.387
Head Position (*Pos*)	**-0.0124**	**0.00375**	**103**	**-3.315**	**0.0013***
D x *Pos*	-0.00376	0.00452	103	-0.831	0.4077

(D) Estimated seed production per flower head (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
Estimated Potential Seeds by Head Position					
Intercept	183.8833	9.461253	274	19.4354	0
Apical Damage (*D*: N)	3.22079	14.20232	127	0.226779	0.821
Herbivory (*H:* A)	-1.19875	17.71206	127	-0.06768	0.9461
Head Position (*Pos*)	-0.07501	0.019652	274	-3.81683	0.0002*
D x *H*	-10.4521	23.65633	127	-0.44183	0.6594
D* x *Pos	**-0.06946**	**0.033732**	**274**	**-2.05922**	**0.0404***
H x *Pos*	-0.04333	0.049557	274	-0.87433	0.3827
D x *H* x *Pos*	0.11616	0.064562	274	1.799157	0.0731

(E) Realized seed production per flower head (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
Percent Realized Seed by Head Position					
Intercept	0.874947	0.073764	274	11.86139	0
Apical Damage (*D*: N)	-0.01512	0.110129	127	-0.13731	0.891
Herbivory (*H:* A)	**-0.37526**	**0.136411**	**127**	**-2.75094**	**0.0068***
Head Position (*Pos*)	-0.00056	0.000149	274	-3.76582	0.0002*
D x *H*	0.095597	0.182247	127	0.524546	0.6008
D* x *Pos	**-0.00068**	**0.000256**	**274**	**-2.65776**	**0.0083***
H x *Pos*	-0.00027	0.000377	274	-0.72299	0.4703
D x *H* x *Pos*	0.000457	0.00049	274	0.932217	0.352
(ii.) Reduced Herbivory					
Intercept	0.87312	0.079597	171	10.96925	0
Apical Damage (*D*: N)	-0.01858	0.119426	64	-0.1556	0.8768
Head Position (*Pos*)	-0.00055	0.000165	171	-3.35596	0.001*
D* x *Pos	**-0.00066**	**0.000283**	**171**	**-2.31703**	**0.0217***
(iii.) Ambient Herbivory					
Intercept	0.518232	0.094236	103	5.499275	0
Apical Damage (*D*: N)	0.079903	0.120107	63	0.665266	0.5083
Head Position (*Pos*)	**-0.00093**	**0.000274**	**103**	**-3.40359**	**0.0009***
D x *Pos*	-0.00022	0.00033	103	-0.6569	0.5127

Chapter 2.

Effects of Apical Damage and Insect Herbivory on the iterocarp *Cirsium undulatum* Spreng.

Abstract Plants that experience steep reproductive losses from insect herbivores should favor strategies that promote tolerance or resistance against insect damage. However, the degree to which such strategies influence plant fitness in the field remains inconclusive, particularly for iterocarpic plants. Therefore, we examined whether modifying reproductive effort would result in predictable variation in reproductive success, given ambient levels of herbivory over two seasons (2007, 2008). We manipulated the strength of apical dominance, as well as subsequent insect herbivory on non-apical flower heads, in the native iterocarpic perennial *Cirsium undulatum* Spreng (wavyleaf thistle) in sand prairie. We evaluated whether *C. undulatum* plants under strong herbivore pressure had the potential to tolerate apical flower head loss by increased reproductive effort in later flower heads, and whether such tolerance influenced total seed production each flowering season. We found that plants compensated in seed production for apical head loss through increased seed contributions by lower positioned, later-flowering heads. Levels of insect floral herbivory varied among plants and among years. Although some compensation for apical head loss was possible, total seed production per plant was low in each season; this may have obscured the overall fitness consequences of altered reproductive allocation within this plant. We conclude that variation in insect load and in growing conditions may limit the contribution of within-season compensation for overall plant fitness through time.

Keywords: Insect herbivory, plant tolerance, Cirsium undulatum, apical dominance

INTRODUCTION

Insect floral herbivores and predispersal seed predators are common (e.g., Janzen 1971). Interactions with these organisms can considerably reduce plant seed production (Louda 1982, 1983, Louda and Potvin 1995, Kelly and Dyer 2002, Maron and Crone 2006), as well as population density and lifetime fitness (Louda and Potvin 1995). Tolerance mechanisms that promote compensation for reproductive losses provide one way for individual plants to ameliorate the negative effects of such herbivory on reproductive fitness. However, the potential for compensatory responses often depends on changes in source-sink dynamics, and investment in alternative functions such as competition and resource capture that are important for other ecological interactions (Aarssen and Irwin 1991, Kotanen et al. 1998, Tiffin 2000). Therefore, the magnitude of positive compensatory contribution by plant herbivory tolerance can be constrained by environmental context. Debate continues over whether insect herbivore effects are strong enough relative to other costs in the environment for tolerance mechanisms to be consistently adaptive (Aarssen 1995, Ehrlén 2003).

Whether herbivory tolerance mechanisms provide a consistent benefit may also vary with life history strategy and reproductive mode (Hendrix 1984, Karlsson and Méndez 2005, Maron and Crone 2006). For monocarpic plants, previous studies examining tolerance have shown that plants can modify expression of reproductive characters in response to floral herbivory (Chapter 1, Pilson and Decker 2002, Kliber and Eckert 2004, Östergård et al. 2007, Wise et al. 2008). Monocarpic plants, dependent on their reproductive effort in a single season, should favor strategies that increase fitness for their one, fatal, flowering episode, leading to the prediction of successful compensatory responses. We know much less about the actuality and role of tolerance to floral herbivores in the current reproductive success of iterocarpic plants (Doak 1992, Kelly and Dyer 2002). In iterocarpic perennials, investment in reproduction in a single season should be prioritized to optimize current reproductive effort with plant survival and fitness over successive seasons (Crawley 1997).

The degree to which an iterocarpic plant compensates for herbivory within any particular season is predicted to depend heavily on the environmental conditions present as well as the consistency of insect pressure on reproductive output (i.e., Maschinski and Whitham 1989, Gonzáles et al. 2008). For instance, in a year of low resources, the allocation cost of compensating for loss of reproductive effort may offset the fitness advantages of that compensation (Brody et al. 2007). Further, mechanisms, such as apical dominance, that can restrain reproductive effort in years with weak herbivore pressure may be offset by mechanisms that produce over-compensatory reproduction in years with high herbivory pressure (Tuomi et al. 1994, Nilsson et al. 1996). Alternately, however, seed limitation does not need to occur every year to have negative effects on population growth (Maron and Gardner 2000), and herbivore/predator effects that reduce, rather than suppress, population growth can still have important implications for plant fitness and recruitment (Kelly and Dyer 2002). In fact, although the potential for future reproduction might buffer a plant against within season fitness losses, optimizing annual reproductive success should reduce variation across seasons (Crawley 1997). Further examination of the degree to which iterocarpic plants compensate, within season and between years, for insect floral herbivory provides needed insight into how plants under high ambient insect pressure might balance the tradeoff between both proximate and lifetime reproduction.

Investment in alternate patterns of reproductive effort over time provides a potential mechanism to compensate for reproductive losses to insect consumers, to increase overall individual fitness, and to explain the variation in success among individuals within a population. We tested whether apical damage, and consequent changes in the distribution of reproductive effort, resulted in differences in reproductive success within a season, over two years, among individuals of the iterocarpic perennial *Cirsium undulatum* Spreng. (wavyleaf thistle). In order to manipulate plant reproductive effort, we altered the strength of apical dominance and the amount of herbivore pressure on later-flowering, non-apical, flower heads. The ability to respond to apical head damage that impairs apical dominance can be an important component of realizing seed set under intense herbivory (Aarssen 1995). Further, the breaking of apical dominance, through release of dormant buds that leads to an increased number of flowering heads, has been hypothesized to provide a tolerance strategy for plants under herbivory (Marquis 1996, Strauss and Agrawal 1999).

Our previous study of the co-occurring, monocarpic congener, *Cirsium canescens* (Platte thistle), showed the potential to compensate for apical head damage through increased seed production from the lower, later flower heads (Chapter 1). However, this potential was unrealized under ambient levels of herbivory; the plant response did not fully compensate for total reproductive losses to insects (Chapter 1). The flowering phenology of *C. undulatum* overlaps the latter half of the flowering period of *C. canescens* and these two congeners share the same suite of specialist floral herbivores

(Lamp 1980, Russell and Louda 2005). Therefore, we expected insect herbivory to impose high within-season costs on seed reproduction, providing a situation in which within-season compensation should be advantageous.

We predicted apical dominance created a meristem reserve of dormant buds that would allow compensation for apical flower head loss, reducing the negative effects of insect floral herbivory on seed production (Aarssen 1995, Marquis 1996). Further, we expected that protection of the later, non-apical flower heads, simulating years or situations with lower levels of seasonal herbivory, would increase compensation and the probability of high seed set when the apical flower head was damaged. Alternatively, however, delayed flowering of those later flower heads might not allowe sufficient development time or resources, or potentially reduce the probability of successful seed set through longer exposure to insect attack (Aarssen 1995, Freeman et al. 2003, Piippo et al. 2009). If so, we expected reproductive success to depend primarily on seed production by the initial early apical flower head. The results suggest that both the apical and subsequent flower heads played a role in reducing the net effect of floral herbivores, thus contributing to plant tolerance of herbivory.

METHODS

Study System

Cirsium undulatum (wavyleaf thistle) occurs in dry prairie meadows and pastures throughout the Great Plains (Kaul et al. 2007). The light purple flowers are produced from late June (early season) through August into September (late season). In the Sand Hills prairie of Nebraska, *C. undulatum* plants are often iterocarpic (S. M. Louda, unpublished data). Reproduction can occur by asexual shoots from the perennial taproot as well as by seed (Kaul et al. 2007, Brozek 2009). Flowering begins with the terminal apical flower head of the main stem. Subsequent flower head development occurs sequentially by branch down the stem, and down a branch from its terminal flower head (unpublished data).

Herbivores. The five main native floral- and seed-feeding herbivores at our site were: *Pyrausta subsequalis* Gn. and *Homoeosoma eremophasma* Neunzig [complex] (pyralid moths), *Paracantha culta* Wiedemann and *Orellia occidentale* Snow (tephritid flies), and *Baris* nr. *subsimilis* Walker (weevil) (Lamp 1980, Louda and Potvin 1995). In addition, the Eurasian flower head weevil (*Rhinocyllus conicus* Frölich) entered the floral-feeding guild in 1994 (Louda et al. 1997, Louda 1998). The patterns of feeding and the population level impacts of floral herbivory by these floral herbivores on the closely related, co-occurring monocarpic thistle, *Cirsium canescens* (Platte thistle) have been published (Lamp and McCarty 1982, Louda and Potvin 1995, Rose et al. 2005, Russell and Louda 2005). Less research has been published on *C. undulatum* (Louda and Arnett 2000, Russell and Louda 2005), and this previous work has focused on overall seed loss with vs. without attack by the flower head weevil, *R. conicus*. Whether *C. undulatum* is able to compensate for extensive ambient floral herbivory via altered patterns of reproductive investment has not been examined.

Study Site. We studied reproductive responses of *C. undulatum* to experimental modification of apical dominance and subsequent herbivory in 2007 and 2008 in Arthur County, western Nebraska, in the upper Great Plains, USA. Sites were located within Arapaho Prairie, a 1,200 ha Sand Hills prairie reserve owned by The Nature Conservancy and managed for research by the University of Nebraska-Lincoln Cedar Point Biological Station. Management since 1978 has involved the exclusion of cattle grazing, plus hay mowing in successive quarters on a four-year rotation (Keeler et al. 1980, Louda and Potvin 1995).

Experimental Protocol

In order to test for compensatory responses, we manipulated the level of apical head damage, and so apical dominance (D treatments), in two experiments (2007, 2008). The two D treatments consisted of an undamaged, insecticide-protected, control apical head (N), and an intentionally damaged apical head (D). In addition, to separate any limits on plant capacity for compensatory response from the effects of insect herbivory on plant reproduction, we tested the interaction of the apical damage treatments with two different levels of subsequent floral herbivory to non-apical heads (H treatments). The herbivory treatments were: reduced herbivory (R), using insecticide-in-water, and ambient herbivory (A), with water-only as a control. We used a completely randomized 2 x 2 factorial experimental design.

In early season each year, we marked plants that were initiating an apical flower head (20 - 22 May 2007, 30 May - 4 June 2008). We had to select new individuals each year, as aboveground ramets are usually monocarpic and new rosettes take several seasons to mature (S. M. Louda, unpublished data). In addition, using different plants each year eliminated the chance that individual effects would cloud identification of general mechanisms promoting within year tolerance. We quantified initial plant size by measuring: rosette diameter (cm), apical head bud diameter (mm), and number of flower head buds initiated. Each replicate block consisted of four plants matched by initial plant size, to control for any effects of variation in initial size on treatment response. Within each replicate block, we randomly assigned the four treatment combinations: no apical head damage (N): reduced (insecticide, R) versus ambient (water control, A) herbivory; and apical head damage (D): reduced (insecticide, R) versus ambient (water control, A) herbivory) randomly within each replicate. We established 15 replicate blocks of four treatments (total n = 60 adult plants) in 2007. We increased the number of replicate blocks to 25 (total n = 100 adult plants) in 2008. Only plants that survived to anthesis were included in the final analysis. As a result, in 2007, in the no apical damage (D_N) treatment, we had 10 surviving plants each in both the reduced (H_R) and ambient (H_A) herbivory treatments; whereas in the apical damage (D_D) treatment, we had 11 surviving plants with the reduced (H_R) herbivory treatment, and 10 surviving with the ambient (H_A) treatment. In 2008, in the no apical damage (D_N) treatment there were 21 and 15 plants with reduced (H_R) and ambient (H_A) herbivory, respectively; whereas in the apical damage (D_D) treatment, there were 19 and 12 plants with reduced (H_R) and ambient (H_A) herbivory, respectively.

The apical head damage treatment was intended to simulate the severe damage observed in the field that significantly slows or ends apical flower head development (see Lamp 1980). Two randomly chosen plants in each replicate block received apical damage. To impose damage in 2007, we caged three, field collected, native insects from the resident floral feeding guild onto the flower head in 1 mm-mesh bags for 1 wk (1 one moth larva, *P. subsequalis;* 2 weevils. *B. subsimilis*). We also hand-drilled a small hole (1mm diameter) into the lower part of each flower head to facilitate moth larval entry. At the end of the week, we removed the bag and checked the level of damage imposed. If the damage did not appear to be similar to levels observed to impede flower head development, we partially severed the vascular transport from the stem below the apical flower head using a razor blade, further mimicking the girdling observed with insect feeding. In 2008, early insect abundances were lower than in 2007. Therefore, we set up five replicates with insects as in 2007, but also added 20 replicates with only the mechanical damage (drilled hole + partial girdling). Because the effects of both techniques of apical head damage (insect + mechanical damage; mechanical damage only) were similar (ANOVA, $P > 0.10$), we present the pooled data.

Further, because herbivory mid-to-late in the season contributes most to the variability in overall floral herbivory (Louda and Potvin 1995; unpublished data), we also manipulated subsequent floral herbivory. Our aim with this treatment was to quantify the effects of variation in mid-to-late season herbivory on reproductive success when the first, apical, head was versus was not subject to floral herbivory, i.e., when apical dominance was broken versus not. Thus, we sprayed two plants within each replicate (one with apical damage, one without) with the appropriate herbivory treatment. We used insecticide-in-water to reduce floral herbivory, and water only to provide a control with ambient levels of herbivory. For the insecticide, in 2007, we used acephate (Isotox, Chevron Corp), and applied it every 7 – 10 d in a 1% solution as recommended. However, in 2008, in an effort to increase the effectiveness of insect exclusion, we used bifenthrin (FMC Corporation Pty Ltd.), and applied it every 14 d in a 0.06% solution as recommended. As found in other studies (i.e., Louda and Potvin 1995), the insecticide treatment was only partially effective; it reduced floral herbivory on the subsequent, lower flower heads by about 40% (see Results).

Data Collection

After quantifying initial plant and flower head sizes when the treatments were imposed (20 - 22 May 2007, 30 May - 4 June 2008), we recorded the number and position of each flowering head on each plant every 2 wk in 2007 (to 31 July), and every 4 wk in 2008 (to 1 August). On each sampling date, for each plant, we recorded flower head diameters of the apical head and terminal flower heads on branches, noted external evidence of insect damage, and we counted the total number of all smaller, subtending flower heads beneath the terminal head on each branch. On each sampling date, for each plant, we also recorded: plant size, as plant height (cm); average rosette diameter (the average of two perpendicular diameters, cm); and flowering effort. Flowering effort was defined as total number of flowering branches per plant and total number of heads where flowering had been initiated. Herbivory was quantified at the end of the flowering season (see below).

We covered each flower head with a mesh bag as it finished flowering to prevent seed dispersal. After flower heads matured and their subtending branches senesced, we collected all of the matured flower heads for dissection. For each mature flower head collected, we recorded: dry weight (g); diameter (mm); number of developed, undamaged seeds; and amount of insect damage to the inflorescence receptacle and to the developing seeds. To quantify the amount of insect damage, we divided each flower head into four sections and recorded damage in each quarter based on the percent area of the receptacle and seeds in that quarter that were insect-damaged. We calculated damage per flower head as the average of the four quarter values, and we divided damage into five categories, each represented by the midpoint of the category range. The categories were:

0 = 0 - 1% (very little evidence of damage); 1 = 1 - 5%; 2 = 10- 30%; 3 = 30 - 50%; 4 = 50 - 75%; 5 = 75 - 100% (heavily damaged).

Data Analysis

To evaluate and compare initial size differences, we analyzed initial measurements for number of flower heads per plant, mean rosette diameter and apical head diameter, using a multivariate analysis of variance (MANOVA) in R (R Core Development Team 2011). Initial plant size parameters were significantly larger in 2007 than in 2008 ($p < 0.001$). However, we found no significant differences among treatments in initial size within years (Treatment x Year: $p > 0.10$ for all variables). Therefore, the data were pooled for analysis, and year was treated as an additive effect in the MANOVA for initial size differences. At season end, the average insect damage per flower head was greater in 2008 than in 2007 ($p = 0.025$). However, no interaction between treatment and year occurred ($p_D = 0.67$, $p_H = 0.15$). Therefore, we evaluated the average damage per flower head by treatment from dissection data using a mixed model GLM, with plant and year as random effects.

Treatment effects on final plant size were examined in MANOVA, with final plant height, rosette diameter, number of branches, and number of flower heads as the composite dependent variable. We examined both treatment effects and the potential interaction of treatments with year. We then used subsequent ANOVAs to determine treatment effects for each significant individual dependent variable to identify factors that contributed to a treatment or year effect in the MANOVA.

To examine treatment effects on plant reproductive effort, we used MANOVA, with total number of flower heads that developed to maturity (reached anthesis) and total number of flower heads that produced seed as the composite dependent variable, followed by subsequent ANOVAs of significant individual dependent variables (as above).

Plant seed set had a severely left biased distribution, because many plants produced zero or very few seeds under the high levels of ambient floral herbivory. We used maximum likelihood to select the most appropriate distribution against which to test treatment effects on whole plant seed set. As a result, to evaluate plant seed production by treatment, we used a generalized linear model with a negative binomial distribution in R (function glm.nb).

Because the consequences of reducing herbivory varied between years ($p_{HxYear} < 0.001$ for most variables measured), each analysis incorporated a potential interaction of treatments with year. Tables of complete statistical results are presented in Appendix 2.1. This experiment mirrors a parallel study of co-occurring, monocarpic, *Cirsium canescens* (Chapter 1), and the main comparative results of these two studies can be found in Appendix 2.2.

RESULTS

Treatment effects by year

Plant sizes were significantly larger in 2007 ($p > 0.001$, see above), and many response variables displayed a treatment by year interaction (see below). Therefore, results are presented separately for each year (e.g., Table 2.1).

Seed production

The average number of filled, undamaged, seeds per plant did not vary between years ($p = 0.28$). Apical damage did not affect total plant seed production ($p = 0.46$,

Table 2.1). However, the effect of reducing herbivory by insects varied between years ($p_{HxYear} < 0.001$, Figure 2.1). Seed production in *C. undulatum* increased when subsequent herbivory was reduced by insecticide spray in 2008 (Figure 2.1B, $p < 0.001$), but there was no average herbivory treatment effect in 2007 ($p = 0.38$, Figure 2.1A). Therefore, in 2007, plants did compensate for herbivory and apical damage; however, in 2008, plants under-compensated for overall insect herbivory.

Apical damage treatments did not differ in internal feeding damage levels overall per plant ($p = 0.81$, Table 2.1). However, herbivory treatments differed in floral damage per plant ($p < 0.001$, Table 2.1). The flower heads of plants in the reduced subsequent herbivory treatment had less internal feeding damage than did control plants in the ambient herbivory treatment ($p < 0.001$, Table 2.1). Plants averaged 38 - 44% damage (2007), and 46 - 48% damage (2008) with insecticide-reduced herbivory, compared to 61 - 67% (2007) and 80 - 86% (2008) internal insect damage with water-only treatment under ambient herbivory. Therefore, while flower head damage per plant did not differ between apical damage treatments, the insecticide treatment reduced herbivory on subsequent flower heads by roughly 40%.

Seed production per flower head came from fewer heads and fewer seeds per head under ambient herbivory than with reduction of subsequent herbivory in 2008 ($p < 0.001$, Figure 2.2). Overall, however, plants with apical damage produced on average more seeds per lower head position compared to plants without apical damage in both herbivory treatments. Therefore, plants with apical damage compensated for early apical head loss with increased seed production in later heads (Fig. 2.3), although the number of heads in lower positions contributing was reduced in plants under ambient insect herbivory.

Both apical damage and herbivory on subsequent heads affected seed production per flower head, but these effects varied between years. In 2007, there were no discernible differences among treatments ($p > 0.10$ for apical damage, herbivory, flower head position, and all interactions, Figure 2.2A). In 2008, apical damage interacted with head position to influence per-flower head seed production ($p_{DxPosition} = 0.009$, Figure 2.2B). Apical damage increased the contribution from lower heads (Fig. 2.3B), but it did not change the result that the majority of seed came from the first few heads. Reducing insects increased the number of seeds per flower head overall ($p < 0.001$) and, further, it centered seed contributions into higher-positioned heads.

Plant Size

Plants were larger in 2007 compared to 2008, and apical damage did not affect plant size (MANOVA: $p_D = 0.31$). However, reducing herbivory on the later heads had a positive influence on final plant size in both years (MANOVA: $p_{Year} < 0.001$; $p_H = 0.016$, Table 2.1). Plants with reduced levels of herbivory on subsequent heads were taller than plants in the control spray treatment under ambient herbivory ($p_{Height} = 0.013$). Reducing subsequent herbivory, however, did not affect any of the other measured size variables ($p > 0.10$ for rosette diameter, number of flower heads, and number of branches). Thus, apical damage had no significant effect on either non-apical head damage or final plant size. Reducing herbivory on non-apical flower heads reduced insect damage per flower head (above) and increased plant height.

Flowering Effort

The treatments had mixed effects on flowering effort. Apical damage increased both the number of heads that flowered, and the number of heads that succeeded in producing seed per plant (Table 2.1). Reduction of herbivory on later heads, however, varied in its effect on the number of heads that flowered and the number of flower heads that set seed between years (MANOVA: $p_D = 0.031$; $p_{HxYear} < 0.001$, Table 2.1). Reduction of subsequent insect herbivory increased the number of heads that set seed in both years ($p = 0.001$), but had no effect of the number of heads that flowered (reached anthesis) ($p_{Flowering} = 0.87$). Overall, reproductive effort was higher in 2007 than in 2008 ($p_{Flowering} = 0.014$; $p_{with\ seeds} <0.001$). No herbivory x year interaction occurred in the univariate analyses ($p_{Flowering} = 0.60$; $p_{with\ seeds} = 0.053$), although there was a trend toward greater effects of herbivory in 2008 (Table 2.1). Thus, apical damage and reduction of subsequent herbivory on later heads increased the realized reproductive effort of the non-apical flowering heads, although the magnitude of difference varied between years.

DISCUSSION

In this study of an iterocarpic plant, *C. undulatum,* plants on average demonstrated the ability to compensate for damage to the apical flower head. Plants with deliberate early apical damage tended to produce more heads that flowered, and more flower heads that succeeded in maturing some seeds, than did plants without apical damage. These responses increased overall seed set by plants with damage to the apical head to a level equivalent to plants without experimental damage to the apical head (Fig. 2.3). However, this compensatory ability did not provide consistent tolerance between years for overall herbivory effects.

The compensation for apical damage seen here parallels responses reported for several other plant species, including *Haplopappus spp., Cirsium canescens, Helianthus annuus,* and *Solanum carolinense* (Louda 1982, 1983, Louda and Potvin 1995, Pilson and Decker 2002, Wise et al. 2008). These previous studies also found alteration in patterns of subsequent reproductive effort compensated, at least in part, for early season reproductive losses to insects. Here, plants with and without apical damage and experimental reduction of subsequent insect feeding had similar average seed production in 2007. However, in 2008, we found that *C. undulatum* plants encountered significant within-season reductions in reproductive fitness due to insect herbivory, evidenced by substantial increases in seed production when herbivory was reduced. Neither apical seed contribution nor increased investment in subsequent flower heads was sufficient to compensate for the high average ambient floral herbivory.

Life history theory predicts an iterocarpic plant like *C. undulatum* may not maximize fitness under high herbivory within an unfavorable season (Crawley 1997). In 2008, both relatively lower reproductive effort, due to smaller mean plant size, and higher average damage level per flower head contributed to the lack of herbivory tolerance and particularly low seed set (Table 2.1). However, differences in plant size were insufficient to explain tolerance consequences, because average seed set per plant did not differ between years. Plants with reduced herbivory in 2008 contributed more seeds than did their 2007 counterparts, offsetting the effects of extremely low seed set in plants exposed to ambient levels of herbivory. This result suggests plants had a reproductive potential in

2008 that was not realized under ambient herbivore pressure, and it highlights the importance of herbivore effects on maternal seed reproduction of this iterocarpic species. Apical dominance plays an important role in plant architecture and phenology (Cline 1991). The investment hierarchy maintained by apical dominance induces positional effects that can influence the effectiveness of such dominance as a tolerance mechanism (Rosenthal and Kotanen 1994). Architectural effects and competition for resources among flower heads means the relative condition of non-apical flower heads is strongly influenced by flower head position and the interactions among sinks (Lloyd 1980, Rosenthal and Kotanen 1994). Because of hormone-driven dynamics and optimization for vertical growth, the first inflorescences may better avoid light limitation by surrounding vegetation, and these inflorescences occupy hormonally-favored, resource rich positions at the cost of decreasing investment along plant axes (Honkanen and Haukioja 1998, Naber and Aarssen 1998, Ortiz et al. 2009). If seeds in upper head positions get better provisioning, and contribute disproportionately to plant fitness, then even increases in seed number from later heads may not compensate for fitness losses of higher positioned seed heads (Cline 1991, Aarssen 1995, Pilson and Decker 2002). We evaluated these predictions for *C. undulatum* by imposing apical damage on plants early in the flowering season, predicting they would maximize their potential for compensation from lower, later heads. However, while there is evidence of some compensation, successful plant seed set was still centered in the higher positioned heads. This result suggests that herbivore damage to the apical flower head merely shifted priority control to nearby, early-flowering branch terminal heads, as predicted (i.e., Cline 1991).

The quality of later reproductive effort may not always equal early effort, and it may actually be hindered by initial effort. Tolerance may not be realized, despite greater numbers of flowers, if lower flower heads lack the time or resources to compensate for higher positioned reproductive losses. Theory suggests that, as resources become scarce, plants should stop investing in flowering once primary heads have produced seeds to maximize seed provisioning and store up reserves for subsequent seasons (Lloyd 1980). High levels of ambient herbivory may give rise to similar effects. For example, in *Solanum carolinense*, incidence of higher floral herbivory led to greater investment in root growth (Wise et al. 2008). Also, in *Erigeron glaucus*, increases in shoot biomass under insect herbivory came at the expense of root biomass (Karban and Strauss 1993), and compensation for within season herbivory led to reduced reproduction in the next year in *Ipomopsis aggregata* (Brody et al. 2007). Finding that plants with reduced herbivory in our study were taller on average than plants under ambient herbivory suggests a cost of herbivory beyond reproductive effects.

In addition, logistics limit what we know about below-ground dynamics of *C. undulatum* (Brozek 2009, Louda et al. unpublished data). We do not yet know to what degree allocation to storage or clonal reproduction in *C. undulatum* contributes to population growth or affects flowering effort or seed allocation. Even in a reproductive year, iterocarpic plants should allocate some resources to storage reserves (Iwasa 2000), although this allocation might be low under herbivore pressure (Klinkhamer et al. 1997). Further studies examining the interaction between sexual and asexual allocation in this species could lend more insight into the degree to which clonal reproduction might buffer the negative effects of seed loss to insects (i.e., Maron and Crone 2006). We focused on within-year effects to identify general mechanisms that might confer tolerance under the intense herbivory experienced by this species. Future studies that examine to what degree floral herbivore damage affects structures and processes associated with long term survival and growth will be better able to identify the relative contributions and costs of tolerance to lifetime fitness.

Previous investments in growth or reproduction, as well as conditions of past seasons, also may affect current reproduction in iterocarpic plants (Aragón et al. 2010). Further, different environments can select for different optimal flowering sizes and reproductive effort (Kelly and Dyer 2002, Hesse et al. 2008). The number of flowering individuals can vary substantially between years (Maron et al. 2002, Hesse et al. 2008, Sletvold and Ågren 2011), and differences in tolerance may also reflect a variation in the range of individuals available to take advantage of favorable flowering conditions. The aboveground ramets of *C. undulatum* are monocarpic in Sand Hills prairie, and plants at our site can remain in the rosette stage for multiple years before flowering (Louda et al. unpublished data). Disproportionate flowering by a particular subset of individuals may reduce the pool of individuals that initiate flowering in the following year. A previous study of *C. undulatum* and its co-occurring congener, *C. canescens*, found more thistle heads were produced in years following cool, dry, summers (Russell and Louda 2005), suggesting environmental conditions in the previous year influence plant reproductive effort in this species.

That timing, frequency, and intensity of herbivory affect tolerance potential is well known (Strauss and Agrawal 1999, Stowe et al. 2000, García and Ehrlén 2002). We would expect differences in herbivory tolerance between years might arise, in part, from variation in resources as well as variation in herbivore attack among years. For instance, differences in resource availability may result in differences in plant sizes among years. Smaller plants with higher average damage, as in 2008, might reflect increased herbivore feeding per flower head as a result of limited flower head availability and lack of floral predator saturation (Crawley 1989). Larger plants, as in 2007, should be less vulnerable to numerical herbivory effects on total seed production and, thus, be better able to invest in higher numbers of non-apical heads (Crawley 1989, Bonser and Aarssen 2003); this response may be modified, however, if higher reproductive effort also results in higher relative herbivore attraction (Miller et al. 2008, Brys et al. 2011). Also, resource differences that affect compensation potential, e.g., that result in low numbers of flower buds or a limited growing season, might also influence the strength of apical dominance. Low resource availability can lead to an increased strength of apical dominance, if early apical suppression of lateral buds conserves limited resources to maximize reproductive success in high positioned heads. In high resource environments, plants might better benefit from weaker apical control that enables release and provisioning of a greater number of buds (Bonser and Aarssen 2003).

For *C. undulatum*, apical control could constrain the tolerance potential offered by non-apical flower heads, as well as exacerbate seed reduction already affected by floral herbivores. However, apical dominance would be advantageous if it confers a potential phenological escape from adapted floral herbivores. For instance, *C. undulatum* shares a suite of specialized thistle-feeding floral herbivores with *C. canescens*, an earlier-flowering, co-occurring congener. Previous work has shown that greater phenological overlap with *C. canescens* results in a lower average attack rate on *C. undulatum* by the

Eurasian flower head weevil, *Rhinocyllus conicus* (Russell and Louda 2005). Weevils preferentially oviposited on the earlier flowering *C. canescens*, resulting in associational resistance for *C. undulatum*. The *C. undulatum* plants that can realize a large reproductive effort in successful seed set while *C. canescens* is still flowering might lower or resist the effects of damage by this herbivore. Alternatively, delayed investment in later heads might decrease flower head susceptibility to a prominent native floral herbivore, the tephritid fly *Paracantha culta*, that oviposits preferentially on flower heads 10 – 15 mm in diameter (Lamp and McCarty 1982). For instance, in *Erigeron glaucus*, plants that flowered longer were more likely to avoid herbivory by another tephritid fly (English-Loeb and Karban 1992). If damage is contingent upon the timing and synchrony with plant flowering phenology, plants that distribute reproductive effort over different or longer time periods may reduce the probability of damage per head.

Classical bet hedging theory predicts that plants should maintain alternative resource allocation strategies in an uncertain, high herbivory environment (Crawley 1997). In our study, early priority investment by *C. undulatum* in a large apical head, along with regrowth potential from subsidiary, later-flowering, dormant buds after apical damage, likely provided two parts of an optimized bet-hedging strategy to reduce herbivory effects in the uncertain, high risk, herbivory environment. More information is required to understand under what circumstances the demonstrated compensation potential is realized and contributes to lifetime fitness. The results of this study demonstrate the magnitude and dynamics of potential reproductive compensatory response to both apical and subsequent floral herbivory by an iterocarpic plant species within season (over two years), and it furthers our understanding of tolerance mechanisms that contribute to ameliorate temporally and spatially variable insect effects on populations of this characteristic prairie species.

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Table 2.1. *Cirsium undulatum* final, end-of-season, plant performance measures (mean, ± SE) for plants in each of the four treatments (2007 and 2008 experiments; D = Apical damage, H = Herbivory on subsequent flower heads). Best plant performance was expected with no apical damage imposed and reduced herbivory (H_R:D_N), whereas poorest plant performance was expected with apical damage imposed under ambient herbivore pressure (H_A:D_D). Variables contributing significantly to treatment effects in MANOVA were analyzed individually using ANOVA (p values presented in Results). (^) indicates a significant treatment interaction with year. (*) indicates significant treatment differences within year. Letters indicate significant treatment differences.

		Herbivory Reduced (H_R)		**Herbivory Ambient (H_A)**	
		D_N	**D_D**	**D_N**	**D_D**
Seeds Matured per Plant^	2007	88.4 ± 31	60 ± 19.6	53.2 ± 17.6	52.3 ± 20.6
	2008*	138.4 ± 27.3^a	151.9 ± 25.6^a	2.7 ± 2.3^b	8.9 ± 3.7^b
% Damage per Flower Head	2007	41.2 ± 4.8^a	49.4 ± 3.8^a	67.3 ± 4.9^b	70.6 ± 3.8^b
	2008	50.6 ± 4.2^a	52.2 ± 3.6^a	85.9 ± 1.4^b	82.7 ± 2.5^b
Structural Effort^					
Plant Height	2007^a	63.2 ± 4.0	63 ± 2.4	62.4 ± 2.3	64 ± 4.6
	2008^b*	55.9 ± 1.9^a	58.8 ± 2.1^a	50.4 ± 3.1^b	47.4 ± 2.1^b
Rosette Diameter	2007^a	29.6 ± 2.4	30.7 ± 2.2	28.5 ± 1.3	32.7 ± 2.9
	2008^b	22.3 ± 1.5	24.9 ± 2.4	23.6 ± 2.1	21.2 ± 1.2
# of Branches	2007	3.1 ± 0.3	3.7 ± 0.3	3.0 ± 0.4	4.6 ± 0.5
	2008	2.7 ± 0.3	3.2 ± 0.4	3.3 ± 0.6	2.9 ± 0.3
# of Flower Buds	2007^a	7.7 ± 1.2	9.6 ± 1.4	7.7 ± 1.4	11.0 ± 1.0
	2008^b	3.1 ± 0.4	4.8 ± 0.7	5.1 ± 0.8	3.9 ± 0.4
Reproductive Effort^					
# Mature Flower Heads	2007^a	1.7 ± 0.5^a	2.4 ± 0.6^b	1.6 ± 0.4^a	1.6 ± 0.5^b
	2008^b	1.0 ± 0.2^a	1.8 ± 0.3^b	0.2 ± 0.1^a	0.6 ± 0.1^b
# Flowered with Seeds	2007^a	2.3 ± 0.6^{a,b}	3.2 ± 0.6^{a,c}	2.2 ± 0.5^{b,d}	2.4 ± 0.5^{c,d}
	2008^b	1.2 ± 0.2^{a,b}	2.2 ± 0.3^{a,c}	1.5 ± 0.3^{b,d}	1.9 ± 0.4^{c,d}

FIGURE LEGENDS

FIG 2.1. *Cirsium undulatum* whole plant seed production (mean ± SE) by treatment in 2007 (A) and 2008 (B). Treatment effects differed between years. Plants compensated for apical head damage in both years, but compensated for insect herbivory to all heads only in 2007.

FIG. 2.2. Average seed contribution per flower head position. Average proportion of undamaged, developed seeds per flower head (mean ± SE) contributed by each flower head position in 2008: (A) with reduced herbivory on subsequent flower heads, and (B) with ambient subsequent herbivory (control), in the no apical damage treatment (control, dark bars) and the apical damage treatment (light bars). Zeroes indicate positions where heads flowered but produced no undamaged seeds. Half positions (i.e., 2.5) indicate all the subsequent (subordinate) heads that occurred below the terminal flower head on a particular lower branch (e.g., branch 2).

FIG. 2.3. Relative seed contribution of apical versus non-apical flower heads in *C. undulatum* in 2007 (A) and 2008 (B). The height of the bars indicate total plant seed production (mean ± SE) by treatment; the black lower portion indicates the average contribution of the apical head, and the upper gray portion indicates the average contribution per plant from all lower positioned, non-apical, flowering heads.

FIGURE 2.1.

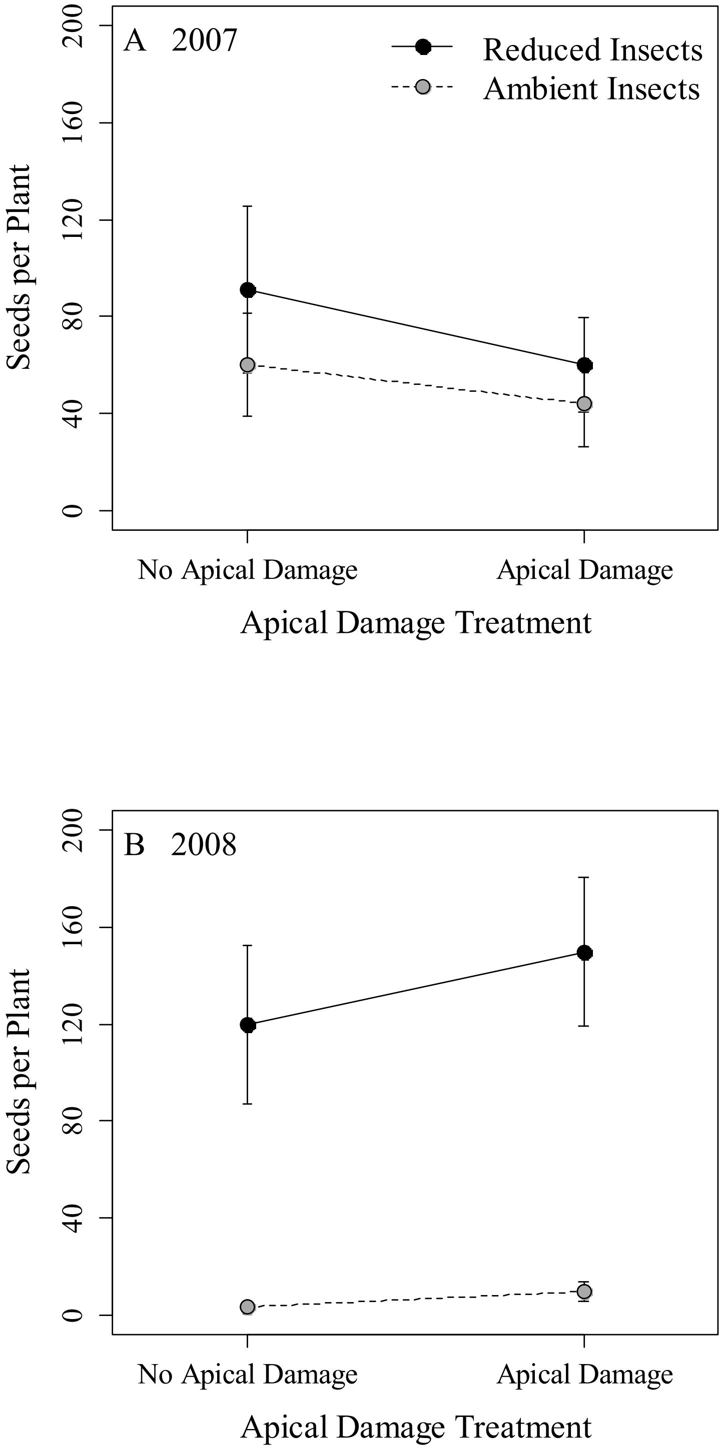

A 2007
Reduced Insects
Ambient Insects
Seeds per Plant
0
40
80
120
160
200
No Apical Damage
Apical Damage
Apical Damage Treatment
B 2008
Seeds per Plant
0
40
80
120
160
200
No Apical Damage
Apical Damage
Apical Damage Treatment

FIGURE 2.2.

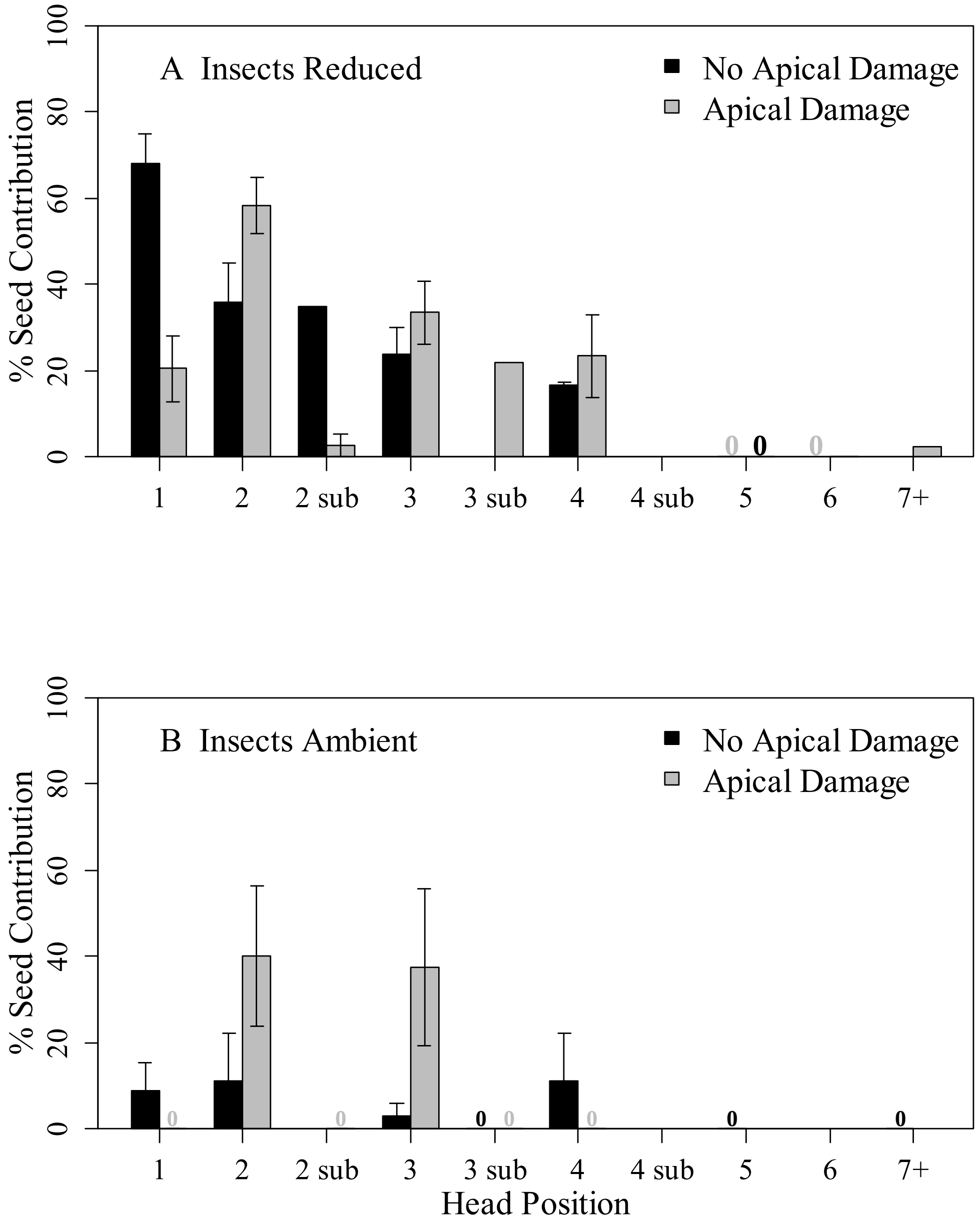
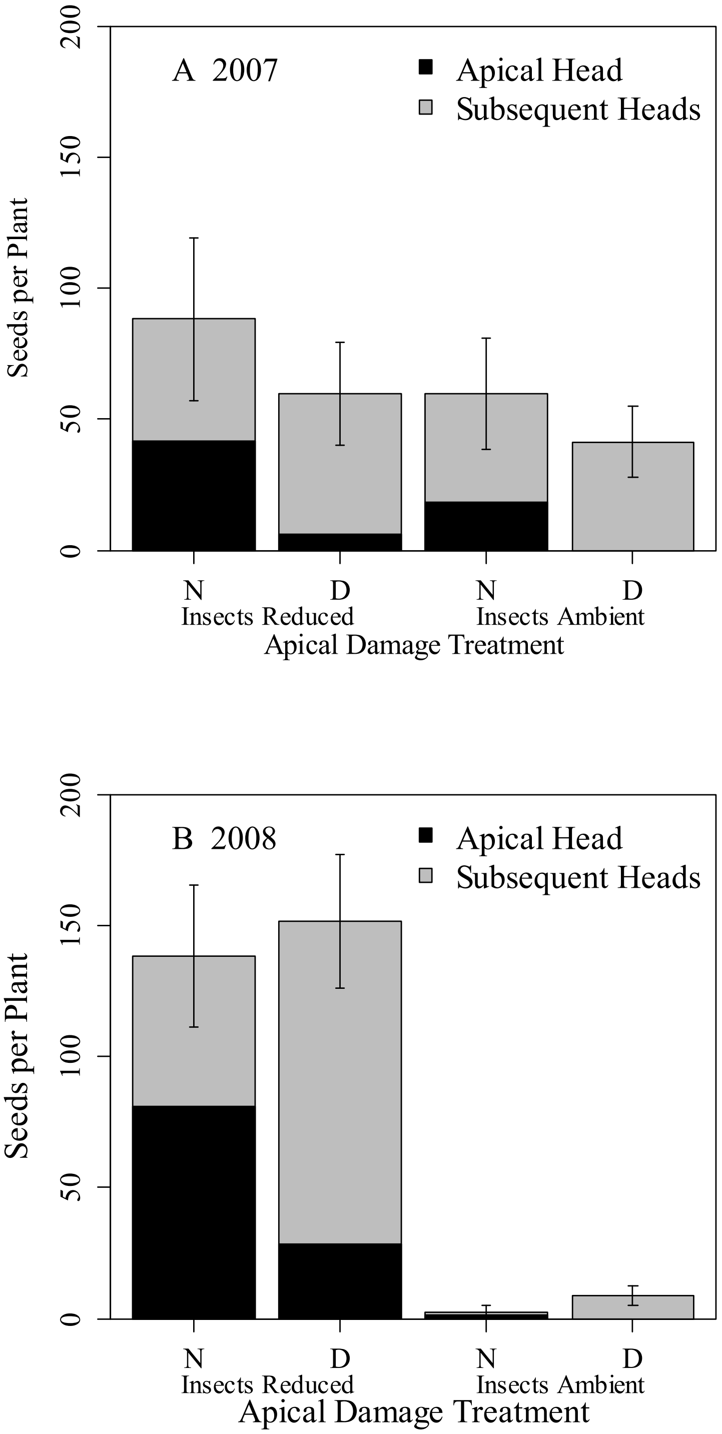

A Insects Reduced
■ No Apical Damage
▨ Apical Damage
% Seed Contribution
0
20
40
60
80
100
0
0
0
1
2
2 sub
3
3 sub
4
4 sub
5
6
7+
B Insects Ambient
■ No Apical Damage
▨ Apical Damage
% Seed Contribution
0
20
40
60
80
100
0
0
0
0
0
0
0
1
2
2 sub
3
3 sub
4
4 sub
5
6
7+
Head Position

FIGURE 2.3.


A 2007
■ Apical Head
▨ Subsequent Heads
Seeds per Plant
0
50
100
150
200
N
D
N
D
Insects Reduced
Insects Ambient
Apical Damage Treatment
B 2008
■ Apical Head
▨ Subsequent Heads
Seeds per Plant
0
50
100
150
200
N
D
N
D
Insects Reduced
Insects Ambient
Apical Damage Treatment

Appendix 2.1.

Statistical results for key *Cirsium undulatum* response variables: (A) Seeds per plant; (B) Average damage per flower head; (C) Treatment effects on plant structure, with subsequent ANOVA's; (D) Plant Reproductive Effort with subsequent ANOVA's; (E) Seed Set per Flower Head by Head Position. "D" refers to the Apical Damage treatment (N: No Damage v. D: Damage), "H" refers to the Herbivory treatment (R: Reduced v. A: Ambient). Bolded items within tables indicate significant p-values reported in the Results.

A. Seeds per Plant (GLM, negative binomial distribution)

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1860.09	925.2229	-2.01	0.044386	*
Apical Damage (*D*: N)	965.162	1317.067	0.733	0.463673	
Herbivory (*H*: A)	5414.583	1408.922	3.843	0.000122	***
Year	0.9288	0.4609	2.015	0.043853	*
D X H	1514.932	1975.512	0.767	0.443167	
D x Year	-0.4807	0.656	-0.733	0.463706	
H x Year	**-2.6979**	**0.7018**	**-3.844**	**0.000121**	*******
D x H x Year	-0.755	0.984	-0.767	0.442927	

2007 (GLM, negative binomial distribution)

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	4.2976	0.2616	16.427	<2e-16	***
Herbivory	-0.3255	0.3703	-0.879	0.379	

2008 (GLM, negative binomial distribution)

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	4.9754	0.2049	24.277	<2e-16	***
Herbivory	**-3.2808**	**0.3328**	**-9.857**	**<2e-16**	*******

B. Average Damage per Flower Head (Mixed Model GLM, plant and year random effects)

	Value	Std Error	DF	t-value	p-value
(Intercept)	0.451025	0.033215	117	13.57898	0
Apical Damage (*D*: N)	-0.00524	0.051312	90	-0.10215	0.9189
Herbivory (*H*: A)	**0.289335**	**0.053142**	**90**	**5.444569**	**0**
D x H	0.028681	0.079199	90	0.362139	0.7181

C. Effect of Treatment on Plant Structure (MANOVA, composite size variable)

	Df	test stat	approx F	num Df	den Df	Pr(>F)	
Apical Damage (*D*)	1	0.0546	1.2283	4	85	0.30497	
Herbivory (*H*)	**1**	**0.1321**	**3.2368**	**4**	**85**	**0.01599**	*****
Year	**1**	**0.4685**	**18.7349**	**4**	**85**	**4.49E-11**	*******
D x *H*	1	0.0165	0.3571	4	85	8.38E-01	
D x Year	1	0.0526	1.1809	4	85	0.32507	
H x Year	1	0.0583	1.3176	4	85	0.27002	
D x *H* x Year	1	0.0325	0.7145	4	85	0.5843	

Number of Heads (ANOVA)

	SS	Df	F	Pr(>F)	
Herbivory	9.71	1	0.8796	0.3505	
Year	570.6	1	51.6712	1.12E-10	***
Residuals	1126.37	102			

Plant Height (ANOVA)

	SS	Df	F	Pr(>F)	
Herbivory	**632.9**	**1**	**6.3709**	**0.01314**	*****
Year	2352.6	1	23.6801	4.16E-06	***
Residuals	10133.6	102			

Rosette Diameter (ANOVA)

	SS	Df	F	Pr(>F)	
Herbivory	4.2	1	0.0842	0.7724	
Year	1264.4	1	25.2961	2.35E-06	***
Residuals	4698.5	94			

Number of Branches (ANOVA)

	SS	Df	F	Pr(>F)
Herbivory	1.56	1	0.6976	0.40553
Year	7.674	1	3.431	0.06688
Residuals	228.133	102		

D. Reproductive Effort (MANOVA, composite reproductive variable)

	Df	test stat	Approx. F	num Df	den Df	Pr(>F)	
Apical Damage (*D*)	**1**	**0.06695**	**3.5881**	**2**	**100**	**0.03125**	*****
Herbivory (*H*)	1	0.19166	11.8558	2	100	2.40E-5	***
Year	1	0.11652	6.5945	2	100	0.00204	**
D x *H*	1	0.00632	0.3183	2	100	0.72811	
D x Year	1	0.01012	0.5112	2	100	0.60136	
***H* x Year**	**1**	**0.09610**	**5.3162**	**2**	**100**	**6.40E-3**	******
D x *H* x Year	1	0.01076	0.5439	2	100	0.58216	

Number Heads that Succeeded in Flowering (Matured heads; ANOVA)

	SS	Df	F	Pr(>F)	
Apical Damage (D)	**1.6774**	**1**	**6.9678**	**0.009576**	******
Herbivory (*H*)	0.0063	1	0.0262	0.871841	
Year	**1.5126**	**1**	**6.2833**	**0.013737**	*****
H x Year	0.0669	1	0.278	0.599139	
Residuals	25.0371	104			

Number Heads that Flowered that Produced Viable Seeds (ANOVA)

	SS	Df	F	Pr(>F)	
Apical Damage (*D*)	**1.3414**	**1**	**5.3614**	**0.022551**	*****
Herbivory (*H*)	**3.2192**	**1**	**12.8669**	**0.000511**	*******
Year	**3.3678**	**1**	**13.4609**	**0.000386**	*******
H x Year	0.959	1	3.833	0.052932	.
Residuals	26.0203	104			

E. Seed set per Head Position (Mixed Model GLM, plant as random effect)

	Value	Std.Error	DF	t-value	p-value	
(Intercept)	-162541	36802.54	112	-4.41657	0	*
Apical Damage (*D*: N)	193015.4	67912.33	89	2.842126	0.0056	*
Herbivory (*H*: A)	**195495.5**	**72376.83**	**89**	**2.701079**	**0.0083**	*****
Head Position (*Pos*)	24853.75	10901.51	112	2.279845	0.0245	*
Year	81	18.33	89	4.418391	0	*
D x *H*	-187912	104581.5	89	-1.7968	0.0758	
D x *Pos*	-47534.3	22238.37	112	-2.13749	0.0347	*
H x *Pos*	-24658.1	23906.65	112	-1.03143	0.3046	
D x Year	-96.14	33.83	89	-2.84211	0.0056	*
H x Year	-97.4	36.05	89	-2.70146	0.0083	*
Pos x Year	-12.38	5.43	112	-2.28055	0.0245	*
D x *H* x *Pos*	42542.99	34920.39	112	1.218285	0.2257	
D x *H* x Year	93.59	52.09	89	1.796614	0.0758	
***D* x *Pos* x Year**	**23.68**	**11.08**	**112**	**2.137346**	**0.0347**	*****
H x *Pos* x Year	12.28	11.91	112	1.031427	0.3046	
D x *H* x *Pos* x Year	-21.19	17.39	112	-1.21808	0.2258	

2007 (Mixed Model GLM, plant as random effect)

	Value	Std.Error	DF	t-value	p-value	
(Intercept)	23.89634	11.27778	62	2.118887	0.0381	*
Apical Damage (*D*: N)	25.89396	18.15045	36	1.426629	0.1623	
Head Position (*Pos*)	-1.62755	3.259052	62	-0.49939	0.6193	
Herbivory: (*H*: A)	-5.40726	6.586237	36	-0.82099	0.4171	
D x *Pos*	-7.66754	5.853479	62	-1.30991	0.1951	

2008 (Mixed Model GLM, plant as random effect)

	Value	Std.Error	DF	t-value	p-value	
(Intercept)	92.15663	10.76299	55	8.562366	0	*
Apical Damage (*D* : N)	-41.3985	13.56846	55	-3.05108	0.0035	*
Head Position (*Pos*)	-11.6674	3.348197	54	-3.48467	0.001	*
Herbivory (*H*: A)	**-53.3851**	**7.954483**	**55**	**-6.71132**	**0**	*****
D* x *Pos	**11.31765**	**4.16291**	**54**	**2.718687**	**0.0088**	*****

Appendix 2.2.

Additional data on *Cirsium undulatum* (Wavyleaf thistle) and summarized results of a qualitative comparison with co-occurring congener *Cirsium canescens* (Platte thistle, Chapter 1).

Table A2.2:1. Initial *C. undulatum* measurements. As in *C. canescens* (Chapter 1), there were no significant differences in early season sizes among treatments, though plant size did vary between years (see *Results*).

		Reduced Herbivory (H_R)		Ambient Herbivory (H_A)	
Variable	Year	D_N	D_D	D_N	D_D
Rosette Diameter					
	2007	33.2 (±2.0)	37.3 (±2.6)	37.5 (±2.0)	32.7 (±1.3)
	2008	29.6 (±2.2)	26.9 (±1.6)	27.2 (±1.7)	25.3 (±1.4)
	Overall	31.1 (±1.5)	31.1 (±1.7)	31.9 (±1.6)	28.4 (±1.1)
Apical Bud Diameter					
	2007	29.9 (±1.6)	31.4 (±1.9)	33.2 (±2.2)	29.6 (±1.6)
	2008	17.4 (±1.7)	17.5 (±1.6)	16.4 (±1.5)	15.5 (±1.3)
	Overall	22.8 (±1.6)	23.2 (±1.7)	24.0 (±1.9)	21.5 (±1.9)
Total Number of Buds					
	2007	3.9 (±0.5)	5.4 (±1.0)	5.6 (±0.9)	4.5 (±0.4)
	2008	2.8 (±0.5)	3.0 (±0.5)	2.9 (±0.5)	2.3 (±0.3)
	Overall	3.2 (±0.4)	4.0 (±0.5)	4.1 (±0.5)	3.2 (±0.3)
N	2007	15	13	15	14
	2008	35	32	33	33

Table A2.2:2. Combined experimental results on the effect of apical damage and subsequent herbivory on co-occurring *C. undulatum* and *C. canescens* (Chapter 1). *Cirsium undulatum* results are separated by year, as they were analyzed by year. Numbers in gray represent results from variables that were unaffected by treatments. Bolded vs. italicized numbers illustrate whether herbivory or apical damage had the principle effect; high values in the comparison are bolded, and a summarized comparison is provided in the last column.

Variable	**H**	***C. undulatum* 2007**		***C. undulatum* 2008**		***C. canescens* (2007, 2008)**		**Results**
		D_N	**D_D**	**D_N**	**D_D**	**D_N**	**D_D**	
% Flower head Damage	**H_R**	**41.2** ± 4.8	**49.4** ± 3.8	**50.6** ± 4.2	**52.2** ± 3.6	**48.1** ± 2.6	**48.4** ± 2.9	H effects, H_R Hi
	H_A	*67.3* ± 4.9	*70.6* ± 3.8	*85.9* ± 1.4	*82.7* ± 2.5	*78.5* ± 2.5	*72.9* ± 4.3	
Plant Reproductive Effort								
Seeds per Flower head	**H_R**	**28.6** ± 8.6	**12.0** ± 3.5	**48.6** ± 7.8	**0.9** ±0.7	**69.6** ± 7.5	**99.0** ± 6.8	H effects H_R Hi
	H_A	*14.7* ± 3.9	*20.7* ± 5.2	*59.3* ± 7.2	*4.7* ±2.1	*30.7* ± 5.3	*31.5* ± 6.5	
Non-apical position contributing most seed	**H_R**	2.6 ± 0.2	2.9 ± 0.4	2.4 ± 0.1	2.2 ± 0.1	2.4 ± 0.1	3.0 ± 0.2	n.s.
	H_A	2.3 ± 0.3	2.3 ± 0.3	3.0 ± 1.0	2.4 ± 0.2	2.5 ± 0.2	2.4 ± 0.1	
# Heads Flowered	**H_R**	*1.7* ± 0.5	**2.4** ± 0.6	*1.0* ± 0.2	**1.8** ± 0.3	*2.9* ± 0.4	**4.2 ± 0.6**	AD_D Hi, PT: H_R only
	H_A	*1.6* ± 0.4	**1.6** ± 0.5	*0.2* ± 0.1	**0.6** ± 0.1	*2.8* ± 0.4	*2.3* ± 0.3	
# Flowered with Seeds	**H_R**	*2.3* ± 0.6	**3.2** ± 0.6	*1.2* ± 0.2	**2.2** ± 0.3	*1.9* ± 0.3	**3.5 ± 0.5**	AD_D Hi, PT: H_R only
	H_A	*2.2* ± 0.5	**2.4** ± 0.5	*1.5* ± 0.3	**1.9** ± 0.4	*1.5* ± 0.2	*1.3* ± 0.2	
Plant Structural Effort								
Plant Height	**H_R**	**63.2** ± 4.0	**63** ± 2.4	**62.4** ± 2.3	**64** ± 4.6	53.3 ± 2.0	53.9 ± 2.1	H effects, WL only
	H_A	*50.4* ± 3.1	*47.4* ± 2.1	*55.9* ± 1.9	*58.8* ± 2.1	50.6 ± 1.7	47.5 ± 1.9	
Rosette Diameter	**H_R**	29.6 ± 2.4	30.7 ± 2.2	22.3 ± 1.5	24.9 ± 2.4	32.2 ± 1.6	34.6 ± 1.7	n.s.
	H_A	28.5 ± 1.3	32.7 ± 2.9	23.6 ± 2.1	21.2 ± 1.2	34.0 ± 1.6	30.6 ± 1.4	
# of Branches	**H_R**	3.1 ± 0.3	3.7 ± 0.3	3.3 ± 0.6	2.9 ± 0.3	5.2 ± 0.9	6.6 ± 0.6	n.s.
	H_A	3.0 ± 0.4	4.6 ± 0.5	2.7 ± 0.3	3.2 ± 0.4	5.9 ± 1.0	5.4 ± 0.4	
# of Flower Buds	**H_R**	7.7 ± 1.2	9.6 ± 1.4	3.1 ± 0.4	4.8 ± 0.7	9.6 ± 0.9	12.6 ± 1.4	n.s.
	H_A	7.7 ± 1.4	11.0 ± 1.0	5.1 ± 0.8	3.9 ± 0.4	10.4 ± 1.8	10.2 ± 0.8	

Variable	**H**	***C. undulatum* 2007**		***C. undulatum* 2008**		***C. canescens* (2007, 2008)**		**Results**
		D_N	D_D	D_N	D_D	D_N	D_D	
Overall Effects on Plant Fitness through Seed Production								
Seeds per Plant	H_R	88.4 ± 31	60 ± 19.6	**138.4** ± 27.3	**151**.9 ± 25.6	**355.9** ± 49.0	**477.8** ± 81.8	W: H 2008
	H_A	53.2 ± 17.6	52.3 ± 20.6	*2.7* ± 2.3	*8.9* ± 3.7	*186.3* ± 29.6	*112.0* ± 27.9	PT: AD_D:H_R

Figure Legends

Figure A2.2:1. Average damage per individual plant with (A) herbivory reduced and (B) herbivory ambient. Dashed vertical lines represent the mean damage per head for each herbivory treatment. Reduction of insects did not totally exclude herbivores, but it did lower the amount of flower head damage. Plants are presented in a random order.

Figure A2.2:2. Evaluation of apical damage treatment. (A) Variation in apical seed production among plants in the apical damage treatment when herbivory was reduced (black) versus ambient (gray) and (B) Average total number of filled, undamaged seeds in the non-apical flower heads by herbivory treatment for plants with either low imposed damage (>50 seeds produced, black) or high imposed damage (< 50 seeds produced,gray) (n = 5 per category). Only one plant in the ambient herbivory treatment produced more than 50 seeds, and there was little difference in the number of seeds produced from subsequent heads between the high and low imposed damage.

Figure A2.2:1.

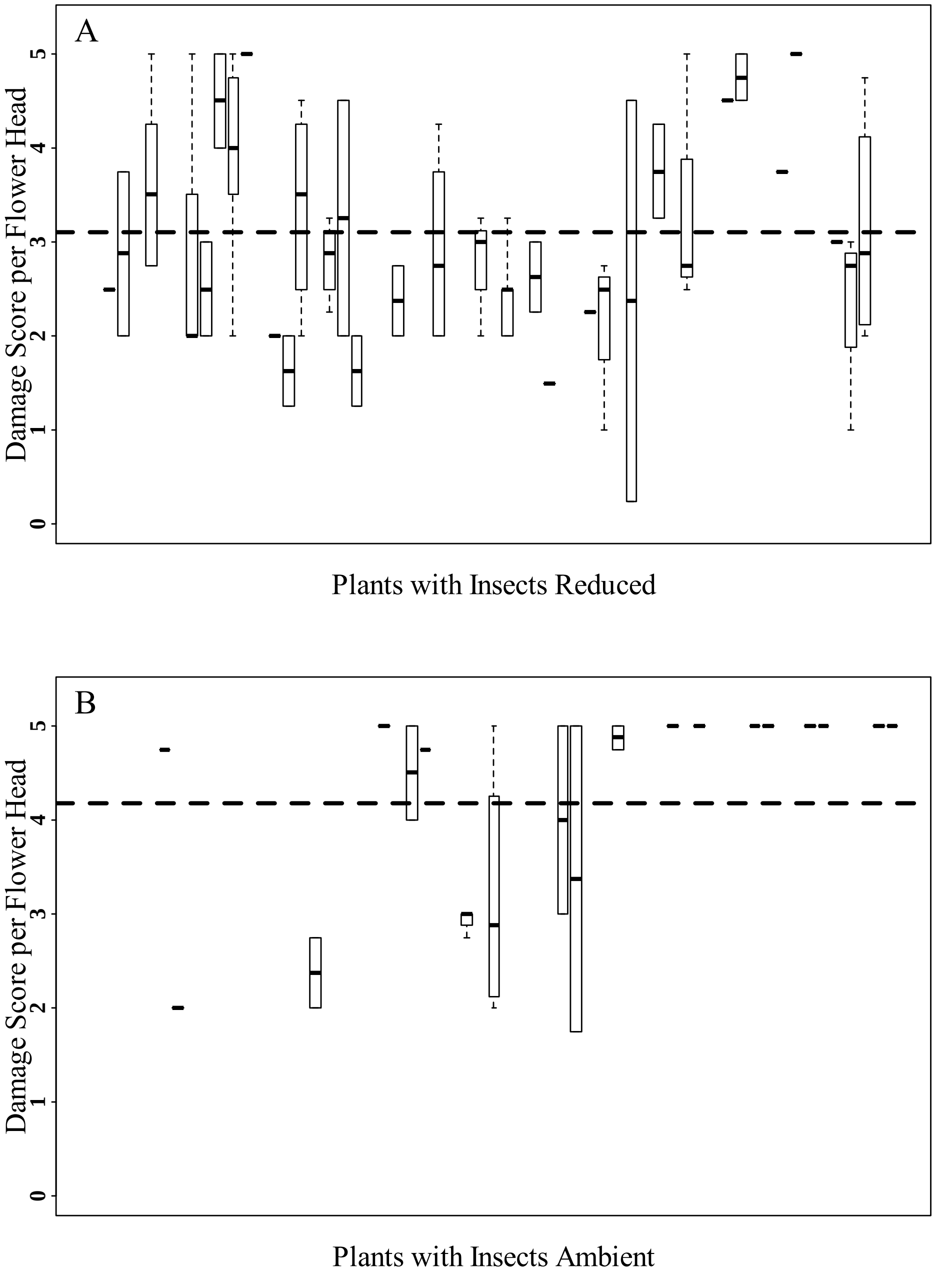
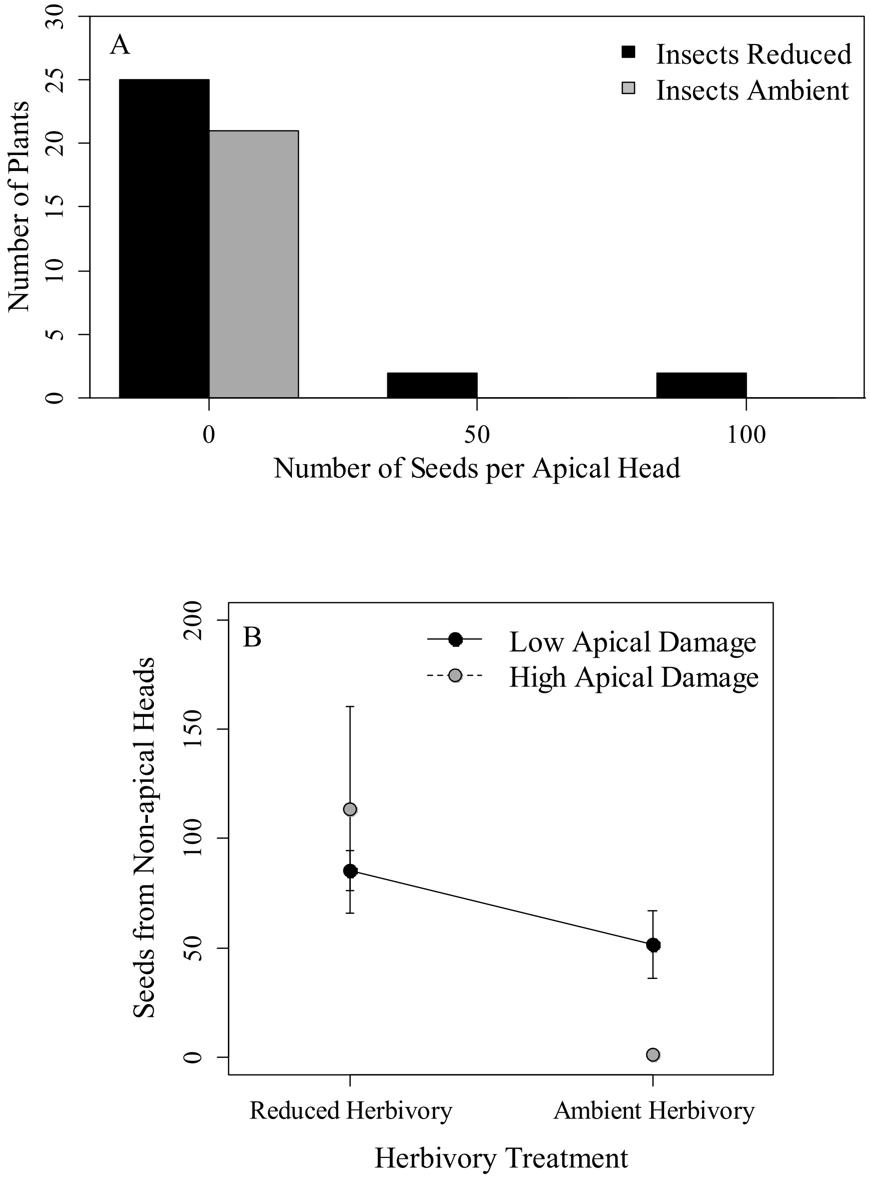

A
Damage Score per Flower Head
0
1
2
3
4
5
Plants with Insects Reduced
B
Damage Score per Flower Head
0
1
2
3
4
5
Plants with Insects Ambient

Figure A2.2:2.


A
■ Insects Reduced
■ Insects Ambient
Number of Plants
0
5
10
15
20
25
30
0
50
100
Number of Seeds per Apical Head
B
Low Apical Damage
High Apical Damage
Seeds from Non-apical Heads
0
50
100
150
200
Reduced Herbivory
Ambient Herbivory
Herbivory Treatment

Chapter 3.

Apical dominance is an optimal resource allocation strategy under a constant risk of flower head destruction by herbivores

ABSTRACT: Apical dominance is important to plant architecture and resource partitioning, but its influence on the consequences of plant-herbivore interactions remains relatively uncertain. Prolonged priority investment in apical regions, accompanied by lateral bud suppression, may constrain fitness through limits on the number or size of flowers. Alternatively, under high herbivory risk, apical dominance may increase fitness if it provides a temporal herbivory escape through either large early-season investments in apical regions or high late-season investments from early suppressed lateral buds. High priority investment in the apical flower head can be an advantage if herbivore attacks are infrequent at the beginning of the flowering season and the apical head is likely to escape herbivores. Disruption of apical dominance releases lower flower heads, but the degree to which these heads contribute to fitness depends on their probability of survival. The degree to which strong apical dominance affects plant fitness if the risk of insect damage remains high throughout the season is not clear. Using a stochastic dynamic programming (SDP) approach, we identified optimal resource allocation among different flower heads, and optimal timing of flowering, assuming no temporal variation in mortality risk of the flower heads. The model addresses trade-off between the longer flower head growth, resulting in higher the potential number of seeds produced (larger heads produce more seeds), versus the risk that the resulting longer exposure time to herbivores increases the likelihood of being destroyed by herbivores and receiving no fitness (zero seeds). Our motivating example is *Cirsium canescens* Nutt., a well-studied prairie species with intense but variable insect floral herbivory. We found that strong apical dominance did emerge as an optimal strategy in this system, and that both optimal growth investment patterns and flowering size varied with flower head survival probability. When survival between flower heads was equal, the small initial size advantage afforded the early emerging apical head resulted in prolonged priority investment. However, when apical and non-apical heads had unequal survival probabilities, the identity of the priority head varied with the overall herbivory risk environment. In a high risk environment (high herbivore attack rate), plants invested initially in the lower risk head until flowering, and both heads flowered at the same size. In a low risk environment (low herbivore attack rate), plants invested initially in the relatively higher risk head and the lower risk head flowered at a slightly larger size compared to the higher risk head. The model suggests that maintaining apical dominance can provide a fitness advantage under a constant risk of herbivory.

Keywords: apical dominance, reproductive allocation, herbivory, stochastic dynamic programming (SDP)

Introduction

Apical dominance refers to the control exerted by the apical regions of the plant shoot over the growth and development of later, dormant, axial buds. The resultant unequal partitioning of resources among individual flower heads leads to disproportionate investment between the apical region and the axial bud regions. The influence of apical dominance on flowering head size and pattern varies with the strength and duration of apical control (Cline 1991, Honkanen and Haukioja 1998, Obeso 2002). Therefore, apical dominance is an important determinant of plant architecture, phenology and resource allocation (Cline 1991, Marquis 1996).

Consequently, apical dominance may also influence the interactions of plants with their herbivores. For instance, the risk of damage and seed loss from floral herbivores and predispersal seed predators is often highest during flowering peaks (Elzinga et al. 2007). If so, then theory postulates that if there is a sufficiently high chance of floral and seed losses, as well as a chance of compensating for those losses, a plant will restrain the magnitude of its initial investment in favor of later investments (Vail 1992). Gradual release of lateral axillary buds also can extend the plant flowering period, allowing development of a subset of flower heads to escape herbivory temporally (English-Loeb and Karban 1992, Pilson and Decker 2002).

Further, the strength of apical dominance, along with its relative contribution to plant fitness under herbivory, varies among different environments. Optimization models allow a theoretical prediction for how plants should allocate resource investment to reduce fitness losses to insect herbivores. In this study, we developed a model to examine how the optimal resource allocation among flower heads should vary in relation to insect floral herbivore pressure in high versus low herbivory risk environments.

Apical dominance can confer a fitness advantage directly, through its effect on plant competitive ability for light and subsequent resource capture, and indirectly, through its influence on flowering phenology and patterns of resource allocation (Aarssen and Irwin 1991). Since apical dominance represents a disproportionate meristem commitment to vertical growth and development, it can be important for faster initial growth, and such growth can lead to competitive preemption of incoming light and reduction of shading from neighbors (Cline 1991, Aarssen 1995).

Also, the apical meristem, as a high priority resource sink, can produce larger inflorescences that are also more conspicuous to pollinators. Thus, such flowers can make substantial early contributions to plant fitness (Tiffin 2000, Chapters 1 and 2). By unequal investment among flower heads, plants can speed up the growth of priority flower buds and, thus, reduce the duration of time a portion of flower head buds remain highly vulnerable to herbivores. For instance, *Arabadopsis halleri* plants that flowered and developed fruit early avoided herbivory by beetle larvae that feed extensively on its flowers and buds (Kawagoe and Kudoh 2010). Earlier flowering also increased fruit set in *Lupinus lepidus* despite greater late season fruit production, because early flowers avoided high fruit predation by the relatively common butterfly larvae that damaged both flowers and developing seeds (Bishop and Schemske 1998).

Additionally, because favored apical sinks inhibit investment in lower positioned buds, the duration and strength of apical dominance represents a bet hedging mechanism by which plants can partition resource investment in flowering through time. Delayed investment in later flower heads can allow buds to compensate for early season conditions or early losses, or to escape herbivores altogether. For example, *Ipomopsis aggregata* increased tolerance to early season damage by regrowth of numerous branches after ungulate herbivory (Juenger and Bergelson 2000). The delayed flowering induced by ungulate herbivores also decreased the magnitude of subsequent insect damage and, so, led to increased seed production by *I. aggregata* (Freeman et al. 2003). Also, *Helianthus annuus* was able to compensate for apical damage by an extended flowering period and by seed production in high positioned branches (a consequence of sustained apical control), as well as by an investment in later flower heads that escaped the peak in insect herbivory (Pilson and Decker 2002).

Alternately, apical dominance can incur costs. For example, initial disproportionate investment, such as into a single, large composite apical head, increases risk of a significant loss of resource investment that may not be replaceable (Aarssen 1995). Furthermore, priority apical investment that delays or limits resource investment in non-apical heads might reduce the developmental rate and size potential of these later heads, as well as increase their exposure time to herbivores; it could also lead to reduction in overlap with pollinators that consequently lowers the contribution of those heads to plant fitness (Cline 1991, Aarssen 1995, Tiffin 2000). Further, total plant seed set may also be reduced if dormant buds are activated relatively late, i.e., without enough time in the season to reach flowering size or to successfully develop seeds (Huhta et al. 2000, Hesse et al. 2008).

The net fitness consequence of strong apical dominance depends on the tradeoff between the aforementioned costs and benefits, as well as the predictability of herbivore damage. For instance, if the damage risk is relatively high only during a crucial developmental time, such as during bud expansion or seed development, priority investment could speed up development and the resulting early flowering individuals would experience a shorter period of risk, providing them with a better chance of avoiding herbivores (Järemo et al. 1999). Alternatively, if herbivory events are most likely early in the season plants may benefit from reserves of dormant buds maintained through apical dominance (Marquis 1996). For example, when early ungulate herbivory is likely, investment in initial apical reproductive structures should be low; in this case, fitness is expected to be maximized through release of later, undamaged flower buds after apical damage impairs dominance (Vail 1992, Tuomi et al. 1994, Nilsson et al. 1996). Finally, if there are multiple brief herbivores attacks throughout the season, plants should gradually activate buds over time to increase the likelihood of overlap with conditions allowing some buds to develop (Lehtilä 2000). Thus, if herbivory is intense but variable in time, fewer flower buds should remain dormant (Nilsson et al. 1996). Haphazard variation in the timing and duration of herbivory would eliminate any predictability of a cost of apical dominance (Aarssen 1995).

Given these considerations, we constructed a stochastic dynamic programming (SDP) model to examine the optimal allocation of resources over a growing season between two, large, composite flower heads (apical, non-apical) exposed to a constant risk of herbivory. In many monocarpic species, the total seed production of lower level heads is similar to the seeds produced from the apical head alone. Thus, the non-apical head in our model can be thought of as a proxy for all lower level flower heads. As commonly observed, resource allocation determined the growth rate of flower heads in the model, and the resulting flower head size determined potential seed production. The model predicted optimal allocation strategies in response two life history tradeoffs. First, it predicted the optimal resource allocation between flower heads; prioritized investment in one head would delay investment and subsequent growth of the other head. Delayed growth influenced head survival because it increased the exposure time to herbivores. Second, the model predicted optimal flowering time. The longer a flower head grows, the larger its size and the higher is the potential seed production, but an extended growing period also extends exposure time to herbivores, resulting in a reduced flower head survival.

We parameterized our model with field data for *Cirsium canescens* Nutt. (Platte thistle) in sand prairie. In this thistle species, insect herbivory on flower heads is common and intense, but variable; floral herbivory can cause significant reductions in plant fitness that has population-level consequences (Louda and Potvin 1995, Rose et al. 2005). Our model predicted strong apical dominance as the optimal strategy when a small size advantage of the apical head at the beginning of the season was the only difference between the flower heads. If survival risk varied between the two heads the optimal resource allocation to the apical head depended on the intensity of the overall herbivore pressure (high vs. low herbivory risk environments) as well as the relative survival difference between the two heads.

Methods

Model Structure

Stochastic dynamic programming (SDP) models identify state-dependent optimal decisions for all possible combinations of the state variables. In this study, the decisions represented state-dependent reproductive allocation strategies that were expected to be optimized over evolutionary time. The model considered five state variables: the size of the apical flower head (M_A), the size of the second flower head or all non-apical flower heads (M_B), the flowering state of the apical (A) head (H_A*: yes or no*), the flowering state of the non-apical (B) head(s) (H_B*: yes or no*), and time (t). The model only considered two flower heads to keep the state space manageable. We considered 45 different size classes of each flower head, 21 time steps (t), and two flowering states for each head, which produced a state space of 170,100 ($t * M_A * H_A * M_B * H_B$). Adding only one additional flower head would have increased the state space to over 15 million (15,309,000) and was too large to get an exact solution. For plants that commonly only produce one to three seed-producing inflorescences, as is often seen in the Asteraceae and Apiaceae, the interpretation of the non-apical head (B) was relatively straightforward; it represented investment in only one or two lower heads with combined seed production comparable to that of the apical inflorescence. Similarly, the non-apical head (B) might correspond to the combined total investment in all other lower heads; in this paper we assumed that the total seed production of all other flower heads was the same as the apical head (Chapter 1 and 2).

A SDP model uses backward iteration to find the optimal solution starting at the final time horizon (*T*), which in our model was the end of the growing season, and then stepping backward through time. At each time step for each combination of states, the SDP model calculated the fitness consequences of all possible decisions in the next time step, and chooses the decision that maximizes expected future fitness (see detailed descriptions of SDP models in Bellman (1957) and Clark and Mangel (2000)).

The model incorporated two life history decisions: the optimal flowering size and, thus, flowering time (trade-off between current and future reproduction) and the optimal resource allocation to growth of the apical (A) head versus the non-apical (B) head(s) before flowering. In the model, if one of the heads flowered or was destroyed by herbivores, all subsequent resource inputs were allocated to the growth of the remaining head. The expected fitness produced by flowering heads generally increased with head size; expected fitness based on head size (*q(M))* at time *t* was described by the equation:

$$q(M) = 1/(1 + e^{-c*\left(\frac{M}{M_{max}}-v\right)}) \qquad Eq.\ 1$$

where M is the head size, M_{max} represents the largest possible head size, and c and v are constants that affect the shape of the S-shaped fitness curve (from Kokko 2007). *q(M)* varied between 0 (no fitness) and 1 (maximum expected fitness). This function incorporates the rarity with which small flower heads produce any seeds, and that at very large head sizes, partitioning resources among an increasing number of seeds would decrease the fitness advantage of continuing to increase in size (a diminishing return). *q(M)* indirectly incorporated the survival of developing seeds. For instance, if a head of size M produces an average of n seeds, and y is the proportion of seeds surviving until the end of seed maturation, then $q(M)=ny$.

The model considered allocation of available resources, R, between the apical (A) and non-apical (B) heads. We specified r as the proportion of R allocated to the A-head, and $(1-r)$ the proportion of resources allocated to the B-head. For each time step, the model determined the optimal r-value for each size combination of the two heads (M_A, M_B). The expected size of a flower head in the next time step (t+1) depended on the resource allocation it received for growth (see below) and on its size at time t. We assumed that flower head size at time t+1 is a linear function of flower head size at time t. This is consistent with empirical observations for many plant species, and it is a common way to model size changes from t to t+1 in integral projection models (Ellner and Rees 2006, Briggs et al. 2010).

$$M(t+1) = a + b\,M(t)$$

In the model, flower heads could not decrease in size, thus if zero resources were allocated to a flower head then the growth function represented the 1:1 line (a=0, b=1). If 100 % of the resources were allocated to a single flower head then the intercept of the growth function, a, specified the maximum size increment of flower heads at their smallest possible size; the slope b <1 ensured that the growth increment of small heads exceeded that of large heads. This growth function produced a concave down growth curve of individual head sizes over time (fig. 3.1, inset).

The growth functions of flower heads that received less than 100% of the resources fell between $M_A(t+1, r=1)$ or $M_B(t+1, r=0)$ and the 1:1 line. The growth increment, g, at head size M was a linearly decreasing function of resource allocation. For example, a head that received 50% of the resources ($r = 0.5$) would grow half its potential growth increment in one time step (fig. 3.1). So

$$M(t+1, r) = g(M(t), r) + M(t), \qquad \textit{Eq. 2}$$

We denoted $g(M_A(t), r)$ as the growth increment for head A, and $g(M_B(t),1\text{-}r)$ the growth increment for B. Since size is a continuous variable, we discretized the size distribution by slicing it into equally spaced intervals. Typically, the growth increment from one time step to the next fell between two size categories. Thus, we used linear interpolation (see Clark and Mangel 2000 for details) to calculate the size of both flower heads resulting from a particular resource investment, r, from time t to t+1.

Each time step, a vegetative flower head could start flowering. Flowering decisions could not be reversed, i.e. a head that flowered at time t could no longer increase in size, but also could not be destroyed by insect herbivores attacking vegetative heads. In the field, heads can be partially or completely destroyed during or after flowering. The resource partitioning between vegetative flower heads and the time when a flower head switched to the flowering state should not influence the chances of herbivore attacks after flowering; hence, this post flowering mortality risk could be included as a scaling factor in the expected fitness calculation associated with a flower head of size M.

The longer a plant delays flowering and continues growing, the higher the potential fitness of each flower head. However, delay also increases the probability of destruction by insect herbivores prior to flowering (fig. 3.2), so even if 92% of the flower heads survive herbivore attack for one time step, only half of the flower heads survive 11 time steps ($0.92^{11} = 0.5$). Thus, postponed flowering initially increased the expected fitness (increase in flower head size) up to a point beyond which it began to decrease because the additional mortality risk incurred by growing one more time step exceeds the benefit of attaining a larger size (fig. 3.3). A consequence of the humped shape expected fitness curve was to flower before the end of the season. We assumed that the mortality risk for apical and non-apical flower heads were independent probabilities.

Our model found the solution that maximized the expected fitness of the entire plant, i.e. the sum of the fitness contributions of both flower heads. At each time step, the SDP model identified which of four possible life history decisions maximized the plant's future fitness. The general programming equation was:

$$F\,[M_A, M_B, H_A, H_B, t] = \qquad \textit{Eq. 3}$$

$$\max(\text{“}\textit{A and B flower”,” only A flowers”,” only B flowers”,” A and B grow"}),$$

where M_A and M_B were the size of flower heads A and B, and H_A or H_B denoted their reproductive state. A reproductive state of one indicated that the head was flowering, whereas a reproductive state of zero indicated that the head was growing. We denoted the survival probabilities (S) of the apical (A) head or non-apical (B) as S_A and S_B. The expected future fitness was zero for a vegetative flower head destroyed by insect herbivores. In the model, we indicated this by setting the head size M to zero. For example, if the A-head flowered at size M_A and the B-head was going to flower in the next time step then the expected future fitness was $F[M_A(t), M_B(t), 1, 1, t+1]$. However, if the B-head was to continue growing, it automatically got all resources (r=0) to grow to size $M_B(t)+g(M_B(t), r=0)$ with probability S_B. Thus, for this scenario, the expected future fitness resulting from the decision for the B-head to keep growing is

$$(1-S_B)\ F\,[M_A(t), 0, 1, 0, t+1] + S_B\ F\,[M_A(t), M_B(t) + g(M_B(t), r=0), 1, 0, t+1].$$

The future fitness associated with each of the four life-history decisions in *Eq 3* was:

"A and B flower":

$$F\,[M_A(t), M_B(t), 1, 1, t+1]$$

"Only A flowers":

$$S_B\ F\,[M_A(t), M_B(t)+g(M_B(t), 1), 1, 0, t+1]\ +\ (1-S_{\boldsymbol{B}})\ F\,[M_A, 0, 1, 0, t+1]$$

"Only B flowers"

$$S_A\ F\,[M_A(t) + g(M_A(t), 1), M_B(t), 0, 1, t+1] + (1-S_{\boldsymbol{A}})\,F\,[0, M_B(t), 0, 1, t+1]$$

"A and B grow"

$$\max_r\ \{S_A S_B F\,[M_A(t) + g(M_A(t), r), M_B(t)+g(M_B(t), 1-r), 0, 0, t+1]\} +$$

$$(1-S_A)\,S_B F\,[0, M_B(t)+g(M_B(t), 1-r), 0, 0, t+1] +$$

$$S_A\,(1-S_B)\,F\,[M_A(t)+g(M_A(t), r), 0, 0, 0, t+1]$$

The possibility that both heads die is not presented here for the sake of brevity, as the fitness if neither head survived was always zero (Clark and Mangel 2000). If both heads were equal in size the expected fitness associated with r was equal to 1-r. When fitness was tied, the A-head received a slight priority investment.

Motivating Example

We parameterized the growth and fitness functions of the model using field data for *Cirsium canescens* (Platte thistle, Appendix 3.1). *Cirsium canescens* is a short-lived, taprooted, monocarpic perennial plant native to sand and gravel soils of the upper Great Plains and southern Rocky Mountains (Kaul et al. 2007). This plant grows as a rosette for two – eight years (Louda and Potvin 1995) prior to its single, fatal reproductive year. As a determinate flowering adult, *C. canescens* produces several large flower heads, starting with the apical head (unpublished data). All heads open from mid- to late May through late June/early July, and reproduction is solely by seed (Lamp 1980, Kaul et al. 2007). Because flowering is determinate, the terminal, apical, flower head emerges first. Over the season, subsequent flower heads (capitula) develop basipetally, sequentially down the stem and down toward the stem on each branch. The apical flower head is critically important to fitness in this plant; this single flower head often produces 40-60% of whole plant seed production (Louda and Potvin 1995, Chapter 1), though it may also have an up to 50% chance of destruction by insects (Lamp 1980). The six main thistle-specific insect floral herbivores in this system, including two noctuid moths, two tephritid flies and two weevils, maintain consistent, but a quantitatively variable, pressure on *C. canescens* within each growing season and among years (Lamp and McCarty 1982, Louda et al. 1990, Louda and Potvin 1995, Rose et al. 2005, Russell and Louda 2005). Insect herbivore damage on *C. canescens* in the field is high and can result in complete abortion of all developing flower heads (Louda and Potvin 1995)

Estimation of plant flower head growth

In early spring 2009, we selected 30 individual plants with an apical flower bud within the rosette that indicated they were preparing to flower. We quantified subsequent flower head growth over time by measuring the diameters of the apical and first branch terminal head. Measured flower heads were marked with permanent markers to ensure measurements were taken at the same location on the flower head each time, and we used the average of two perpendicular measurements. In addition, the area of the flower head receptacle, which produces the florets and, so, seeds, was estimated using the two diameter measurements. Because growth measurements in receptacle area and head diameter produced qualitatively similar patterns, we used diameter as the direct estimate of flower head size in our model. To quantify (maximum) growth rate per head, we divided the 30 plants into three treatment groups, in which we removed all but the apical head (N = 10), all but the second head (N = 10), or all but the first two heads (apical and second bud, N = 10).

REDUCTION OF INSECT HERBIVORY: Because insect herbivory is frequent and severe in this system, and because we wanted to quantify maximum growth rate, we also protected these developing flower heads with insecticide. We sprayed individual flower head buds on experimental plants with bifenthrin (FMC Corporation Pty Ltd.) at 14 day intervals in a 0.06% solution, as recommended. Once flowering was initiated, we only applied insecticide to the flower head base, to avoid discouraging pollination; however, this caution allowed some floral herbivory to continue. After pollination, we covered flower heads with 1- mm mesh bags to prevent post-senescence seed dispersal. We collected flower heads in their bags after senescence and dissected them in the lab, quantifying seed production as well as insect damage that might have influenced growth rate estimates. The average internal insect damage was 20.5% (± 4.2%), which was considerably lower than the average damage sustained by untreated plants (68 - 71% per flower head: Chapter 1). On our experimental plants, we observed little external evidence of insect damage that was sufficient to affect final head size.

Estimation of size-dependent seed production

We recorded the seed production per head as a function of head size. We assumed that the highest number of seeds per flower head recorded in our growth estimation experiment (450 seeds) was the maximum seed fitness value. This maximum fitness value was a conservative estimate because our model predicted that that flower heads should flower before reaching the maximum size, and it is larger than average seed maximums recorded from flower heads without insecticide protection (Louda and Potvin, Chapter 1). Flower heads < 10 mm rarely flowered, and if they did, produced no seed (unpublished data). We used a logistic function to describe the relationship between head size and fitness in our data (*Eq. 1* above, Appendix 3.1) and assumed that fitness was approximately zero for heads <10 mm diameter. We rescaled the parameters such that the maximum possible fitness value was 1. Our sensitivity analysis suggested that the qualitative predictions of the model were insensitive to parameter variation in the fitness function (Appendix 3.2).

Model Implementation

We programmed the SDP model in R v. 2.14.0 (v. 2.14.0; R Development Team, 2011). Time steps were three days, consistent with the data collected on flower head growth (above). Since a typical growing season was ~ 9 wks, we used 21 time steps as the final time horizon, T, consistent with the observation that plants typically completed flowering by the end of the growing season (unpublished data). We chose the range over which we varied flower head survival probabilities per time step using field estimates; probabilities ranged from 0.80 to 0.94, which was equivalent to 17 to 62% flower head survival during the season assuming all heads flowered by $t = T$.

We explored three scenarios. In the first scenario, we assumed that the risk of being destroyed by insect herbivores was equal for both the apical (A) and non-apical (B) heads. We tested this scenario over a range of ambient survival probabilities (S) from S= 0.80 to S = 0.92 per time step. In the second and third scenarios, we assumed unequal survival probability between the A and B heads. For example, if we envision the non-apical (B) head as representing all non-apical flower heads, the complete destruction of all seed production by insect herbivores was less likely compared to that of the single apical (A) head. We examined the plant decisions with unequal flower head survival in an environment with a relatively low overall survival risk (second scenario) versus a higher overall survival risk (third scenario), in order to determine whether the optimal strategy changed with ambient risk. Because heads were identical in the first scenario, which led to an initial fitness tie, for all scenarios, we allowed the apical (A) head a small initial size advantage, as seen in the field.

Forward Simulation

The SDP predicted optimal life history decisions in a five-dimensional space, given five state variables. In order to make the results of the SDP more easily understood, we performed a forward simulation using 10,000 plants for each survival parameter combination. In the simulation, the plants followed the optimal life history decisions from the SDP model. Every time step, the SDP results determined whether a flower head should flower. If it was best for flower heads to remain vegetative, the SDP determined the resource allocation given the time of the season, and the size and flowering states of the two flower heads. Then the simulation used a random number generator to determine how many vegetative flower heads survived until the next time step. Based on the simulation results, we calculated the means for the flowering times of the different heads, the proportion of heads surviving to flowering, the size of flowering heads, the change in resource allocation over time, and the average plant fitness for each scenario.

Results

The model predicted a plant should prioritize initial investment into a single flower head under all parameter combinations. However, the predicted degree of optimal apical dominance, and the identity of the head with prioritized investment, depended upon the survival scenario. The proportion of heads surviving until flowering was dependent both on the survival probabilities of the two heads in each time step and the optimal flowering date, as flowering date determined the number of time steps a flower head was subject to mortality.

Both heads with equal probability of being destroyed by herbivory

The model predicted apical dominance was the optimal strategy for all survival scenarios. In the first time step, the expected fitness of equally-sized flower heads was identical, resulting in a fitness tie. In order to break the tie, the apical (A) head received the priority investment in the the first time step, in congruence with field data. Our model predicted that, at the beginning of the season, all resources should be allocated to the larger, hence, the apical (A), head (fig. 3.4) until it flowered (10 time steps, ~ 30 days). However, in the simulation, the apical head frequently died before flowering, in which case all resources were allocated to the remaining head. In general, a higher risk of being destroyed by herbivores resulted in earlier flowering of the non-apical B heads (fig. 3.4), and smaller head sizes at flowering (fig. 3.5A). Interestingly, within the survival scenarios considered in this model, the flowering time of the apical-head was not influenced by survival risk. The combination of both smaller flower heads and a reduced proportion of heads surviving until flowering drastically reduced the average fitness of plants in environments with a high risk of herbivory (fig. 3.6).

Both heads with unequal probability of being destroyed by herbivores

Our model predicted two distinct reproductive strategies for the high herbivory risk environment versus the lower herbivory risk environment (fig. 3.7). In the high risk environment, the model predicted that the head with high survival probability (low risk) received initial priority in resource investment, continuing until it flowered or was destroyed by insect herbivores (~70%: S = 0.88, fig. 3.2). Resources were then allocated to the head with low survival probability (high risk), if it was still alive; there was on average only a 20% chance that the low survival head (S = 0.84 after 10 time steps, fig.3. 2) had not already been destroyed. Only 0.86% of plants had both heads survive to flowering. If, however, the head with low survival probability did survive, it flowered at the same size as the head with priority resource acquisition (fig. 3.5B).

In the low risk environment, in contrast, the model predicted the opposite strategy. The head with low survival probability (high risk, S = 0.88) had initial priority resource investment, rather than the head with high survival probability (low risk: S = 0.92, fig. 3.7), until the low survival probability head flowered (~30% of heads) or was destroyed by insect herbivores (~70% of heads, fig. 3.2). Then, resources were allocated to the low risk head (high survival probability), which subsequently grew to a larger size than did the high risk head (low survival probability) that initially received priority investment (fig. 3.7). This flowering strategy produced 20% survival of the high risk head, and 30% survival of the low risk, though only 1.5% of plants had both heads survive. As a consequence, the relative fitness of the plant as a whole was higher in the low risk environment than in the high risk environment (fig. 3.6).

The switching point between the different strategies for high versus low risk environments occurred between $S = 0.84$ and $S = 0.86$ survival probability per head per time step. This same pattern occurred regardless of whether A or B had the survival advantage.

Discussion

Both plant tolerance and resistance of herbivory can provide strategies to decrease the effects of herbivory (Järemo et al. 1999, Boege and Marquis 2005). Through these general mechanisms, plants can minimize losses to herbivory by resource investment decisions that decrease the likelihood of strong negative effects on plant performance (Strauss et al. 2002). Plant tolerance involves growth responses after herbivory that minimize the consequences of herbivores (Tiffin 2000). Conversely, plant resistance involves strategies to avoid or minimalize the likelihood or severity of herbivory (Agrawal 2005). Our model identifies optimal resource allocation patterns that reduce the likelihood that herbivores will destroy reproductive investment (resistance). Plants can replace losses caused by herbivory to some extent. Regrowth ability after herbivory, a form of plant tolerance, is often influenced by apical dominance (Strauss and Agrawal 1999), and has been studied extensively (Strauss and Agrawal 1999, Stowe et al. 2000, García and Ehrlén 2002). However, how phenological variation in resource allocation and flowering might aid in decreasing the effects of herbivory is less understood (Strauss and Whittal 2006).

In this study, we focused on determining whether apical dominance would emerge as an optimal strategy to minimize the effect of herbivory on plant reproductive fitness. Priority investment in a single flower head provided an optimal strategy under all three fitness scenarios. In the first scenario, both flower heads were assumed to be identical and have equal probability of survival. An initial small size advantage was sufficient for strong apical dominance, realized here as initial priority investment in only one of the two developing heads at a time, to emerge as the optimal strategy, regardless of the ambient herbivory risk. The initial size advantage is congruent with field observations, as it was reasonable to assume that one of the heads, the apical head, should emerge first and, as a consequence, grow somewhat larger than the secondary, later, non-apical head(s).

Priority investment in a single flower head produced one head that grew to flowering size as quickly as possible. In the model, as in the field, plants can be destroyed by herbivores at any time, and flower heads need to become large quickly to achieve a high reproductive fitness payoff. Regardless of the population-level predictability of herbivory in this system (Louda and Potvin 1995, Rose et al. 2005), the chance that a particular individual will suffer herbivore damage, and the magnitude of that damage, are always uncertain (Simons and Johnston 1999). Rapid growth will reduce the number of time steps that a flower head is exposed to herbivore-imposed mortality before reaching flowering and setting seed. In our model, the apical head had a slight initial size advantage and, as a consequence, was one step closer to flowering. This advantage led to the prediction that the apical head should receive the priority in resource investment when the probability of survival was equal for apical and non-apical flower heads. Because the increase in fitness per unit head size increase decreased as size increased (diminishing return, fig 3.3), there came a point at which it became more advantageous to stop allocating resources to the apical (A) flower head in favor of the non-apical (B) head.

In the second and third scenarios, when survival probability for apical and non-apical flower heads was unequal, the optimal strategy depended on the overall survival probability, and relative survival differences between flower heads, independent of the initial size difference. We examined the consequences of unequal flower head survival in both a relatively low herbivory risk environment with a relatively higher probability of head survival overall (hereafter, low risk environment, second scenario) versus a higher herbivory risk environment with a low probability of head survival overall (hereafter, high risk environment, third scenario). In a high risk environment, the model predicted that initial investment should focus on the flower head with the relatively high survival probability. However, in a low risk environment, the optimal strategy was to invest initially in the flower head with the lower survival probability. This strategy is counterintuitive at first, but there is > 40% chance that the low risk head will not be destroyed by herbivores by the time the priority head flowers (fig. 3.2, $S = 0.92$ after 10 times steps), and hence, there is a good chance that the second head will also survive until flowering. In contrast, in the high risk environment it is rather unlikely that both heads will survive until flowering, so it was best to be safe and invest in the low risk head first.

The optimal strategies in the different environments were robust regardless of whether A or B had the relatively higher herbivory risk. Hence, when survival probabilities of the apical and non-apical head were unequal, it was the difference in survival probabilities, rather than in initial head sizes, that determined the optimal investment strategy. These results show how apical dominance that influences patterns of resource investment can contribute to optimizing reproductive fitness under floral herbivory in three reasonable ecological scenarios.

Survival probability of a head also influenced predicted optimal flowering size. In general, the model predicted that plants should flower relatively later at larger sizes if, and only if, the survival probability per time step was relatively high (i.e., low risk). When survival probabilities were the same for both flower heads, the optimal flowering size was equal for both heads if the survival was low (high risk), but the head with priority investment flowered earlier at smaller sizes if survival was high (low risk). If survival was unequal between the two flower heads, both flower heads flowered at the same size in the high risk environment, but in the low risk environment the head with the priority investment flowered first at a smaller size.

The results here illustrate that risk of insect herbivory influenced the optimal resource allocation between reproductive structures within a plant. Previous empirical evidence shows that plant phenology and resource allocation can affect the magnitude of herbivory losses by avoidance of a large overlap with potential principal predators (Russell and Louda 2005, Elzinga et al. 2007). For instance, insect herbivores influenced optimal plant resource allocation to growth versus reproduction in *Opuntia imbricata* (Miller et al. 2008). Further, plants of *Erigeron glaucus* that allocated flowering through time avoided floral herbivory by tephritid flies more successfully (English-Loeb and Karban 1992). Also, Pilson (2000) found selection for later-flowering heads of *Helianthus annuus* reduced total damage by a complex of seed predators. Thus, our results are consistent with prior theoretical and empirical work suggesting that the fitness costs imposed by herbivores have the potential to shape plant life history strategies.

The role of herbivory risk in plant life history has received extensive attention in research on the evolution of bud dormancy. The timing and type of herbivory experienced may directly determine the degree to which plants are susceptible or resistant to herbivore effects (Honkanen and Haukioja 1998). If herbivores are large grazers roaming through the landscape, herbivory can be envisioned as an isolated event followed by a lull in herbivory risk during which plants can replace investment from protected buds. In this case, bud dormancy models predict that plants should release all buds early in the season (no dormancy) when risk of herbivory is less than 0.5, but release all buds late (full dormancy) when risk of herbivory is more than 0.5 (i.e., Vail 1992, Tuomi et al. 1994, Simons and Johnston 1999). Bet-hedging by partially investing in both early and late reproduction was found to be optimal only when herbivory risk was exactly 0.5, or when there were other influences determining the effects of herbivory; such influences include: low fitness returns from late season reproduction relative to early season reproduction (Simons and Johnston 1999); size-selective herbivory (Vail 1992); variation in bud release potential at different levels of damage (Tuomi et al. 1994); and variation in herbivory risk between years (Nilsson et al. 1996). Bud dormancy models also suggest that repeated risk of herbivory should lead to the evolution of some sort of bet-hedging (Nilsson et al. 1996), such as gradual activation of the entire bud bank, rather than a release triggered by damage (Tuomi et al. 1994, Lehtilä 2000).

In contrast to the effect of large grazers, insect herbivore communities can impact individual plant fitness consistently throughout the growing season; thus, vulnerable plants have a more or less constant risk of being attacked by insect herbivores. In this model, we did not find any evidence of bet-hedging, as defined above, as partial investment in both heads simultaneously. Resource investment in apical versus non-apical heads was optimized by investing in one flower at a time. Partial investment in the two flower heads at once would have reduced the growth rate of both, and so decreased the probability that either bud would survive to flower and set seed under constant herbivore risk.

Our basic model did not incorporate the effect of apical dominance on the positional hierarchies among multiple lower, non-apical, heads nor resource investment in seed maturation. As a result of architectural position effects, and competition for resources among flower heads, the relative condition of non-apical flower heads are strongly influenced by flower head position and the interactions among such resource sinks (Lloyd 1980, Rosenthal and Kotanen 1994). In this model, we wanted the optimal strength of apical dominance under constant herbivory risk to be predicted by the model; thus, position effects were incorporated very simply. Subsequent research could incorporate the role of positional effects to address more of the complexity and influence of plant modular nature on the dynamics of allocation among flower heads, as heads close together are most likely to compete and be influenced by similar considerations (Lehtilä 1999, Vuorisalo and Mutikainen 1999). Future models that included analysis of positional effects, such as a greater fitness payoff or a higher growth rate in the apical head, could broaden our understanding of how apical dominance might mediate a bet-hedging strategy for the intense, but variable, fitness effects of insect herbivores.

In summary, we explored whether initial priority investment in a single developing flower head, defined as strong apical dominance, could confer an optimal strategy under a constant high risk of damage and seed loss, similar to that which plants can experience under intense insect floral herbivory. We found that priority investment provided an optimal strategy under herbivory, but the relative allocation of investment varied with differences in survival probability and the overall level of risk in the environment. The model and our results provide a framework for future studies, as well as furthering our understanding of how herbivory can contribute to the evolution of plant reproductive strategies.

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Figure Legends

Figure 3.1. Flower head growth trajectories. The solid black line represents the change in head size from one time step to the next if all resources are allocated to a single head. The narrower gray line represents the 1 : 1 line (if no resources are allocated, the head stays the same size from one time step to the next). As a result of this growth function, the growth trajectory of flower heads is a concave down function (inset). A head that gets half the resource investment can only realize half the maximum growth increment, which is indicated by the grey circle. The dashed line in the inset indicates the growth trajectory of a flower head that receives fewer resources compared to the flower head indicated by the solid line.

Figure 3.2. Proportion of flower heads surviving over time. The curves illustrate the cumulative mortality over the growing season resulting from the different survival probabilities per time step, *S*, used in our model.

Figure 3.3. Expected fitness for different flowering times. This assumes all resources were allocated to a single flower head. Initially, postponing flowering increases expected fitness because it produced larger flowers. However, the cumulative probability of surviving until flowering is lower the later the flowering date. As a consequence, the expected fitness curve is humped shaped (unless survival probability is 1, dashed line); circles represent the peak fitness value for different survival probabilities. The lines indicate different survival probabilities (*S*) per time step: 1.0 (black dashed line) 0.92 (black solid line), 0.8 (dark gray solid), and 0.84 (light grey solid line). The inset displays the change in head size over time.

Figure 3.4. Optimal resource allocation if survival probability of all heads is the same. The lines indicate different survival probabilities (*S*) per time step (gray line, *S* = 0.92; black line, *S* = 0.84). Diamonds indicate initial flowering time for the apical (A) head (black diamond, *S* = 0.84; grey diamond, *S* = 0.92) and non-apical (B) head in each herbivory risk environment (black circle, *S* = 0.84; grey circle, *S* = 0.92). The results show that both heads tended to initiate flowering earlier when the survival probability was lower (i.e., risk was higher).

Figure 3.5. Comparison of average flowering sizes from the forward simulation when head survival rates were equal (A) versus unequal (B). The x-axis shows the (A-head; B-head) survival probabilities. The black bars indicate the apical (A) head (equal survival, fig. A), or the low survival head (unequal survival, fig. B); the grey bars indicate the non-apical (B) head (equal survival, fig. A), or the high survival head (unequal survival, fig. B).

Figure 3.6. Average plant fitness from the forward simulation represented by total number of seeds per plant (seeds from apical head + seeds from non-apical head). The x-axis shows the (A-head; B-head) survival probabilities.

Figure 3.7. Optimal resource allocation when flower head survival was unequal. The gray line depicts the scenario for the low herbivory risk environment (*S* = 0.924 and 0.880) and the black line depicts the scenario for the high herbivory risk environment (*S* = 0.882 and 0.840). The diamonds indicate flowering times for the relatively low survival head (*S* = 0.880 in the low risk environment, and *S* = 0.840 in the high risk

environment), and the squares indicate flowering times for the relatively high survival head ($S = 0.924$ in the low risk environment, and $S = 0.882$ in the high risk environment).

Figure 3.1.

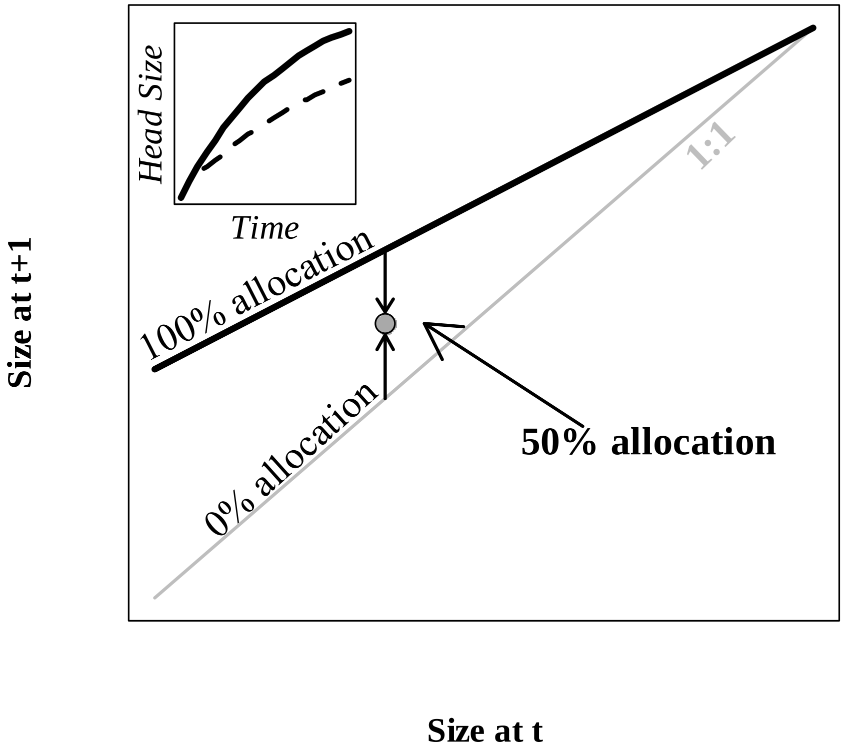

Head Size
Time
1:1
100% allocation
0% allocation
50% allocation
Size at t+1
Size at t

Figure 3.2.

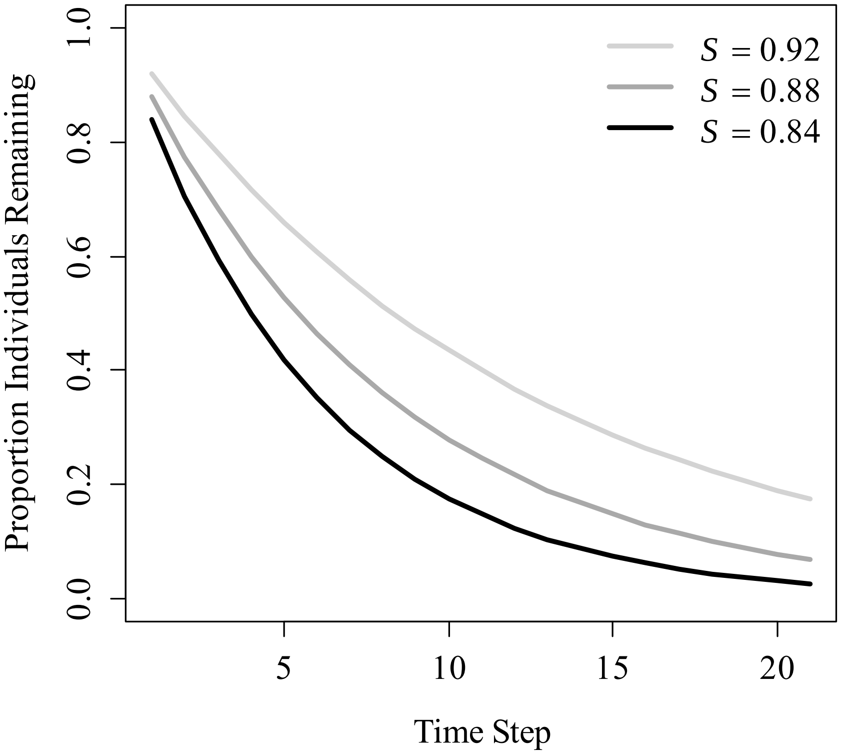

S = 0.92
S = 0.88
S = 0.84
Proportion Individuals Remaining
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
Time Step

Figure 3.3.

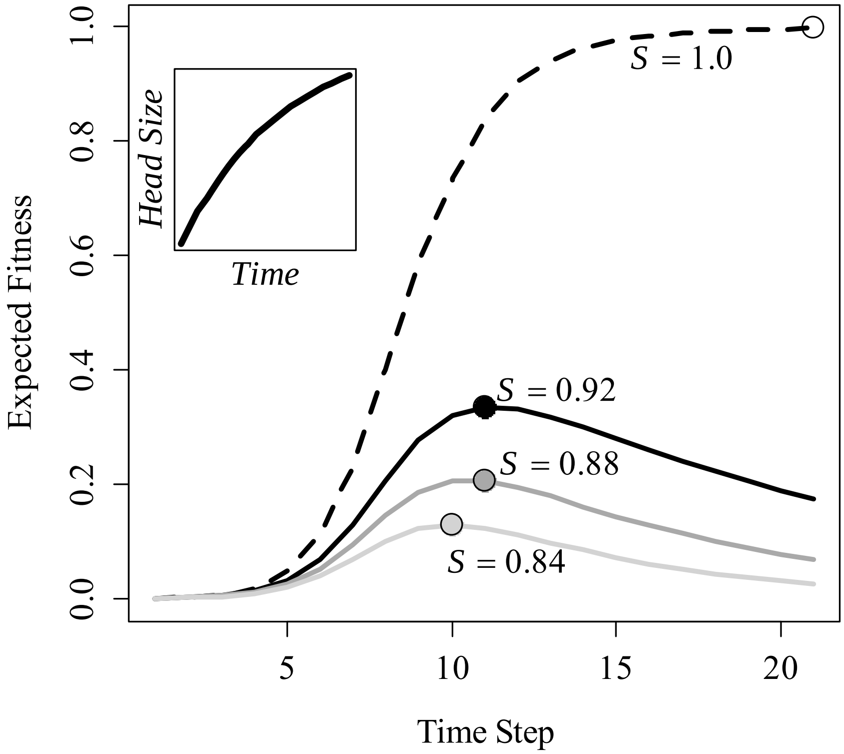

Expected Fitness
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
Time Step
Head Size
Time
S = 1.0
S = 0.92
S = 0.88
S = 0.84

Figure 3.4.

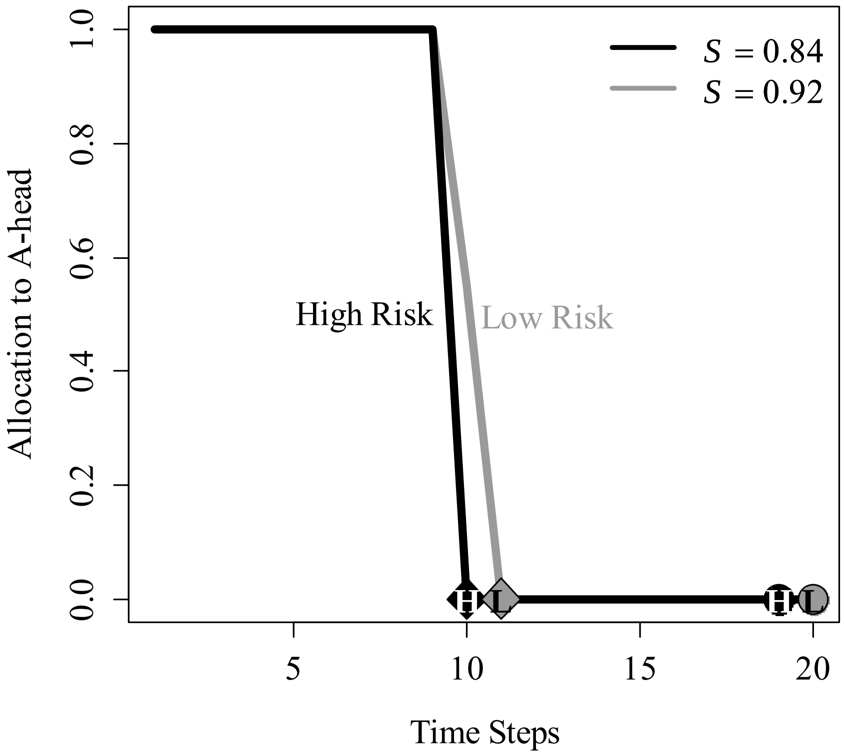

S = 0.84
S = 0.92
High Risk
Low Risk
H
L
H
L
1.0
0.8
0.6
0.4
0.2
0.0
Allocation to A-head
5
10
15
20
Time Steps

Figure 3.5.

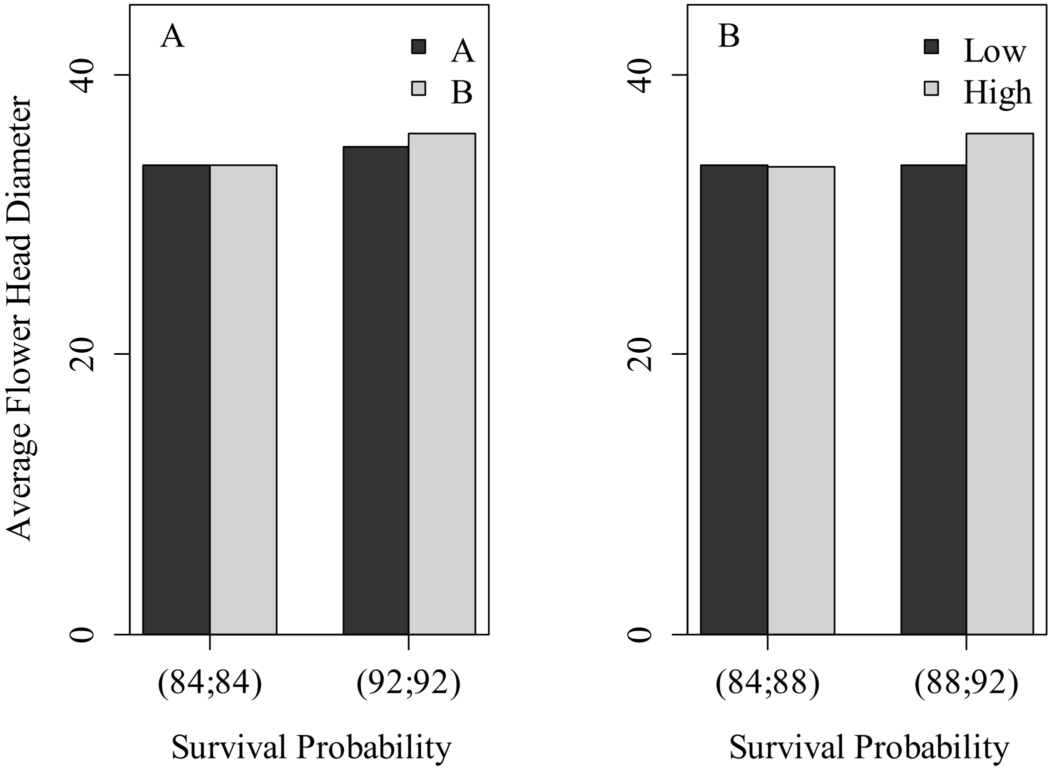
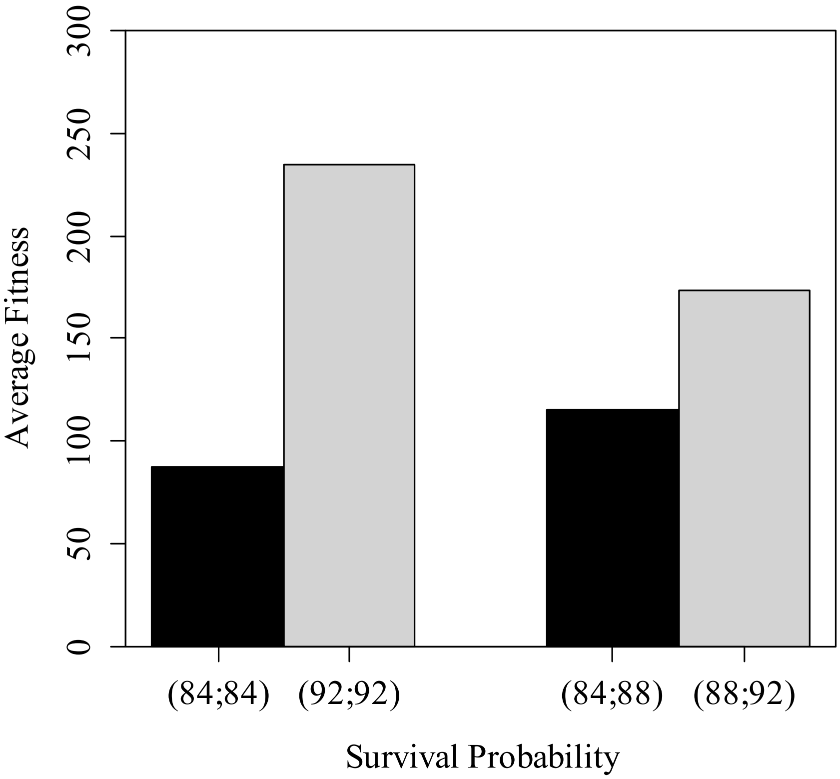
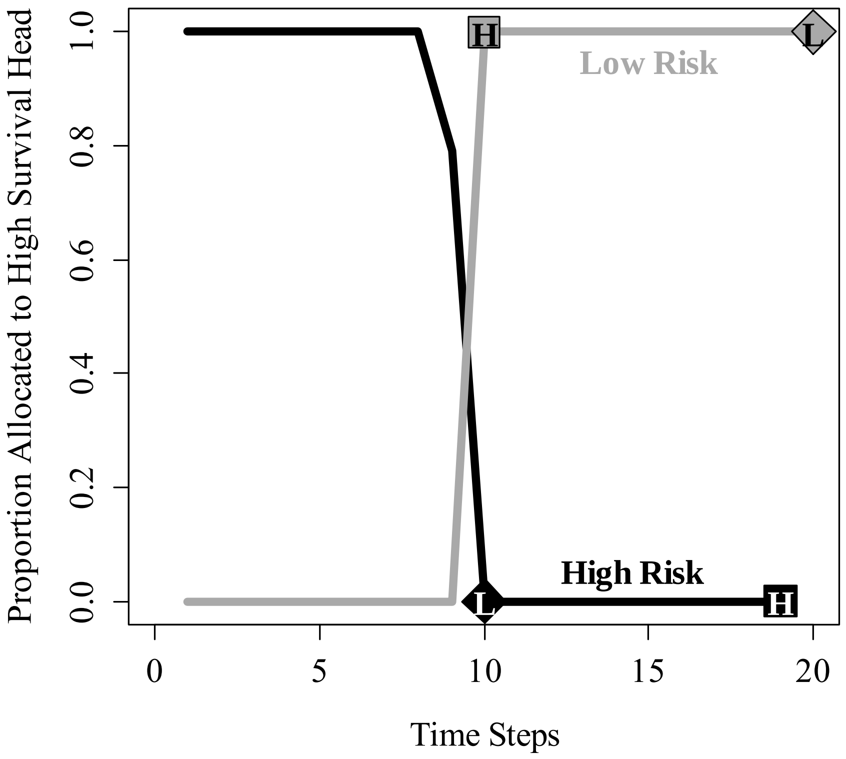

A
■ A
□ B
Average Flower Head Diameter
0
20
40
(84;84)
(92;92)
Survival Probability
B
■ Low
□ High
0
20
40
(84;88)
(88;92)
Survival Probability

Figure 3.6.



Average Fitness
0
50
100
150
200
250
300
(84;84)
(92;92)
(84;88)
(88;92)
Survival Probability

Figure 3.7.


Proportion Allocated to High Survival Head
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Time Steps
Low Risk
High Risk
H
L
L
H

.

Appendix 3.1

Flower head growth

For our motivating example, *Cirsium canescens*, we estimated flower head growth as a function of size using field data (see *Methods*), and modeled the growth relationship as

$$M_{t+1} = 0.922M_t + 4.97 \qquad \textit{Eq. 1}$$

where M is the head diameter in millimeters (fig. A3.1:1A). The resulting growth increment decreased as flower head size increased (fig. A3.1:1B).

Fitness by flower head size

To model fitness, we chose parameter values that qualitatively fit the relationship between flower head diameter and number of seeds produced estimated from lab dissections of field collected flower heads (see *Methods*). We used a fitness equation from Kokko (2007), and modeled the fitness relationship as

$$q(M) = 1 \div (1 + e^{-c*\left(\frac{M}{M_{max}}-v\right)}) \qquad \textit{Eq. 2}$$

where M is head diameter in millimeters, M_{max} is the maximum head size from our field collection, and c and v are constants that affect the shape of the curve (fig. A3.1:2). In the model, $c = 12$ and $v = 0.66$. The maximum number of seeds produced in one flower head in our growth estimate study was 450 (see *Methods*), and was used to predict the seed production that resulted from the optimized reproductive strategies (fig. 3.6). For the fitness estimation, we included data from an additional 488 lab dissected flower heads collected over three years to incorporate a greater range of sizes; the average maximum fitness of field collected heads among years, under ambient herbivory levels, was approximately 350 (fig. A3.1:2). As this field maximum was more similar to what would be expected for plants under ambient herbivory (Chapter 1) and to earlier studies of seed production in this system (Louda and Potvin 1995, see below), we used this maximum to qualify the fitness curve (fig. A3.1:2).

Figure Legends

Figure A3.1:1. Size change per time step by flower head size from field data. A. Size change per time step. The line represents the growth increment used in the model (*Eq. 1*, above) estimated from regression. B. Resulting flower head growth over time. The line represents the resulting growth progression over time.

Figure A3.1:2. Seeds produced by flower head size from field data. The curve represents the fitness relationship used in the model (*Eq. 2*, above).

Figure A3.1:1

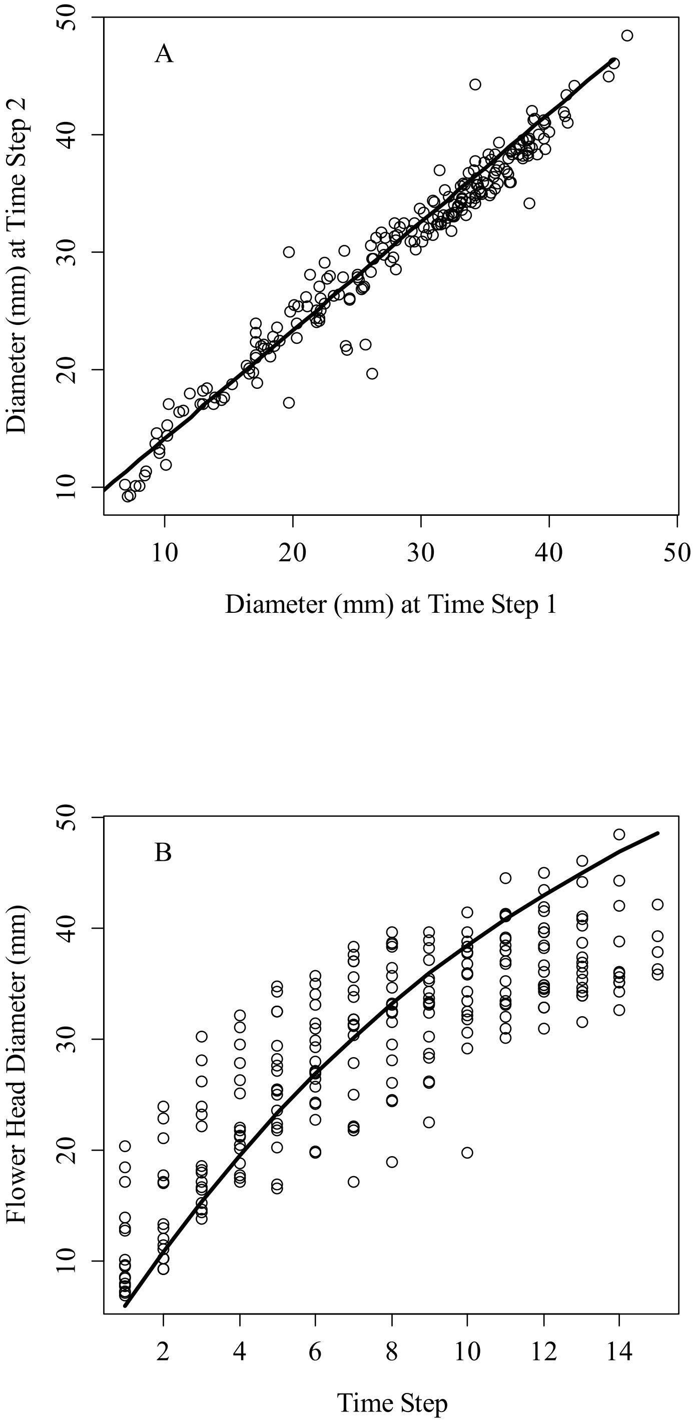
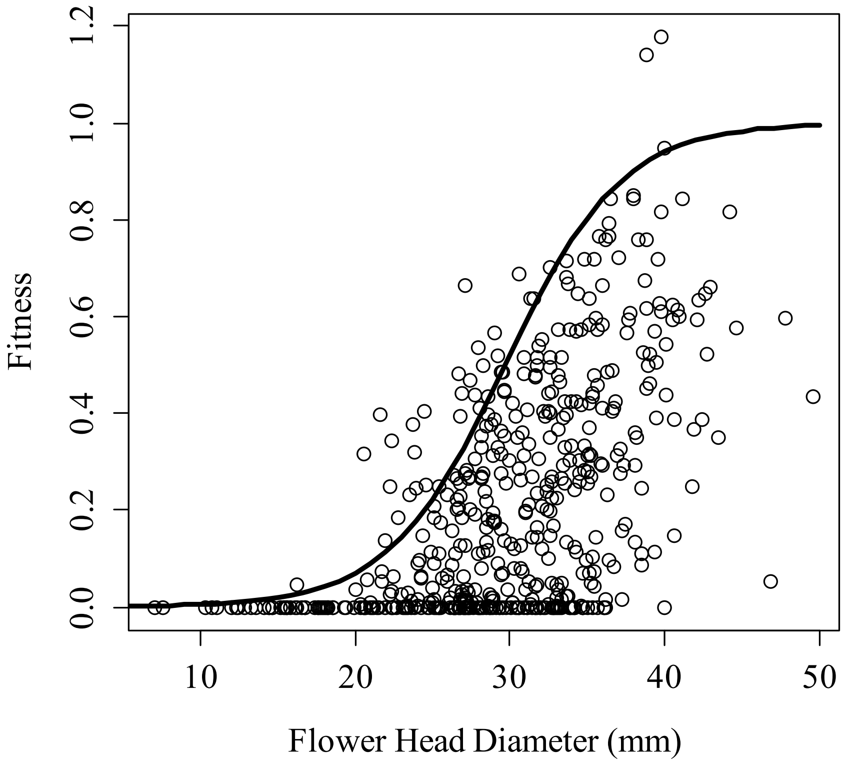

A
Diameter (mm) at Time Step 2
10
20
30
40
50
Diameter (mm) at Time Step 1
10
20
30
40
50
B
Flower Head Diameter (mm)
10
20
30
40
50
Time Step
2
4
6
8
10
12
14

Figure A3.1:2


Fitness
0.0
0.2
0.4
0.6
0.8
1.0
1.2
10
20
30
40
50
Flower Head Diameter (mm)

Appendix 3.2

We examined how the functions we used to model growth and fitness affected the overall model results.

Variation in fitness function parameters

We examined the effect of *c* and *v* on model results by using values 40% higher and lower than each model value in the SDP model and subsequent simulations, with a survival probability of 0.88. Fitness was modeled as

$$q(M) = 1 \div \left(1 + e^{-c*\left(\frac{M}{M_{max}} - v\right)}\right) \qquad \textit{Eq. 1}$$

where *M* was flower head diameter, and *c* and *v* were constants that affected the shape of the curve. In the model, *c* = 12 and *v* = 0.66; 40% lower and higher values for *c* were 7.4 and 16.8, (fig. A3.2:1A), and for *v* were 0.53 and 0.79, respectively (fig. A3.2:1B). Changing *c* had little effect on resulting flowering diameter, but changing *v* resulted in slightly larger (0.79, high *v*) and lower (0.53, low *v*) flowering sizes (fig.A3.2:1C).

Influence of diminishing returns on model results

Both the growth and fitness functions used in the SDP model incorporated diminishing returns. The growth increment decreased with increasing flower head size and the fitness benefit from growing one additional size increment also decreased with increasing flower head size. We evaluate the effect of this diminishing return on the flowering and allocation decisions predicted. We compared our model results (dotted line, G_N:F_N, fig. A3.2:2A and B) to models with a linear growth function (solid line in inset of fig.A3.2:1A, G_L), a linear fitness function (solid line in fig A1:1B, F_L), and a combination of the two.

LINEAR GROWTH FUNCTION. To evaluate the effect of the diminishing return in growth on optimal flowering and allocation decisions, we compared our model results (dotted line, fig. A3.1:2A) to models with linear functions of growth (solid line, fig.A3.2:2A). To eliminate the growth increment decline we used the intercept value from our growth equation (Appendix 3.1, *Eq. 1*: 4.97) as a constant growth increment, such that

$$M_{t+1} = M_t + 4.97 \qquad \textit{Eq. 2}$$

where M is the head diameter in millimeters.

LINEAR FITNESS FUNCTION. To eliminate the diminishing fitness return, we used the linear fitness estimates of seed production calculated from a regression equation in Louda and Potvin (1995) that estimated seed production under ambient herbivory

$$\text{Seeds produced} = 3.52M - 42.7 \qquad \textit{Eq. 3}$$

where M is head diameter in millimeters. At small sizes, using this equation, fitness estimates were negative, which is unrealistic, so in our model we truncated all negative fitness values to zero (fig. A3.2:2B).

Overall, altering the fitness and growth functions, and changing the shape of the fitness function, did not qualitatively change the main results (figs. A3.2:3 and A3.2:4). Heads flowered slightly earlier with a linear growth function (fig. A3.2:3A and C), and predicted flowering sizes were greater when using a linear fitness function (fig. A3.2:4). However, priority investment emerged from all models (fig. A3.2:3).

Figure Legends

Figure A3.2:1. Effect of varying the *c* and *v* in the fitness equation (*Eq. 1*) on optimal resource allocation (A and B), and average flowering size in the forward simulation (C). A. and B.: The dotted lines indicate the optimal resource allocation using the parameters in the main text ($c = 12$; $v = 0.66$), and 40% higher (solid black line, $c = 16.8$; $v = 0.79$) and 40% lower values (solid grey line, $c = 7.4$; $v = 0.53$). Triangles show average flowering time of the A head, and the dots indicate the average flowering time of the B head using the same fill color as the associated line. Average flowering diameter resulting from the optimal resource allocation and flowering decision are presented in fig. C.

Figure A3.2:2. Flower head growth and fitness. A. In our model the size increment from *t* to *t*+1 decreased with flower head size (the dashed line gets closer to the 1:1 lines with increasing flower head size). This results in a concave down flower head growth (dotted line, inset). The solid line depicts the change in size from time *t* to *t*+1 that is parallel to the 1:1 line (grey solid line); this produces a linear change in flower head size over time (solid line, inset). B. The dotted line indicates the sigmoid fitness function used in the main paper, the solid line indicated a linear fitness function (solid line).

Figure A1:3. Effect of linear growth and fitness functions on flower head allocation with $S = 0.88$ per time step. A. Linear growth function. B. Linear fitness function taken from Louda and Potvin (1995). C. Linear fitness and growth function. D. Nonlinear growth and fitness functions used in the main paper.

Figure A1:4. Effect of linear growth and fitness functions on flowering size with a survival probability per time step of 0.88. G_L:FL = both linear growth and fitness, G_N:F_L

= Nonlinear growth and linear fitness, G_L:F_N = linear growth and nonlinear fitness, G_N:F_N = both nonlinear growth and fitness, as presented in the main text. The model that included both linear growth and fitness predicted larger flowering sizes than the other intermediate models or the original model.

Figure A3.2:1.

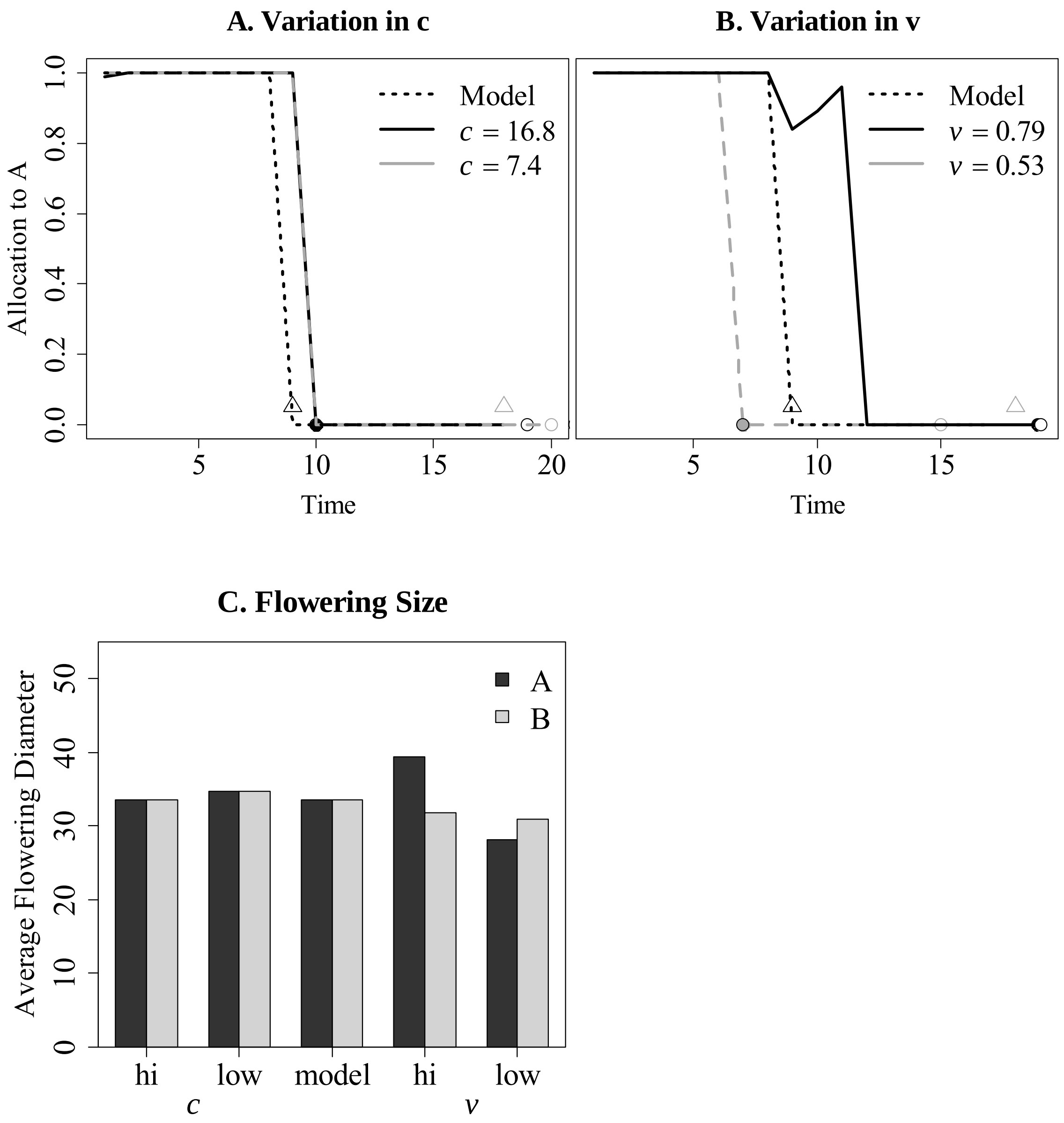

A. Variation in c
B. Variation in v
Allocation to A
0.0
0.2
0.4
0.6
0.8
1.0
Time
5
10
15
20
Model
c = 16.8
c = 7.4
v = 0.79
v = 0.53
C. Flowering Size
Average Flowering Diameter
0
10
20
30
40
50
A
B
hi
low
model
c
v

Figure A3.2:2.

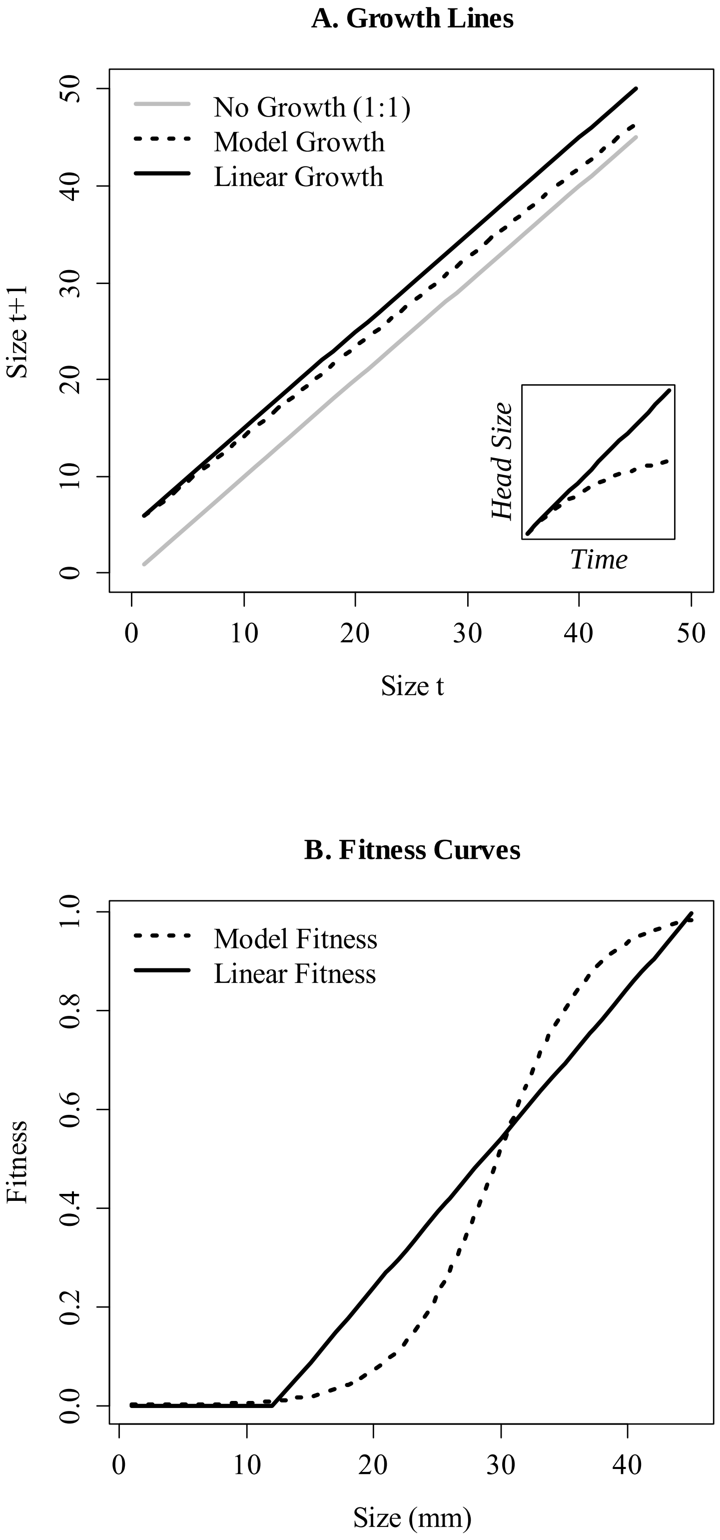

A. Growth Lines
No Growth (1:1)
Model Growth
Linear Growth
Size t+1
Size t
0
10
20
30
40
50
Head Size
Time
B. Fitness Curves
Model Fitness
Linear Fitness
Fitness
Size (mm)
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40

Figure A3.2:3.

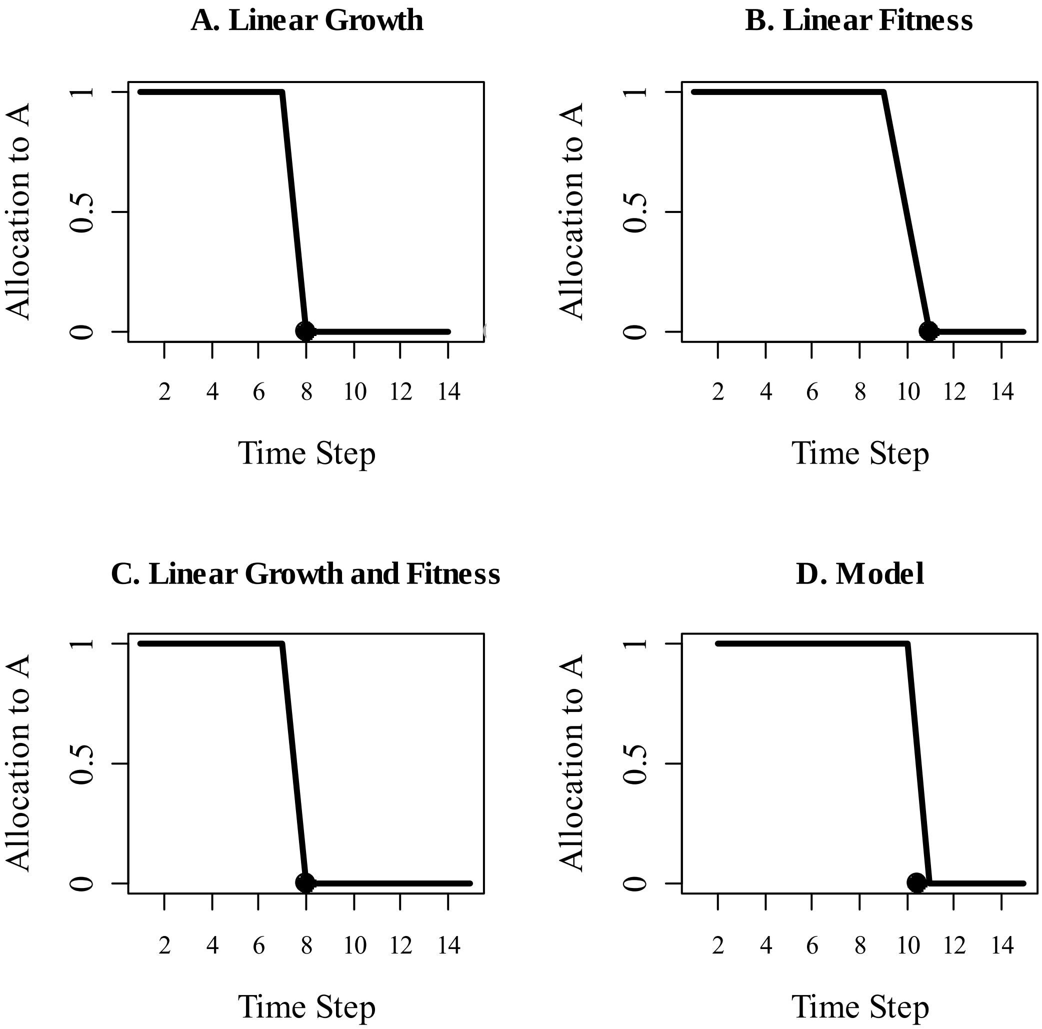
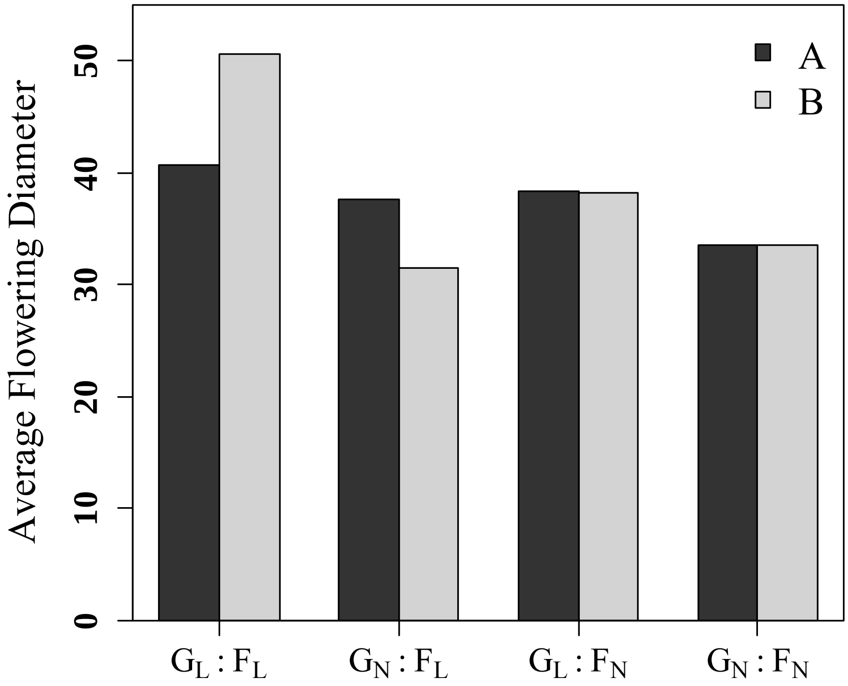

A. Linear Growth
B. Linear Fitness
C. Linear Growth and Fitness
D. Model
Allocation to A
0
0.5
1
2
4
6
8
10
12
14
Time Step

Figure A3.2:4.


Average Flowering Diameter
0
10
20
30
40
50
A
B
$G_L : F_L$
$G_N : F_L$
$G_L : F_N$
$G_N : F_N$

Appendix 3

Population level allocation decisions

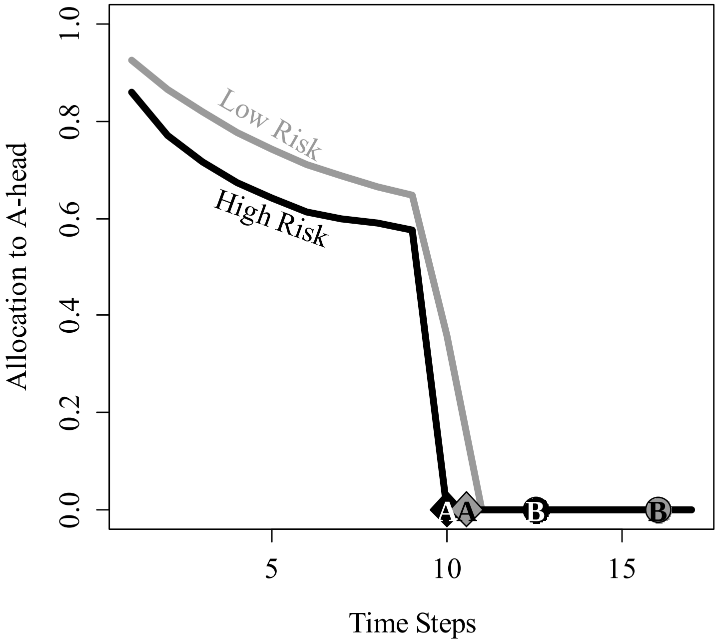
Regardless of survival scenario, in the forward simulation, fewer than half of the plants had at least one flower head survive to flowering, and in less than 10% of individuals both heads survived. If one flower head was destroyed by herbivores, then all resources were allocated to the surviving flower head. As a consequence, in the forward simulation, the resource allocation to the A head averaged over the entire surviving population differs from the optimal strategy assuming both flower heads are alive.

Figure Legend

Figure A3.3:1. Average resource allocation over time to the apical head by surviving individuals. A. Equal flower head survival: Diamonds and squares indicate the average flowering time of the apical and non-apical head, respectively. The black line depicts a low survival environment (S = 0.84), and the grey line a high survival environment (S = 0.92). B. Unequal survival: The black line depicts a low survival environment (S = 0.84 and 0.88), and the grey line a high survival environment (S = 0.88 and 0.92). The diamonds indicate the flowering time of the flower head with the relatively lower risk (S = 0.84 and 0.88), and the square is the flower head with the relatively higher risk (S = 0.88 and 0.92).

Figure 3.3:1.

A. Population: Equal Survival



B. Population: Unequal Survival