

Increased photosynthesis and water potentials in *Silphium integrifolium* galled by cynipid wasps

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Abstract. Interactions between drought, insect herbivory, photosynthesis, and water potential play a key role in determining how plants tolerate and defend against herbivory, yet the effects of insect herbivores on photosynthesis and water potential are seldom assessed. We present evidence that cynipid wasp galls formed by *Antistrophus silphii* on *Silphium integrifolium* increase photosynthesis (A), stomatal conductance (g), and xylem water potential (Ψ). Preliminary data showed that in drought-stressed plants galled shoots had 36% greater A, and 10% greater stem Ψ than ungalled shoots, while in well-watered plants leaf gas exchange was not affected by galls. We hypothesized that 1) galled shoots have higher Ψ , g, and A than ungalled shoots, but this difference diminishes if plant drought stress is reduced, and 2) galls can reduce decreases in A and g if water availability decreases. A field experiment testing the first hypothesis found that galls increased g and Ψ , but that differences between galled and ungalled shoots did not diminish after plants were heavily watered. A laboratory test of the second hypothesis using potted *Silphium* found that galled plants had smaller drops in A and g over a 4-day dry-down period. A vs g and A vs intercellular CO₂ concentration relationships were consistent with the explanation that increased Ψ allows galls to increase A by reducing stomatal limitation of A, rather than by altering sink-source relationships or by removing low- Ψ limitations on non-stomatal components of A. Our working hypothesis is that galls increase Ψ and A by reducing the shoot:root ratio so that the plant is exploiting a greater soil volume per unit leaf area. We argue that increased A is an ineffective way for *Silphium* to compensate for negative effects of gall insect attack. Instead, increased Ψ and A may protect gall insects from variation in resource availability caused by periodic drought stress, potentially reducing negative effects of drought on plant quality and on gall insect populations.

Key words: Photosynthesis – Water potential – Gall insect – *Silphium integrifolium* – Plant-insect interactions

The interactions between drought, insect herbivory, photosynthesis, and water potential play a key role in determining how plants tolerate and defend against herbivory. For example, several authors (Bryant et al. 1983; Tuomi et al. 1984; Coley et al. 1985; Bazzaz et al. 1987) suggest that plant carbon-nutrient balances control the amount and type of anti-herbivore defenses in plants. Plant physiological functioning is an important determinant of a plant's ability to compensate for tissues lost to herbivores (Maschinski and Whitham 1989; Whitham et al. 1991). Mattson and Haack (1987) have suggested that drought stress causes a suite of changes in plants which can culminate in insect outbreaks. However, if insect herbivores modify levels of plant drought stress then they may have an important effect on the quality of their host plants as a resource.

The effect of insect herbivores on plant photosynthesis and water potential has received relatively little attention compared to interactions between insect herbivores and plant secondary chemistry (e.g. Rosenthal and Janzen 1979; Spencer 1988). This seems surprising because insect herbivores damage leaves, shoots, roots, and other plant parts directly involved in the acquisition of carbon, nutrients, and water. In contrast, the effect of drought on photosynthesis and water potential has been relatively well studied (e.g. Fitter and Hay 1988; Hale et al. 1987), but how insects modify plant photosynthesis and water potential (Parker 1985) remains to be examined in natural systems.

In this paper we present evidence from field and laboratory studies showing that cynipid wasp galls formed by *Antistrophus silphii* on the composite *Silphium integrifolium* increase photosynthesis and water potential. These species are well-suited for studying the effects of insects on plant physiological processes because *Antistrophus* converts normal apical meristems into galls which are vascularly integrated with the rest of the plant, leaving other plant organs intact.

Study organisms

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 which form a tightly packed clump. *Silphium* shoot growth begins in spring from belowground buds initiated the previous year on a stout woody rhizome. Stems reach 1–2 m tall and bear 15–25 pairs of opposite leaves. Flowering occurs from July to October. Each shoot produces a terminal inflorescence of 1–15 flower heads (capitula). All aboveground parts die back by the end of October, and are completely replaced the following year.

Antistrophus silphii Gil. (Cynipidae) is a common insect herbivore on *Silphium*. *Antistrophus*' life cycle starts in early May, when *Silphium* shoots are beginning to elongate. Female *Antistrophus* emerge from previous year's galls, mate, locate a shoot, and oviposit into its apical meristem. Within 2 weeks, the shoot's height growth slows and the apical meristem swells into a sphere 1–4 cm in diameter. Up to 30 larvae feed within individual chambers in the gall, developing to their final larval instar (III) before *Silphium* becomes dormant. Larvae overwinter in the gall, then pupate in April. Further details on the biology of *Silphium* and *Antistrophus* can be found in Fay and Hartnett (1991).

Methods

Field portions of this study were conducted in an annually burned old field at 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.

1. Observations on drought-stressed and well-watered plants

In June 1989 we made preliminary observations comparing leaf net photosynthesis (A , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance (g , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), intercellular CO_2 concentration (C_i , ppm) and stem xylem pressure potential (Ψ , MPa) of galled and ungalled *Silphium* shoots in drought-stressed plants found in natural field conditions and in well-watered plants in a common garden established from rhizome cuttings in March, 1989.

Drought stressed plants: Leaf A and g were measured on the first leaf beneath the gall on a galled shoot and the first fully expanded leaf beneath the apical meristem on an ungalled shoot in each of eight plants. Leaves were at similar heights on the shoots and so did not differ greatly in age. A and g were measured with a portable infrared gas analyzer (IRGA) system (LI-COR LI-6200) using a 1 liter cuvette.

In another set of 8 plants, midday stem Ψ was measured using a pressure chamber (PMS Model 1000) on a galled and an ungalled shoot from each plant cut between the second and third leaf below the gall or apical meristem.

Well-watered plants: A and g of one galled and one ungalled shoot in each of eight plants were measured as in the drought-stressed field plants. Each leaf was measured immediately after being detached from the shoot. Ψ was not measured in the well-watered plants. However these plants were irrigated approximately 4h/d, 3–4 d/wk, so that soil water was definitely abundant compared to the drought-stressed plants.

Paired *t*-tests were used to evaluate differences between galled and ungalled shoot means.

2. Field watering experiment

In June 1990 leaf g was compared on galled and ungalled shoots before and after plants were heavily watered to experimentally examine how galls and water availability interact to affect stomatal conductance and stem Ψ .

Pre-watering measurements: Ten plants were chosen from the same field population used in 1989. Predawn shoot Ψ was measured on a galled and an ungalled shoot in each plant using a pressure chamber. Then 20 plants were randomly chosen and from each a galled and an ungalled shoot with equal leaf area were selected. Shoots were matched for leaf area to equalize their potential for transpiration. Stomatal conductance was measured on the abaxial side of the third and seventh leaf below the gall or apical meristem using a transient porometer (Delta T Instruments, Ltd.). Measurements were made between 0900–1200 h during cloud-free conditions. The average of the two leaf measures was used as the shoot response. Leaves were measured under the illumination conditions in which they were found. After porometry, galled and ungalled shoots were collected at midday for Ψ determination.

Watering treatment. For 9 days after pre-water g and Ψ measurements, the 20 plants were each given a total of 34 liters of water, applied slowly to minimize runoff. An additional 51.0 mm of precipitation fell during this period.

Post-watering measurements: Predawn Ψ was measured on one ungalled shoot from each of the 20 irrigated plants. Predawn Ψ was not measured on galled shoots because galls had no effect on predawn Ψ in the pre-watering measurements. Then g and midday Ψ measurements were repeated (1000–1300 h) on another leaf area-matched pair of galled and ungalled shoots.

Design and analysis. Two different sized experimental units were involved in the watering experiment. The whole plant ($n=20$) was a blocking factor and was the experimental unit watered. The shoot was the unit galled ($n=40$ galled + 40 ungalled). The experimental design was a split-plot. *F*-tests were constructed using these error terms: mean square (MS) plant \times water for the block and the water effect, and the remaining model MS error for the galling and water \times galling effects.

3. Laboratory measurements

Leaf A , g , C_i , and Ψ were determined on experimentally galled and ungalled potted *Silphium* plants allowed to dry after watering.

Silphium rhizomes were transplanted into soil in 4 l pots in spring 1990, and allowed to overwinter outdoors. In April 1991, immediately before gall wasp emergence, 3 plants were covered with nylon tulle to exclude wasps and prevent gall formation. Three more plants were galled by placing a gall containing soon-to-emerge gall wasps in the pot so that the gall was at roughly the height of the growing meristems. Gall wasps were then allowed to freely oviposit. Galls formed on all shoots in plants exposed to gall wasps, while covered plants remained gall-free.

Plants were fertilized with slow release fertilizer (Sierra 17-6-10 with micronutrients), watered as required, and grown outdoors until galls were fully enlarged. Plants were then brought indoors and allowed to acclimate for 24 h under an 800 W multivapor high intensity discharge lamp at 14:10 L:D photoperiod at 24–27°C.

A , g , and C_i were measured between 0900 and 1400 h on the first, second, and fourth days after plants were watered to saturation on a leaf 7–8 nodes above the soil surface on two shoots per galled and per ungalled plant. The same leaves were measured each day of the experiment.

Leaves were measured with a null-balance gas exchange system (Pacsys 9900) capable of maintaining constant CO_2 concentration, leaf temperature, and relative humidity during the course of the measurement. Conditions at measurement were 320 ppm CO_2 , 25°C, 40% RH and 1200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ photosynthetic photon flux density.

Leaf Ψ was measured concurrently with photosynthetic determinations. A 1×3 cm leaf strip was taken from a leaf 1 node below the gas exchange leaf. Its Ψ was determined in a thermocouple psychrometer sample chamber (Decagon SC-10A) calibrated with NaCl solutions. Leaf strips were allowed to equilibrate in the sample chamber for 15 min and the Ψ determination made after 1 min.

Design and analysis. This experiment used a repeated-measures design, which was treated as a split-plot for analysis. The potted plant ($n=6$) was the whole plot factor and day was the subplot factor.

Results

1. Field and garden observations

In the well-watered garden plants, A, g, and Ci did not differ between galled and ungalled shoots (Table 1). In drought-stressed field plants A and g were less than half that of the well-watered plants, reflecting low water availability in the field. In galled shoots A was 36% greater, stem Ψ was 10% greater, but g and Ci did not differ compared to ungalled shoots, suggesting that galled shoots in drought-stressed plants were less affected by low water availability than ungalled shoots.

When A vs g for the drought-stressed and well-watered plants are plotted on the same graph (Fig. 1), regression analysis shows that g explains 90% of the variation in A, suggesting galls may be altering the degree of stomatal limitation on A. Also, in the drought-stressed plants, ungalled shoot A vs g values were mostly clustered at the low end of the gradient, suggesting consistently limited access to water compared to galled shoots.

These observations suggest two specific hypotheses:

1. Galled shoots have higher Ψ , g, and A than ungalled shoots, but the difference diminishes when plant drought stress is reduced.
2. Galls can reduce decreases in A and g if water availability decreases.

2. Field watering experiment

The field watering experiment tested the first hypothesis.

Pre-watering predawn Ψ (Fig. 2a) was equal in galled and ungalled shoots (paired $t=0.452$, $p=0.662$), indicating no apparent differences in soil water availability to these shoots. Predawn Ψ was higher at the post-watering measurement (two-sample $t=12.793$, $p=0.0001$), indicating

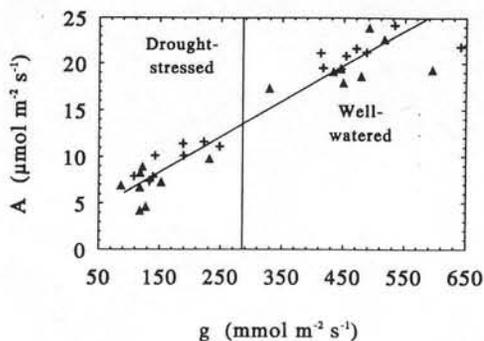


Fig. 1. Regression of A vs g for galled (+) and ungalled (▲) shoots from drought-stressed and well-watered *Silphium integrifolium* measured in 1989. $A=3.308+0.035(g)$ $F=287.28$ $p<.0001$, $r^2=0.902$. The vertical line separates data values for drought-stressed field plants, left, from data for well-watered common garden plants, right

the watering treatments increased soil water availability to the plants.

Midday Ψ (Fig. 2b) and leaf g (Fig. 2c) were increased by heavy watering, and galled shoots maintained higher midday Ψ and g than ungalled shoots (Table 2). Since galled and ungalled shoots were matched for leaf area, this result suggests that galled shoots had greater access to soil moisture than did ungalled shoots from the same plant. Galls increased g and Ψ equally before and after the plants were watered (Table 2), suggesting that differences between galled and ungalled shoots in water status did not diminish when drought stress was reduced.

3. Laboratory experiment

The lab experiment tested the second hypothesis.

Galled plants had smaller drops in A and g over the 4-day dry-down period (Fig. 3a, b, Table 3). A and g were equal in galled and ungalled plants on day 1. By day 4, A and g in ungalled plants had dropped over 50%, while A and g in galled plants had dropped about 25%.

Ci and Ψ also decreased as soil moisture was depleted (Fig. 3c, d, Table 3). Galling had no effect on Ci, and caused only a marginal increase in Ψ because of the unexpected increase in ungalled plant Ψ on Day 2.

These data are consistent with the explanation that increased Ψ allows galls to increase A by reducing stomatal limitation of A, rather than by altering sink-source

Table 1. Mean (± 1 SE) leaf A, g, Ci, and stem Ψ of galled and ungalled *Silphium integrifolium* shoots in plants growing in a drought-stressed field site and leaf A, g, and Ci from plants in a well-watered common garden

| | Drought Stressed | | | | Well-Watered | | | |
|--|--------------------|--------------------|-------|-------|--------------------|--------------------|-------|-------|
| | Galled | Ungalled | t | p< | Galled | Ungalled | t | p< |
| A ($\mu\text{moles m}^{-2} \text{s}^{-1}$) | 9.66 \pm 0.62 | 7.07 \pm 0.69 | 2.799 | .0142 | 21.20 \pm 0.53 | 19.76 \pm 0.81 | 1.336 | .2234 |
| g ($\text{mmoles m}^{-2} \text{s}^{-1}$) | 171.24 \pm 17.11 | 134.06 \pm 15.26 | 1.622 | .1272 | 482.04 \pm 26.50 | 466.96 \pm 26.91 | 0.836 | .4310 |
| Ci (ppm) | 212.25 \pm 5.35 | 221.13 \pm 10.93 | 0.729 | .4780 | 235.63 \pm 3.97 | 238.63 \pm 4.36 | 0.771 | .4660 |
| Ψ (MPa) | -1.53 \pm 0.03 | -1.70 \pm 0.02 | 5.400 | .0010 | | | | |

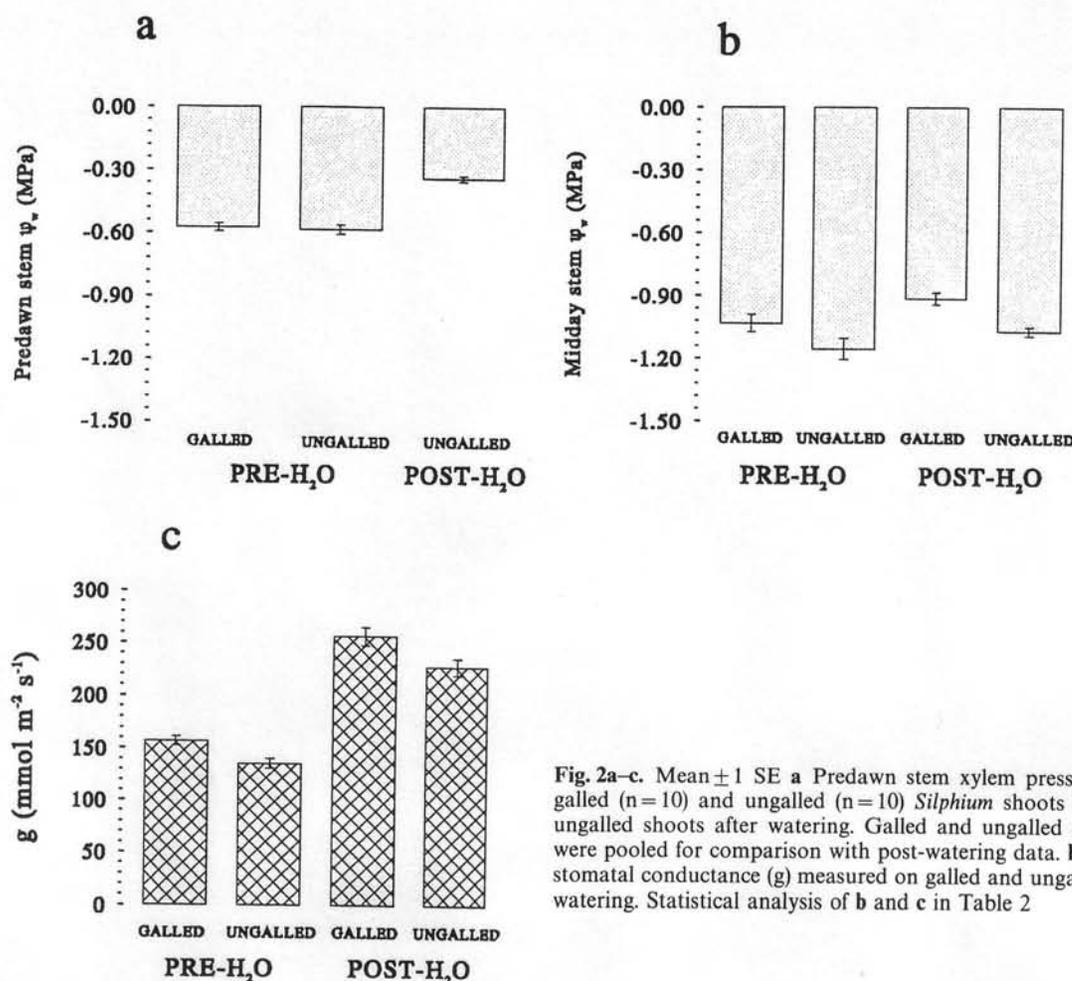


Fig. 2a-c. Mean \pm 1 SE a Predawn stem xylem pressure potential (Ψ) of paired galled ($n=10$) and ungalld ($n=10$) *Silphium* shoots before watering, and of 20 ungalld shoots after watering. Galled and ungalld pre-watering measurements were pooled for comparison with post-watering data. b Midday stem Ψ and c leaf stomatal conductance (g) measured on galled and ungalld shoots before and after watering. Statistical analysis of b and c in Table 2

Table 2. Analysis of variance of midday stem water potential (Fig. 2b) and leaf stomatal conductance data (Fig. 2c) from galled and ungalld *Silphium integrifolium* shoots measured in the 1990 field watering experiment

| Source | df | Midday Ψ | | | Stomatal Conductance | | |
|------------------------|----|---------------|-------|-------|----------------------|--------|-------|
| | | MS | F | $p <$ | MS | F | $p <$ |
| Block (= Plant) | 19 | 5.364 | 1.91 | .0843 | 2861.467 | 1.66 | .1384 |
| Water | 1 | 21.321 | 7.58 | .0126 | 183164.475 | 106.41 | .0001 |
| Block \times Water | 19 | 2.813 | | | 1721.299 | | |
| Galling | 1 | 38.921 | 28.02 | .0001 | 12557.803 | 32.34 | .0001 |
| Water \times Galling | 1 | 0.578 | 0.42 | .5228 | 235.065 | 0.61 | .4414 |
| Error | 38 | 52.784 | | | 388.360 | | |

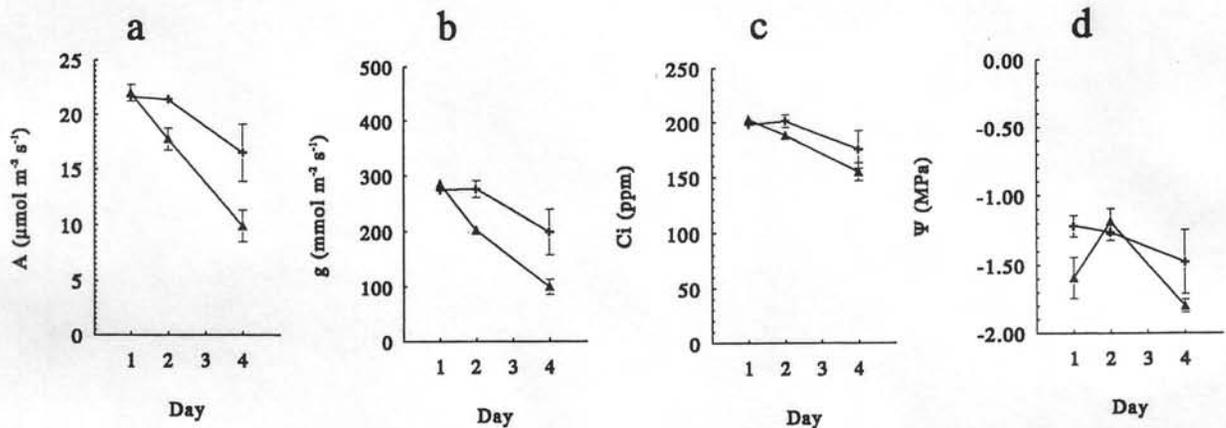
relations or by removing low Ψ limitations on non-stomatal components of A. If galls were increasing A through non-stomatal means, then at a given g or Ci galled plants might be expected to have higher A than ungalld plants. Plots of A vs g (Fig. 4) and A vs Ci (Fig. 5) indicate no such pattern. Furthermore, multiple regression using g and Ci as predictor variables explained 95% of the variation in A, but Ci could not explain significantly more variation ($t=1.391$, $p=.1846$) after that explained by g ($t=9.248$, $p<.0001$).

Discussion

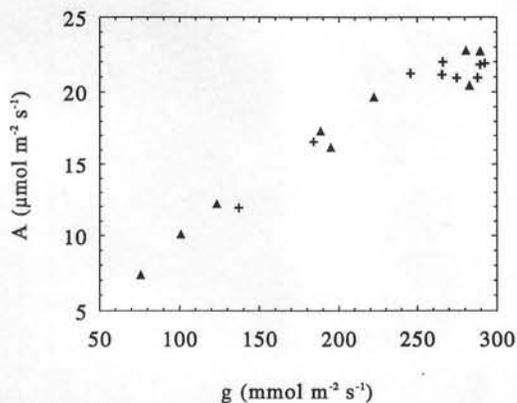
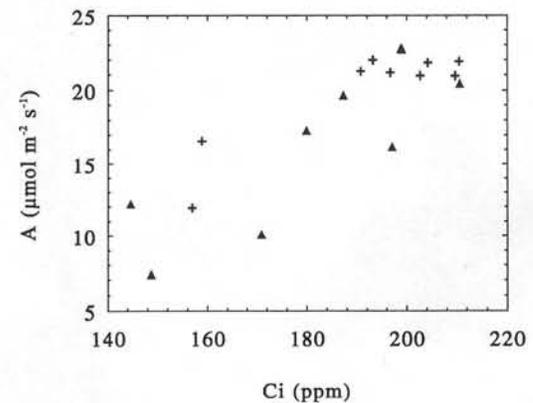
Our results showed that *Antistrophus silphii* galls on *Silphium integrifolium* increased leaf photosynthesis, stomatal conductance, and water potential over ungalld shoots, and that galled plants experienced a smaller drop in A and g over a 4-day period after watering. These results contrast significantly with those from other systems. For example, when leaves are damaged by aphids, leafhoppers, scale insects, mites, leaf miners, or artificial defoliation

Table 3. Analysis of variance of leaf A, g, Ci, and Ψ from galled and ungalled *Silphium integrifolium* plants measured in the 1991 laboratory experiment (Fig. 3)

| Source | df | Photosynthetic Rate | | | Stomatal Conductance | | | Intercellular CO ₂ | | | Leaf Ψ | | |
|----------------------|----|---------------------|-------|-------|----------------------|-------|-------|-------------------------------|-------|-------|-------------|------|-------|
| | | MS | F | p < | MS | F | p < | MS | F | p < | MS | F | p < |
| Galling | 1 | 49.175 | 5.29 | .0830 | 13060.426 | 7.41 | .0529 | 417.133 | 1.79 | .2550 | 19.137 | 5.36 | .0815 |
| Plant (Galling) | 4 | 9.303 | | | 1762.917 | | | 236.601 | | | 3.568 | | |
| Day | 2 | 119.985 | 37.09 | .0001 | 26482.293 | 33.66 | .0001 | 2175.319 | 10.00 | .0067 | 25.882 | 4.77 | .0434 |
| Galling \times Day | 2 | 18.010 | 5.57 | .0305 | 4920.018 | 6.25 | .0232 | 253.22 | 1.16 | .3599 | 9.145 | 1.68 | .2453 |
| Error | 8 | 3.235 | | | 786.669 | | | 217.508 | | | 3.235 | | |

**Fig. 3a–d.** Mean \pm 1 SE a leaf photosynthesis a, b stomatal conductance (g), c intercellular CO₂ concentration (Ci), and d leaf water potential (Ψ) of galled (+) and ungalled (▲) potted *Silphium* plants 1,

2, and 4 days after being watered to saturation in the 1991 laboratory experiment. Statistical analysis in Table 3. Standard errors not shown fall within the symbols

**Fig. 4.** Individual plant A vs g for galled (+) and ungalled (▲) *Silphium* from the laboratory experiment**Fig. 5.** Individual plant A vs Ci for galled (+) and ungalled (▲) *Silphium* from the laboratory experiment

their photosynthetic rates are reduced (Hall and Ferree 1976; Poston et al. 1976; Andrews and La Pré 1979; Sances et al. 1979, 1982; Johnson et al. 1983; Womack 1984; Trumble et al. 1985; Wood et al. 1985; Warrington et al. 1989; Flinn et al. 1990; Schaffer and Mason 1990; but see Daly and McNeil 1987). An important distinction between our study and those just cited is that cynipid galls leave *Silphium* leaves intact, and our results are consistent with

studies finding that photosynthetic rates appear to generally increase in undamaged foliage remaining after defoliation (Hodgkinson 1974; Martens and Trumble 1987) and in regrowth foliage (Heichel and Turner 1983).

Few studies have considered interactions between insects, photosynthesis, and drought; those which did considered the consequences for the insect (Waring and Price 1990; Youngman et al. 1988; Talhouk et al. 1990). In

studies focusing on consequences for the plant, results have been equivocal. Spider mites feeding on almond leaves were found to reduce leaf A more at high than at low water stress in one year, but to reduce A more at low than at high water stress levels the next year (Youngman and Barnes 1986). Another study of the effects of citrus red mites on orange leaves found no consistent relationship between mite damage, water stress, and leaf gas exchange (Hare et al. 1989).

In the field experiment, the effect of galls on g did not depend on the overall level of drought stress experienced by the plant. In contrast, in the laboratory experiment galls increased A and g when plants were drought stressed (Fig. 3, Day 4) but not when plants were well-watered (Day 1). This discrepancy in results is likely due to differences in the range of Ψ occurring in the two experiments. In the field experiment average midday Ψ ranged from -0.90 to -1.15 Mpa, which is probably in a Ψ range where A and g are relatively little affected by changes in Ψ . In the lab experiment, average midday Ψ ranged from -1.20 to -1.80 Mpa, which is probably in a range where A and g are more strongly affected by changes in Ψ . We predict that had conditions been dryer when the field experiment was conducted its results would agree with the results of the laboratory experiment. Taken together, the results of the two experiments support the conclusion that galls reduce drops in A and g usually exhibited by drought stressed *Silphium*.

An ineffective compensatory response

The gall-induced increase in leaf photosynthesis can be interpreted as a compensatory response by the plant lessening the negative effect of galls on plant performance. The extent to which increased photosynthesis enables *Silphium* to compensate for gall damage depends on how much galls increase whole plant carbon uptake compared to how much fixed carbon is pre-empted by the gall and unavailable for normal growth. Galls increased A as much as 36% in leaves near the gall (Table 1) but galls also reduce shoot leaf numbers by 37% and cause a 1/3 loss in biomass production (Fay and Hartnett 1991). These data suggest that whole plant carbon uptake is most likely reduced in galled compared to ungalled plants, therefore increased A appears to be relatively ineffective as a means of *Silphium* compensating for the effects of galls.

The fate of the additional carbon fixed in galled shoots by more rapidly photosynthesizing leaves is uncertain, and depends on the gall's sink strength compared to the sink strength of the normal shoot parts the gall replaced and the strength of other sinks in the plant. Observational and experimental data (Figs. 1, 3–5, Table 3) suggest that cynipid galls are no stronger as sinks than the normal growth they replace because there was no evidence that leaf A differed between galled and ungalled shoots when compared at the same stomatal conductance or C_i (Figs. 1, 4–5). Biomass allocation studies on this system are consistent with this interpretation. Dry matter allocation to stems in lightly-galled plants equals dry matter allocation to stems + galls in heavily galled plants (Fay and Hartnett 1991). Greater allocation to stems + galls is expected if

galls are strong sinks. The other major sinks in the plant are flower heads and the rhizome. Carbon isotope studies will be required to assess patterns of carbon movement among the major sinks in galled *Silphium* (e.g. Larsen and Whitham 1991).

The evidence so far argues that galls increase A solely by improving *Silphium's* water status, rather than through altered sink-source interactions. We suspect that galls increase Ψ by altering the shoot:root ratio. Recent experimental evidence (Fay et al. unpublished work) has shown that heavily galled plants have reduced leaf area but unchanged root biomass compared to gall-free plants, suggesting that galls increase Ψ by reducing transpiring area supported per unit of root. However, increased Ψ may result from increased root growth in individual galled shoots. Although shoots are connected by a stout root-stock-like rhizome, each shoot is supported by a cluster of roots at its base. Increased root growth on galled shoots is a possible explanation for higher Ψ and g compared to leaf area-matched ungalled shoots from the same plant (Fig. 2).

Benefits to the insect

Price et al. (1987) have argued that protection of the gall insect against hygrothermal stress was a major selective benefit in the evolution of gall formation. Based on our data we hypothesize that protection of the insect from variation in resource supply caused by plant responses to drought stress is another selective benefit in the evolution and maintenance of gall-insect life histories. During the hotter and dryer parts of the growing season many plants experience large diurnal fluctuations in Ψ causing closure of stomata and reduction in carbon uptake until later in the day when conditions moderate. Similar effects also occur over days or weeks between periods of rainfall. Since galled shoots and plants maintain higher Ψ , daily variations in A may be reduced or eliminated, and decreases in A over longer periods may be delayed. As a result, more carbon would be fixed than if the gall did not increase Ψ , and more resources potentially available for the insect. This may provide a mechanism by which insects which are completely committed to one shoot for a full year could exert some control over their food resource.

Drought and plant quality

A large body of evidence reviewed by Mattson and Haack (1987) suggests that drought stress has a positive effect on populations of free-feeding insects by increasing nutrient availability, facilitating the insect's ability to detoxify defense compounds, and bolstering insect immune systems until herbivore populations become so large they begin to degrade the quality of their resource. Our results are consistent with the trend in gall-formers that their density, growth, and reproduction are highest on non-drought stressed or more vigorous plant parts (Whitham 1978; Craig et al. 1986; Preszler and Price 1988; Fay and Whitham 1990; but see Waring and Price 1990), indicating that drought stress has negative effects on gall-forming insect populations. Our results show that some gall for-

mers can reduce plant drought stress, potentially increasing host plant quality and reducing any negative effects of drought stress on gall insect populations.

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References

- Andrews KL, La Pré LF (1979) Effects of Pacific Spider Mite on physiological processes of almond foliage. *J Econ Entomol* 72: 651–654
- Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF (1987) Allocating resources to reproduction and defense. *Bioscience* 37: 58–67
- Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357–368
- Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. *Science* 230: 895–899
- Craig TP, Price PW, Itami JK (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* 67: 419–425
- Daley PF, McNeil JN (1987) Canopy photosynthesis and dry matter partitioning of alfalfa infested by the alfalfa blotch leafminer (*Agromyza frontella* (Rondani)). *Can J Plant Sci* 67: 433–443
- Fay PA, Hartnett DC (1991) Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp. *Oecologia* 88: 243–250
- Fay PA, Whitham TG (1990) Within-plant distribution of a galling adelgid (Homoptera: Adelgidae): the consequences of conflicting survivorship, growth, and reproduction. *Ecol Entomol* 15: 245–254
- Fitter AH, Hay RKM (1988) *Environmental Physiology of Plants*, 2nd ed. Academic Press, London
- Flinn PW, Hower AA, Kniewel DP (1990) Physiological response of alfalfa to injury by *Empoasca fabae* (Homoptera: Cicadellidae). *Environm Entomol* 19: 176–181
- Hale MG, Orcutt DM, Thompson LK (1987) *The physiology of plants under stress*. Wiley, New York
- Hall FR, Ferree DC (1976) Effects of insect injury simulation on photosynthesis of apple leaves. *J Econ Entomol* 69: 245–248
- Hare JD, Pehrson HE, Clemens T, Youngman RR (1989) Combined effects of differential irrigation and feeding injury by the Citrus Red Mite (Acari: Tetranychidae) on gas exchange of orange leaves. *J Econ Entomol* 82: 204–208
- Heichel GH, Turner NC (1983) CO₂ assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia* 57: 14–19
- Hodgkinson KC (1974) Influence of partial defoliation on photosynthesis, photorespiration and transpiration by Lucerne leaves of different ages. *Austr J Plant Physiol* 1: 561–578
- Johnson MW, Welter SC, Toscano NC, Ting IP, Trumble JT (1983) Reduction of tomato leaflet photosynthesis rates by mining activity of *Liriomyza sativae* (Diptera: Agromyzidae). *J Econ Entomol* 76: 1061–1063
- Larson KC, Whitham TG (1991) Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interactions. *Oecologia* 88: 15–21
- Mani MS (1961) *Ecology of plant galls*. W. Junk, The Hague
- Martens B, Trumble JT (1987) Structural and photosynthetic compensation for leafminer (Diptera: Agromyzidae) injury in Lima Beans. *Environm Entomol* 16: 374–378
- Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *Am Nat* 134: 1–19
- Mattson WJ, Haack RA (1987) The role of drought stress in provoking outbreaks of phytophagous insects. In: Barbosa P, Schultz JC (eds) *Insect Outbreaks*. Academic Press, San Diego, pp 365–407
- Poston FL, Pedigo LP, Pearce RB, Hammond RB (1976) Effects of artificial and insect defoliation on soybean net photosynthesis. *J Econ Entomol* 69: 109–112
- Preszler RW, Price PW (1988) Host quality and sawfly populations: a new approach to life table analysis. *Ecology* 69: 2012–2020
- Price PW, Fernandes GW, Waring GL (1987) Adaptive Nature of Insect Galls. *Environm Entomol* 16: 15–24
- Rosenthal GA, Janzen DH (1979) *Herbivores, their interaction with secondary plant metabolites*. Academic Press, New York
- Sances FV, Wyman JA, Ting IP (1979) Physiological responses to spider mite infestation on strawberries. *Environm Entomol* 8: 711–714
- Sances FV, Toscano NC, Hoffmann MP, La Pre LF, Johnson MW, Bailey JB (1982) Physiological responses of avocado leaves to avocado brown mite feeding injury. *Environm Entomol* 11: 516–518
- Schaffer B, Mason LJ (1990) Effects of scale insect herbivory and shading on net gas exchange and growth of a subtropical tree species (*Guaiacum sanctum* L.). *Oecologia* 84: 468–473
- Spencer KC (1988) *Chemical Mediation of Coevolution*. Academic Press, San Diego
- Talhok SN, Nielsen DG, Montgomery ME (1990) Water deficit, defoliation, and birch clones: short-term effect on gypsy moth (Lepidoptera: Lymantriidae) performance. *Environm Entomol* 19: 937–942
- Trumble JT, Ting IP, Bates L (1985) Analysis of physiological, growth, and yield responses of celery to *Liriomyza trifolii*. *Entomologia Experimentalis et applicata* 38: 15–21
- Tuomi J, Niemelä P, Chapin FS, Bryant JP, Sirén S (1984) Defensive responses of trees in relation to their carbon/nutrient balance. In: Mattson WJ, Levieux J, Bernard-Dagan C (eds) *Mechanisms of woody plant defenses against insects*. Springer, New York, pp 57–72
- Waring GL, Price PW (1990) Plant water stress and gall formation (Cecidomyiidae: *Asphondylia* spp.) on creosote bush. *Ecol Entomol* 15: 87–95
- Warrington S, Cottam DA, Whittaker JB (1989) Effects of insect damage on photosynthesis, transpiration and SO₂ uptake by sycamore. *Oecologia* 80: 136–139
- Whitham TG (1978) Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* 59: 1164–1176
- Whitham TG, Maschinski J, Larson KC, Paige KN (1991) Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, New York, pp 227–256
- Womack CL (1984) Reduction in photosynthetic and transpiration rates of alfalfa caused by potato leafhopper (Homoptera: Cicadellidae) infestations. *J Econ Entomol* 77: 508–513
- Wood BW, Tedders WL, Thompson JM (1985) Feeding influence of three pecan aphid species on carbon exchange and phloem integrity of seedling pecan foliage. *J Am Soc Horticul Sci* 110: 393–397
- Youngman RR, Barnes MM (1986) Interaction of spider mites (Acari: Tetranychidae) and water stress on gas-exchange rates and water potential of almond leaves. *Environm Entomol* 15: 594–600
- Youngman RR, Sanderson JP, Barnes MM (1988) Life history parameters of *Tetranychus pacificus* McGregor (Acari: Tetranychidae) on almonds under differential water stress. *Environm Entomol* 17: 488–495