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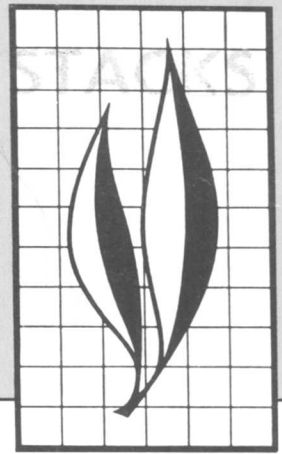
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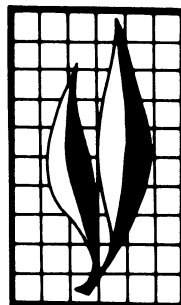
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## Distribution and Dynamics of Aphid (Homoptera: Drepanosiphidae) Populations on *Betula pendula* in Northern California

Ann E. Hajek and Donald L. Dahlsten



## ABSTRACT

Three species of autoecious aphids, *Callipterinella calliptera* (Hartig), *Euceraphis betulae* (Koch), and *Betulaphis brevipilosa* Börner, commonly occur on European white birch trees, *Betula pendula* Roth, in northern California. Populations were sampled from 1981 through 1984 at two sites. Within-tree populations of all three species were more abundant in the lower and middle vertical thirds of tree canopies. Optimal sample sizes were estimated for individual trees as well as tree populations, given variable mean aphid densities, sampling reliability levels, and sampling costs. An aesthetic injury level for honeydew production was estimated.

At both sites, all species exhibited spring and fall peaks with a summer decline in numbers. *Callipterinella calliptera* and *B. brevipilosa* populations increased during late summer while feeding on mature leaves. *Euceraphis betulae* preferred developing and senescing leaves and was reproductively inactive during summer. At the warmer inland site, *C. calliptera* and *E. betulae* were present only early in spring and late in fall and *B. brevipilosa* populations were virtually absent.

Natural enemies associated with these aphids did not prevent the development of large populations, although coccinellids and syrphids demonstrated numerical responses. The only ant-tended aphid species, *C. calliptera*, developed the largest populations of all three aphid species.

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### THE AUTHORS:

Ann E. Hajek, formerly a graduate student, Division of Biological Control, Department of Entomological Sciences, University of California, Berkeley, is currently Research Affiliate, U.S. Department of Agriculture, Agricultural Research Service, Plant Protection Research Unit, Boyce Thompson Institute, and Visiting Fellow, Department of Entomology, Cornell University, Ithaca, NY 14853. Donald L. Dahlsten is Professor of Entomology and Chair of the Division of Biological Control, and Entomologist in the Experiment Station, University of California, Berkeley, CA 94720.

# Distribution and Dynamics of Aphid (Homoptera: Drepanosiphidae) Populations on *Betula pendula* in Northern California<sup>1</sup>

## INTRODUCTION

THREE AUTOECIOUS SPECIES of aphids, *Callipterinella calliptera* (Hartig), *Euceraphis betulae* (Koch), and *Betulaphis brevopilosa* Börner, commonly occur on European white birch, *Betula pendula* Roth, in northern California. The aphids and their host trees are European in origin. The natural histories of aphids on *B. pendula* have been reported from Denmark where they are native (Heie 1972). During 1974, the biologies of California populations of two birch aphids, *C. calliptera* and *E. betulae* (= *Euceraphis punctipennis* (Zetterstedt)), were studied on four birch trees in San Leandro, California (Grushkowitz 1976).

In California, *B. pendula* is a commonly planted ornamental tree. The three aphids frequently develop large populations on ornamental birches and produce copious amounts of honeydew, thus constituting a nuisance in the urban environment. As a result of the high potential for outbreaks in populations, many homeowners spray their birches with insecticides on a preventive basis for aphid control.

Studies of aphid population dynamics often implicate natural enemies, intraspecific competition, host quality, weather, and production of emigrants as potential regulatory factors (Dixon 1977). Research efforts in aphid population ecology have often highlighted only the dynamics of one aphid species at a time. A few exceptions include studies of aphid complexes on potatoes (Robert 1979), cereal crops (Honěk 1985; Wiktelius and Ekbohm 1985), and fireweed (Addicott 1978). Recent models with subsequent field validation have most elegantly compared those factors with the greatest impact on population levels of two sympatric alfalfa aphid species (Gutierrez and Baumgaertner 1984a, b; Gutierrez, Baumgaertner, and Summers 1984).

In the present study our initial goals were to determine the within- and between-tree distributions of these three aphids and to develop a sampling strategy. Sampling was conducted to study the influence of abiotic and biotic factors on populations of *E. betulae*, *C. calliptera*, and *B. brevopilosa*. The impact of natural enemies, ant attendance, host quality, and alate production on the population dynamics of each species was compared.

## METHODS

### Study Sites

Birch aphid populations were studied from 1981 through 1984 in Albany, Berkeley, and Walnut Creek, California. Albany and Berkeley are directly adjacent to San Francisco Bay; Walnut Creek is approximately 32 km inland. European white birch is

<sup>1</sup>Approved for publication on October 8, 1987.

frequently grown ornamentally in yards of homeowners in these cities (Hajek and Dahlsten 1986b). In a 1.6-km<sup>2</sup> residential area in both Albany and Walnut Creek all birch trees were mapped. Throughout this study, sample trees were chosen randomly from among those 4.6- to 10.7-m trees, without obvious injury or lack of vigor. Included were only trees belonging to homeowners who agreed to cooperate in this study and not treat their trees for insect pests. At both sites, hygrothermographs were operated within the study area.

## Distributional Studies

### Egg distribution

Birch aphids overwinter as eggs on the wood of dormant trees. Egg distributions on branch terminals were evaluated in 1984 on five trees in Berkeley and Albany, California. Ten branch terminals, composed of the previous year's growth, were clipped on January 19 and 20 from each of six quadrants: three vertical levels and inner and outer canopy locations. Samples were chosen randomly from all sides of the trees (method described below) within each quadrant. Eggs of each species were identified, using size and shape characteristics (Hajek and Dahlsten 1987b), and counted under a dissecting microscope.

### Distribution of nymphal and adult viviparae

In 1981, 209 *B. pendula* east of San Pablo Avenue in Albany matched the selection criteria for inclusion in this study. A commonly planted cultivar named cutleaf birch, *B. pendula* 'Dalecarlica', comprised 15 percent of all birches in the study area and was included in the 1981 study design.

Fifteen trees of *B. pendula* and *B. pendula* 'Dalecarlica' were chosen for study. They were divided vertically into thirds and radially into inner and outer canopy, for a total of six quadrants. The outer canopy was defined as the outermost portions of branches. Ladders were used for sampling to reduce foliage disturbance since both *E. betulae* and *C. calliptera* can be fairly mobile. The outer canopy of the top third of the trees could not be reached for sampling and therefore was excluded. Sampling by cardinal direction was not used as directional effects were obscured because of frequent proximity of sample trees to houses or other trees (Hajek, unpublished data). Sampling was nondestructive and all counts were taken in the field since the three aphid species can be easily distinguished (Hajek and Dahlsten 1987b).

The sampling unit chosen was the branch terminal. Birch trees have two types of shoots that produce leaves: (1) short shoots that produce two to three leaves at the beginning of each year and (2) long shoots that continue to grow through much of the season, producing at least three leaves as well as the present year's twig growth (Maillette 1982). To encompass potential differences in aphid preference for leaf types and ages, samples of branch terminals included both short and long shoots. For each sampling unit, leaves were sampled on the length of new twig produced by a long shoot as well as on short shoots occurring along an equal length of the previous years' twig, proximal to the long shoot. Sample branches were randomly chosen using a random numbers table to find percentage height in each quadrant and radial position around the tree (out of 360°, with 0° to the north).

On the initial sample date, sample branches were marked with red tape and were repeatedly sampled thereafter to reduce variability from one date to the next. The influence of tagging on aphid density was tested by randomly sampling 15 tagged and untagged branch terminals on each of 15 trees in Albany once between July 7 and 12, 1982. Tagging did not influence the total aphid density ( $p \geq 0.05$ ) or the occurrence of any of the three individual aphid species ( $p \geq 0.05$ ).

To evaluate population distributions in 1981, 10 branches were sampled in each of the 5 quadrants with a total of 50 branches per tree, or 750 branches per sample date. All trees were sampled three times: June 20–July 23, August 6–27, and September 8–24. Only species trees, and not cutleaf, were also sampled once in spring: May 21–June 11. During 1982, 30 branches per tree in the lower and middle crowns of 14 cutleaf and species birches were sampled twice in Albany: July 16–August 6 and September 3–28.

### Statistical analysis

Egg, nymphal, and adult distributions were analyzed using the general analysis of variance (ANOVA) approach proposed by Morris (1955). Aphid densities were transformed using  $\log_{10}(x + 1)$  to normalize data. To evaluate those factors necessary for inclusion in a sampling design, a multiway ANOVA (program BMDP 8V [Jennrich and Sampson 1981]) of 1981 data tested relationships between the density of nymphal and adult viviparae on branches and sample date, cutleaf versus species trees, crown level, radial location, and individual trees. Since 1981 quadrants were unbalanced because the outer canopy of the top third of the trees was not sampled, distribution was tested in two ways for each aphid species: ANOVA I tested inner and outer crown samples for the two lower vertical levels and ANOVA II tested the three inner canopy vertical levels. The experimentwide error level of  $\alpha = 0.10$  for each ANOVA was partitioned between main effects and interactions. Aphid distribution by the two lower vertical canopy levels was retested with 1982 data. For main effects that were not significant in ANOVAs of nymphs and adults, statistical power was calculated based on formulas presented by Scheffé (1959) for 1981 data and Swartz and Dahlsten (1980) for 1982 data.

### Sample Size Determination

Estimates of variances and means from 1981 aphid populations were used to determine the sample sizes necessary for population estimation. Variances of many plant and animal populations have been shown to increase with the mean (Taylor 1961). This relationship is commonly referred to as Taylor's Power Law:

$$s^2 = ax^b \quad \text{or} \quad \log s^2 = \log a + b \log x \quad [1]$$

The slope and intercept coefficients of this regression equation provide species- and sample unit-specific values that can vary due to age-specific dispersal, mortality, and sample unit size (Wilson 1985). These coefficients are extremely useful for estimating variances at differing population densities. Coefficients derived with Taylor's Power Law were therefore used to describe aphid distributions for sample size calculation.

Sample size calculations were generally based on equations from Karandinos (1976) that provide a statistical probability for the reliability of sample size estimates. Reliability was calculated as the number of samples necessary for an estimate of the mean with half-width confidence intervals that are a given proportion (D) of the mean (Karandinos 1976). To calculate the numbers of samples necessary per individual tree:

$$n = \frac{Z_{\alpha/2}^2}{D^2} * (a\bar{x}^{b-2}) \quad [2]$$

where a, b = coefficients from the within-tree variance/mean regression, n = number of branches to sample per tree, D = a fixed proportion of the mean used to define a half-width of the confidence interval ( $1/2$  C.I. =  $D\bar{x}$ ), and  $Z_{\alpha/2}$  = upper  $\alpha/2$  point of the standard normal distribution.

To evaluate aphid populations on an areawide basis, a two-stage method for calculation of sample size was adapted for use with Taylor's Power Law coefficients. Cochran (1963) defined the standard error of the mean ( $V(y)$ ) as being composed of variance components from both stages in two-stage systems. In terms of the present study:

$$V(y) = \frac{\sigma_t^2}{n_t} + \frac{\sigma_b^2}{n_t n_b} \quad [3]$$

where  $\sigma_t^2$  = variance among trees,  $\sigma_b^2$  = variance within trees,  $n_b$  = number of branches per tree, and  $n_t$  = number of trees. Incorporating this partitioned variance into sample size calculations (Equation 2) and substituting Taylor's Power Law relationships to help calculate variances:

$$n_t = \frac{Z_{\alpha/2}^2}{D^2} * \frac{a_b \bar{x}^{b_b-2}}{n_b} + a_t \bar{x}^{b_t-2} \quad [4]$$

where  $a_t$ ,  $b_t$  = coefficients from the among tree variance/mean regression and  $a_b$ ,  $b_b$  = coefficients from the within-tree variance/mean regression.

The time necessary to obtain samples of various sizes at differing levels of reliability and aphid densities was evaluated. The cost of sampling a population of trees was calculated as:

$$C = n_t(c_t + (n_b * c_b)) \quad [5]$$

where C = total cost (in person-hours),  $c_t$  = cost of moving between trees,  $c_b$  = cost to sample a branch. The number of branches to sample per tree, with the greatest cost effectiveness, was calculated according to Southwood (1978):

$$m = \sqrt{\frac{C_t * \sigma_b^2}{C_b * \sigma_t^2}} \quad [6]$$

An estimate of the aesthetic injury level was developed using 1983 data. For each sample date, each tree was subjectively judged by the first author as to whether aphid populations were creating a nuisance through honeydew production, premature leaf fall, or both. The midpoint between the lowest aphid density causing problems and the highest aphid density that did not cause problems was calculated. This density provides an approximation of the threshold density of aphid populations that are a nuisance, or an aesthetic injury level.

## Population Studies

For population studies, aphid populations were compared on species birches only. Within-tree distribution information, sample size calculations, and time constraints determined the quadrants and numbers of branches and trees sampled during 1982 and 1983. During 1983, 20 lower- and middle-crown branches from each of 12 species birches were sampled every 2 to 4 weeks from bud burst until approximately 50 percent abscission. Trees were sampled a total of 17 times in Albany and 13 times in Walnut Creek, between March 25 and November 20. To maintain a fairly consistent number of leaves sampled on each sample date, on the first date, the leaves of five bursting buds were examined at each of 20 randomly selected locations within each tree canopy. Since twigs grew from these buds and added more leaves as the season progressed, during the next three sample dates, progressively fewer samples were examined at each location so that by mid-May, the leaves from only one branch (previously, a bud) were examined at each of the 20 locations within each tree crown.

For all species, counts of nymphs (specifying fourth instars with wing buds), apterous and alate adult viviparae, and sexuales were made in the field. Three age classes of leaves were identified in 1983 (developing leaves that were still unfolding, mature leaves, and yellowing leaves) and aphid abundance by leaf age was recorded.

The differential suitability of these three aphid species as food sources for *Adalia bipunctata* (L.) larvae was evaluated. Coccinellid eggs were collected from the field in Albany or from a colony fed *Acyrtosiphon pisum* (Harris) that had been maintained for one generation in the laboratory. When eggs hatched, coccinellid larvae were individually transferred to 5 × 8.5-cm plastic vials and reared at 20°C with a 16:8 photoperiod. Aphids of the three species were field-collected and transferred separately onto one-leaf bouquets. Bouquets were made by tightly wrapping the petiole of a birch leaf with cotton and placing this in a water-filled, 2 × 5-cm vial. Leaf bouquets were placed inside of vials with coccinellid larvae. Each day, the number of aphids eaten was recorded and aphids were added so that excess aphids would remain the next day. A fresh bouquet was made every third day.

All Aphidiidae parasitizing birch aphids were field-collected as mummies and laboratory-reared. Diptera larvae collected on birch were reared in the laboratory on a diet of birch aphids. Other natural enemies were brought to the laboratory for rearing and identification when necessary.

Student's t-test was used to test for increases in coccinellid and syrphid egg density with increasing aphid density. To maintain independence between samples, separate regression lines were calculated for each tree and the common slopes were tested against 0 and each other. Parasitism levels were calculated by counting each mummy on only the first sample date it was present.

## RESULTS AND DISCUSSION

### Aphid Distribution and Sampling Design

#### Distribution of eggs

Means and standard errors for *E. betulae* and *C. calliptera* eggs by quadrant are presented in table 1. ANOVA results demonstrated no differences among horizontal or vertical quadrants for either species ( $p \geq 0.05$ ). Although viviparae prefer the lower and middle canopy during spring, summer, and autumn (see following), these findings suggest that oviparae disperse throughout the canopy.

During this study, *E. betulae* and *C. calliptera* eggs were primarily found in cracks and crevices where buds lay alongside twigs, in leaf scars, and under the apices of bracts of male aments. Grushkowitz (1976) also found eggs of *E. betulae* and *C. calliptera* on branch terminals. Branch terminal samples contained almost no eggs of *B. brevopilosa*. This suggests an alternate site for oviposition of *B. brevopilosa* since populations of oviparous *B. brevopilosa* inhabited sample trees during the autumn preceding this sample period. Other dendrophilous aphid species are known to oviposit preferentially on 1- to 2-cm diameter branches (*Chromaphis juglandicola* (Kaltenbach); Nowierski and Gutierrez 1986) and in bark crevices  $> 50$  cm from the terminal buds of branches (*Drepanosiphum platanoidis* (Schrank); Dixon 1976).

#### Distribution of nymphal and adult viviparae

Mean population estimates of untransformed 1981 aphid densities by sample date, vertical crown level, horizontal crown location, and tree type are presented in table 2. The overall results demonstrate that variation between dates and between individual trees was frequently significant ( $p \leq 0.01$ ). Vertical crown level differed significantly for all species when comparing three crown levels (ANOVA II;  $p \leq 0.01$ ), although it did not differ between the lower and middle strata (ANOVA I;  $p \geq 0.01$ ). Density estimates support these results since very few aphids inhabited the upper third of tree canopies (table 2). Two-way interactions indicated that vertical distribution varied in individual trees for *E. betulae* and *B. brevopilosa* ( $p \leq 0.005$ ) and by date for *B. brevopilosa* and *C. calliptera* ( $p \leq 0.005$ ). Despite these differences in distribution by date, for all sample dates *B. brevopilosa* and *C. calliptera* densities in the upper third of trees never exceeded 5.0 percent or 1.6 percent, respectively, of the total populations. The extremely low populations in the upper vertical third of trees indicates that omitting this level from sampling is adequate for population estimation.

Since tree type, crown level (comparing two levels), and horizontal location were not significant, the power of ANOVAs ( $1-\beta$ ) to prove that these factors had no effect was tested. Variation between samples was so high that these results do not prove that these factors had no effect ( $p \geq 0.05$ ).

To further test for differences between lower- and middle-crown levels, data were collected in 1982 (table 3). Aphid distributions for *C. calliptera* and *E. betulae* were similar to results from 1981 (table 2) with higher densities in the lower canopy compared with the middle canopy. *Betulaphis brevopilosa* distributions in 1982 demonstrated a different trend during the summer with higher densities in the middle canopy (table 3). However, for all species, statistically significant differences in the

TABLE 1. DISTRIBUTION OF EGGS OF *CALLIPTERINELLA CALLIPTERA* AND *EUCERAPHIS BETULAE* ON BRANCH TERMINALS WITHIN *BETULA PENDULA* CANOPIES IN BERKELEY AND ALBANY, CALIFORNIA, 1984

Aphid species/location	Inner canopy		Outer canopy	
	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
(eggs/cm of branch)				
<i>Callipterinella calliptera</i>				
Lower canopy	0.976	0.229	1.108	0.289
Middle canopy	1.152	0.418	2.214	0.782
Upper canopy	1.078	0.443	1.520	0.561
<i>Euceraphis betulae</i>				
Lower canopy	0.228	0.106	0.266	0.175
Middle canopy	0.140	0.105	0.267	0.139
Upper canopy	0.102	0.083	0.342	0.186

TABLE 2. DENSITIES OF THREE SPECIES OF APHIDS ON *BETULA PENDULA* BY DATE, TREE TYPE, AND CANOPY POSITION IN ALBANY, CALIFORNIA, 1981

Aphid species	Sample date*			Tree type*		Vertical crown level†			Horizontal location*	
	Jun 23- Jul 21	Aug 6-27	Sept 9-24	Cut- leaf	Spe- cies	Lower	Middle	Upper	Inner	Outer
	( $\bar{x}$ aphids/100 cm of twig)									
<i>Callipterinella calliptera</i>	5.44	21.09	28.94	25.92	11.06	23.02	18.79	0.54	16.07	20.90
<i>Betulaphis brevipilosa</i>	1.12	1.54	33.30	17.82	15.39	21.82	12.47	0.70	16.06	17.15
<i>Euceraphis betulae</i>	0.94	2.04	3.85	2.23	2.31	2.35	1.54	0.00	2.60	1.94

\*Omitting the upper vertical third, inner canopy location.

†Values for inner canopy samples only.

TABLE 3. DISTRIBUTION OF THREE APHID SPECIES ON *BETULA PENDULA* BY SAMPLING DATE AND LOWER AND MIDDLE VERTICAL CANOPY LEVELS IN ALBANY, CALIFORNIA, 1982

Aphid species/ sampling dates	Lower canopy		Middle canopy	
	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
(aphids/100 leaves)				
<i>Euceraphis betulae</i>				
July 21–August 6	7.03	2.68	5.63	2.46
September 3–28	1.22	0.47	0.78	0.29
<i>Callipterinella calliptera</i>				
July 21–August 6	16.97	9.37	7.70	2.95
September 3–28	81.06	31.01	46.43	20.90
<i>Betulaphis brevipilosa</i>				
July 21–August 6	1.74	0.62	8.99	5.13
September 3–28	6.74	3.11	5.88	3.28

two lower vertical levels were not indicated ( $p \geq 0.01$ ). Power calculations demonstrated that there was only a 50 percent chance of demonstrating a lack of difference between lower- and middle-crown level populations of *B. brevopilosa*. By contrast, tests of *E. betulae* and *C. calliptera* strongly suggested that no differences in density actually existed between lower- and middle-crown levels. Additional sampling during this study included both lower and middle strata to potentially improve the resolution of *B. brevopilosa* population estimates.

### Within-tree distributions for tree-dwelling aphids

Within-tree distributions of tree-dwelling aphids that have been studied were evaluated to see if common trends occur. Several studies have investigated the within-tree distributions of dendrophilous aphids, although emphasis thus far has been on aphids on apple (Hull and Grimm 1983), walnut (Nowierski and Gutierrez 1986), and pecan trees (Shepard 1973; Gentry, Malstrom, and Blythe 1975; Polles and Mullinix 1977; Edelson and Estes 1983) in orchards. Within-tree distributions of urban shade tree aphids are known only for linden aphids (Dahlsten, unpublished data) and the three species of birch aphids discussed in this study. Orchard trees provide a very different micro-environment that is potentially more homogeneous than urban shade trees. Within an orchard, trees are evenly spaced and are often maintained using the same practices, while in urban areas, trees are planted in varied environments and are maintained by a variety of methods.

No all-encompassing distributional pattern could be found for the tree-dwelling aphid species that have been investigated. However, some general trends are evident. Density by cardinal directions has usually been found not to vary (Gentry, Malstrom, and Blythe 1975; Edelson and Estes 1983; Nowierski and Gutierrez 1986; Dahlsten, unpublished data). As with birch aphids, increased densities have been found in the lower vertical canopy levels for pecan aphids (Shepard 1973; Gentry, Malstrom, and Blythe 1975), pecan aphids at only lower densities (Polles and Mullinix 1977), and linden aphids (Dahlsten, unpublished data). By contrast, *Aphis pomi* DeGeer inhabited the actively growing shoots in the tops of apple tree canopies (Hull and Grimm 1983). Walnut aphids, *C. juglandicola*, were found vertically throughout the tree canopy, while horizontally, their distribution differed throughout the season, but did not demonstrate a consistent trend (Nowierski and Gutierrez 1986). These results suggest that within-tree distributions of dendrophilous aphids definitely vary in different systems.

### Taylor's Power Law relations

The coefficients  $a$  and  $b$  of Taylor's Power Law were derived for within-tree populations of each species separately and as a total aphid population (table 4). Slope coefficients have been considered as demonstrating random distributions when  $b = 1$  and aggregated distributions when  $b \rightarrow \infty$  (Taylor 1961), although Wilson (1985) suggests that this is untrue when  $a$  values are  $\ll 1$ . Within-tree populations of all birch aphids were very similar and all would be considered aggregated based on the aforementioned criteria. Within-tree variance/mean regressions all explained a large proportion of the variance.

Using branch terminals as a sample unit, slope values demonstrate that between-tree distributions for all aphid species were generally more aggregated than within-tree

TABLE 4. VARIANCE/MEAN REGRESSION COEFFICIENTS FOR BETWEEN- AND WITHIN-TREE POPULATIONS OF THREE SPECIES OF APHIDS ON *BETULA PENDULA* IN ALBANY, CALIFORNIA, 1981

Aphid species	Between tree				Within tree			
	n	a	b	r <sup>2</sup>	n	a	b	r <sup>2</sup>
<i>Callipterinella calliptera</i>	21	1.652	2.020	0.949	105	21.777	1.667	0.952
<i>Betulaphis brevopilosa</i>	20	2.606	1.943	0.989	105	17.947	1.624	0.973
<i>Euceraphis betulae</i>	21	1.151	2.000	0.806	105	13.677	1.662	0.893
Total aphids	21	5.058	2.013	0.991	105	28.314	1.711	0.914

(table 4). However, at low densities, birch aphids were less aggregated between trees than within trees. A large proportion of the variation was once again explained by the variance/mean regressions. At low densities, *E. betulae* populations were the least aggregated of the three species. All adults of this species are winged and can easily disperse. At low population levels, when preferred foliage is often scarce, *E. betulae* may readily fly and thereby decrease aggregation levels.

Since all three species were of interest, both within- and between-tree variance/mean regressions were calculated for total aphids. These comprehensive regressions also explained a large proportion of the variation both within and between trees.

### Estimation of aphid populations and injury levels

Sample size values were calculated using Taylor's Power Law coefficients for total aphids. The numbers of branch terminals to be sampled on individual trees are presented for differing levels of reliability and differing aphid densities (table 5). The aggregated distribution of these aphids requires an extensive number of branches to be sampled from each tree for even low levels of sampling reliability. Increasing aphid density and decreasing sampling reliability clearly decrease the number of samples necessary.

Individual homeowners or pest control operators wanting to monitor individual trees may sample the appropriate number of branches (table 5) at differing estimated aphid densities and at chosen levels of reliability. Since variations in aphid density can alter sample size estimation, the threshold aphid density causing damage was approximated.

TABLE 5. SAMPLE SIZE IN NUMBER OF BRANCHES FOR ESTIMATION OF APHID POPULATIONS ON INDIVIDUAL *BETULA PENDULA* TREES AT VARYING LEVELS OF RELIABILITY AND APHID POPULATION DENSITIES

Mean aphid density	Reliability with 70% confidence intervals (± % of the mean)				
	20%	30%	40%	50%	60%
(/100 cm)	(numbers of branches)				
10	391	174	98	63	43
20	320	142	80	51	36
30	285	126	71	46	32
40	262	116	65	42	29
50	245	109	61	40	27

Using the proposed protocol, the aesthetic injury level was estimated at 40 aphids per 100 cm of branch (or 88 aphids per 100 leaves). Using the approximate aesthetic injury level, sampling at a mean aphid density of 40 could help with decisions on the necessity of control.

Figure 1 presents the numbers of trees necessary to sample with varying levels of reliability and the numbers of branches to sample at both high and low aphid population densities. The large variability in aphid populations both within- and between-trees causes sample sizes to be prohibitive at higher levels of reliability ( $D \leq 0.1$ ). Once again, sample size clearly decreases with decreasing reliability and increasing aphid density. More trees must be sampled for equivalent reliability at lower density aphid populations. Sampling additional branches over 10 or 20 per tree has little effect on the numbers of trees to be sampled (fig. 1).

### Optimal numbers of samples

Sampling time varied with aphid density. The greater aphid densities in spring and fall required approximately 1.88 minutes/branch and the lower summer populations required 1.35 minutes/branch. The average time necessary to drive between trees and prepare to sample was approximately 10 minutes throughout the year. To optimize the time spent sampling, five branches per tree should be sampled at lower population levels (estimated 5 aphids/100 leaves) while three branches should be sampled per tree when populations are abundant (estimated 40 aphids/100 leaves).

The cost of sampling sufficient trees to attain prescribed reliability was calculated using person-hours for aphid densities of 5 and 40 aphids/100 leaves (fig. 2). Although optimal sample sizes have been calculated, at lower population densities sampling is more expensive because more trees must be sampled and more branches are sampled per tree.

## POPULATION DYNAMICS

### Phenology

During 1983, aphid populations of all three aphid species at both sites peaked in spring and fall with a summer decline (fig. 3). Relative levels of these aphids differed greatly between years but data for 1981 and 1982 also suggest a pattern of spring and fall peaks (fig. 4). Both *C. calliptera* (1983) and *B. brevipilosa* (1981) populations were able to increase during summer after declines in numbers. *Euceraaphis betulae* populations never reached the high densities observed during peak numbers of *C. calliptera* or *B. brevipilosa*. Walnut Creek populations of both *E. betulae* and *C. calliptera* demonstrated a much longer period of summer population decline than Albany populations (fig. 3). *Betulaphis brevipilosa* was virtually absent all years that Walnut Creek was sampled.

Maximum summer temperatures in Albany and Walnut Creek have great potential impact on aphid populations. During summers in Walnut Creek the daily maximum temperature frequently exceeded 29.4°C (85°F) (43.2 percent of days over the three summers) (fig. 5). The average maximum 1983 temperatures in Walnut Creek surpassed Albany temperatures beginning in May and Walnut Creek populations of *E. betulae*

(continued on page 16)

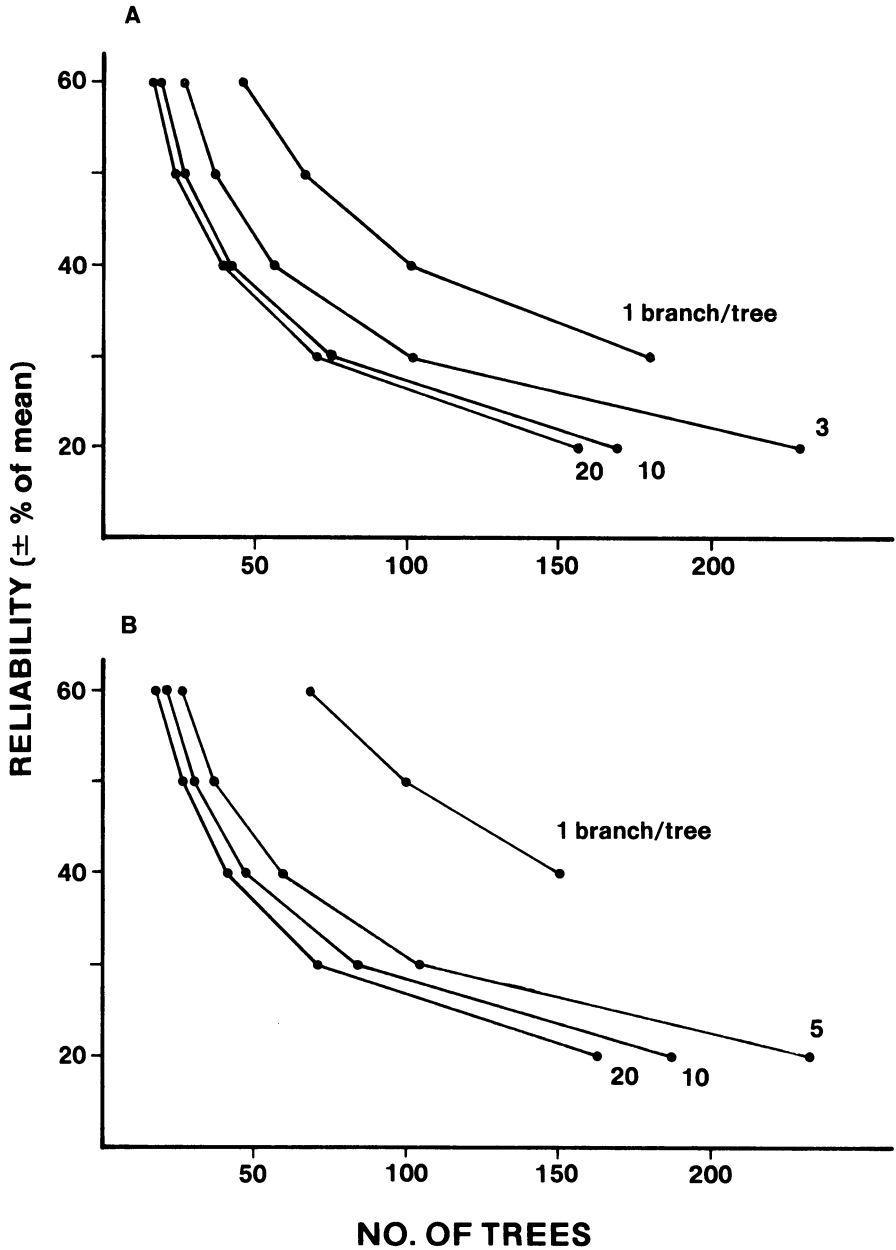


Fig. 1. Numbers of trees to sample for estimation of aphid populations on *Betula pendula* with varying levels of reliability and numbers of branches per tree (70 percent confidence limits). (A) 40 aphids/100 leaves; (B) 5 aphids/100 leaves.

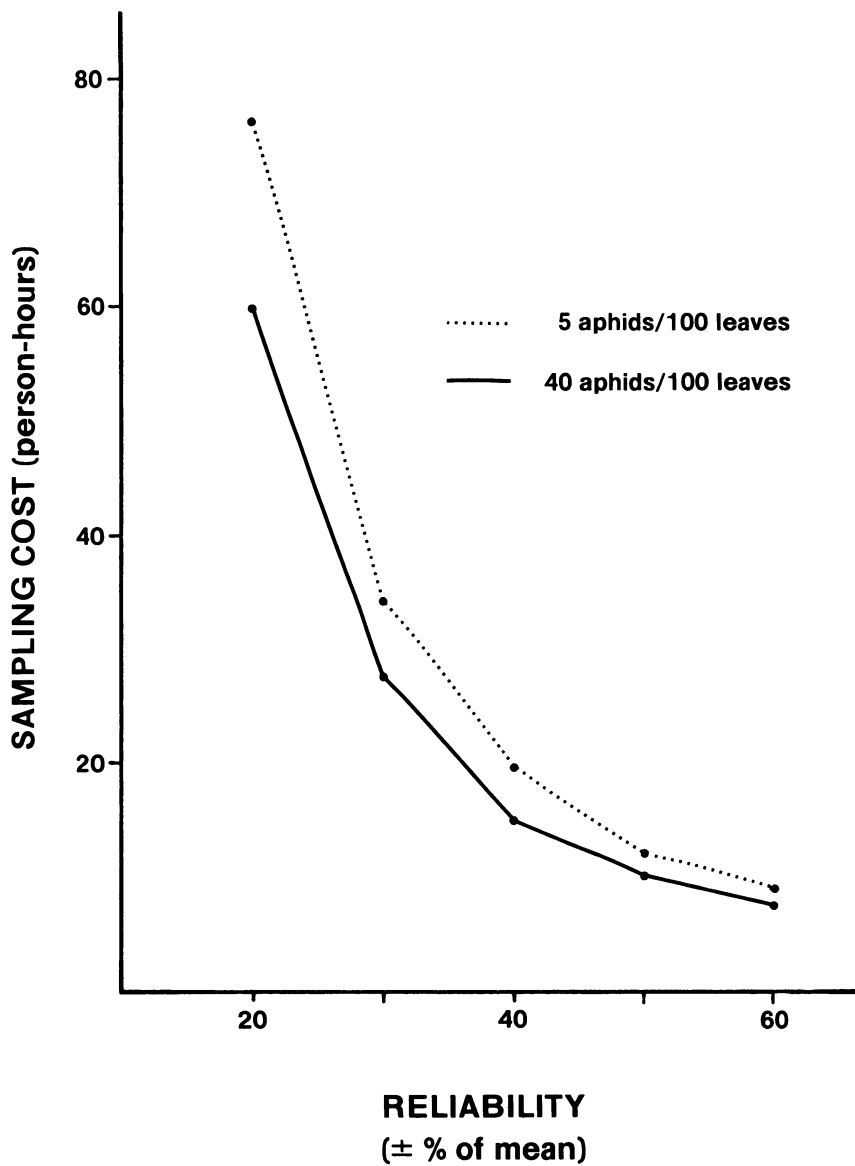


Fig. 2. Sampling costs (in person-hours) to optimally estimate aphid population densities on *Betula pendula* for varying levels of reliability (70 percent confidence limits).

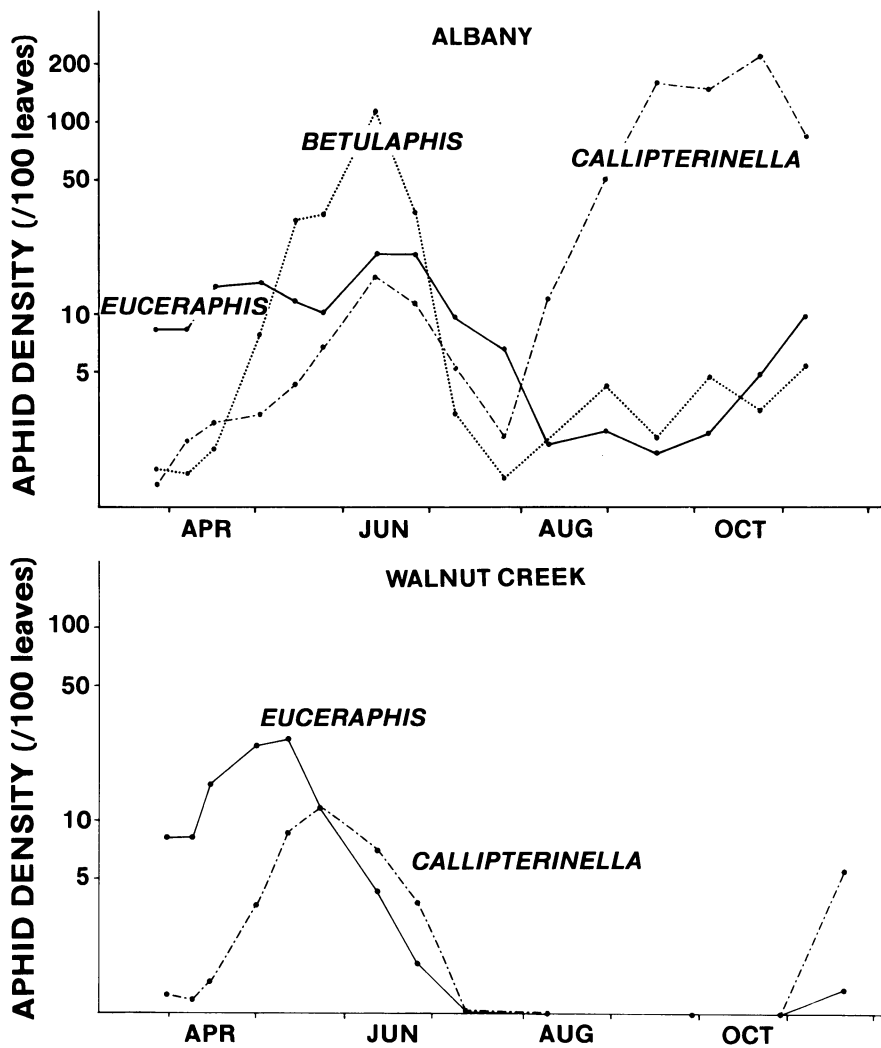


Fig. 3. Seasonal abundance of three aphid species on *Betula pendula* in Albany and Walnut Creek, California, 1983 (density/100 leaves).

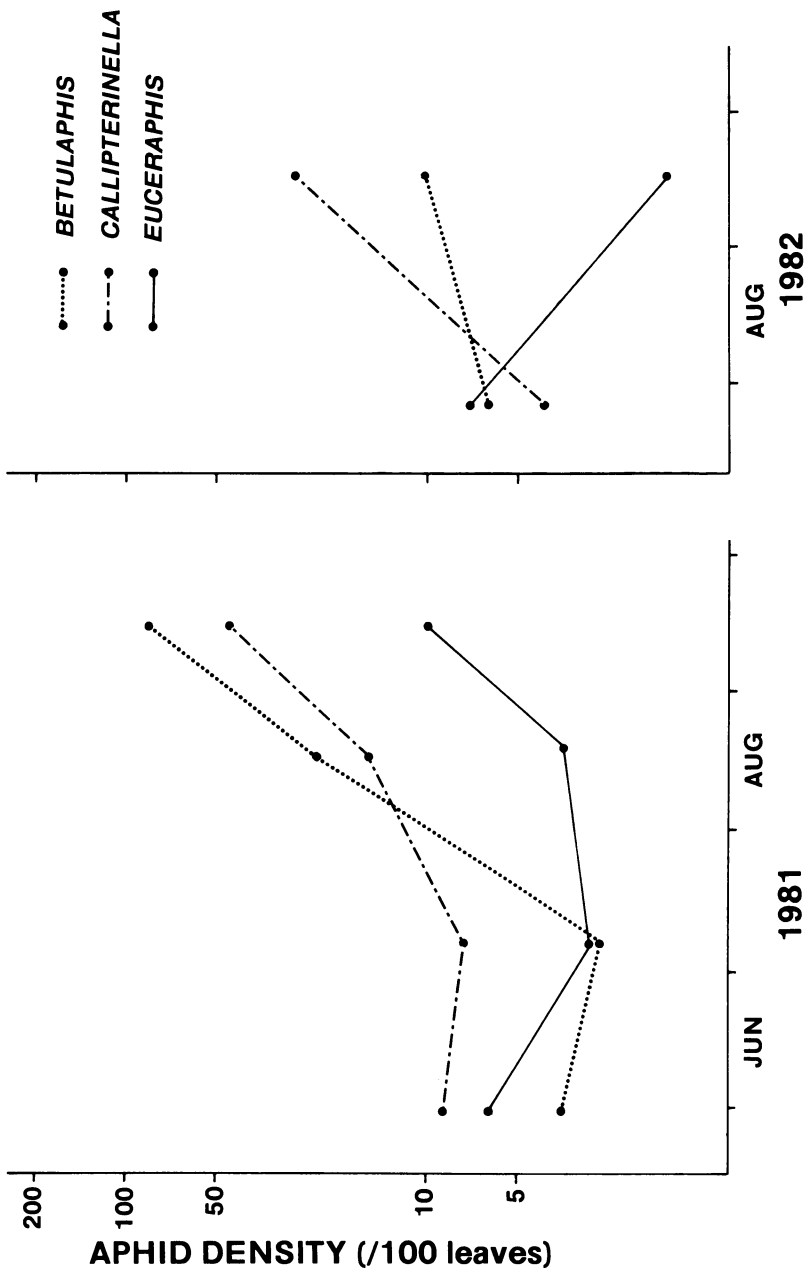


Fig. 4. Seasonal abundance of three aphid species on *Betula pendula* in Albany, California, 1981 and 1982 (density/100 leaves).

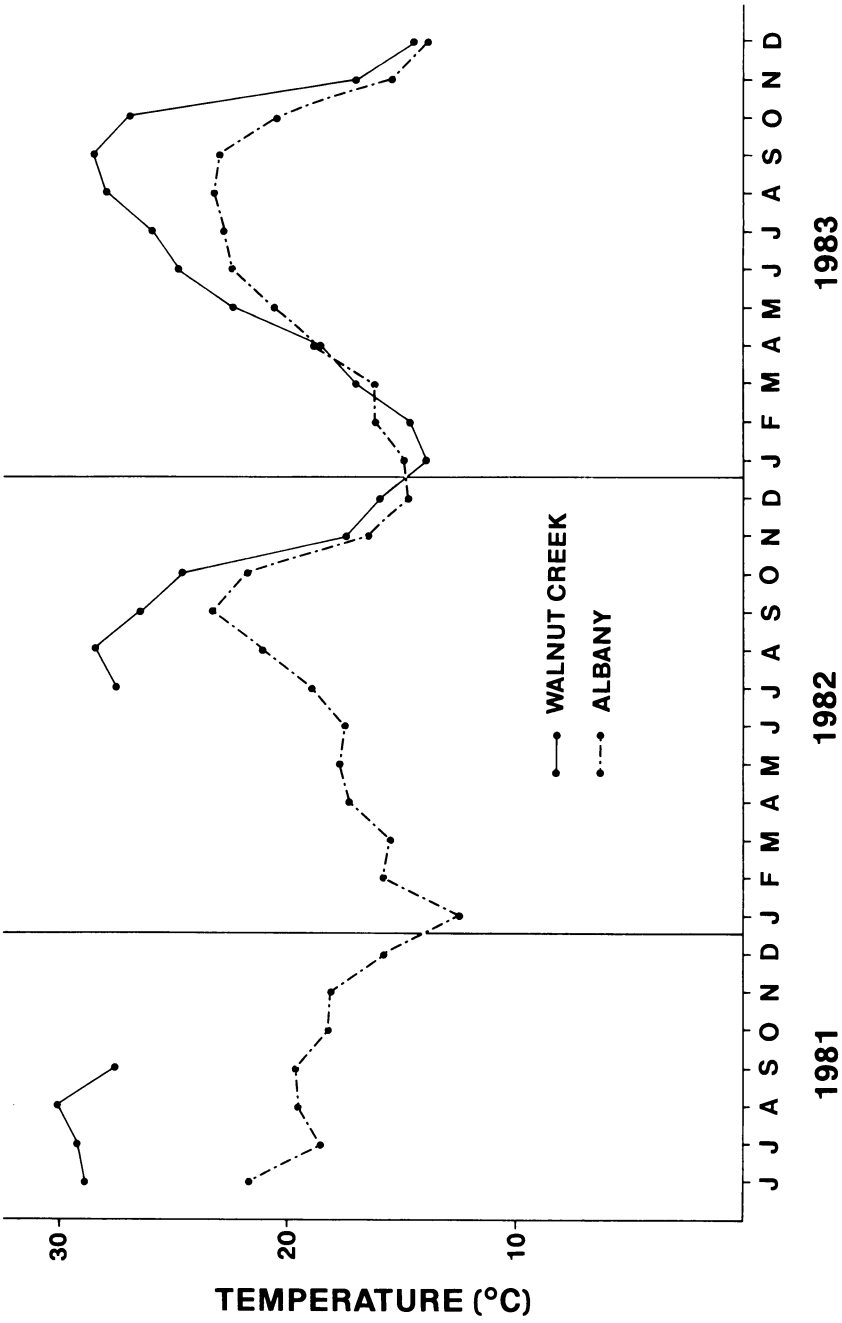


Fig. 5. Mean monthly maximum temperatures in Albany and Walnut Creek, California, 1981-1983.

(continued from page 10)

and *C. calliptera* both began decreasing in May. In autumn, when temperatures decreased from summer highs, *E. betulae* and *C. calliptera* were once again collected in Walnut Creek.

In Albany, average summer maximum temperatures were lower than in Walnut Creek (fig. 5) due to the coastal influence and temperatures seldom reached 29.4°C (1.8 percent of days over three summers). During 1983, *E. betulae*, *B. brevopilosa*, and *C. calliptera* populations in Albany peaked one month later in spring than Walnut Creek populations. Summer populations of *E. betulae* and *C. calliptera* were never as rare in Albany as in Walnut Creek. Summer populations of *B. brevopilosa* in Albany increased only during 1981 when average maximum temperatures from July to September were cooler than in 1983 (t-test;  $p \leq 0.05$ ) (fig. 5). Therefore, at both sites *B. brevopilosa* populations were not abundant during intervals with higher temperatures.

## Influence of Natural Enemies

The most common natural enemies collected in California were aphid-specific predators and polyphagous predators. Parasitoids were found infrequently and diseased aphids were never seen. The species of natural enemies associated with birch aphids

TABLE 6. NATURAL ENEMIES ASSOCIATED WITH THREE SPECIES OF APHIDS ON *BETULA PENDULA* IN NORTHERN CALIFORNIA

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### Parasitoids

#### Hymenoptera

##### Aphidiidae

- Praon flavinode* (Haliday); host: *Eucera phis betulae* (Koch); Albany.  
*Betuloxys compressicornis* (Ruthe); host: *E. betulae*; Albany, Berkeley.  
*Aphidius aquilus* Mackauer; host: *Callipterinella calliptera* (Hartig); Albany, Berkeley.  
*Lysiphlebus testaceipes* (Cresson); host: *C. calliptera*; Albany, Lafayette.

#### Predators

#### Hemiptera

##### Reduviidae

- Empicoris rubromaculatus* (Blackburn); Berkeley.

##### Anthocoridae

- Anthocoris antevolens* White; Albany, Berkeley, Marin County.  
*Anthocoris bakeri* Poppius; Berkeley, Walnut Creek.  
*Anthocoris nemoralis* (F.); Albany, Walnut Creek.

##### Nabidae

- Nabis (Reduviolus) alternatus* Parshley; Walnut Creek.

##### Miridae

- Campyloneura virgula* (Herrich-Schaeffer); Walnut Creek.  
*Deraeocoris brevis* (Uhler); Albany, Berkeley.  
*Diaphnocoris provancheri* (Burque); Albany.  
*Diaphnocoris* sp.; Berkeley.  
*Paraprobea pendula* Van Duzee; Walnut Creek.  
*Phytocoris* sp.; Albany, Walnut Creek.  
Phylinae, genus unknown, near *Stenarus*; Walnut Creek.

#### Neuroptera

##### Hemerobiidae

- Hemerobius pacificus* Banks; Albany, Berkeley.
- 

(continued)

and their collection locations are presented in table 6. Some of these species were observed feeding on birch aphids, or were collected from aphid colonies, while others are considered to be aphid predators based on their biologies or biologies of related species. The total number of adult and larval predators sampled in Albany during 1983 was 326 compared with a total of 56 individuals in Walnut Creek. Albany and Walnut Creek exhibited somewhat different natural enemy faunas with differing dominants (Hajek and Dahlsten 1986c) although, at both sites, coccinellids and spiders were most abundant.

*Betula pendula* is inhabited by few insects beside the three aphid species under study and their natural enemies, although low populations of leafhoppers were occasionally noted. Therefore, predatory insects on *B. pendula* had to specialize on aphids. Sampling techniques did not measure potential preference of predators for individual aphid species, although such preferences could exist.

### Coleoptera: Coccinellidae

In Albany, coccinellids were the most abundant natural enemies during spring. *Adalia bipunctata*, a Holarctic species that prefers habitats over 2 m in height (Ipert 1966), was the dominant species of coccinellid, comprising 86 percent of adults

TABLE 6. (continued)

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Chrysopidae	<i>Chrysopa plorabunda</i> Fitch (= <i>carnea</i> Stephens); Berkeley. <i>Chrysopa nigricornis</i> Burmeister; Albany. <i>Chrysopa rufilabris</i> Randall; Albany.
Coleoptera	
Anthicidae	<i>Isbyropalpus nitidus</i> (LeConte); Albany.
Coccinellidae	<i>Adalia bipunctata</i> (L.); Albany, Arcata, Berkeley, Marin County, Walnut Creek. <i>Coccinella californica</i> Mannerheim; Albany, Walnut Creek. <i>Hippodamia convergens</i> Guérin; Albany, Berkeley, Lodi. <i>Olla v-nigrum</i> (Mulsant); Lodi, Walnut Creek.
Diptera	
Cecidomyiidae	<i>Aphidoletes aphidimyza</i> (Rondani); Albany.
Syrphidae	<i>Allograpta obliqua</i> (Say); Albany. <i>Syrphus opinator</i> Osten Sacken; Albany. <i>Metasyrphus</i> sp.; Albany.
Chamaemyiidae	<i>Leucopsis</i> sp.; Albany.
Hymenoptera	
Formicidae	<i>Iridomyrmex humilis</i> (Mayr); Albany, Walnut Creek.
Sphecidae	<i>Passaloecus monilicornis</i> Dahlbom; Albany. <i>Psenulus pallipes</i> (Panzer); Albany.

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sampled in 1983. The endemic species *Coccinella californica* Mannerheim composed the remaining 14 percent of total coccinellid adults. Seasonal abundance of eggs, larvae, and adults for total coccinellids are presented in figure 6.

The spring ladybird peak coincided with the spring peak in total aphid density during 1983. Coccinellids did not check total spring aphid populations during the initiation or first increase phases described by Hodek (1973). Rather, ladybird egg and larval population levels tracked aphid population levels during spring. Coccinellid adults responded positively to aphid density by laying increasing numbers of eggs as total aphid densities rose during spring (t-test;  $p \leq 0.05$ ) (fig. 7). However, coccinellid eggs were not observed on trees with fewer than 6.3 aphids/100 leaves. This lack of ovipositional response to low aphid populations may explain why coccinellids did not prevent the large spring aphid increase.

Total aphid values are actually composed of the population fluctuations of the three aphid species. Not all aphid species are always suitable or acceptable as food for coccinellids (Hodek 1973). Therefore, the three species of aphids on *B. pendula* were compared as potential food for coccinellids. *Adalia bipunctata* larvae that were fed diets consisting solely of each aphid species successfully developed from egg to adult (table 7). Since all three aphids feed on *B. pendula*, these results are consistent with Blackman's (1967) suggestion that successful coccinellid development may depend on the species of host plant of aphids. The developmental rates of coccinellid larvae fed these three aphid species were very similar, although the numbers of aphids consumed and the resulting coccinellid pupal weights differed by aphid species. These differences may partially be due to the differences in the body sizes of these three aphid species (Hajek and Dahlsten 1987b). However, the preferential acceptability of these three aphid species may also not be equivalent.

On the population level, all three aphid species comprise food sources for *A. bipunctata* larvae, although different population levels of the different birch aphid species would be necessary for coccinellid development. Concurrent studies of aphid defensive behavior demonstrated that *A. bipunctata* larvae capture *B. brevipedosa* more readily than either *C. calliptera* or *E. betulae* (Hajek and Dahlsten 1987a). The same relationship may hold for adult coccinellid capture efficiency since capture rates of larvae and adults of several coccinellid species were similar (Dixon 1958; Brown 1972, 1974). Adult coccinellids oviposit only when they find sufficient food (Ibrahim 1955; Honěk 1978) and coccinellid eggs were found only on trees with *B. brevipedosa* populations. The spring increase in *A. bipunctata* eggs and larvae specifically followed the large increase in *B. brevipedosa* while *C. calliptera* and *E. betulae* populations were low and few alternative prey were present on trees.

By the end of July, coccinellid numbers had declined and coccinellid populations remained low, not responding to aphid densities, throughout fall. Since the aphid species that was predominant during this period, *C. calliptera*, is ant tended, coccinellid adults may have been deterred from oviposition (Way 1963). A small second generation of coccinellids was produced on birch trees during August and September. Hodek (1973) noted that coccinellids often remain in habitats until dormancy if aphid populations remain following a spring peak.

One factor that diminishes the effectiveness of spring populations of *A. bipunctata* is its habit of cannibalizing eggs that are laid in batches (Mills 1982). Eggs that were cannibalized, or nonviable, accounted for roughly 12 percent of the total eggs sampled in spring.



The most abundant coccinellid species in Albany, *A. bipunctata*, was largely replaced in Walnut Creek by the endemic species, *Olla v-nigrum* (Mulsant). Habits of *O. v-nigrum* differ from those of *A. bipunctata* in that eggs are often laid on the tree trunk. The sampling design used did not evaluate tree trunks and therefore, oviposition by coccinellids could not be evaluated for Walnut Creek.

### Diptera: Syrphidae

During 1983 in Albany, syrphid larvae and adults exhibited increases during both spring and autumn aphid peaks (fig. 6) and were the most abundant predators during autumn. Syrphids in Albany displayed a numerical response to aphid density from April

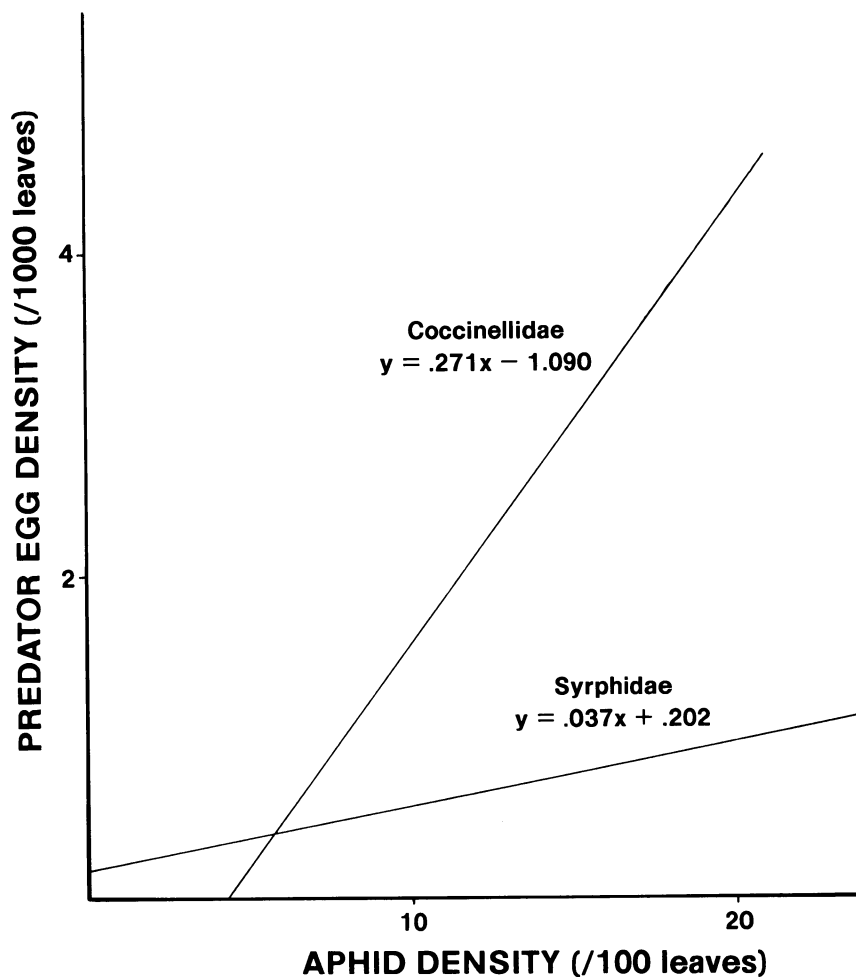


Fig. 7. Oviposition by Coccinellidae and Syrphidae in response to aphid density on *Betula pendula* in Albany, California, 1983.

TABLE 7. DEVELOPMENT OF *ADALIA BIPUNCTATA* (L.) LARVAE REARED ON THREE SPECIES OF BIRCH APHIDS\*

	No. <i>A. bipunctata</i> larvae	Time to pupation (days $\pm$ SE)	Pupal weight (gm $\pm$ SE)*	No. aphids eaten ( $\pm$ SE)*
<i>Callipterinella</i> <i>calliptera</i>	12	11.67 $\pm$ 0.31	8.97 $\pm$ 0.27 a	322.3 $\pm$ 19.70 b
<i>Betulaphis</i> <i>brevipilosa</i>	16	11.18 $\pm$ 0.15	12.07 $\pm$ 0.75 b	493.3 $\pm$ 8.67 c
<i>Euceraphis</i> <i>betulae</i>	10	11.20 $\pm$ 0.13	15.95 $\pm$ 0.67 c	116.7 $\pm$ 1.90 a

\*Means in a row followed by different letters are statistically significantly different; Student-Newman-Keuls test,  $\alpha = 0.05$ .

through September, 1983 (t-test;  $p \leq 0.05$ ) (fig. 7). Comparison of the slopes of responses by coccinellids and syrphids, however, demonstrated that syrphid response was much weaker than coccinellid response (t-test;  $p \leq 0.05$ ). Syrphids clearly did not control the autumn populations of *C. calliptera*. Many of the syrphids that were reared for identification were parasitized by either solitary ichneumonids or the multiple parasite, *Pachyneuron albutius* (Walker). Both of the two syrphids identified to species are native to western North America (Cole 1969).

### Hymenoptera: Aphidiidae

The aphidiid species reared from trees sampled during this study (table 6) and collected during surveys in the area were uncommon. *Lysiphlebus testaceipes* (Cresson), a highly polyphagous species native to North and South America, was reared from *C. calliptera* only a few times. The other species of aphidiids reared, *Aphidius aquilus* Mackauer, *Betuloxys compressicornis* (Ruthe), and *Praon flavinode* (Haliday), are probably of European and eastern North American origin (Mackauer and Stary 1967). The occurrence of *A. aquilus* in California may be due to a biological control introduction of an *Aphidius* sp. from Japan in 1975 (Dahlsten et al. 1982). *Praon flavinode* was introduced into the San Francisco Bay Area in 1972 for biological control of birch aphids (Dahlsten et al. 1982). Birch aphids and their natural enemies had not been studied extensively in this area before 1972. Since *P. flavinode* was collected in British Columbia in 1960 (J. W. Johnson, personal communication), it remains unknown whether *P. flavinode* occurred in the San Francisco Bay Area before the 1972 introduction.

*Praon flavinode*, a parasite of *E. betulae*, was the most common aphidiid reared. *Praon flavinode* parasitizes several species of arboricolous aphids (Mackauer and Stary 1967), although during this study, it was reared only from *E. betulae*. In Albany, the first parasitized *E. betulae* nymph was recorded on March 28 and populations of *P. flavinode* reached a maximum of 1.5 percent parasitism on July 12. The total of 38 mummies sampled throughout 1983 were collected on 7 out of the 12 trees sampled. Comparing the density of *E. betulae* on trees with *P. flavinode* populations and those trees without, parasite abundance was not correlated with *E. betulae* density from mid-April through mid-July when most mummies were seen (t-test;  $p \geq 0.05$ ). *Praon flavinode* populations therefore did not respond to increases in *E. betulae* population levels.

Beginning on June 12, many of the *P. flavinode* mummies found had been eaten by predators or contained dried remains of larvae or adults. Failure to develop or emerge could be due to the predation by anthocorids that was observed. High levels of hyperparasitism by seven species of Hymenoptera also decreased emergence. Of the five hyperparasites identified to the species level, four are endemic to western North America and have shifted onto this introduced host. The fifth species, *Psilonotus achaeus* Walker, an associate of *Betula* (Burks 1979), has not previously been reported from western North America.

Aphidiids overwinter as mummies on leaves or on woody parts of plants (Stary 1970). One *P. flavinode* mummy was found on an ivy leaf (*Hedera helix* L.) attached to a vine growing up a birch trunk. In urban environments, pruning of trees and other garden plants, along with collection and disposal of deciduous leaves in autumn, may deplete the overwintering aphidiid generations each year.

### Hymenoptera: Formicidae

Ants are well known to tend aphids for their honeydew but the role of ants in harvesting aphids as a food source is poorly known (Way 1963). *Iridomyrmex humilis* was commonly found on *B. pendula* trees tending *C. calliptera* colonies. During September 1981 and June and July 1983, ants were seen walking down a tree trunk in Albany carrying dead nymphs of *B. brevopilosa* and *E. betulae*. Pontin (1958) and Skinner and Whittaker (1981) reported ant predation of aphids that are not adapted to ant attendance. *Betulaphis brevopilosa* is usually not ant tended in Denmark (Heie 1980) and was never tended in California. *Euceraphis betulae* is not ant tended in either Denmark (Heie 1980) or California. Therefore, the aphids harvested by ants were not myrmecophilous and were potential competitors with the aphid species that is tended.

In September 1983, when levels of *B. brevopilosa* and *E. betulae* were low, *I. humilis* individuals descended a birch tree with dead *C. calliptera* nymphs. Predation by ants on the aphids they tend provides solid protein and not only honeydew for the ant colony when alternative prey is absent. The importance of this food source varies with different ant species (Way 1963) and is not known for *I. humilis*. However, this behavior by *I. humilis* has also been reported for another aphid it tends, *Eucallipterus tiliae* L. (Olkowski 1973).

### Effect of Ant Attendance

During June, *Callipterinella calliptera* populations began to decline from their spring peak and *I. humilis* was associated with < 25 percent of the trees sampled. During late July, *C. calliptera* populations began to increase and remained abundant (> 50 aphids/100 leaves) from late August through October. By late July continuous trails of *I. humilis* occurred on six out of twelve trees, with scattered ants on the trunks of four more trees (fig. 8). *Iridomyrmex humilis* colonies remained on most trees through October. This ant species chases away coccinellid adults (Dechene 1970), and, during this study, ants were seen descending a tree with two dead aphid predators, a chrysopid larva and a mirid nymph. Protection of *C. calliptera* colonies by *I. humilis* may have helped allow *C. calliptera* populations to increase during summer and remain at high levels into October, protected from attack by natural enemies.

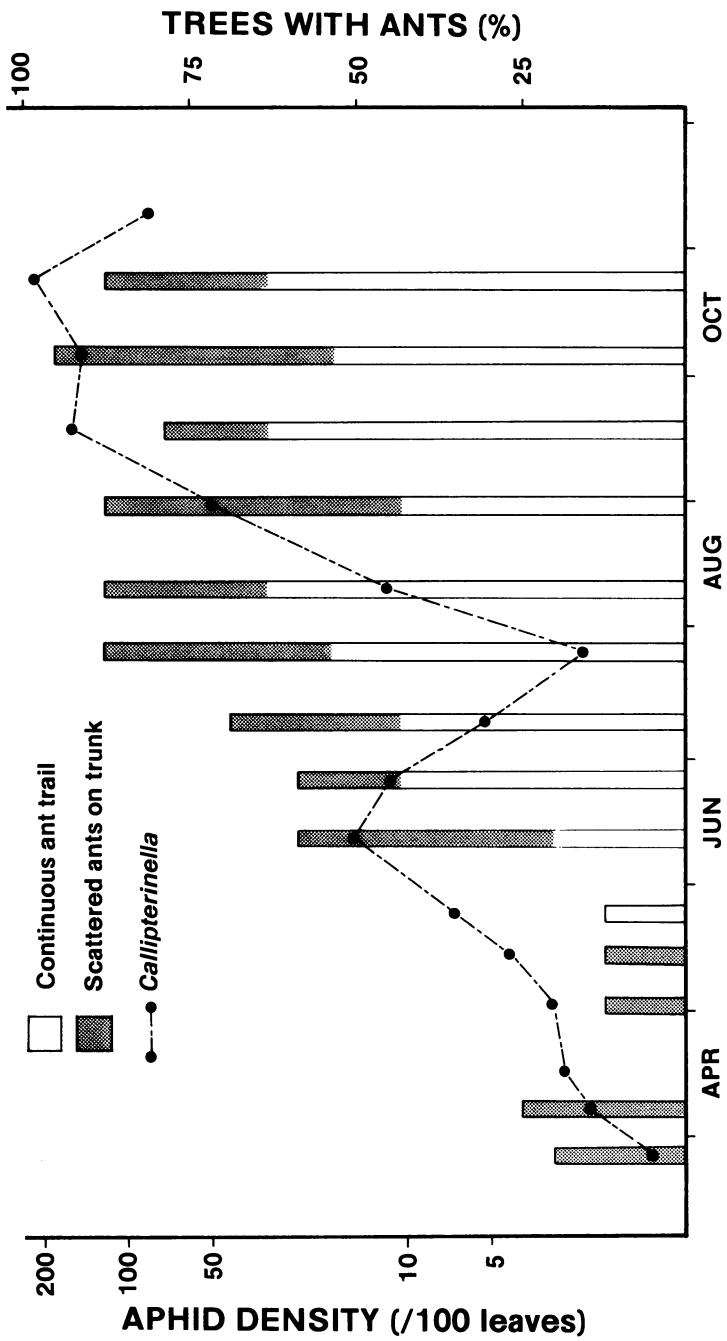


Fig. 8. Dispersion of *Iridomyrmex humilis* associated with *Callipterinella calliptera* on *Betula pendula* in Albany, California, 1983.

## Influence of Temporal Variation in Host Quality

On *B. pendula*, a large portion of each tree's foliage was present at the end of March, when buds burst. However, many buds formed long shoots that continued to grow in length (producing twigs) and produced new leaves until mid-June. *Euceraphis betulae* prefers the new, developing leaves present through spring (Hajek and Dahlsten 1986a). During this time, the ratio of nymphs to adults was high, since *E. betulae* was reproductively active (fig. 9). The ratio of nymphs to adults began to decline noticeably in May, as the percentage of developing leaves on trees declined (fig. 10). By July, the percentage of nymphs in *E. betulae* populations had decreased markedly (fig. 9), demonstrating a low reproductive level when little tree growth was occurring. During summer, when all leaves were mature, the density of *E. betulae* was low (figs. 3, 4).

*Euceraphis betulae* also prefers senescing leaves in early autumn (Hajek and Dahlsten 1986a). The summer phase of reproductive quiescence of *E. betulae* was fairly brief because birch trees began producing senescent leaves even before developing leaves

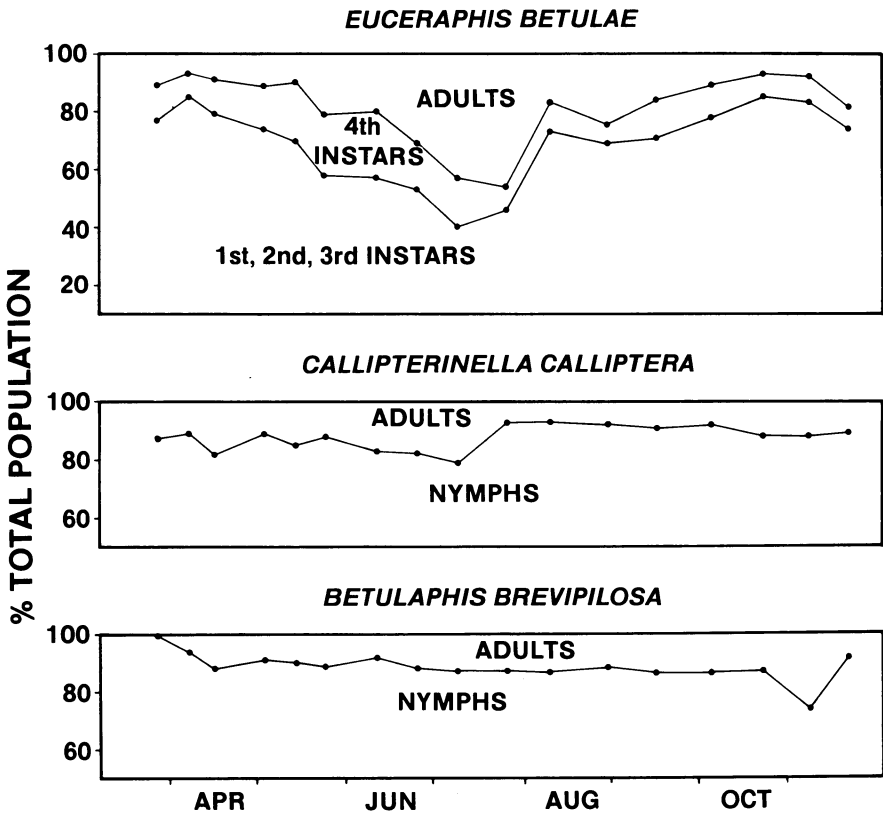


Fig. 9. Seasonal percentages of age classes of three aphid species on *Betula pendula* in Albany, California, 1983.

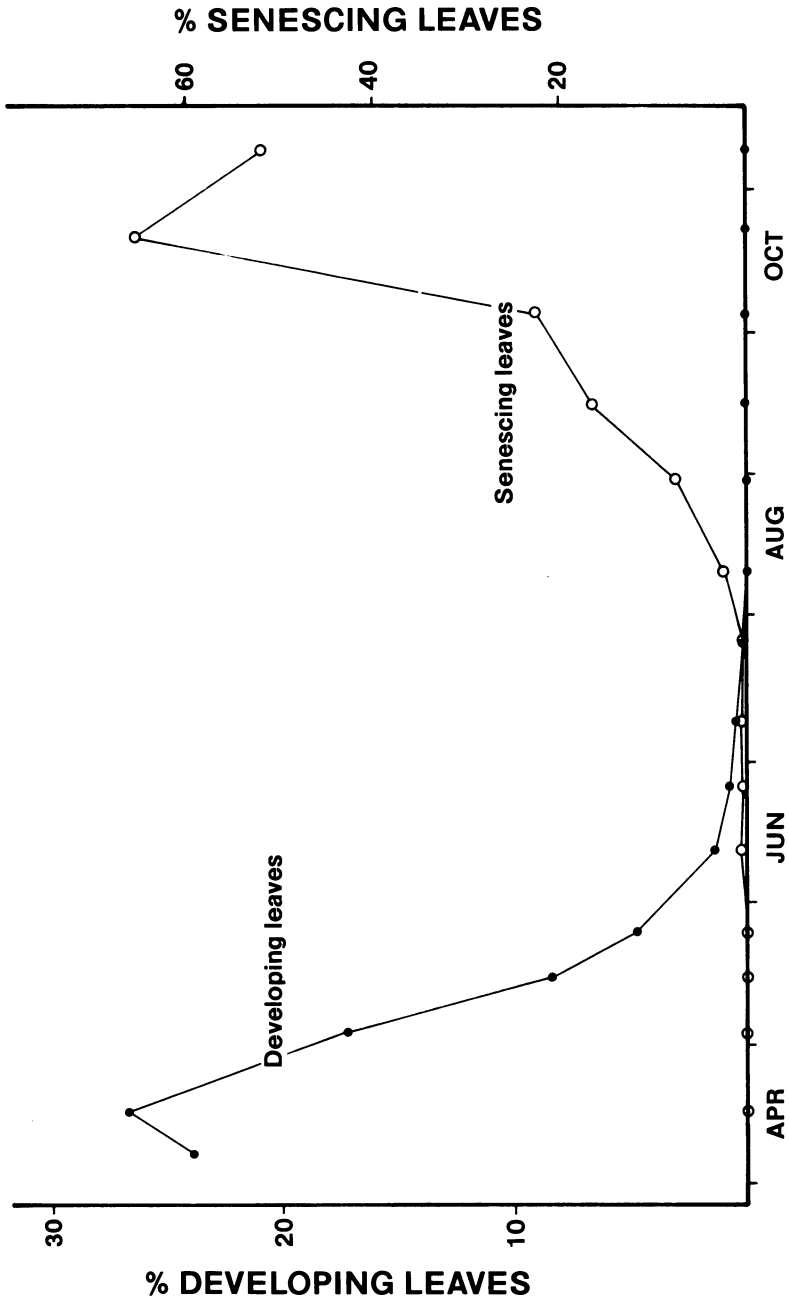


Fig. 10. Incidence of developing and senescing leaves on *Betula pendula* in Albany, California, 1983.

were all produced (fig. 10). In this way, birch trees never completely lacked the preferred foliage of *E. betulae*. As senescent leaves became more abundant on birches, a higher proportion of nymphs was again seen (fig. 9) and *E. betulae* populations increased.

Many aphid species prefer feeding on growing or senescing leaves instead of mature leaves (Dixon 1977). Dixon (1970) has shown that growing and senescing leaves of sycamore are high in amino-nitrogen, a limiting nutrient for aphids. Similar nitrogen fluctuations have been demonstrated for many plants, including birch. High nitrogen is present during spring in the leaves of several birch species (Haukioja et al. 1978; Schultz, Nothnagle, and Baldwin 1982) and nitrogen levels in leaves dropped during summer. Chapin and Kedrowski (1983) have shown that nitrogen is retranslocated in *Betula papyrifera* var. *humilis* (Reg.) Fern and Raup during autumn before leaf abscission. Both *E. betulae* and *E. punctipennis* (Wratten 1974), a sister species, undergo midsummer depressions in adult reproductive activity when highly nutritious foliage is not present.

*Callipterinella calliptera* exhibited a less marked preference for new leaves in spring (Hajek and Dahlsten 1986a). This resource was gone by the end of July and *C. calliptera* density declined. Unlike *E. betulae*, however, this species soon increased again long before senescent leaves were abundant, feeding on mature leaves. The ratio of nymphs to adults decreased only slightly during spring and did not vary substantially throughout summer (fig. 9). During this study, the rate of reproduction by *C. calliptera* was influenced little by the seasonal changes in host quality.

*Betulaphis brevipilosa* feeds on mature leaves throughout the season (Heie 1972; Hajek and Dahlsten 1986a) so the incidence of new and senescent leaves does not influence this species. The proportion of nymphs to adults remained fairly constant through spring, summer, and early autumn (fig. 9). The ratio of nymphs to adults decreased in November, probably due to egg production by sexuales.

Host quality changes had little association with reproduction of *C. calliptera* and *B. brevipilosa*. Many aphids exhibit life histories that allow them to avoid feeding on mature leaves of woody plants during summer, e.g., host alternation, aestivation, production of quiescent summer morphs (Heie 1980). It is less common for aphids to be abundant on mature leaves during the summer (Shaposhnikov 1959; Dixon 1977). However, both *C. calliptera* and *B. brevipilosa* deviate from this more common trend, as both species became abundant while feeding on mature leaves during summer.

## Effect of Alate Production

*Eucерaphis betulae* is unusual among aphid species because all adults are alate and can easily disperse. By contrast, many aphid species produce alate virginoparae only in response to crowding, decreased host quality, and/or day length (Dixon 1977). Production of alatae was evaluated for both *C. calliptera* and *B. brevipilosa* in Albany during 1981 and 1983. Only fourth instar aphids with wing buds were analyzed because alatae that were present could have immigrated from other birches.

*Betulaphis brevipilosa* produced winged forms during spring and early summer in 1983 (table 8). Alatae were produced while the population was most dense and directly afterward. A clear association was noted between aphid density and alate production:

$$y = 0.033 x + 0.096; r^2 = 0.90; n = 16 \quad [7]$$

where y = fourth instar prealatae per 100 leaves and x = total aphid density per 100 leaves.

The highest percentages of alatae were found as the *B. brevipilosa* population declined in 1983 (table 8). There may be a lag between reception of cues to produce alatae and detection of alate production, i.e., growth of fourth instars with wing buds. In 1981, alatae were not found during spring when aphid populations were low but instead, were produced only by the dense autumn populations. When alate production was maximal in 1983, the majority of the leaves on trees were mature.

*Callipterinella calliptera* produced some alatae through much of 1983 (table 8) although in both 1981 and 1983, alate production increased during the fall, when populations were most dense and leaves were senescing. As with *B. brevipilosa*, alatae were produced by denser aphid populations:

$$y = 0.016 x + 0.039; r^2 = 0.643; n = 16 \quad [8]$$

where y = fourth instar prealatae per 100 leaves and x = total aphid density per 100 leaves.

The maximum alate percentages of 7.69 for *B. brevipilosa* and 3.88 for *C. calliptera* were not typical for these two species through most of the season. The percentages of

TABLE 8. ALATE PRODUCTION BY *CALLIPTERINELLA CALLIPTERA* AND *BETULAPHIS BREVIPILOSA* POPULATIONS IN ALBANY, CALIFORNIA, 1981 AND 1983

Date	<i>Callipterinella calliptera</i>			<i>Betulaphis brevipilosa</i>		
	Aphids	Alatae & fourth instar prealatae	Alatae & prealatae	Aphids	Alatae & fourth instar prealatae	Alatae & prealatae
	(/100 leaves)	(/100 leaves)	(%)	(/100 leaves)	(/100 leaves)	(%)
<b>1981</b>						
May 21-Jun 9	7.29	0	0	2.58	0	0
Jun 23-Jul 21	6.53	0	0	1.67	0	0
Aug 6-27	14.36	0.03	0.21	21.97	0.01	0.05
Sept 9-24	43.15	0.65	1.51	82.69	0.09	0.11
<b>1983</b>						
Mar 25-29	0.33	0	0	0.61	0	0
Apr 5-8	1.24	0	0	0.52	0	0
Apr 14-18	1.74	0.02	1.15	1.04	0	0
Apr 18-May 6	2.04	0	0	6.96	0.02	0.29
May 10-17	3.33	0	0	29.77	0.34	1.14
May 24-26	5.72	0	0	33.07	0.29	0.88
Jun 10-15	14.50	0.13	0.90	110.10	3.13	2.84
Jun 24-28	10.61	0.16	1.51	33.47	1.39	4.15
Jul 7-12	4.26	0.13	3.05	2.09	0.05	2.39
Jul 25-27	1.29	0.05	3.88	0.39	0.03	7.69
Aug 10-11	11.04	0.03	0.27	1.06	0	0
Aug 29-31	49.57	0.11	0.22	3.26	0	0
Sept 14-19	160.88	1.20	0.75	1.28	0	0
Oct 3-7	148.95	4.45	2.99	3.66	0	0
Oct 21-26	218.51	2.20	1.01	2.20	0	0
Nov 7-9	85.72	1.09	1.27	4.40	0	0

alatae suggest that alate production impacts local population levels to a minimal extent and operates only occasionally. Both species produced most alatae under crowded conditions. The influence of leaf quality on alate production is questionable since both species feed on mature leaves a large portion of the year (Hajek and Dablssten 1986a).

Alate production has an unknown influence on aphid populations on individual trees, as well as on regional populations. While local populations may decrease through emigration of alatae (Way 1973), regional populations may be influenced to a lesser extent. The percentage of the weakly flying emigrant aphids that never find their host plant species is unknown.

## CONCLUSIONS

The factors regulating populations of these three species of aphids in Europe, where they are native, have not been studied quantitatively. Heie (1972) reports that *C. calliptera* is uncommon in Denmark due to the influence of parasites and predators. However, there are no other European records of parasites of *C. calliptera* (Mackauer and Stary 1967; Stary 1978) and no further studies have suggested regulation of this aphid in Europe by natural enemies. In Albany, this species increased to the highest population levels of the three aphid species sampled. *Euceraphis betulae* is not considered abundant in Denmark (Heie 1972), although it was plentiful on some trees during spring in Albany. The major parasites of *E. betulae* in Europe are *P. flavinode* and *B. compressicornis* (Mackauer and Stary 1967). Both of these parasitoid species were reared from *E. betulae* in California, although they did not control populations of this aphid. *Betulaphis brevopilosa* is frequently attacked by hymenopterous parasitoids (Heie 1972) in Denmark, although in California, this species was never found to be parasitized. Although both European and Nearctic species of natural enemies are associated with birch aphids in California, populations of aphids still reached outbreak levels.

Maximum summer temperatures were associated with lower aphid population levels in both Walnut Creek and Albany. While this study cannot determine if this effect is due to the direct effect of temperature on birch aphids or to changes in the host plant, this pattern has also been reported previously for other aphid species. The abundance of three species of cereal aphids has also been negatively correlated with the number of days the ambient maximum temperature exceeded 27°C (Honěk 1985). Simulation models of two species of alfalfa aphids have been used to validate field data and prove that high temperatures were one of the major factors limiting alfalfa aphid populations (Gutierrez, Baumgaertner, and Summers 1984).

Populations of these three aphid species were differentially impacted by host quality while alate production, and therefore, potential emigration, by both *C. calliptera* and *B. brevopilosa* was not extensive. Another potential source of aphid population regulation may be intra- and interspecific competition. Lawton and Strong (1981) state that among herbivores, population levels high enough to produce interspecific competition are rarely seen in nature. Studies of coexistence of these aphid species (Hajek and Dablssten 1986a) did not implicate regulation by interspecific competition. Birch aphid species partition resources differently and occur randomly in association with each other on leaves, or even aggregate with each other. Both of these findings suggest an absence of negative interactions between species.

Several authors have suggested regulation of aphids by intraspecific mechanisms through aphid-induced deterioration in food quality (Sluss 1967; Dixon 1971). Aphid developmental rate, size, and survival ability can all be impacted. McClure (1983) suggested that introduced insects which have been removed from the strong influence of their native natural enemy faunas often reach extremely high population levels and offer examples of intraspecific competition. The only birch aphid species following this description is *C. calliptera*. During 1983, only *C. calliptera* populations were at high densities for a prolonged period. These large populations were probably protected from natural enemies by ants and did not seem to be regulated by weather, alate production, or presence of new or senescing leaves.

One problem in identifying the regulatory factors influencing birch aphids is that these factors are interconnected. The weather provides a background that alters the actions of all other factors (e.g., host quality, aphid growth rate, etc.). The various species of natural enemies on birch may also influence each others' abundance. Predators were the most abundant natural enemies, although many predators eat alternative prey, including other predators, as well as aphids. Feeding on alternative prey may be advantageous, maintaining predator populations during low host densities and allowing a density dependent response.

The differences in seasonal abundance and factors regulating these aphid species demonstrate the importance of evaluating the ecologies of these species separately. Due to the different ecologies of these aphid species, the impact of specific control measures will vary between species. A comparison of the honeydew production by each species will be necessary to determine if these aphid species are differentially detrimental in the urban environment and should be individually sampled and controlled.

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