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Effects of leaf and sap feeding insects on photosynthetic rates of goldenrod

Gretchen A. Meyer¹ and Thomas H. Whitlow²

¹ Section of Ecology and Systematics and ² Department of Floriculture and Ornamental Horticulture, Cornell University, Ithaca, NY 14853, USA

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Summary. Herbivory can alter the balance between sources and sinks within a plant, and changes in the source-sink ratio often lead to changes in plant photosynthetic rates. We investigated how feeding by three insect herbivores affected photosynthetic rates and growth of goldenrod (*Solidago altissima*). One, a phloem-sap feeding aphid (*Uroleucon caligatum*), creates an additional sink, and the other two, a leaf-chewing beetle (*Trirhabda* sp.) and a xylem-sap feeding spittlebug (*Philaenus spumarius*) both reduce source supply by decreasing leaf area. Plants were grown outside in large pots and insects were placed on them at predetermined densities, with undamaged plants included as controls. All insects were removed after a 12-day feeding period. We measured photosynthetic rates both of damaged leaves and of undamaged leaves that were produced after insect removal. Photosynthetic rates per unit area of damaged leaves were reduced by spittlebug feeding, but not by beetle or aphid feeding. Conductance of spittlebug-damaged leaves did not differ from controls, but internal carbon dioxide concentrations were increased. These results indicate that spittlebug feeding does not cause stomatal closure, but impairs fixation within the leaf. Effects of spittlebug feeding on photosynthetic rates persisted after the insects were removed from the plants. Photosynthetic rates per unit area of leaves produced after insect removal on spittlebug-damaged plants were lower than control levels, even though the measurements were taken 12 days after insect removal. The measurement leaf on spittlebug-damaged plants was reduced in area by 27% relative to the controls, but specific leaf area (leaf area/leaf weight) was increased by 18%. Because of the shift in specific leaf area, photosynthetic rates were also examined per unit leaf weight, and when this was done there were no significant differences between control and spittlebug-damaged plants. Beetle and aphid feeding had no effects on the photosynthetic rate of the leaves produced after insect removal. Plant relative growth rates (in terms of height) were reduced by spittlebugs during the period that the insects were feeding on the plants. Relative growth rates of

spittlebug-damaged plants were increased above control levels after insect removal, but these plants were still shorter than controls 17 days after insect removal. Beetles and aphids did not affect plant relative growth rates or plant height. Feeding by both spittlebugs and beetles reduced leaf area, and the effect of the spittlebug was more severe than that of the beetle. These results show that effects of herbivory on photosynthetic rates cannot be predicted simply by considering changes in the source-sink ratio, and that spittlebug feeding is more damaging to the host plant than beetle or aphid feeding.

Key words: Herbivory – *Solidago* – Aphid – Spittlebug – Defoliation

Plant tissues can be divided into two general categories: sources, which are net exporters of photosynthate, and sinks, which are net consumers of carbohydrates. Photosynthetic rates appear to be controlled, at least in part, by the balance between sources and sinks within the plant. Photosynthetic rates rise when source supply is reduced relative to sink demand (through leaf shading or removal), and tend to fall if sink demand is reduced by removal of buds or roots (Sweet and Wareing 1966; King et al. 1967; Neales and Incoll 1968; Wareing et al. 1968; Gifford and Evans 1981; Hartnett and Bazazz 1983). Although much remains to be learned about controls on photosynthetic rates, these ideas have been extended to make predictions about the impacts of herbivores on plants. Photosynthetic rates might increase in response to leaf-chewing insects, which decrease leaf area, or phloem-sap feeding insects, which act as an additional sink (Crawley 1983). Increased photosynthetic rates following damage have been suggested as a mechanism contributing to plant compensation for herbivory (McNaughton 1979, 1983; Crawley 1983; Verkaar 1988). Compensatory photosynthesis is defined as an increase in photosynthetic rate per unit area of leaves of damaged plants compared to similar-aged leaves on undamaged plants, to exclude changes that occur simply because new leaves on the damaged plants are younger than leaves remaining on undamaged plants (Nowak and Caldwell 1984).

Increases in photosynthetic rates per unit area following damage are well-documented (review by Welter 1989), although alteration of the source-sink balance may not be the sole cause (Mooney and Chiariello 1984). However, the majority of studies reviewed by Welter (1989) reported no change or decreased photosynthetic rates per unit area following herbivory. Differences in methodology among these studies make generalized conclusions difficult. Much of the research demonstrating compensatory photosynthesis has simulated herbivore damage by clipping leaves (e.g. Gifford and Marshall 1973; Bassman and Dickmann 1982; Detling and Painter 1983; Heichel and Turner 1983; Nowak and Caldwell 1984; Wallace et al. 1984). Comparative studies have shown that photosynthetic rate changes are sensitive to the technique used to damage leaves (Hall and Ferree 1976; Poston et al. 1976), and artificial damage is rarely an adequate mimic of real herbivore damage for a variety of plant responses (Baldwin 1990). Experiments with actual herbivores (insects or mites) generally show that photosynthetic rates decrease following damage (e.g. Hall and Ferree 1975; Andrews and LaPre 1979; Sances et al. 1982; Johnson et al. 1983; Whittaker 1984; Parrella et al. 1985; Trumble et al. 1985; Brito et al. 1986; Youngman et al. 1986). However, much of the work with actual herbivores has compared the photosynthetic rates of damaged leaves to undamaged leaves on the same plant (studies cited above, Welter 1989). To show compensatory photosynthesis, a leaf on an undamaged plant must be used as a control. Because of these problems of methodology, we cannot assess whether compensatory photosynthesis is a general mechanism that improves a plant's ability to recover from damage.

The objective of this study was to determine photosynthetic rate responses of goldenrod (*Solidago altissima* L.) to damage by leaf and sap-feeding insects. The insects used were a xylem-sap feeding spittlebug (*Philaenus spumarius*), a phloem-sap feeding aphid (*Uroleucon caligatum*), and a leaf-chewing beetle (*Trirhabda* sp.). Photosynthetic rate determinations were made on leaves present during an 11-day period of insect feeding, and also on undamaged leaves produced after the insects were removed from the plants. Undamaged plants were used as controls. To our knowledge, this is the first study to examine the effects of xylem-sap feeding insects on photosynthetic rates. A second objective was to relate physiological changes to the impacts of these insects on their host plant. Plant height, leaf number, leaf area, and aboveground dry weight were used to assess impacts. Past work with these 3 insects has shown that they differ greatly in their effects on the plant; the spittlebug was the most damaging and the aphid had no detectable effects on vegetative growth (Meyer 1992a). Hartnett and Bazzaz (1984) showed how the distribution of *U. caligatum* on *Solidago* stems was related to leaf demography.

Methods

Natural history of the system

Solidago altissima L. (Compositae) is a native, rhizomatous perennial that occupies open, disturbed sites (particularly abandoned agricul-

tural fields) where it can persist for many years. Numerous insects feed on *S. altissima*; 138 species have been recorded in central New York and the fauna is taxonomically and functionally diverse (Root and Cappuccino 1992). There are two species of *Trirhabda* (Coleoptera: Chrysomelidae) which cannot be told apart in the larval stage; *T. virgata* is very common and is most likely the species used in this study (Messina and Root 1980). *P. spumarius*, the spittlebug (Homoptera: Cercopidae) is also an abundant insect on *S. altissima*. Both the beetle and the spittlebug are univoltine, with immature stages appearing in mid to late May and completing development in about 3 weeks. The aphid used in this study, *U. caligatum* (Homoptera: Aphididae), also appears in fields in the spring, but reaches its maximal abundance in late summer and fall, when the plants are flowering (Cappuccino 1987). Information on the population dynamics and community-level patterns of the goldenrod insects in central New York can be found in Root and Cappuccino (1992). For more details on the biology of the insects used in the present study, see Messina and Root (1980) for *Trirhabda*, Cappuccino (1987) for *Uroleucon*, and Weaver and King (1954) for *Philaenus*.

Experimental design

All seeds came from one maternal parent in an effort to reduce variability. Because *S. altissima* is an obligate outcrosser (Melville and Morton 1982), these seeds were half to full sibs. The experiment was set up in a randomized complete block design. There were 4 treatments: spittlebug, beetle, or aphid feeding and a control (no damage), with 10 replicates of each treatment. The plants were arranged by size and appearance into 10 blocks of 4 plants each, and treatments were randomly assigned within each block.

Plants

Seeds were collected from a field near Ithaca, N.Y. in October 1989, and were sown in the greenhouse on March 25, 1990, using a peatmoss-based potting medium (obtained from the Department of Plant Breeding, Cornell University and described in Meyer 1992b) in 8 oz styrofoam cups. Plants were started early so that the seedlings would be approximately the same size at the start of the treatments as ramets emerging from overwintering rhizomes in the field. Because of high thrips infestation in the greenhouse, all seedlings were sprayed with Orthene on April 27 as a preventive measure. Seedlings were thinned to one per cup on May 1. On May 8 plants were moved outside, out of direct sunlight, and hardening off was begun. The seedlings were transplanted into large pots (20 cm in diameter by 15 cm deep) on May 17. On May 19 the plants were moved to full sun on the roof of Corson Hall, Cornell University. The plants were started from seed and grown individually in pots to provide more uniform conditions than would be possible in the field. However, the experimental plants differed in several ways from field-grown plants. The experimental plants were grown free from competition in a fertile soil and were watered as necessary; thus they did not experience many of the stresses that would be found in field populations. Because the plants were started from seed, they did not have stored reserves in a rhizome. The plants initially grew as a single stem. Midway through the experiment, buds at the base of the main stem began developing so the plants consisted of a main, central stem surrounded by several lateral stems. These lateral stems probably developed because the lack of competition resulted in high light levels at the base of the main stem; the fertile soil may also have stimulated their growth. Lateral stems at the base of the main stem generally would not be found on field-grown plants. However, plants in the field usually have several stems connected by rhizomes; thus the experimental plants and field-grown plants both consisted of a group of connected stems.

Insects

Insects were placed on the plants on May 26 for all treatments. Beetle larvae and spittlebug nymphs were collected from fields surrounding Ithaca, N.Y. on May 25 and May 26, respectively. A density of 20 per plant was used for both insects. Spittlebugs are not commonly found at densities this high on goldenrod in central New York (GAM, pers. obs.). However, *P. spumarius* does have the potential to reach high densities: McEvoy (1986) recorded 406 nymphs/m² on natural vegetation, and Wiegert (1964) observed 1280 nymphs/m² on alfalfa. Beetle densities in this experiment were lower than the highest levels seen in the field; *Trirhabda* is an irruptive species and can reach densities where entire fields of goldenrod are defoliated (Messina 1981, GAM, pers. obs.). Aphids came from a greenhouse colony; 40 nymphs of mixed ages were placed on each plant. Ten more aphids were added to each plant on May 27 for a total of 50. Beetles were counted on May 31, and plants which had lost insects were supplemented on June 1. Aphids were added to the one or two plants with the lowest densities on May 31, June 4, and June 5 so that all plants supported approximately equal aphid densities.

Cages were not used since all of these insects are relatively sedentary in the immature stage. Plants were inspected every few days. While a few insects moved from their assigned plant to adjacent plants, they were easily spotted and removed. Dry weight of the insects at the start of the experiment was determined from a sample of 100 insects for each species. Insects were removed from the plants on June 7, after 12 days of feeding, and were counted, dried to constant weight at 70°C, and weighed.

Photosynthetic rate determinations

Photosynthetic rates and two associated parameters, conductance and internal CO₂, were measured using a Li-Cor 6200 portable photosynthesis system equipped with a quarter-liter cuvette. Conductance refers to the rate at which gases pass through the stomates, and internal CO₂ is the concentration of carbon dioxide inside the leaf. These two parameters greatly aid in interpreting photosynthetic rate data, by separating effects on the diffusion of gases into the leaf (conductance) from effects on biochemical reactions inside the leaf (internal CO₂).

Measurements were taken on June 6 (after 11 days of insect feeding) and on June 19 (12 days after the insects were removed from the plants). To insure that the leaf used was the same age for all of the treatments, leaves were marked by tying a thread loosely around them prior to measurement. The first unfurled leaf at the time treatments began was used for the June 6 measurement; this leaf was 11 days old when photosynthesis was measured. The first leaf produced after the insects were removed was marked on June 9, but on some plants this leaf showed signs of insect damage. On June 12 another leaf was marked; this leaf was used for the June 19 run and was 7 days old.

Plants were moved into a greenhouse (adjacent to the roof where they were at other times) early in the morning for photosynthetic rate measurements, and measurements were begun 1–2 hours later. Measurements were taken under a high pressure sodium lamp that provided a photon flux density of approximately 1000 μmol m⁻² s⁻¹, with an external fan that blew on the cuvette and helped to keep it cool. On June 6 the marked leaf was examined for insects and they were removed before the measurement was taken. Most plants did not have insects feeding on the marked leaf at the time of measurement. Photosynthetic rate was determined for all plants in approximately 2 h for both June 6 and June 19, so heating of the greenhouse was not a problem. After the measurements were taken, the marked leaf was excised and both the area within the cuvette and the total area were determined. The leaf was then dried and weighed.

Harvest and plant measurements

The height of the main stem was measured before the treatments began (May 24), after the treatments ended (June 8), and at the

harvest (June 24). Leaves on the main stem were counted to determine the number of leaves added over the treatment period, and the number of leaves produced after the insects were removed. Plants were harvested on June 24. They were separated into main and lateral stems. Lateral stems were counted, then separated into leaves and stems which were dried and weighed. Leaves and stem for the main stem were also dried and weighed. All plant parts were dried to constant weight at 70°C. Buds were pooled with leaves for both the main and lateral stems. In addition leaf area was measured for 6 leaves on the main stem. The leaf marked on June 9 was used to divide the stem into a zone of leaves produced during the treatment period, and leaves which were produced following damage. Four leaves (every second or third leaf, depending on plant size) were taken from the zone of insect damage (the stub of the leaf that was excised for the first photosynthetic rate determination was the lower boundary). The leaf marked on June 9, and the leaf at the midpoint of the growth following damage were also taken. Leaves were xeroxed, then a hand-held scanner was used to digitize the xeroxed leaf image, and a pixel-counting program was used to estimate the area. This method allowed per cent leaf area loss for leaves from beetle-damaged plants to be quantified easily. The holes on damaged leaves were filled in to create an image of an undamaged leaf; the undamaged area was then estimated with the pixel-counting program. After xeroxing, the leaves were dried and weighed with the other leaves from the main stem. The dry weights of the two leaves removed after photosynthetic rate was measured were added in for the total leaf dry weight.

Data analysis

All data were analyzed with a randomized complete block ANOVA. Homogeneity of variance was checked with Hartley's F_{\max} test (Sokal and Rohlf 1981); no heterogeneity of variance was detected. Differences between treatment means were tested with Fisher's protected least significant difference using a series of planned comparisons (Sokal and Rohlf 1981). Each insect treatment was first compared with the control. Insect treatments were compared against each other only when they were significantly different from the control.

Results

Herbivore loads

Insect number per plant and mean weight per insect are shown in Table 1. To account for differences in insect size, herbivore loads are expressed both in terms of insect number and insect weight gain per plant. Insect weight gain is used rather than insect biomass to correct for the initial weight. For each insect species, the pooled weight of all insects recovered from the plants was divided by the total number to yield a mean weight per insect. For spittlebugs and beetles, weight gain was calculated by multiplying insect number per plant by the mean weight gain (weight at removal – initial weight). This procedure was essentially the same for aphids, except that the initial and final numbers were used to estimate the initial and final weights.

Aphid numbers increased dramatically over the treatment period from the 50 that were set out initially. Mean weight per aphid fell over time because on June 7 a greater proportion of the colonies consisted of newly produced nymphs. Although individual aphids were much smaller than the other two insects, because of their large colonies weight gain per plant was over twice as high for the aphid

Table 1. Insect number and weight gain (mg)

Insect	Mean weight/insect		Insect number/plant		Insect weight gain/plant	
	Initial	June 7	Mean	Range	Mean	Range
Aphid	.26	0.134	466.2	263 to 674	47.10	8.67 to 77.16
Beetle	.27	1.470	15.1	6 to 19	18.06	7.18 to 22.72
Spittlebug	.31	1.405	18.6	16 to 20	20.37	17.52 to 21.90

than for the spittlebug or beetle. Beetle and spittlebug herbivore loads were similar in terms of both number and weight gain.

Photosynthetic rates

Spittlebug feeding decreased photosynthesis 17% below control levels after 11 days of insect feeding, while beetle and aphid feeding had no detectable effects (Table 2). Leaf conductance was not affected by insect feeding, but internal CO₂ was increased above control levels by both spittlebug and beetle damage. Spittlebug feeding increased internal CO₂ more than beetle feeding, but this difference was not significant.

Leaf area, dry weight, and specific leaf area (leaf area/leaf weight) for the leaf used for measuring photosynthesis are shown in Table 3. The leaf used on June 6 was the youngest leaf at the time treatments were started and developed during the period of insect damage. Spittlebug feeding, but not beetle or aphid feeding, decreased the area and dry weight of this leaf, although the dry weight effect was of borderline significance ($p < .06$). Although specific

leaf area was reduced relative to controls for both spittlebug and beetle-damaged plants, this difference was not significant.

The analysis of variance did not detect a decrease in area for the June 6 leaf on beetle-damaged plants; however light chewing damage was visible on these leaves. Per cent leaf-area loss was estimated for each individual leaf; it ranged from a low of .05% to a high of 14%. Chewing damage was variable because the insects were moving freely over the plant, and their densities and time spent on the plants were not enough to insure that all leaves were damaged. The relationship between the amount of damage that a leaf received and photosynthetic rate was explored using regression analysis. The results were consistent with those shown by the ANOVA: there was no relationship between damage and photosynthetic rate or conductance, but there was a highly significant increase in internal CO₂ with greater leaf area loss (Fig. 1).

Spittlebug feeding still had effects on photosynthetic rates 12 days after the insects were removed from the plants (Table 2). Photosynthetic rates of leaves produced after insect removal on spittlebug-damaged plants were depressed 12% below control levels, and again there were

Table 2. Effects on photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), conductance ($\text{mol m}^{-2} \text{s}^{-1}$), and internal CO₂ (ppm). Means and standard errors are shown. June 6 measurement: leaf present during treatment period. June 19 measurement: leaf produced following damage

	Photosynthesis	Conductance	Internal CO ₂
A. June 6 measurement			
Control	13.9 (0.54)	.322 (.062)	233 (4.7)
Aphid	12.9 (0.53)	.220 (.028)	223 (7.5)
Beetle	13.0 (0.43)	.294 (.029)	249 (4.0)
Spittlebug	11.5 (0.67)	.354 (.062)	258 (5.6)
<i>ANOVA statistics</i>			
Treatment	$p < .03$	ns	$p < .0001$
Block	ns	ns	$p < .008$
<i>Comparisons of means</i>			
Control vs. aphid	ns	–	ns
beetle	ns	–	$p < .02$
spittlebug	$p < .004$	–	$p < .0006$
Beetle vs. spittlebug	–	–	ns
B. June 19 measurement			
Control	18.4 (0.74)	.595 (.024)	261 (3.4)
Aphid	17.6 (0.48)	.599 (.032)	264 (3.8)
Beetle	18.3 (1.07)	.573 (.048)	257 (2.5)
Spittlebug	16.2 (0.64)	.546 (.021)	266 (2.8)
<i>ANOVA statistics</i>			
Treatment	$p < .05$	ns	ns
Block	$p < .005$	ns	$p < .04$
<i>Comparison of means</i>			
Control vs. aphid	ns	–	–
beetle	ns	–	–
spittlebug	$p < .01$	–	–

Table 3. Effects on leaf area (cm²), leaf dry weight (g), and specific leaf area (SLA, cm²/g) for the leaves used in photosynthetic rate determinations. Means and standard errors are shown. June 6 measurement: leaf present during treatment period. June 19 measurement: leaf produced following damage

	Leaf area	Leaf dry wt.	SLA
A. June 6 measurement			
Control	19.6 (1.45)	.098 (.008)	202 (4.5)
Aphid	22.3 (2.66)	.111 (.013)	202 (5.0)
Beetle	18.8 (2.13)	.097 (.011)	194 (4.3)
Spittlebug	15.0 (1.67)	.078 (.008)	190 (3.8)
<i>ANOVA statistics</i>			
Treatment	$p < .009$	$p < .03$	ns
Block	$p < .0003$	$p < .0002$	$p < .05$
<i>Comparisons of means</i>			
Control vs. aphid	ns	ns	-
beetle	ns	ns	-
spittlebug	$p < .03$	$p < .06$	-
B. June 19 measurement			
Control	39.5 (2.35)	.138 (.009)	288 (5.7)
Aphid	41.9 (2.26)	.151 (.008)	279 (9.2)
Beetle	42.9 (2.36)	.158 (.010)	274 (7.9)
Spittlebug	28.9 (3.27)	.087 (.011)	340 (13.9)
<i>ANOVA statistics</i>			
Treatment	$p < .002$	$p < .0001$	$p < .0002$
Block	ns	ns	ns
<i>Comparisons of means</i>			
Control vs. aphid	ns	ns	ns
beetle	ns	ns	ns
spittlebug	$p < .007$	$p < .0004$	$p < .0008$

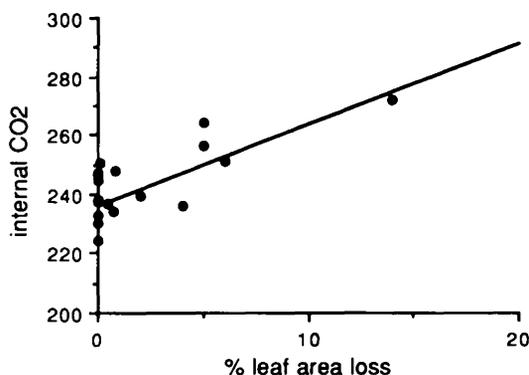


Fig. 1. Relationship between internal carbon dioxide and per cent leaf-area loss for beetle-damaged leaves. Per cent leaf-area loss for leaf used in June 6 photosynthetic rate determination. Regression equation: $y = 236 + 2.82x$, $p < 0.003$

no detectable effects of beetle or aphid feeding. Like the earlier measurement, insect damage had no effect on leaf conductance; however there was also no effect on internal CO₂. The leaf used for this set of measurements was marked as the youngest leaf 5 days after the insects were removed from the plants. Although the insects had been removed, leaf area and dry weight were still reduced for plants in the spittlebug treatment, by 27% and 37%, respectively (Table 3). In addition, spittlebug feeding caused a 18% increase in specific leaf area.

The change in specific leaf area for spittlebug-damaged plants suggested that photosynthetic rates should also be examined in terms of leaf weight. To express photo-

synthetic rate per gram of leaf tissue, photosynthetic rate per unit area was multiplied by the specific leaf area (units were m²/g, rather than cm²/g as shown in Table 3). The differences between the control and the spittlebug-damaged plants disappeared when photosynthesis per gram of leaf was analyzed (photosynthesis in $\mu\text{mol g}^{-1} \text{s}^{-1}$, mean and s.e: control: .531 (.026), spittlebug: .549 (.027); ANOVA showed no significant treatment differences). In summary, the leaf produced after the insects were removed was less dense on spittlebug-damaged plants and had a lower photosynthetic rate per unit area, but photosynthetic rate per unit weight was equivalent to control plants.

Growth rates, height and leaf number

Relative growth rates in terms of height were calculated for the main stem for the period of insect feeding and for the interval from insect removal to plant harvest (Table 4). The log of the height at the beginning of the interval was subtracted from the log of the height at the end of the interval; this number was then divided by the time period in days. The spittlebug caused a dramatic decrease in relative growth rate over the treatment period; the mean for spittlebug-damaged plants was less than 1/3 that of the other treatments. However, after the insects were removed, spittlebug-damaged plants showed relative growth rates that were 12% above control levels. There was no effect of beetle or aphid feeding on relative growth rate, either during or after the treatment period.

The decrease in relative growth rate for spittlebug-damaged plants resulted in reduced height of the main

Table 4. Effects on relative growth rate ($\text{cm cm}^{-1} \text{ day}^{-1}$), height (cm, natural log), and leaf number for the main stem. Means and standard errors are shown. Height was measured at end of period, leaf number is number of leaves added over period

	RGR (ht)	log height	Leaf number
A. During insect feeding			
Control	.023 (.001)	2.89 (.083)	12.7 (0.82)
Aphid	.023 (.003)	2.84 (.139)	12.4 (0.86)
Beetle	.024 (.003)	2.86 (.128)	12.1 (1.01)
Spittlebug	.007 (.002)	2.59 (.096)	11.1 (0.66)
<i>ANOVA statistics</i>			
Treatment	$p < .0001$	$p < .0003$	ns
Block	$p < .0001$	$p < .0001$	$p < .0001$
<i>Comparisons of means</i>			
Control vs. aphid	ns	ns	–
beetle	ns	ns	–
spittlebug	$p < .0001$	$p < .0001$	–
B. Following insect feeding			
Control	.072 (.003)	4.05 (.048)	28.8 (1.23)
Aphid	.076 (.004)	4.06 (.080)	29.2 (2.13)
Beetle	.075 (.002)	4.06 (.095)	28.2 (2.25)
Spittlebug	.081 (.003)	3.88 (.079)	25.3 (1.72)
<i>ANOVA statistics</i>			
Treatment	$p < .02$	$p < .02$	ns
Block	$p < .0001$	$p < .0001$	$p < .0003$
<i>Comparisons of means</i>			
Control vs. aphid	ns	ns	–
beetle	ns	ns	–
spittlebug	$p < .003$	$p < .01$	–

stem at the end of the treatment period (Table 4). Spittlebug-damaged plants were shorter than controls, while beetle and aphid feeding did not affect plant height. Although relative growth rate for spittlebug-damaged plants increased after removal of the insects, they were still shorter than the other treatments 17 days after the insects were removed.

The number of leaves produced on the main stem was not affected by insect damage, either during the period of insect feeding or following insect removal (Table 4). Plants in all treatments added about one leaf per day during the treatment period; this rate increased to almost 2 per day following insect removal.

Plant dry weight and leaf area at harvest

Average area per leaf for the period of insect feeding was computed from the 4 leaves taken from the zone of insect damage at the harvest (Table 5). Both spittlebug and beetle feeding decreased mean area per leaf, while aphid feeding had no effect. Spittlebug feeding caused more severe reductions in leaf area than did beetle feeding: average area per leaf was reduced by 19% for beetle-damaged plants, but was reduced by 63% for spittlebug-damaged plants.

As was noted for the leaves used for photosynthetic rate measurements, effects of spittlebug feeding on leaf area

Table 5. Effects on leaf area (cm^2) at harvest. Leaf 1: first leaf produced after insect removal. Leaf 2: leaf from mid-point of growth following insect removal. Means and standard errors are shown

Treatment	Treatment period		Post-treatment	
	Mean Area per leaf		Leaf 1	Leaf 2
Control	24.3 (1.69)		26.7 (1.42)	24.4 (0.88)
Aphid	26.3 (1.60)		29.5 (1.57)	26.5 (1.35)
Beetle	19.6 (1.92)		29.5 (1.96)	29.4 (1.41)
Spittlebug	9.1 (1.32)		18.0 (2.81)	22.7 (1.03)
<i>ANOVA statistics</i>				
Treatment	$p < .0001$		$p < .0005$	$p < .007$
Block	$p < .0007$		ns	ns
<i>Comparisons of means</i>				
Control vs.				
Aphid	ns		ns	ns
Beetle	$p < .009$		ns	$p < .01$
Spittlebug	$p < .0001$		$p < .004$	ns
Beetle vs Spittlebug	$p < .0001$		–	–

Table 6. Effects on harvest dry weights (g) of main and lateral stems. Means and standard errors are shown

Treatment	Main stem		Lateral stems		
	Leaf weight	Stem weight	Number	Leaf weight	Stem weight
Control	7.50 (0.69)	2.72 (0.38)	4.9 (0.23)	3.42 (0.30)	1.02 (0.17)
Aphid	6.99 (0.82)	2.70 (0.48)	4.5 (0.27)	3.21 (0.34)	0.92 (0.14)
Beetle	6.74 (0.73)	2.51 (0.48)	4.0 (0.33)	2.61 (0.36)	0.69 (0.18)
Spittlebug	3.85 (0.55)	1.23 (0.23)	4.7 (0.37)	3.61 (0.42)	0.84 (0.12)
<i>ANOVA statistics</i>					
Treatment	$p < .0001$	$p < .0001$	ns	ns	ns
Block	$p < .0001$	$p < .0001$	ns	ns	ns
<i>Comparisons of means</i>					
Control vs.					
Aphid	ns	ns	-	-	-
Beetle	$p < .07$	ns	-	-	-
Spittlebug	$p < .0001$	$p < .0001$	-	-	-

were still evident on leaves produced after the insects were removed from the plants. Spittlebug feeding decreased the area of the first leaf produced following insect removal by 32%, while beetle feeding and aphid feeding had no effect (Table 5). Leaf area on spittlebug-damaged plants recovered for the leaf taken from the midpoint of the growth following insect removal; this leaf showed no significant difference between the spittlebug treatment and the control. However, this leaf showed a significant 20% increase in area on beetle-damaged plants.

At the harvest, 17 days after the insects were removed from the plants, spittlebug-damaged plants had reduced main-stem leaf weight and stem weight (Table 6). Beetle-damaged plants also had lower main-stem leaf weight, but this effect was of marginal significance ($p < .07$). There were no effects on the number of lateral stems, or on their leaf or stem weight. Aphid feeding had no detectable effects on any variable.

Discussion

Effects of insect damage on photosynthesis

This study does not support the idea that photosynthetic rates increase in response to either aphid feeding or partial defoliation, as suggested by Crawley (1983) and McNaughton (1979, 1983). The aphids used in this study achieved high densities and their feeding caused no obvious damage to the plant. This study and previous work (Meyer 1992a) failed to detect any significant effects of aphid feeding on plant growth rates or size. Since these aphids are not particularly damaging to the plant, this system would seem to be a good one for detecting increased photosynthetic rates due to increased sink demand from aphid feeding. With a few exceptions, most studies show that aphids have either no effect or decrease photosynthetic rates (Welter 1989). Other phloem sap-feeding insects, such as scale insects, can also cause reduced photosynthetic rates (Schaffer and Mason 1990).

Partial defoliation by beetle feeding also had no effect on photosynthetic rates in this experiment. The measure-

ment leaf that was present during feeding was lightly damaged on most plants. While there was no significant effect on photosynthetic rate, the rise in internal carbon dioxide with per cent leaf area loss suggests that decreases in photosynthetic rate were probably occurring. If the photosynthetic rate slows down, CO_2 within the leaf is not drawn down as quickly and the internal CO_2 concentration increases. Beetle feeding significantly reduced mean leaf area in the zone of insect damage, but there was no effect on photosynthetic rate for an undamaged leaf produced after the beetles were removed. However, there was evidence that leaves produced following insect removal were changing in ways that would increase the plant's potential carbon gain; the leaf taken from the midpoint of the growth following insect removal showed a 20% increase in area (relative to leaves on control plants). The increase in area for this leaf may have been accompanied by physiological changes, but since no measurements were taken this possibility cannot be tested. In a study of simulated herbivory on *S. altissima*, Schmid et al. (1988) found that defoliation increased stomatal conductance of the remaining, undamaged leaves, but that photosynthetic rates were not affected.

The only insect in this study to significantly affect photosynthetic rates was the spittlebug, with decreased photosynthesis observed for the leaf that was present during the period of insect feeding. The lower photosynthetic rate was accompanied by an increase in internal CO_2 , as would be expected if the photosynthetic machinery was less efficient than in controls. The lack of an effect on conductance suggests that the decreased photosynthetic rate was not due to stomatal closure. These results indicate that the stomates on spittlebug-damaged plants were open, but that the fixation of carbon dioxide within the leaf was impaired relative to undamaged plants. Previous work (Meyer 1992a) has shown that spittlebug feeding decreases leaf per cent water but leaf per cent nitrogen is not affected. Because leaf nitrogen concentrations are maintained, spittlebug feeding probably does not reduce the production of photosynthetic enzymes. It is possible that the reduction in leaf water content caused by spittlebug feeding affects the biochemical reactions within the leaf and slows down the rate of photosynthesis.

The results for the leaf produced 5 days after the insects were removed are difficult to interpret. Photosynthetic rates per unit leaf area were reduced on spittlebug-damaged plants, but this difference appeared to be explained by an increase in specific leaf area. When photosynthetic rates were examined per unit weight, there were no detectable differences between spittlebug-damaged plants and controls. The significance of the increase in specific leaf area is not clear. All other things being equal, an increase in specific leaf area will lead to an increase in relative growth rate (Dijkstra 1990), but in this case increased specific leaf area was accompanied by decreased photosynthetic rates per unit area. The effects of insect feeding on specific leaf area are virtually unexplored. The few studies that report specific leaf area show either decreases or no change with insect feeding (Dixon 1971a and b; Mallott and Davy 1978; Vranjic and Gullan 1990). Increased specific leaf area on leaves produced following artificial defoliation has been found (Bassman and Dickmann 1982); these leaves also had increased area and photosynthetic rates. Artificial defoliation of *S. altissima* caused decreased specific leaf area of the remaining leaves (Schmid et al. 1988).

The differences in photosynthetic rate between spittlebug-damaged plants and control plants were small (even though they were statistically significant). A decline in photosynthetic rate of less than 20%, as observed here, may not greatly affect whole plant carbon gain. Previous work has shown that spittlebug feeding does not reduce net assimilation rate, a measure of the balance of photosynthesis over whole-plant respiration over a period of days (Meyer 1992a). This result suggests that compensation for the reduced photosynthetic rates of some leaves does occur, but the mechanism could have been reduced respiration rates in non-photosynthetic tissues rather than increased photosynthetic rates of other leaves.

Welter (1989) concluded from a literature review that compensatory photosynthesis is much more likely to occur following defoliation than for other types of damage (e.g. feeding by mites, leafhoppers, and leaf miners). Welter reviewed 77 studies: 21 concluded that photosynthetic rates per unit area increased following damage, and 18 of these examined defoliation. However, these studies are not easily compared because of methodological differences (see Introduction). Most studies that examine the effects of defoliation use artificial damage to simulate herbivory, but simulated damage may not accurately mimic feeding by real herbivores (Baldwin 1990). In a comparative study, Poston et al. (1976) found that across-the-midrib bisections of soybean leaves increased photosynthetic rates, while caterpillar feeding or paper-punch defoliation had no effect. Hall and Ferree (1976) also found that the type of damage influenced the response: reductions in photosynthetic rates on damaged leaves were greater if the veins were damaged, and for many small holes in the leaf compared to fewer but larger holes.

We lack the information necessary to assess whether compensatory photosynthesis generally occurs in undamaged leaves of naturally damaged plants. The likelihood of compensatory photosynthesis in naturally damaged plants will depend critically on the feeding style of the herbivore. If herbivores damage most or all of the leaves

on a plant, or if the plant fails to add new leaves following partial defoliation, then compensatory photosynthesis would probably not be important. Compensatory photosynthesis has been frequently found in grasses (Gifford and Marshall 1973; Detling et al. 1979; Detling and Painter 1983; Nowak and Caldwell 1984; Wallace et al. 1984; Welter 1989), where there is the possibility that some tillers of a plant may be damaged while others are not, and there is generally vigorous regrowth following herbivory.

This study focussed on the responses of the main stem, but each plant also had several smaller lateral stems that appeared from buds at the base of the main shoot midway through the experiment. Most insect feeding occurred on the main stem, and the lateral stems were generally undamaged. Increases in photosynthetic rate on the lateral stems in response to damage on the main stem cannot be ruled out. Hartnett and Bazzaz (1983) found that unshaded ramets of *Solidago* increased their photosynthetic rates when a connected ramet was shaded. Presumably, the shaded ramet drew assimilates from the unshaded ramet, and this increase in sink demand resulted in an increased photosynthetic rate. The species used was *S. canadensis* var. *scabra*, which is now considered to be *S. altissima* (Melville and Morton 1982). If the main stems of the damaged plants in the present study were drawing resources from the lateral stems, a similar response is possible.

In summary, this study provided no evidence for increased photosynthetic rates following insect damage. However, the possibility of compensatory photosynthesis cannot be ruled out, since photosynthetic rates were not measured for lateral stem leaves, or for main stem leaves produced more than 5 days after the insects were removed. These results do suggest that the conditions under which compensatory photosynthesis is most likely to occur need to be more carefully defined. Other mechanisms for compensation, such as increases in leaf area or specific leaf area, may also be important.

Impacts on the host plant

No significant effects of the aphid were detected for any variable, even though insect weight gains per plant were more than twice as high for the aphid as for the other two insects. Herbivore loads of beetles and spittlebugs were very similar, whether measured as insect number per plant or as insect weight gain per plant. The spittlebug was the most damaging insect, causing strong decreases in main-stem height and relative growth rate, leaf area, leaf weight, and stem weight. Although spittlebug-damaged plants increased their relative growth rates above control levels after the insects were removed, they were still shorter than control plants at the harvest. Beetle feeding mostly affected the main-stem leaves, which showed decreases in area in the zone of insect damage, and a marginally significant decrease in weight at the time of the harvest. These results are consistent with other experiments using the same system (Meyer 1992b). Overcompensation in whole-plant dry weight following artificial defoliation of *S. altissima* has been reported (Schmid et al. 1988).

As was found previously (Meyer 1992a), the spittlebug caused more severe decreases in leaf area than did the beetle, even though the beetle was feeding directly on the leaf tissue. The spittlebug's effects on leaf size persisted after the insects were removed from the plants. The leaf marked 5 days after the insects were removed showed decreased area and dry weight on spittlebug-damaged plants. This leaf was probably forming in the bud near the end of the insect feeding period, suggesting that spittlebug feeding damages leaves while they are developing in the bud. Buds were not measured separately from leaves in this study, but spittlebug feeding can cause strong decreases in bud weight (Meyer 1992a). The plant's ability to replace lost leaf area is thus impaired, even after the spittlebugs are no longer feeding. The beetle, although it will feed on young leaves (particularly in the early instars), does not damage the buds (Meyer 1992a). There were no reductions in leaf area for leaves produced after insect removal on beetle-damaged plants, even for the leaf marked 2 days after insect removal.

These results help to explain why spittlebug feeding is more damaging to the plant than beetle or aphid feeding. Spittlebugs were the only insect to significantly decrease photosynthetic rates in this study, and effects persisted after the insects were removed. In addition, spittlebug feeding reduced leaf area to a much greater extent than did beetle feeding. Finally, the effects of spittlebugs on plant buds and developing leaves limits the ability of the plant to replace leaf area lost to herbivory.

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