

## HABITAT SELECTION BY *PEMPHIGUS* APHIDS IN RESPONSE TO RESOURCE LIMITATION AND COMPETITION<sup>1</sup>

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**Abstract.** The leaf galling aphid, *Pemphigus betae* Doane can be highly resource and habitat limited and has evolved to reduce these limitations.

Over a 3-day period in spring as much as 83% of the overwintering population migrates to immature leaves of *Populus angustifolia* where individuals are rapidly entombed by expanding leaf tissue. The size of the mature leaf is critical to the ultimate fitness of the individual colonizing stem mother. Probability of stem mother failure, body weight of stem mother and progeny, number of progeny, development rate of progeny to maturity, and number of embryos in mature progeny are all correlated with leaf size. Due to these selection pressures, stem mothers search out and colonize large leaves. Thirty-two percent of the tree's leaves were so small as to result in an 80% probability of total aphid failure. Nearly all of these leaves were avoided. In comparison, only 1.6% of the tree's leaves were so large as to result in a 0% probability of failure, and 100% of these leaves were colonized. Even though most stem mothers were forced to colonize suboptimal leaves because competitor density (35/100 leaves) was much > the availability of optimal leaves, the average stem mother colonized a leaf 60% > the mean leaf size of the tree. Resulting from this degree of selectivity, the minimum increase in fitness was 2 times > expected if leaves had been selected at random. At low competitor densities reproductive output would still be limited by energy intake such that if there were only 1 gall on a tree, the colonizing stem mother and her progeny would still be resource limited. Apparently, no leaf produced by the tree is so large that a further increase in leaf size would not result in a further increase in fitness. Thus, even at low competitor densities, resources would still be important in the habitat selection process and in determining the parasite distribution.

**Key words:** aphids; coevolution; colonization; competition; fitness; foraging; habitat selection; host; migration; parasite; *Pemphigus*; *Populus*; resource limitation; Utah.

### INTRODUCTION

The school of evolutionary ecology expanded upon by Hutchinson (1958, 1959), MacArthur (1958, 1968, 1970, 1972) and others has made critical assumptions concerning the extent that resources are limiting and the resultant importance of competition in structuring communities. According to Connell (1975) evidence supporting competition is sparse, probably because predation holds populations below the threshold at which resources become limiting. The result of this lack of evidence is that many have begun to question the importance of competition in natural systems (Birch and Erlich 1967, Paine 1971, Dayton 1971, 1973, Culver 1975, Menge and Sutherland 1976, Rathcke 1976, Weins 1977).

This skepticism is particularly prevalent concerning insects which comprise 70–80% of all species. The basis for this skepticism is the belief that insects are *r*-selected (Pianka 1970), fugitive species (Hutchinson 1951). Because so little quantitative information is known about resources or individual fitness in virtually all currently examined field systems, it is difficult to accurately assess the importance of competi-

tion in structuring or in determining individual strategies in these communities. Fortunately, with the aphids used in this study one can quantify the distribution of available resources, the subset of resources utilized by each individual throughout its life, and the resultant fitness achieved by every individual.

Previous studies of aphid systems have stated that intraspecific competition for the resources of the host plant can be severe (Way and Banks 1967, 1968, Way 1968, Way and Cammell 1970, Dixon 1970a, b, Perrin 1976) and that the level of amino-nitrogen in the phloem sap is thought to be the limiting factor in growth and development of aphids (Auclair et al. 1957, Kennedy 1958, Kennedy and Stroyan 1959, Auclair 1963, van Emden 1966, 1973, van Emden and Bashford 1971, Dixon 1970a, b, 1971a, Forrest 1971). Since most aphids feed from phloem tissues by siphoning sap as it flows under positive pressure from the leaves of the host plant, the quality, quantity, or both, of the phloem sap should determine which leaves will be selected as feeding sites.

In this paper I will examine the patterns of leaf exploitation exhibited by the gall-forming aphid, *Pemphigus betae*, which colonizes the leaves of narrowleaf cottonwood, *Populus angustifolia*. These patterns are supplemented by observations of *Pemphigus populivenae* on Fremont cottonwood, *Populus fremontii*. For both aphid species, correct choice of a leaf is crit-

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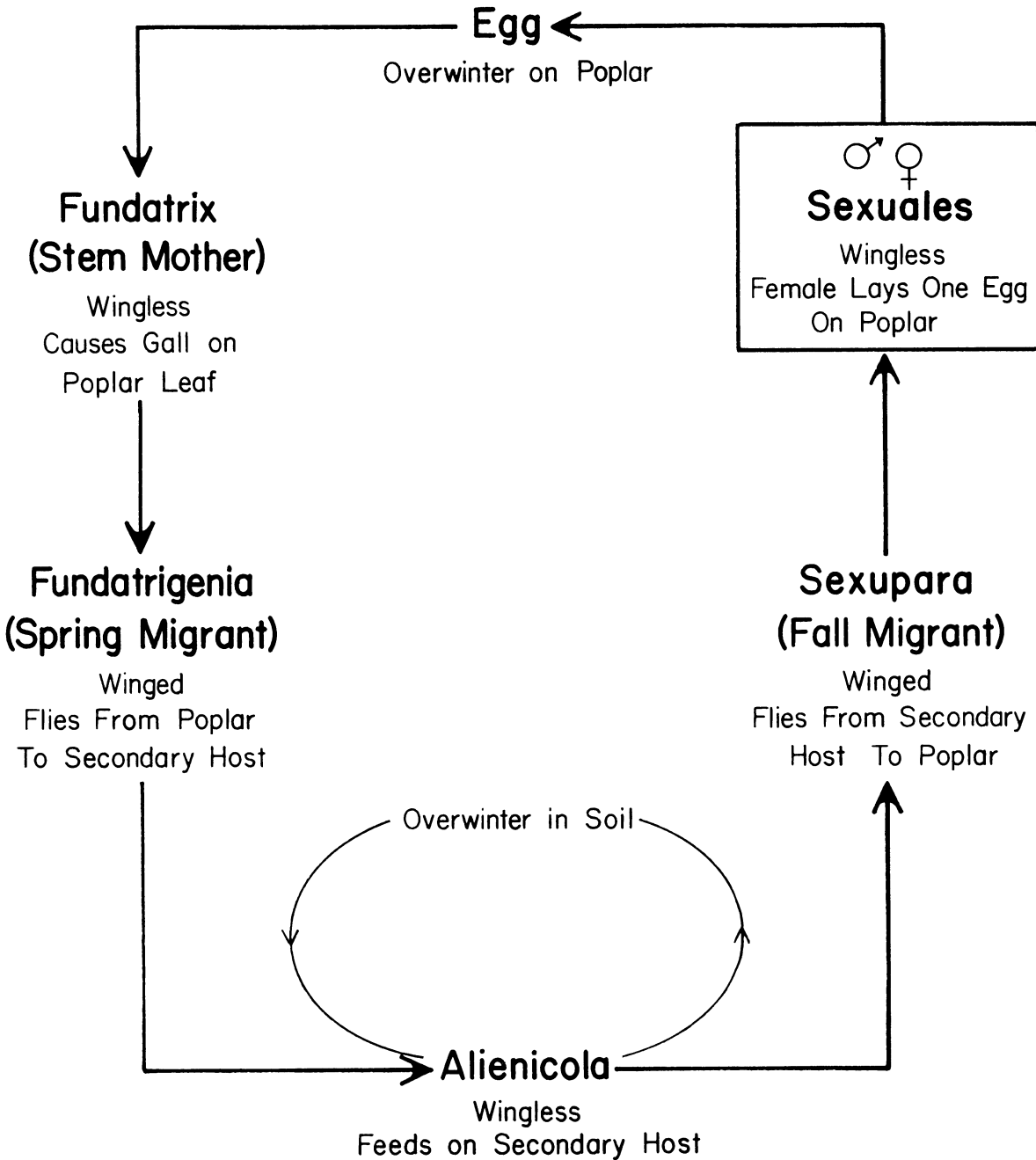


FIG. 1. Life cycle of *Pemphigus betae*, adapted from Harper 1963.

ical and within a few days of settling on a leaf the reproductive fate of each female is sealed. *Pemphigus* aphids are characterized by a complex life cycle which involves migration between a primary and secondary host as well as parthenogenetic and bisexual reproduction in alternate generations (Fig. 1). In northern latitudes most *Pemphigus* species overwinter as eggs in the deeply fissured bark of the main branches and trunk of cottonwoods. In early spring when the pro-

ductive leaf bud scales 1st separate (bud burst), wingless stem mothers emerge and disperse to developing leaves where they feed, inducing gall formation. The hollow galls, which may attain a diameter of 1.5 cm, are generally formed on the midrib at the base of the leaf blade and completely enclose the stem mother. Within the confines of the gall a mature stem mother parthenogenetically and viviparously produces a colony of winged offspring which may number as many

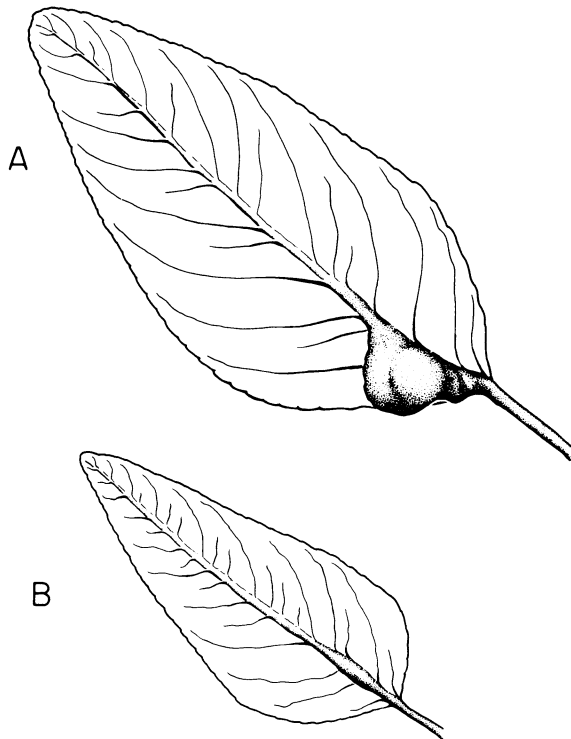


FIG. 2. Each stem mother, whether she survives or dies during the colonization attempt, produces 1 of 2 possible kinds of galls. A. Successful gall of *Pemphigus betae* on *Populus angustifolia*. B. Aborted gall which failed to develop due to the death of the stem mother.

as 700 depending on the species. In midsummer the gall dehisces and progeny migrate to the secondary host where they produce a generation of wingless females. These wingless forms in turn produce the fall winged migrants which return to the primary host. Here, with the production of wingless sexuals (2N – 1 males and 2N females), sexual reproduction occurs for the only time in the life cycle and the result is the laying of a single overwintering egg by each female.

#### METHODS

This paper is concerned with that portion of the *Pemphigus* life cycle spent on the primary host. Analyses of the secondary host have not been included. This, however, does not detract from the overall results because regardless of events occurring on the secondary host, individual colonizers should settle on the primary host so as to maximize their reproductive success. Most of the data were collected in the springs and summers of 1974–1976 near Ogden, Utah. Three trees were sampled extensively and another 4 trees were sampled in less detail. In no instance were data from different trees and/or years pooled. In most cases branches were randomly selected from the lower 4 m of mature trees and all shoots were measured. A shoot is defined as the current year's growth of 1 leaf bud.

All leaves were mapped as to their position on the shoot, which is a measure of their relative age. Leaves which emerge in the initial burst of spring growth are termed "early" leaves and those which develop later are termed "late" leaves (Critchfield 1960). Terminal shoots, the most active growing centers of the tree, characteristically produce more than 6 leaves, have considerable supportive tissue and are located at the periphery of the tree. Lateral shoots have fewer leaves, produce less wood and, by definition, are anywhere but at the apex of branches.

Since studies of net primary productivity are often related to photosynthetic surface area, the size of an individual leaf should be correlated with the quality and/or quantity of resources translocated via leaf vascular tissues. J. C. Gordon (1971, and *personal communication*) found that for leaves of similar age, the amount of nitrogen in a leaf was a function of its size. Other physiological and anatomical evidence for *Populus deltoides* indicates that leaf size may affect vascular sap availability to aphids (P. R. Larson *personal communication*). In this study, greatest length  $\times$  greatest width of mature *Populus angustifolia* leaves was used as an accurate correlate of actual leaf area ( $r = 0.998$ ,  $N = 27$ ,  $P < .001$ ). Actual leaf area was measured by tracing representative leaves on finely lined paper and summing the number of  $1 \text{ mm}^2$  within the leaf outlines. By using the linear equation,  $y = .624x + .127$ , all length  $\times$  width measurements were converted into leaf areas.

To study the reproductive success of individual stem mothers, *P. betae* galls were sampled over a 4-day period (2–5 July) when their progeny were starting to mature. Since all galls were initiated on virtually the same day in spring (14 May), the data represent a cohort having the same developmental period of about 51 days. Galls were placed in 85% alcohol. In the laboratory galls were examined for the presence of predators and number of progeny was counted. Stem mothers and winged migrants were oven dried, allowed to equilibrate to a relative humidity of 32% at 25°C and individually weighed on a Cahn electrobalance. Winged migrants were then rehydrated and dissected to count the number of embryos within their bodies. These embryos are well-formed, complete with eyespots, and represent most of the body weight of the adult migrant. From these data not only can relative fitness of the stem mother be examined, but expected fitness of her daughters, the winged migrants, can be predicted.

Because emerging stem mothers must crawl from overwintering sites at the base of the tree to developing leaves, a sticky barrier (Tanglefoot) placed at the base of small branches is highly effective in limiting dispersal. If barriers are in place before dispersal occurs, few or none can cross; if barriers are established at a later time, density is limited to those already on the branch. This method was used to study the

confined movements and colonization success of a constant number of stem mothers. Galls which failed to develop due to the death of the stem mother during the colonization attempt are termed abortions. Figure 2 shows successful and aborted galls of *Pemphigus betae*. The colonization attempts of *P. betae* and *P. populivenae* were examined to determine if even those stem mothers which failed in the colonization attempt survived long enough to produce an identifiable scar or rudimentary gall. This is important in determining the validity of counting galls as an accurate measure of the colonizing population.

To test the hypothesis that *Pemphigus* aphids are nutrient limited, parameters of reproductive success for aphids maturing on leaves treated with a foliar fertilizer were compared to those maturing on control leaves. Branches receiving fertilizer were sprayed with high analysis Rapid-Gro 23-21-17 at 1 week intervals for 6 weeks commencing at bud burst while the control leaves on adjacent branches were sprayed with water only. The advantages of using the same genotype and root system with associated soils for treatment and control are obvious.

## RESULTS

### *Dispersal and colonization of leaves*

Dispersal from overwintering sites is rapid and within 4 or 5 days after bud burst most *P. betae* have selected leaves and permanently settled. Although dispersing stem mothers are <0.5 mm in length, they are highly mobile and crawl at an average rate of 2.2 cm/min. The linear distance from overwintering sites to leaves ranges from about 300 to 1000 cm. The distance actually traveled, however, is probably much greater because stem mothers often crawl to a developing leaf, make several feeding probes with their stylets and then move to another leaf. Figure 3 shows the pattern of dispersal in which 215 leaf buds (1306 leaves) were monitored once each day and all arriving stem mothers were removed. Of the 699 stem mothers that attempted colonization, 83% arrived over a 3-day period that peaked just after bud burst. The ability of stem mothers to synchronize their movements with bud burst is undoubtedly aided by the nearly simultaneous expansion of buds throughout the tree.

This synchronization of a parasite with its host is very likely an adaptation to a selection pressure which favors the colonization of immature developing leaves. Prat (1955) demonstrated that plant resistance to gall formation increases with cell differentiation and age and that meristematic tissues are the most affected by gall-inducing organisms. Although leaf maturity has not been quantified in this study, it is estimated that 7 days after bud burst most leaves are no longer available for colonization because nearly all have fully expanded and lignified. It is probably accurate to assume that the most favorable period for successful coloni-

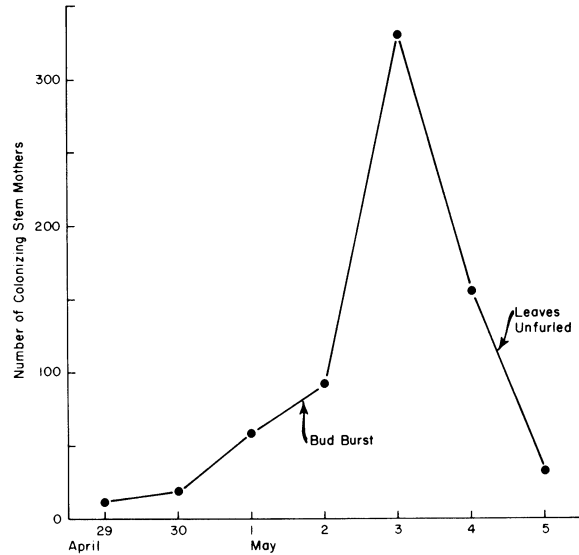


FIG. 3. Pattern of arrival of 699 stem mothers onto 1306 leaves of *Populus angustifolia*. Stem mothers were removed once each day as they arrived at the buds and leaves of several small branches. Eighty-three percent of all stem mothers arrived over a 3-day period that peaked just after bud burst.

zation is limited to the first 3 days after bud burst before leaves have unfurled. During this time when most leaves are colonized, leaves are less than 2 cm long, extremely soft and easily damaged.

Although many stem mothers fail to successfully colonize a leaf and die within the first few days after bud burst, even those that die leave a small identifiable scar or aborted gall on the leaf as seen in Fig. 3B. Thus, a census of aborted and successful galls accurately reflects the number of stem mothers that survived dispersal from the tree trunk to developing leaf buds. Four days after bud burst when most leaves had just unfurled and stem mothers could be easily viewed, 34 *P. betae* stem mothers were removed with a fine brush from leaves of *P. angustifolia*. Every stem mother had initiated the rudimentary beginnings of an oval gall that could be perceived as a slight depression about .5 mm deep and 3 mm long in the leaf blade. Several weeks later the artificially aborted galls of all 34 stem mothers were easily spotted. Damage inflicted upon immature leaves is magnified as the leaf tissues expand and mature. In another experiment on *Populus fremontii*, 4 days after bud burst the leaves occupied by 135 stem mothers from several small branches were marked and recorded. At this time, approximately half of the stem mothers had not formed any visible rudimentary galls. To prevent potential interbranch movement, Tanglefoot was applied at the base of each branch. Nine weeks later, of the 135 stem mothers originally recorded, 133 could be accounted for. Forty-one had died but left aborted galls as evidence of their colonization attempt and the remainder had success-

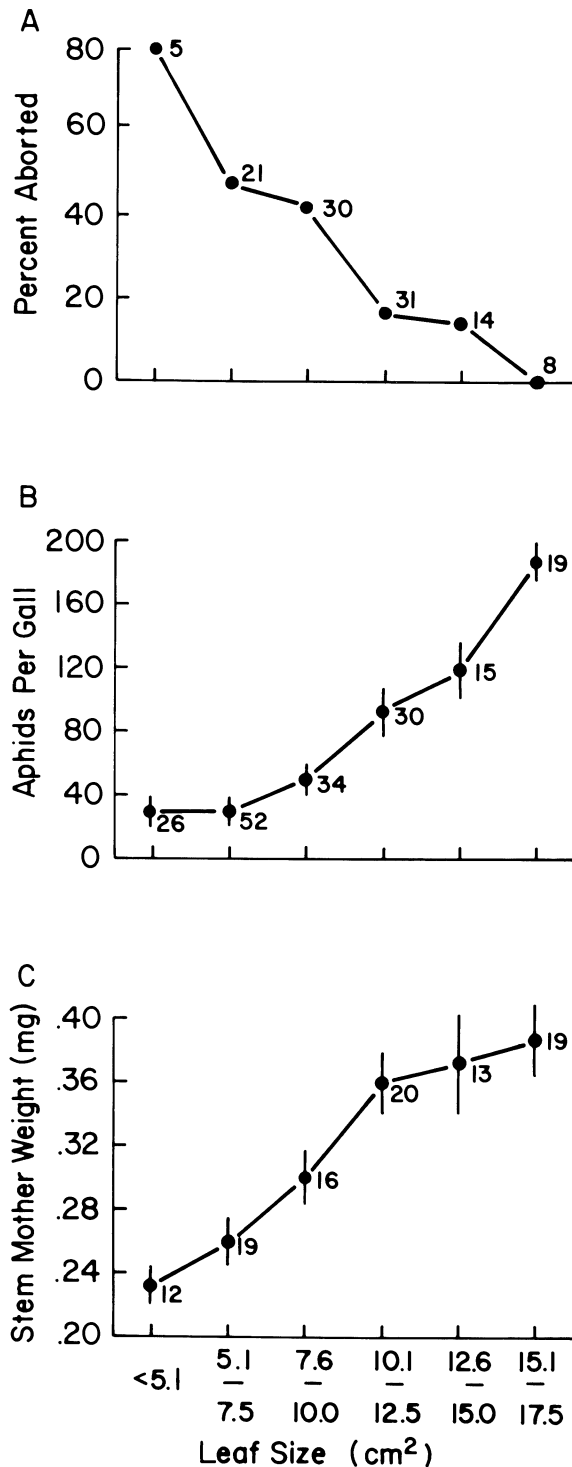


FIG. 4. Effect of mature leaf size on three estimates of relative fitness. A. Percent galls that aborted in their development due to death of the stem mother. B. Number of aphids per gall. C. Dry body weight of surviving stem mothers. To eliminate effects of competitor density and predation, only leaves with single, predator-free galls were used. Sample size and 1 SE are indicated for each mean. Spearman rank correlation of A and linear regression analysis of B and C show these relationships to be highly significant ( $P < .01$  or greater).

fully formed galls and produced offspring. Thirty-one of the stem mothers that had not formed rudimentary galls when the 1st census was taken had moved to different leaves where they were recorded during the second census. Importantly, even those stem mothers which abandoned 1 leaf and moved to another produced *either* 1 successful or 1 aborted gall throughout their lifespan. Of the 31 stem mothers that moved, 61% died; of the 102 that did not move from their original sites, only 22% died. These highly significant differences ( $\chi^2 = 17.593$ ,  $df = 1$ ,  $P < .001$ ) indicate that stem mothers which settle last are far more likely to fail in the colonization attempt. Furthermore, during the 1st census 15% of all stem mothers were clumped in groups of 5 per leaf. At the 2nd census groups of 5 per leaf no longer existed while leaves with 1 or 2 stem mothers had increased in frequency. Apparently, many stem mothers are attracted to the same leaves at bud burst where, due to density effects (present paper and Whitham 1978), continued dispersal results in reduced clumping.

*Pemphigus populivivae* stem mothers become irreversibly committed to a single leaf and will not move even if the leaf will no longer support their existence. Seven days after bud burst, 128 leaves of *Populus fremontii* containing 1 stem mother each were cut from the tree and reattached with a rubber band to determine if stem mothers would disperse as the leaves withered. Sixty-four stem mothers had formed rudimentary galls and 64 had not. Twenty-four hours after the leaves were severed, 87% of the stem mothers that had not formed galls moved to adjacent normal leaves, whereas only 52% that had initiated rudimentary galls moved ( $\chi^2 = 19.508$ ,  $df = 1$ ,  $P < .001$ ). The reluctance of the latter group to move may indicate that a physiological change or cost prohibits further movement. Schaller (1968) showed that the saliva of gall-forming aphids contained a plant growth hormone, indole acetic acid, and Miles (1968) has suggested that gall aphids produce proteins which are injected into the plant to induce gall formation. If these proteins are costly or limited, once used the stem mother may be permanently committed.

#### *Relationship between leaf size and parameters of fitness*

Because galls of *Pemphigus betae* are located at the base of the leaf blade on the midrib, the total translocated production of the leaf should be available to the aphid colony. If these aphids are resource limited, then various parameters of relative fitness should correlate with leaf area. To test this hypothesis, leaves with single predator-free galls were sampled from the same cohort over a 4-day period (2–5 July).

As leaf size increased the percent stem mothers that died during the colonization attempt declined (Fig. 4A). Eighty percent of those stem mothers on the smallest leaves ( $\leq 5.0$  cm<sup>2</sup>) died, while 0% failed on

TABLE 1. Effect of leaf size on the success of colonization and development time of *Pemphigus betae* stem mother progeny to adult migrants

| Maturity of Progeny                | Leaf Size Occupied (cm <sup>2</sup> )<br>$\bar{x}$ | N  |
|------------------------------------|--|----|
| 1. Zero progeny (Stem mother died) | 7.3 ± .32  | 73 |
| 2. Immatures only                  | 7.4 ± .63  | 35 |
| 3. Both adults and immatures       | 11.5 ± .49   | 73 |

Analysis of variance (Student-Newman-Kuels test) yields no significant difference between the means of category 1 and 2 but both are significantly < category 3 ( $P \ll .01$ ).

the largest leaves (>15 cm<sup>2</sup>). This result has been verified with several other *Pemphigus* species on different host plants (*personal observations*). Undoubtedly, this must represent a strong selection pressure favoring the colonization of leaves with the potential of becoming large.

Even more impressive is the effect of leaf size on reproductive success. Including stem mothers which died as having zero progeny, the average reproductive success on the largest leaves was  $189 \pm 11.7$  while on the smallest leaves only  $32 \pm 7.3$  offspring (Fig. 4B). If only those stem mothers which survived to reproduce are considered, then on the smallest leaves an average of  $59 \pm 8.3$  progeny were produced and since none failed on the largest leaves their average success remained at 189. This basic relationship has also been confirmed using several other *Pemphigus* and *Populus* species (*personal observations*).

Other evidence that resources are limiting to individuals is the sharp increase in body weight with increased leaf size (Fig. 4C). Dry body weights of mature stem mothers on the smallest leaves averaged only  $.23 \pm .014$  mg, whereas those individuals on the largest leaves were 70% heavier and averaged  $.39 \pm .023$  mg. This feature is important because parent body weight is related to number and size of offspring (Figs. 5A and 5B). Stem mothers with dry body weights less than .20 mg gave birth to an average of  $59 \pm 6.3$  progeny that weighed  $.17 \pm .005$  mg when mature. In comparison, stem mothers heavier than .40 mg produced  $180 \pm 8.0$  offspring that weighed  $.23 \pm .005$  mg when mature. One further extension of the importance of body weight on reproductive success is the number of preformed embryos contained within individual winged migrants (Fig. 5C). Winged migrants weighing <.18 mg contained an average of  $11 \pm .3$  embryos, whereas those weighing >.30 mg contained  $18 \pm 1.2$ , or 64% more, potential progeny.

Leaf size also affects the rate at which the stem mother's daughters mature to become adult winged migrants. Table 1 compares the mean leaf size occupied by stem mothers which died (7.3 cm<sup>2</sup>), those which successfully initiated galls but contained only immatures (7.4 cm<sup>2</sup>), and those galls containing both

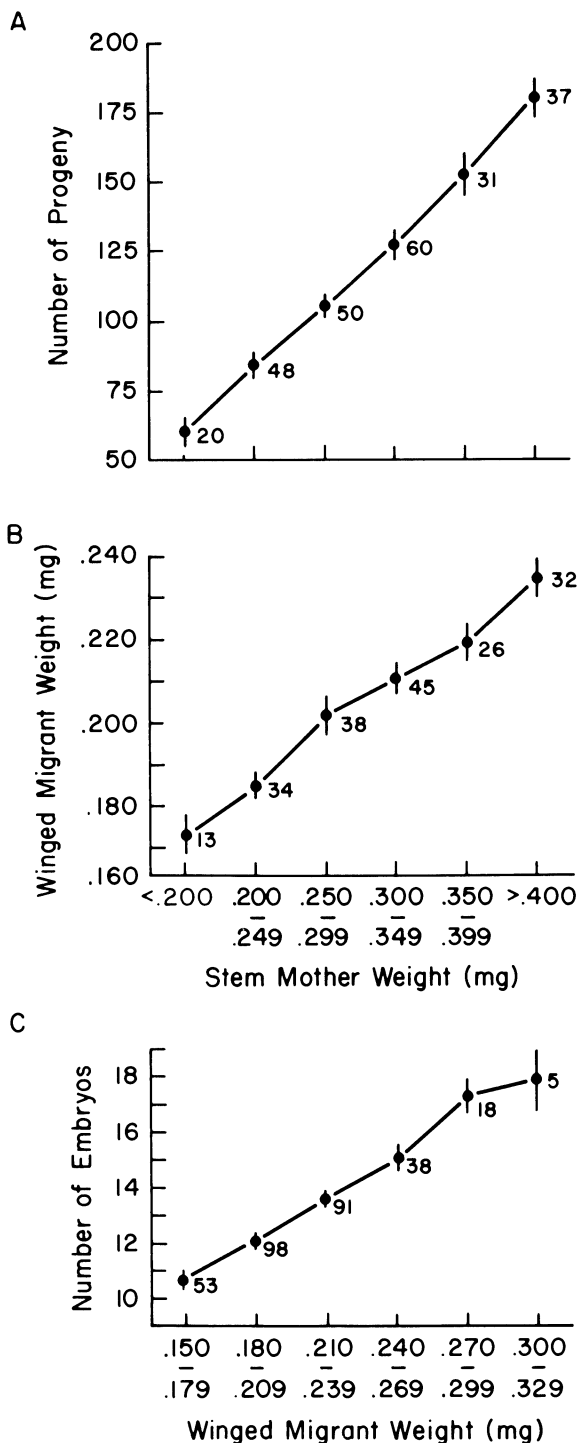


FIG. 5. A. Mean number of progeny per gall. B. Mean dry body weight of winged migrants as a function of the dry body weight of the stem mother. C. Mean number of embryos in winged migrants as a function of parent dry body weight. Only leaves with single, predator-free galls were used. Sample size and 1 SE are indicated for each mean. Linear regression analyses show these relationships to be highly significant ( $P < .001$  in all cases).

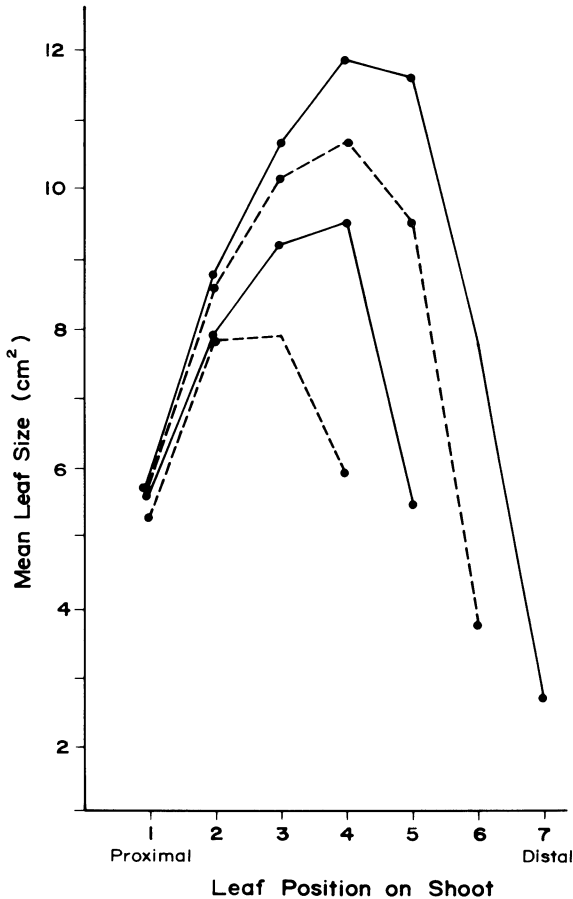


FIG. 6. Leaf size as a function of leaf position on shoots with 4, 5, 6, and 7 leaves per shoot in which the oldest or proximal leaf is numbered 1. Each point represents the mean of at least 50 leaves and in all cases each point represents the mean of at least 50 leaves and in all cases  $1 \text{ SE} \leq .5 \text{ cm}^2$ . The largest leaves are predictably located in the middle section of shoots with many leaves.

immatures and adults ( $11.5 \text{ cm}^2$ ). Note that these galls were sampled at the same time from a cohort and only predator-free galls were included. Analysis of these data show that when adults 1st appear in the population they are far more likely to be found in galls which had developed on large leaves (Student-Newman-Keuls test,  $P \ll .01$ ). This is an important observation because as the season progresses, the probability of detection by predators increases. During the first couple of weeks after bud burst no predators were seen, but by the time adult migrants 1st appeared and were dispersing, 30% of all galls containing aphids were being preyed upon by 1 or more predators (*Syrphus* [Diptera], *Leucopis* [Diptera] and *Anthocoris* [Hemiptera]).

The advantages of colonizing large leaves could be negated by predators selectively foraging on large leaves where aphid reproductive success is greatest. To test this hypothesis, leaves with single galls con-

TABLE 2. Effect of supplemental nutrients on 2 measures of relative fitness for *Pemphigus populivinae*

|                             | Fertilized Leaves          |    | Control Leaves             |    | t-statistic          |
|-----------------------------|----------------------------|----|----------------------------|----|----------------------|
|                             | $\bar{x} \pm 1 \text{ SE}$ | N  | $\bar{x} \pm 1 \text{ SE}$ | N  |                      |
| Leaf Size ( $\text{cm}^2$ ) | $28.7 \pm 1.08$            | 50 | $27.0 \pm 1.29$            | 52 | .988,<br>$P < .4$    |
| Aphids per Gall             | $217 \pm 8.4$              | 50 | $159 \pm 8.5$              | 52 | 4.850,<br>$P < .001$ |
| Adult Migrant Wt. (mg dry)  | $.191 \pm .0045$           | 20 | $.147 \pm .0061$           | 20 | 5.795,<br>$P < .001$ |

taining aphids were examined to see if there was any difference between the mean leaf size of galls with and without predators. The mean leaf size of both categories was identical (with predator  $\bar{x} = 11.0 \pm .70 \text{ cm}^2$ ,  $N = 20$ ; without  $\bar{x} = 11.0 \pm .44 \text{ cm}^2$ ,  $N = 55$ ) ( $t = .034$ ,  $P < .9$ ). Since no differences were found it can be concluded that predators do not forage in any systematic fashion which would reduce the selective advantage of colonizing large leaves. One factor which may account for this seemingly inefficient foraging is the fact that as leaf size increases, leaves become increasingly rare; thus predator foraging costs increase. The distribution of leaf sizes will be more thoroughly examined in this paper.

Fertilization experiments conducted on *Populus fremontii* significantly increased parameters of reproductive success for *Pemphigus populivinae* indicating that nutrients are limiting. Approximately 9 weeks after bud burst galls from fertilized and unfertilized branches were collected from a single tree and comparisons made (Table 2). Even though the mean leaf size occupied by stem mothers on fertilized and unfertilized branches was the same, fertilization significantly increased the number of progeny by 37% and their mature body weights by 30%. It would appear that on *Populus fremontii* stem mothers are nutrient limited and with the addition of nutrients by foliar fertilization a dramatic increase in aphid fitness can be achieved. Similar experiments conducted on *Populus angustifolia* with *Pemphigus betae* did not produce significant differences between treatment and control. It is not clear why no differences were observed; however, these experiments require that most of the fertilizer be utilized within the leaves to which it is applied and that resultant products translocated to adjacent branches be sufficiently low as to have a minimal effect on aphid fitness. Clearly, this and other factors such as waxy layers which might prevent the uptake of fertilizer can affect results. Therefore, an absence of significant differences between treatment and control cannot be interpreted as a lack of resource limitation; only results showing significant differences are meaningful.

*Distribution of leaves and galls on the host plant*

If stem mothers do indeed prefer large leaves, then one would also expect that the time of colonization would not only correspond to the time when leaves were most susceptible to gall initiation but also to the time when the largest leaves were available. To establish the size and location of leaves produced by the tree, in mid-summer after most plant growth had occurred 1100 mature leaves of *P. angustifolia* were measured from branches collected from all sides and heights of a 15 m tree. Figure 6 shows that regardless of the number of leaves per shoot the proximal and distal leaves are small while leaves in the middle section are significantly larger. Most importantly, the largest leaves are predictably located in the middle section of shoots which contain 6 or more leaves.

To establish the pattern of when new leaves first emerge and become available for colonization, 200 shoots were sampled at 1 week intervals commencing at bud burst. Early leaves, those produced at bud burst, expand rapidly and almost simultaneously. These leaves accounted for 81% of the leaf production from bud burst to early July when winged migrants began to disperse from the primary host. About 4 weeks after bud burst, late leaves were produced during a secondary spurt of growth which added approximately 2 new leaves to terminal shoots with 8 leaves and no new leaves to lateral shoots with 4 leaves. The average shoot added 1 new leaf. Since Fig. 6 includes both early and late leaves it shows that leaves added to terminal shoots in the secondary spurt of growth were small leaves. It is also likely that the production of late leaves is dependent on growing conditions and therefore quite variable. Thus, the largest and most favorable leaves are preformed in the leaf bud and available when stem mothers colonize immature leaves at bud burst.

The most important comparison remains to be demonstrated; do aphids select large leaves for colonization? Figure 7A shows the distribution of leaf sizes available on the tree ( $\bar{x} = 6.9 \pm .17 \text{ cm}^2$ ) and Fig. 7B shows the percent of each leaf size class that was colonized. Leaves resulting in a 0% abortion rate and the highest measures of relative fitness measured  $15.0 \text{ cm}^2$  or more. Although they accounted for only 1.6% of the tree's leaf production, 100% were colonized. Leaves resulting in an 80% abortion rate and the lowest measures of relative fitness measured  $5.0 \text{ cm}^2$  or less. Even though these leaves were numerous, 31.7% of the total, only 3.0% were colonized. Since the observed density of stem mothers was 35 per 100 leaves, most were forced to occupy leaves smaller than the largest available with a resultant decline in expected fitness. The mean leaf size colonized by stem mothers was  $10.9 \pm .27 \text{ cm}^2$ , which is 60% larger than the mean leaf size of the tree ( $t = 11.552, P \ll .001$ ). From

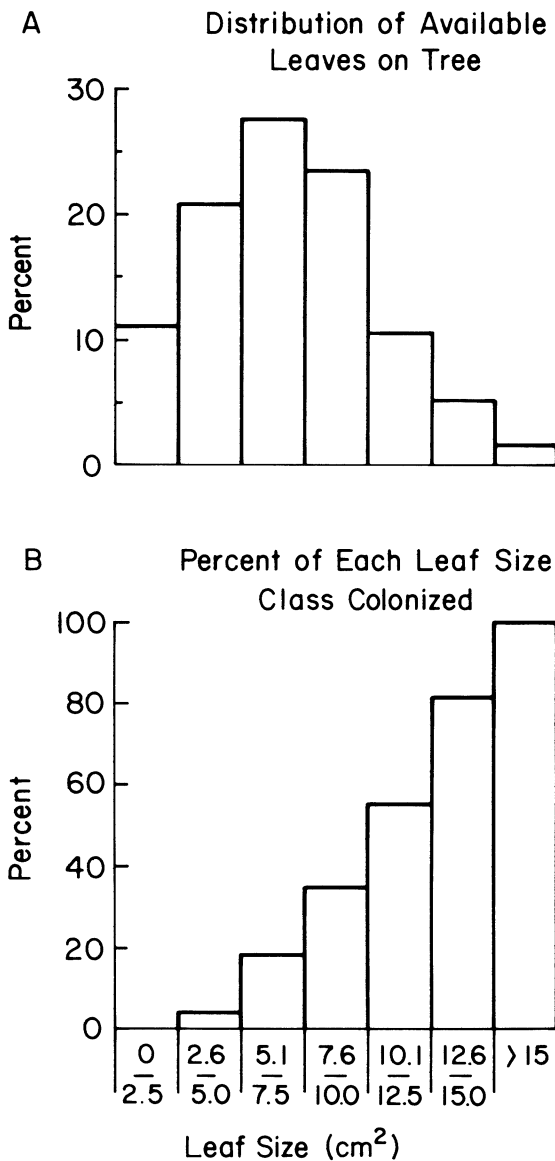


FIG. 7. A. Distribution of leaves available for colonization (mean leaf size =  $6.9 \pm .17 \text{ cm}^2, N = 422$ ). B. Percent of each leaf size class colonized by stem mothers (mean leaf size colonized =  $10.9 \pm .27 \text{ cm}^2, N = 153$ ). Comparisons of A and B show that stem mothers discriminate between leaves of different size by colonizing those leaves with the greatest potential for becoming large.

these data there can be little doubt that stem mothers occupy the largest leaves on the tree.

An alternative to the reasoning developed here is one which suggests that feeding activity and gall-inducing substances injected into the plant by the stem mother and her progeny cause galled leaves to become larger than nongalled leaves. The best test of this hypothesis is to examine only those leaves with the same potential for becoming large and then compare the resultant leaf size of galled and nongalled leaves. Most



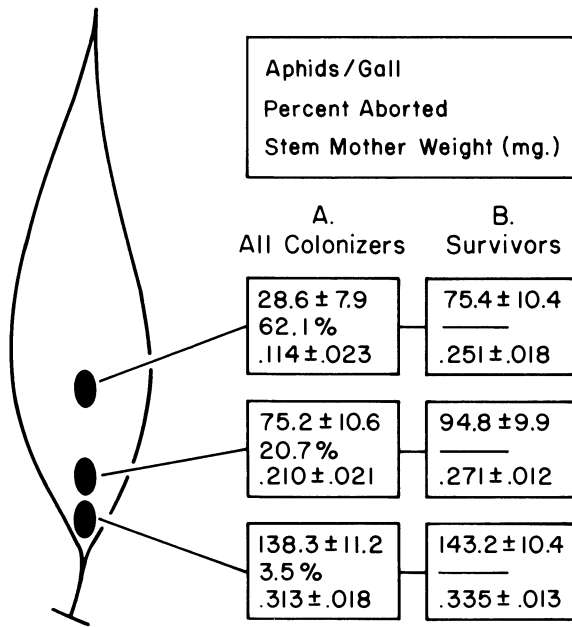


FIG. 8. Effect of gall position on measures of relative fitness when 3 *Pemphigus betae* stem mothers colonize the same leaf blade ( $N = 35$  leaves). Shown are the mean number of aphids per gall  $\pm 1$  SE, the percent stem mothers that died in attempting colonization (column A only) and the mean dry body weight of stem mothers  $\pm 1$  SE. Column A includes all colonizing stem mothers while column B considers survivors only. Probability of stem mother death is greatly reduced at the base of the leaf ( $\chi^2 = 25.708$ ,  $df = 2$ ,  $P \ll .001$ ). Analyses of variance (Student-Newman-Kuels test) show all means of column A to be significantly different ( $P < .01$ ). In column B, means of basal galls differ significantly from both distal galls ( $P < .01$ ) but distal galls do not differ significantly. In the latter comparisons, high abortion rates reduced sample size to low levels.

of the variance in leaf size is a result of leaf position on the shoot and number of leaves per shoot (Fig. 6). Therefore, if a comparison of mean leaf size of galled and nongalled leaves from a specific position and shoot size show no significant differences, this alternative hypothesis can be eliminated. In this study, the most commonly galled leaf was the 4th leaf on shoots with 6 leaves (Fig. 6). It was found that the mean leaf size of galled leaves ( $11.0 \pm .39$  cm<sup>2</sup>,  $N = 45$ ) did not differ significantly from the mean leaf size of nongalled leaves ( $10.4 \pm .39$  cm<sup>2</sup>,  $N = 35$ ) ( $t = 1.003$ ,  $P < .4$ ). This test was conducted for several other specific leaf positions and shoot sizes with identical results. The conclusion is that on *Populus angustifolia*, *Pemphigus betae* does not inject substances which result in increased leaf size and that leaves with the greatest potential of becoming large are actively sought and colonized.

#### Selection for optimal position on the leaf

Gall position on the leaf blade is a critical determinant of expected fitness of individual stem mothers.

For vascular feeders the base of the leaf blade at the junction of the petiole should represent an optimal position for gall formation because everything translocated into or out of the leaf must flow by that point. To determine if the selection of this site is evolutionarily favored, fitness parameters of individual stem mothers on leaves with  $>3$  galls were examined. Leaves with  $>1$  gall are common on trees with high densities of aphids. The most conservative comparisons using only surviving (nonaborted) galls of *P. betae* show that basal galls contain 90% more progeny and their stem mothers are 34% heavier than distal galls (Fig. 8). Furthermore, the abortion rate of basal galls is  $1/18$  that of the most distal galls. When there is  $>1$  gall per leaf, the basal gall clearly realized much greater fitness.

It is hypothesized that the position of the gall on the leaf influences the effective size of the leaf from which the colony draws resources and that a more accurate measure of leaves as resources is the area distal to the gall. For the purposes of the following correlations an attempt was made to collect galls so that the sample would be composed of galls uniformly distributed at various distances along the midrib of the leaf blade. Furthermore, to avoid density effects (intraspecific competition) only leaves with 1 gall were examined. Since almost all galls were clumped at the base of the leaf, the desired distribution was unattainable. Consequently, the following correlations are very conservative in demonstrating the effects of leaf area distal to the gall on colony size. By correlating colony size as a function of total leaf area, 39% of the variance was accounted for ( $r^2 = .389$ ,  $N = 58$ ,  $P < .001$ ). However, by using the same galls and considering only leaf area distal to the gall, 61% of the variance is accounted for ( $r^2 = .609$ ,  $N = 58$ ,  $P < .001$ ). Thus, if stem mothers colonize anywhere but at the base of the leaf blade their expected fitness is more accurately related to leaf area distal to the gall.

The rate at which colonies produce winged migrants is also affected by the position of the gall on the leaf blade. The data in Table 3 were collected when aphid progeny had matured to the point at which some galls contained adult migrants and others did not. At this time, 75% of those galls at the base of leaves (bottom 1 cm) contained adult migrants whereas only 42% of the galls more distal on the leaf blade contained adult migrants ( $\chi^2 = 7.734$ ,  $P < .01$ ). It should be noted that for the above comparison of leaves with 1 gall to be valid, the distance from gall center to leaf base must be independent of leaf size. The mean leaf size of galls situated within the basal 1 cm of the leaf ( $9.1 \pm .31$  cm<sup>2</sup>,  $N = 174$ ) is nearly identical to the mean of those more distally located ( $9.3 \pm .63$  cm<sup>2</sup>,  $N = 39$ ) ( $t = .315$ ,  $P < .9$ ). Thus, not only do galls located at the base of leaves have larger colonies, they also mature at a faster rate which allows them to avoid rising predation rates.

TABLE 3. Effect of *Pemphigus betae* gall position on the growth of immatures to adult migrants

| Distance from leaf base to gall center (cm) | Galls without winged migrants (N) | Galls with winged migrants (N) | Galls containing winged migrants (%) |
|---|-----------------------------------|--------------------------------|--------------------------------------|
| ≤1.0  | 22                                | 65                             | 74.7                                 |
| >1.0  | 11                                | 8                              | 42.1                                 |

$\chi^2 = 7.734$ ,  $df = 1$ ,  $P < .01$ ; aborted galls not included.

Since expected fitness of stem mothers which colonize the base of leaves is much greater than those that colonize more distally, natural selection should favor those that colonize the base. Examination of 109 leaves of *Populus angustifolia* containing 1 gall each revealed that 84% of all *Pemphigus betae* galls were situated within the bottom centimeter of leaves averaging  $6.7 \pm .13$  cm in total length. The mean distance from the center of each gall to the leaf base was  $0.7 \pm .05$  cm. Clearly, stem mothers are discriminating in their microhabitat selection behavior.

If one is willing to accept the hypothesis that the area of leaf damage is correlated with the level of resources harvested by the aphid colony, then the importance of gall position on the leaf blade can be demonstrated visually. *Pemphigus populivenerae* causes galled leaves of *Populus fremontii* to become chlorotic and produces a chevron pattern of yellowing distal to the gall. With galls located at the base of the leaf, the entire leaf yellows; however, as galls are more distally located, the leaf area affected is lessened. Thus, position of the gall on the leaf blade determines the extent of leaf damage or chlorosis. Damaged leaves characteristically fall from the tree 1 to 2 months earlier than normal leaf fall.

#### DISCUSSION

Differential reproduction due to leaf size has resulted in the evolution of strategies and mechanisms by which *Pemphigus betae* search out and colonize large leaves with considerable accuracy. Those stem mothers which fail to colonize the largest leaves available forfeit potential fitness by having a greater probability of dying, increased predation due to a slower rate of development, and fewer and smaller progeny which contain less preformed embryos for the next generation. By combining these measures of relative fitness one may obtain a collective estimate of the fitness gained by stem mothers which discriminate between leaves of varying quality. If stem mothers selected leaves at random; the mean leaf size colonized would be the same as the mean leaf size of the tree,  $6.9 \text{ cm}^2$ . The mature progeny from a single stem mother would collectively contain within their abdomens approximately 544 preformed embryos. However, stem moth-

ers selectively colonized the largest leaves and even though most were forced to colonize suboptimal leaves due to high competitor densities, the mean leaf size colonized,  $10.9 \text{ cm}^2$ , was 60% larger than the mean leaf size of the tree. In this case, mature offspring from a single stem mother contained about 1096 preformed embryos which for the average stem mother represents a 101% increase in fitness over stem mothers which selected leaves at random. These estimates are conservative because it was not possible to include effects of development rate to maturity.

Selection for leaf size discrimination operates not only on stem mothers initiating galls on the largest leaves within a tree, but also on fall migrants (sexupara) which select a tree on which the eggs of their progeny will overwinter. Whitham (1973) studied colonization and mortality of *Pemphigus populitransversus* on Eastern cottonwood, *Populus deltoides*. In this study 10 trees of similar size and in close proximity were selected on the basis of having different average leaf sizes in which a 5-fold difference existed between the largest and smallest leafed trees. The percent stem mothers that died was inversely correlated with the mean leaf size of the tree with the smallest-leafed tree having an abortion rate of 76% and the largest leafed tree only 28%. Apparently, individual trees vary greatly in suitability. Since the difference in bud burst of these trees spanned not more than 3 days of similar environmental conditions, the different survival rates can hardly be attributed to weather. It was found that the number of colonizing stem mothers was positively correlated with leaf size, such that the largest-leafed trees had densities at least  $4 \times$  the smallest-leafed trees. If density of stem mothers is positively correlated with the number of fall migrants, it appears that fall migrants preferably colonize those trees which have the greatest potential to produce large leaves the following spring. This may account for the wide range of aphid densities encountered in the field which varies from a few galls per tree to 50% of all leaves being galled.

Although the advantages of colonizing large leaves are great, in this study the number of large leaves was far less than the number of stem mothers, resulting in severe competition. Even though the best habitats represented only 1.6% of the total leaves available, 100% were colonized. Since there were 35 stem mothers for every 100 available leaves most were forced to occupy either suboptimal leaves or suboptimal positions on leaves (Figs. 7 and 8). This result is particularly interesting because *r*-selected, fugitive species are not generally thought to compete for resources and aphids with their characteristic parthenogenetic reproduction, alternation of hosts, and literally billions of dispersing migrants are the epitome of these traits.

Even in the absence of competitors, resources may still be limiting to individuals. This would be the case for species whose reproductive output is limited only

by energy intake. Figure 4B demonstrates this point because the number of progeny per stem mother did not approach an upper limit as leaf size increased to the maximum available on the tree. These same data have been collected using several other *Populus* species which have considerably larger leaves and the *Pemphigus* aphid species which colonize them not only produce more progeny, they similarly show no evidence of being asymptotic as leaf size increases (*personal observations*). Similar results are obtained for the number of stem mothers that die as a function of leaf size (Fig. 4A). Only on the largest leaves does the failure rate drop to zero. Parthenogenesis and the telescoping of generations in which newly born parthenogenetic females contain embryos may allow these aphids to utilize all available resources regardless of the size of leaf found on *Populus angustifolia*. Thus, in the absence of competitors, the reproductive output of *Pemphigus betae* is limited by the quality of leaves on *P. angustifolia* and at the lowest density of 1 gall on a single tree, that stem mother and her progeny could realize even greater fitness on a larger leaf. Increased competitor density forces stem mothers to colonize smaller leaves simply because large leaves are very limited, but increased density only heightens an effect that exists at the lowest densities.

Resource limitation is not a surprising result if one views gall insects and their host plants as coevolved systems. Mani (1964) contends that the often complex life cycle of many galling insects is imposed upon them by plants evolving to minimize the impact of their parasites and with evolutionary time plants may even be capable of shedding parasites. Logically, counter-adaptations by the plant may restrict aphids in some way, such as limiting the availability of resources. The viewpoint of a coevolved system requires that the impact of aphids upon their host plants be sufficient that it evolutionarily pays the plant to adapt. Mittler (1958) calculated that a single willow aphid could, in 1 day, ingest the photosynthetic product of 5–20 cm<sup>2</sup> of leaf. Dixon (1971b) stated that a sycamore tree with 116,000 leaves may support  $2.25 \times 10^6$  sycamore aphids and in the absence of aphids, sycamores could produce as much as 280% more stem wood. Sycamore aphids can become so numerous that their feeding negatively affects the growth of the host plant and subsequently causes a decline in the aphid population (Dixon 1970b).

When considering potential counteradaptations employed by plants to resist herbivory, one usually thinks of toxic biochemical compounds (Feeny 1975) or exotic mechanisms such as cuticular trichomes which kill larvae (Gilbert 1971). This study has suggested some rather subtle but potentially effective alternative mechanisms. Because selection favors stem mothers which succeed in colonizing the largest leaves of host cottonwood, the smallest leaves on individual trees and small leafed trees are avoided. Through differential colonization, *Pemphigus* aphids may act as a selective pres-

sure in which trees with the least favorable leaf size distribution are favored. Obviously, there are physiological and photosynthetic constraints which determine optimal leaf size (Parkhurst and Loucks 1972), but there may be additional constraints as well.

Another interesting feature of cottonwoods is the number of gall-forming aphid species which colonize them. Palmer (1952) lists 537 aphid species occurring in the Rocky Mountain Region, of which 49 or 9% produce either galls or pseudogalls. However, of the 26 recorded species occurring on *Populus*, 65% or 17 species from 5 genera produce galls. Most aphids do not produce galls, yet on *Populus*, gall-forming aphids are clearly in the majority. This fact may be due to the characteristic leaf motion of some *Populus* species. According to Dixon and McKay (1970), when leaves brush against one another, the feeding activity of aphids is interrupted and reproduction declines. Consequently, gall aphids may be selected for or are preadapted to survival on cottonwoods.

Although the mechanism used by *Pemphigus* stem mothers to find superior habitats is unknown, it is well documented that aphids excel as phytochemists and with a few stylet probes are capable of sampling the chemical makeup of the phloem sap and either accepting or rejecting the food source (van Emden 1972). The results of this study also show that large leaves are predictably located on the middle section of terminal shoots (Fig. 6). This predictability should aid stem mothers in saving valuable search time by allowing them to proceed directly to the terminal portion of each branch. During a 26-minute period of observation, one *P. betae* stem mother moved directly from 1 terminal shoot to another, bypassing 6 lateral shoots.

Due to the vascular anatomy of the leaf it appears that there is only 1 optimal site for gall formation. For leaf blade galls of *P. betae* when there was more than 1 gall on the same leaf, the aphids at the base consistently achieved the highest measures of relative fitness (Fig. 8). For petiole galls of *P. populitransversus* just the reverse is true (Whitham 1973). When there was >1 gall on the same petiole, those nearest the leaf blade realized the greatest fitness. Thus, 2 factors appear to determine the optimal position for gall initiation. First, the gall should be located at a site that has the highest concentration of vascular tissues. Secondly, the site should be located so near the point where vascular traces fan out to different portions of the leaf that a potential competitor stationed more distally cannot cut off the phloem supply. Such a position would be found at the junction of the leaf blade and petiole. Although this simple explanation accounts for the observed patterns, a more complex answer may be required once detailed anatomical and physiological studies are completed.

The observation that leaf galls of *Pemphigus populivivae* cause all portions of the leaf distal to the gall to become chlorotic while basal portions retain their normal green color is revealing of the vascular phenome-

non involved. Characteristically, nongalling aphids have 2 peak feeding periods when the primary host is particularly rich in amino-nitrogen, in early spring when the leaves and tree are most actively growing and translocation is greatest and in the fall just prior to abscission when valuable nutrients are translocated out of the leaves (Dixon 1970a). The level of amino-nitrogen in phloem sap of leaves that are just beginning to yellow is much higher than in nonchlorotic mature leaves (Mittler 1958). It seems that *P. populivinae* has telescoped these 2 discontinuous favorable feeding periods into 1 by causing physiological changes in the leaf resembling fall senescence in early summer just before migration to the secondary host.

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