

## RELATIVE IMPORTANCE OF PLANT ONTOGENY, HOST GENETIC VARIATION, AND LEAF AGE FOR A COMMON HERBIVORE

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**Abstract.** Using an experimental eucalypt forest of known pedigree and laboratory feeding trials, we examined the relative importance of plant ontogeny (heteroblasty), genetic variation among host trees, canopy height, and leaf age as potential drivers that could affect the distribution and feeding preference of a common insect herbivore, *Chrysophtharta agricola*. We found that ontogeny is a major factor affecting this insect. Its importance rivaled leaf physiological age, a well-documented factor, which served as our standard for judging the relative importance of other effects. Three patterns emerged: (1) In the field, beetle feeding was nine times greater in the adult zone than in the juvenile zone of heteroblastic trees (i.e., trees with both adult and juvenile foliage). (2) Laboratory feeding trials confirmed their strong preference for adult foliage. (3) Although eucalypt species, hybrid cross type ( $F_1$ ,  $F_2$ , and backcrosses), and canopy height also exhibited significant effects on beetle feeding in laboratory trials, their relative importance was much less than ontogeny and leaf physiological age. We conclude that beetles perceive greater variation in host quality within individual plants than between different eucalypt species and their hybrids. The magnitude of these effects argues that ontogeny may rival other better studied plant traits that affect herbivores. We discuss how genetic regulation of phenotypic expression in plants may affect herbivore populations and structure communities.

**Key words:** canopy height; *Chrysophtharta agricola*; common garden; chrysomelid; *Eucalyptus globulus*; *Eucalyptus nitens*; heteroblasty; hybridization; insect preference; ontogeny; physiological age; synthetic hybrids.

### INTRODUCTION

Plant development is known to affect the distribution of pathogens and herbivores (Zagory and Libby 1985, Kearsley and Whitham 1989, 1998, Waltz and Whitham 1997, Karban and Thaler 1999, Brennan et al. 2001, Swihart and Bryant 2001). Developmental processes in plants can be generalized into two broad categories: ontogenetic and physiological or environmental (e.g., Lawson and Poethig 1995). Environmental changes result from alteration of the local meristem environment by factors such as shading, water, and nutrient relations. In contrast, ontogenetic variation arises from changes in gene expression in plant meristems (Poethig 1990, Wiltshire et al. 1994), is widespread, and results in changes in vegetative structures across whole plant gradients (Jones 1999). These morphological changes can be gradual (e.g., *Populus*; Kearsley and Whitham 1998) or abrupt, with heteroblasty representing the extreme case. The genus *Eucalyptus* contains many heteroblastic species in which foliage may rapidly change from juvenile to adult leaves (Fig. 1; Jordan et al. 1999).

Brennan et al. (2001) states that little is known about the effects of heteroblasty on host plant selection by herbivores. In addition, very few studies have clearly separated the ontogenetic and environmental components of plant developmental processes, especially as they relate to other community members. This distinction is important, because only ontogenetically derived traits are heritable and thus subject to natural selection. Previous studies have shown that the height and age of the ontogenetic change in eucalypt leaf morphology are under strong genetic control (Wiltshire et al. 1998, Dutkowski and Potts 1999, Jordan et al. 2000). Because the findings of Jordan et al. (2000) clearly established the genetic basis of the timing of the transition from juvenile and adult plant traits of *E. globulus* used in our studies, our findings are not confounded by alternative environmental interpretations. Associated with the changes in leaf morphology and biochemistry in juvenile and adult zones of individual trees, we predicted that these changes in gene expression could be ecologically important by affecting the distribution of a common herbivore.

Most importantly, using the same study trees, we sought to quantify the relative importance of plant ontogeny in comparisons with other factors such as the genetic variation between two eucalypt species and their hybrids, canopy height, and leaf age. Although

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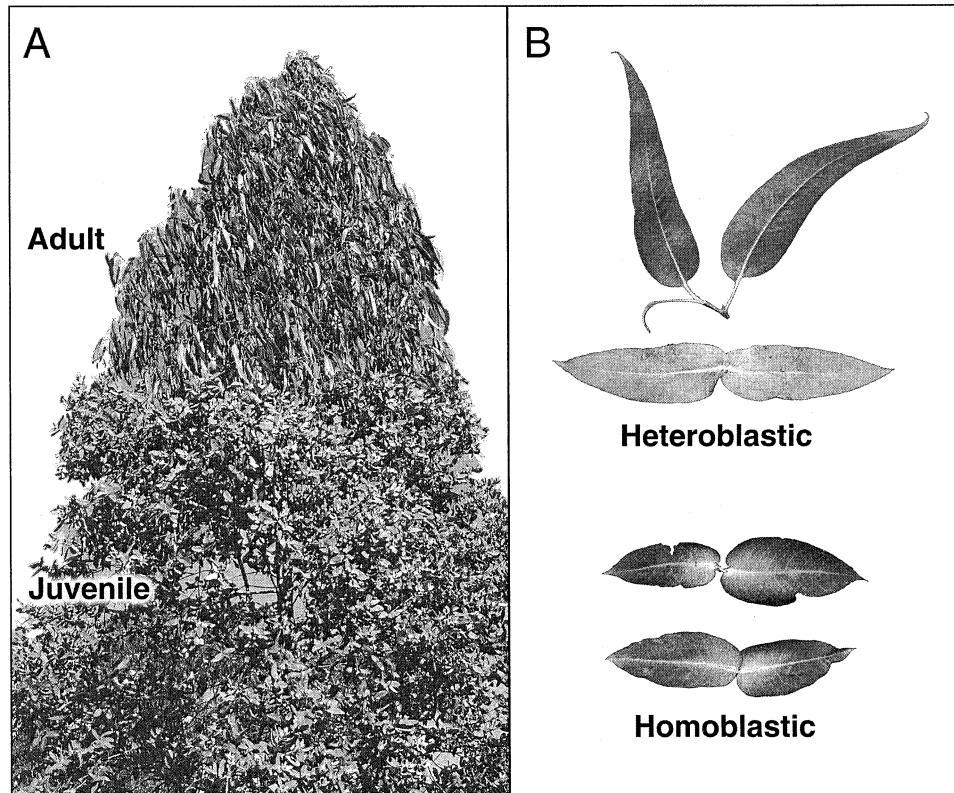


FIG. 1. Leaves from homoblastic and heteroblastic trees exhibit dramatically different leaf morphologies in which the height and age of the transition from juvenile to adult morphology is highly heritable. (A) A single heteroblastic tree illustrating the sharp boundary between juvenile and adult leaf types. (B) These photos show the morphologies of leaves collected from the upper and lower canopies of two trees. The lower canopy of a heteroblastic tree produces glaucous, broadly ovate, opposite, and sessile juvenile leaves, whereas the upper canopy produces green, lanceolate, alternate, and petiolate adult leaves. A homoblastic tree of the same size produces juvenile foliage in both the upper and lower canopies. Photos by Tom Whitham.

other studies cited above argue that plant ontogeny can be an important driver of herbivore populations and communities, we are aware of no studies that have evaluated the importance of plant ontogeny relative to other better studied factors. As our standard for comparison, we quantified the effects of leaf age on beetle preference. Many insects are well known to exhibit greater preference and performance on young leaves relative to old leaves (review by Raupp and Denno 1983), and these effects can be so pronounced as to affect their geographic distribution (Floate et al. 1993). Relative to young leaves, older leaves are tougher due to higher levels of fiber, lignin, and tannins, and they often lack sufficient levels of nitrogen or sugars for insect development (e.g., Coleman 1986).

#### Study system

To study the effect of plant ontogeny on herbivore distribution, we quantified the feeding patterns of *Chrysophtharta agricola* (Coleoptera: Chrysomelidae) beetles on homoblastic and heteroblastic trees of *Eucalyptus globulus*, *E. nitens*, and their synthetic hybrids of the same age and size. *Eucalyptus globulus* and *E.*

*nitens* are two of the most important plantation eucalypts in temperate Australia (Eldridge et al. 1993, Tibbits et al. 1997). They are taxonomically close (Brooker 2000), and both are markedly heteroblastic (Fig. 1). They normally switch to adult foliage when two to four years old. Due to genetic variation in the timing of this transition (*E. globulus*: Jordan et al. 1999, 2000; *E. nitens*: Dutkowski et al. 2001), homoblastic and heteroblastic trees of the same age often grow in close proximity during this transition period. We contrasted beetle feeding on homoblastic trees, which had juvenile foliage throughout the canopy, with their feeding on trees that had recently shifted to become heteroblastic. In the laboratory, we also presented beetles with foliage collected from different foliage types and heights.

To quantify how other sources of genetic variation might affect beetle distributions, we used controlled crosses to examine the effects of plant species and hybridization on *C. agricola*. Numerous studies have shown that natural hybridization in the wild can have important evolutionary consequences for plants (e.g., Stace 1987, Rieseberg et al. 1996, Arnold et al. 1999),

and their pathogens and herbivores (Fritz 1999, Moulia 1999, Whitham et al. 1999, Dungey et al. 2000).

#### METHODS

##### *Experimental forest*

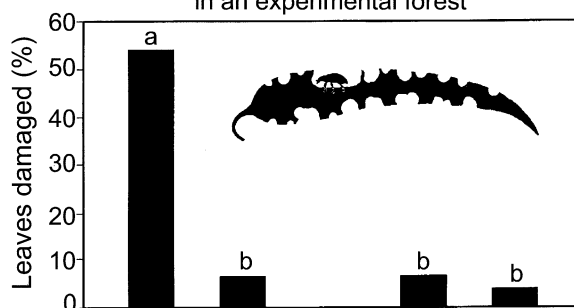
Trees were from full-sib families derived from unrelated crossing amongst *E. globulus*, *E. nitens*, and their  $F_1$  hybrids to produce six different cross types: the two parental species, *Eucalyptus globulus* and *Eucalyptus nitens*; the  $F_1$  hybrid; outcrossed  $F_2$ 's ( $F_1 \times F_1$ ); backcrosses to *E. nitens* (BCnitens = *E. nitens*  $\times$   $F_1$  or  $F_1 \times E. nitens$ ); and backcrosses to *E. globulus* (BCglob = *E. globulus*  $\times$   $F_1$  or  $F_1 \times E. globulus$ ). These six genetic classes provided a complete genetic continuum between the two parental types. These full-sib families were grown in a field trial at Tyenna (42°20' S, 146°39' E) in southern Tasmania, Australia, where they were surrounded by native eucalypts (mainly *E. regnans*) that served as a natural source of insects. The trial was a randomized, complete block design of seven replicates, with each replicate containing a single plant from each of the 126 full-sib families.

##### *Chrysophtharta agricola in the field*

Our studies focused on the chrysomelid beetle, *C. agricola*, a pest of eucalypt plantations in Tasmania (Ramsden and Elek 1998). To quantify its field distribution, we randomly selected a heteroblastic and homoblastic tree from each of the six cross types. This was repeated across six replicates in the field trial. On each of the 72 trees, we censused beetle feeding in the upper and lower canopies at a consistent height. At each position, the percentage of leaves that exhibited the characteristic "scallop" cuts of adult beetle feeding (see silhouette Fig. 2A) were determined from a random sample of 50 leaves of the current growing season. At the time of field censuses, beetles were abundant in the common gardens, and all trees were actively growing and producing new leaves. Thus, young and old foliage of the current year's growth for both juvenile and adult leaf types were available for foraging beetles to choose among.

This sampling design enabled the simultaneous examination of three independent gradients: the ontogenetic gradient, the genetic gradient, and a height gradient. The effect of changing ontogeny, independent of canopy height, was examined by comparing juvenile and adult foliage at the top of homoblastic and heteroblastic trees. Responses to the genetic gradient could be examined independently of ontogenetic and height effects by comparing the distributions of beetles on the cross types for one or the other ontogenetic foliage types at a comparable height. The height gradient was supplied by the high and low juvenile foliage on the homoblastic trees, which allowed us to examine the effects of height independent of confounding ontogenetic factors associated with changing foliage types.

##### A) Feeding by adult *Chrysophtharta agricola* in an experimental forest



##### B) Feeding preference in the laboratory

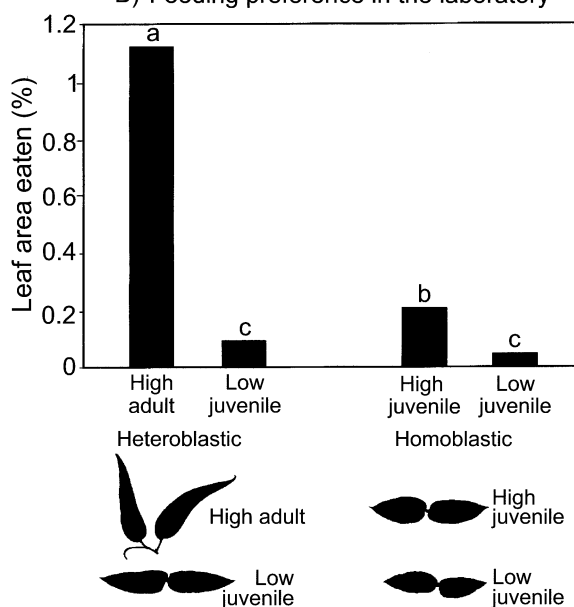


FIG. 2. (A) In the field, adult beetles are far more likely to feed on the adult foliage of heteroblastic trees than on the juvenile foliage of either heteroblastic or homoblastic trees. (B) In laboratory feeding trials, the same general pattern emerged, but high juvenile foliage is also preferred more than low juvenile foliage indicating either a height effect or innate differences in leaf quality not reflected in foliage morphology. While significant, this latter effect is small in comparison to beetle preferences for adult foliage over juvenile foliage. Leaf and beetle silhouettes indicate the typical mode of feeding in which adult beetles scallop the leaves. Different letters indicate significant differences among groups.

##### *Laboratory feeding trials*

Feeding trials were conducted using single 25–30-cm shoots of foliage from the upper and lower canopy of each of the 72 trees censused in the field. The foliage was collected by replicate, and all shoots from a field replicate were allocated to the same laboratory cage (150  $\times$  35  $\times$  35 cm), resulting in 24 randomly arranged shoots in each cage. The base of each shoot was placed in water in an individual cup, which was covered to prevent beetles from falling into the water. On each shoot there was very young (newly expanded) foliage

at the tips, intermediate age (fully expanded, still succulent) foliage, and old (sclerophyllous) foliage of the current season's growth. Thus, in each replicate cage, beetles were exposed to high and low foliage of three different physiological ages from each of the twelve trees. Cages were maintained at constant temperature (22°C) and humidity (55%) with a photoperiod of 16 h daylight and 8 h of darkness. Because we found no significant pattern of cross type use in the field, for our laboratory experiments we collected beetles from all cross types in the common garden and pooled them for choice experiments in the laboratory. Thirty-six even-aged beetles were placed in each cage and allowed to feed for 72 h. Leaves were then removed from the cage, classified into the three different physiological ages, and a leaf area meter was used to quantify the percent leaf area eaten.

#### Analysis of data

The significance of factors that affected beetle feeding in the laboratory trial were tested using a three-way, repeated-measures mixed model ANOVA with the factors of cross type (six levels), leaf age (young, intermediate, or old physiological age of the foliage), foliage type (homoblastic low juvenile, homoblastic high juvenile, heteroblastic low juvenile, and heteroblastic high adult), and replicate (six levels). The first three factors and their interactions were treated as fixed effects, replicate was treated as a random effect, and the shoot was treated as the subject. Pairwise comparisons between cross types, ontogenetic types, and height types were undertaken with specific contrasts. The data best fitted the assumptions of normality using an exponential transformation ( $X^{0.25}$ ), but least squares means were back-transformed for presentation. For the field experiment, a similar statistical model without the effect of age and its interactions, but with tree as the subject, was fitted to the angular transformed data. These analyses were undertaken using the MIXED procedure in SAS (SAS Institute 1997).

### RESULTS

#### Field trials

Consistent with our observations that adult beetles were far more abundant on adult foliage than juvenile foliage, our censuses of feeding damage revealed that adult foliage was 9.3 times more likely to suffer damage than juvenile foliage, regardless of canopy height (Fig. 2A). There was no evidence that beetles might selectively forage higher in the canopy, as there was no significant difference in beetle feeding in the upper crown and at the base of homoblastic trees (Fig. 2A). There was also no significant difference between juvenile foliage at the base of heteroblastic trees and juvenile foliage either high or low on homoblastic trees (Fig. 2A).

We also examined the genetic effect of cross type and found no significant effect of any hybrid or parental

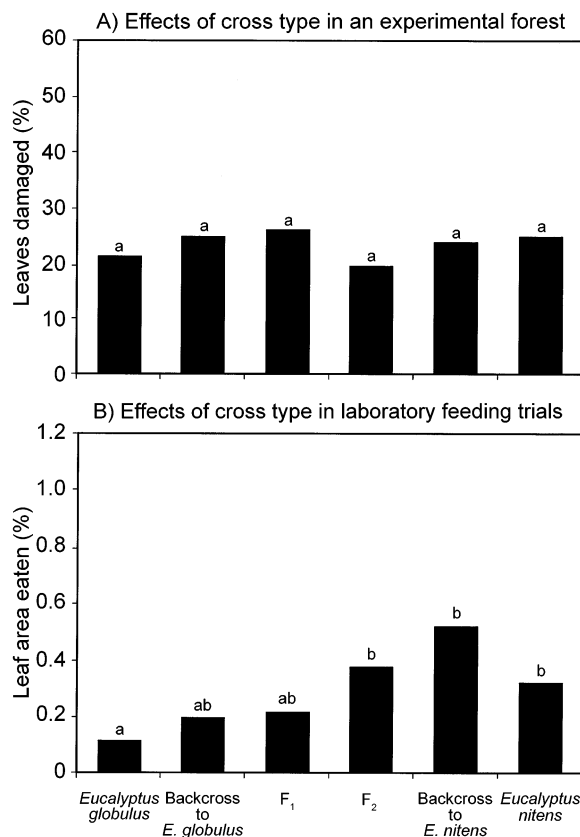


FIG. 3. (A) In field trials, adult beetles did not feed more on one cross type than another. (B) In laboratory feeding trials, cross type had a significant effect on feeding preference, but the effect was much smaller than the ontogenetic effect shown in Fig. 2B. Different letters indicate significant differences among groups.

species on beetle feeding in the field (Fig. 3A). Thus, in our field analyses of ontogeny, height, and the genetic effects of cross type and parental species, only ontogeny demonstrated a significant effect on beetle feeding. Furthermore, the nine-fold magnitude of the effect suggested that ontogeny is a major factor affecting the distribution of adult beetles.

#### Laboratory trials

Our laboratory feeding trials showed that adult beetles exhibited preferences for ontogenetic type, foliage height, cross types, and foliage age (Table 1). In close agreement with our field studies, our laboratory feeding trials showed that adult beetles respond strongly to plant ontogeny by feeding selectively on adult foliage (Fig. 2B). This result is not confounded by other effects because it compares high adult foliage of heteroblastic trees with high juvenile foliage of homoblastic trees of the same cross type. Thus, when other effects such as height are eliminated, adult beetles fed 5.6 times more on adult foliage than on juvenile foliage ( $P < 0.001$ ).

It is possible that the feeding preference for adult foliage is simply a result of physical characteristics of

TABLE 1. The three-way mixed model analysis of variance of feeding preferences by *Chrysopharta agricola* in the feeding trial.

| Effects and contrasts                            | df | F    | P     |
|--|----|------|-------|
| Effect   |    |      |       |
| Foliage  | 3  | 22.8 | 0.000 |
| Age  | 2  | 70.5 | 0.000 |
| Genetic  | 5  | 3.0  | 0.012 |
| Foliage × age                                    | 6  | 0.9  | 0.534 |
| Genetic × foliage                                | 15 | 1.5  | 0.100 |
| Genetic × age                                    | 10 | 0.3  | 0.969 |
| Genetic × foliage × age                          | 30 | 0.7  | 0.883 |
| Contrasts  |    |      |       |
| Ontogenetic                                      |    |      |       |
| Homo high (juvenile) vs. hetero high (adult)     | 1  | 23.2 | 0.000 |
| Position   |    |      |       |
| Home high (juvenile) vs. homo low (juvenile)     | 1  | 7.3  | 0.007 |
| Ontomorph  |    |      |       |
| Homo low (juvenile) vs. hetero low (juvenile)    | 1  | 1.0  | 0.326 |
| Genetic  |    |      |       |
| <i>E. globulus</i> vs. <i>E. nitens</i>          | 1  | 4.9  | 0.027 |
| Pure vs. hybrids                                 | 1  | 3.0  | 0.087 |
| F <sub>1</sub> vs. F <sub>2</sub>                | 1  | 1.6  | 0.207 |
| F <sub>1</sub> vs. mid-parent                    | 1  | 0.1  | 0.739 |
| F <sub>2</sub> vs. mid-parent                    | 1  | 3.1  | 0.081 |
| <i>E. globulus</i> vs. backcross <i>globulus</i> | 1  | 1.4  | 0.241 |
| <i>E. nitens</i> vs. backcross <i>nitens</i>     | 1  | 1.6  | 0.211 |

Notes: Effects are: foliage (homoblastic high juvenile, homoblastic low juvenile, heteroblastic low juvenile, heteroblastic high adult), age (young foliage, intermediate-aged foliage, old foliage), and genetic (*E. globulus*, backcross *globulus*, F<sub>1</sub>, F<sub>2</sub>, backcross *nitens*, *E. nitens*). The homoblastic and heteroblastic trees are compared using low juvenile foliage to test for inherent differences in susceptibility. Error degrees of freedom = 206.

the foliage such as leaf habit or orientation, as these factors differ between adult and juvenile foliage and could affect feeding both in the field and laboratory trials. We therefore tested whether or not beetle preference for adult foliage was a direct response to leaf quality in an additional feeding trial in which 52 adult beetles were fed on cut pieces of foliage placed on filter paper in petri dishes. Of the 52 individual trials, 73% (38 beetles) took their first bite from the adult foliage while only 23% (12 beetles) ate the juvenile foliage first, and 4% (2 beetles) ate neither ( $\chi^2_1 = 13$ ,  $P < 0.001$ ). This selective “first bite” analysis suggests that ontogenetic variation directly affects foliage quality rather than habit, orientation or interspecific interactions.

When other effects were eliminated, foliage height also had a significant effect on beetle feeding ( $P < 0.007$ ). Beetle feeding was significantly greater on juvenile foliage collected from the top as opposed to juvenile foliage from the bottom of homoblastic trees (Fig. 2B). Although this effect was not found in the field experiment and is very small relative to ontogenetic effect, it suggests that even within the juvenile foliage class, there may be subtle differences that affect feeding preferences.

It is also important to note that the low juvenile foliage on heteroblastic trees did not differ significantly ( $P = 0.326$ ) from the low juvenile foliage on hom-

oblastic trees (Table 1, Fig. 2B). This is the same pattern observed in the field trials (Fig. 2A), and suggests that the quality of low juvenile foliage does not change when a tree shifts from being homoblastic to heteroblastic. There is no flow-over effect from the adult foliage, nor are there any inherent genetic differences between homoblastic and heteroblastic trees that affect beetle feeding.

Beetles were selective in their feeding from different cross types (Fig. 3B). Beetles had a significant preference for the introduced *E. nitens* over the native *E. globulus* ( $P < 0.001$ ). Beetle preference for the F<sub>1</sub> hybrid was intermediate to the parental types and not significantly different from the mid-parental value. These data are inconsistent with our field trials, which found no significant differences among cross types. However, the magnitude of the cross type effect is small relative to the ontogenetic effect (i.e., contrast laboratory results of Figs. 2B and 3B).

Beetles exhibited a pronounced preference for young foliage relative to older foliage from the current year's growth (Fig. 4). Beetles ate 2.4 times more young foliage than intermediate aged foliage, and far more young foliage than old foliage, as the latter was left virtually untouched. The absence of significant interaction effects (Table 1) indicates that the preference for different foliage ages did not change between adult and juvenile foliage or between the different cross

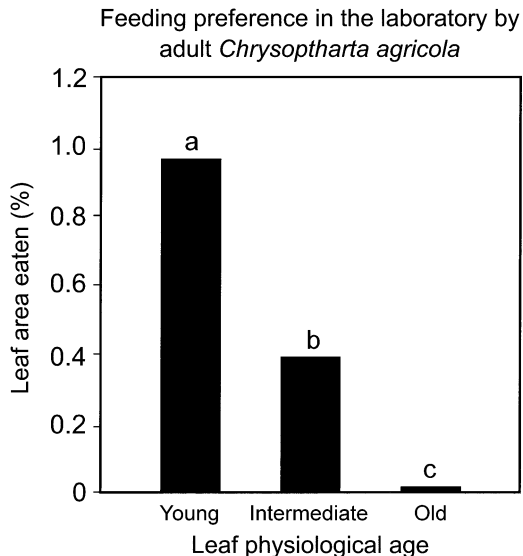


FIG. 4. In laboratory feeding trials, leaf physiological age greatly affected feeding preference by *Chrysopharta agricola*.

types. These results are consistent with field observations in which beetles fed on young foliage, but were never observed feeding on old foliage.

#### DISCUSSION

##### *The relative importance of ontogeny*

Few studies have examined how multiple factors act in concert to affect herbivores (e.g., Harrison and Cappuccino 1995, Wimp and Whitham 2001). Regarding the factors we examined, this lack of integration is likely due to few systems having both common gardens in which the pedigree of all trees is known, and traits whose ontogenetic basis has been clearly established.

In our study, foliage age followed by ontogeny emerged as the clear factors that most accounted for the distribution of adult beetle feeding. Because leaf age is recognized as being very important in numerous studies (review by Raupp and Denno 1983), the importance of ontogeny in other systems warrants further study. There were inconsistencies regarding the small, but significant effects of canopy height and cross type in the laboratory, but not in the field. It is not likely that beetles were systematically preconditioned as the source of beetles for the laboratory experiment was from many trees of all cross types in the common garden. Overall, these differences were minor relative to the major differences we detected for ontogeny and leaf age, which were consistent in both field and laboratory trials.

These combined effects create a habitat mosaic in which adult beetles most preferred feeding on young, adult foliage from the crown of *Eucalyptus nitens* and its backcross hybrids. In contrast, they least preferred old, juvenile foliage from the base of *E. globulus* and

its backcross hybrids. However, the effect of plant ontogeny goes beyond the feeding of adult beetles. While adult *C. agricola* beetles preferentially feed on the adult foliage, egg laying is virtually restricted to the juvenile foliage, and it is here where nearly all larval feeding occurred (Nahrung and Allen 2002; R. Lawrence, unpublished data). In this case, it appears that the beetle may have evolved to allow exploitation of different ontogenetic phases of the tree host, thereby avoiding resource competition between adult and larval stages. Ontogenetic preference has been reported for several other insect herbivores of eucalypts (Edwards 1982, Farrow et al. 1994, Brennan and Weinbaum 2001, Brennan et al. 2001), but none of these compared the relative importance of ontogeny with other well-known factors such as leaf age. Our findings show that beetles perceive far greater variation in host quality within individual plants than between two different eucalypt species and their hybrids.

##### *Ontogeny as a community organizer*

Our findings argue that plant ontogeny affects the distribution of a common herbivore that can be an important defoliator of a dominant plant species. As such, this selective herbivory has the potential to affect both the plant and the distribution of many other species that feed on eucalypts. Because few studies have actually documented the genetic basis of variation in phenotypic expression within individual plants, most examples refer to developmental variation, which encompasses both ontogenetic and environmental processes. Developmental variation is known to have major impacts on diverse organisms including pathogens (Zagory and Libby 1985, Dungey et al. 1997), insects (Karban and Thaler 1999, Brennan et al. 2001), and vertebrates from rodents to elephants (Bryant et al. 1992, 1994).

Because many of the plants that exhibit developmental variation are dominant species (e.g., conifers, broadleaf evergreens, and deciduous trees), the effects of plant ontogeny on common or keystone consumers has the potential to affect many other community members. For example, with *Populus angustifolia*, *P. fremontii* and their natural hybrids, Kearsley and Whitham (1989, 1998) showed that plant development predictably affected the survival, performance, and distribution of the gall aphid, *Pemphigus betae*, whose presence subsequently affected other diverse taxa, including fungi, insect herbivores and predators, and birds (Dickson and Whitham 1996, Waltz and Whitham 1997). Thus, in this system, the effects of plant development on a common species cascade to have community-wide consequences. Swihart and Bryant (2001) reviewed 128 studies of the effects of plant development on vertebrates, and in 96% of the studies, vertebrates favored adult over juvenile growth. They argued that plant development is ecologically and evolutionarily important; selective feeding by these com-

mon mammals can alter the composition and successional trajectories of plant communities (e.g., Bryant and Chapin 1986, Ritchie et al. 1998). Because the ontogenetic component of plant development is genetically based and subject to natural selection, these studies suggest a genetic component to community structure that few ecologists have explored.

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