

# PLANT RESOURCE ALLOCATION AND HERBIVORY FOR *HELIANTHELLA QUINQUENERVIS* (ASTERACEAE) OVER AN ELEVATIONAL GRADIENT

Davis, Stacey R., Biology Departmental Honors Senior Thesis

---

## ABSTRACT

Resources obtained from the environment are allocated to many plant parts and functions. Resource allocation into defense, growth, and reproduction was examined for *Helianthella quinquenervis*, the Aspen sunflower, for three field sites over an elevational gradient. *H. quinquenervis* has evolved a mutualism with ants for defense against seed predators. Timing of flower opening and pollination success for plants were also studied. The results indicated that ratios of defense to reproduction and reproduction to growth are statistically equivalent for *Helianthella* at all the field sites. Defense to growth ratios were different for the high and middle, and the high and low elevations. Timing of flower opening was statistically different for the middle elevation site, however pollination success was similar over sites.

## KEY WORDS

|                                   |                     |
|-----------------------------------|---------------------|
| ant-plant mutualism               | insect herbivory    |
| biotic defense                    | pollination success |
| extrafloral nectar                | resource allocation |
| <i>Helianthella quinquenervis</i> | seed predation      |

---

## INTRODUCTION

Plants acquire resources from the environment and allocate them to a variety of plant parts and functions (Bazzaz 1997). The proportions of investment into growth, defense, chemical manufacturing, reproduction, storage, etc., differ among species and populations. Limiting resources, environmental conditions (Bazzaz 1990; Roger et al. 1994), and community-level interactions (Tremmel and Bazzaz 1995) influence plant resource allocation.

Plant resource allocation is a fairly recent field of investigation. Most allocation experiments have been conducted within the past three decades. Numerous computer and mathematical models have been developed to predict and explain shifts in resource allocation in response to changing environmental conditions (Coley et al. 1985; Zangerl and Bazzaz 1992; and Basey and Jenkins 1993). Many experiments have also examined the role of important elements such as nitrogen, carbon, oxygen, potassium, phosphorous, and magnesium on resource allocation (Field and Mooney 1986; Agren and Ingestad 1987; Benner and Bazzaz 1987; Hilbert 1990). Plant allocation responses to added soil

nutrients have also been examined (Gleeson and Tilman 1992). Heavy metals in the soil have been noted to alter plant resource allocation (Saikkonen 1998).

Allocation to biomass has been studied for many plant populations under varying environments, including both field and greenhouse research. Biomass allocation over altitude and season was contrasted in two tropical, montane plants (Calero and Baruch 1986). Biomass allocation patterns under varying resource gradients (light, nutrients, and water) have been monitored for three annual plant species in controlled greenhouse conditions (McConnaughay and Coleman 1999).

The issue of plant defense allocation has been closely examined and remains controversial. The Optimal-Defense Hypothesis suggests that plant defense has an associated cost for the plant, and that resources invested into defense cannot be simultaneously invested into other plant parts and functions (McKey 1974; Rhoades 1979). Other researchers have challenged this theory by stating that an associated cost does not exist for the plant (Wink and Witte 1985; Harborne 1990). The Optimal-Defense Hypothesis also assumes that herbivory is the primary selective force shaping plant defense (Feeny 1976; Rhoades and Cates 1976; Fagerstrom et al. 1987).

Two contradictory hypotheses exist: the Growth Rate Hypothesis and the Environmental Constraint Hypothesis (Herms and Mattson 1992). The Growth Rate Hypothesis states that investment into defense varies with the growth of the plant and the rate of herbivory (Janzen 1974; Bryant et al. 1983; Coley 1987). High resource environments yield faster growing plants and lower allocations into defense (Coley et al. 1985). Conversely, poor resource environments contribute to slower plant growth and larger defense investment (Coley et al. 1985). The Environmental Constraint Hypothesis speculates that investment into defense is strictly governed by resource availability and not herbivory (Bryant 1988; Tuomi 1988; Chapin 1988).

Plants subject to herbivory can employ physical, chemical, and biotic defense systems to counteract predation. Toughened leaves, trichomes, and thorns are physical defenses that limit herbivory (Herms and Mattson 1992). Plants may also produce secondary metabolites (i.e. alkaloids, tannins, terpenes) for chemical defense. Obligate ant-plants (myrmecophytes), such as the desert shrub, *Acacia constricta*, have evolved a biotic defense system (Wagner 2000).

*Helianthella quinquenervis*, the Aspen sunflower, has evolved an ant-plant mutualism for defense against seed predators/herbivores (Inouye and Taylor 1979). *H. quinquenervis* is a temperate, montane species found at elevations from 2741 to 3257 meters. *H. quinquenervis* has a wide geographic distribution, ranging as far south as Nuevo Leon, Mexico, and as far north as southern Canada (Inouye and Taylor 1979). Modified leaves, called bracts, are found on the back of the sunflower head. Extrafloral nectar (EFN) is secreted at the margins of the bracts and attracts at least six species of ant, primarily of the genus *Formica* (Inouye and Taylor 1979). EFN is rich in sucrose and amino acids (Inouye and Inouye 1980). The ants collect EFN for food, and they provide protection from insect herbivores, including three species of tephritid flies, an

agromyzid fly, and three species of Lepidoptera (Inouye and Taylor 1979). Adult dipteran seed predators often mate on the plant and females then oviposit on the sunflower head. The fly larvae hatch from the eggs and eat ovules and developing seeds, thereby causing reproductive damage to the plant. While ants wait for nectar to be produced, they patrol the flower head and chase off potential herbivores (Inouye and Taylor 1979). Therefore, the Aspen sunflowers have developed a biotic defense system, or ant guard.

The following study examines herbivory rates and plant resource allocation for the Aspen sunflower at three field sites over an altitudinal gradient. The objectives of the study were 1) to measure levels of insect herbivory; 2) to compare allocation to reproduction, defense, and growth for the three field site populations; 3) to observe interactions between ants and seed predators, and characterize insect densities; and 4) to investigate timing of flowering and pollination for plant populations.

Several hypotheses were generated prior to conducting the study. First, a gradient of herbivore abundance was hypothesized to exist over elevation, with the lowest site having a greater herbivore abundance. A difference in plant resource allocation with regards to defense was expected. Maxfield Meadow was hypothesized to have a greater ratio of defense to growth than the other sites due to the proposed higher rates of herbivory. Pollination success was hypothesized to be different for the three field sites if the timing of flower opening varied.

## MATERIALS AND METHODS

Field research was conducted over a course of nine weeks, starting mid-June, in the vicinity of the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado. RMBL is situated in the West Elk Range of the Rocky Mountains (38°57'30"N, 106°59'15"W) at an elevation of 2871 m (Inouye and Taylor 1979). Three sites of increasing elevation were used: Maxfield Meadow (2871 m), Bellview (3091 m), and Virginia Basin (3505 m). These field sites represent the upper 75 percent of the total range for *Helianthella* plants. Sites along an elevational gradient were used because it was previously noted that insect herbivore abundance decreased with elevation. The research was performed in two parts.

For the first part, 50 *Helianthella* plants were tagged with field flags over a section of each site and the plants were visited frequently throughout the summer. At the end of the growing season, *H. quinquenervis* disperses its seeds. Prior to seed dispersal, the capitulae were collected in plastic vials and shipped back to the Maryland lab. Flower heads were dissected and seed herbivore damage was assessed over winter break and the spring semester. The number of fertilized and unfertilized seeds, the number of damaged fertilized and unfertilized seeds, the number of caterpillar larvae present, the number of puparia, and the number of emerged flies were counted for each flower head. A measure of herbivory rates was obtained by finding the percentage of damaged seeds to total seeds. The groups of percentages for each field site were compared between sites

using an ANOVA single factor test. A Tukey-Kramer Means Comparison Test was used to determine statistical significance within pairs of groups.

For the second part, 30 *Helianthella* plants were tagged at each site with field flags. Physical attributes were measured and characterized as defensive, reproductive, or growth structures. Growth attributes included stalk height, stalk thickness, leaf area, leaf weight, basal leaf area, basal leaf weight, and basal plant diameter. The number of stalks per plant and the number of axillary flower heads were also noted. *H. quinquenervis* plants had an average of 2-4 stalks, however, a maximum of 21 stalks was observed. Stalk height was roughly between .28-.84 meters (1-3 feet). Axillary flower heads were absent or present in 1-2 pairs. Growth characteristics were measured with calipers, a tape measure, a balance, or leaf area meter. Leaves were left to dry 2-3 days prior to weighing.

Reproductive attributes included size of flower head, the number of fertilized seeds, the number of unfertilized seeds, the total number of seeds, and the weight of fertilized seeds. The diameter of the flower heads was measured in the field using calipers, and the area was calculated to determine flower head size. The latter four reproductive attributes were determined upon dissection of the flower heads. The capitulae were collected in plastic vials and shipped to the Maryland lab.

The number of bracts was counted as a measure of defense. The volume and concentration of EFN secreted from the bracts would be the ideal attribute to measure for defense investment, but the EFN is difficult to collect because of the small quantities and high viscosity. The ratio of bract numbers to flower head size was determined for each flower head. The group of ratios from the lowest field site was compared to the group of ratios from the upper site using an ANOVA single factor test.

A Principal Components Analysis test was used to reassign values for growth, reproduction, and defense for each flower. Ratios for reproduction to growth, defense to growth, and defense to reproduction were calculated for each field site plant population. The ratios between pairs of sites were compared using ANOVA single factor tests. In addition to plant resource allocation, timing of flower opening and pollination success were examined across sites. Flower opening was defined as the moment the central disc of the terminal flower head became visibly yellow, to the moment the petals were fully opened. Timing was measured in number of days. An ANOVA single factor test was used to compare between sites. A Tukey-Kramer Means Comparison Test determined the statistical significance within pairs of sites. Pollination success was examined by calculating the percentage of fertilized seeds to total ovules for each flower head. An ANOVA single factor test was used for comparison between sites. Total ovules per plant were calculated and compared between sites using an ANOVA single factor test. Statistical analyses were conducted using Microsoft Excel and Statistica.

## RESULTS

A histogram presents the mean percent seed damage for each field site: Maxfield Meadow (56%), Bellview (15.8%), and Virginia Basin (8.8%) (Figure 1). Mean percent data were compared with an ANOVA single factor test ( $p < .01$ ;  $SE \pm 5\%$ ). A Tukey-Kramer Test revealed that Maxfield Meadow and Virginia Basin, and Maxfield Meadow and Bellview were statistically different.

An additional histogram shows the mean percents of numbers of bracts to flower head size for the field sites Virginia Basin and Maxfield Meadow (ANOVA:  $p$ -value between sites  $< .05$ ;  $SE = \pm .23$ ) (Figure 2). Results indicate a statistical difference between sites.

Three bar graphs compare reproduction to growth ratios for pairs of field sites (Figure 3). Mean ratios were found through Principal Component Analysis. The Bellview-Maxfield Meadow comparison was not statistically significant (ANOVA:  $p > .05$ ;  $SE \pm .29$ ), the Virginia Basin-Maxfield Meadow pair was not statistically significant (ANOVA:  $p > .05$ ;  $SE \pm 1$ ), and Bellview-Virginia Basin pair was not statistically significant (ANOVA:  $p > .05$ ;  $SE \pm .9$ ).

Three bar graphs contrast defense to growth ratios for pairs of field sites (Figure 4). Mean ratios were found through Principal Component Analysis. The Bellview-Maxfield comparison was not statistically significant (ANOVA:  $p$ -value  $> .05$ ;  $SE \pm 68.1$ ). However, both additional pairs, Maxfield Meadow-Virginia Basin (ANOVA:  $p$ -value  $< .05$ ;  $SE \pm 80.1$ ) and Bellview-Virginia Basin (ANOVA:  $p$ -value  $< .01$ ;  $SE \pm 86.7$ ), were different.

Three bar graphs compare defense to reproduction ratios for pairs of field sites (Figure 5). Mean ratios were again determined through Principal Component Analysis. The pairs Bellview-Maxfield Meadow (ANOVA:  $p$ -value  $> .05$ ; and  $SE \pm 136.6$ ), Bellview-Virginia Basin (ANOVA:  $p$ -value  $> .05$ ; and  $SE \pm 188.2$ ), and Virginia Basin-Maxfield Meadow (ANOVA:  $p$ -value  $> .05$ ; and  $SE \pm 171.3$ ), were all found to have no significant difference.

Total ovules per plant were compared for Bellview, Maxfield Meadow, and Virginia Basin (ANOVA:  $p$ -value between sites  $> .05$ ;  $SE \pm 95.8$ ) (Figure 6). Maxfield Meadow had an average of 376 seeds, Bellview had an average of 427 seeds, and Virginia Basin had an average of 491 seeds.

Mean flower opening time (days) over field sites was compared (ANOVA:  $p$ -value between sites  $< .01$ ;  $SE \pm .587$ ) (Figure 7). Bellview flowers took an average of 6.5 days to open, Virginia Basin flowers 8.8 days, and Maxfield Meadow 8.5 days. A Tukey-Kramer procedure found a significant difference between Virginia Basin and Bellview, and Maxfield Meadow and Bellview.

Pollination success was examined by calculating the mean percentage of fertilized seeds to total ovules as seen for each field site (Figure 8). All three sites had a mean percent between .44-.48 (ANOVA: p-value between sites > .05; SE  $\pm$  .037).

## DISCUSSION

The goal of part one was to determine if the field sites were associated with high or low herbivory rates. Figure 1 depicts a trend in decreasing insect herbivory with higher elevations. Since an herbivore gradient was established, resource allocation was compared between sites with statistically different rates of herbivory (Virginia Basin and Maxfield Meadow, and Virginia Basin and Maxfield Meadow). Resource allocation was also examined between sites of similar herbivory rates (Bellview and Virginia Basin).

Comparisons between growth to reproduction ratios were similar over all three field sites. The ratio of growth to reproductive investment appears to be stable for *H. quinquenervis* plant populations in a variety of environmental conditions. The same appears true for ratios of defense to reproductive investment. Defense to growth ratios, however, differed in two pairs of field sites: Maxfield Meadow and Virginia Basin, and Bellview and Virginia Basin. Because defense to growth ratios were different between sites of different insect herbivory rates (Virginia Basin-Maxfield Meadow) and similar herbivory rates (Bellview-Virginia Basin), herbivory may not be the primary selective agent for defense investment. This contradicts the Optimal-Defense Hypothesis. To support one of the three hypotheses more conclusively, this study must be replicated and environmental resources (water, nutrients, and light) must be measured.

The three hypotheses have only been suggested by researchers examining plants with chemical defenses. A biotic defense, such as that evolved by the Aspen sunflower, may not be compared to these hypotheses. Defense allocation by the Aspen sunflower appears to be influenced by both herbivory and environmental conditions. Therefore, this contradicts the Environmental Constraint Hypothesis. The Growth Rate Hypothesis was originally proposed through research on tropical trees. The Growth Rate Hypothesis cannot be directly applied to the Aspen sunflower system. This experiment is the only one of its nature. More research on biotic and physical defenses must be conducted.

A comparison of the Maxfield Meadow and Virginia Basin pair indicates that Maxfield Meadow is investing more into defense than growth. This suggests that sites with high herbivory rates, invest more into defense to reduce seed damage. Plants found at higher elevations have been previously noted to have a reduced number of ovules per flower head. Plants with fewer ovules were proposed by other researchers to invest more into defense to protect their smaller numbers of ovules from herbivores. The results from this study contradict these previous thoughts. The results from Figure 6 indicate that total ovules per plant do not change over elevation for *Helianthella*. Fertilized seeds from Bellview and Maxfield Meadow weighed more than seeds from Virginia Basin. Therefore, the seed dimensions were greater for the lower two sites, or the seeds had a thicker, protective casing. Increases in seed thickness may inhibit some herbivores from penetrating the seeds, thereby reducing damage.

It is unclear why Bellview and Maxfield Meadow are not statistically different with regards to defense and growth ratios, despite being statistically different in herbivory rates. Bellview was more diverse in its plant community than either Virginia Basin or Maxfield Meadow. The Bellview sunflowers were more densely arranged with other wildflowers and plants. Community level effects may have changed resource allocation patterns at Bellview. Communities of plants actively compete for resources (Tremmel and Bazzaz 1995). Comparisons between Maxfield Meadow and Virginia Basin are probably more accurate.

An additional importance of the ratio findings is that while defense to growth ratios varied, defense to reproduction ratios did not change statistically over the field sites. This suggests that to accommodate defense investment, plants pull resources from growth instead of reproduction. Reproduction is possibly too important to the plant.

Figure 6 shows that flowers open up faster on average at Bellview. Many researchers have previously proposed that the timing of flower opening represents a trade-off between herbivory and pollination. The longer the flower takes to open up, the more pollinators the plant attracts. However, if flowers open up slowly, they are perhaps subject to increased herbivory. An examination of pollination success, however, indicates that plants at each field site have very similar ratios of fertilized seeds to total ovules. The flowers at Bellview did not have a decreased success of pollination despite opening earlier.

There were some associated problems with the study. Many flowers in the field were damaged by heavy frost that persisted through the middle of July. Large mammal herbivores (deer, elk, sheep, chipmunks, ground squirrels, etc.) also ate some flower heads. Sample sizes were still adequate to conduct the experiment for statistical significance.

Another significant problem is that bract number has never been previously reported to be a substantial measure for defense investment. Therefore, this assumption may be incorrect. The results of figure 2 indicate that bract numbers to flower head size did vary over the sites. Therefore, bract number may not simply be constrained by flower head size. Assuming bract number is an inadequate measure of defense, differences in allocation strategies over the sites are still evident. While reproduction and growth remained similar over sites, bract numbers did change. Chemical analyses of primary metabolites in the bracts are suggested for future projects. The nectar is a byproduct of primary metabolite production.

Plant resource allocation experiments are important for understanding how plants strategize for survival. Predictions of plant resource allocation in future environmental conditions may be assessed. Global warming is a large concern because of its unknown impacts for plants. Global warming will be associated with higher nitrogen deposition, greater atmospheric carbon dioxide, and higher temperatures. A future experiment examining *Helianthella* resource allocation under global warming conditions may illustrate changes in current patterns.

## ACKNOWLEDGEMENTS

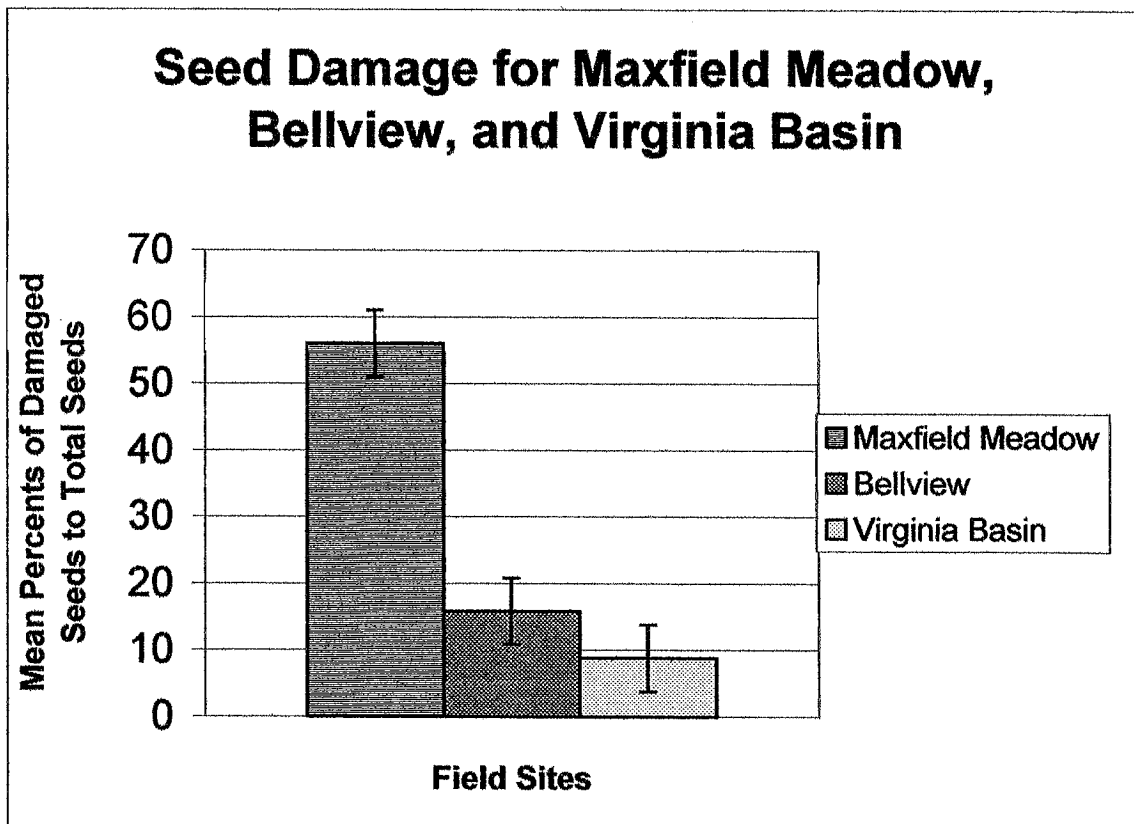
Financial support for this research was provided by the Howard Hughes Undergraduate Fellowship and Senior Summer Scholars Programs. Many sincere thanks to Dr. David Inouye for his mentorship, assistance, and support. Additional thanks to Dr. Manuel Morales, Gary Dodge, Mike Leigh, and Dr. Marjorie Reaka-Kudla. The Rocky Mountain Biological Laboratory and Gunnison National Forest provided access to study sites.

## REFERENCES

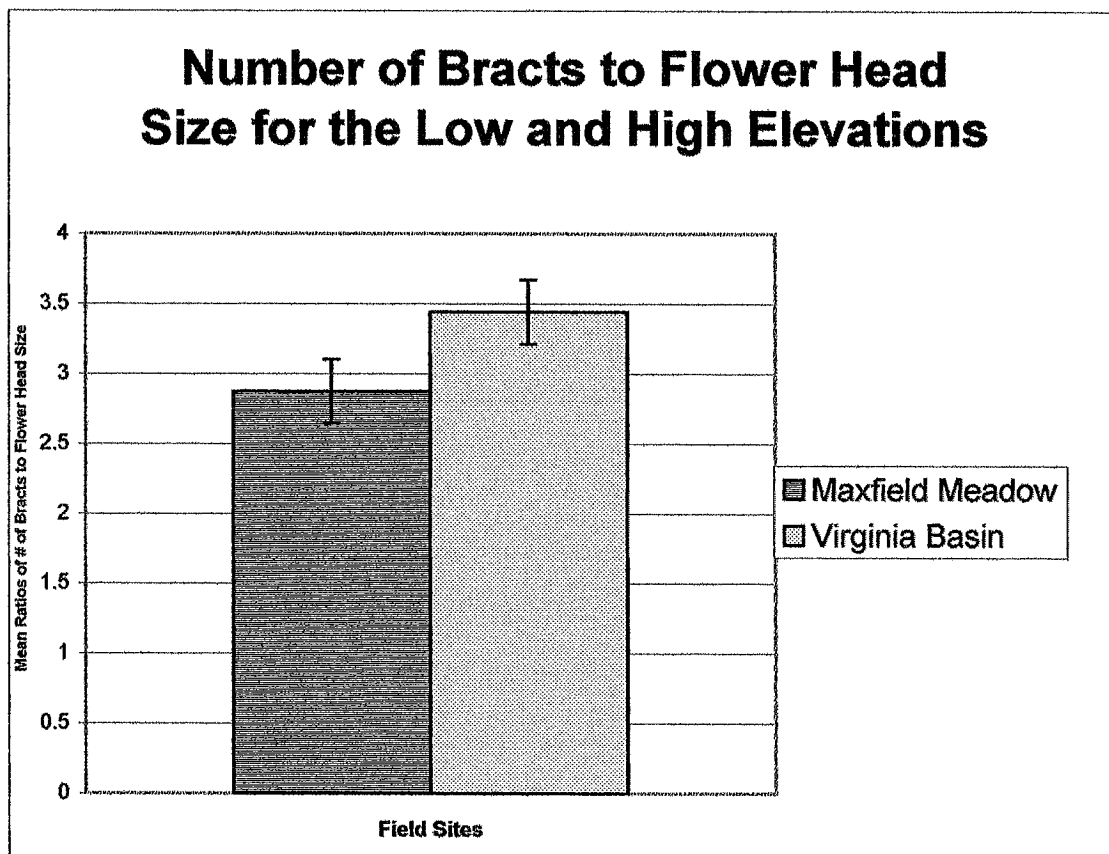
- Agren, G.I. and T. Ingestad (1987). Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant Cell Environment* 10, pp 579-586.
- Basey, J.M. and S.H. Jenkins (1993). Production of chemical defenses in relation to plant growth rate. *Oikos* 68, pp 323-328.
- Bazzaz, F.A. (1990). The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Annual Review of Ecological Systems* 21, pp 167-196.
- Bazzaz, F. (1997). "Allocation of resources in plants: state of the science and critical questions" in *Plant Resource Allocation* (Bazzaz, F. and J. Grace, eds.). Academic Press: San Diego; pp 1-37.
- Benner, B.L. and F.A. Bazzaz (1987). Effects of timing of nutrient addition on competition within and between two colonizing annual plants. *Journal of Ecology* 75, pp 229-245
- Bryant, J.P., Chapin III, F.S., and D.R. Klein (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40, pp 357-368.
- Calero, A.G. and B. Zdravko (1986) Patterns in altitudinal and seasonal biomass allocation in two contrasting plant life forms from a tropical mountain biome. *Biotropica* 18 (3), pp189-194.
- Coley, P.D. (1987). Intraspecific variation in plant antiherbivore properties: the role of habitat quality and rate of disturbance. *New Phytology* 106 (suppl.): 251-263.
- Coley, P.D., Bryant, J.P., and F.S. Chapin III (1985). Resource availability and plant antiherbivore defense. *Science* 230, pp 895-899.
- Fagerstrom, T. (1989). Anti-herbivory chemical defense in plants: a note on the concept of cost. *American Naturalist* 133, pp 229-257.
- Feeny, P. (1976). Plant apparency and chemical defense. *Recent Advances in Phytochemistry* 10, pp 1-40.

- Field, C.B. and H.A. Mooney (1986). "The photosynthesis-nitrogen relationship in wild plants" in *On the Economy of Plant Form and Function* (Givnish, T.J., ed.) Cambridge University Press: Cambridge; pp 25-55.
- Gleeson, S.K. and D. Tilman (1992). Plant resource allocation and the multiple limitation hypothesis. *The American Naturalist* 139 (6) pp 1322-1343.
- Harborne, J.B. (1990). Constraints on the evolution of biochemical pathways. *Biological Journal of Linnean Society* 39, pp 135-151.
- Harms, D.A. and W.J. Mattson (1992). The dilemma of plants: To grow or defend. *The Quarterly Review of Biology* 67 (3), pp 283-335.
- Hilbert, D.W. (1990) Optimization of plant root:shoot ratios and internal nitrogen concentrations. *Annals of Botany* 66, pp 91-99.
- Inouye, D.W. (1984). The ant and the sunflower. *Natural History* 93 (60), pp 48-53.
- Inouye, D.W. and R.S. Inouye (1980). The amino acids of extrafloral nectar from *Helianthella quinquenervis* (Asteraceae). *American Journal of Botany* 67, pp 1394-1396.
- Inouye, D.W. and O.R. Taylor, Jr. (1979). A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. *Ecology* 60 (1), pp 1-7.
- Janzen, D.H. (1974). Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* 6, pp 69-103.
- McConaughay, K.D.M. and J.S. Coleman (1999). Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80 (8), pp 2581-2593.
- McKey, D. (1974). Adaptive patterns in alkaloid physiology. *American Naturalist* 108, pp 305-320.
- Rhoades, D. F. (1979). "Evolution of plant chemical defense against herbivores" in *Herbivores: Their interaction with secondary plant metabolites*. (G.A. Rosenthal and D. H. Janzen, eds.) Academic Press: New York; pp 3-94.
- Rhoades, D.F., and R.G. Cates (1976). Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry* 10, pp 168-213.
- Rogers, H.H., Runion, G.B., and Krupa, S.V. (1994). Plant responses in atmospheric CO<sub>2</sub> enrichment with emphasis on roots and rhizosphere. *Environmental Pollution* 83, pp 155-189.

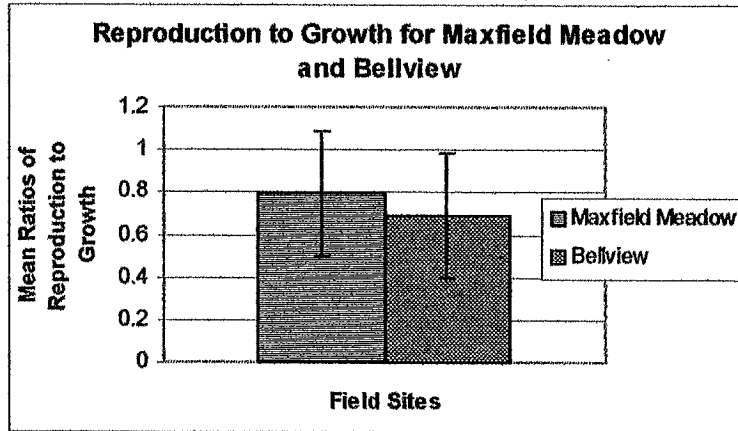
- Saikkonen, K., Koivunen, S., Vuorisalo, T., and P. Mutikainen (1998) Interactive effects of pollination and heavy metals on resource allocation in *Potentilla anserina* L. *Ecology* 79 (5), pp1620-1629.
- Tremmel, D.C. and F.A. Bazzaz (1995). Plant architecture and allocation in different neighborhoods: implications for competitive success. *Ecology* 76 (1), pp 262-271.
- Tuomi, J., Niemela, P., Chapin III, F.S., Bryant, J.P., and S. Siren (1988). "Defensive responses of trees in relation to their carbon/nutrient balance" in Mechanisms of Woody Plant Defenses Against Insects: Search for Pattern (Mattson, W.J., Levieux, J., and C. Bernard-Dagan eds.). Springer-Verlag: New York; pp57-72.
- Wagner, D. (2000). Pollen viability reduction as a potential cost of ant association for *Acacia constricta* (Fabaceae). *American Journal of Botany* 87(5), pp 711-715.
- Wink, M., and L. Witte (1985). Quinolizidine alkaloids as nitrogen source for lupin seedlings and cell cultures. *Zeitschrift für Naturforschung* 40c, pp 767-775.
- Zangerl, A.R., and F.A. Bazzaz (1992). "Theory and pattern in plant defense allocation" in Plant Resistance to Herbivores and Pathogens (Fritz, R.S. and E.L. Simms, eds.) University of Chicago Press: Chicago; pp 363-391.



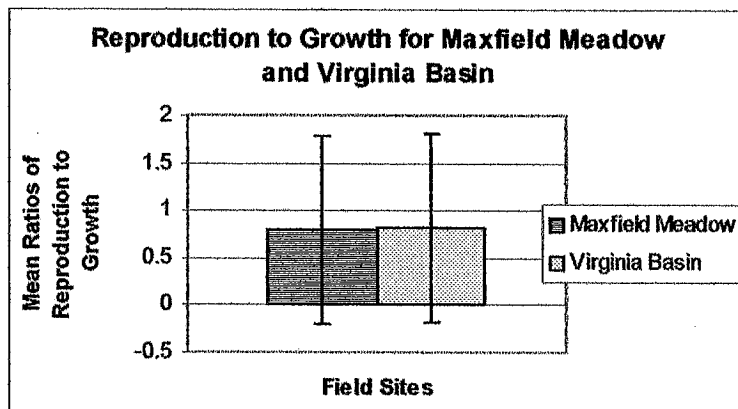
**FIGURE 1:** Percent of damaged seeds to total seeds as measures of herbivory for the field sites Maxfield Meadow, Bellview, and Virginia Basin. P-value between sites < .01; SE=  $\pm$  5.



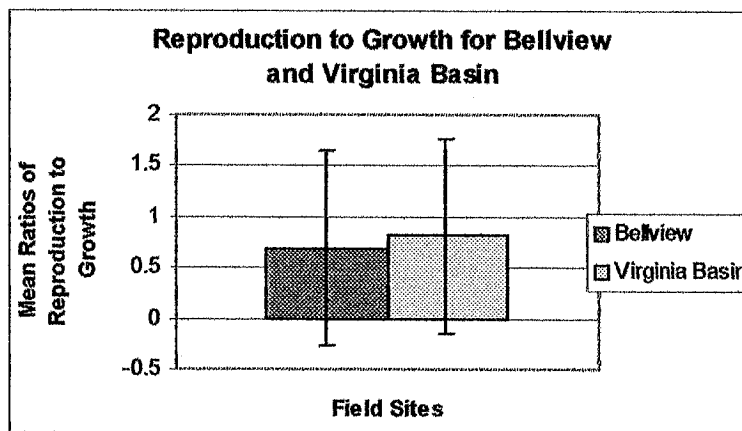
**FIGURE 2:** Mean ratios of numbers of bracts to flower head size for the field sites Virginia Basin and Maxfield Meadow. P-value between sites < .05; SE=  $\pm$  .23.



p-value > .05; SE =  $\pm .3$

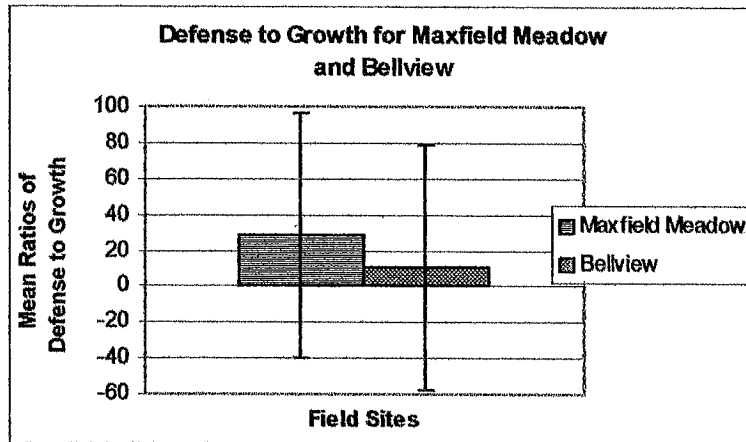


p-value > .05; SE =  $\pm 1$

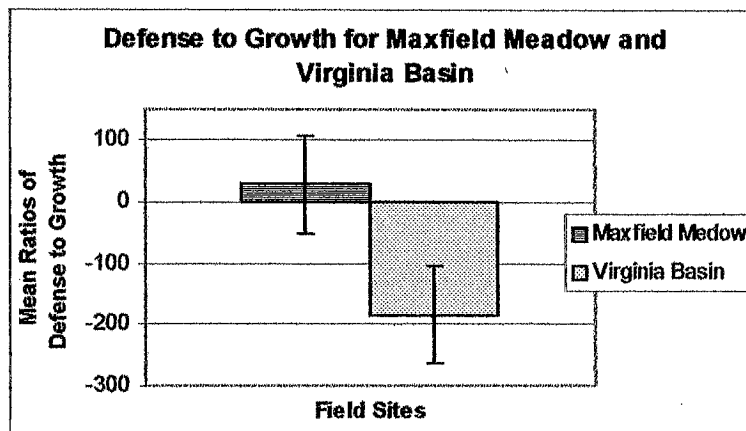


p-value > .05; SE =  $\pm .9$

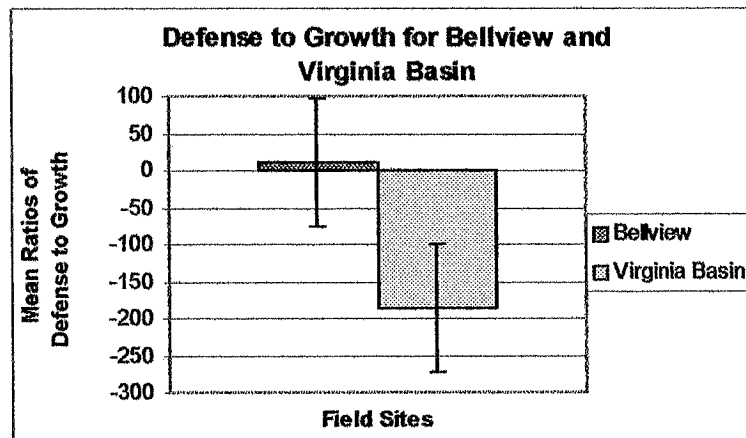
**FIGURE 3:** Comparisons of reproduction to growth ratios between pairs of field sites: Bellview-Maxfield Meadow, Virginia Basin-Maxfield Meadow, and Bellview-Virginia Basin.



p-value > .05; SE =  $\pm 68.1$

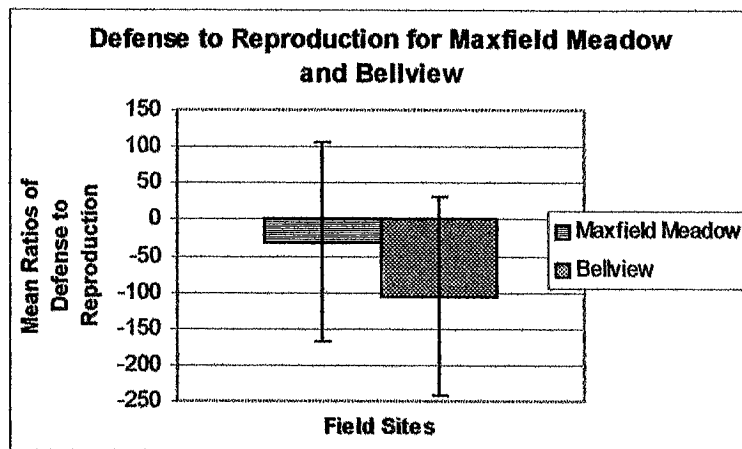


p-value < .05; SE =  $\pm 80.1$

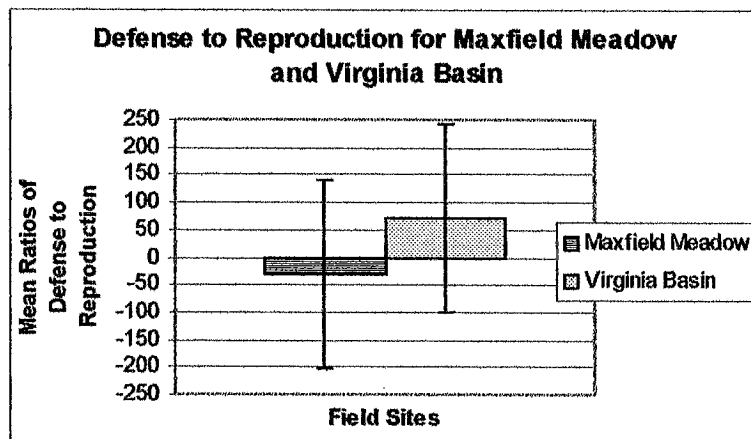


p-value < .05; SE =  $\pm 86.7$

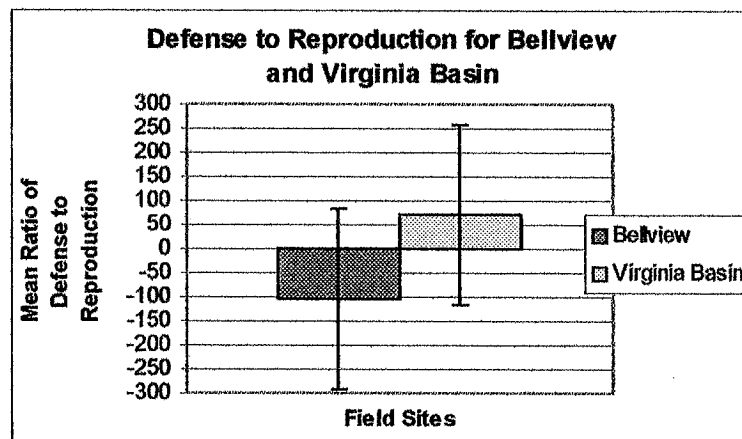
**FIGURE 4:** Comparisons of defense to growth ratios between pairs of field sites: Bellview-Maxfield Meadow, Virginia Basin-Maxfield Meadow, and Bellview-Virginia Basin.



p-value > .05; SE =  $\pm 136.6$

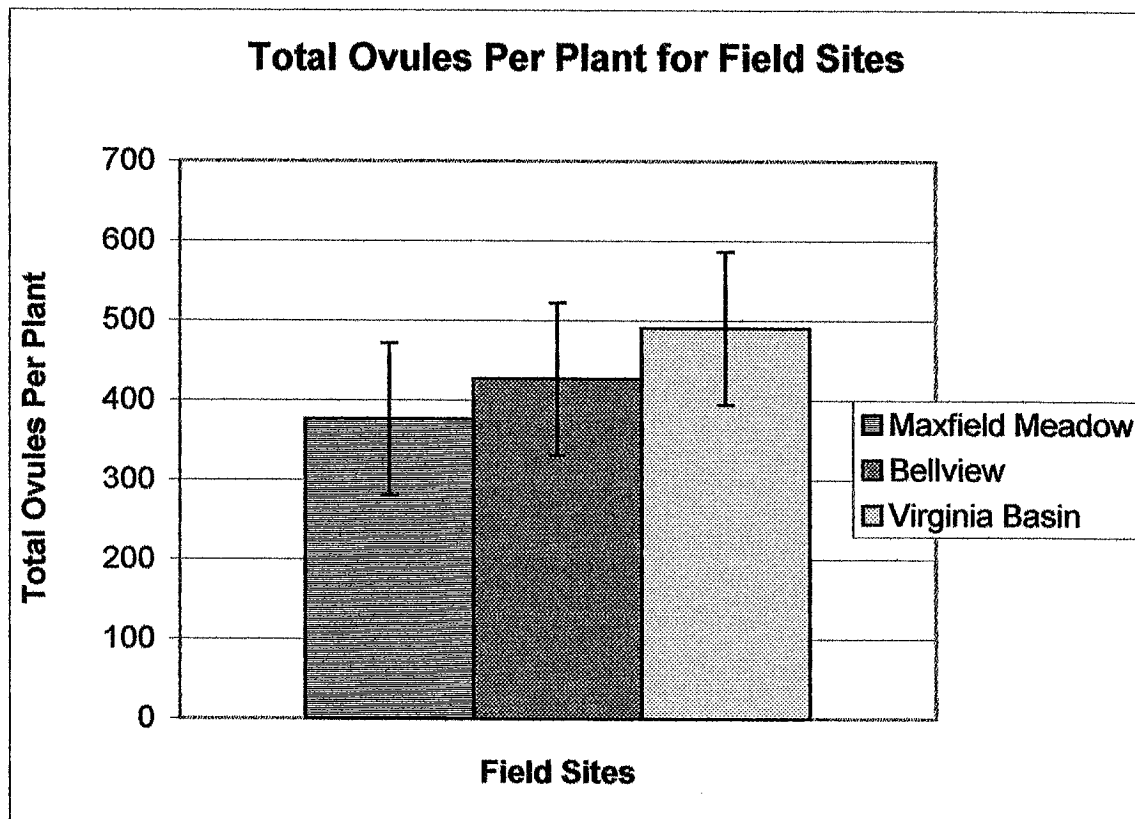


p-value > .05; SE =  $\pm 171.3$

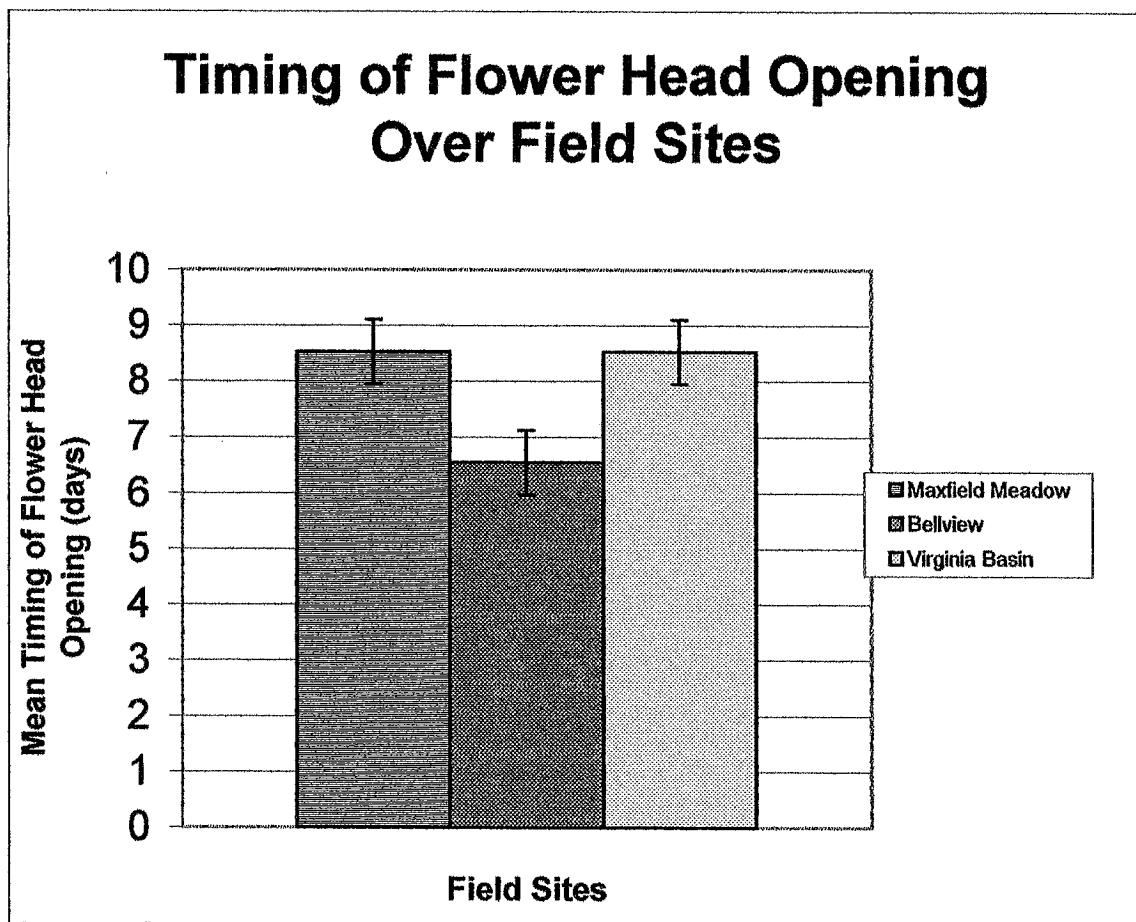


p-value > .05; SE =  $\pm 188.2$

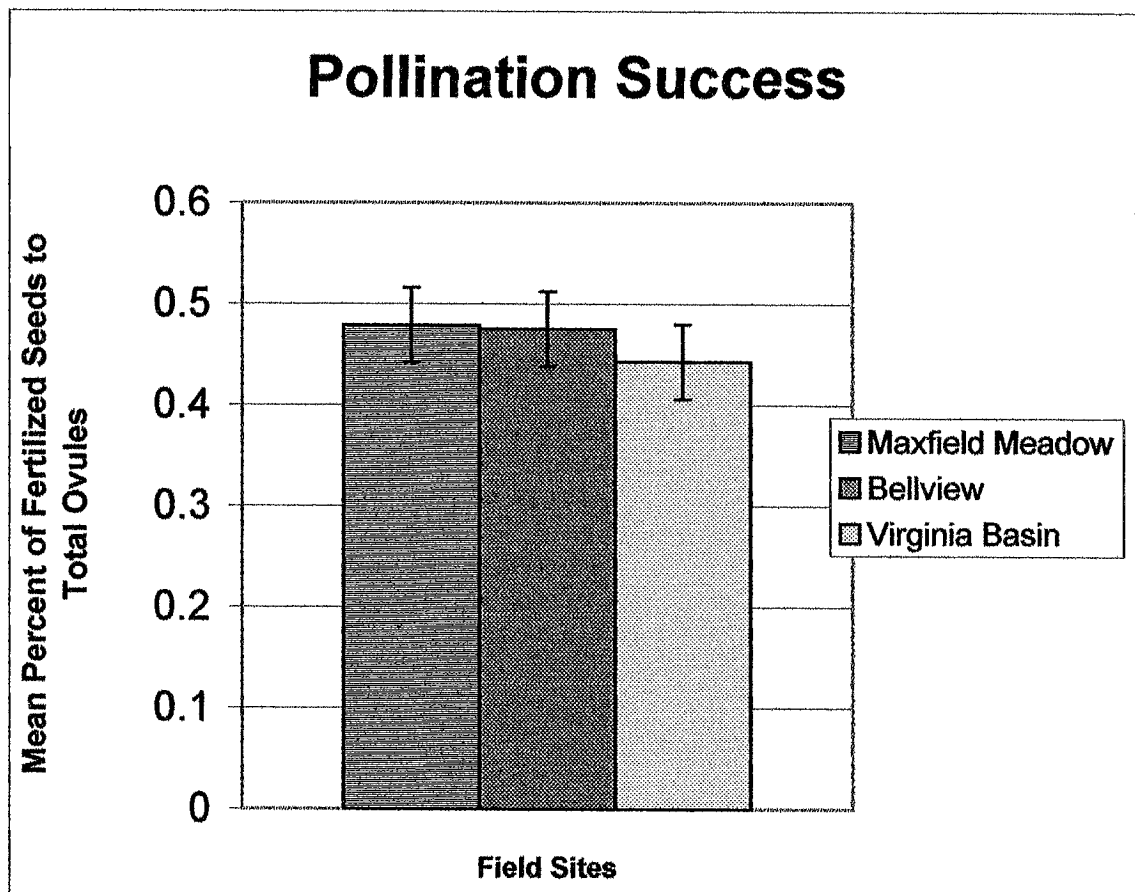
**FIGURE 5:** Comparisons of defense to reproduction ratios between pairs of field sites: Bellview-Maxfield Meadow, Virginia Basin-Maxfield Meadow, and Bellview-Virginia Basin.



**FIGURE 6:** Total ovules per plant for three field sites: Maxfield Meadow, Bellview, and Virginia Basin. P-value between sites > .05; SE=  $\pm$  95.8.



**FIGURE 7:** Mean timing of flower head opening for plants measured in days, for three field sites: Maxfield Meadow, Bellview, and Virginia Basin. P-value between sites  $< .01$ ;  $SE = \pm .587$ .



**FIGURE 8:** Percentage of fertilized seeds to total ovules as a measure of pollination success over three field sites: Maxfield Meadow, Bellview, and Virginia Basin. P-value between sites  $>.05$ ; SE=  $\pm .037$ .