PREMATURE LEAF ABSCISSION: AN INDUCED PLANT DEFENSE AGAINST GALL APHIDS[1]

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Abstract. We hypothesized that premature leaf abscission represents an adaptive plant response to herbivore attack. To the extent that this host response reduces the pest population and is cost effective, it should be considered an induced plant defense. To test this hypothesis we examined the patterns of abscission by two species of cottonwoods (*Populus*), quantified the impacts of abscission on the survival of two *Pemphigus* gall aphid species, and examined aphid behavioral and life history countermeasures to this host response. These studies revealed that premature leaf abscission is induced by gall aphid attack. This host response reduced the aphid population by 25% on narrowleaf cottonwood and by 53% on Fremont cottonwood. Galled leaves rapidly declined in quality; only 1 wk after colonization ungalled leaves contained 10.9% more chlorophyll than galled leaves, and differences continued to increase with time. This induced host response is selective and dosage dependent; leaves with 3 or more galls were four times as likely to be dropped as leaves with 1 gall, and 20 times as likely to be dropped as ungalled leaves. Selective abscission is effective even at low aphid densities. At least 98% of the aphids in the galls of abscised leaves died, 90% within 48 h of abscission. Mature aphids on senescing leaves had lower body masses than those on green leaves, demonstrating that the process of leaf abscission is detrimental to aphids before leaves actually fall. A few aphids (<1%) escaped leaf drop by migrating from deteriorating galls to nearby galls in less danger of imminent abscission. Since the effects of premature leaf fall force gall aphids to emigrate, shifting to new hosts may have evolved as a counteradaptation to escape this induced plant defense. Sessile plant pests should be particularly susceptible to induced leaf abscission, and this may explain why galling aphid species are 3.5 times as likely to host-shift as nongalling aphids.

Key words: abscission; aphids; galls; host shifting; induced defense; migration; mortality; Pemphigus betae; Populus angustifolia; Populus fremontii; *Utah.*

INTRODUCTION

Previous studies showing that premature leaf abscission results from psyllid (Clarke 1962, 1963, Clarke et al. 1967) and leaf miner attack (Faeth et al. 1981) have assumed that abscission negatively affects the insect population. Kahn and Cornell (1983) point out the need to document mortality of insects after leaf drop, because premature abscission may actually benefit the insects (Hering 1951, Askew 1962, Shorthouse et al. 1980).

We report the results of an examination of patterns of premature leaf abscission by narrowleaf cottonwood, *Populus angustifolia,* and the resulting impact on the gall aphid, *Pemphigus betae.* These investigations were supplemented by observations of *Pemphigus* sp. on Fremont cottonwood, *P. fremontii.* The following questions were examined: (1) Does early leaf fall result in significant aphid mortality? (2) Is early leaf fall utilized by most host trees and is it effective over a wide range of aphid densities? (3) Do aphids respond to lessen the impacts of abscission? (4) Can the effects of induced leaf abscission account for the evolution of host-alternating life cycles by gall aphids? Our findings to these questions demonstrate that herbivore-induced leaf abscission should be included in the suite of fungal-, insect-, and mammal-induced de-

fensive responses by plants (see reviews by Rhodes 1983, Ryan 1983).

Pemphigus aphids are characterized by a complex life cycle (Harper 1959, 1963) that involves migration between the primary host (*Populus*) and a secondary host. In early spring, wingless stem mothers emerge from overwintered eggs on the primary host and move onto newly expanding leaves, where they become encased within a hollow gall (Whitham 1978). Within each gall, a mature stem mother parthenogenetically produces up to 300 progeny. In midsummer, the gall dehisces and the mature progeny migrate to the secondary host (*Chenopodium* or *Rumex* species in this system). In the fall, another winged generation returns to cottonwood trees where, after a brief sexual phase, overwintering eggs are laid.

Methods

Data were collected in the springs and summers of 1981–1983 near Ogden, Weber County, Utah. Individual trees and populations of trees were sampled.

To examine the selective abscission of galled leaves on a single tree, three data sets were collected. First, we censused 800 to 1200 leaves on the tree and recorded the number of leaves with 0, 1, 2, and 3 or more galls per leaf. Leaves were sampled from all heights and sides of the tree to obtain an accurate estimate of gall densities. Second, from these same samples, leaf scars on the stems were counted to determine how

many leaves had dropped. Third, we collected abscised leaves in a wide circle around the base of each tree daily and recorded the number of leaves with 0, 1, 2, and 3 or more galls. By combining these three data sets, we calculated the original gall density on the tree and the probabilities that leaves with 0, 1, 2, and 3 or more galls would be abscised. For example, if the tree drops 10 out of every 100 leaves and if 3 out of every 10 leaves on the ground have a single gall, then the leaves on the ground with single galls represent 3.0% of the tree's total leaf production. If, out of an initial 100 leaves, 9 out of every 90 remaining on the tree (10 have already dropped) have a single gall, then the initial starting density of leaves with one gall was 9.0% + 3.0% = 12.0%. Once the initial density is known, the probability of being dropped can also be calculated. In the previous example, 3.0/12.0 or 25.0% of the leaves with one gall were dropped by the host tree up to the time of the census. This same method was also used for calculating the probabilities of leaf fall for leaves with 0, 2, and 3 or more galls.

The above method was used to determine the degree of selective leaf abscission on a population of 100 trees. To characterize gall densities on these trees, 40 leaves were haphazardly collected from all sides and heights of each tree, for a total of 4000 leaves. Every 2 d until aphid maturation, leaves were collected from beneath the trees to characterize the population of leaves that had abscised.

To test the validity of the above technique another method was used that did not rely upon collecting fallen leaves but directly censused the changes in parasite loads. The density and distribution of galls on each tree were estimated by examining 800–1200 leaves per tree before any leaves had fallen. Eight weeks later, when the aphids were first beginning to emigrate, the densities and distribution of galls on each tree were again censused by examining an additional 800–1200 leaves per tree. In addition, leaf scars were counted directly to quantify the actual number of leaves abscised, and the total reduction in parasite loads was calculated.

In the laboratory, galls were examined and the number of progeny counted. The mature progeny (winged migrants) were oven-dried, allowed to equilibrate to a relative humidity of 32% at 25°C, and individually weighed on a Cahn electrobalance. Because the number of embryos contained within a winged migrant is correlated with body mass ($r = 0.784$, $P \ll .001$), mass was used as a predictor of relative fitness (Whitham 1978).

To determine the number of winged migrants escaping from abscised galls, individual leaves were enclosed in traps constructed of vials, foam rubber, and netting (Addicott 1981). These traps were 100% effective in retaining known numbers of aphids inside.

Two methods were used to determine how soon a leaf would abscise. First, leaves close to abscission fall at the lightest touch, while vigorously growing leaves are difficult to remove. A spring scale was attached to the petiole of the leaf and the force needed to remove the leaf from the stem was recorded. Second, the chlorophyll content of the leaf tissue was used as an index of the imminence of abscission. It is well known that leaves recycle many constituents prior to abscission, chlorophyll disappears, and leaves characteristically turn yellow (Milborrow 1974, Addicott 1982). Leaves were removed from the tree, immediately frozen, and stored in the dark at −20°. Chlorophyll content was quantified following Harborne (1973).

RESULTS

Selective abscission of galled leaves by a single tree

Although leaf abscission is usually associated with the autumn of the year, on narrowleaf cottonwood galled leaves commence to drop in early spring, shortly after bud break. Most stem mothers settle during the first 3 d of bud burst. The leaves continue to expand for another 4 wk, adding ≈400% to their surface area. In 1982, galled leaves began falling only 3 wk after colonization, at least 1 wk prior to full leaf expansion. In 1981, leaf drop commenced 6 wk after bud burst. At this time, even though only 7.4% of the 800 leaves examined on the tree were galled, 95% of the 200 leaves found on the ground were galled. Galled leaves were far more likely to be dropped by the host tree than gall-free leaves ($\chi^2 = 790.8$, df = 1, $P \ll .001$).

Although galled leaves are selectively dropped at all times of the year, the effect of leaf ascission on aphids was most pronounced early in the season, before the aphids matured. Data from a single isolated tree that was intensively sampled illustrate two points. First, the absolute number of leaves falling decreased through time ($r = -0.61$, $n = 16$, $P < .05$; Fig. 1A). For example, the number of leaves falling into the sampling area decreased from >100 leaves/d to ≈10 leaves/d by the time the first aphids emigrated. The number of leaves falling also varied from day to day, primarily due to variable wind and weather patterns; a wind storm on 28 June resulted in increased leaf fall (Fig. 1A). Second, selective leaf drop is greatest in early spring but decreases with time. For example, in early spring 95% of dropped leaves contained galls, whereas by early summer only 30% contained galls ($r = 0.93$, $n = 17$, $P < .001$; Fig. 1B).

The probability a leaf will fall was correlated with the density of galls on a leaf. Fig. 2A shows that by 2 July 1981, on a tree with 29.8 galls per 100 leaves, an ungalled leaf had only a 1.8% probability of premature abscission; by comparison, a leaf with 1 gall had a 10.0% chance of being dropped. At increased gall densities, the probability of early leaf fall increased from 26.8% (at 2 galls per leaf) to 37.5% (3 galls per leaf) and 53.7% (4 or more galls per leaf) ($\chi^2 = 905$, df = 4, $P \ll .001$).

Attacked leaves still providing photosynthate to the

tree have a lower probability of being dropped than leaves whose photosynthetic production is lost to the aphids. Leaves in which gall formation was attempted but was unsuccessful had a distinct scar where the stem mother probed the leaf and died during the first few days of the gall-forming attempt (Whitham 1978). Compared to single galls with actively reproducing stem mothers, leaves on which the stem mother died were less likely to be abscised ($\chi^2 = 5.84$, $n = 140$, $P < .05$). Consequently, even when gall densities were constant, abscission was selective; only leaves supporting living aphids were dropped.

The probability a leaf will fall is also dependent on leaf size; larger leaves are less likely to be dropped. The mean leaf size of all galled leaves that were abscised was 7.6 ± 0.20 cm², whereas the mean leaf size of all galled leaves remaining on the tree was 10.0 ± 0.18 cm² ($t = 3.5$, $P < .001$, $n = 988$).

Selective abscission by the tree population

The pattern of early leaf fall demonstrated for a single tree represents a general population phenomenon. A stand of 100 contiguous trees was sampled in 1982 using procedures similar to those for a single tree. Even at low densities, galled leaves were selectively dropped. At a density of only 4 galls per 100 leaves, 25.0% of the gall population was dropped. Additionally, leaf drop increased as gall density increased on leaves. Leaves with 1 or 2 galls suffered 19.8% and 10.6% leaf fall, respectively, whereas 100% of the leaves with 3 or more galls were dropped (Fig. 2B; $\chi^2 = 76.29$, df = 4, $P \ll .001$).

Similar patterns were observed with *Pemphigus* sp. on *Populus fremontii*. Leaves with only 1 gall had nearly a 50% chance of being dropped while leaves with 2 or more galls always abscised (Fig. 2C; $\chi^2 = 688.58$, df = 4, $P \ll .001$). This selective abscission of galled leaves reduced the number of galls by 53.0%.

Alternative hypotheses

The first of three alternative hypothesis to the selective abscission of galled leaves is that galled leaves fall closer to the tree than ungalled leaves, resulting in artificially high estimates. In field experiments with galled and gall-free leaves of the same size, leaves were dropped from a height of 3.65 m at three different wind velocities. At the two highest wind velocities, galled leaves fell significantly closer to the tree than ungalled leaves (Table 1). To avoid this problem, large areas beneath the trees were sampled to include all leaves that fell, and/or sampling was conducted only on trees in protected areas where the effect of wind velocity was greatly reduced.

These precautions were adequate; the same patterns of selective leaf drop were observed when another censusing technique not relying on leaf collection from the ground was used. Forty-two trees were individually censused before any leaf fall had occurred. Six weeks
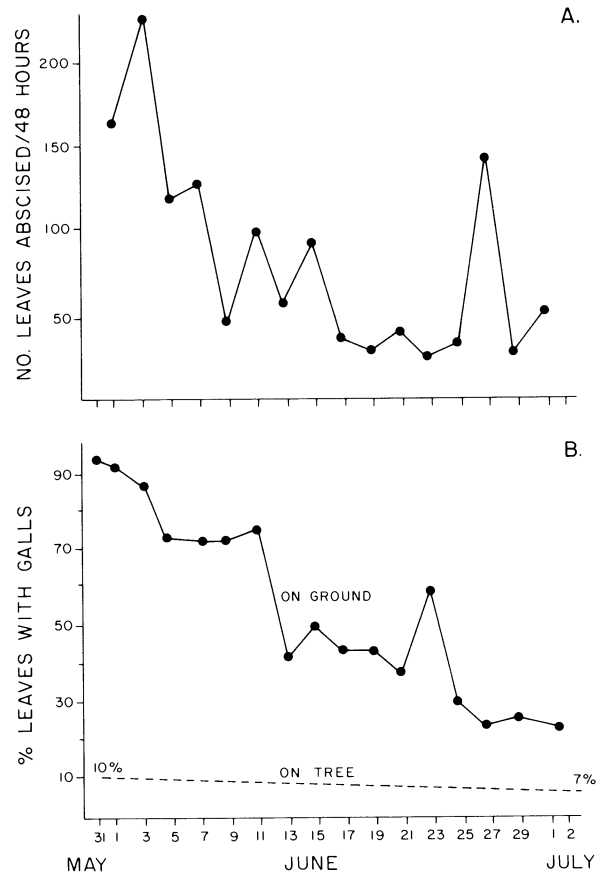

FIG. 1. Temporal changes in (A) the number of leaves falling into the collection area in 48 h and (B) the percentage of leaves with galls, for a single narrowleaf cottonwood tree. Leaf abscission was greatest in early spring and declined to its lowest levels in July, when aphids abandoned the gall and emigrated to the secondary host. In each of the 48-h leaf collections, the percentage of abscised leaves that had galls was greater than the percentage of leaves still attached to the host tree that had galls.

later, the same trees were recensused and gall densities were found to have declined. With a starting gall density of 9.1 galls per 100 leaves, 21.3% of the galls were dropped ($\chi^2 = 5.77$, df = 1, $P < .02$). Additionally, leaf fall was strongly correlated with gall density; 15.6% of the leaves with only 1 gall were abscised, whereas 45.7% of the leaves with 2 or more galls were dropped ($\chi^2 = 1403$, df = 2, $P \ll .001$).

A second alternative hypothesis is that the increased mass of galled leaves results in early leaf fall. To test this hypothesis, 100 ungalled leaves were artificially weighted with putty to simulate the effect of gall mass. Despite having 4 times the mass of a single gall, weighted leaves were no more likely to fall than gall-free control leaves of equal size ($\chi^2 = 0.352$, df = 1, $P > .50$).

A third alternative hypothesis is that premature leaf fall is induced by aphids to obtain increased nutrients while feeding. Because leaves hydrolize reserves and
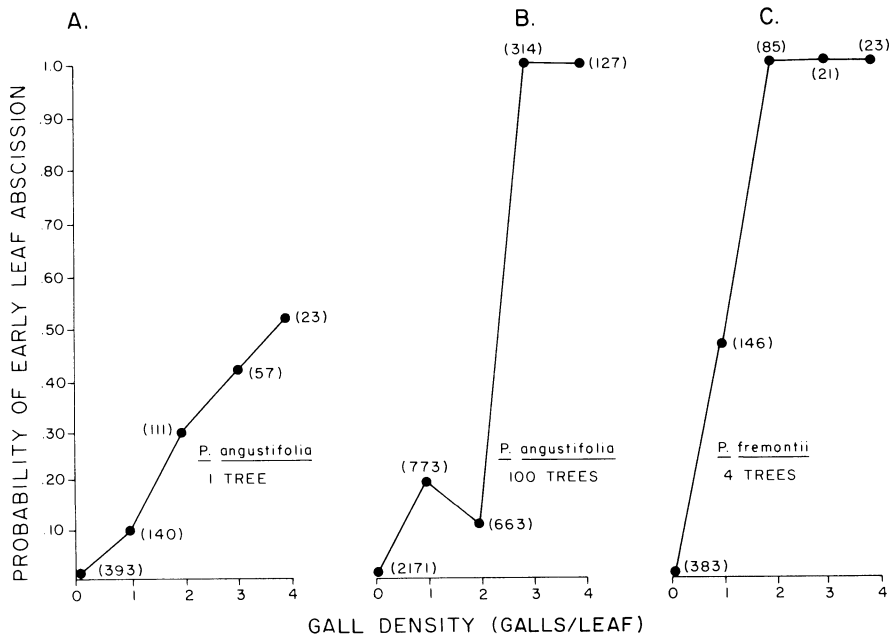
FIG. 2. Probability of early leaf abscission, as a function of gall density, on (A) one *Populus angustifolia* tree with a gall density of 29.8 galls per 100 leaves, (B) 100 *P. angustifolia* trees pooled, with an average gall density of 4.0 galls per 100 leaves, and (C) four *P. fremontii* trees pooled, with average gall density of 25.0 galls per 100 leaves. Galled leaves were selectively dropped, and the probability of abscission was highly dependent upon the number of galls occupying an individual leaf. Each comparison represents the accumulated leaf drop occurring prior to aphid emigration to the secondary host.

export nutrients prior to abscission (Ishikura and Tazaki 1980, Addicott 1982), the aphids occupying these leaves may enjoy superior resources relative to those occupying unaffected leaves (Whitham 1978). If so, then the aphids on leaves collected a few hours after abscission should exhibit evidence of increased relative fitness compared to aphids on leaves showing no signs of approaching leaf drop. Two lines of evidence negate this alternative. First, 57% of all aphids in the gall are dead soon after the leaf falls. We cleared the ground of all abscised leaves, then returned 12 h later and collected the 30 least desiccated leaves; this permitted us to make a conservative estimate of aphid survival on leaves that had been dropped only a few hours previously. Fifteen of these leaves were immediately sampled to determine aphid mortality compared to mortality on 15 galled control leaves still attached to the tree. Aphids on leaves that had just been abscised suffered 11.4 times the mortality of aphids on leaves still attached to the host tree (855 dead or 57% mortality on abscised leaves vs. 75 dead or 5% mortality on controls; $t = 3.8$, df $= 29$, $P < .001$). The observation that many aphids were already dead within 12 h of the abscission of their leaves suggests that the negative effects of abscission begin to take their toll before the leaf actually drops.

Secondly, of the aphids that survive the first 12 h after leaf drop, nearly all die. The remaining 15 galls of the 30 collected were placed in traps to determine if any of the living aphids could escape as winged migrants. Of the 700 aphids that survived initial leaf fall, only 14 winged migrants, or $<1\%$ of the total progeny, escaped. When this experiment was replicated with 61 newly fallen leaves placed in a large, common trap, only 0.17% of all aphids escaped. In total, at least 99% of aphids in the gall at the time of leaf fall die.

Behavioral response to early leaf fall

In response to the deteriorating resource of an abscising leaf, some immature aphids emigrate and seek safety in another gall. Since leaf damage induces abscission (Addicott 1982), abscission was artificially induced by removing the leaf blade distal to the gall, and aphid responses were monitored. Uncut, galled leaves of the same size were used as controls. Both sets of leaves were enclosed in traps and aphids counted daily. Five days following damage, twice as many aphids on damaged leaves emigrated (16.4% of the total, or 328 aphids

TABLE 1. Distance ($\bar{X} \pm 1$ se) that galled and ungalled leaves traveled at various wind speeds when dropped from a height of 3.65 m. Galled and ungalled leaves were of identical surface area.

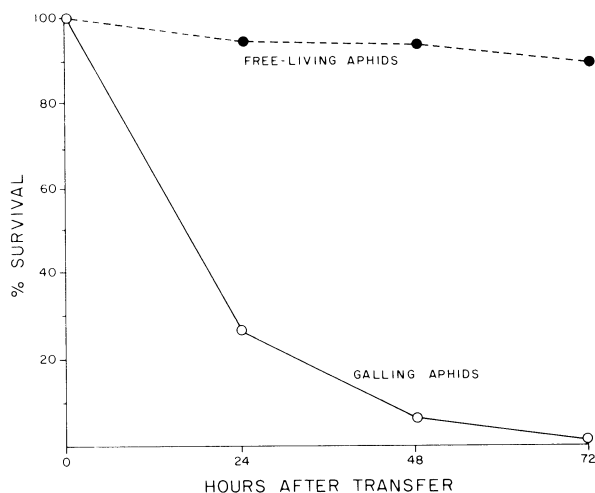| Wind speed (m/s)	Distance traveled (m)		t value	n	P
	Galled leaves	Ungalled leaves			
0	0.93 ± 0.11	1.00 ± 0.08	1.07	94	$>.5$
4.5	3.80 ± 0.22	5.25 ± 0.30	6.51	94	$<.001$
8.9	10.55 ± 0.42	15.46 ± 0.77	7.26	96	$<.001$

FIG. 3. The mortality curve for *Pemphigus betae* forced to live outside their galls shows that they are physiologically constrained to the gall environment. *Chaitophorus* sp., a free-living aphid used as a comparison, showed low mortality and actually reproduced freely. Half of the *P. betae* aphids are estimated to have died within 13.86 h ($n = 20$ replicates with 20 aphids per replicate).

moved) as did those on the controls (8.35%, or 167 aphids; $\chi^2 = 70.36$, df $= 1$, $P \ll .001$).

Emigration by immature *P. betae* is very risky because they rapidly become desiccated and die when exposed to the external environment. Immature aphids were removed from their galls, and 20 were placed onto each of 45 shoots of a cottonwood tree and enclosed in traps to prevent emigration. Mortality was recorded every 24 h for 3 d. By using the standard decay equation ($a = pe^{rt}$), we estimated that the lethal "dose" for 50% of the population was 13.86 h of exposure to the external environment (Fig. 3). This mortality rate is conservative because the traps protected the aphids from wind and predators and probably increased the humidity around the leaf. Furthermore, in comparison with free-living aphids, *P. betae* is much more physiologically constrained to the specialized gall environment. When immature free-living aphids of *Chaitophorus* sp. were similarly transferred to new leaves, they suffered only 5% mortality over the same period (Fig. 3).

The results of three manipulation experiments show that only 0.98% of the aphids within a gall facing abscission could potentially emigrate to another gall. First, aphids were removed from their galls and placed on the twig near their galled shoot. Their movement was then monitored and the total distance traveled during the observation period of up to 3 h was recorded. By comparing the aphids' rate of travel with the average distance to the next galled shoot, we concluded that only 34.7% of the aphids could travel far enough in 13.9 h to find a galled shoot. Second, aphids were then placed at the bases of galled shoots to determine if they could locate galled leaves. Only 34.7% of the aphids

migrated onto the galled leaf of the infected shoot. Third, aphids were placed on galled leaves to determine if they would enter the gall. Only 55.4% of the aphids entered the gall once on the leaf. The others emigrated or died on the leaf. Combining of these results reveals that only 6.7% ($0.347 \times 0.347 \times 0.554$) of the emigrating immature aphids could potentially find a new gall. Since only 16.7% of the immatures even attempted migration, total cohort success (i.e., migrants plus immatures) in escaping to a new gall is only 0.98%.

Decline in leaf quality and early maturation of aphids

Galled leaves rapidly become chlorotic. Because leaf wounding and chlorosis precede abscission (Addicott 1982), leaf quality to aphids and the rapidity of the induced host response can be quantified by monitoring the concentration of chlorophyll in leaves. Although there was no significant difference in the concentration of chlorophyll in galled and ungalled leaves at the time of colonization ($t = 1.90$, df $= 39$, $P > .05$), only 1 wk after colonization ungalled control leaves from the same shoots contained 10.9% more chlorophyll than galled leaves ($t = 2.11$, df $= 39$, $P < .05$; Fig. 4). In gathering these data, leaves were chosen at random with respect to size and position on the shoot.

Differences in chlorophyll concentration between galled and gall-free leaves continued to be significant during spring and early summer, with a maximum difference in chlorophyll levels of 27.5% 5 wk after leaf colonization. These differences are conservative be-
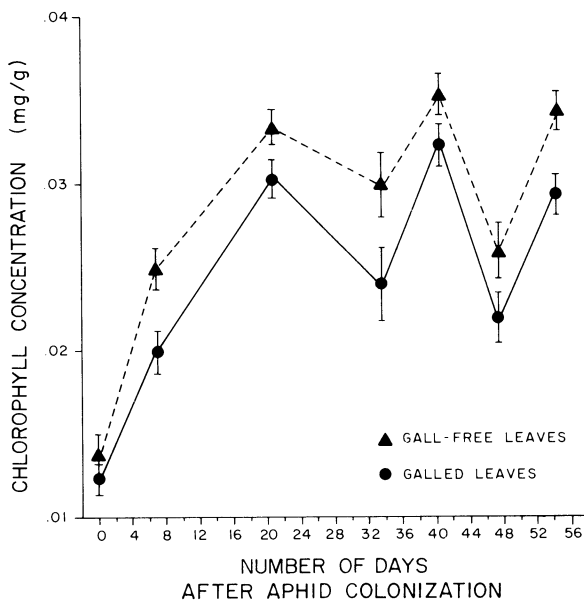

FIG. 4. Galled leaves rapidly became yellow compared to gall-free leaves. Although there was no significant difference in chlorophyll concentration (mass of chlorophyll per unit fresh leaf mass) at the time of colonization, 1 wk later and at all subsequent collections differences between galled and gall-free leaves were significant (*t* tests). $n = 39$ for each point; ± 1 SE is indicated for each mean.

TABLE 2. Comparison of green leaves and chlorotic leaves. Aphids on chlorotic leaves near abscission matured at a smaller size than those occupying green leaves. Leaves were matched to eliminate size effects. Data are means ± 1 SE.

	Leaf area (cm^2)	Force needed to remove leaf (N)	No. progeny per gall	Winged migrant aphids	
				No. per gall	Dry mass per aphid (mg)
Chlorotic leaves	16.06 ± 0.83 (43)*	3126.8 ± 240.8 (43)	119 ± 5.28 (43)	2.78 ± 0.50 (43)	0.151 ± 0.003 (120)
Green leaves	16.12 ± 0.77 (43)	8242.2 ± 254.2 (43)	117 ± 3.64 (43)	1.98 ± 0.34 (43)	0.164 ± 0.003 (85)
Difference (%)	0.04 $t = 0.05$ df = 83 $P = .96$	163.6 $t = 14.6$ df = 83 $P < .001$	1.8 $t = 0.34$ df = 83 $P > .9$	41.2 $z = 1.2$ df = 83 $P = .15$	8.8 $t = 3.3$ df = 203 $P < .002$

* Numbers in parentheses indicate sample size.

cause leaves with the least amount of chlorophyll dropped before they could be collected and were not included in the analysis. Much greater differences were observed on another tree when aphids were first beginning to emigrate: ungalled leaves had 61.4% more chlorophyll than galled leaves ($t = 36.9$, $n = 118$, $P \ll .001$).

Aphids in galls facing imminent abscission have a high probability of dying, but may respond by maturing at a small size, thereby escaping before leaf drop. Galls on chlorotic and green leaves of the same size were censused for aphid mass, number, and maturity (Table 2). Mature aphids on green leaves were 8.8% heavier than aphids from chlorotic leaves ($t = 3.30$, df = 203, $P < .002$). No significant differences were detected in the absolute number of aphids in galls from chlorotic and green leaves or in the number of mature aphids.

DISCUSSION

Leaf abscission as an induced plant defense

Although abscission represents an ancient plant trait that evolved in response to many environmental and ecological factors (Addicott 1982), it seems likely that gall aphids and other sessile pests contribute to its maintenance. Addicott (1982:17) listed removal of injured or infected leaves as one of the benefits of leaf abscission and stated that "leaf abscission can serve as a valuable defense mechanism" (Addicott and Lyon 1973).

Our findings support this viewpoint. First, selective leaf abscission is induced by the presence of gall aphids. Galled leaves are far more likely to abscised than gall-free leaves. Additionally, the induced host response is rapid and can be observed as a 10.9% decline in chlorophyll content in galled leaves only 1 wk after colonization, and galled leaves begin to fall 2 wk later.

Second, pre- and post-abscission changes negatively affect gall aphids in several ways. The body masses of mature aphids on leaves near abscission significantly declined relative to those on healthy nonchlorotic leaves. Because body mass is correlated with the number of embryos contained within the abdomen of the

spring migrant (Whitham 1978), the observed decline in body mass translates into a 7.5% decline in embryo production. Thus, the negative effects of abscission begin before leaf drop. The most significant impact arises after leaf drop; 98% of the aphids occupying abscised leaves die due to desiccation. Even at relatively low aphid population densities the average narrowleaf cottonwood dropped 25% of its gall load (53% on Fremont cottonwood). Considering that gall densities can be as high as 84 galls per 100 leaves (T. Whitham, *personal observation*), a 25% reduction in the parasite load translates into the removal of $\approx 3 \times 10^6$ aphids.

Third, when a galled leaf is dropped, not only is the parasite load reduced, but adjacent ungalled leaves are freed from indirect attack. Phloem feeders create "sinks" that attract resources from nearby uninfested leaves (Miles 1968, Way 1968, Hori 1974, Norris 1979). Way and Cammell (1970) incorporated ^{14}C-labeled sucrose into aphid-free leaves and showed that nearby aphid-infested leaves attracted 81 times more labeled sucrose than aphid-free leaves. By abscising a galled leaf the host plant should recover much of its otherwise lost photosynthetic capacity in nearby leaves.

Fourth, in an effort to avoid induced leaf abscission aphids attempt to emigrate to another gall even though most die. The results of our experiments indicate that <1% of the aphids within a deteriorating gall may survive by migrating to a nearby gall in less danger of imminent abscission. Other studies indicate higher movements between galls. Setzer (1980) used electrophoresis to separate *Pemphigus* aphid clones. He found that, on average, 17.2% of all aphids in a gall are apparently unrelated to the stem mother that formed the gall. Aoki (1979) also found that *P. marsupialis* migrate from gall to gall on *Pachypappa masimowiczii*. Although small immature aphids may escape abscission by emigrating to another gall, larger aphids near their final moult may mature as smaller adults and thus escape leaf abscission by flying to the secondary host. This is suggested by the observation that winged migrants in deteriorating galls were significantly smaller than those in galls in less danger of abscission.

Although this study has shown that aphids are neg-

atively affected by leaf abscission and that abscission is an induced response triggered by gall aphids, in the strictest sense we have not demonstrated that leaf abscission is a plant defense. A defense must be genetically based, and must result in enhanced plant fitness in spite of the cost of the defense. We are unaware of experimental studies in which the costs and/or benefits of a heritable defense have been quantified in terms of plant fitness. This represents an important goal for future plant-herbivore studies.

Leaf-by-leaf defense

As an induced plant defense, abscission should be most effective against galling or mining species in which an individual is restricted to a single leaf and cannot move. With these parasites the surgical removal of only infected leaves should be much more efficient than a systemic defense that both defended galled leaves and unnecessarily defended gall-free leaves. This would be particularly true when parasite densities are low and few leaves need defending. In our study, at densities of only 4 galls per 100 leaves, host trees dropped 25% of their parasite load while leaving gall-free leaves unaffected (Fig. 2B). A systemic defense that affected the other 96 gall-free leaves would have provided no real protection and perhaps have been very costly. Although other plants can respond to low levels of herbivory (McFarland and Ryan 1974), their known responses are systemic (Green and Ryan 1972, Graham and Ryan 1981, Ryan et al. 1981) and thought to be costly (Gustafson and Ryan 1976).

Because the cottonwood response is confined to the infected leaf, the cost to the tree is only the loss of that leaf, a cost already incurred since the photosynthate production of that leaf has already been lost to aphids. Llewellyn (1975) calculated that with a density of lime aphids (per unit leaf area) of 0.67 aphids/cm², the entire net primary production of the leaf would be lost to aphids. In comparison, a narrowleaf cottonwood leaf with one gall supports 15 times as many aphids per square centimetre of leaf area (an average of 142 aphids, or 10.2 aphids/cm²; Whitham 1986a). Considering that the infected leaf contributes little to the tree and that the aphids act as sinks drawing resources from other leaves (K. Larson and T. Whitham, *personal observation*), it seems likely that the costs of abscission are minimal and should result in a net savings.

With leaf-by-leaf defenses the host can also respond disproportionately to higher levels of attack in a dosage-dependent fashion. As the aphid population increases on the host tree, more stem mothers will be forced to colonize the same leaves. T. Whitham (*personal observation*) found that as the aphid population increased from 0.5 to 84 galls per 100 leaves, leaves with multiple galls comprised 10% and 79% of the aphid population, respectively. Because leaves with 4 galls are 5.4 times as likely to be dropped as leaves with 1 gall, as gall densities rise leaf abscission should

TABLE 3. The relationship, for the aphid species of the Rocky Mountain region, between the species propensity to form galls and the propensity to migrate between a primary and a secondary host. Data from Palmer (1952).

	Aphid species producing galls or pseudogalls		Aphid species without galls		Total no. species
	No.	%	No.	%	
Species with primary and secondary host	15	30.6	43	8.8	58
Species with no known alternation of hosts	34	69.4	445	91.2	479
Total	49		488		537
			$\chi^2 = 21.97, P < .001$		

become increasingly effective. Interestingly, such dosage-dependent host responses to attack may have been important in the evolution of territoriality by these aphids (Whitham 1986a, b); stem mothers that share leaves clearly run a greater risk of triggering abscission than solitary stem mothers.

Dixon and Logan (1973) describe a mechanism for an individual leaf to respond to aphid attack. They suggest that vascular blockage and wounding occurs when aphid feeding exceeds some threshold rate of sap extraction that is dependent upon sieve tube diameter. Consequently, small leaves or leaves with multiple infections are first to suffer the effects of wounding and subsequently senescence and abscise soonest.

Evolution of host alternation

Various explanations have been proposed for host alternation by aphids. The best known hypothesis suggests that aphids leave the primary host only because new resources, usually rapidly growing herbaceous plants, become available later in midsummer, when the woody primary hosts generally decline in quality (Kennedy and Stroyan 1959, Dixon 1971). A second hypothesis suggests that two hosts are necessary, one to provide suitable overwintering sites and a secondary one for suprior nutrient value (Moran 1983). Both of these hypotheses imply a passive role for the host plant.

Alternatively, we propose that emigration and host shifts may be forced upon aphids by the induced defenses of the host plant. In the *Pemphigus–Populus* system, selective leaf drop forces aphids to shift hosts or die. Because these aphids can only form galls on immature leaf tissues, the option of forming a new gall on another leaf is precluded after the initial spring growth. To survive, these gall aphids must emigrate before leaf abscission. In contrast to the galling aphid, the free-living aphid has more options. Because these aphids do not require immature leaves to survive, they can freely move from one leaf to another and do not need to find a new host species.

If induced defenses are important in the evolution

of host shifting we would predict that host shifting would be more commonly observed with the sessile galling species than with the more mobile nongalling species. Of the 537 aphid species that Palmer (1952) lists as occurring in the Rocky Mountain region, galling aphids are 3.5 times as likely to host-shift than nongalling species ($\chi^2 = 21.97$, df = 1, $P \ll .001$; Table 3).

These data suggest that leaf abscission may represent a generalized defense that is particularly effective against galling species and has contributed to the evolution of host shifts. We note that it is not possible to separate those species that have evolved host shifts independently of one another from those that possess the trait due to descent from shared, host-shifting ancestors. It is known, however, that closely related aphid species exhibit very different life history traits. For example, *Uroleucon gravicorne* shifts hosts, but its sister species, *U. cadens,* does not (Moran 1985). This indicates that recent ecological factors may be as important in determining whether an aphid species host-shifts as are longer-term historical factors. Although broader surveys are now warranted, these data are promising because they suggest that some of the complexities of herbivore life cycles may be understood through studies of plant defensive traits.

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