EFFECTS OF SIMULATED FOLIAGE AND ROOT HERBIVORY ON GROWTH, REPRODUCTION, AND INSECT DAMAGE OF THREE ANNUAL PLANT SPECIES

by

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B.S., Kansas State University, 1983

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1987

Approved by:

Major Professor

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ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. O.J. Reichman, for many aspects of my research, including editorial assistance, field equipment and laboratory facilities, and especially the many constructive ideas in the formulation of my experiments and data analysis. I would also like to thank my committee members: Dr. Donald W. Kaufman and Dr. Chris C. Smith for their ideas. Dr. Ted Barkeley also provided helpful suggestions.

I had help in the field from a number of friends, including Gregg Farley, Susan Farley, Cindy Rebar, Rob Gendron, and especially Phil Bollinger. Rob Gendron was also very helpful with statistical analyses and with development of the computer program for randomly assigning plants and treatments. Craig Frank provided helpful suggestions for statistical analyses. Others who provided assistance include Lisa Smith, Joe Gelroth, Linda Davis, Richard Inouye, and Nancy Huntly.

I also wish to thank two very special people who helped make this project possible: my parents, Stan and Jean Smith, who provided endless encouragement and moral and financial support. Last, I wish to thank my wife, Kim, who gave constant emotional support; and my two sons, Micheal and Ryan, who make everything I do seem very important.

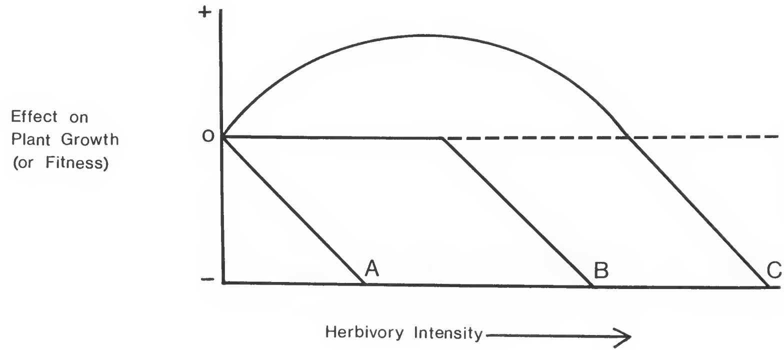
INTRODUCTION

The effects of defoliation on plants have been considered extensively by ecologists and agriculturists for at least fifty years (e.g. Mortimer and Ahlgren 1936; Jameson 1963; Belsky 1986). A wide variety of effects have been attributed to defoliation by herbivores. On a broad scale, defoliation by insects is known to influence growth and nutrient dynamics of forest ecosystems (e.g. Mattson and Addy 1975; Swank et al. 1981; Seastedt et al. 1983). Some researchers have attempted to measure the effects of grazing or clipping on the net primary production of entire plant communities (e.g. Pearson 1965, Vickery 1972). The majority of studies have looked at responses of single plant species to herbivore damage. Most of the literature can be divided into studies of effects of herbivory on plant growth and a smaller number of studies analyzing plant reproduction or yield in relation to herbivory.

Effects of Herbivory on Plant Growth

The effects of herbivory on plant growth are variable. There are three major contrasting views of the effects of herbivores on plant growth or fitness (see Figure 1). The first of these is the hypothesis that plant growth always decreases in response to herbivory. Lacey and Van Poolen (1981), in a review of studies of grazed and ungrazed rangelands, concluded that production of grazed rangelands averaged 68% lower than protected land. Ruess et al.

Figure 1. Three alternative hypotheses for how herbivory affects plant growth or fitness. The first is that any herbivory causes a decrease in growth or fitness (line A). The second is that plants are able to compensate for moderate herbivory (line B) but not when herbivory exceeds a particular level. The third hypothesis is that plant growth or fitness increases with moderate herbivory (line C) but decreases beyond a particular level of herbivory. Redrawn from McNaughton (1983) and Belsky (1986).


Effect on
Plant Growth
(or Fitness)
+
O
–
A
B
C
Herbivory Intensity

(1983) found that, except when grown in increased ammonia, Killinga nervosa exhibited a decrease in green leaf production in response to clipping. Stanton (1983) found that the biomass of all plant parts (including roots and shoots) of blue grama decreased significantly with three levels of both above-ground and below-ground herbivory.

The second hypothesis is that plants are able to compensate for tissue removal by herbivores, with no significant decrease in growth, up to a threshold level of herbivory. There is substantial evidence that grasses can partially or fully compensate for lost biomass (Lee and Bazzaz 1980; Solomon 1983). Seastedt et al. (1983) suggest that a problem with many studies of the effects of herbivory (particularly with forests) is that low-level, natural consumption effects are included in the "controls" of defoliation studies. They compared biomass production of black locust and red maple trees that were sprayed with insecticide to those that were not sprayed. Biomass production, however, was unaffected by the low levels of herbivory of the untreated trees (Seastedt et al. 1983).

The third hypothesis concerning the effects of herbivores on plant growth is that plants are able to compensate for lost tissue, with significant increases in growth, up to a threshold level of herbivory. This has been a continuing subject of controversy (see reviews by Owen and Wiegert 1976, 1981; Owen 1980; McNaughton 1983, 1986; Belsky 1986). There are very few studies that report overcompensation by individual species in total biomass as a result of herbivory (Belsky 1986). Numerous studies, however, report increases in above-ground biomass. It has repeatedly been documented that shoot production in turfgrasses may be stimulated by moderate clipping (see McNaughton 1983). Belsky (1986), however, argues that many of these studies had inadequate controls, insufficient replication, or no statistical evaluations (see Jameson 1963 for a similar conclusion). Also, few studies of noncrop dicots report overcompensation for lost tissue. Lowman (1982) found that, for seedlings of coachwood (Ceratopetalum apetalum) in controlled conditions, growth was stimulated beyond the rate of the controls with 25% leaf removal, but was suppressed with 50% leaf removal. Torres et al. (1980) reported increased vegetative growth following several levels of leaf removal in two Chilean matorral shrubs. Biomass was not measured, however, and below-ground growth was not taken into account. Heichel and Turner (1984) found that defoliation of red oak (Quercus rubra) and red maple (Acer rubrum) stimulated lateral shoot formation. Terminal bud and branch formation, however, was reduced. After two years of defoliation the numbers of all shoots on the defoliated trees declined, as compared to undefoliated trees. Some authors have argued (e.g. Stanton 1983; Belsky 1986) that most studies of net primary production following herbivory do not present convincing evidence of overcompensation because they measure above-ground production only. And a large number of studies show that defoliation initiates reallocation of assimilates from the roots to the shoot, causing little reduction in growth of foliage but causing a reduction in root growth (e.g. Branson 1956; Richards 1984).

Effects of Root Damage on Plant Growth

Some studies of herbivory have also included analyses of the removal of below-ground plant parts. Due to the abundance of below-ground invertebrate herbivores, below-ground herbivory may be extremely important, perhaps more so than above-ground herbivory (Detling et al. 1980). For example, James and Hutto (1972) found an increase in the growth of *Lolium perenne* following the removal of root apices. Andrews and Newman (1968) found an increase in growth rate of wheat following root removal when the soil was relatively dry, but found a decrease in growth rate in wet soil. Totsuka et al. (1960) found a decrease in biomass of cultivated *Helianthus annuus* following partial root excision. Humphries (1958) and Detling et al. (1980) also found reductions in biomass production following root removal. In another study, involving actual herbivores rather than clipping, Stanton (1983) found reduced total biomass in plants subjected to several levels of phytophagous nematodes. The majority of studies suggest that the effects of root removal is reduced total biomass production.

Overall, overcompensation in growth of plants following root or shoot removal has been demonstrated in a limited number of studies, and usually under controlled conditions. It could theoretically occur in natural systems, but probably only under limited conditions. For instance, herbivory would have to occur early enough in the growing season for plants to recover, water and nutrients must be adequate for regrowth, and other plant species must not be in a position to gain a competitive advantage.

Even if biomass compensation could occur in a natural situation, it may not be an accurate measure of plant fitness. Increased biomass production benefits plants only when it is associated with an increase in reproduction. This may not occur if new production occurs too late in the season or is consumed before it is transferred to reproductive tissue. The question remains: do herbivores increase plant reproductive output, or do they decrease it?

Effects of Herbivory on Plant Reproduction

The three alternative hypotheses regarding the effects of herbivores (Figure 1) may be applied to plant fitness as well as biomass production. The first possibility is that any amount of tissue removal results in a decrease in reproduction. The majority of relevant studies report results of this nature. Reed and Stephenson (1972) found severe reduction in seed production in the annual _Ambrosia artemisiifolia_ with increasing levels of simulated herbivory. Seed number in the biennial _Arctium minus_, however, is determined very early in the reproductive phase, and is not greatly affected by defoliation, but the size and weight of the seeds was decreased with increasing defoliation (Reed and Stephenson 1974). Likewise, Maun and Cavers (1971) found that defoliation of the panicle of _Rumex crispus_ had little effect on the number of seeds produced but led to a severe reduction in total seed weight per panicle and size of individual seeds. In _Catalpa speciosa_, Stephenson (1980) found that branches that have experienced simulated herbivory have significantly more fruit abortions than control branches. Many crop plants also show a decrease in seed production with defoliation. Kittock and Williams (1967) reported lower yields in castorbeans with four levels of defoliation than in the controls. Stickler and Pauli (1961) found that removal of 33%, 50%, 67%, and 100% of the leaves resulted in yield decreases of 23%, 35%, 43%, and 95% in sorghum. Sackston (1959) and Johnson (1972) showed significant decreases in seed yield and seed weight in sunflowers with several levels of defoliation.

Although the majority of studies report decreases in reproductive tissue following herbivory, a few suggest that some species actually benefit from herbivory by producing more reproductive tissue than they would without herbivory. In a widely cited paper, Dyer (1975) concluded that the ear weight of corn (Zea mays) was increased by moderate damage to immature corn ears by red-winged blackbirds. The results of this study were complicated by the fact that red-winged blackbirds selectively feed on larger ears. In a later study however, simulated bird damage was applied to ears of corn that were similar in size, stage of growth, and other relevent characteristics. In this case the damaged ears did not fully compensate for the lost tissue (Woronecki et al. 1980). In the thistle Jurinea mollis, multiple stalks are produced when lepidopteran larvae eat the central part of the basal rosette. Plants with multiple stalks can produce up to three times as many seeds as those without multiple stalks (Inouye 1982). Several other types of herbivory on this species were reported to decrease the reproductive potential.

Crop species are sometimes reported to overcompensate, in reproductive tissue, following tissue loss. Binnie and Clifford (1980) found that the remaining tissues of defoliated and decapitated french beans had numbers of fruits and weights of seeds that were 2 to 3 times greater than control plants. For winter rye, winter wheat, and winter oats, Sprague (1954) found that fall grazing significantly increased grain production. Furthermore, Taylor (1972) found that several levels of defoliation before and during tillering resulted in significantly greater grain yields in several varieties of rice.

Effects of Herbivory on Reproductive Strategies

In addition to affecting production of seeds, herbivory has also been shown to directly alter the immediate reproductive strategies of plants. The removal of leaves of subterranean clover (Trifolium subterraneum) was found to cause a delay in flowering time by up to 30 days (Collins and Aitken 1970). Boscher (1979) found that moderate defoliation of leek (Allium porrum) results in a shift from asexual reproduction (bulblets in inflorescences and underground off-set bulbs) to a greater level of sexual reproduction than in control plants. Another example of altered reproductive strategy was reported in a study by Hendrix and Trapp (1981) in which they found that wild parsnip (Pastinaca sativa) responded to insect herbivory by producing a greater proportion of hermaphroditic flowers. In the damaged plants there was also a larger total number of flowers and a larger proportion of hermaphroditic flowers producing seeds. This did not translate into greater reproductive output, however, because the first inflorescences were destroyed by the herbivory. Although these studies do not prove that defoliated plants have lesser or greater overall reproductive potential, they do suggest that reproductive strategies may be altered by herbivores.

Overall, although some would suggest that moderate levels of herbivory maximize plant fitness (Owen and Wiegert 1976, 1981; Owen 1980), the relevant literature seems to provide little support for this idea. The cases in which total plant biomass or seed numbers are increased following defoliation are limited. Many of those presented are for crop species or are conducted under laboratory or agricultural conditions.

My study was designed to investigate experimentally the effects of root removal and several levels of defoliation on seed production of the annual _Helianthus annuus_ L. and total biomass of the two annuals _Chenopodium album_ L. and _Chenopodium berlandieri_ Moq. var. _zschackei_ Murr. Objectives were: 1) To determine the effects of defoliation or root removal on biomass of _Chenopodium_ spp.; 2) to determine whether or not total biomass is an accurate indicator of seed production in _Chenopodium_ spp.; 3) to determine the effects of defoliation and root removal on numbers of seeds and seed heads produced by _H. annuus_; 4) to determine the effects of defoliation and root removal on the level of herbivory by sunflower moth larvae on _H. annuus_; and 5) to assess the general implications of these observed responses for plant-herbivore relationships. The approach involved artificial damage of the leaves and roots of plants, followed by direct measurement of the biomass of the shoots, roots, and reproductive tissue. Results of this study may provide insights into plant-herbivore relationships, particularly the question of whether plants benefit from the animals that eat them.

METHODS

All plants were transplanted, treated, and collected during spring and summer of 1985.

Transplanted Plants

Seedlings of two annual plants were transplanted in an old corral just south of the main barn on Konza Prairie Research Natural Area. The plot was mowed to 2-3 in. and sprayed with Roundup herbicide one week prior to the first transplantings to prevent the existing plants from reestablishing. Seedlings of C. album (10-15 cm tall) were collected from a disturbed site just south of Manhattan, KS., using a bulb puller, and transported in plastic pans to Konza Prairie. Seedlings of H. annuus (30-40 cm tall) were collected in the same fashion from a diversion ditch just west of the corral. C. album were transplanted on May 13, 14, and 15, and H. annuus were transplanted on June 5 and 6.

All plants were watered at least twice within one week of transplanting and sprayed with Ortho liquid Sevin insecticide to facilitate adaptation to the site. Mortality of the original C. album totalled 9%, with 0% mortality of H. annuus. The dead C. album were replaced as soon as they were detected.

The study plot consisted of a 24 x 50 grid. Rows and columns were .5 m apart. A computer program was designed to randomly place the transplants into each of the 1200 sites, so that the end result was approximately equal numbers of the two species distributed randomly throughout the plot (Figure 2). The seedlings were transplanted to the grid according to this distribution. One of 14 possible treatments was also randomly assigned to each plant site (see later section for explanation of treatments).

Naturally Occurring Plants

Naturally occurring plants were also used in the experiment. The site was located approximately 150 m south of the plot of transplanted plants. *H. annuus* and *C. berlandieri* were both abundant at this site (*C. album* was not found to occur in a suitable natural site). 560 naturally occurring *H. annuus* and 560 *C. berlandieri* seedlings were tagged. The individual plants were chosen as follows. Forty areas were located, each area containing at least 14 *H. annuus* and 14 *C. berlandieri*. A typical sized *H. annuus* was selected near the center of each site, and the 13 nearest *H. annuus* were picked for the experiment. The nearest 14 *C. berlandieri* to the 14 *H. annuus* were also picked for the experiment. Plants that were visually determined to be considerably larger or smaller than average were not included.

Treatments

Fourteen treatments were used for *H. annuus* and *Chenopodium* spp. (see Table 1). Using a random number table, each plant site was assigned one of the 14 possible treatments (7 treatments x early or late) for the transplanted plants (Figure 3). For the naturally

Figure 2. Grid of plant sites for transplanted *Helianthus annuus* (H) and *Chenopodium album* (C). For each site, one of the plant species was randomnly assigned. Sites at which plants died before application of treatments are represented by an X. Rows and columns both are 0.5 m apart.

1 C H C C C C C H X C H C H C C H H H H H C H H C

2 H C C H C H H H C H H H H H H H H C H C H C C H

3 C H C H H H C C C C C C H C H H H H H C H C C C

4 H H C C C C H H C C C C H C C C C C H H H H C C

5 C H C C H C C C C C H C H C H C H H H H H C C C

6 C H H H H H C H H C H C H H C H C C C H C H H C

7 C H C H C H C C H C C H C C C H C C H H C H H C

8 H C H H H H H C H H C H C C C H H H C C C C C C

9 C C X C C H C C H C C C H H C C C H C H C C H C

10 H H H H H C H C H H C H H H H H C H H C H H C H

11 H H H H C H H H H C C C H C C X H C C H H C C H

12 H H H H C H H C C H C C H H C H C H H C C H C H

13 H H H C C H C H H C C H C H C C H H H H C C H C

14 H H H C H C C C H H C H H H H H C H H H H C H C

15 H H H C H C H H H H C H H H C H H H C H H H C H

16 C H C H C C H C C H H C H H C C H C H H H C C C

17 C C C C C C H C C H H C H C H H C H H H H C C C

18 H H H C X C H C H C C H C C C C H C H H H H H H

19 H C H C C H C H C C C H H H C H C H C H H H H C

20 C H H H C H C C H C C H H H C H C C C H H C H H

21 C C H H H H C H C H H C C H H H C H H H H C H H

22 C C C C C H C C H H X C H H C H C C H C H H H H

23 H H H C H C C H C H C C H H H H H C C H H H H C

24 H C H C H C C H H H H H H H H H C C H C C C H C

25 C C C H C C C H H H C C H H C H C H H C C H C C

26 H C C H C C C C C H H C C H C H C H H H C C H H

27 C H C H C H C H H C H C H C H C C H H C H H H H

28 C C C C H H C C C C C H C H H C C H H H H H H H

29 H H C H H C H H C C H H H H H C C H C H H H H H

30 C H H C C C C H H C C C C C C H H C H C C H H H

31 H C C H C C H C C H C H C H C H H C C H H C C H

32 C C C H H H C C H C C C H H H H C C C C C C C C

33 H H H H H H H H H C C C H C C H H C C H X H C H

34 C C C C C H H H C C H H H H C C H C H H X C H C

35 H H C X C C C C H C C C H H H H C H C C X C H H

36 H C C C C C H C H H C H H H H H C H H H C H C H

37 C H C H C H H H H H H H C H C H C H H H H C C C

38 C H C C H H C C H H C H C C H C H H H C C H H H

39 H C H C C C H H H C H H C C H C H H H H H C X H

40 H C H H C H C H H C C H H H C H H C H H C H C H

41 H H C C C C H H H C H H H C H H C C C C H C C C

42 C H C H C H H H H C H C H C H C C C C H H H H H

43 H C C C H H C H C H H C C C H C H H C H H C C H

44 H H H H C H C C C H C H H C H C H C X C C C C C

45 H C C H C C C C C H H H H H C H C C X C C C H H

46 H C H H C C C H H C H C C H C H C H H C H C H C

47 C C H H H C C C C H C H H C C C H C H H H C H H

48 C C C H C C H C H H C C C C C H C H H C C H C H

49 H H C C C H H C H C C H C C H H H C H C C C H C

50 C H H C H C C H C H C C C H H H C C H H C H C H

Table 1. Fourteen simulated herbivory treatments used for both the natural and transplanted plants. These treatments were applied to each of the three species. See text for details of each treatment.

Early	treatment 1: control
	treatment 2: 25% area of each leaf removed
	treatment 3: 25% of leaves removed
	treatment 4: 75% area of each leaf removed
	treatment 5: 75% of leaves removed
	treatment 6: roots trimmed
	treatment 7: roots trimmed and 25% of leaves removed
Late	treatment 1: control
	treatment 2: 25% area of each leaf removed
	treatment 3: 25% of leaves removed
	treatment 4: 75% area of each leaf removed
	treatment 5: 75% of leaves removed
	treatment 6: roots trimmed
	treatment 7: roots trimmed and 25% of leaves removed

Figure 3. Grid of plant sites for transplanted *Helianthus annuus* and *Chenopodium album*, showing randomly assigned treatments (1-7). Those which are underlined were treated late in the growing season and those not underlined were treated early (see text for description of treatments).

1	5	4	4	6	3	2	2	6	6	2	6	5	5	7	6	3	5	3	6	5	6	7	3	2
2	2	5	6	3	1	4	7	5	1	6	1	5	3	5	2	5	1	5	3	2	2	6	4	2
3	2	4	6	6	6	3	2	5	2	3	2	4	6	3	2	2	6	2	7	5	4	1	4	7
4	5	6	2	4	1	4	2	1	5	1	3	5	7	3	1	6	2	2	6	5	7	1	3	5
5	1	5	3	4	5	6	1	1	4	6	4	4	1	1	6	2	2	1	5	2	5	3	6	3
6	5	2	6	2	6	7	3	3	3	3	4	4	5	1	7	7	4	5	5	5	2	1	1	6
7	1	1	6	5	1	6	7	7	2	5	1	1	5	4	5	2	7	2	5	3	4	6	3	7
8	5	5	7	7	4	1	4	1	7	3	2	6	7	7	1	2	2	4	4	6	6	1	4	5
9	4	6	4	6	2	2	7	3	6	5	3	7	6	2	2	5	7	4	7	2	6	5	2	3
10	5	7	7	4	1	6	2	4	7	5	1	2	1	1	4	5	5	2	1	7	4	7	2	6
11	7	6	3	5	1	7	7	3	1	5	1	6	3	1	1	5	3	2	6	4	6	6	3	1
12	6	2	4	1	4	1	7	7	7	5	7	7	4	5	4	2	2	1	5	6	6	6	2	7
13	3	2	6	4	7	4	6	2	6	6	7	7	3	7	2	7	2	5	6	4	1	5	7	6
14	6	1	6	4	4	1	1	1	4	1	7	5	7	7	2	5	6	4	6	2	3	7	2	2
15	1	6	7	5	4	1	7	6	7	6	5	5	6	5	4	4	1	5	4	7	3	6	1	3
16	4	3	3	6	6	7	2	3	3	5	3	2	4	2	7	3	3	4	3	5	7	4	5	3
17	3	6	4	7	1	7	2	6	4	5	6	6	6	3	3	4	6	3	3	2	2	2	5	5
18	4	6	7	1	1	1	3	6	3	1	3	7	4	3	4	2	7	5	7	7	1	5	5	4
19	2	2	6	7	3	7	2	6	3	1	1	6	4	2	1	5	5	1	2	6	2	1	1	1
20	5	2	2	7	2	4	3	7	3	1	2	2	4	7	6	7	5	6	3	7	3	4	7	2
21	2	2	7	1	1	5	5	1	4	7	5	3	4	2	4	3	6	7	7	5	4	4	2	3
22	4	1	1	2	7	4	2	2	4	4	3	2	4	1	3	4	1	2	1	4	7	5	3	4
23	4	4	6	7	2	4	6	5	4	4	1	4	2	2	4	7	3	7	3	4	4	3	4	1
24	6	7	3	4	5	2	4	5	6	3	6	4	4	4	3	5	1	7	5	1	6	5	4	7
25	3	7	6	5	7	1	5	3	6	5	4	1	4	6	7	1	2	4	7	6	2	1	6	2
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27	1	1	2	1	4	7	2	4	2	1	5	7	7	4	3	7	3	7	6	7	2	6	5	2
28	6	4	5	3	2	5	4	4	3	3	2	6	1	5	6	5	5	5	2	5	3	7	3	1
29	2	3	7	6	6	3	6	2	2	5	2	7	2	5	1	3	6	4	1	4	3	4	7	3
30	6	6	4	1	6	7	7	5	4	5	2	5	5	3	3	1	2	5	2	4	3	1	5	7
31	2	3	5	6	4	6	2	7	3	1	5	2	4	5	3	7	5	5	4	3	2	1	6	7
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33	7	4	1	3	1	6	2	4	6	2	3	5	3	7	7	2	7	7	7	3	3	2	2	1
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39	1	1	6	7	1	7	1	4	4	3	5	4	7	6	7	6	6	3	7	2	3	6	7	7
40	5	4	3	3	4	5	2	1	2	1	3	1	6	6	4	6	1	5	7	1	2	6	2	7
41	7	6	5	7	6	6	7	3	6	3	7	7	5	7	7	4	2	6	6	2	4	6	6	1
42	2	1	7	6	4	6	6	7	6	4	2	5	4	5	2	6	2	3	7	5	3	2	3	4
43	5	2	2	7	4	3	5	7	5	6	5	6	2	3	7	6	4	3	7	1	6	4	4	7
44	4	1	5	4	3	7	3	3	1	3	1	6	3	4	2	6	2	6	6	1	5	6	5	5
45	6	7	5	4	7	1	3	2	5	2	5	4	7	2	4	3	4	1	7	1	2	2	5	6
46	5	1	3	3	7	6	3	5	7	1	4	1	6	7	5	2	5	4	4	5	1	3	1	5
47	5	4	5	6	2	5	4	1	3	2	6	6	3	1	2	4	4	2	7	6	4	7	3	3
48	5	5	4	4	7	5	4	2	1	1	4	6	7	1	7	1	1	7	3	5	5	7	4	5
49	3	7	4	7	2	6	5	5	5	4	7	4	3	2	4	1	6	4	5	1	2	1	1	4
50	3	7	4	7	2	6	5	5	5	4	7	4	3	2	4	1	6	4	5	1	2	1	1	4

occurring plants, one H. annuus was picked and the 13 plants nearest to this individual were used. Treatments were assigned to plants at increasing distances from the first plant in the order of treatments 1-7 for early and 1-7 late. The C. berlandieri were selected simply by picking the plant nearest to each H. annuus and assigning the same treatment as for that plant. A metal tag, with the assigned treatment written on it, was attached to each naturally occurring plant.

Control plants (treatment 1) were unmanipulated. Treatment 2 consisted of removal of 25% of the area of each leaf on the plant. This was accomplished by cutting off the distal 1/2 of the leaf area on one side of the midvein with scissors for H. annuus. For Chenopodium spp., which have much smaller and more numerous leaves, the distal 1/4 of each leaf was pinched off, including the midvein. Treatment 4 was similar except 75% of the area of each leaf was removed. The entire area of the leaf blade on one side of the midvein was cut off, as well as 1/2 the area on the other side of the midvein for H. annuus. The distal 3/4 of each leaf was pinched off for Chenopodium spp. (Figure 4). The location of the cuts for all leaves was estimated by eye and the proportions of leaf material removed is therefore approximate rather than exact.

Treatments 3 and 5 consisted of removal of entire leaves rather than a proportion of the area of each leaf. For treatment 3 every fourth leaf was removed with scissors at the base of the petiole, and for treatment 5 three out of every four leaves were removed in a similar fashion, starting at the bottom of the plant. When counting

Figure 4. Diagrams of *Chenopodium* sp. leaf and *H. annuus* leaf showing positions of cuts (dotted lines) used to remove 25% or 75% of leaf area. With the *Chenopodium* leaf (top) the cut was made through the midvein because of their small size and the large number of leaves per plant. The midvein was left intact on the *H. annuus* leaves.

up from the bottom, the starting number (1,2,3 or 4) for the lowermost leaf was changed for each plant in order to spread the error due to larger bottom leaves.

Treatment 6 consisted of removal of approximately 30% of the length of the central tap root of H. annuus and C. album. C. berlandieri were significantly smaller, and since the roots of these plants were cut at the same depth, a smaller proportion of the tap root was removed. Roots were cut at a specific depth by forcing a shovel into the ground at a specific distance from the shoot and at a specific angle from vertical. For plants that were treated early in the growing season, roots were cut at a depth of 10 cm. The average height of the H. annuus at the time of clipping was 37 cm, with an average root length of 14 cm. For the early treatments a shovel was positioned with its point 10 cm from the base of the shoot, with the blade at an angle of 45 degrees. Accurate positioning of the shovel was accomplished by attaching a cord of appropriate length, with a weight on the end, to the shovel handle. the shovel was placed 10 cm from the shoot and lowered from vertical until the weight touched the ground. It was then driven into the ground at this angle so that the blade intersected a point exactly 10 cm below the base of the shoot. This process was repeated on the opposite side of the plant to ensure that the root had been severed in the event that it did not grow directly beneath the shoot. The roots were cut at a depth of 13 cm for the late treatments, which again removed approximately 30% of the length of the roots. At this time the average height of H. annuus was 106 cm, with an average root length of 18 cm. This process was identical except that the shovel blade was pushed into the soil 13 cm from the base of the shoot instead of 10 cm. The roots of C. berlandieri were cut at the same depth as those of C. album. The average root length of the transplanted C. album was similar to H. annuus, but the roots of the smaller, naturally occurring C. berlandieri were somewhat shorter.

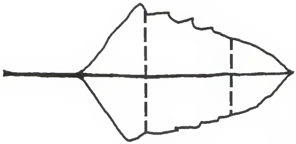
Treatment 7 consisted of both root trimming (at the same depth as treatment 6) and removal of one out of every four leaves, as in treatment 3.

Treatments were applied to one group of plants early in the growing season (transplanted: June 27 - July 2; naturally occurring: July 12 - July 18), and another group later in the season (transplanted: Aug. 8 - Aug. 15; naturally occurring: Aug. 19 - Aug. 24). Individual plants were treated only once, either early or late.

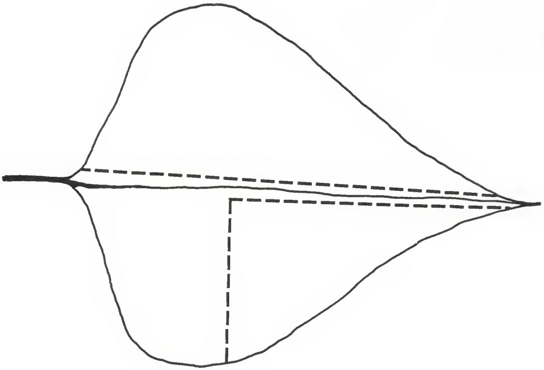
All treatments were applied to the transplanted plants first. It was later found that transplanting delayed maturation by two weeks compared to naturally occurring plants (both H. annuus and Chenopodium spp.). Because of this delay in maturation of the transplanted plants, collection of natural plants was done before collection of transplanted plants to insure that all plants were collected at approximately the same developmental stage (see Table 2 for a schedule of transplanting, phenology, treatments, and collection).

Collection of Plants

The flower heads of all naturally occurring H. annuus were removed and placed in paper bags between Sept. 22 and Sept. 27.



Chenopodium



Helianthus

Table 2. Schedule of transplanting, phenology, treatments, and collection of *Helianthus annuus* and *Chenopodium* spp.

Inclusive Dates	Activity
May 13 - 15	*C. album* transplanted to plot.
June 5 - 6	*H. annuus* transplanted to plot.
June 7	Sprayed with Sevin insecticide.
June 13	Sprayed with Sevin insecticide.
June 27 - July 2	All early treatments applied to transplanted plants.
July 14 - 17	All early treatments applied to natural plants.
Aug. 5 - 15	All late treatments applied to transplanted plants.
Aug. 19 - 24	All late treatments applied to natural plants.
Aug. 20	All natural plants have started flowering.
Sept. 8	All natural plants producing mature fruits, all transplanted plants have started flowering.
Sept. 20	All transplanted plants producing mature fruits.
Sept. 22 - 27	Seed heads collected from natural *H. annuus*.
Oct. 1 - 5	Seed heads collected from transplanted *H. annuus*.
Oct. 6 - 7	Natural *C. berlandieri* collected.
Oct. 7 - 9	transplanted *C. album* collected.

Those of the transplanted plants were collected from Oct. 1 to Oct. 5. These bags were allowed to air dry at room temperature for 4 months before measurements were made. The entire naturally occurring C. berlandieri, including roots, were collected on Oct. 6 and 7 and placed in paper bags. These plants were allowed to air dry at room temperature for approximately 5 months. Transplanted C. album were collected from Oct. 7 to Oct. 9. Due to the large size of these plants they were allowed to air dry in a storage shed for approximately 6 months.

Data Collection

To determine that seed head diameter is a reliable indicator of number of seeds, a subsample of 30 H. annuus seed heads from each of treatments 1 through 7 (lumping early and late, with unequal numbers of each) was analyzed. The exact number of seeds was determined for each seed head by counting the number of seeds present and the number of spaces on the head where seeds were missing. Then the diameter of the empty seed head was measured (not including leafy bracts) and the head was weighed on an electric balance. The seeds themselves were weighed to determine average seed mass. Linear regressions indicated a highly significant relationship between seed head mass (independent variable) and number of seeds (dependent variable; $r=0.78$, $n=210$, $p<<.0005$), and seed head diameter and number of seeds ($r=0.84$, $n=210$, $p<<.0005$). Seed head diameter proved to be the best indicator of seed number so this parameter was used for the remainder of the seed heads.

Number of seed heads per plant and average diameter of seed heads was determined for each H. annuus. In addition, the proportion of seed heads occupied by sunflower moth larvae (Homoeosoma electellum Hulst.) was calculated for each plant. During their normal feeding activity on the seed head, sunflower moth larvae create a pulpy mass of material that is easily recognizable, facilitating their detection.

An original objective of this study was to count or estimate the number of seeds produced by Chenopodium spp. Because counting the seeds of C. album proved to be extremely difficult, subsamples of approximately 30-40 plants were analyzed to determine a relationship between total plant biomass and seed biomass. Subsamples of transplanted and natural plants of treatment 1 and treatment 5 (lumping early and late, with unequal numbers of each), were weighed. The seeds, including the pericarp, were then removed from the plants and weighed seperately. Linear regressions indicated a highly significant relationship between total plant biomass (independent variable) and seed biomass (dependent variable) for both groups of plants (treatment 1: $r=0.91$, $n=41$, $p<<.0005$; treatment 5: $r=0.91$, $n=36$, $p<<.0005$). The same procedure was performed with naturally occurring C. berlandieri, with similar results (treatment 1: $r=0.99$, $n=33$, $p<<.0005$; treatment 5: $r=0.96$, $n=33$, $p<<.0005$). Total plant biomass, therefore, was used to estimate seed biomass for the remainder of the transplanted and naturally occurring Chenopodium spp. Root biomass was also determined. Plants were cleaned of all residual soil, and weighed on an electric balance. Those that were too large for the electric balance (most of the transplanted C. album) were weighed with a Pesola field scale.

Analysis

Plant data for H. annuus (number of seed heads per plant, average head diameter, and percent heads infested with moth larvae) and Chenopodium spp. (root biomass, shoot biomass, and total biomass) were analyzed by ANOVA (Sokal and Rohlf 1981). Two-way ANOVAs were used on data from H. annuus of six treatments (it was innappropriate to include the control groups in the two-way ANOVAs in this case, as they were identical in the early and late groups) and the two treatment times (early and late). Two-way ANOVAs were also used on data from Chenopodium spp. of these six treatments and the two treatment times. One-way ANOVAs were used on data from H. annuus and Chenopodium spp. of all seven treatments, for plants treated early and late, to detect differences between treatments. The Tukey-Kramer method (Sokal and Rohlf 1981, p.251) was used to determine differences between means at the 0.05 level.

Linear regressions were used for data on H. annuus, relating number of seed heads (independent variable) to percent heads infested with sunflower moth larvae (dependent variable), and relating average head diameter (independent variable) to percent heads infested (dependent variable). This was done for plants of all seven treatments in each of the four groups (transplanted/early, transplanted/late, natural/early, natural/late). Linear regressions were used for data from most of the natural H. annuus, relating shoot biomass (independent variable) to number of seed heads (dependent variable). This test did not include all of the plants in this group because there was not time to weigh all of them in the field. In order to detect general relationships that may not show up in tests of the small groups of plants of each treatment, tests were also conducted for larger groups of H. annuus. Plants of all treatments were combined, including early and late, for both the transplanted group and the natural group. For both of these groups linear regressions were used to relate number of heads (independent variable) to percent heads infested (dependent variable), average head diameter (independent variable) to percent heads infested (dependent variable), average head diameter (independent variable) to number of seed heads (dependent variable), and shoot biomass (independent variable) to number of seed heads (dependent variable) for most of the natural plants.

Linear regressions were used to relate root mass (independent variable) to shoot mass (dependent variable) for the two Chenopodium species. These tests included data from plants in each of the four main groups. In order to detect general relationships, plants of all treatments were combined, including early and late, for the transplanted group and the natural group. Linear regressions were used to relate root mass (independent variable) to shoot mass (dependent variable) for both of these groups.

RESULTS

Chenopodium album and *Chenopodium berlandieri*

The results of two-way ANOVAs indicated no significant interaction effects of timing of treatment (early/late) and treatment type for both the natural and transplanted *Chenopodium* species. Seperation procedures using values from the one-way ANOVAs revealed virtually no significant treatment effects in total mass (Table 3), shoot mass (Table 4), and root mass (Table 5). There was a great deal of variation in the sizes of both species of plants, so that moderate differences may not be detectable. Because of this variation, it is not conclusive that the *Chenopodium* species were able to fully compensate for lost tissue, even though differences were not detected between plants of each treatment.

Linear regressions revealed a strong relationship between root mass and shoot mass for the natural and transplanted *Chenopodium* spp. (Table 6). Regressions of the same two variables were also done on plants of each individual treatment (both early and late). Virtually all of these tests showed a highly significant relationship, with no obvious differences in regression values between plants of different treatments.

Reproduction in *Helianthus annuus*

Number of Seed Heads

The results of two-way ANOVAs on numbers of seed heads indicated

Table 3. ANOVAs for total mass (*Chenopodium* spp.).

Plant group	df(Among)	df(Within)	F	P
Transplanted/Early	6	271	.95	n.s.
Transplanted/Late	6	275	.26	n.s.
Natural/Early	6	266	1.65	n.s.
Natural/Late	6	261	.99	n.s.

Table 4. ANOVAs for shoot mass (*Chenopodium* spp.).

Plant group	df(Among)	df(Within)	F	P
Transplanted/Early	6	270	1.11	n.s.
Transplanted/Late	6	275	.29	n.s.
Natural/Early	6	266	1.69	n.s.
Natural/Late	6	261	1.01	n.s.

Table 5. ANOVAs for root mass (*Chenopodium* spp.).

Plant group	df(Among)	df(Within)	F	P
Transplanted/Early	6	271	.78	n.s.
Transplanted/Late	6	275	1.23	n.s.
Natural/Early	6	266	1.77	n.s.
Natural/Late	6	261	.80	n.s.

Table 6. Regressions of root mass with shoot mass for transplanted and natural *Chenopodium*. Plants of all treatments have been combined.

Plant group	r	n	p
Natural	.90	541	<<.0005
Transplanted	.89	559	<<.0005

no significant interaction effects of timing of treatment (early/late) and treatment type for both the natural and transplanted H. annuus. One-way ANOVAs for number of seed heads indicated significant differences between treatments in all four plant groups (transplanted/natural X early/late; Table 7). Separation procedures using values from the one-way ANOVAs revealed the location of these differences (Figures 5-8). The control plants (treatment 1) produced the most seed heads in the transplanted plants treated early (Figure 5). The only statistically significant differences in this group were between treatment 1 and 5 and between treatment 1 and 6. Although the mean for treatment 7 is quite low for the transplanted plants treated early (X=21.1), there was an unusually low number of individuals in this group. The seperation procedure, which incorporates the sample size, indicated that the difference between treatment 1 and 7 was marginally insignificant. The control plants produced the most heads in the transplanted plants treated late (Figure 6). Plants of treatment 1 produced significantly more heads than plants of treatments 4, 5, and 7. There were no other significant differences in this group. The control plants produced the most heads in the natural plants treated early (Figure 7). In this case the plants of treatment 1 produced significantly more heads than those of treatments 3, 5, 6, and 7. The control plants again produced the most heads in the natural plants treated late (Figure 8). The plants of treatment 1 produced significantly more heads than those of treatments 5, 6, and 7.

When considering all four of these plant groups (Figures 5-8),

Table 7. ANOVAs for number of seed heads per plant (*H. annuus*).

Plant group	df(Among)	df(Within)	F	P
Transplanted/Early	6	252	3.17	.005
Transplanted/Late	6	301	4.53	<.0005
Natural/Early	6	254	5.13	<.0005
Natural/Late	6	249	2.86	.01

Figure 5. Histogram showing means for number of seed heads per plant for the transplanted _H. annuus_ treated early. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

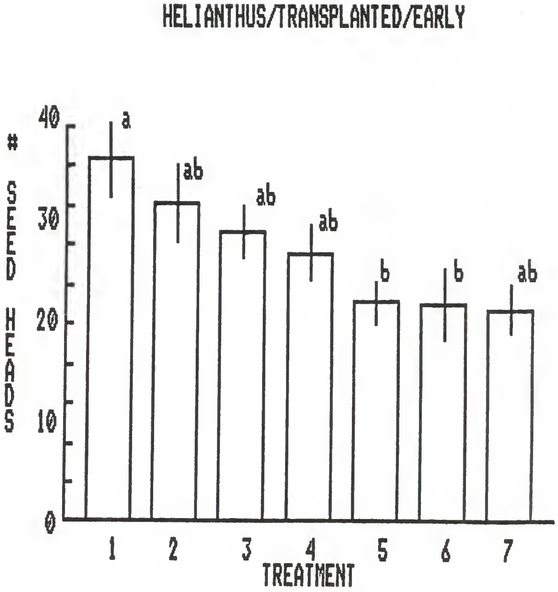

HELIANTHUS/TRANSPLANTED/EARLY
SEED HEADS
40
30
20
10
0
a
ab
ab
ab
b
b
ab
1
2
3
4
5
6
7
TREATMENT

Figure 6. Histogram showing means for number of seed heads per plant for the transplanted *H. annuus* treated late. See text for description of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

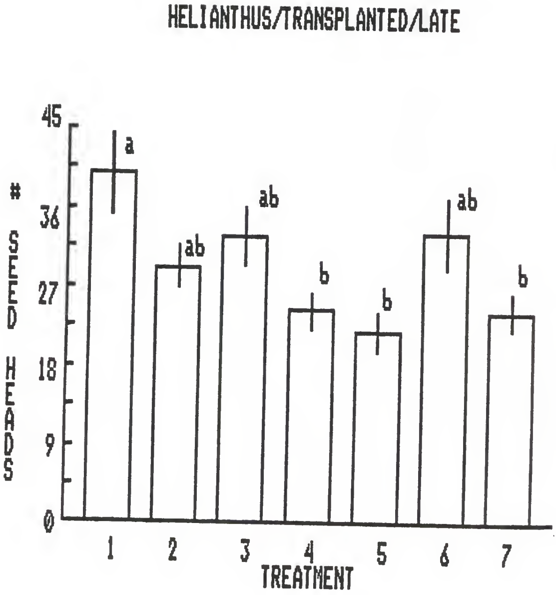

HELIANTHUS/TRANSPLANTED/LATE
SEED HEADS
45
36
27
18
9
0
a
ab
ab
b
b
ab
b
1
2
3
4
5
6
7
TREATMENT

Figure 7. Histogram showing means for number of seed heads per plant for the natural *H. annuus* treated early. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

HELIANTHUS/NATURAL/EARLY

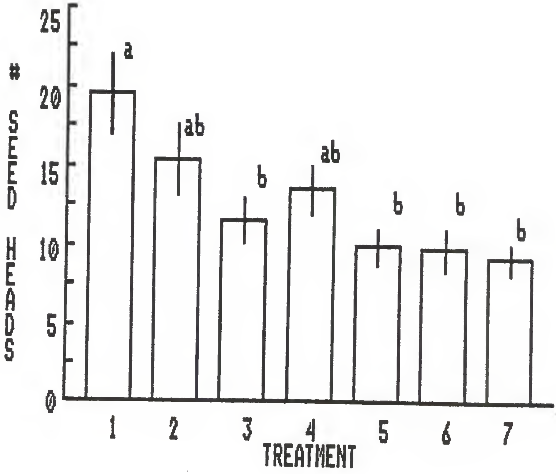
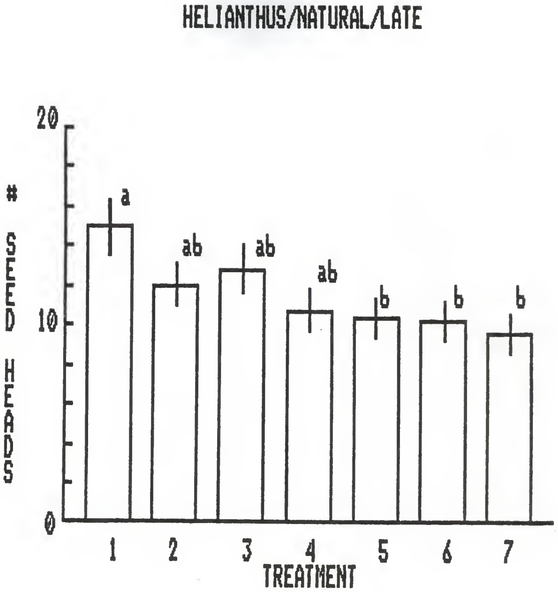


Figure 8. Histogram showing means for number of seed heads per plant for the natural *H. annuus* treated late. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.



HELIANTHUS/NATURAL/LATE
SEED HEADS
20
10
0
a
ab
ab
ab
b
b
b
1
2
3
4
5
6
7
TREATMENT

some consistent patterns emerge. The most striking feature is that, in every case, the control plants (treatment 1) developed more seed heads than plants of any of the defoliation or root-trimming treatments. In nearly every case, plants of treatments 2 and 3 (25% leaves removed) produced more heads than those of treatments 4 and 5 (75% leaves removed). Plants of treatment 6 (roots trimmed) produced relatively few heads in every case except for the transplanted plants treated late. In every case plants of treatment 7 produced the fewest heads.

Overall it is apparent that severity of leaf removal significantly affects the number of flower heads produced. Control plants consistently produced more seed heads than plants experiencing moderate defoliation, which produced more heads than those experiencing relatively heavy defoliation.

The two methods of leaf area removal (removing a portion of entire leaves and removing a proportion of each leaf) did not result in statistically significant differences in seed head production. Although differences are not significant, in all four plant groups plants of treatment 4 (75% of leaf area removed from each leaf) produced more seed heads than those of treatment 5 (75% of leaves removed). This pattern was not as obvious for plants of treatments 2 and 3 (more moderate defoliations); only the two groups treated early show the pattern in which plants with entire leaves removed (25% of leaves removed) produced fewer seed heads than plants with 25% of the area of each leaf removed.

Root trimming, especially in combination with leaf removal, also transplanted plants treated late (Figure 10). Plants of treatment 5 had significantly smaller average head diameters than those of treatments 1-3, and those of treatment 4 were significantly smaller than plants of treatment 3. The early treatments for the natural plants produced no significant differences in average seed head diameter (Figure 11). The late treatments for the natural plants produced differences in average head diameter similar to the late treatments of those that were transplanted (Figure 12). Plants of treatment 5 had significantly smaller average head diameters than those of treatments 1-3, and those of treatment 4 were significantly smaller than plants of treatment 1. In this case, plants of treatments 6 and 7 had significantly smaller average head diameters than those of treatment 1.

Overall it is apparent that severe defoliation significantly affects seed head diameter in H. annuus only when it occurs late in the growing season. All of the early treatments were applied by the middle of July. Late treatments were applied from early to late August, which overlapped significantly with flower head production of the natural plants (Table 2). Flower head production in transplanted plants was well under way in early September. Apparently, severe defoliation had a heavier impact on seed head diameter when it occurred during (or near) the time when plants were actually producing the heads, rather than earlier in the growing season, before flowering began. Less severe defoliation (treatments 2 and 3) had less impact on head diameter.

Treatments involving root removal (treatments 6 and 7), even when

Table 8. ANOVAs for mean diameter of seed heads (*H. annuus*).

Plant group	df(Among)	df(Within)	F	P
Transplanted/Early	6	252	2.62	.025
Transplanted/Late	6	301	4.95	<.0005
Natural/Early	6	254	1.41	.25
Natural/Late	6	249	7.39	<.0005

had a significant effect on the number of seed heads produced. In 3 out of the 4 plant groups (transplanted H. annuus treated late was the exception), plants of treatment 6 had numbers of seed heads at least as low as those of treatments 4 and 5, the more severe defoliations. Therefore root damage alone seems to significantly affect the number of seed heads produced. Root damage in combination with moderate defoliation caused plants to produce even fewer seed heads, although not significantly different from plants of treatment 6.

Average Seed Head Diameter

The results of two-way ANOVAs on average seed head diameter indicated no significant interaction effects of timing of treatment (early/late) and treatment type for both the natural and transplanted H. annuus. One-way ANOVAs for average head diameter indicated significant differences between plants of different treatments in three out of the four plant groups (Table 8). Separation procedures using values from the one-way ANOVAs revealed where these differences occurred (Figures 9-12). Whereas number of seed heads was effected by manipulations both early and late in the growing season, average head diameter was significantly affected only when treatments were applied late in the growing season. The early treatments for the transplanted plants produced no significant differences in average head diameter (Figure 9; in this case the ANOVA indicates marginally significant differences between treatments, but the separation procedure failed to detect where the differences exist). Plants of treatments 4 and 5 had the smallest average head diameter in the

Figure 9. Histogram showing means for average seed head diameter per plant for the transplanted *H. annuus* treated early. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

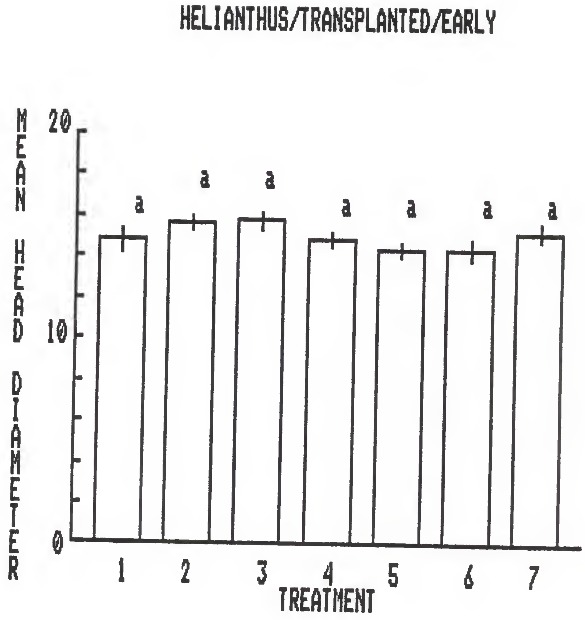

HELIANTHUS/TRANSPLANTED/EARLY
MEAN HEAD DIAMETER
20
10
0
a
a
a
a
a
a
a
1
2
3
4
5
6
7
TREATMENT

Figure 10. Histogram showing means for average seed head diameter per plant for the transplanted H. annuus treated late. See text for descriptions of the treatments the vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

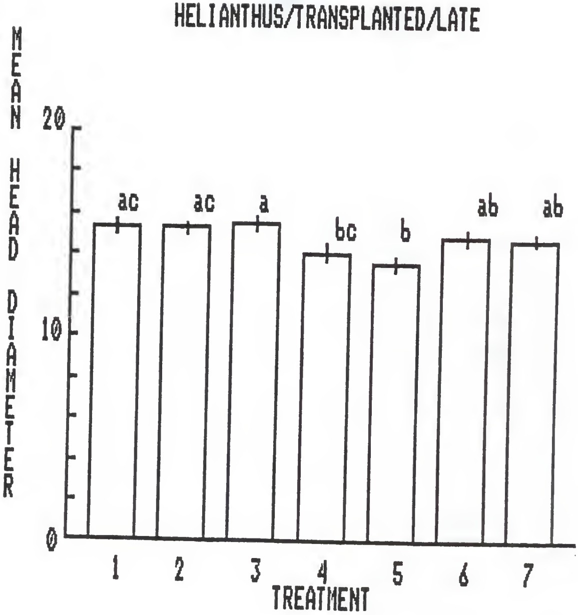

HELIANTHUS/TRANSPLANTED/LATE
MEAN HEAD DIAMETER
20
10
0
ac
ac
a
bc
b
ab
ab
1
2
3
4
5
6
7
TREATMENT

Figure 11. Histograms showing means for average seed head diameter per plant for the natural H. annuus treated early. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

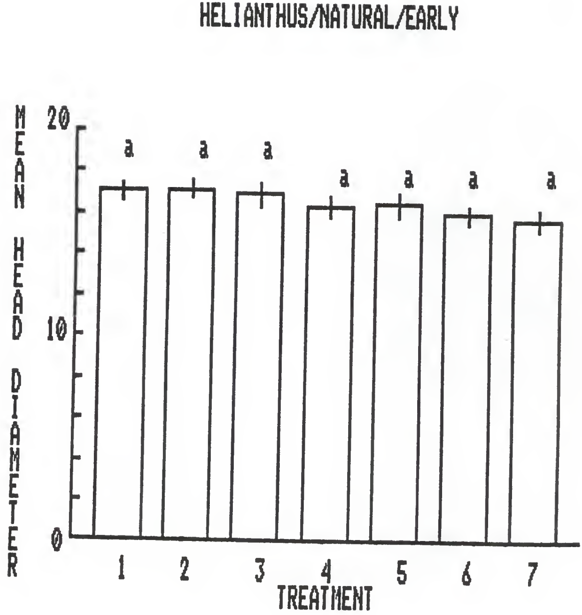
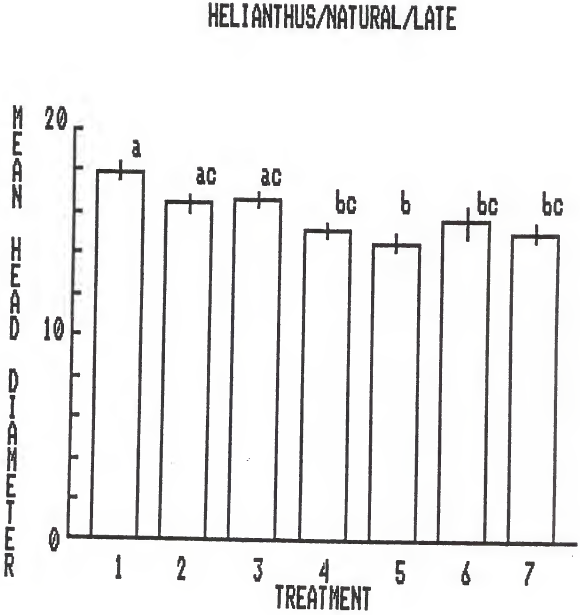

HELIANTHUS/NATURAL/EARLY
MEAN HEAD DIAMETER
20
10
0
a
a
a
a
a
a
a
1
2
3
4
5
6
7
TREATMENT

Figure 12. Histogram showing means for average seed head diameter per plant for the natural *H. annuus* treated late. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.


HELIANTHUS/NATURAL/LATE
MEAN HEAD DIAMETER
20
10
0
a
ac
ac
bc
b
bc
bc
1
2
3
4
5
6
7
TREATMENT

combined with moderate defoliation, had less impact on average head diameter than severe defoliation. This is in contrast to their obvious detrimental affect on number of heads produced.

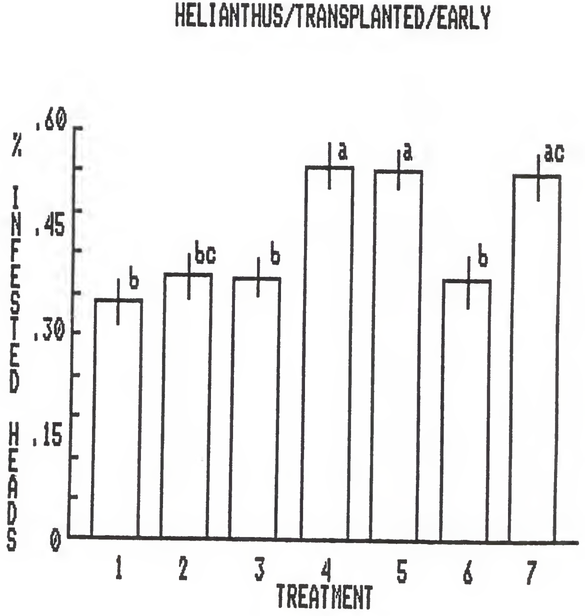
Sunflower Moth Density on Helianthus annuus

The results of two-way ANOVAs on percent of seed heads infested with sunflower moth larvae indicated no significant interaction effects of timing of treatment (early/late) and treatment type for both the natural and transplanted H. annuus. One-way ANOVAs for percent infested heads indicated significant differences between plants of different treatments in all four plant groups (Table 9). Separation procedures using values from the one-way ANOVAs revealed where these differences occurred (Figures 13-16). The effects of various treatments on the proportion of seed heads infested with sunflower moth larvae were particularly striking. The control plants had the lowest mean proportion of infested heads in the transplanted plants treated early, with treatments 2, 3 and 6 only slightly higher (Figure 13). Plants of these four treatments had significantly lower mean proportions of infested heads than those of treatments 4, 5 and 7. The control plants again had the lowest mean proportion of infested heads in the transplanted plants treated late (Figure 14). In this case the plants of treatment 2 had relatively higher mean proportions, as compared to those of treatment 2 in the early treated transplants. The plants of treatments 4, 5 and 7 again had the highest mean proportions of infested heads (Figure 14). Plants of treatments 1 and 2 had the lowest mean proportions of infested heads

Table 9. ANOVAs for percent of seed heads infested with sunflower moth larvae (*H. annuus*).

Plant group	df(Among)	df(Within)	F	P
Transplanted/Early	6	252	8.53	<.0005
Transplanted/Late	6	301	5.24	<.0005
Natural/Early	6	254	3.67	.0025
Natural/Late	6	250	7.86	<.0005

Figure 13. Histogram showing means for proportion of seed heads infested with sunflower moth larvae for the transplanted *H. annuus* treated early. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicated statistically indistinguishable means at the .05 level.



HELIANTHUS/TRANSPLANTED/EARLY
% INFESTED HEADS
.60
.45
.30
.15
0
b
bc
b
a
a
b
ac
1
2
3
4
5
6
7
TREATMENT

Figure 14. Histogram showing means for proportion of seed heads infested with sunflower moth larvae for the transplanted *H. annuus* treated late. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

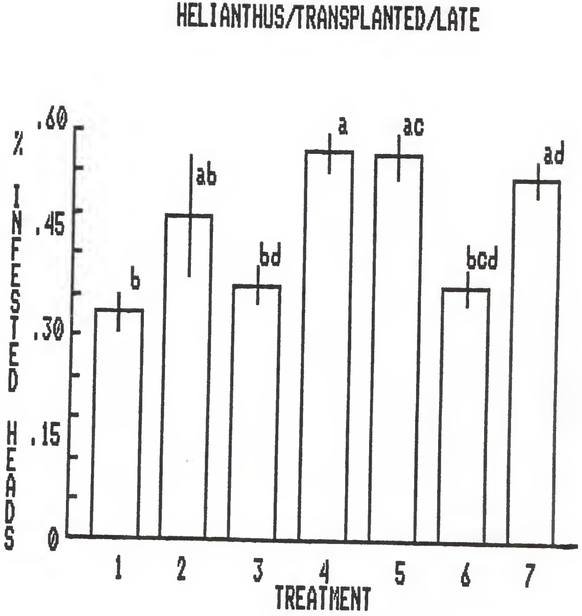

HELIANTHUS/TRANSPLANTED/LATE
% INFESTED HEADS
.60
.45
.30
.15
0
b
ab
bd
a
ac
bcd
ad
1
2
3
4
5
6
7
TREATMENT

Figure 15. Histogram showing means for proportion of seed heads infested with sunflower moth larvae for the natural H. annuus treated early. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.

HELIANTHUS/NATURAL/EARLY

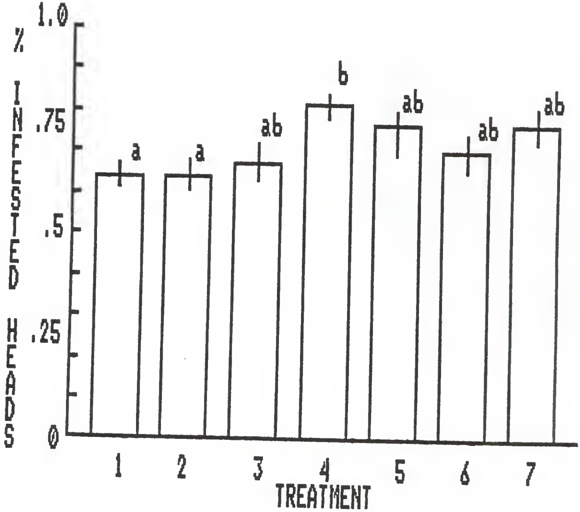
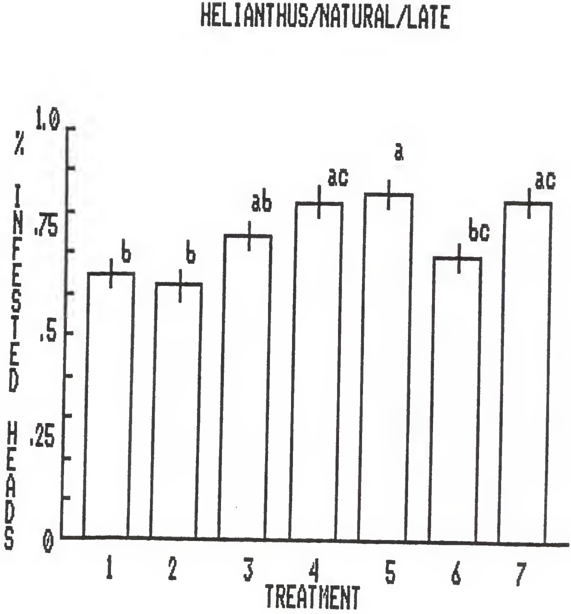


Figure 16. Histogram showing means for proportion of seed heads infested with sunflower moth larvae for the natural *H. annuus* treated late. See text for descriptions of the treatments. The vertical lines represent one standard error on each side of the mean. Shared lower case letters indicate statistically indistinguishable means at the .05 level.


HELIANTHUS/NATURAL/LATE
% INFESTED HEADS
1.0
.75
.5
.25
0
b
b
ab
ac
a
bc
ac
1
2
3
4
5
6
7
TREATMENT

in the natural plants treated early (Figure 15). Although a pattern similar to that of the two plant groups described above is clear in the natural plants treated early, the only statistically significant differences are between treatments 1 and 4 and between treatments 2 and 4. Plants of treatments 1 and 2 again had the lowest mean proportions of infested heads in the natural plants treated late (Figure 16), with plants of treatments 4, 5 and 7 having the highest mean proportions of infested heads.

When considering all four (natural/transplanted X early/late) of these plant groups (Figures 13-16), some consistent patterns emerge. In all four groups the control plants had the lowest incidence of the moth larvae (for the natural plants treated late, plants of treatment 2 had slightly lower infestations than the control plants). Plants of treatments 4 and 5 (severe defoliation) consistently had the highest infestation, with plants of treatment 7 (root and leaf removal) only slighly lower. Those of treatments 2 and 3 (moderate defoliation) and 6 (root removal) showed intermediate levels of infestation. It is clear that the degree of defoliation in some way affected the number of moth larvae inhabiting each plant.

Linear regressions of number of seed heads and percent infested heads revealed very little information when they were done for plants of each treatment (Table 10). Likewise, linear regressions of average seed head diameter andpercent infested heads also revealed very little when they were done for plants of the same small groups (Table 11). These groups of plants of each treatment are not large enough to uncover any obvious patterns. The results of linear

Table 10. Regressions of seed heads (independent) and percent of heads infested with sunflower moth larvae (dependent) for *H. annuus* of each treatment, within each plant group.

Treatment	r	n	p
Natural/Early			
1	-.07	37	>.25
2	.12	39	>.25
3	.09	38	>.25
4	.09	40	>.25
5	.18	38	.25
6	-.002	33	>.25
7	.28	36	.10
Natural/Late			
1	.08	40	>.25
2	.35	40	>.25
3	-.12	39	>.25
4	.27	34	.10
5	.10	35	>.25
6	-.12	37	>.25
7	-.06	31	>.25
Transplanted/Early			
1	.39	29	.05
2	-.19	46	.25
3	.12	35	>.25
4	-.23	45	.10
5	.20	45	.25
6	.04	35	>.25
7	.11	24	>.25
Transplanted/Late			
1	-.02	46	>.25
2	-.22	48	>.25
3	-.09	44	>.25
4	.06	44	>.25
5	-.03	38	>.25
6	-.10	38	>.25
7	-.06	50	>.25

regressions in which plants of all treatments were lumped are, however, quite interesting (Table 12). There was a significant negative relationship between number of seed heads and percent heads infested with sunflower moth larvae in the transplanted plants ($r=-0.12$, $n=567$, $p=.005$), but not in the natural plants ($r=0.01$, $n=517$, $p>.25$). This negative relationship in the transplanted plants is not surprising, since the plant groups that produced the most seed heads were the same groups that had the lowest proportions of infested heads. This negative relationship was not seen in the natural plants, however. In general, there was a higher proportion of infested seed heads in the naturally occurring plants (71.9%) than in the transplanted plants (42.2%). If this represents a true difference in the density of moth larvae between the two sites then this difference may be due to the fact that the natural plants began flowering 2-3 weeks earlier than the transplanted plants, perhaps during a time of peak egg-laying. Cultivated sunflowers blooming before late July stand greater chances of heavy infestations (Higgins 1986). The transplanted plants had considerably more flower heads per plant ($\bar{x}=27.8$) than the natural plants ($\bar{x}=11.9$), however. The total number of larvae per plant in the natural plants, therefore, was not markedly different from the transplanted plants. Nevertheless, the significant negative relationship of number of heads with percent infested heads for the transplanted plants suggests that, in a situation where there is a higher proportion of uninfested heads, female moths selectively oviposit on (or more larvae survive on) plants with fewer heads over plants with more

Table 11. Regressions of average seed head diameter (independent) and percent heads infested with moth larvae (dependent) for *H. annuus* of each treatment, within each plant group.

Treatment	r	n	p
Natural/Early			
1	.55	37	.0005
2	.37	39	.025
3	.12	38	>.25
4	.27	40	.10
5	.35	38	.025
6	.26	33	.10
7	.51	36	.001
Natural/Late			
1	.19	40	.25
2	.19	40	.25
3	-.14	39	>.25
4	-.02	34	>.25
5	.25	35	.10
6	.20	37	.25
7	.005	31	>.25
Transplanted/Early			
1	.15	29	>.25
2	.13	46	>.25
3	.17	35	>.25
4	-.15	45	>.25
5	.51	45	.0005
6	.44	35	.01
7	.19	24	>.25
Transplanted/Late			
1	.48	46	.0005
2	-.05	48	>.25
3	.25	44	.10
4	.25	44	.25
5	.19	38	.25
6	.17	38	.25
7	.06	50	>.25

Table 12. Regressions of number of seed heads with percent infested heads and average head diameter with percent infested heads of *H. annuus*. Plants of all treatments are combined.

Independent/Dependent	r	n	p
Natural			
heads/% infested	.01	517	>.25
avg. diam./% infested	.13	517	.005
Transplanted			
heads/% infested	-.12	567	.005
avg. diam./% infested	.10	567	.10

heads.

There was a significant positive relationship between average head diameter and percent infested heads for the natural plants ($r=0.13$, $n=517$, $p=.005$). Although it might be expected that female moths would selectively oviposit on (or more larvae survive on) heads of larger diameter, this finding is somewhat surprising, since those plant groups with larger head diameters were the same groups with lower proportions of heads infested with larvae. The only plant groups that showed significant differences in average head diameter, however, were those treated late (Figures 10 and 12). Table 11 reveals that only the early treatments show a significant positive relationship between head diameter and percent heads infested with larvae (this cannot be determined from Table 12 because these regressions combine plants treated early and late). This may explain why there was a positive relationship between average head diameter and percent of heads infested with larvae for the natural plants. This relationship of average head diameter and percent infested heads was marginally insignificant for the transplanted plants ($r=0.10$, $n=567$, $p=.10$). It is clear that moths either selected heads of larger diameter for egg-laying, or more larvae survived on these heads, at least on the natural plants treated early. Regressions were carried out on plants of all treatments in the natural group and in the transplanted group, comparing number of heads per plant to average head diameter. A significant positive relationship was found for the natural plants ($r=0.13$, $n=514$, $p=.005$) and the transplanted plants ($r=0.12$, $n=564$, $p=.005$).

DISCUSSION

What little information is available on the influence of leaf and root removal on plant success suggests that several primary factors may determine how plants respond to damage. The severity of leaf area removal may determine whether biomass and seed production decrease, increase or remain unchanged (Sackston 1959; Stickler and Pauli 1961; Lowman 1982). Different specific patterns of leaf area removal may have varying effects on biomass and seed production (Stickler and Pauli 1961; Lowman 1982). The timing of defoliation, relative to flowering time, may determine the severity of decrease in seed production (Mortimer and Ahlgren 1936; Kittock 1967; Mueggler 1967). Also, plants that are grown in controlled, agriculture-like conditions may respond differently to damage, as compared to those growing in a more natural community (Lee and Bazzaz 1980; Belsky 1986). The results of this study elucidate the relative importance of these factors to the seed head production of Helianthus annuus and biomass production of Chenopodium album and Chenopodium berlandieri. These data also suggest certain relationships between root and leaf removal of H. annuus and levels of a seed eating insect, the sunflower moth, Homoeosoma electellum (Hulst.).

Biomass Production

The fact that there were no significant differences in biomass between the various treatments of Chenopodium spp. suggests that the two species of Chenopodium may be able to at least partially compensate for the damage. Often, when only shoots are measured, there is a potential for overestimation of biomass because shoot damage is known to increase shoot growth at the expense of root growth (Branson 1956; Richards 1984). Since both above- and below-ground plant parts were weighed in the present study, there is no chance of overestimation of the mass of damaged plants due to reallocation of resources from the root to the shoot. The findings of this study support the idea that some plants can compensate in biomass production following damage. There is substantial evidence that some species of dicots compensate partially or exactly for lost tissues (Bazzaz 1980; Solomon 1983). Although some studies report overcompensation in biomass production following herbivory, the majority of cases in the literature suggest that plants do not respond with a net gain in biomass following herbivore attack.

The two Chenopodium species showed no significant reductions in total biomass, regardless of the severity of defoliation and timing of defoliation. Apparently, species of the genus Chenopodium are able to tolerate a wide variety of types of damage without any appreciable decrease in final total biomass. Due to high variation in plant size however, these results are not entirely conclusive.

Seed Production

Regressions indicated that amount of reproductive tissue produced is strongly correlated with total biomass in Chenopodium spp. The fact that there were no significant differences in mean biomass between plants of different treatments therefore, may suggest that these plants are able to tolerate severe tissue loss with no appreciable decrease in seed production. Due again to high variation in plant size, however, this is not conclusive.

Both measures of seed production in H. annuus (number of seed heads and head diameter) decreased significantly following simulated herbivory. Measuring offspring production is a reasonable measure of plant fitness. Since seed production was significantly reduced in H. annuus, the hypothesis that some forms of herbivory decrease plant fitness is supported.

There appeared to be no appreciable difference between the effects of the early treatments and effects of the late treatments on seed head production. Data on average seed head diameter, however, show different effects between the early and late treatments. There was no significant reductions in seed head diameter in the plants treated early, while those treated late, at the time of flowering, did show significant reductions in seed head diameter, particularly with 75% defoliation. There is substantial evidence that the timing of herbivore damage may be important in determining the extent of recovery of plants. Mueggler (1967) found that native vegetation, composed of a mixture of grasses and forbs in Montana, were most harmed by clipping during the period from flower stalk formation to seed ripening, which was probably too late in the season to allow regrowth prior to the period of carbohydrate storage. Production of herbage and flower stalks were compared (Mueggler 1967). Using several levels of defoliation of cultivated sunflowers, Sackston (1959) found that seed yield decreased more following defoliation at flowering than defoliation of seedlings or maturing plants. Similar results have been found with soybeans (Thomas et al. 1974) and castorbeans (Kittock and Williams 1967).

It is worth noting that the two methods of leaf area removal (removing a portion of entire leaves and removing a portion of each leaf) did not result in statistically significant differences in seed head production. Sackston (1959) found that cultivated sunflowers (H. annuus) had lower seed yields when all leaves were removed from the upper half of the stem than when 50% of each leaf was removed along the midrib. The plants with the highest seed yields, however, were those from which all leaves were removed from the lower half of the stem. This was probably due to the fact that leaves in the top half of the plant are younger, and therefore more productive, than those in the lower part of the plant. Stickler and Pauli (1961) found removal of alternate leaves to be more deleterious to seed yield than removing half of each leaf in grain sorghum. Additionally, Lowman (1982) found that rainforest seedlings of coachwood (Ceratopetalum apetalum) with all leaves partially clipped recovered more successfully than those with some leaves completely removed. Although differences are not significant, in all four plant groups (transplanted/natural X early/late) of the present study, plants of treatment 4 (75% of leaf area removed from each leaf) produced more seed heads than those of treatment 5 (75% of leaves removed). The increased impact of removing entire leaves, rather than area from each leaf, is consistent with Stickler and Pauli (1961) and Lowman (1982). This pattern was not as obvious for plants of treatments 2 and 3 (more moderate defoliations); only the two groups treated early show the pattern in which plants with entire leaves removed (25% of leaves removed) produced fewer seed heads than plants with 25% of the area of each leaf removed.

In the present study plants were treated in a natural setting and in a more controlled, agricultural-like plot. There were no apparent differences, however, in the way that the plants responded to damage. Therefore, it remains to be shown that a particular species of plant responds differently to herbivory under these two types of conditions. Overcompensation in reproductive output, although rare, is usually reported for plants in controlled laboratory or agricultural conditions. It is possible that factors such as competition and resource availability would limit the chances of overcompensation in natural communities.

The treatments involving root removal caused significant reductions in number of seed heads and, in at least one plant group, average head diameter. There is very little information in the literature on the effects of root damage on seed production. Totsuka et al. (1960) reported that, following removal of 21% total dry weight of the root system, cultivated sunflowers produced less flower biomass (0.9 g/plant; 0.65% of total plant biomass) than control plants (1.6 g/plant; 0.73% of total plant biomass). That particular study was designed to measure growth and the plants were harvested before they were mature, so it is not a reliable estimate of the total number of seeds produced. The present study, therefore, is important in showing that root damage can significantly decrease the number of seeds produced by plants.

It is thought that water stress causes an increase in the amount of free amino acids (and hence nitrogen) mobilized and translocated to the plant tissues. Increased flowering and seed production, as a result of this nitrogen mobilization to reproductive tissue, are commonly recorded following drought (see review by White 1984). Conceivably, the root trimming treatments of the present study would produce this type of drought stress (wilting was evident following the treatments), but the _H. annuus_ experiencing root removal did not produce more seeds. In fact, seed production was somewhat lower in most plant groups. This study, therefore, does not support the hypothesis that drought stress triggers increased production of flowers and seeds.

Treatment Effects on Sunflower Moth Density

It is clear that the degree of defoliation in some way affected the number of moth larvae inhabiting each plant. This could have occurred in one or both of two ways. The first is that female sunflower moths selectively oviposited in the florets of plants of certain treatments (presumably those which had the highest proportions of infested heads; treatments 4, 5, and 7). The second possibility is that females were not selective, but differential mortality of the larvae occurred between various treatments. Adult sunflower moths prefer plants in the early stages of flowering for egg-laying. Nearly 80% of the eggs are deposited on a plant within 4 to 7 days after the flower bud begins to open (Higgins 1986). In the present study nearly all of the treatments, including the late ones, were applied before the majority of the buds opened. Since both egg-laying and larval development took place after treatments were applied, it is not possible to determine whether differential egg-laying or differential larval mortality explain the results in question.

Densities of sunflower moth larvae were higher in H. annuus experiencing heavy defoliation and root damage (when combined with moderate defoliation). This is in agreement with a number of studies reporting that herbivores of many plants increase in number following plant damage or stress. Various types of herbivory and clipping are known to increase the density of below-ground consumers, such as nematodes and white grubs (Hutchinson and King 1980; Smolik and Dodd 1983; Stanton 1983; Ingham and Detling 1984; and see review by Seastedt 1985). Above-ground herbivores are also known to increase following plant damage. Lewis (1979) found that grasshoppers feeding on sunflower plants which had experienced previous insect damage, or were wilted, had greater survival, growth rate and fecundity than grasshoppers feeding on undamaged plants. Williams and Myers (1984) found that fall webworm larvae raised on foliage from trees which had been attacked previously by tent caterpillars grew faster and attained heavier pupal weights than those raised on unattacked trees.

Several possible explanations have been proposed to explain the phenomenon of increased herbivores following plant damage or stress. First, the carbon-to-nitrogen ratio of below-ground tissue usually decreases following defoliation, due to a decrease in carbohydrate reserves but an unchanged amount of nitrogen (Ruess et al. 1983; Seastedt 1985). This increase in the relative amount of nitrogen is thought to provide a higher quality food source for below-ground herbivores, and therefore may cause an increase in herbivore density. Second, as with senescing plant tissue, plant tissue experiencing stress contains a larger amount of soluble nitrogen (amino acids), which is being mobilized away from the stressed or senescing tissue (Hagland 1980; and see review by White 1984). Herbivores feeding on this stressed or senescing tissue, as well as tissue receiving the mobilized nitrogen, will have a more readily available source of nitrogen in their food. Again, this higher quality food source may cause an increase in herbivore density. Hagland (1980) found that grasshoppers detect and preferentially feed on grasses treated with the amino acids proline and valine, which are known to increase in plants under stress. This suggests that some herbivores may preferentially feed on plants that have experienced damage. This may explain the higher levels of sunflower moth larvae on the plants experiencing heavy defoliation in the present study.

Another possible explanation for the increase of moth larvae on the seed heads of the heavily defoliated plants is that production of defense chemicals was curtailed. It is likely that, in defoliated plants, the transport of carbohydrates to roots, flowers, and other tissues is reduced. This could stop the production of carbon-based defense chemicals in these tissues (Chew and Rodman 1979; Ingham and Detling 1984). It has been reported that damage by herbivores may cause increased levels of secondary defense chemicals (e.g. Carroll and Hoffman 1980; Schultz and Baldwin 1982; and see reviews by Edwards and Wratten 1985 and Rhoades 1985). None of the treatments of the present study, however, caused a decrease in moth larvae below the level of the control plants. This study therefore does not support the hypothesis that plants increase production of defense chemicals following damage.

Conclusion

In some respects this study is similar to a number of others looking at the effects of tissue removal on plant success. Reports of the effects of tissue removal on plant biomass are abundant. There are fewer studies looking at effects on reproductive success. In general, the results of this study agree with others of this nature: that tissue damage decreases plant success. But it is unique in several respects. Much of the research on effects of tissue damage on seed production include only crop species, and many others examine grasses. This is one of few studies using noncrop annual dicots. It is perhaps the first to consider one species in both cultivated and natural conditions. There have been very few studies that investigated the effects of root removal (particularly in combination with leaf removal) on seed production.

Complete understanding of plant responses to herbivory will require a great deal more research comparing plants under natural conditions to those in laboratory or cultivated conditions. Do plants growing in controlled conditions respond to herbivory in a relevant way? The relationship between natural and artificial herbivory must also be ascertained. The effects of herbivory are no doubt crucial to our understanding of plant-animal interactions, but these effects vary with timing of damage, intensity of damage, pattern of tissue removal, environmental conditions, nutrient and water availability, presence or absence of competitors, and previous damage to the plant. These factors must be thoroughly and carefully investigated.

This study is also unique in reporting increases in insect herbivore densities following tissue damage. It is one of few studies reporting insect densities following defoliation of several intensities, and among the first to report increased above-ground herbivores following root removal. Also, this is the first report of herbivore responses on a single species of plant in both natural and more controlled conditions.

Whether increased densities of sunflower moth larvae on _H. annuus_ is due to differential egg-laying or differential larval survival remains to be demonstrated. Whether defoliation increases the quality of the seed heads of _H. annuus_ for moth larvae by increasing available nitrogen or by decreasing levels of secondary compounds also remains to be demonstrated. It is evident that defoliation may play an important role in determining susceptability of plants to other types of herbivory, but the factors involved are no doubt extremely complex and will require careful investigation.

This research should provide information contributing to our understanding of plant-animal interactions and direction for future studies of the effects of herbivory on the growth, reproduction, and subsequent damage of plants.

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EFFECTS OF SIMULATED FOLIAGE AND ROOT HERBIVORY ON GROWTH, REPRODUCTION, AND INSECT DAMAGE OF THREE ANNUAL PLANT SPECIES

by

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B.S., Kansas State University, 1983

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1987

A wide variety of plant responses have been attributed to defoliation by herbivores. Documented responses range from significant decreases in growth and seed production to significant increases. Most studies suggest that tissue removal decreases plant success but a few suggest that, in certain situations, plants may benefit from some types of damage.

Simulated herbivory experiments were conducted on three annual plant species at Konza Prairie Research Natural Area, Manhattan, Kansas, during the spring and summer of 1985. The experiments investigated the effects of partial root removal and several levels of defoliation on seed production of Helianthus annuus, and total biomass of the two annuals Chenopodium berlandieri and C. album. Of the plants being modified, half were treated early in the growing season and half later in the growing season.

The defoliation and root removal treatments did not cause any differences in biomass of the two Chenopodium species, but did cause significant differences in number of seed heads produced by H. annuus. The general pattern for average number of seed heads per plant for plants of different treatments (from most to least) was as follows: controls (unmanipulated); 25% defoliation; 75% defoliation; roots trimmed; roots trimmed and 25% defoliation. Although this was the observed pattern, the only statistically significant differences were between controls and the last three treatments in the above sequence. The treatments also caused significant differences in average seed head diameter, but only when they were applied late in the growing season. The most obvious pattern was that plants with 75% defoliation had lower average seed head diameters than plants of all other treatments.

An additional finding was that significant differences in the proportions of sunflower moth larvae (an insect that feeds on the developing seeds) occurred among plants of different treatments. The general pattern for proportion of seed heads infested with moth larvae was as follows: root trimmed plus 25% defoliated plants and 75% defoliated plants had the greatest proportion of infested heads, and root trimmed plants and 25% defoliated plants had greater proportions than controls (unmanipulated).

The significant reductions in number of seed heads and average seed head diameter of H. annuus following simulated herbivory suggests that herbivores may play an important role in determining the success of annual plants. Further research into the effects of tissue removal on plants under various ecological conditions may help us to better understand the interrelationships of plants and their herbivores.