Oecologia (1991) 88:243–250

Oecologia

Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp

P.A. Fay and D.C. Hartnett

Division of Biology, Ackert Hall, Kansas State University, Manhattan, KS 66506, USA

Received January 7, 1991 / Accepted in revised form May 30, 1991

Summary. Insect herbivory can have important effects on plant life histories and architecture. We quantified the impact that a cynipid gall wasp, *Antistrophus silphii,* had on growth, reproduction, and biomass allocation patterns of *Silphium integrifolium* growing in the tallgrass prairie of northeastern Kansas. Experimentally galled individual *Silphium* shoots (ramets) had reduced shoot growth, leaf and flower head production, and delayed flowering compared to gall-free control shoots. Gall formation completely halted normal apical growth in 65% of the shoots. Galling did not affect individual flower head weight, the numbers of achenes per flower head or achene weight. *Silphium* plants (genets) with a high proportion of galled shoots had lower total biomass, a lower proportion of total biomass allocated to flower heads, higher allocation to leaves, but no change in allocation to stems or rhizome. High gall densities reduced the number of flower heads per plant and shortened the time between flower head initiation and maturity. An adaptive interpretation of these results would be that the survivorship and future performance of galled *Silphium* may be promoted by maintaining allocation to rhizome. However, reduced shoot growth and delayed reproduction in galled *Silphium* may weaken its competitive ability and reduce pollination success, so that any adaptive advantage to *Silphium's* allocation responses to galls may be outweighed by disadvantages from its growth and flowering phenology responses. We conclude that a more parsimonious interpretation of these results is that gall-induced allocation changes are due to architectural constraints placed by galls on meristem activity, rather than to any adaptive response on the part of the plant.

Key words: Life history – Allocation – Gall insect – *Silphium integrifolium* – Plant insect interactions

To understand the selective role of herbivory on plants and the adaptive value of plant responses to herbivory it is necessary to understand the nature of the impact of herbivore damage on the plant. Numerous studies have documented how insect herbivory can significantly affect the survivorship, growth and reproduction of plants (Harper 1977; Crawley 1983, 1988). Insect feeding can reduce plant growth rates (Rausher and Feeny 1980; Kinsman and Platt 1984), alter plant growth form (Whitham and Mopper 1985; Craig et al. 1986), or exacerbate the effects of shading (Dirzo 1984) or other stresses. Plant fecundity is often reduced by insect damage (Dennill 1988; Marquis 1984; Fedde 1973; Kinsman and Platt 1984; Sacchi et al. 1988), especially when the damage occurs directly to reproductive structures (Schowalter and Haverty 1989). Insect damage can also affect fecundity indirectly if the feeding disrupts a plant's synchrony with its pollinators by altering the timing or duration of flowering (Jennersten et al. 1988).

Relatively few studies have documented the effects of insect damage on plant resource allocation patterns. Knowledge of allocation patterns is particularly important for understanding the impact of herbivory on perennial plant species, which store a proportion of their resources for future growth. Resource allocation patterns are the result of the physiological interactions of carbon sources and sinks in the plant. Herbivores remove carbon sources by removing leaf area (Caldwell et al. 1981), and carbon sinks are removed when herbivores damage or remove meristems or flower buds (Weis and Kapelinski 1984). New sinks are added when herbivores feed directly on phloem sap (Puritch and Talmon De L'Armee 1971) or induce galls (Hartnett and Abrahamson 1979). Carbon sinks and sources are connected by the plant's vascular system, and herbivores are capable of disrupting this connection (McCrea et al. 1985).

Interpretations of the adaptive value of plant allocation responses to herbivores are difficult, because potential adaptive advantages of plant responses to the herbivore may be countered by disadvantages of those plant responses. Furthermore, since herbivory disrupts the sink-vascular system-source continuum, growth and allocation effects which could be interpreted as adaptive plant responses (Antonovics 1980) to insect herbivory may instead be the results of phylogenetic or architec-

Offprint requests to: P.A. Fay

tural restrictions on allocation imposed by the removal of leaves, vascular tissue, apical meristems, or other parts (Watson and Casper 1984).

In this paper we examine the impacts of herbivory on the life history and architecture of a perennial tallgrass prairie forb *Silphium integrifolium,* wholeleaf rosinweed. Specifically, we quantified the impact of a gall forming cynipid wasp, *Antistrophus silphii,* on *Silphium* growth, flower head and achene production, flowering phenology, and biomass allocation patterns. Gall insects are particularly appropriate herbivores for studying impacts of herbivory on plant growth and allocation patterns. Gall abundance on the plant is easily quantified, there is little variation in the timing of attack, attack is restricted to meristematically active tissues, damage occurs in the form of a discrete abnormal growth on the plant, and the gall persists on the plant and is capable of affecting plant growth for the duration of the growing season.

Study organisms

This study was conducted during the 1988 growing season in an annually burned old field on the Konza Prairie Research Natural Area, a 3,487 ha preserve near Manhattan in the Flint Hills region of northeastern Kansas (39°05′ N, 96°35′ W). The site is owned by the Nature Conservancy and is managed for ecological research by the Division of Biology, Kansas State University.

Silphium integrifolium var. laeve T. and G. (= *Silphium speciosum* Nutt. Rydberg) (Asteraceae) is a perennial forb of the tallgrass prairie, where it generally occupies relatively moist deep soil. A *Silphium* plant (= genet) consists of from a few up to about 100 shoots (= ramets) which form a relatively tightly packed clump. *Silphium* shoot growth begins in spring from buds initiated the previous year belowground on a compact, woody, branching rhizome. One to three shoots may arise from one branch of the rhizome. The extent of physiological integration among these shoots is unknown. Shoots reach 1–2 m tall and consist of a single apical meristem and 15–25 pairs of opposite leaves. Flowering occurs from July to October. Each shoot produces a terminal inflorescence of 1–15 flower heads (capitula). Fertile achenes are produced on the ray florets. Disk florets are functionally male. Mature achenes dehisce from the flower head starting in August. All aboveground parts die back by the end of October, and are completely replaced the following year.

The most abundant insect herbivore on *Silphium* is the gall wasp *Antistrophus silphii* Gil. (Hymenoptera:Cynipidae). *Antistrophus* oviposits into a shoot's apical meristem, and forms a spherical gall 1–4 cm in diameter. Gall tissue often completely inhibits further normal meristematic activity, halting further shoot growth, leaf production, and flowering. *Antistrophus* gall wasps are very abundant at our study sites on Konza Prairie. On average 36.87 ± 0.02% of *Silphium* shoots were galled over the last 3 years. Gall frequencies on individual plants range from 0 to 100%. In addition to *Antistrophus, Silphium* experiences lower levels of damage from several other herbivores. White-tail deer *(Oedicoleus virginianus)* browse shoots, and blister beetles *(Epicauta fabricius)* feed on foliage. Flower heads are attacked by an unidentified galler which attacks the disk florets, and an unidentified Lepidopteran larva damages approximately 17% of *Silphium* achene production. Damage by these herbivores does not appear to be affected by the presence of *Antistrophus* (Fay and Hartnett, unpublished).

Antistrophus' life cycle is synchronized with the phenology of its host plant. In early May, when *Silphium* shoots are beginning to elongate, adults emerge from previous year's galls. Females mate, locate a shoot, and oviposit. Within 2 weeks, the shoot's height growth slows and the apical meristem begins to swell. Gall formation is complete by early June. Up to 30 larvae feed within the gall, developing to their final larval instar (III) before *Silphium* goes dormant in October. Larvae overwinter in the gall, then pupate in April. Gall wasp larvae are parasitized by two Eurytomid parasitoids (E.E. Grissell, pers. comm.)

Methods

1. Shoot (ramet) responses to galls

The first part of the study focused on the ramet level by determining individual shoot responses to galls. Six shoots were randomly chosen to be galled in each of 8 separate *Silphium* plants. Six more shoots from the same 8 plants, matched for size with the first six, were chosen from throughout the plant to be gall-free controls. Then shoots were experimentally galled to determine the effects of galls on *Silphium* shoot growth, leaf production, and flowering phenology. This design prevented plant genotype or initial shoot size from being confounded with effects of galls on shoot growth.

Galls were induced by enclosing a female *Antistrophus* over the shoot's apical meristem using a cheesecloth bag closed around the shoot with string. Female wasps were obtained by capturing them from other *Silphium* on the site, and placing them in vials which were secured within the cheesecloth bag. Wasps were enclosed on shoots 2 days after they had appeared on the study site, and wasps were kept on shoots for 1 day.

Growth, leaf production, and flowering phenology were measured eight times at 1- to 2-week intervals during the growing season. Shoot growth was quantified by measuring gall diameters and shoot height. A demographic analysis of leaf production was done by marking individual leaves, recording new leaf production and leaf abscission, and calculating the number of live leaves on each shoot at each sampling date. Flowering phenology was determined at each sampling date by recording the number of flower heads on each shoot which were 1) in the bud stage (unopened), 2) flowering, 3) fertilized, or 4) ready to dehisce achenes. Only healthy flower heads not damaged by insects or aborted by the plant were counted.

The effect of galls on shoot achene production and weight was determined using 1–4 flower heads collected from galled and gall-free shoots at achene dehiscal. Intact flower heads were collected from 5 of the 6 galled shoots which flowered, and from all 15 gall-free shoots which flowered. Flower heads were weighed after equilibration to ambient laboratory conditions, the numbers of achenes were counted, and subsamples of up to 100 achenes per shoot were weighed.

This experiment used a repeated-measures design. The whole plant ($n = 8$) was a blocking factor, the shoot ($n = 48$ galled and 48 control) was the experimental unit for galling, and measurements

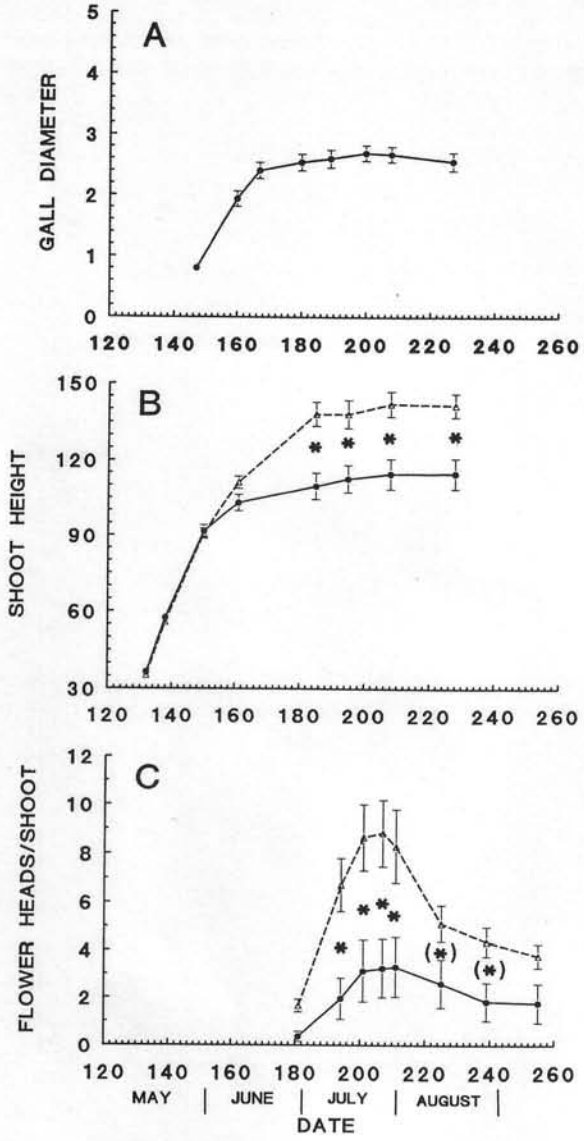

Fig. 1A–C. Mean responses ± 1 SE of galled (———) and gall-free (- - - - -) *Silphium integrifolium* shoots to *Antistrophus silphii* galls. **A** Mean gall diameters (cm) on galled shoots. **B** Mean shoot height (cm) of *Silphium* shoots. $F_{galling} = 8.84$, $p < 0.006$. $F_{date} = 438.49$, $p < 0.0001$. $F_{galling \times date} = 17.40$, $p < 0.0001$. For means comparisons across levels of galling, LSD's at 0.05, 0.01, and 0.001 probabilities are 6.74, 8.88, and 11.40. **C** Mean number of flower heads per shoot. $F_{galling} = 8.27$, $p < 0.007$. $F_{date} = 25.81$, $p < 0.0001$. $F_{galling \times date} = 6.12$, $p < 0.0001$. LSD's at 0.05, 0.01, and 0.001 probabilities are 2.89, 3.87, and 5.14. (*) = significant at 0.01, * = significant at 0.001. Degrees of freedom for B–C are: $F_{galling}$ 1,32; F_{date} and $F_{galling \times date}$ 7,224

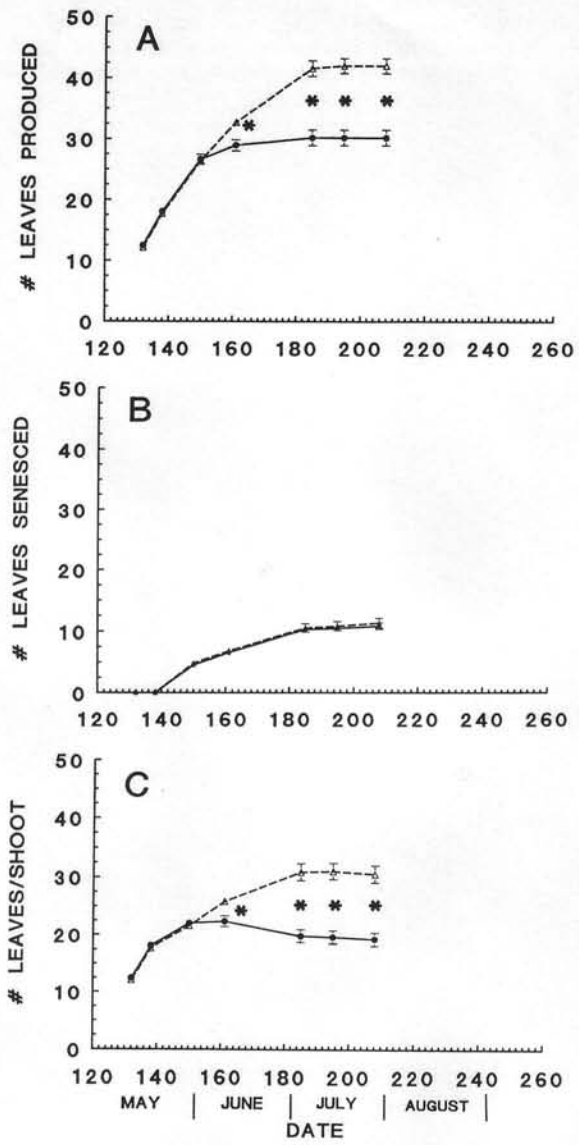

Fig. 2A–C. Mean leaf production ± 1 SE on galled and gall-free *Silphium* shoots. All symbols as in Fig. 1. **A** Number of new leaves produced per shoot. $F_{galling} = 20.62$, $p < 0.0001$. $F_{date} = 669.56$, $p < 0.0001$. $F_{galling \times date} = 65.77$, $p < 0.0001$. LSD's at 0.05, 0.01, and 0.001 probabilities are 2.77, 3.71, and 4.87. **B** Mean number of leaves senesced per shoot. $F_{galling} = 0.25$, $p < 0.6233$. $F_{date} = 463.84$, $p < 0.0001$. $F_{galling \times date} = 0.15$, $p < 0.9880$. **C)** Mean number of live leaves per shoot, = # produced – # senesced. $F_{galling} = 20.06$, $p < 0.0001$. $F_{date} = 140.98$, $p < 0.0001$. $F_{galling \times date} = 49.52$, $p < 0.0001$. LSD's at 0.05, 0.01, and 0.001 probabilities are 2.80, 3.74, and 4.91. Degrees of freedom for A–C are: $F_{galling}$ 1,32; F_{date} and $F_{galling \times date}$ 6,192

of growth and reproduction of the shoots on successive dates were the repeated measures. Control shoots were naturally galled in 20 pairs of shoots, and treated shoots failed to gall in 11 pairs, leaving 17 out of the original 48 pairs where treated shoots had galls and control shoots remained gall-free. The 17 usable pairs were unevenly distributed among 7 of the 8 plants, so the blocking factor was omitted from the analysis. The data were then treated as a split plot, with galling as the whole plot factor and date of measurement as the subplot factor. Means comparisons between galled and ungalled stems on particular measurement dates were made using least significant differences calculated at the 0.05, 0.01 and 0.001 levels. This design was not balanced for the flowering phenology measurements because not all stems flowered, so a modified split plot procedure described in Milliken and Johnson (1984) was used for these F-tests and means comparisons. End of season flower head weights, numbers of achenes per flower head, and achene weights were compared using two-sample *t*-tests.

2. Whole-plant (genet) responses to galls

The second part of the study focused on the genet level by examining whole-plant responses to cynipid galls. We measured total biomass production, proportional biomass allocation, and several

reproductive characteristics of 10 naturally-infested, heavily galled plants and 10 lightly galled plants. These plants were chosen to represent extremes on the continuum of gall density.

We made periodic measurements of the effects of galls on *Silphium* flower head production, weights, and maturation rates. At 5- to 7-day intervals during the flowering period we marked all flower heads produced and recorded the dates of flowering and subsequent achene maturation. At maturation flower heads were collected and weighed after equilibration to laboratory conditions. From these data we determined for each sampling date the weight of mature flower heads, the number of days from flowering to achene maturity, and the cumulative number of flower heads produced per plant.

We harvested the remaining aboveground plant parts when they senesced. Senesced leaves and stems were collected every week to 10 d. Rhizomes and any remaining leaves and stems were collected in early November after the plants had become dormant. Roots are too deep to be adequately retrieved in naturally occurring plants, so they were not collected. Galls were separated from stems and weighed after equilibration to laboratory conditions. Stems, leaves and rhizomes were weighed after oven-drying at 70° C for 48 h.

Biomass allocation patterns were determined for each galled and gall-free plant from the cumulative weights of all flower heads, leaves, galls, stems, and rhizome. Means were compared using two-sample *t*-tests. Because the effects of plant size on plant reproductive output could be confounded with the effects of herbivory on plant reproductive output if herbivory reduces plant size (Samson and Werk 1986), we also performed a covariance analysis of the effects of galls on individual plant flower head biomass using vegetative biomass as the covariate. The repeated measures design used to determine seasonal reproductive output was treated as a split-plot as described earlier. No means separations were required since no significant treatment by date interactions were found.

Results

1. Shoot (ramet) growth and reproduction

Oviposition and gall formation. Oviposition by female gall wasps occurred during the first 3 weeks in May. Gall development began in late May (Fig. 1a), with the most rapid period of gall enlargement occurring during the first half of June.

Shoot growth, leaf and flower production. There were no pre-gall-enlargement differences in *Silphium* shoot growth or leaf production (Figs. 1b, 2a–c). As gall expansion proceeded, galled shoot growth and leaf production fell below that of ungalled shoots. At the last measurement date, galled shoots were 19% shorter ($p<0.001$, Fig. 1b), and had 37% fewer live leaves per shoot than ungalled shoots ($p<0.001$, Fig. 2c). Galls reduced the number of leaves by reducing new leaf production ($p<0.001$, Fig. 2a), without affecting leaf abscission (Fig. 2b) during the period of these measurements.

In some cases galls influenced meristematic activity enough to completely prevent any further apical growth. Eleven of 17 galled shoots (65%) completely failed to flower, compared to 2 of 17 (12%) of gall-free shoots ($X^2=9.52$, $p<0.005$). Galled shoots had fewer flower heads than gall-free shoots throughout the flowering period ($p<0.007$, Fig. 1c). For all shoots, the number of

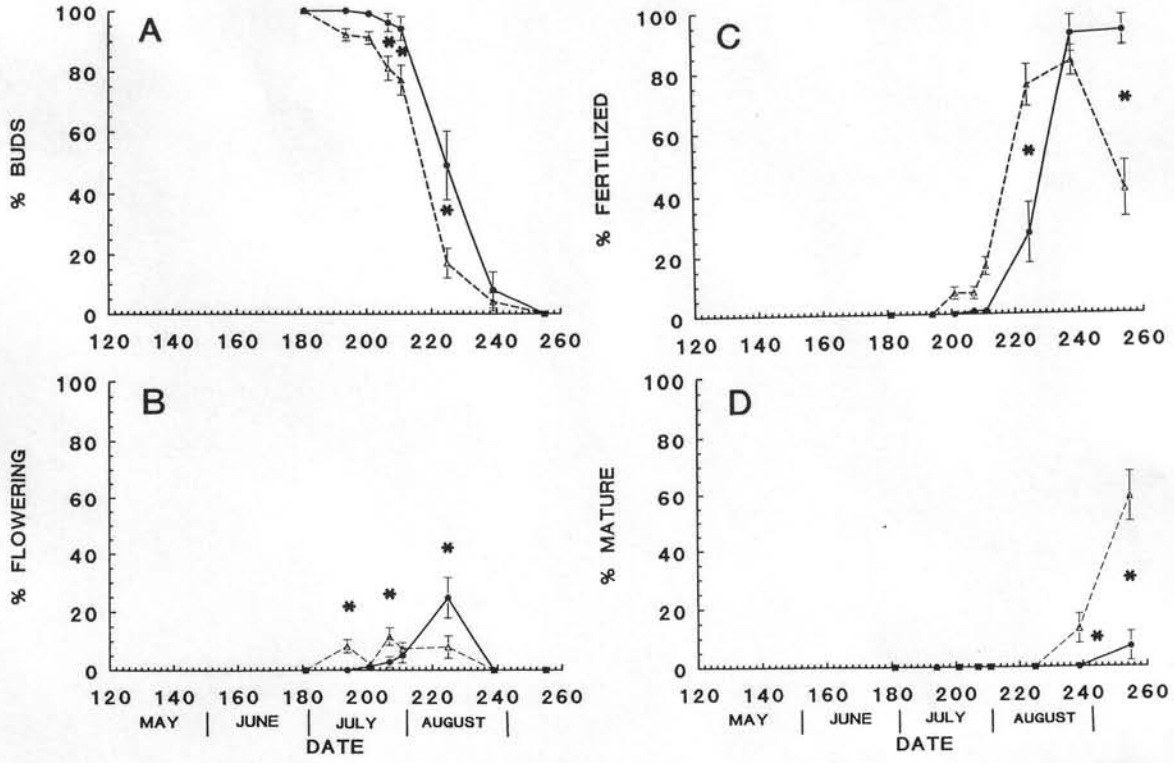

Fig. 3A–D. Mean phenology ± 1 SE of flower heads on galled and gall-free *Silphium* shoots. Symbols as in Fig. 1. Figures **A–D** indicate for a given sample date the percentage of the healthy flower heads on a shoot in each developmental stage. **A** $F_{galling}=13.67$, $p<0.001$. $F_{date}=206.49$, $p<0.0001$. $F_{galling\times date}=3.58$, $p<0.002$. **B** $F_{galling}=0.19$, $p<0.6637$. $F_{date}=8.07$, $p<0.0001$. $F_{galling\times date}=7.09$, $p<0.0001$. **C** $F_{galling}=0.38$, $p<0.5425$. $F_{date}=58.17$, $p<0.0001$. $F_{galling\times date}=11.06$, $p<0.0001$. **D** $F_{galling}=9.56$, $p<0.0044$. $F_{date}=12.44$, $p<0.0001$. $F_{galling\times date}=7.41$, $p<0.0001$. Degrees of freedom for A–D are: $F_{galling}$ 1,25; F_{date} and $F_{galling\times date}$ 7,117

Table 1. Measures of flower head weight, achene production, and achene weight from experimentally galled and ungalled shoots (i.e. ramets) of *Silphium integrifolium*

	Galled shoot		Ungalled shoot		T	$p>T$
	mean	SE (n)	mean	SE (n)		
Flower head weight (g)	1.03	±0.17 (5)	0.89	±0.09 (15)	0.799	0.435
# achenes/ flower head	35.33	±8.47 (5)	29.31	±3.17 (15)	0.834	0.416
achene weight (g)	0.0145	±0.0010 (5)	0.0146	±0.0009 (15)	0.027	0.979

Table 2. End-of-season whole-plant (i.e. genet) dry weights (g) of component tissues of heavily ($n=10$) and lightly ($n=10$) galled *Silphium integrifolium*

	Heavily galled		Lightly galled		T	$p>T$
	mean	SE	mean	SE		
Stem	219.82	±37.08	364.70	± 42.87	2.56	0.020
Gall	46.77	± 9.73	4.77	± 1.69	4.25	0.002
Leaf	125.73	±17.41	142.69	± 19.60	0.65	0.526
Rhizome	173.87	±27.27	236.99	± 38.52	1.34	0.198
Flower	19.41	± 5.83	82.28	± 10.42	5.26	0.000
Total	585.61	±90.87	831.44	±104.57	1.77	0.093

flower heads peaked in late July and then declined for the remainder of the flowering period. Flower head losses were due to abscission or insect damage (not quantified). Flower numbers on gall-free shoots dropped approximately 5 flower heads per shoot from July to the end of the season ($p<0.001$), while on galled shoots over the same period flower numbers dropped approximately 1.5 flower heads/shoot (NS), suggesting that flower head losses to abscission and insect damage were far more severe on gall-free shoots.

Flowering phenology. Galls delayed shoot flowering phenology. Flower heads on galled shoots progressed through each stage of flower head development and achene production after flower heads on gall-free shoots (Figs. 3a–d). For example, the percent of the flower heads in the bud stage on day 225 was 3-fold higher for the galled shoots than for the gall-free shoots ($t=5.277$, $p<0.0001$, Fig. 3a), indicating that fewer of the heads on the galled shoots had developed to the next stage. Consequently, the percent of the heads flowering was 3.1-times less on galled shoots than on gall-free shoots ($t=5.717$, $p<0.0001$, Fig. 3b). The subsequent fertilization of flower heads, and final maturation of achenes (Figs. 3c–d) were similarly delayed on galled shoots.

Reproductive output. Though flowering was delayed by the presence of galls, characteristics of individual flower heads were not affected. Head weights, the number of achenes per flower head, and individual achene weights were equal in galled and gall-free shoots (Table 1).

2. Whole-plant (genet) biomass allocation and reproductive output

Differences in shoot growth and flowering translated into differences in whole-plant growth, biomass allocation, and flower production.

Growth and biomass allocation. Heavily galled plants had 74.3±3.3% of shoots galled, compared to 6.3±1.5% in lightly galled plants. Compared to lightly galled plants, heavy galling reduced total plant biomass by 30%, reduced total biomass of flower heads and stems, but had no effect on leaf or rhizome biomass (Table 2). Heavy galling reduced the proportion of total biomass allocated to flower heads by 70% ($t=5.49$, $p<0.0001$, Fig. 4), to stems by 19% ($t=4.09$, $p<0.0001$), and increased allocation to leaves by 25% ($t=3.91$, $p<0.001$). Heavy galling did not affect proportional allocation to rhizome ($t=1.28$, $p=0.2146$). Plant size has an important effect on the biomass of reproductive structures (Samson and Werk 1987; Hartnett 1990). As a result, reductions in flower head biomass could be due to gall effects on plant size as well as to direct size-independent effects of galls on *Silphium* reproduction. When the effects of individual plant size or total flower head biomass was controlled for by an analysis of covariance using total vegetative biomass (stems+leaves+galls+rhizomes) as the covariate, galls reduced average total flower biomass by 75% (Table

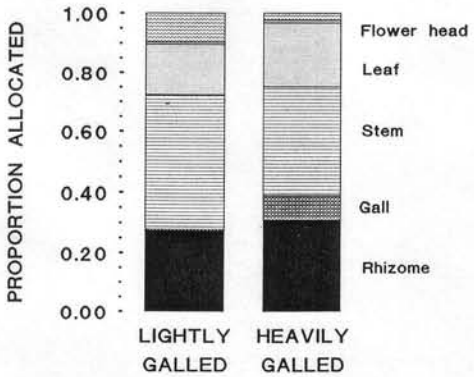

Fig. 4. Proportion of biomass allocated to constituent organs in *Silphium integrifolium* plants with low (6.3±1.5%, $n=10$) or high (74.3±3.3%, $n=10$) percentage of the plant's shoots galled. The largest standard error was ±0.019 for allocation to rhizome

Table 3. Covariance analysis of vegetative biomass and reproductive output in heavily and lightly galled *Silphium integrifolium*

	Heavily galled	Lightly galled	F	$p>F$
	mean SE	mean SE		
Flower head biomass	25.29± 6.38	76.40± 6.38	82.23	0.0001
Y-intercept	−17.00±10.95	34.10±13.46	15.63	0.0001
Slope of covariate (Vegetative biomass)	0.064±0.016		16.28	0.0009

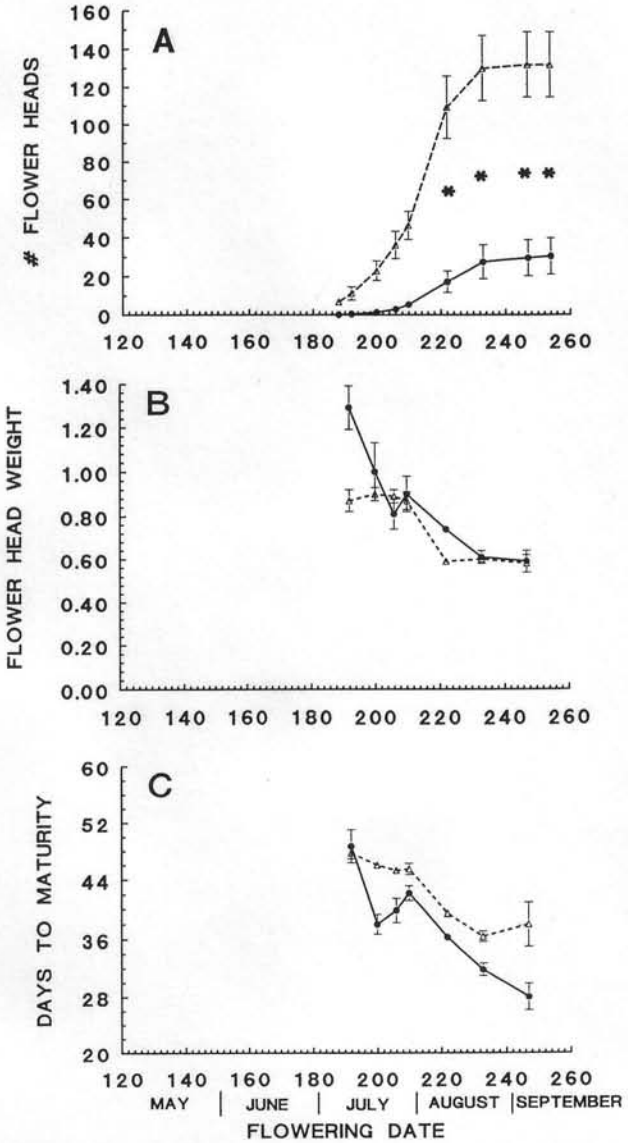

Fig. 5A–C. Mean flower head responses ±1 SE of heavily (———) and lightly (- - - - -) galled *Silphium* plants. **A** Cumulative number of flower heads per plant. $F_{galling}=31.12$, $p<0.0001$. $F_{date}=56.47$, $p<0.0001$. $F_{galling\times date}=21.30$, $p<0.0001$. LSD's at 0.05, 0.01, and 0.001 probabilities are 43.04, 58.12, and 78.35. *=significant at $p<0.001$. Degrees of freedom for A are: $F_{galling}$ 1,18; F_{date} and $F_{galling\times date}$ 8,144. **B** Individual flower head weight. $F_{galling}=1.03$, $p<0.3237$. $F_{date}=22.18$, $p<0.0001$. $F_{galling\times date}=1.38$, $p<0.2363$. **C** Number of days from flowering to maturity for individual flower heads. $F_{galling}=3.19$, $p<0.0909$. $F_{date}=36.27$, $p<0.0001$. $F_{galling\times date}=1.06$, $p<0.3600$. Degrees of freedom for **B–C** are: $F_{galling}$ 1,18; F_{date} and $F_{galling\times date}=6,70$

3). Galls reduced the average sized plant's flower head biomass by approximately 50 g. Using the regression equation from the covariance analysis, we estimate that the reduction in flower head biomass resulting from gall attack is equivalent to a nearly 795 g change in plant size. The reduction in size associated with galls from our biomass data (Table 2) was 245 g. These results show that cynipid galls have a far greater impact on *Silphium* flower head biomass than would be expected from the gall's impact on plant size alone.

Reproductive output. In addition to reducing total flower head biomass, gall formation reduced the number of flower heads per plant and the number of days from flowering to maturation. Heavily galled plants had fewer flower heads than lightly galled plants at all times in the flowering period ($p<0.0001$, Fig. 5a), a difference that widened as the flowering period progressed ($p<0.0001$). Heavy galling did not affect the weight of individual flower heads ($p=0.3237$, Fig. 5b), but flower heads which flowered later weighed less than flower heads initiated earlier ($p<0.0001$). Flower heads on heavily galled plants took marginally fewer days to mature compared to lightly galled plants ($p=0.0909$), and flower heads initiated later took fewer days to mature than flower heads produced earlier in the season ($p<0.0001$, Fig. 5c).

Discussion

This study has examined the impact of cynipid galls on individual *Silphium* shoot growth and reproduction and on whole plant growth, reproduction, and biomass allocation. Cynipid galls had a strong negative effect on *Silphium* reproduction. Galling reduced and delayed flower head production and accelerated flower head maturity, but did not affect individual flower head and achene weights or the numbers of achenes per flower head. Reduced reproduction in galled plants appears to be a common trend in other plant-gall systems, although the stage in the plant's reproductive cycle where the effects occur may vary. For example, shoot galls of the sawfly *Euura* reduced willow *(Salix lasiolepis)* reproductive bud formation by 44% while having no effect on seed weight (Sacchi et al 1988). In contrast, galls on *Solidago canadensis* reduced numbers of flower heads per shoot, numbers of achenes per flower head, and achene weights (Hartnett and Abrahamson 1979). Why galls have different affects on reproduction in different systems is un-

known. Galls that reduce plant reproduction may be restricting resource availability or transport to flowers and ovules during seed production. This is a fundamentally different way of reducing reproduction than occurs with defoliating herbivores. Defoliation reduces plant size and leaf area (Marquis 1984; Kinsman and Platt 1984), so that reduction in seed weight and numbers is more likely due to a lack of available resources rather than restriction of their movement.

Cynipid galls markedly reduced *Silphium* shoot and whole-plant growth and altered biomass allocation patterns. These results might be explained by the reduction or elimination of apical growth beyond the gall. Restriction of the apical meristem by the gall could cause biomass normally allocated to new leaf growth to be shunted instead to the gall or existing leaves. Later in the season, biomass allocated to reproduction in the absence of galls could be shunted to the remaining available sink at that time of year, the rhizome. Disruptions of the plant sink/vascular system/source continuum are another common feature of plant-gall interactions. For example, *Eurosta* galls on *Solidago* reduced leaf and inflorescence allocation (Hartnett and Abrahamson 1979), and ^{14}C tracer studies on this system (McCrea et al. 1985) showed that galls blocked carbon transport in the stem, preventing carbon assimilated on one side of the gall from being transported to the other.

Gall-induced allocation changes in *Silphium* will depend on the sink strength of the gall compared to the strength of the apical meristem, and the effect of galls on photosynthetic capacity. Preliminary evidence suggests that *Silphium* shoot galls are stronger sinks than the apical meristem they replace because galls increase photosynthetic rates of leaves near the gall compared to similar-aged leaves on gall-free shoots (Fay and Hartnett, unpublished). At the same time, galls reduced the number of leaves per shoot by 38% (Fig. 2c), probably reducing total shoot photosynthetic capacity. Increased sink strength combined with reduced source size would account for the smaller overall size of heavily galled plants. More detailed studies are in progress to assess leaf photosynthetic responses to gall formation.

The magnitude of the impact of cynipid galls on *Silphium* suggest that galls have been an important selective agent on *Silphium* life histories. The concept of resource allocation (Antonovics 1980) often used to interpret biomass allocation data would predict that plant allocation responses to galls are adaptive phenotypic responses which ameliorate gall-former impact. An adaptive explanation for allocation changes we observed might be that the stress caused by gall insect attack has selected for plants that 1) increased leaf allocation to offset carbon depletion caused by the gall, 2) reduced flower head allocation in order to maintain allocation to the rhizome, insuring plant survivorship and future reproductive potential, and 3) maintained allocation to achenes to insure maximum viability.

Adaptive explanations for changes in allocation patterns assume that galled and gall-free *Silphium* have the same options available for allocating resources to their constituent organs. However, galled plants did not have the option of allocating to flower heads, because gall restriction of the apical meristem completely prevented flower head formation in 65% of the galled shoots. Also, the adaptive advantages to gall-induced changes in *Silphium* allocation patterns could be offset by changes in plant growth and flowering phenology. For example, height growth and the number of leaves per shoot were reduced by galls, increasing the possibility of suppression of galled plants by intra-or interspecific competition with neighbors (Lee and Bazzaz 1980; Parker and Salzman 1985). Galls also delayed and reduced the flowering period, which could reduce pollination success (Jennersten et al. 1988). If the density of surrounding plants is high, flower heads on shorter galled shoots could be more difficult to find, further reducing *Silphium* achene production. These possible indirect effects of galls on *Silphium* performance must also be accounted for when determining the adaptive value of *Silphium* responses to gall attack.

A more parsimonious explanation of the results is that gall-induced changes in growth, allocation, and reproduction were due to altered sink-source relations resulting from architectural constraints placed by galls on meristem activity (Watson and Casper 1984), effects which may or may not have adaptive value for the plant. Thus biomass allocation patterns resulting from gall attack can also be explained purely in terms of altered meristem availability or activity and altered sink-source relationships, without invoking any adaptive response on the part of the plant.

Acknowledgements. This research was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (BSR 9001047) to P. Fay. We thank E. Muths and M. McCollum for assistance in the field and lab, A.S. Menke for identification of *Antistrophus*, K. Kemp for statistical advice, D. Custer for assistance with preparation of the manuscript, and A. Knapp for comments which improved the content. Computing facilities were provided by the Konza Prairie LTER program (BSR–8514327).

References

Antonovics J (1980) Concepts of resource allocation and partitioning in plants. In: Staddon JER (ed) Limits to action: the allocation of individual behavior. Academic Press, Orlando

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia 50:14–24

Craig TP, Price PW, Itami JK (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. Ecology 67:419–425

Crawley MJ (1983) Herbivory: The dynamics of animal-plant interactions. University of California Press, Berkeley

Crawley MJ (1988) Herbivores and Plant Population Dynamics. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology, 28th Symposium of the British Ecological Society. Blackwell, Oxford

Dennill GB (1988) Why a gall former can be a good biocontrol agent: the gall wasp *Trichilogaster acaciaelongifoliae* and the weed *Acacia longifolia*. Ecol Entomol 13:1–9

Dirzo R (1984) Herbivory: a phytocentric overview. In: Dirzo R, Sarukhán J (eds) Perspectives on plant population ecology. Sinauer, Sunderland MA