

Heteroblasty in *Eucalyptus globulus* (Myricales: Myricaceae) Affects Ovipositional and Settling Preferences of *Ctenarytaina eucalypti* and *C. spatulata* (Homoptera: Psyllidae)

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ABSTRACT Heteroblasty describes plants whose juvenile and adult vegetative shoots differ morphologically. In *Eucalyptus*, heteroblasty is a common source of within-plant variation and an expression of ontogenetic aging that affects the within-tree distribution of psyllids. Using *Eucalyptus globulus* Labillardiere as a model system, we studied the reproductive behavior of adults of two Australian psyllid species (*Ctenarytaina eucalypti* Maskell and *C. spatulata* Taylor) on the glaucous, simple-shaped juvenile leaves and the glossy, sickle-shaped adult leaves under field conditions. We compared the ovipositional preferences and mating site preferences of the psyllids in caged pairs of juvenile and adult shoots, as well as the behavior of the psyllids after they landed on both types of shoots. *Ctenarytaina eucalypti* oviposited only on juvenile shoots and *C. spatulata* oviposited only on adult shoots. *Ctenarytaina eucalypti* mated primarily (88% of the time) on juvenile shoots, and *C. spatulata* mated only on adult shoots. After landing on both shoot types, *C. eucalypti* remained longer than *C. spatulata* on juvenile shoots, but *C. spatulata* remained longer than *C. eucalypti* on adult shoots. This is the first experimental evidence that heteroblasty in *Eucalyptus* affects insect reproductive behavior. These results are discussed in relation to subsequent studies on psyllid performance in this system that found that the epicuticular wax (present only on the juvenile leaves) plays a primary role in the preferences of these psyllid species for the juvenile versus adult shoots.

KEY WORDS *Eucalyptus globulus*, heteroblasty, developmental resistance, herbivory, within-plant variation, phase change

AS PLANTS DEVELOP from seedlings to reproductive individuals they go through the process of *maturation* (phase change or ontogenetic aging) (Kozlowski 1971). This process is associated with biochemical, phenological, morphological, and anatomical changes in the plant (Hackett 1985, Woo et al. 1994, Greenwood 1995). Plant species that exhibit relatively few changes in vegetative shoot morphology at different developmental phases are referred to as homoblastic, whereas species that show pronounced morphological differences between juvenile and adult shoots are considered heteroblastic (Goebel 1900, Jones 1999). Heteroblasty is a conspicuous expression of ontogenetic aging in *Eucalyptus* (Potts and Wiltshire 1997) and several other genera (McLellan 1993, Heenan 1997, Day 1998) that results in considerable within-plant variation. Whitham et al. (1984) speculated that within-plant variation due to ontogenetic aging may affect plant resistance to rapidly evolving pests. However, despite the explosion in herbivory research over the past two decades, relatively little is known about the effects of plant ontogeny and heteroblasty on insect herbivory.

Because insects respond to visual cues (e.g., leaf color and shape) (Bernays and Chapman 1994, Degen and Stadler 1997) that may differ between juvenile and adult shoots of heteroblastic plants, it is likely that heteroblasty affects plant-insect interactions. In observational studies, Brennan (2000) found that heteroblasty in *Eucalyptus globulus* Labillardiere significantly affected the within-tree distribution of two species of Australian psyllids (*Ctenarytaina eucalypti* Maskell and *C. spatulata* Taylor). Nymphs and adults of *C. eucalypti* were found almost exclusively on the juvenile shoots and those of *C. spatulata* occurred only on the adult shoots. There are significant differences in the shape, color and orientation of the glaucous juvenile leaves and the glossy adult leaves of *E. globulus* (Fig. 1) (Johnson 1926, Brennan and Weinbaum 2001) that may affect insect herbivores.

Eucalyptus globulus is an evergreen tree introduced to California from Australia more than 100 yr ago. Both *Ctenarytaina* spp. are native to Australia and specialize on *Eucalyptus*. In California, *C. eucalypti* and *C. spatulata* were first reported in 1991 (Brennan et al. 1999). Both species complete several generations annually and include an egg stage and five nymphal instars before emerging as winged adults. The psyllid populations increase in response to shoot growth beginning in December and peak in July to September (Dahlsten et al. 1998). *Ctenarytaina eucalypti* and *C. spatulata* oviposit in bud crevices, and *C. eucalypti* also oviposits

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Fig. 1. Juvenile (left) and adult (right) shoots of *Eucalyptus globulus*.

on the lamina of expanding leaves. In California, *E. globulus* is a major host of the *Ctenarytaina* spp.

Eucalyptus spp. exhibit five leaf types including cotyledons, seedling leaves, juvenile leaves, intermediate leaves, and adult leaves (Penfold and Willis 1961). Our study focuses on shoots of *E. globulus* with juvenile and adult leaves. In *E. globulus*, reproductive shoots usually exhibit adult leaves at the shoot apex; however, occasionally these shoots have juvenile leaves. In this article, we use the terms 'juvenile' and 'adult' to modify 'leaves' or 'shoots,' and to describe vegetative phase and phenotype.

We address two questions: (1) Do the *Ctenarytaina* spp. preferentially oviposit and settle on juvenile or adult shoots? (2) Do the *Ctenarytaina* spp. differ in retention (i.e., the amount of time that they remain) on juvenile and adult shoots where they have landed?

Materials and Methods

Study Sites and Organisms. The study was conducted in groves of *E. globulus* in the East Bay region of San Francisco, CA. The study sites were El Cerrito High School and Portola Middle School in the city of El Cerrito, and Albany Hill in the city of Albany. The

basal diameter of trees ranged from 5 cm to >2 m, and included planted and volunteer trees.

Distributional and Ovipositional Preferences. To assess the distributional and ovipositional preferences of adult psyllids for the juvenile and adult shoots, we conducted a field experiment with each species from June to August 1998. Experiment 1 (with *C. eucalypti*) and experiment 2 (with *C. spatulata*) occurred simultaneously. We selected adjacent pairs of healthy, vegetative, juvenile and adult shoots from the same trees. The shoots in each pair were approximately the same distance from the root crown. The shoots had approximately the same number of leaves (two to four) and closed axillary buds and were located between 1 and 4 m from the ground. We inspected each shoot with a 10× hand lens to ensure that they were free of psyllid eggs, nymphs and adults. The 1- to 3-cm long tip of each shoot was removed to stimulate axillary bud growth, and to remove any undetected eggs or nymphs. Each pair of juvenile and adult shoots was held together in parallel with a twist tie, and the 10–15 cm long shoot terminal was enclosed in a spun polyester cage (18 cm long by 20 cm base by 26 cm top) made from a Plant Sleeve (Kleen Test Products, Brown Deer, WI, USA). Each cage included two 4 by

16-cm clear acetate viewing windows and a 1 by 1-cm acetate trap door to introduce psyllids. Experiment 1 included 12 pairs (replicates) of caged shoots among four trees, and experiment 2 included nine pairs of caged shoots among three trees. At the beginning of the experiments, two male and two female reproductively mature adult psyllids were captured from nearby trees and introduced to each cage. Eleven days later we began collecting data including the following: the presence of eggs, and the number and distribution of live males, females and mating pairs. Each time data were collected we added psyllids (if needed) so that each cage contained at least two to three pairs of males and females. Data were collected between 1000 and 1500 hours, each day for days 11–18, every 2 d for days 19–37, every 5 d for days 38–57, and on day 63. Within 5 d of oviposition, or at the end of the experiment (which ever came first), each caged pair of shoots was harvested and the number of eggs per shoot was recorded under a dissecting microscope. Both experiments lasted 63 d. We determined a psyllid distribution score for each of the three possible positions in each cage (including the juvenile shoot, adult shoot, and the cage) for each observation day. Each score had a maximum value of 1 and was determined as follows: (1) if the majority of the psyllids were on a single position (e.g., the juvenile shoot), that position received a score of one and other two positions received a 0, (2) if the psyllids were equally distributed on two positions, each received a score of 0.5, and (3) if psyllids were equally distributed on all three positions each received a score of 0.33. The psyllid distribution scores were tallied and converted to a percentage that reflected the proportional number of observation days where the majority of the psyllids were distributed among the three positions. Each cage was considered an experimental unit. Paired *t*-tests were used to compare the distributional preferences of each psyllid species for the juvenile versus adult shoots. To statistically compare the ovipositional preferences of each psyllid species for the juvenile and adult shoots, we calculated the exact binomial probability of oviposition on the preferred shoot type.

Retention on Juvenile and Adult Shoots. To compare the retention of adult psyllids that had landed on juvenile and adult shoots, we conducted the following experiments at El Cerrito High School in July 1999. In experiment 3 we selected two juvenile shoots \approx 50 cm from the ground and in similar microenvironments (e.g., light, aspect). These shoots had two closed axillary buds at the axil of the most recent fully expanded leaf pair, and two to four expanding buds and leaves at more distal nodes, all which were free of psyllid eggs, nymphs and adults. Adult females of both species were collected from nearby trees and held individually in \approx 1-cm³ cages. The psyllids were caged for at least 10 min before the experiment, and were used within 2 h of collection. The psyllids were tested individually in pairs of one of each species based on the time since collection. To measure the retention of a psyllid on a shoot, the cage was opened and gently tapped over the most recent fully expanded, horizon-

tally held leaf to dislodge the psyllid from the cage onto the adaxial leaf surface. Once the psyllid had landed on the leaf and was on its feet, we allowed the leaf to return to its normal position and recorded the amount of time the psyllid spent on the shoot, and its behavior (e.g., settled, walked) for up to 10 min. In each replicate, *C. eucalypti* was tested first followed by *C. spatulata*. There were 16 replicates divided equally among the two shoots. The natural orientation of the juvenile leaf (in relation to the flat ground below the tree) where the first eight replicates landed was 90° and the orientation of the second leaf (replicates 9–16) was 45°. Each psyllid was used once. We used the same procedure to evaluate retention on adult shoots (experiment 4). The two selected adult shoots had two to three closed axillary buds at the tip of the shoot, and were in same region of the tree canopy as the juvenile shoots in experiment 3. The natural orientation of the adult leaves where the psyllid landed was 90°. The shoots used in both experiments lacked reproductive structures. The experiments were conducted between 0800 and 1930 hours, when the psyllids were naturally active. Paired *t*-tests were used to compare retention times of psyllids on the juvenile and adult shoots.

Results

There were significant differences in the distribution of *C. eucalypti* (paired $t = 7.1$, $df = 11$, $P \leq 0.001$) and *C. spatulata* (paired $t = 17.3$, $df = 8$, $P \leq 0.001$) on the juvenile and adult shoots. *Ctenarytaina eucalypti* and *C. spatulata* were observed mainly on juvenile and adult shoots, respectively (Fig. 2). These patterns were consistent for males and females of both species (data not shown). We observed 68 and 48 mating pairs of *C. eucalypti* and *C. spatulata*, respectively. *Ctenarytaina eucalypti* mated on juvenile shoots 88% of the time, and 12% of the time on adult shoots. In contrast, *C. spatulata* mated only on adult shoots.

Ctenarytaina eucalypti oviposited significantly more on the juvenile shoots than on the adult shoots (binomial probability; $P < 0.001$). In all 12 replicates *C. eucalypti* oviposited only on the juvenile shoots. In contrast, *C. spatulata* never oviposited on juvenile shoots and oviposited on adult shoots in three of nine replicates, however, this pattern was not significant (binomial probability; $P = 0.13$). Both species oviposited in grooves of expanding buds and *C. eucalypti* also oviposited on expanding leaves and at the bases of expanding buds, as in the wild.

There were significant differences in the retention of *C. eucalypti* and *C. spatulata* on the juvenile and adult shoots (Fig. 3; Table 1). During the 10-min observation period, all of the *C. eucalypti* remained on the juvenile shoots, whereas 63% of *C. spatulata* left. On the juvenile shoots the majority of the *C. eucalypti* walked from the leaf where they had landed to the stem, and nearly half of the individuals probed the juvenile buds with their ovipositor. In contrast, *C. spatulata* never walked from the leaf to the stem of the juvenile shoots and nearly half flew away within 1 min

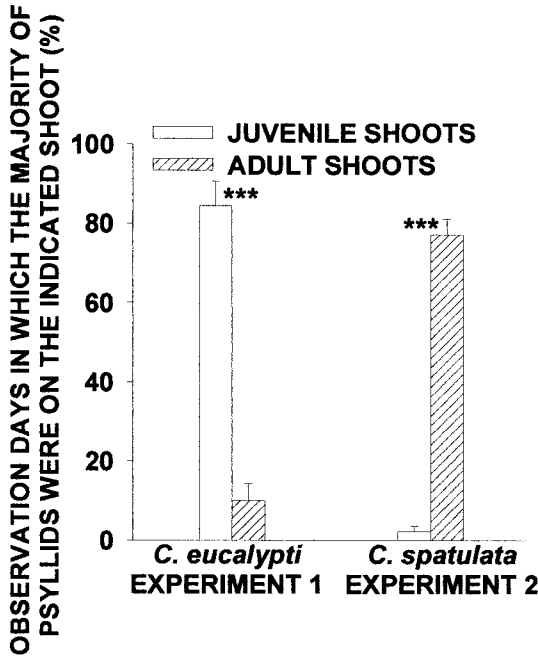


Fig. 2. Distribution of adult psyllids in caged pairs of juvenile and adult shoots of *Eucalyptus globulus*. Experiment 1, $n = 12$. Experiment 2, $n = 9$. Bars = mean \pm 1SE. *** indicates significant difference at $P < 0.001$ based on paired t -tests.

of landing. On the adult shoots, most *C. spatulata* remained for 10 min, a few probed the buds with their ovipositor, and several moved their body up and down as if probing the leaf with their stylets.

Discussion

Our study demonstrated that heteroblasty in *E. globulus* affects the reproductive behavior of *C. eucalypti* and *C. spatulata*. These results are consistent with the natural distributions of these psyllids on the juvenile and adult shoots of their host (Brennan 2000). Despite considerable work on insect herbivory in *Eucalyptus* (Ohmart and Edwards 1991), to our knowledge the current study is the first experimental evidence that heteroblasty in *Eucalyptus* affects the ovipositional preferences of insects, and the first report of developmental resistance due to heteroblasty. Developmental resistance (Kearsley and Whitham 1989) describes plant resistance to herbivores that depends on plant developmental age. Developmental resistance to arthropod herbivores has been studied in relatively few systems (Frankie and Morgan 1984, Kearsley and Whitham 1989, 1997, Waltz and Whitham 1997, Karban and Thaler 1999). Although there were some differences in leaf size and shape of the aphid resistant versus susceptible leaves of *Populus angustifolia* L., Kearsley and Whitham (1997) did not consider this host heteroblastic. In addition, Karban and Thaler (1999) found no difference in mite pop-

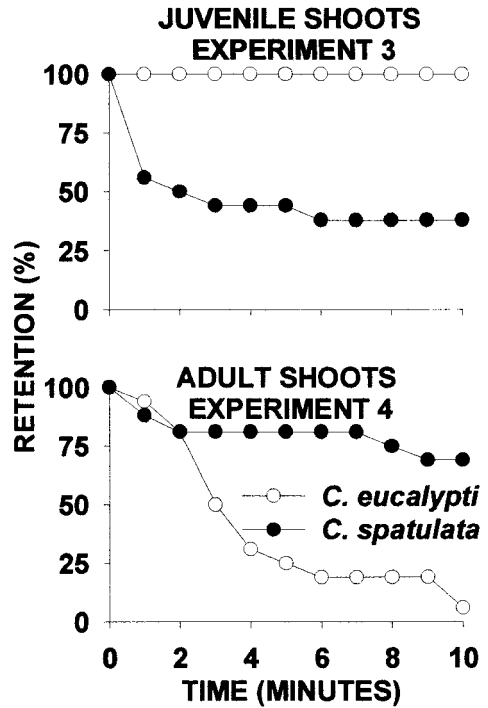


Fig. 3. Retention of adult female psyllids of *C. eucalypti* and *C. spatulata* on juvenile and adult shoots of *E. globulus*. In both experiments, $n = 16$.

ulations on the juvenile and adult leaves of cotton, although both differed from the cotyledons.

Subsequent studies with this system help to explain the ovipositional preference of *C. spatulata* for the adult shoots, and the significantly shorter retention times of this species on the juvenile shoots than on the adult shoots. In no-choice experiments, adults of *C. spatulata* survived significantly longer on adult leaves than on juvenile leaves and also survived longer on 'de-waxed' juvenile leaves than on normally waxy juvenile leaves (Brennan and Weinbaum 2001a). Based on honeydew and stylet track data, we hypothesized that *C. spatulata* died sooner on the waxy juvenile leaves due to starvation (Brennan and Weinbaum 2001b). Furthermore, we found that the epicuticular wax on the juvenile leaves affected negatively the ability of *C. spatulata* to adhere to the juvenile leaves (Brennan and Weinbaum 2001c). Per unit of body weight, *C. eucalypti* males and females respectively had eight and 11 times more total pulvillar area than *C. spatulata* (Brennan and Weinbaum 2001c). This helps to explain why *C. spatulata* walked less on the juvenile leaves than on adult leaves, and often flew away within 1 min of landing on the juvenile leaves.

The reasons that *C. eucalypti* preferred to oviposit on the juvenile leaves are less clear because adults of this species survived equally well on adult and juvenile leaves (Brennan and Weinbaum 2001a). In addition, honeydew production and stylet track behavior of *C. eucalypti* were independent of leaf type and unaf-

Table 1. Retention times and behavior of adult females of psyllids that landed on juvenile and adult shoots of *E. globulus*

	Experiment 3 Juvenile shoots		Experiment 4 Adult shoots	
	<i>C. eucalypti</i>	<i>C. spatulata</i>	<i>C. eucalypti</i>	<i>C. spatulata</i>
Retention time (min) ^a	10 ± 0***	4.5 ± 1.1	4.0 ± 0.8**	7.8 ± 0.9
Psyllid behavior (%) ^b				
Walked on the shoot	100	75	100	100
Walked from leaf to stem	69	0	75	19
Probed buds with ovipositor	44	0	6	13
Moved body up and down as if probing with the stylets	0	0	0	38

^a Mean ± 1SE, n = 16 individuals of each species.

^b Percentage of individuals exhibiting each behavior during the 10 min observation period.

, and * are significant at P < 0.01 and P < 0.001, respectively, for within experiment comparisons of retention times of *C. eucalypti* versus *C. spatulata* in paired t-tests.

fects by the presence of epicuticular wax (Brennan and Weinbaum 2001a, 2001b). However, preliminary data suggest that survival of *C. eucalypti* nymphs may be limited on adult leaves which may explain the ovipositional preference of this species for juvenile shoots (Brennan 2000). It is possible that chemical and nutritional differences between the juvenile and adult shoots affect the preference of *C. eucalypti* for the juvenile shoots.

Brown and Lawton (1991) proposed that insects influenced the evolution of leaf shape. However, in *Eucalyptus*, heteroblasty is most likely an adaptation to climate, rather than herbivory (Cameron 1970, Beadle et al. 1989, Bell and Williams 1997). Furthermore, because heteroblasty increases the spatial complexity and variation within a plant, we hypothesize that heteroblasty influenced the evolution of insects. This speculation is based on the fact that (1) phytophagous insect diversity is highest in structurally and spatially complex plant communities (Lawton 1983), and (2) that hybrid zones are centers of herbivore biodiversity (Whitham et al. 1999). On the level of an individual heteroblastic plant exhibiting juvenile, intermediate and adult shoots, the juvenile and adult shoots may function as 'parental species,' and intermediate shoots as 'transitory phenotypic hybrid zones.' Heteroblastic plant-insect interactions may provide model systems to investigate the questions of both theoretical and practical importance.

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