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DIFFERENTIAL COLONIZATION OF RESISTANT AND SUSCEPTIBLE HOST PLANTS: *PEMPHIGUS* AND *POPULUS*[1]

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Abstract. Plants show extensive intrapopulational variation in quality as hosts for herbivores. Adaptive discrimination among individual host plants depends on the availability of plant traits that are present when plants are colonized and that are correlated with quality. Here, we examine the ability of colonizers to select appropriate hosts when colonization occurs long before feeding, and when traits available as cues may be least associated with host quality. In such systems the precision of host selection may be limited by a lack of appropriate cues at the time of colonization.

In the life cycle of the aphid *Pemphigus betae*, autumn migrants select among host trees (*Populus angustifolia* and natural hybrids with *P. fremontii*) far in advance of the spring feeding stages, while trees are in a very different physiological condition. In order to estimate host quality, we censused successful and aborted galls on 34 trees in a Utah canyon during seven consecutive years, thus obtaining tree-specific rates of stem-mother survivorship. We estimated attractivity of these trees by censusing autumn migrants during 3 yr. Both survivorship and attractivity varied among trees, and differences among trees persisted across years. Tree-specific colonization rates were positively related to gall establishment. These results indicate that the actual colonization pattern is more adaptive than a random colonization process; however, the ability to select better hosts is far from perfect.

To determine how migrants might use cues evident during colonization and correlated with quality, we examined the relationships between tree attributes in autumn and colonization rate and between these same attributes and stem-mother survivorship. One attribute, degree of leaf retention in autumn, was positively correlated with both colonization and subsequent progeny survival. Thus, the tendency to colonize trees retaining leaves longer in autumn may contribute to *P. betae*'s limited ability to preferentially colonize better hosts. These results support the hypothesis that, in life cycles in which colonization and feeding are separated, the evolution of adaptive host discrimination may be constrained by the availability of appropriate cues.

Key words: aphid behavior; gall formation; habitat selection; host alternation; host-plant selection; host-plant resistance; host-plant variability; insect–plant relationships; Pemphigus betae; Populus angustifolia; *sexupara; Utah.*

INTRODUCTION

An increasing number of studies demonstrate that natural plant populations show extensive variation in quality as hosts for their insect herbivores (e.g., Edmunds and Alstad 1978, Journet 1980, Moran 1981, Service and Lenski 1982, Whitham 1983, Marquis 1984, Fritz et al. 1986, Weis and Abrahamson 1986, Papaj and Rausher 1987). The bases of this heterogeneity may be genetic (e.g., Marquis 1984, Service 1984, Berenbaum et al. 1986, Fritz et al. 1986, Weis and Abrahamson 1986, McCrea and Abrahamson 1987, Simms and Rausher 1987), environmental (e.g., Thompson 1978, Carroll and Hoffman 1980, Atsatt 1981, Rausher 1982), developmental (e.g., Kearsley and Whitham 1989), or some combination. Regardless of its origin, variable host quality presents colonizing insects with the evolutionary challenge of adaptive discrimination among conspecific plants. While preferences for more favorable host individuals have been found in some cases (e.g., Rausher and Papaj 1983, Myers 1985, McCrea and Abrahamson 1987, Papaj and Rausher 1987, Sower and Mitchell 1987), as yet too few studies have been directed at detecting conspecific host discrimination to determine its extent in natural systems.

Here, we propose that the evolution of adaptive discrimination among conspecific hosts of variable quality is beset with obstacles not affecting discrimination among different host species. At the level of interspe-

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cific host discrimination, plant species manifest correlated suites of traits that allow them to be distinguished throughout the seasonal cycle. Thus, a female butterfly can select plant species for oviposition based on traits that are distinct from but perfectly correlated with interspecific differences that affect larval feeding. In contrast, within a set of hosts undergoing genetic exchange, such as a species or hybrid swarm, correlations among plant traits available as cues and traits determining quality may be weak, thus constraining this level of discrimination. The extent of these correlations depends on several factors, including (1) how long direct indicators of quality, such as nutrient content, are expressed, (2) possible linkage disequilibrium or pleiotropy involving traits used as cues and traits affecting host quality, or (3) causative links between traits used as cues and those determining quality.

We focus on the timing of events in the herbivore life cycle, particularly the timing of host selection in relation to feeding, as an important factor influencing the potential for adaptive discrimination among conspecific hosts. If selection of hosts is followed promptly by feeding, either by the selecting individual and/or her progeny, direct assessment of nutritive quality is possible, and the evolution of adaptive host selection is relatively straightforward. Examples include (1) grazers, such as grasshoppers (Mulkern 1967, Lewis 1984), mobile lepidoteran larvae using herbs (Chew 1980), and vertebrates (Bryant and Kuropat 1980); and (2) insects in which adults produce progeny that feed soon after colonization, as in most aphids (Klingauf 1987).

In contrast, the stage that selects hosts may occur long in advance of feeding stages, often when plants are in a very different physiological state. For example, in some insects with overwintering eggs, host selection occurs during the season preceding feeding, before the tissues that will serve as food are developed (examples in Funkhauser 1917, Swan and Papp 1972, Scott 1981). In such cases, direct assessment of nutritive quality may be impossible, and adaptive discrimination may be constrained by the availability of host features that are both detectable at the time of colonization and correlated with future quality as a host.

Autumn migrants of *Pemphigus betae* (Aphididae) colonize cottonwood trees near the time of leaf senescence and abscission, whereas feeding and induction of galls begin 6 mo later when trees are in a very different physiological state. This life cycle would appear to limit between-tree discrimination by migrants. However, host trees vary extensively in suitability for spring generations, potentially imposing strong selection for the ability to discriminate. For example, Whitham (1983) showed that tree-specific survivorship varies from 0 to 76%, with extreme trees growing side-by-side in the field. Host quality is largely genetic or cytoplasmically inherited, since 81% of the variation observed in parental trees is maintained when these same trees are cloned and grown in a common garden (Whitham 1989). Having identified a system in which discrimination is clearly advantageous but in which available cues may be poor indicators of future performance, we have an opportunity to examine host selection under unusually demanding circumstances.

We examined discrimination among trees of susceptible developmental stages of the host taxa. At coarser levels, *P. betae* migrants clearly discriminate in their choice of plants. Several tree species in non-host genera, including *Ulmus pumila, Acer negundo,* and *Fraxinus velutina,* were intermixed with the census trees and were completely avoided by colonists in censuses during heavy flights. Cottonwood trees at our study site include narrowleaf cottonwood, *Populus angustifolia,* Fremont cottonwood, *Populus fremontii,* and complex hybrids between them. Studies of nuclear DNA restriction fragment length polymorphisms (RFLPs) show that most of the trees used by *P. betae* are backcrosses with *P. angustifolia* (Paige et al., *in press,* Whitham 1989). This correlation between susceptibility and RFLPs indicates that variation in resistance is at least partly genetic. Fremont cottonwoods and F_1 hybrids are highly resistant and avoided by autumn migrants (N. A. Moran and T. G. Whitham, *personal observation*) and were not included here. Finally, since juvenile trees are resistant to galling and are avoided by migrants (Kearsley and Whitham 1989), only mature trees were included in the present study. While our study included only the most susceptible class of trees, mature *P. angustifolia* and hybrid backcrosses, individual trees in this category vary in resistance.

We tested abilities of migrants to discriminate among these individual trees. The specific questions we addressed include:

1) Do autumn migrants selectively colonize trees that support higher stem-mother survivorship in spring?
2) Does average leaf size, tree size, tree position, or degree of leaf retention in autumn show a correlation with colonization rates?
3) If a correlation between colonization and tree features occurs, does it hinder or facilitate adaptive host selection?
4) Since host-tree characteristics change during the colonization period, is the ability to discriminate affected by the timing of autumn migration by aphids?

STUDY ORGANISMS AND METHODS

The timing of host-tree selection in Pemphigus betae's *life cycle*

Our study area was in the lower Weber Canyon near Ogden, Utah, USA. During summer months at this location, *P. betae* exists as a series of wingless, subterranean, parthenogenetic generations on roots of herbs (*Rumex, Polygonum,* and *Chenopodium*). In September, these root colonies produce winged migratory forms that fly to cottonwood hosts. Abundances of migrants vary widely between years and appear to be dependent on summer rainfall, which affects growth of root colonies (Moran and Whitham 1988*a*). Before emigrating from their natal hosts, the abdomens of these migrants contain well-developed embryos, and the migrants' own digestive tracts degenerate before their flight. Soon after their arrival on a tree, migrants deposit the sexual offspring and die. As in other Pemphiginae, the sexuals have vestigial mouthparts and do not feed; they decrease in size with each of the four moults (Miyazaki 1987). After mating, each female deposits a single overwintering egg.

Eggs hatch in spring to give rise to the parthenogenetic stem mothers, which attempt to initiate galls on new leaves. Although these females can discriminate among leaves within a tree according to their suitability for gall formation (Whitham 1978), they are wingless and do not move between trees. Once a female has selected a leaf, she remains and inserts her stylets in a precise pattern in order to induce formation of a characteristic gall (Dunn 1960, Whitham 1986).

Natural history of host-tree selection

Flights occur over an interval of 4–6 wk during September and October. Under favorable conditions (temperature >16°C and windspeed <1 m/s), flights begin after 1500 and continue until sunset. During flights, aerial migrants are conspicuously more abundant in the immediate neighborhood of host-tree stands along the river, even where root host plants are absent from these areas. Migrants alight on leaves and, if the tree is acceptable, they walk down stems and branches to crevices in bark on dead branches or on the trunk. On heavily colonized trees many migrants can be observed walking down stems. In observations of individual migrants immediately following alightings, each proceeded to walk around, particularly at the margin, apparently periodically contacting the leaf with the apices of the rostrum and of the antennae. In 12 of 50 observed alightings, the migrant walked from the leaf toward the base of the stem, continuing down larger stems toward major branches and the main trunk. In 38 instances, the migrant took flight and could no longer be followed. The time between alighting and entry into a crevice was from 10 to 45 min in the 12 observed cases.

Study site and census trees

The trees included in the present study were selected haphazardly from a 100 m length of riverbank at the mouth of the Weber Canyon, in the zone where *P. betae* migrants and galls are most abundant (Moran and Whitham 1988*b*). For 34 mature trees we quantified colonization rates as well as resistance attributes that might affect colonization by autumn migrants. Secondary host plants, upon which migrants develop, were absent from the immediate vicinity of the stand of census trees.

Estimation of tree-specific survivorship

The susceptibility of individual trees to successful gall formation was measured as the ratio of successful galls to the total number of attempted galls. Total attempted galls can be counted because failed attempts to form galls result in recognizable deformities at the junction of leaf blade and petiole and in the death of the stem mother (Whitham 1978). Censuses of stem-mother survival rates and densities were made in each of 7 yr (1980 through 1986). Pole pruners were used to haphazardly remove 20 samples from each tree crown. Leaves of the terminal and four lateral shoots of each sample (a total of ≈600 leaves per tree per year) were censused for successful and aborted galls. Overall mortality rates were calculated for each tree for the 7-yr period, to give a single best estimate of host resistance to gall formation for each tree. Before analyses, arcsine and log transformations were applied to stem-mother survivorships and gall densities, respectively.

Estimation of colonization rates of individual trees

We sampled migrants directly as they colonized the study trees during three consecutive years, from 1983 through 1985. Direct observation of colonization events was too time-consuming to be feasible as a means of estimating colonization rates of individual trees. In addition, because colonization rates varied among days and with time of day, simultaneous estimates for all trees were needed. The method of sampling was based on the behavioral observations of individual migrants, described above.

Tanglefoot, a sticky resinous substance, was applied to bands of tape that were affixed so that they encircled the trunk just below the main portion of the crown. Colonists encountered these bands as they moved from their positions of alighting on leaves to crevices farther down the trunk where they would deposit their progeny. Following each census, bands were removed and migrants, entrapped in the upper margin of the Tanglefoot or under the upper edge of the tape, were counted.

Bands were applied to and removed from all trees simultaneously so that trees were sampled under identical flight conditions. Most censuses of colonists included a single day's flight, although traps were sometimes left up for >1 d when weather prevented flights on the first day that traps were set. Censuses were conducted at different times of the flight season, with a total of 12 censuses during the 3 yr. On some census dates the height of the river or wind precluded censusing certain trees, resulting in missing values. Three trees were missing more than two of the census dates and were excluded, giving colonization data for 31 trees.

Raw census totals gave estimates of colonization rates per tree. Since trees varied in size, we estimated colonization rates on a per-leaf basis by dividing total number of colonizers by an index of tree crown volume (see Measurement of Tree Characters, below). Colonization rates were log transformed before statistical analysis. Consistency of host choice was examined by estimating correlations between colonization rates during different census years. Simple linear regressions of colonization rates on stem-mother survivorships were calculated to determine whether colonists colonize more favorable trees. The question of whether choice is more successful on some flight days than on others was addressed by calculating correlations between stem-mother survivorships and colonization rates for each census date.

These estimates of relative colonization rates will reflect differences in passive encounter rates due to tree position as well as any pre- or post-alighting phases of active discrimination. Differences in proximity to root-host plants were probably unimportant since distances to root-host stands were great (≈1 km) relative to distance among census trees (≤100 m), which were selected from a continuous stand of cottonwoods. Differential predation between alighting and entrapment could not have been great enough to significantly affect census numbers, since predation on walking migrants was never observed during the 3-yr study. Differential availability of crevices for oviposition distal to our sticky bands could have been a factor; however, we positioned traps so as to minimize numbers of distal oviposition sites. Wind was probably not an important contributor to tree-specific colonization rates since windspeed was effectively zero during flights.

Measurement of tree characters

We measured six tree features, height, crown volume, distance from the riverbank, position ranked from upstream to downstream, leaf size, and degree of autumn leaf retention. These traits varied widely among trees, and were thought likely to influence colonization by autumn migrants. Tree height was measured directly using a telescoping pole. Volumes were estimated by each of us independently, based on an arbitrary unit of the smallest tree crown, and averaged when estimates differed. Distance from the riverbank was measured directly using metre tape. Mean leaf areas were calculated based on samples of 240 to 894 leaves per tree for each of 2 yr (1980–1981). Leaf sizes for the 2 yr were highly intercorrelated, and were averaged to give a single estimate. An index of leaf retention during autumn was obtained by categorizing each tree into one of seven ranked categories, ranging from "all leaves abscised" to "fewer than 10% of leaves abscised." Leaf retention rankings were made three times during 1984 and 1985. Scorings showed high intercorrelations, and were averaged to obtain a single index of autumn leaf retention for each tree. We tested for an influence of tree features on discrimination among hosts by calculating correlations between colonization rates and our measures of tree characteristics. To determine whether such an influence improves or confounds adaptive discrimination, we examined the correlation between gall success rates and host attributes found to influence colonization.

RESULTS

Variation in host-tree quality as reflected by survivorship

Rates of aphid success at gall formation varied substantially among the 34 trees. Tree-specific survivorships for the 7-yr census period ranged from extremes of 12.8% to 79.5% (total successful galls/total attempted galls; $\bar{X} \pm \text{SD} = 56.1 \pm 15.7\%$, $N = 34$). Furthermore, success rates for individual trees were highly intercorrelated between years. We could not calculate correlations for all pairwise combinations of years, since numbers of attempted galls for certain resistant trees were too low to provide meaningful estimates of survivorships for single years. However, correlations between success rates in odd-numbered vs. even-numbered census years, and between the first three vs. the last three census years were both highly significant ([1980, 1982 1984, 1986] vs. [1981, 1983, 1985]: $r = 0.70$, $P < .0001$, $N = 34$; [1980–1982] vs. [1984–1986]: $r = 0.78$, $P < .0001$, $N = 34$). Thus, individual trees maintained characteristic levels of susceptibility across years under natural conditions.

Variation in colonization rates among host trees

Colonization rates by autumn migrants varied widely among individual trees, with averages ranging from 1.0 to 163.4 colonizers in a single day's flight on a per-tree basis, and from indices of 0.5 to 29.5 colonizers per unit of tree crown volume. Furthermore, colonization rates showed high correlations across years (Table 1), indicating that the same trees were favored by colonizers in successive autumns. This consistency among years also indicates that our census method gives a reliable index of autumn colonization rate.

Trees that are colonized more in autumn also have higher densities of attempted (successful and aborted) galls in the spring ($r = 0.47$, $P < .01$, $N = 31$ for the correlation between the 3-yr colonization rate and the 7-yr density estimate).

Relationship between colonization rate and host resistance

Colonization rates, both on a per-tree scale and a per-leaf (or crown volume) scale, showed a significant positive relationship with survival rates, indicating that the observed pattern of colonization resulted in success rates higher than those expected if migrants colonized randomly (Table 2). Significant correlations between

TABLE 1. Intercorrelations of colonization rates by autumn migrants of individual trees between years, as measured on a per-tree basis and on the basis of relative crown volume. Data were log-transformed.

	Colonizers per tree		Colonizers per unit crown volume	
	1984	1985	1984	1985
1983	0.65 (N = 29, P < .0001)	0.47 (N = 28, P < .05)	0.42 (N = 29, P < .05)	0.19 (N = 28, NS)
1984	···	0.80 (N = 29, P < .0001)	···	0.71 (N = 29, P < .0001)

colonization and survivorship are apparent for each of the yearly sums as well as for the 3-yr totals (Table 2, Fig. 1). The low correlation coefficients suggest that discriminatory abilities are far from perfect. Migrants successfully avoided the few very resistant trees present in the sample but did not discriminate among trees on which average survival exceeded 45% (Fig. 1). These correlations cannot be due to positive density dependence, since (1) survivorships in experimental transfers to clones with similar, controlled aphid densities closely matches that on naturally occurring parental trees (Whitham 1989) and (2) increased densities result in reduced survival and reproduction (Whitham 1986), increased predation (Whitham 1987), and higher premature leaf drop that kills nearly all the aphids on abscised leaves (Williams and Whitham 1986).

Influence of leaf size on colonization rates

Variation in leaf size within single trees is known to strongly affect gall development and aphid fitness (Whitham 1980). Variation in stem-mother survivorship among trees is also related to variation in leaf area among trees (r = 0.44, P < .02, N = 33). Thus, leaf size relates directly to differences in habitat quality both within and between trees. Whereas colonizing stem mothers do prefer larger leaves (Whitham 1978, 1980), autumn migrants do not appear to use leaf size in selecting trees (Table 3).

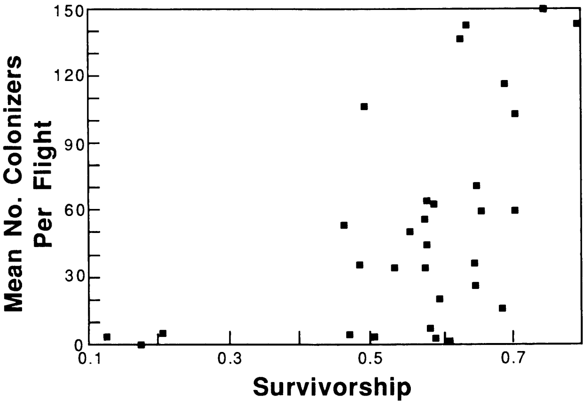

FIG. 1. Relationship between autumn colonization rates and stem-mother survivorships for individual narrowleaf cottonwood trees (r = 0.61, P < .005, N = 31). Colonization rates are based on average number of colonizers per flight per tree for 12 sampling dates during 3 yr, and survivorships are based on the ration of successful galls to attempted galls for 7 yr.

Influence of host-tree size on colonization rates

On a per-tree basis, colonization rates were higher on larger trees, as reflected in the significant correlations between colonization rate and both height and crown volume (Table 3). On a per-leaf basis, however, colonization rate was not significantly related to tree size. Larger trees received more colonists but not a higher density of colonists relative to their crown volumes (Table 3).

Influence of host-tree position on colonization rates

Differences in colonization rates among trees are not a consequence of tree position in relation to the riverbank (Table 3). Since all census trees were near the river, these data do not eliminate the possibility that colonization is affected by greater distances.

Furthermore, colonizers were not concentrated in any one segment of the 100 m length of riverbank where census trees grew (Fig. 2). Trees showing both extremes in colonization rates occurred along the entire length of our study site.

Influence of leaf retention by host tree on colonization rates

Colonization rates on both a per-tree and per-leaf basis were positively related to degree of leaf retention in autumn (Table 3, Fig. 3). A more direct picture of

TABLE 2. Correlation coefficients between autumn colonization rates and spring survivorship rates for individual cottonwood trees. Log and arcsine transformations were applied to colonization rates and to survivorships, respectively.

	Year	N	r	P <
Colonization per tree	1983	29	0.62	.0005
	1984	30	0.56	.005
	1985	31	0.48	.01
	3 year total	31	0.61	.005
Colonization per unit crown volume	1983	29	0.48	.01
	1984	30	0.50	.005
	1985	31	0.35	.05
	3 year total	31	0.48	.01

TABLE 3. Correlation coefficients (r) between colonization rates of autumn migrants and characteristics of individual cottonwood trees. Log transformations were applied to colonization rates.

	Year	N	Height	Crown volume	Distance to river	Leaf retention	Leaf size
Colonization per tree	1983	29	0.52**	0.56**	−0.35	0.35	0.18
	1984	30	0.51**	0.63***	−0.24	0.43**	0.28
	1985	31	0.35*	0.42*	0.01	0.48**	0.15
	3 year total	31	0.47**	0.54**	−0.20	0.47**	0.22
Colonization per unit crown volume	1983	29	0.12	0.07	−0.7	0.23	0.03
	1984	30	0.20	0.31	−0.12	0.43**	0.27
	1985	31	0.01	0.08	0.19	0.43**	0.06
	3 year total	31	0.04	0.07	0.02	0.40*	0.07

* $P < .05$, ** $P < .01$, *** $P < .001$.

the effect of leaf retention on colonization is apparent from Fig. 4, which shows the relationship between leaf colonization and leaf retention assessed simultaneously, on 1 October 1984. Trees with few or no leaves received few or no colonizers; trees with many leaves received few to many colonizers. Thus, more aphids colonized trees with more leaves, whether due to larger crowns or to greater persistence of leaves in autumn.

Implications of leaf retention and tree size for adaptive host discrimination

The positive relationships between colonization rates and both tree size and leaf retention suggest that flying aphids utilize cues, visual and/or chemical, produced by tree leaves in autumn. To determine whether use of measured plant traits facilitates or thwarts adaptiveness of discrimination, we examined the relationship between tree size and stem-mother survivorship, and between leaf retention and stem-mother survivorship.

Trees with larger crowns supported significantly greater rates of spring gall success ($r = 0.45$, $P < .01$, $N = 34$). No relationship was evident between tree height and gall success rates ($r = 0.21$, $P > .2$, $N = 34$).

Of the plant traits measured, the single cue available to the autumn migrants that best reflects the success of stem mothers the following spring is leaf retention. Trees retaining leaves longer in autumn are more favorable for gall formation in spring ($r = 0.60$, $P < .0002$, $N = 34$; Fig. 5).

Influence of the seasonal timing of colonization on discriminatory ability

Correlation coefficients between autumn colonization rates and stem-mother survivorships do not differ significantly between different census dates, whether colonization is on a per-tree or a per-leaf basis (Table 4; comparison of multiple correlation coefficients, for colonization per leaf, $\chi^2 = 4.6$, df = 11, NS; for colonization per tree, $\chi^2 = 5.4$, df = 11, NS; Zar 1984).

DISCUSSION

The choosiness of *P. betae* autumn migrants is restricted by the brevity of their lives once they depart their natal hosts, by their limited power and control in flight, and by the difficulty of their task. Migrants taken directly from their original root colonies on summer hosts and placed in Petri dishes with moist filter

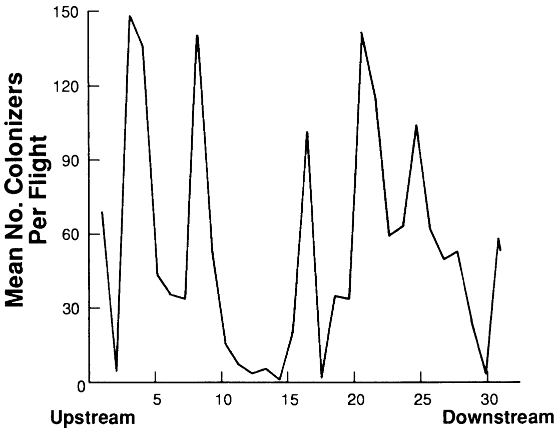

FIG. 2. Relationship between average colonization rates by autumn migrants and rank of tree position along the 100 m length of riverbank.

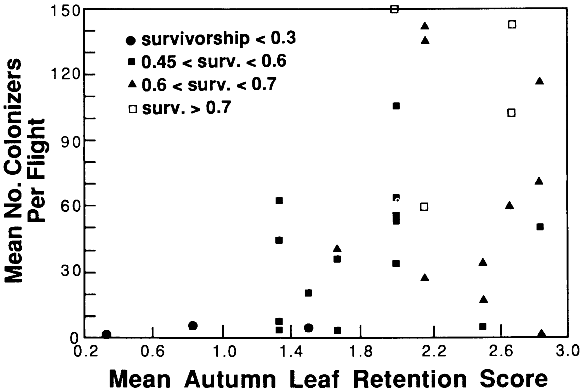

FIG. 3. Relationship between autumn colonization rates and degree of autumn leaf retention for individual trees ($r = 0.47$, $P < .01$, $N = 31$).

TABLE 4. Correlations between autumn migrant colonization rates and stem-mother survivorships for individual trees on different census dates during the three census seasons. All relationships were positive. Log and arcsine transformations were applied to colonization rates and survivorships, respectively.

Date of census	*N*	*r*	*P* <
1983: 24 Sept	27	0.62	.001
28 Sept	28	0.51	.01
17 Oct	25	0.40	.05
1984: 22 Sept	24	0.45	.05
28 Sept	32	0.43	.05
1 Oct	32	0.47	.01
5 Oct	32	0.53	.005
9 Oct	32	0.53	.005
1985: 2 Sept	31	0.18	.35
29 Sept	31	0.44	.01
3 Oct	31	0.55	.005
8 Oct	31	0.54	.005

paper produce their sexual offspring and die within 12 to 48 h at field temperatures. This commitment to depositing all of their progeny quickly implies that migrants must find a host during the first, or possibly second, evening following their flight from root colonies. Thus, *P. betae* migrants may have little opportunity to discriminate, due to the lack of detectable cues correlated with quality, and to their own clumsiness and ephemerality. Yet, failure to discriminate can result in complete reproductive failure.

The significant relationships between colonization rate and spring survivorship show that *P. betae* migrants do manage to preferentially colonize host trees that are more favorable for descendants. Individual trees do vary in traits that might be detected in autumn. For example, we found variation in leaf retention and leaf size, and clones of other *Populus* species have been shown to differ in leaf chemistry (Garbaye 1972) and in architecture (Nelson et al. 1981). Adaptive discrimination by *P. betae* migrants depends on the existence of correlations between detectable autumn characteristics and susceptibility in spring. We have not identified the cues used by migrants; the traits we measured may correlate with others that are used as cues. Because crown volume and, especially, degree of leaf retention correlate with subsequent stem-mother survivorship (Fig. 5), a simple attraction to leaf-produced stimuli, whether visual or chemical or both, could explain the differential colonization of superior hosts. More *P. betae* colonizers go to trees that retain their leaves longer and that are larger (Table 3, Figs. 3 and 4), suggesting that attraction to leaf-produced cues does contribute to the ability to select more favorable hosts. These findings do not imply that attraction to leaf-produced stimuli evolved in the context of conspecific host discrimination. Possibly, leaf-produced cues must be used due to constraints on sensory capabilities, and, by chance, trees with more leaves are superior hosts. In either case, use of leaf-based cues positively affects future success.

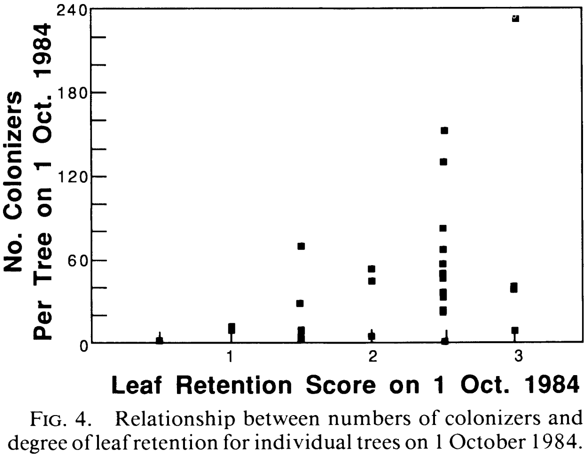

FIG. 4. Relationship between numbers of colonizers and degree of leaf retention for individual trees on 1 October 1984.

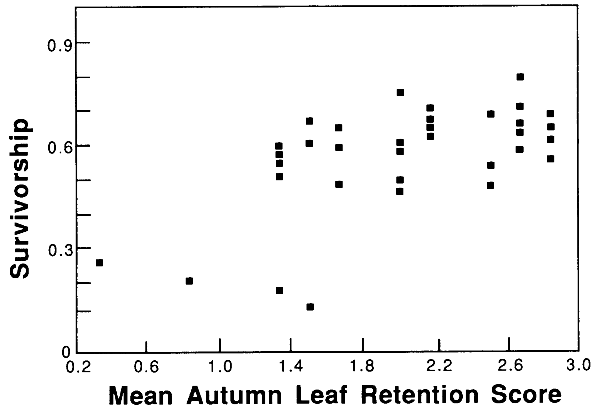

FIG. 5. Relationship between degree of leaf retention in autumn and survivorship of stem mothers in spring ($r = 0.60$, $P < .0002$, $N = 34$).

Colonization data are consistent with a simple discrimination between two categories of trees, those that are resistant (stem-mother survivorship < 0.45) and those above an apparent threshold of susceptibility (stem-mother survivorship > 0.45, Fig. 1). The relationship between attributes of susceptible (>45% survival and resistant (<45% survival) trees in autumn and stem-mother survivorship in spring is strong, implying that these features are useful as indicators of host quality. However, the ability to discriminate among superior hosts (trees with 45–80% aphid survival) is weak (Table 2, Fig. 1), suggesting that more highly informative cues are absent. Of course, other cues not examined by us, particularly leaf chemical characteristics, may play a role in discrimination, and may aid or hinder the ability to select good hosts. Observations of colonizing migrants in the field suggest some role of leaf chemical cues after contact. Upon alighting, a migrant frequently spends several minutes on a leaf and appears to contact it both with the tip of the labium, which is known to have mechanoreceptors in aphids, and with the antennae, which have chemoreceptors in aphids (Anderson and Bromley 1987). Some ability to discriminate among chemicals, at least enough to ascertain that a plant is the correct host species, is very likely, since other tree genera (*Ulmus, Fraxinus,* and *Acer*) in the vicinity of the censused cottonwoods did not intercept any *P. betae* migrants, despite the large number of leaves still persisting on these non-host taxa. Interestingly, in a study of clone-specific differences in nutrient content of *Populus* leaves, Garbaye (1972) concluded that tree-specific nutrient status is best characterized by sampling leaves near the top of the crown during early autumn. Thus, *P. betae* may be sampling under conditions best suited for discriminating among individual trees.

In some other insects, correlates of host-plant quality have been found to exist, and to be utilized for discrimination among conspecific hosts. For example, females of *Battus philenor* preferentially oviposit on individual plants that have larger buds, and these support better larval growth and survival (Papaj and Rausher 1987). The bud-galling sawfly, *Euura mucronata,* oviposits more frequently on longer shoots that support higher rates of larval establishment and survival (Price et al. 1987). The western pine shoot borer, *Eucosoma sonomana,* selectively oviposits on ponderosa pines with the largest terminal buds, and these produce the longest shoots (Sower and Mitchell 1987). In each case, a direct mechanistic link between cue and nutritive quality is evident. In some other insects, colonists do not seem to use host features that correlate with quality. For example *Euphydryas editha* does not show adaptive discrimination among conspecific hosts (Mackay 1984), and in several species, pre-alighting or post-alighting ovipositional preferences among different host species did not correspond with quality for developing larvae (Wiklund 1975, Courtney 1981, Singer 1983).

The average survivorship actually achieved by *P. betae* stem mothers is ≈60%. (The summation of products of proportions of attempted galls per tree times tree-specific survivorship gives 59.6%; the summation of products of proportions of autumn migrants per tree times tree-specific survivorship gives 63.8%.) Thus, ≈40% of hatching spring females fail to reproduce at all, due to the resistance of their individual hosts, and 25% of the remainder suffer from early leaf abscission (Williams and Whitham 1986). Possibly, the lag between colonization and feeding limits the discriminatory powers of *P. betae* and other pemphigines as compared to most aphids in which winged colonists themselves and their immediate progeny feed on selected hosts.

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