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PLANT TOLERANCE OF GALL-INSECT ATTACK AND GALL-INSECT PERFORMANCE[1]

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Abstract. We examined plant tolerance of gall-insect attack and gall-insect performance in rosinweed (*Silphium integrifolium,* Asteraceae) and its apical meristem galler *Antistrophus silphii* (Hymenoptera: Cynipidae). Gall densities were varied in field rosinweed populations, while gall densities, water, and nutrients were varied for rosinweed in an experimental garden. Field plants grew under prevailing resource and competitive conditions, but garden plants grew free from competition, so gall-insect impacts, rosinweed regrowth, and gall-insect performance were observed under widely different growing conditions. Seasonal measures of rosinweed growth and leaf physiology, and end-of-season measures of biomass, reproduction, gall-wasp emergence, growth, sex ratios, and parasitism were made for both experiments.

Rosinweed poorly tolerated *Antistrophus* gall damage in the field. Galls reduced plant height, leaf area, and inflorescence production. Rosinweed diverted biomass to stems, but produced no regrowth from axillary meristems. In the garden, rosinweed was much more tolerant of *Antistrophus* gall damage. Galls initially reduced plant height and leaf area, but axillary meristems grew profusely after gall formation, producing nearly all galled plant inflorescences and more than replacing leaf area initially lost to gall formation. Water- and nutrient-supplemented rosinweed were most tolerant of gall damage, experiencing little loss of total biomass or reproductive output. Field rosinweed failed to mount a tolerance-enhancing regrowth response because galls, resource availability, and competition combined to constrain axillary meristem growth. Gall-wasp performance was largely independent of rosinweed tolerance. Emergence, growth, sex ratios, and parasitism were comparable in field and garden, and only slightly affected by resource availability. Gall-insect performance may be buffered from environmental variation, disconnecting plant and herbivore population dynamics. Rosinweed's poor tolerance of gall damage may typify forb responses to herbivory in highly competitive grassland plant communities.

Key words: Antistrophus; *biomass allocation; compensation; Cynipidae; gall insect; herbivory; Konza Prairie; meristems; parasite; sex ratio;* Silphium; *tallgrass prairie.*

Introduction

The ability of plants to tolerate herbivory depends strongly on the environmental conditions surrounding the interaction. For example, tolerance of herbivory is enhanced when light, water, and nutrients are more abundant, and when competition from neighboring plants is less intense (Crawley 1983, Parker and Salzman 1985, Louda et al. 1990, Whitham et al. 1991, McEvoy et al. 1993, Rosenthal and Kotanen 1994). Herbivory tolerance also depends on plant growth rates, post-damage allocation patterns, photosynthetic rates, and reserves of carbohydrates, nutrients, and meristems (Rosenthal and Kotanen 1994). In particular, the ability to reallocate resources to reserve meristems provides developmental plasticity in a variable environment and is necessary for compensatory regrowth after damage (Maschinski and Whitham 1989, Aarsen and Irwin 1991, Paige 1992, Rosenthal and Kotanen 1994).

The factors affecting tolerance of herbivory can also have consequences for herbivores. Host-plant resource availability can affect herbivore attack rates (Horner and Abrahamson 1992, Rossi et al. 1992), survivorship, growth, and sex ratios (Preszler and Price 1988, Waring and Cobb 1989, Craig et al. 1992), and attractiveness to herbivore natural enemies (Fox et al. 1990). Since plant resources have such widespread effects on the plant and on the herbivore, there may be complex feedbacks in their interactions (Haukioja 1990), with uncertain consequences for plant and herbivore population dynamics.

We conducted simultaneous studies of a plant/gall-insect interaction under natural field conditions and in a competition-free experimental garden where nutrient and water availability were manipulated. These experiments examined (1) plant regrowth responses after gall formation on apical meristems, (2) how a plant's growing conditions might affect plant tolerance of gall-insect damage, and (3) how factors affecting plant tolerance might affect gall-insect performance.

Gall-insect/plant interactions are complex and poorly understood. Galls are an integrated part of the plant (Weis et al. 1988, Shorthouse and Rohfritsch 1992) that can alter plant architecture and reproduc-

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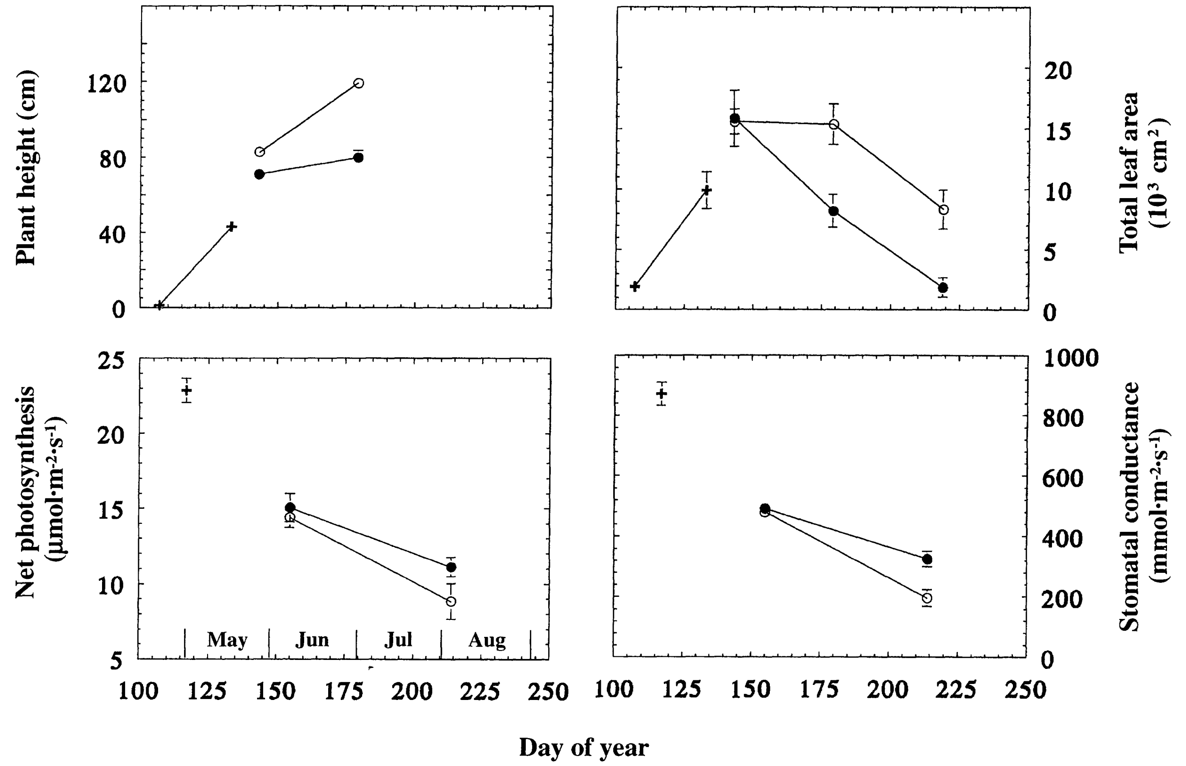

FIG. 1. Plant height, leaf area, net photosynthesis, and stomatal conductance of *Silphium integrifolium* galled by *Antistrophus silphii* in the field experiment (means ± 1 SE). + = before gall formation; ● = galled rosinweed; ○ = ungalled rosinweed. Standard errors not shown fell within the symbols. Statistical analysis is presented in Table 1.

tion (Dennill 1985, Sacchi et al. 1988, Fay and Hartnett 1991, DeClerck-Floate and Price 1994). Galls often play active physiological roles, regulating lateral or adventitious regrowth after gall formation (Weis 1984, Craig et al. 1986, DeClerck-Floate and Price 1994), redirecting resource movement (Jankiewicz et al. 1970, McCrea et al. 1985, Larson and Whitham 1991), and increasing photosynthetic rates (Weis and Kapelinski 1988, Fay et al. 1993). These physiological effects possibly continue for the duration of the metabolically active life of the gall, which is several months in some species. Thus, galls may play a more active role in plant regrowth responses than free-feeding herbivores, which typically "eat and run," leaving the plant to respond based on its own physiological constraints.

These studies focused on the tallgrass prairie perennial forb *Silphium integrifolium* var. *laeve* T. and G. (=*Silphium speciosum* Nutt. Rydberg, Asteraceae; hereafter "rosinweed") and the cynipid gall wasp *Antistrophus silphii* Gil. (Hymenoptera). *A. silphii* galls form on shoot apical meristems, causing conflicting effects on shoot growth and physiology. Galls reduce shoot growth, leaf area, and inflorescence development but increase photosynthetic rates and stem water potential (Fay and Hartnett 1991, Fay et al. 1993). Since prairie plants are nitrogen limited (Owensby et al. 1970, Knapp and Seastedt 1986), periodically

TABLE 1. ANOVA *F* statistics (df in parentheses) for gall and date main effects and the gall × date interaction affecting *Silphium integrifolium* shoot growth, leaf area, and gas exchange in the field experiment.

	Plant height	Total leaf area	Net photosynthesis	Stomatal conductance to H_2O vapor
Galls	35.78**** (1, 18)	5.56* (1, 36)	2.48NS (1, 18)	5.82* (1, 18)
Date	226.97**** (1, 18)	66.10**** (2, 36)	25.69**** (1, 18)	66.84**** (1, 18)
Galls × Date	86.75**** (1, 18)	9.64*** (2, 36)	1.72NS (1, 18)	3.68† (1, 18)

NS = not significant, † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

TABLE 2. Characteristics (mean ± 1 SE) of galled and ungalled *Silphium integrifolium* plants in the field experiment.

	Galled	Ungalled	*t*	df
Midday leaf-water potential (MPa, 1 Aug)	−1.46 ± 0.10	−1.68 ± 0.09	1.59NS	14
Biomass (g)				
Leaf	46.18 ± 4.31	66.08 ± 4.83	6.41****	18
Stem	103.68 ± 14.61	32.42 ± 12.92	3.37***	18
Galls	56.31 ± 7.67	0	…	…
Flower heads	0.72 ± 0.64	8.25 ± 1.25	10.62****	18
Total	206.88 ± 20.81	107.39 ± 14.70	3.90***	18
Axillary (%)	2.36 ± 0.87	0.99 ± 0.75	2.03*	18
% of ungalled shoots senesced (26 Aug)	49.10 ± 11.70	17.41 ± 4.00	2.25*	10.3
Achene characters				
Mass (mg)	5.82 ± 0.68	9.36 ± 0.89	1.68NS	10
% damaged	48.64 ± 27.75	46.60 ± 0.02	0.14NS	2.0
% germinated	0	1.64 ± 0.85	1.91NS	9
Leaf chemistry				
Midseason (5 July)				
%C	42.27 ± 0.17	43.42 ± 0.19	4.59***	18
%N	1.93 ± 0.09	1.90 ± 0.06	0.82NS	18
Insects				
No. gall wasps/gall	1.51 ± 0.36	…	…	…
Sex ratio (females:total)	0.66 ± 0.09	…	…	…
Female mass (mg)	1.34 ± 0.08	…	…	…
Male mass (mg)	0.78 ± 0.04	…	…	…
No. parasites/gall	0.71 ± 0.18	…	…	…

NS = not significant, † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

drought stressed, and can be shaded by neighbors (Fay 1992), resource availability should be an important factor in *Silphium* regrowth responses and gall-insect performance.

Life histories of rosinweed and the gall wasp

Rosinweed grows on sites with deep soils and a history of disturbance (Great Plains Flora Association 1986). A rosinweed plant (genet) usually consists of 20–50 shoots forming a tightly packed clump. Rosinweed's architecture is simple, and typical of many prairie forbs. Each spring new growth emerges from belowground buds set the previous year on a stout, rootstock-like rhizome. During April the buds form a rosette, then in May they rapidly elongate into a 1–2 m tall primary shoot bearing 15–25 pairs of sessile opposite leaves (Fay and Hartnett 1991). Primary shoot growth ends in July when the apical meristem produces a terminal inflorescence of 1–15 flower heads (capitula). Shoots are normally unbranched. As a result, an intact apical meristem is required for sexual reproduction and to grow above the surrounding plant canopy. Deer occasionally browse rosinweed, causing axillary shoot growth and inflorescence production. However, shoot height is reduced and shading by neighbors becomes more severe (P. Fay, *personal observation*). Achenes mature in August. All aboveground parts die back by the end of October, and are completely replaced the following year.

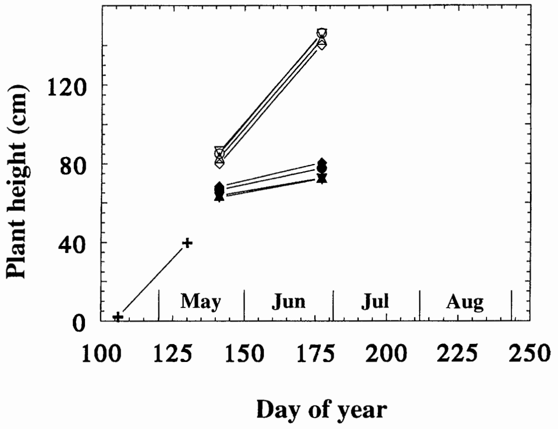

FIG. 2. Plant height of *Silphium integrifolium* receiving factorial combinations of *Antistrophus silphii* galls, water, and fertilizer in the garden experiment (means ± 1 SE). + = before gall formation; closed symbols = galled plants; open symbols = ungalled plants. ● = no added resources; ▲ = added H_2O; ▼ = added fertilizer; ◆ = added H_2O and fertilizer. Standard errors not shown fell within the symbols. Statistical analysis is presented in Table 3.

Antistrophus silphii is one of eight *Antistrophus* species known from North America (Krombein et al. 1979). All form galls on Asteraceae, most on the genus *Silphium*. Galls form after a female *A. silphii* oviposits into a rapidly elongating apical meristem (P. Fay, *personal observation*). Within 2 wk, the meristem swells into a spherical gall eventually reaching 1–4 cm in diameter. Up to 30 larvae feed in individual chambers. Larvae develop through three instars before shoots and gall senescence, pupate in April, and emerge for the next generation by May. Since *A. silphii* occupies its gall for all but a few weeks of the

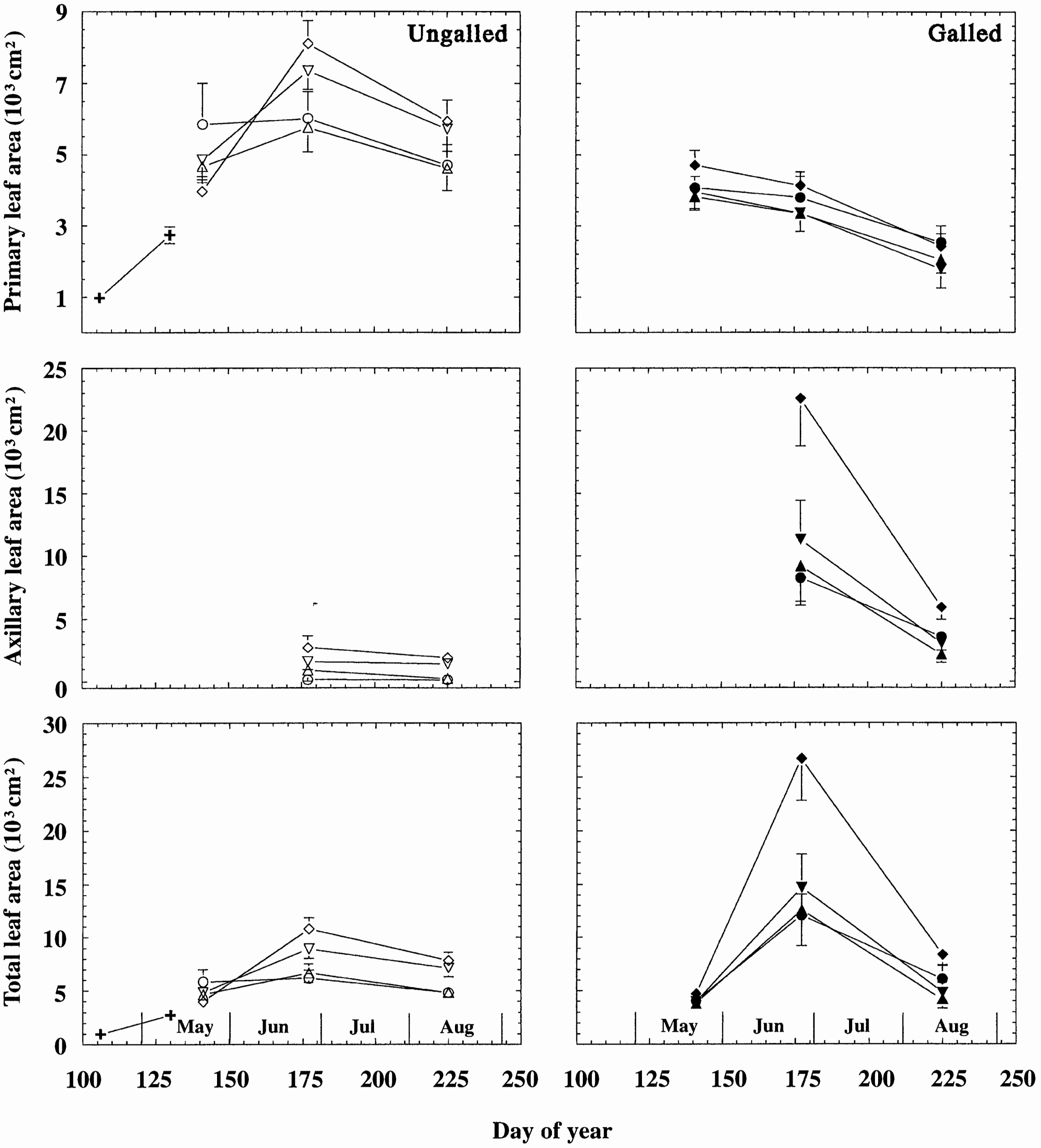

FIG. 3. Leaf area components (cm²) of *Silphium integrifolium* receiving factorial combinations of galls, water, and fertilizer in the garden experiment. Primary leaf area consists of leaves on the primary shoots, axillary leaf area results from growth of axillary buds on the primary shoot, and total leaf area is their sum. Symbols as in Fig. 2; statistical analysis is presented in Table 3.

year, host-plant characteristics may assume special importance for this species. The limited oviposition period means there is little variation in the timing of attack that might affect plant regrowth abilities, and later lateral growth is not subject to gall-wasp attack. *A. silphii* larvae are parasitized by an undescribed *Eurytoma* species (E. E. Grissell, *personal communication*). Disk florets are attacked by an unidentified galler (possibly *A. laciniatus*), and an unidentified capitulum feeder damages the achenes.

METHODS

Research sites

Experiments were conducted at Konza Prairie Research Natural Area, a 3487 ha tract of Flint Hills tall-

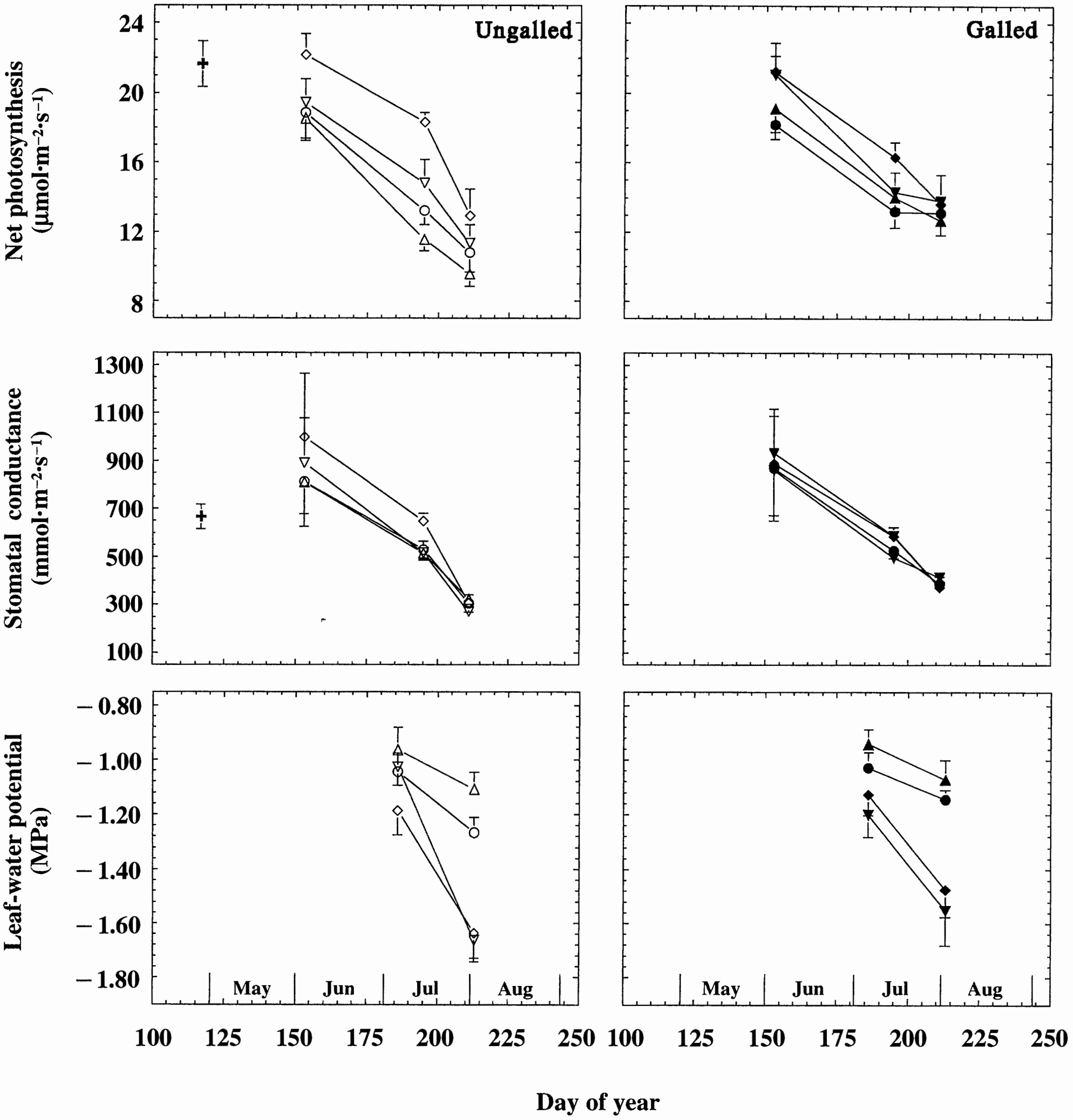

FIG. 4. Photosynthesis, stomatal conductance, and midday leaf-water potential of galled, watered, or fertilized *Silphium integrifolium* in the garden experiment. Symbols as in Fig. 2; statistical analysis is presented in Table 3.

grass prairie near Manhattan in northeastern Kansas (39°05′ N, 96°35′ W).

Field experiment

Gall densities were manipulated on naturally established rosinweed to measure baseline plant responses to gall damage and gall-insect performance under field nutrient, water, and competitive conditions. The field site was an annually burned old field dominated by Eastern gamagrass (*Tripsacum dactyloides*), switchgrass (*Panicum virgatum*), and several forbs, primarily goldenrod (*Solidago canadensis*) and Baldwin ironweed (*Vernonia baldwinii*). The site was burned in early April 1991. April fires eliminate *Antistrophus* populations (Fay and Samenus 1993), so galled shoots were removed from the site before the burn for later use establishing galls in experimental plants.

Twenty plants were arbitrarily chosen to be gall free. Nylon tulle cages (1.2 m high × 0.6 m in diameter) were placed over plants immediately before gall-wasp emergence (23 April 1991). Plants remained caged for 3 wk until gall-wasp activity ceased. Another 20 plants were arbitrarily chosen to be heavily galled. The previously collected galled shoots were placed five per plant among the elongating shoots at roughly the height of their apical meristems. Gall wasps then freely

TABLE 3. ANOVA *F* statistics (df in parentheses) for main effects and interactions affecting *Silphium integrifolium* plant height, leaf area, gas exchange, and carbon/nitrogen content in the garden experiment.

	Plant height	Primary leaf area	Axillary leaf area	Total leaf area
Source plant (= block)	4.37*** (14, 98)	2.85**** (14, 98)	2.05* (14, 98)	1.61† (14, 98)
Galls	337.09**** (1, 98)	52.96**** (1, 98)	62.79**** (1, 98)	11.71* (1, 98)
Water	0.37NS (1, 98)	0.02NS (1, 98)	5.03* (1, 98)	3.31† (1, 98)
Fertilizer	0.02NS (1, 98)	1.81NS (1, 98)	12.98*** (1, 98)	12.97*** (1, 98)
Galls × Water	1.49NS (1, 98)	0.41NS (1, 98)	2.43NS (1, 98)	2.51NS (1, 98)
Galls × Fertilizer	0.18NS (1, 98)	0.90NS (1, 98)	3.53† (1, 98)	1.33NS (1, 98)
Galls × Water × Fertilizer	2.22NS (1, 98)	0.20NS (1, 98)	3.71† (1, 98)	3.26† (1, 98)
Galls × Date	238.50**** (1, 112)	38.88**** (2, 224)	44.92**** (1, 112)	32.56**** (2, 224)
Galls × Water × Date	0.01NS (1, 112)	2.98* (2, 224)	3.26† (1, 112)	1.89NS (2, 224)
Galls × Fertilizer × Date	0.03NS (1, 112)	12.85**** (2, 224)	6.11* (1, 112)	2.97† (2, 224)
Water × Fertilizer	0.69NS (1, 112)	1.73NS (2, 224)	4.61* (1, 112)	5.56* (2, 224)
Water × Date	0.00NS (1, 112)	2.01NS (2, 224)	5.31* (1, 112)	5.80** (2, 224)
Fertilizer × Date	0.00NS (1, 112)	7.78*** (2, 224)	6.74* (1, 112)	12.16**** (2, 224)
Water × Fertilizer × Date	0.24NS (1, 112)	0.32NS (2, 224)	1.33NS (1, 112)	2.65† (2, 224)

NS = not significant, † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

emerged and oviposited. Cages were not used for galled plants because they disrupt gall-wasp behavior, making them congregate in the top of the cage, ignoring the shoots (P. Fay, *personal observation*). Cages caused negligible effects on rosinweed growth, with no differences in leaf area or gas exchange, and with minor shoot elongation seen in measurements immediately after cage removal.

Plant growth and physiology.—Plant growth measurements were made on a subset of 10 plants per treatment chosen to be of similar size (mean ± 1 SE = 29 ± 4 shoots per plant). Plant growth was characterized by estimating plant height and leaf area. These were measured on five randomly chosen shoots per plant. The same shoots were measured throughout the experiment. Plant height was measured from the ground to the apical meristem or gall. Leaf-area estimates were based on the number of leaves and average individual leaf area on primary and axillary shoots. Average individual leaf area was derived from leaf lengths and widths by linear regression ($R^2 = 0.97$). Each shoot's primary leaf area was the product of average individual leaf area and the number of primary leaves. Each axillary shoot's leaf area was calculated similarly and summed over the primary shoot. Total, primary, and axillary leaf area was the product of shoot primary and axillary leaf areas and the number of shoots per plant. Measurements were made four (plant height) or five (leaf area) times through the season: after rosette emergence, just before and after gall-wasp oviposition, and at mid- and late-season.

Early-, mid-, and late-season measurements of net photosynthesis and stomatal conductance to H_2O vapor were made with an infrared gas analyzer (LICOR LI-6200) on a sixth marked shoot. Similar-aged leaves were measured in each plant on clear days at saturating photosynthetic photon flux densities (>1700 $\mu mol \cdot m^{-2} \cdot s^{-1}$).

Midday leaf-water potential during the last gas-exchange measurement was determined with a thermocouple psychrometer (Decagon SC–10A, Decagon Devices, Pullman, Washington, USA) on 1 × 3 cm leaf strips. The psychrometer was calibrated with NaCl solutions. Leaf strips were equilibrated in the sample chamber for 15 min before water potential determination.

Midseason leaf C and N contents were measured in a carbon–nitrogen analyzer (Carlo Erba NA 1500 NC, Carlo Erba Strumentagione, Milan, Italy) on oven-dried, finely-ground samples from two or three randomly collected leaves per plant. The instrument was calibrated with an acetanilide standard. C and N contents were expressed as a percentage of dry mass.

End-of-season measurements.—All aboveground plant parts were collected as they senesced to determine the end-of-season masses of galls and all primary and axillary flower heads, leaves, and stems. Stems and leaves were oven dried at 70°C for 48 h and weighed. Galls and flower heads were air dried, weighed, and

TABLE 3. Continued.

Stomatal conductance to H_2O vapor	Net photosynthesis	Midday leaf-water potential	Leaf % N (5 July)	Leaf % C
30.22****	5.16****	7.02****	4.16****	3.77****
(11, 77)	(11, 77)	(14, 98)	(14, 98)	(14, 98)
2.78†	3.03†	1.21NS	0.69NS	27.69****
(1, 77)	(1, 77)	(1, 98)	(1, 98)	(1, 98)
2.15NS	2.64†	3.34†	7.25**	1.55NS
(1, 77)	(1, 77)	(1, 98)	(1, 98)	(1, 98)
3.93†	21.23****	67.10****	1199.25****	0.62NS
(1, 77)	(1, 77)	(1, 98)	(1, 98)	(1, 98)
3.38†	0.17NS	0.33NS	0.02NS	0.30NS
(1, 77)	(1, 77)	(1, 98)	(1, 98)	(1, 98)
0.47NS	3.45†	0.02NS	4.84*	2.46NS
(1, 77)	(1, 77)	(1, 98)	(1, 98)	(1, 98)
1.47NS	2.35NS	1.00NS	3.74†	3.03†
(1, 77)	(1, 77)	(1, 98)	(1, 98)	(1, 98)
0.31NS	3.34*	1.73NS	...	...
(2, 112)	(2, 112)	(1, 64)		
0.04NS	0.42NS	0.82NS	...	...
(2, 112)	(2, 112)	(1, 64)		
0.11NS	0.67NS	5.97**	...	...
(2, 112)	(2, 112)	(1, 64)		
1.71NS	2.44NS	4.02*	12.61***	0.08NS
(2, 112)	(2, 112)	(1, 64)	(1, 98)	(1, 98)
0.02NS	0.95NS	1.01NS	...	...
(2, 112)	(2, 112)	(1, 64)		
0.55NS	1.34NS	10.96**	...	...
(2, 112)	(2, 112)	(1, 64)		
0.04NS	0.79NS	0.02NS	...	...
(2, 112)	(2, 112)	(1, 64)		

stored at 4°C. In April 1992 gall wasps and parasites were allowed to emerge at room temperature from 10 galls per plant. Insects were immediately preserved in 70% ethanol and later sorted, sexed, and counted. Gall wasps were weighed after oven drying. A random sample of 20 undamaged achenes per plant was collected from flower heads, weighed, and germinated on moist filter paper in petri dishes in a controlled environment chamber at 14:10 L:D photoperiod and 25:15°C day : night temperature. Achenes were checked daily, and scored as germinated if the hypocotyl extended 3 mm from the achene.

Design and analysis.—The plant was the experimental unit for galling (n = 10 ungalled, 10 galled). Responses measured more than once during the season required a repeated-measures analysis. This was done with the split-plot method, where galling was the whole-plot factor and measurement date (=day of year) the sub-plot factor. Pretreatment measurements before day 140 were not included in the analysis. Biomass data were first analyzed by multivariate analysis of variance (MANOVA) to evaluate effect of galls on overall biomass distribution, then differences in masses of individual plant parts were compared with two-sample t tests (Johnson 1995). Other factors measured once during the season were compared with two-sample t tests.

Garden experiment

Gall-wasp attack and nutrient and water availability were manipulated in rosinweed established in an experimental garden near the field site to determine how variation in plant resource availability influenced plant responses to gall-insect attack under competition-free conditions. Rosinweed plants were grown from rhizomes in 1.2 m × 30 cm galvanized steel tubes spaced 1.5 m apart in a 15-row × 8-column grid. The tubes completely contained rosinweed's root system, excluded roots from neighboring vegetation, and allowed retrieval of roots and rhizomes at the end of the experiment. Surrounding vegetation was periodically mowed and tubes were continually weeded, so competition was excluded from this experiment. The tubes contained a sand/vermiculite mixture up to the level of the surrounding soil. This mixture offered important experimental benefits over native soil. Its low nutrient and water holding capacity allowed establishment of broad treatment differences in resource availability, and roots could be more rapidly and completely recovered than from native soils.

Rosinweed rhizomes for transplant came from the field experiment site. Fifteen plants having high natural gall densities the previous growing season were excavated while dormant (March 1990). Their rhizomes were washed, separated into pieces, weighed, and stored in a cold room in wet sand. Rhizome pieces were planted in the tubes in early April 1990 and fertilized (Alljack 15-30-15, recommended concentration) once to aid establishment. Resulting plants had 7.0 ± 0.7 shoots/plant (mean ± 1 SE).

Experimental treatments.—Plants (n = 120) were

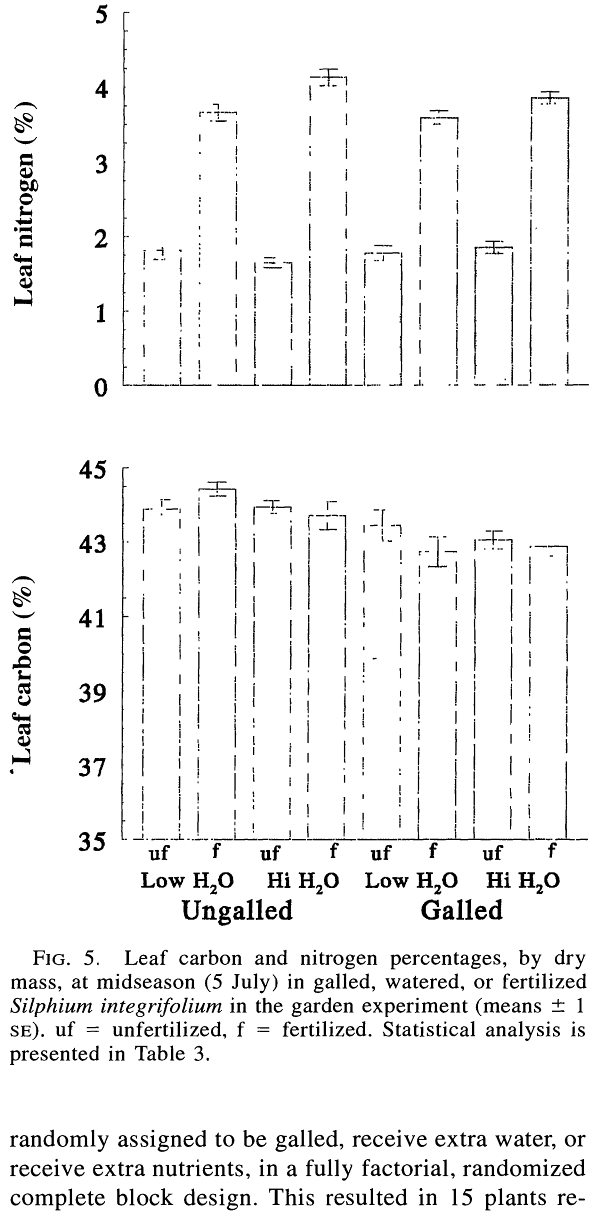

FIG. 5. Leaf carbon and nitrogen percentages, by dry mass, at midseason (5 July) in galled, watered, or fertilized *Silphium integrifolium* in the garden experiment (means ± 1 SE). uf = unfertilized, f = fertilized. Statistical analysis is presented in Table 3.

randomly assigned to be galled, receive extra water, or receive extra nutrients, in a fully factorial, randomized complete block design. This resulted in 15 plants receiving one of eight galling × water × fertilizer combinations.

Attempts to establish galls in May 1990 were unsuccessful, so the plants grew in the tubes during the 1990 growing season, receiving one more fertilizer application and water as required. In 1991, galling treatments were successfully established using field experiment methods: plants were caged to exclude gall wasps, or left uncaged and given two previous-year galls whose gall wasps freely oviposited on the plants. Cage effects on plant growth were again negligible.

Fertilizer and water treatments began after oviposition, to prevent uneven oviposition on plants receiving different resource treatments. Fertilized plants were top-dressed with 356 g (4 kg/m^3) of slow-release fertilizer pellets (Sierra 17-6-10 with micronutrients). Watered plants received water to soil saturation three times per week. Unwatered plants received only natural precipitation. Unfertilized plants had low nutrient availability. Pre-experiment soil analysis showed that all macronutrients and most micronutrients in the sand/vermiculite mixture were 10–33% of field soil values.

Plant and insect responses.—Treatment effects on plant height, leaf area, and leaf physiology were assessed through the season using field experiment methods at similar intervals on two randomly chosen marked shoots per plant. Biomass distributions were also determined using field experiment methods. In addition, rhizomes and roots were retrieved, washed free of sand/vermiculite, and oven dried in late November after aboveground organs had senesced. Rhizome buds were counted as an indicator of the effects of galls on the next year's potential shoot (ramet) production. Flower heads and galls were handled as in the field experiment to assess achene responses and insect performance.

Design and analysis.—This experiment used a repeated-measures design treated as a split plot for analysis. Source plant (n = 15) was the blocking factor. The plant was the whole-plot experimental unit for gall, water, and fertilizer treatments (total n = 120), and measurements of plant growth and physiology on successive dates were the repeated measures. F tests were

TABLE 4. ANOVA F statistics for rosinweed biomass responses to galls, water, and fertilizer in the garden experiment. MANOVA tested for overall significance of biomass distributions between flower heads, leaves, galls, stems, rhizome, and roots. If an effect was significant by MANOVA, univariate ANOVA is then presented. Total plant biomass, number of

	MANOVA	Flower heads	Leaves	Galls	Stems
Source plant (= block)	···	2.85**	4.56****	2.95***	5.20****
Galls	30.29*	24.11****	19.07****	98.83****	40.56****
Water	5.90*	7.63****	1.34NS	0.69NS	3.36†
Fertilizer	12.07*	44.25****	15.18***	1.32NS	40.44****
Galls × Water	0.74NS	···	···	···	···
Galls × Fertilizer	2.11*	0.07NS	2.32NS	1.64NS	0.34NS
Water × Fertilizer	3.73*	17.54****	6.65*	2.20NS	9.74**
Galls × Water × Fertilizer	0.62NS	···	···	···	···

NS = not significant, † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

constructed using these error terms: mean square (MS) block × galls × water × fertilizer for the block effect and the gall, water, fertilizer main effects and their interactions. The remaining model MS error was used for the date main effect and its interactions with galls, water, and fertilizer.

Biomass data were first analyzed by MANOVA to evaluate main and interactive effects of galls, water, or fertilizer on overall responses (Johnson 1995). For effects where MANOVA was significant, the responses of individual organs were analyzed with randomized complete blocks analysis of variance (ANOVA). Other factors measured once during the season were analyzed by ANOVA. The achene and insect data contained missing values, so least-square means and standard errors are reported.

RESULTS

Field experiment

Caged plants were gall free, while galls formed on 87 ± 2% of shoots (mean ± 1 SE) in galling treatment plants. The growth of these plants and insects reflect ambient field nutrient, water, and competitive conditions, and serve as a baseline for comparison with the garden experiment.

Plant growth and physiology.—Galls had generally negative effects on field rosinweed. Galling reduced plant height and total leaf area, and caused earlier leaf and shoot senescence, and higher late-season stomatal conductance (Fig. 1, Table 1). At midseason, galling reduced leaf C percentage, but did not affect midday leaf-water potential, or N percentage (Table 2).

Plant biomass and reproduction.—Galling doubled rosinweed aboveground biomass (Table 2). The galls themselves accounted for half the increase, and stem mass made up the rest. The increased mass of galls and stems easily replaced mass lost from leaves and flower heads. Galling caused small but negligible (≤2% of total biomass) growth of axillary leaf buds. Achene damage, germination, and mass were unaffected by galling (Table 2).

Gall insects.—Gall-wasp emergence (Table 2) from field galls was low at ≈1.5 gall wasps/gall. Sixty-six percent of gall wasps were female, and females were twice as heavy as males. One parasitic *Eurytoma* wasp emerged per two gall wasps.

Garden experiment

Caged plants were gall free, while galls formed on 69 ± 4% of shoots (mean ± 1 SE) in galling treatment plants. We focus here on the most important gall and resource main effects and interactions, especially those differing from field plants. Most minor but significant interactions are not emphasized.

Plant growth and physiology.—In general, galls were considerably less damaging to rosinweed than under typical field conditions. As in field plants, galling resulted in shorter plants with less primary leaf area (Figs. 2, 3, Table 3). But unlike field plants, galling stimulated extensive axillary leaf production, resulting in greater total leaf area than in ungalled plants. The greatest response occurred in galled + watered + fertilized plants. They produced twice the axillary leaf area of other galled plants, and at least 5 times the axillary area of ungalled plants (Fig. 3). However, galled + watered + fertilized plants also lost axillary leaf area most rapidly. By mid-August galls and resources had little effect on total leaf area. Despite rapid leaf loss, axillary growth gave galled plants 28% more total leaf area than ungalled plants averaged from May through August.

Fertilizer generally increased photosynthesis and stomatal conductance (Fig. 4, Table 3) while galls and water had little effect. However galls became important later in the season, by slowing the decline in photosynthesis seen in ungalled plants. Fertilizer decreased midday leaf-water potential (Fig. 4, Table 3), particularly during August and in ungalled plants.

Leaf N and C percentages in unwatered, unfertilized plants were close to field-plant levels. Fertilizer strongly increased leaf N percentage, especially in high-water plants, but less in galled plants (Fig. 5, Table 3). Galls reduced leaf C by a few percentage points.

Plant biomass and reproduction.—Unlike in field

rhizome buds, axillary biomass, and axillary reproduction were analyzed with ANOVA (df: MANOVA 7, 92; Source plant 14, 98; all others 1, 98).

Rhizome	Roots	No. rhizome buds	Total biomass	Axillary biomass	Axillary reproduction
10.30****	5.29****	1.26NS	5.38****	3.36***	1.92*
2.93†	0.17NS	1.04NS	16.04***	167.75****	445.85****
3.02†	30.61****	2.90†	8.82**	4.03*	0.11NS
0.05NS	5.62*	7.30**	28.80***	33.29****	12.01***
···	···	0.21NS	2.25NS	0.05NS	1.88NS
2.88†	0.72NS	0.38NS	0.01NS	0.34NS	10.13**
8.19**	9.57**	6.27*	13.77***	1.88NS	1.21NS
···	···	0.06NS	0.31NS	0.15NS	0.70NS

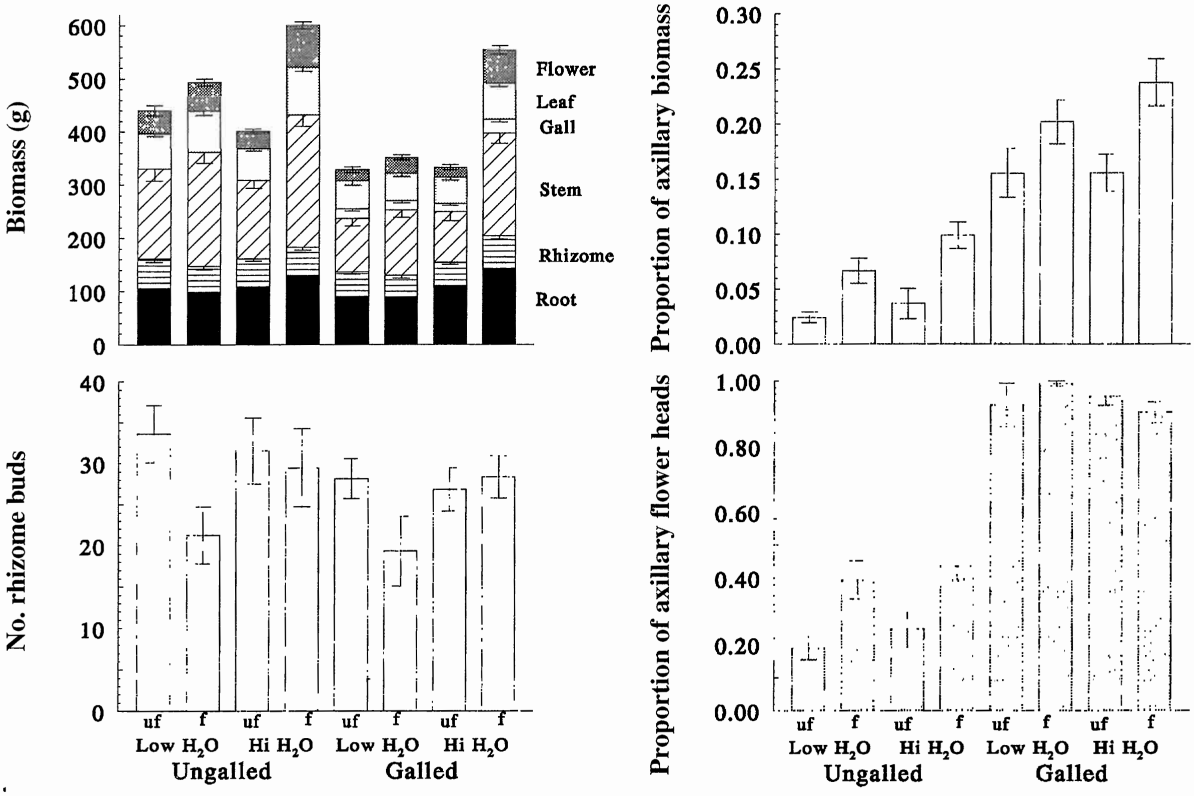

FIG. 6. Biomass patterns, rhizome bud production, and contribution of axillary growth to total flower-head production in *Silphium integrifolium* in the garden experiment (means ± 1 SE). Symbols as in Fig. 5; statistical analysis is presented in Table 4.

plants, galling reduced total rosinweed biomass by 20% (Fig. 6, Table 4). Galls made up <5% of plant biomass, but reduced all aboveground parts except rhizome and root mass and rhizome bud production. Axillary biomass (Fig. 6, Table 4) was a major biomass component in galled plants, and accounted for nearly all of their flower-head biomass.

Resources increased the mass of most plant parts (Fig. 6, Table 4). When watered and fertilized, galled plants at least equalled the mass of ungalled plants. However, when limited by absence of water, fertilizer, or both, galled plants were the smallest of all the treatments. Gall mass was notably unaffected by resources. Rhizome buds were decreased by fertilizer, especially at low water. Axillary biomass was increased by water and fertilizer. Resources only affected axillary flower-head production in ungalled plants.

Galls and fertilizer both caused small decreases in achene mass (Fig. 7, Table 5), but there were no significant gall × resource interactions. Galls did not affect germination rates, (Fig. 7, Table 5), but fertilizer doubled the rate of germination.

Gall insects.—Garden gall wasps had similar emergence, parasitism, sex ratios, and growth as field gall wasps (Fig. 8, Table 5). Plant resources caused little additional variation. Small increases in gall-wasp and parasite emergence occurred when plants received either water or fertilizer, compared to receiving both, or compared to control plants. Water slightly increased male gall-wasp mass, but resources did not affect female gall-wasp mass or gall-wasp sex ratio.

DISCUSSION

Rosinweed tolerance of galling

Rosinweed's tolerance of galling by *Antistrophus silphii* depended on the conditions in which their interaction occurred. In the garden experiment, rosinweed's responses suggested considerable tolerance of galls. For example, galled plants produced extensive axillary regrowth that replaced leaves and inflorescences normally arising from apical meristems, but inhibited by galls. With added water and nutrients, rosinweed mounted a sizeable axillary regrowth response, in the end experiencing little or no loss of biomass or reproductive output.

In contrast, in the field experiment rosinweed's responses indicated much less tolerance of galls. Axillary meristems were present but failed to grow in galled plants, so their leaf area and reproductive output were reduced. The lack of axillary regrowth in galled field plants was unexpected for several reasons. First, ax-

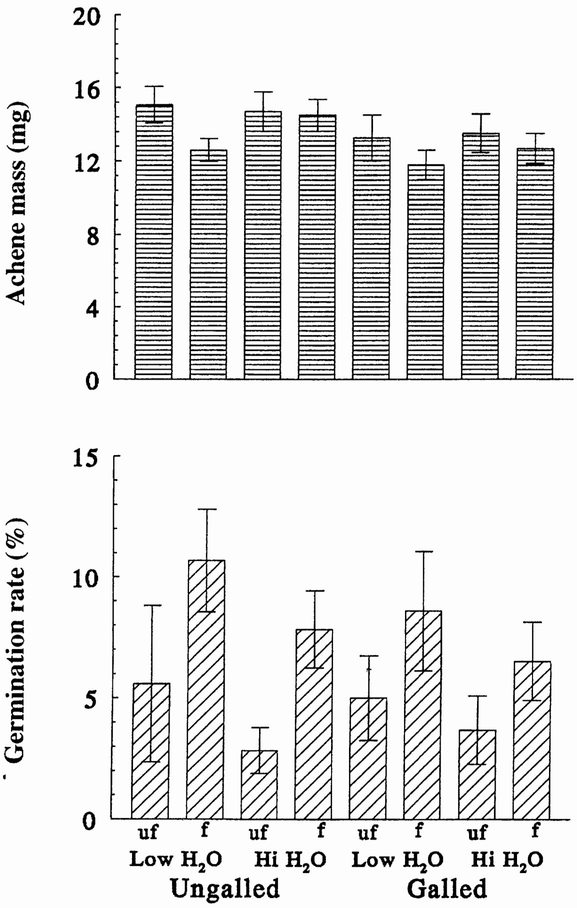

FIG. 7. Achene mass and germination rates from *Silphium integrifolium* in the garden experiment. Data from undamaged achenes only, primary and axillary capitula pooled (means ± 1 SE). Symbols as in Fig. 5; statistical analysis is shown in Table 5.

illary regrowth is a common response to meristem damage (Islam and Crawley 1983, Stamp 1984, Paige and Whitham 1987, Doak 1991, Belsky et al. 1993, Karban and Strauss 1993, DeClerck-Floate and Price 1994). Second, axillary regrowth should be favored, since gall damage occurred during a short period early in the season, when rosinweed shoots grow most rapidly (Fay and Hartnett 1991). Third, axillary regrowth could effectively replace lost reproductive structures and help maintain normal size/fecundity allometry (Hartnett 1990, Fay and Hartnett 1991, Aarsen and Taylor 1992).

Resources, competition, and the galls themselves appear to have constrained a tolerance-enhancing axillary regrowth response in galled field rosinweed. Resources clearly limited rosinweed's regrowth response, since water and fertilizer strongly increased axillary biomass. Competition also limited axillary growth, since ungalled, unsupplemented garden plants produced more axillary biomass than ungalled field plants, despite lower soil nutrient availability, equal N reserves, and similar photosynthetic capacity and water availability. Field rosinweed grew amid a matrix of grasses and other forbs, and resulting low canopy light levels probably inhibited axillary meristem activity (Hillman 1984).

Galls appeared to further limit axillary growth by mimicking the apical meristem. Galls share several physiological traits with meristems, including auxin and cytokinin production (Byers et al. 1976, Weis et al. 1988), high metabolic rates (Bronner 1992), and effects on distant plant parts (Weis and Kapelinski 1984, Larson and Whitham 1991, Fay et al. 1993). Axillary growth limitation by galls is also suggested because other kinds of meristem damage (e.g., browsing by deer) typically stimulate axillary growth in field rosinweed (P. Fay, *personal observation*). However, axillary limitation turned to axillary stimulation in the garden when resource and competitive constraints were removed. This interaction may be unique, because few herbivores can actively mediate a plant's ability to tolerate the resulting damage.

Gall-insect performance

Gall wasps were mostly unaffected by changes in competition and resources that so strongly affected rosinweed's tolerance of gall damage. As a result, *Antistrophus* appears distinct from other gall-insect species, since plant vigor often governs gall-insect fitness (Whitham 1978, Preszler and Price 1988, Waring and Cobb 1989). From rosinweed's perspective, competition and resource availability are unlikely to affect future gall-insect population levels. This avoids a positive feedback loop where plant regrowth after gall-insect attack favors further attack in later years (Craig et al. 1986).

From *Antistrophus*' perspective, independence of rosinweed tolerance and gall-wasp performance suggest that gall-wasp populations are not limited by rosinweed resource availability. Instead, fire likely constitutes the major population control for *Antistrophus*. Spring fires cause extensive *Antistrophus* mortality (Fay and Samenus 1993) and are implicated in population cycling in several other grassland gall-insect species (D. Hartnett and P. Fay, *unpublished data*). *Antistrophus* may actively avoid varying rosinweed resource availability. For example, by suppressing axillary meristems, galls eliminate potential competitors for resources (Sachs et al. 1993) and may make extra resources available for gall and gall-insect growth.

The independence of rosinweed tolerance and gall-insect parasitism rates suggests there may be no benefit to rosinweed to attract *Antistrophus* natural enemies. Plant characteristics affect parasitism rates in some herbivores (Price et al. 1980, Shepard and Dahlman 1988, Fox et al. 1990). However, once *Antistrophus*' gall has formed, its damage is done and gall-insect parasitism cannot restore the damaged apical meristem and recover lost plant fitness.

Conclusions

Under normally encountered growing conditions, rosinweed poorly tolerates galls formed by *Antistro-*

TABLE 5. ANOVA *F* statistics (df in parentheses) for main effects and interactions affecting *Silphium integrifolium* achene characteristics and gall-insect performance, and *Eurytoma* emergence.

	Achene mass (mg)	Germination rate (%)	No. gall wasps per gall	No. *Eurytoma* per gall	Sex ratio (females: total)	Gall-wasp mass (mg)	
						Males	Females
Source plant (= block)	4.65† (14, 98)	1.91* (14, 98)	2.46* (14, 39)	2.22* (14, 39)	0.91NS (13, 25)	15.82† (11, 13)	6.73† (13, 20)
Galls	6.74* (1, 98)	0.28NS (1, 98)	...	...	...	...	...
Water	1.57NS (1, 98)	2.99† (1, 98)	0.01NS (1, 39)	0.43NS (1, 39)	2.34NS (1, 25)	7.14* (1, 13)	2.96† (1, 20)
Fertilizer	4.73* (1, 98)	9.10** (1, 98)	0.02NS (1, 39)	0.02NS (1, 39)	0.66NS (1, 25)	0.10NS (1, 13)	0.08NS (1, 20)
Galls × Water	0.01NS (1, 98)	0.12NS (1, 98)	...	...	...	...	...
Galls × Fertilizer	0.06NS (1, 98)	0.55NS (1, 98)	...	...	...	...	...
Water × Fertilizer	1.60NS (1, 98)	0.01NS (1, 98)	3.29† (1, 39)	5.12* (1, 39)	0.48NS (1, 25)	0.08NS (1, 13)	1.79NS (1, 20)
Galls × Water × Fertilizer	0.65NS (1, 98)	0.00NS (1, 98)	...	...	...	...	...

NS = not significant; † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

phus silphii, despite possessing the mechanisms required to counteract gall damage. Multiple constraints imposed by the herbivore and rosinweed's growing conditions prevented a tolerance-enhancing axillary regrowth response. We view this as the typical situation for forbs in highly competitive grassland plant communities, distinguishing them from species in more open environments where equal compensation for herbivory may be more common (e.g., Maschinski and Whitham 1989). Like many galling species (Hartnett and Abrahamson 1978, Dennill 1985, Sacchi et al. 1988), *Antistrophus* exerted strong structural and re-

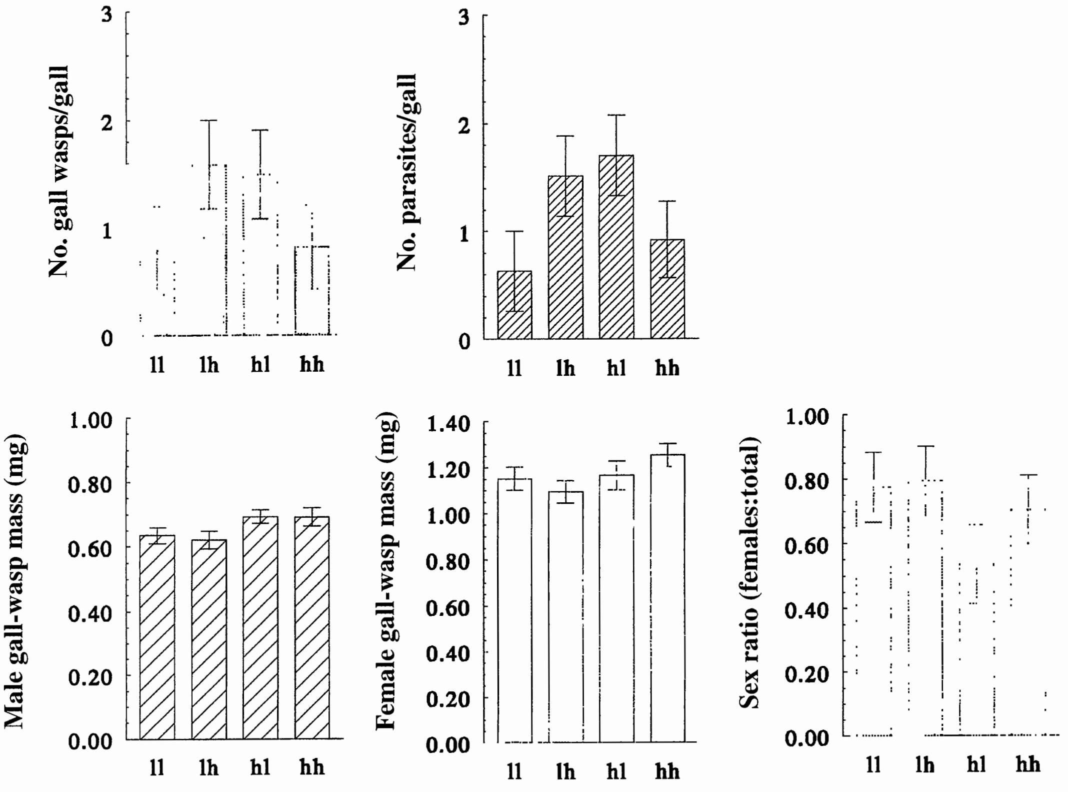

FIG. 8. Gall-wasp and parasite emergence, and gall-wasp body masses and sex ratios in watered or fertilized *Silphium integrifolium* (means ± 1 SE). ll = low H_2O, low fertilizer, lh = low H_2O, high fertilizer, etc. Statistical analysis is presented in Table 5.

productive impacts on rosinweed, but rosinweed exerted minor reciprocal impacts on gall-insect performance. Gall insects may be buffered from environmental variation (Fay et al., *in press*), disconnecting plant and herbivore population dynamics.

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