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Corymbia Species and Hybrids: Chemical and Physical Foliar Attributes and Implications for Herbivory

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Abstract Hybridization is an important biological phenomenon that can be used to understand the evolutionary process of speciation of plants and their associated pests and diseases. Interactions between hybrid plants and the herbivores of the parental taxa may be used to elucidate the various cues being used by the pests for host location or other processes. The chemical composition of plants, and their physical foliar attributes, including leaf thickness, trichome density, moisture content and specific leaf weight were compared between allopatric pure and commercial hybrid species of *Corymbia*, an important subtropical hardwood taxon. The leaf-eating beetle *Paropsis atomaria*, to which the pure taxa represented host (*C. citriodora* subsp. *variegata*) and non-host (*C. torelliana*) plants, was used to examine patterns of herbivory in relation to these traits. Hybrid physical foliar traits, chemical profiles, and field and laboratory beetle feeding preference, while showing some variability, were generally intermediate to those exhibited by parent taxa, thus suggesting an additive inheritance pattern. The hybrid susceptibility hypothesis was not supported by our field or laboratory studies, and there was no strong relationship between adult preference and larval performance. The most-preferred adult host was the sympatric taxon, although this species supported the lowest larval survival, while the hybrid produced significantly smaller pupae than the pure species. The results are discussed in relation to plant chemistry and physical characteristics. The findings suggest a chemical basis for host selection behavior and indicate that it may be possible to select for resistance to this insect pest in these commercially important hardwood trees.

Keywords Forestry · Gas chromatography-mass spectrometry · *Paropsis atomaria* · Plant resistance

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Introduction

Hybridization occurs in every major plant taxon (Floate and Whitham 1994) and represents an important process that may elucidate the evolutionary process of speciation of plants and their associated herbivores (Strauss 1994). Additionally, artificial hybridization is a common procedure in agriculture and silviculture, as it has long been recognized that hybrids can combine desirable features of parental types, or even display novel phenotypes as a result of increases or changes in genetic composition (Strauss 1994).

An important aspect of hybridization is the interactions between hybrid plants and the pests and diseases of the parental taxa. The comparison of herbivore preference and performance on parental plants with that on hybrids can provide insights into the inheritance of potential resistance mechanisms (O'Reilly-Wapstra et al. 2005), and host-shift mechanisms that may in turn explain the distribution of insect species among plants (Thompson 1988). There are four generally hypothesized outcomes expressed in hybrids with respect to herbivory: hybrid susceptibility (arising either through dominance to a susceptible parent, or a hybrid that is more susceptible to herbivory than either parent); hybrid resistance (arising either through dominance to a resistant parent, or a hybrid that is more resistant than

either parent); an additive pattern, whereby hybrid traits are intermediate between the two parental types; or no difference between hybrids and parental taxa (Fritz et al. 1999). None of these responses dominates in studies published to date. In 127 studies of susceptibility of plant species and their hybrids to attack by herbivorous insects, hybrid susceptibility appears the most common pattern (39%), and hybrid resistance appears to be reasonably rare (10%), while 22% of studies identified an additive pattern, and almost one-third (29%) found no differences between parents and hybrids (Fritz et al. 1999; Dungey and Potts 2003; Hallgren et al. 2003; O'Reilly-Wapstra et al. 2005). An additive pattern has been found in interactions between eucalypt hybrids and mammalian herbivores (Scott et al. 2002).

Development of interspecific eucalypt hybrids for forest plantations is a silvicultural strategy adopted in many eucalypt-growing regions worldwide to maximize tree performance by combining the desirable traits of different species (de Assis 2000). Eucalypts are known to form hybrids readily with related species (Griffin et al. 1988). Traits for improvement through hybridization include growth rate, coppicing and propagation ability, pulp yield, wood density, and resistance to frost, drought, salinity (Dale and Dieters 2007), and pests and diseases (Potts and Dungey 2004). The eucalypts are a diverse group of trees and shrubs (> 800 species), generally considered to belong to the genera *Eucalyptus* (Brooker 2000), *Angophora,* and *Corymbia* (Ladiges and Udovicic 2000; Ochieng et al. 2007a, b) in the family Myrtaceae. One prominent characteristic of the group is the high essential oil content of the leaves, and the oils vary substantially among taxa (Bignell et al. 1998; Dunlop et al. 1999; Asante et al. 2001; Keszei et al. 2008), thus affecting feeding preferences of insect herbivores (Edwards et al. 1993; Steinbauer et al. 2004). An understanding of how characters important to plant herbivores (e.g., secondary chemicals and physical leaf characteristics) vary between species and their hybrids enables an understanding of the mechanisms of host choice by insect herbivores (Hallgren et al. 2003).

We examined variations in foliar chemical composition, leaf physical characteristics, and feeding by herbivorous beetles with three taxa: two allopatric species (*Corymbia citriodora variegata* (CCV) and *C. torelliana* (CT)) and their hybrid (CT × CCV). All are important in subtropical hardwood plantation forestry where the hybrids have significant advantages in growth, and tolerance to disease, insects, and frost, and also have been successfully vegetatively propagated (Lee 2007; Lee et al. in press). This tolerance to insects is, however, anecdotal, and needs quantification. The model pest species chosen to examine patterns of herbivory was *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae: Paropsina), a major pest of the commercially valuable CCV (Carnegie et al. 2008). *Paropsis atomaria* is an ideal model for this study, as adults and larvae feed on the same foliage, and thus allow a test of linkages between oviposition preference and larval performance. In addition, the test taxa represented a known host (CCV), a novel host (CT), and their F1 hybrid (CT × CCV).

Methods and Materials

Study System

Corymbia citriodora subsp. *variegata* (CCV) belongs to the Section Politaria, and recent studies have shown that it is genetically indistinguishable from *C. citriodora* subsp. *citriodora* and *C. henryi* (Ochieng et al. 2008; Shepherd et al. 2008), although the taxa are chemically distinct (Asante et al. 2001). It has a sympatric distribution with *P. atomaria*, although it was recorded only recently as a host (Nahrung 2006). *Corymbia torelliana* (CT) occurs naturally in about a 350×80 km zone in northern Queensland (Boland et al. 1992), a vicinity to which *P. atomaria* has recently expanded its range (Nahrung 2006). *Corymbia torelliana* (CT) is not a host for *P. atomaria*, although around 20 other eucalypt species are (CAB International 2005). An artificial hybrid between CT and CCV has been prepared for commercial purposes, and is planted widely throughout the insect's range (Lee 2007). All lifestages (except pupae) of *P. atomaria* occur on the host plant, with oviposition by females determining subsequent larval feeding habitat, and the long-lived adults and all four larval instars feeding on new growth, removing apical leaves. This results in a characteristic broom-topped appearance to trees (Carne 1966).

Foliage Collection

Seed was collected from one open-pollinated tree of each pure taxon (i.e., CT and CCV), thus ensuring that all samples had the same mother (were at least half-sibs). Hybrid (CT × CCV), seed was collected from one CT mother artificially pollinated from a single CCV father (i.e., full sibs). Neither of the hybrid parents were the same trees (families) as the pure taxon, so as to ensure a more representative sampling rather than looking only at intra-familial responses. Plants were sown from seed in potting mix comprising 50% pine bark fines, 25% peat (Aussie Peat) composted, and 25% perlite to which Osmocote® and Ag lime were added each at 4 kg/m^3, and gypsum, Micromax (fertilizer) and Hydroflow (wetting agent) were added each at 1 kg/m^3. Seedlings were raised in the glasshouse for the first 6 wk under mist, and then put under shadecloth for 2 wk before being put out into full

sun. Plants were repotted later into 130 mm diam pots and housed in a glasshouse (24°C, ambient light) for several months prior to use in experiments.

Foliage used in all experiments (physical analysis, chemical analysis, and feeding trials) was sourced from about 20 individual plants of each taxon. Only the first two—four fully expanded apical leaves were used for all trials to standardize the age of foliage during testing.

Foliar Analyses—Physical Analysis

Moisture content and specific leaf weight (SLW) (used as an indicator of leaf toughness—see Steinbauer 2001) were determined by measuring the fresh weight (FW) of leaves (to nearest 0.001 g), drying them in paper envelopes at ambient temperature for 3 wk, and re-weighing them (DW). Leaf area (mm^2) was estimated by using Compu Eye Leaf and Symptom Area software (Bakr 2005). Moisture content was calculated as (FW - DW)/FW, while SLW was determined as DW/area.

Foliar glabrousness was determined as the mean number of leaf trichomes in the field of view of a dissecting microscope (×40). The thickness (width) of the leaf lamina was measured under a dissecting microscope (×40) by cutting 4 small strips (~5 mm wide) and averaging the measurements per leaf (N=12). Data were analyzed using StatView (V 5.0.1). One-way *ANOVA* was used to analyze moisture content (following arcsine-square root transformation), SLW, and lamina thickness, with *Fishers LSD* test used for *post-hoc* comparisons. *Kruskall Wallis* test was used for leaf glabrousness, as data were not normally distributed. Twelve replicates of each foliage type were conducted for each parameter.

Foliar Analyses—Chemical Analysis

Replicate samples (N=5) of foliage (2.07±0.019 g FW) from 5 randomly chosen plants of each taxon were collected, and cut into squares (≤ 1 cm^2), and extracted with hexane (Sigma-Aldrich ≥ 99%) (≈ 15 ml) for 50 min, stirring for 1 min, three times within this period. The extract was filtered through filter paper (Whatman) and stored in the freezer (−20°C) until analysis (Jones et al. 2002; Rapley et al. 2004c).

Samples (1 µl) were analyzed with a gas chromatograph (GC) (Agilent 6890 Series) coupled to a mass spectrometer (MS) (Agilent 5975) and fitted with a silica capillary column (Agilent, model HP5-MS, 30 m×250 µm ID × 0.25 µm film thickness). Data were acquired under the following GC conditions—inlet temperature: 250°C, carrier gas: helium at 51 $cm.s^{-1}$, split ratio 13:1, transfer-line temperature: 280°C, initial temperature: 40°C, initial time: 2 min, rate: 10°$C.min^{-1}$, final temperature: 260°C, final time: 6 min. The MS was held at 280°C in the ion source with a scan rate of 4.45 $scans.s^{-1}$.

Peaks that were present in blank hexane (control) samples were discarded from analysis in test samples. Tentative identities were assigned to peaks with respect to a Kovats Retention Index analysis and the National Institute of Standards and Technology (NIST) mass spectral library. Mass spectra of peaks from different samples with the same retention time were compared to ensure that the compounds were indeed the same.

The presence of peaks in the chromatograms, and their relative areas were analyzed by nonparametric methods (*Bray-Curtis* cluster analysis and multidimensional scaling (*MDS*) ordination) (Clarke 1993) to ascertain whether any differences could be detected among the samples. The use of relative percentage area for the peaks removes the need for standardizing concentrations from samples where slightly different total mass of components has been extracted from leaf material. Instead, it is the relative amount of each component that is compared, thus ensuring that comparisons can be made among samples of unknown total concentrations.. Each point in the *MDS* plot represents an individual plant, and points that are close together (clumped) correspond to individuals with similar peak composition (presence and abundance). Since they represent relative differences among samples, the axes of an *MDS* plot are dimensionless. *MDS* has been used successfully in previous studies to analyze chromatographic data (e.g., Hayes et al. 2006).

To determine whether clusters of individual plants relating to the taxa investigated were significantly different from each other, we used an analysis of similarity (*ANOSIM*). The *ANOSIM* tests are a range of Mantel-type permutations of randomization procedures, which make no distributional assumptions. These tests depend only upon rank similarities, and thus are appropriate for this type of data. We used a similarity percentages (*SIMPER*) analysis to determine which peaks were the most important in contributing to any differences between groups, and to assess similarity between individuals within each group. The software used for the multivariate analysis was Primer 5 for Windows (V 5.2.9, Clarke and Gorley 2001).

Herbivory Trials—Field Assessment

Two field sites in Queensland (Site I S 26.595° E 151.915°; Site II S 26.101° E 151.623°) containing CT, CCV and CT × CCV were monitored for the incidence (proportion of trees with damage) of characteristic damage caused by *Paropsis atomaria*. Both plantations were established in March 2004 so were the same age at time of sampling (January 2008). Site I comprised a single tree plot design with each family/seedlot represented by one randomly

allocated individual in each of twenty blocks of 100 trees each. One half (i.e., 10 blocks) of the entire site was sampled. Site II comprised 20 lines of 10 trees each. Each plant type was represented by at least 4 such line-plots, each representing a different family/seedlot except CCV which was represented by only one line-plot. Larvae, beetles, and egg batches were present at both sites when censuses were conducted. Each tree was scored for its suitability as a host for *P. atomaria* by recording the presence or absence of *P. atomaria* lifestages. χ^2-pairwise comparisons were made for each site to compare the beetle incidence on each taxon.

Herbivory Trials—Laboratory Bioassays

The same plants used in the chemical and physical foliar attribute studies were used to provide foliage for laboratory bioassays with *P. atomaria*.

Herbivory Trials—Larval (No-Choice) Trials

Field-collected egg batches were held in a controlled-temperature cabinet at 25°C, 16L:8D photoperiod. Unfed (except on egg chorion) neonate larvae were transferred with a soft paintbrush, with larvae from different egg batches divided among treatments to control for possible maternal effects. Eight larvae were placed directly onto test foliage for each replicate (N=11 per taxon). The experiment was conducted in a controlled temperature cabinet at 16°C, 16L:8D. The group size was selected as that above which mortality was constant (Duffy et al. 2008), while 16°C represented the temperature at which mortality was lowest (Nahrung et al. 2008) in previous laboratory studies. A piece of moist filter paper was provided to slow desiccation of treatment foliage. Mortality was recorded, old foliage and filter paper were removed, and fresh filter paper and foliage were added every 3–4 days. Care was taken to ensure that larvae were provided an excess of foliage, such that they never consumed all foliage present. When larvae reached the fourth instar, the replicate was transferred to a larger plastic cage (160×110×35 mm), and upon pre-pupation (dorso-ventral flattening and cessation of feeding) individuals were transferred to separate, numbered, sterilized-soil-filled cells of a plastic modular tray (cell dimensions 20×20 mm). When pupae formed, they were weighed (to nearest 0.001 g) on an electronic balance, and returned to their cell until adult emergence. On emergence, sex was determined under a dissecting microscope (×40), using tarsal differences of the foreleg as the discriminating factor (Baly 1862).

Overall larval mortality, development time and pupal weight were used to assess larval performance on the different foliage types. One-way *ANOVA* was used to compare foliage type among these performance parameters, with proportion data arcsine-square root transformed prior to analysis, and *Fisher's LSD* test used to *post-hoc* test. A *Kaplan-Meier* survival curve (Kaplan and Meier 1958) was plotted for each foliage type, and non-parametric pairwise comparisons were made (P<0.05) to compare larval survival rate on different taxa.

Herbivory Trials—Adult Feeding (Choice) Trials

Field collected beetles were housed in gauze cages and provided with fresh *Eucalyptus cloeziana* foliage prior to use. Twenty-four hours before the start of the trial, beetles were removed from foliage, their sex determined as above, and deprived of foliage until the trial began. For each replicate, one male-female beetle pair was placed into a plastic arena (160×110×70 mm). An apical branch comprising the first 2–4 fully expanded leaves of each foliage type was inserted through holes in the base of the cage into water below. Visually-estimated equivalent biomass was provided of each type in each replicate; twelve replicates were run simultaneously under ambient laboratory conditions. The experiment ran for 3 d, after which adults were removed and the remaining area of each leaf was estimated by placing it under a clear plastic sheet of grid-squares (3×3 mm) and counting the number of squares (to nearest 0.25 of a square) of foliage. The amount of foliage eaten was determined by multiplying the number of grid-squares by 9 mm^2. One-way *ANOVA* was used to detect differences between treatments, and a *Fisher's LSD* test was used to identify where those differences lay. Data for all herbivory trials were analyzed with StatView (V 5.0.1).

Results

Foliar Analyses

Moisture content was the only parameter measured not to differ significantly among different taxa (Table 1). *C. ciriodora* subsp. *variegata* (CCV) had the highest specific leaf weight and lamina thickness, and no leaf hairs (Table 1). In almost all cases, results for the hybrid either lay between that of each parent, or was not different from CT.

The compounds identified in extracts were primarily mono- and sesquiterpenes, as well as some waxes and long-chain hydrocarbons that could not be identified unambiguously. The percentage of individuals in each taxon group from which the component was identified is shown (Appendix 1). Chromatograms produced from hexane extracts of leaves of the three taxa were distinctly different from each other. The composition of components was consistent between replicates / individuals, however, the relative amounts varied among

Table 1 Moisture content, SLW, lamina thickness and glabrousness of *Corymbia citriodora* subsp. *variegata* (CCV), *Corymbia torelliana* (CT) and their hybrid (CT × CCV). The final row shows analysis results, and different letters within columns designate significant differences between taxa

Taxon	Moisture content (%)	Specific Leaf Weight (mg/mm^2)	Lamina thickness (μm)	Leaf surface glabrousness (# trichomes)
CCV	77.2±1.6	0.098±0.007 a	126.2±5.4a	0a
CT × CCV	74.0±1.9	0.052±0.006 b	102.4±4.3b	87.3±25.3b
CT	80.0±0.8	0.054±0.007 b	88.7±3.9c	106.9±23.6b
ANOVA/Kruskall-Wallis results	$F_{2,30}$ = 2.3 P=0.12	$F_{2,30}$ = 13.9 P<0.001	$F_{2,33}$ = 17.4 P<0.001	H_2 = 23.79 P=0.03

taxa. The CT samples were highest for the late-eluting components, the CCV samples highest for the early-eluting components, and the CT × CCV samples either intermediate between the two parental species or showing an additive response (Fig. 1).

In addition to visual chromatographic differences, the samples were statistically distinguishable, and pairwise comparisons demonstrated that all taxa differed from each other (*ANOSIM*: *Global* R=0.814, P=0.001; CCV, CT: R=0.964, P=0.008; CCV, CT × CCV: R=0.834, P=0.008; CT, CT × CCV: R=1, P=0.008). The *MDS* output (Fig. 2), provides a visual representation of the data described by the *ANOSIM*. Each point on the figure represents an individual extract. Points that are close together are more similar, and those farther away are more different.

The *SIMPER* analysis is a measure of the similarities of samples within a defined grouping (in this case taxa studied). All groups have high levels of similarity, but the CCV samples are the most dispersed (Fig. 2).

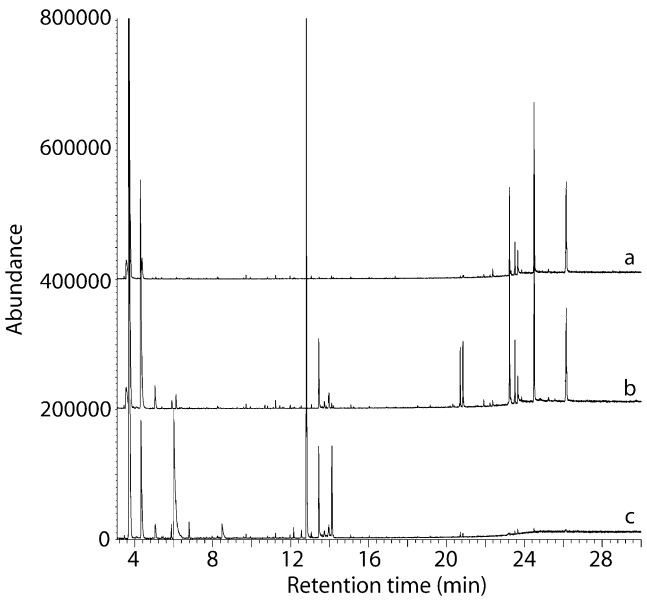

Fig. 1 Chromatograms produced by hexane extracts of *Corymbia* leaves. A typical extract from *Corymbia torelliana* (CT) is shown on top (**a**), a typical extract from *Corymbia citriodora* subsp. *variegata* (CCV) is shown on the bottom (**c**), and a typical extract from the hybrid (CT × CCV) is shown in the center (**b**)

The mean percentage area (± s.e.) under the peak for the most important peaks used to distinguish between the taxa are listed (Appendix 2). These peaks account for over 50% of the total dissimilarity between the groups. The peaks are listed in the table in order of increasing dissimilarity between the groups, i.e., the first peak contributes most to the overall dissimilarity. Retention time is as given in Appendix 1.

Herbivory Trials

The proportion of trees associated with *P. atomaria* did not differ between sites (χ^2 = 3.04, P=0.08) so data from the two sites were combined for subsequent taxa-level analysis. Three-quarters (153/204) of CCV trees were damaged by *P. atomaria*, while less than 30% (67/232) of CT trees exhibited damage symptoms. Sixty-five percent (202/313) of hybrid CT × CCV trees were associated with *P. atomaria.* Again, the hybrid was intermediate between the parental taxa. Pairwise comparisons (Bonferroni-adjusted, P=0.02) demonstrated that each taxon differed significantly from the others (CCV, CT χ^2 = 92.4, P<0.001; CCV, CT × CCV χ^2=6.3, P=0.01; CT, CT × CCV χ^2 = 67.8, P<0.001).

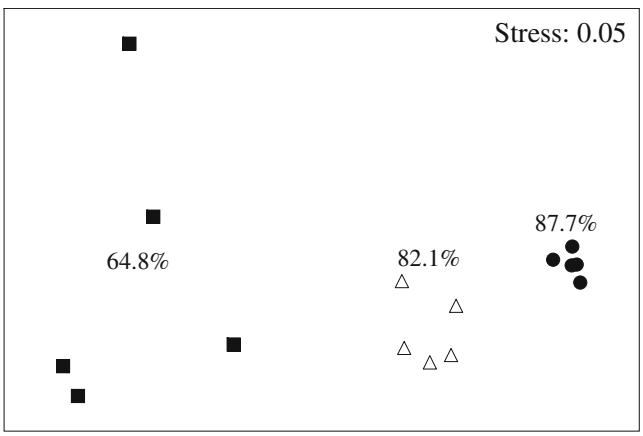

Fig. 2 Two-dimensional MDS ordination of the 15 *Corymbia* extracts including SIMPER measures of average similarity. The plot is based on fourth-root transformed abundances and a Bray-Curtis similarity matrix. Extracts from each taxon cluster separately. Symbols: *Corymbia citriodora* subsp. *variegata*-CCV (■), *Corymbia torelliana*-CT (●), their hybrid-CT × CCV(△)

Table 2 Mean ± s.e. mortality, development time and pupal weights of *Paropsis atomaria* larvae reared on *Corymbia* taxa. Different letters within columns designate significant differences between taxa

Taxon	Larval mortality (%)	Development time (days)	Pupal weight (g)	
			male	female
CCV	84.1±6.8 a	42.6±1.0	0.12±0.01 a	0.18±0.01 a
CT × CCV	54.5±8.3 b	42.6±0.9	0.10±0.01 b	0.14±0.01 b
CT	51.1±6.4 b	40.9±0.5	0.12±0.01 a	0.17±0.01 a

Overall larval mortality (proportion dying before pupation) was highest on CCV (Table 2) (*ANOVA*: $F_{2,30}$ = 8.5, P=0.001), although mortality *rate* differed significantly only between the two parent taxa (Fig. 3) (test statistic = 5.1, P=0.02). Larval development time did not differ according to rearing host (*ANOVA*: $F_{2,21}$ = 1.5, P=0.25), but pupal weight differed depending on sex (males were smaller than females) and natal host taxon (*ANOVA*: sex: $F_{1,36}$ = 70.0, P<0.001; taxa: $F_{2,36}$ = 9.2, P=0.0006, sex*taxa: $F_{2,36}$ = 2.2, P=0.13; Table 2), with hybrids resulting in significantly smaller adults than parent taxa for both sexes.

Feeding occurred on CCV in all replicates, whereas only 40% of replicates of CT and CT × CCV sustained adult feeding damage. The amount (mm^2) of foliage eaten differed among taxa (*ANOVA*: $F_{2,27}$ = 17.12, P<0.001), with CCV the most-preferred host (Fig. 4).

Discussion

Although there is some variability in the response, the hybrid exhibited traits intermediate to the parent species for several of the foliar characteristics investigated, and the feeding preference of *P. atomaria* followed a similar trend in both the laboratory and field (Table 3). The known host, CCV, recorded the highest field incidence of *P. atomaria*, and laboratory trials supported this pattern, with CCV the most-preferred taxon in adult feeding trials. Almost one-fifth of the foliar chemical components identified were detected only in CCV, and it may be one (or many) of these compounds that are involved in host location and selection for this species. The one with the greatest concentration was elemol, a sesquiterpenoid that has been reported previously as a dominant component of CCV leaf chemistry (Asante et al. 2001). Similarly, limonene was present in CCV and the hybrid, but was not detectable in CT. Limonene is a well known attractant for a range of insects, especially beetles (Chenier and Philogene 1989; Miller 2007). The monoterpene α-pinene is a common component of eucalypt leaf chemistry (Asante et al. 2001; Bignell et al. 1998), that varies among the taxa in this study, with high levels in both the host plant and the hybrid, and low levels in CT. α-Pinene is a known kairomone for Colorado potato beetle (*Leptinotarsa decemlineata,* Coleoptera: Chrysomelidae), and attracts the beetle (Panasiuk 1984). The high levels of both limonene and α-pinene in the host taxon and hybrid, and its lack of detectibility in extracts of the non-host plant, may explain some of the variation in behavior observed in our study.

Only two compounds were detectable in the non-host parent (CT) alone, and it is possible that these are repellent to *P. atomaria*. Ohmart (1991) speculated that adult paropsine beetles were repelled or unattracted to the volatile

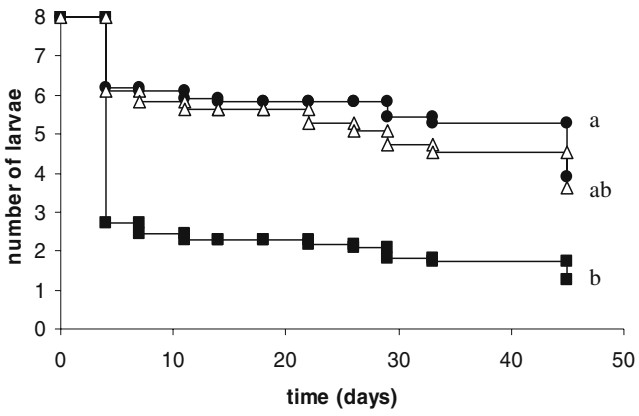

Fig. 3 Kaplan-Meier survival curve illustrating the mortality rate of *Paropsis atomaria* larvae reared on *Corymbia citriodora* subsp *variegata*-CCV (■), *Corymbia torelliana*-CT (●) or their hybrid-CT × CCV (Δ)

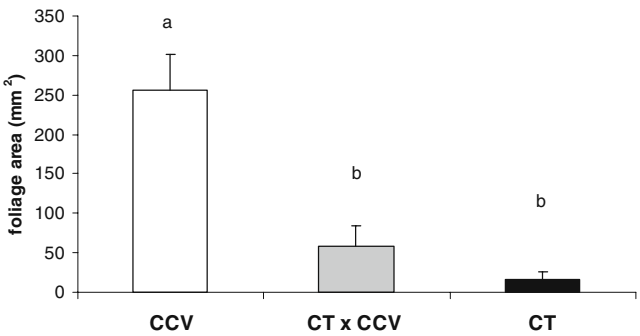

Fig. 4 Mean + s.e. amount of *Corymbia* taxa foliage consumed (mm^2) by one male-female pair of *Paropsis atomaria* adults

Table 3 Summary of foliar attributes and responses of *Paropsis atomaria* to different *Corymbia* taxa: *dark grey* = highest, *white* = lowest, *light grey* = intermediate, *stippled* = no differences. These rankings were statistically significant except where otherwise shown

	CCV	CT × CCV	CT
leaf thickness			
specific leaf weight			
leaf glabrousness			
moisture content		*all equal*	
chemical profile			
field incidence			
adult feeding pref (lab)			
larval mortality rate (lab)	*a*	*ab*	*b*
overall larval mortality (lab)			
larval development time (lab)		*all equal*	
pupal weight (lab)			

compounds produced by juvenile foliage of shining gum, since larvae develop just as well on this foliage type as on adult foliage on which adults feed and oviposit. There often is not a tight linkage between paropsine oviposition preference and larval performance (Carne 1966; de Little and Madden 1975; Baker et al. 2002; Nahrung and Allen 2003), and since larval habitat is determined principally by the placement of eggs by females, oviposition preference is probably a more pertinent indicator of the plant attributes used for host selection.

Assuming that *P. atomaria* adult feeding preference reflects oviposition preference, larvae would rarely encounter CT under field conditions. Larval development time was unaffected by rearing host in these trials, but subsequent pupal mass was significantly lower on the hybrid. Increased pupal weight confers increased adult fecundity in *P. atomaria* (Carne 1966), suggesting a reduction in herbivore fitness arising from larvae developing on the hybrid. This result cannot be attributed to foliar physical characteristics, since the hybrid displayed intermediate or CT-equivalent traits, but there were five chemical components detected only in CT × CCV foliage, including 1,8-cineole, α-cubebene, and β-patchoulene, which may have contributed physiologically to lower pupal weight. 1,8-Cineole and α-cubebene were detected in very low amounts in CCV foliage (Asante et al. 2001), and were probably present in trace amounts in parental foliage here, representing an additive (*sensu* Fritz et al. 1999) effect in the hybrid.

Overall larval mortality was highest on *P. atomaria*'s sympatric host, CCV, and we attribute this to the high SLW and lamina thickness in this species: leaf toughness impedes feeding establishment of neonate paropsine larvae (Ohmart et al. 1987; Larsson and Ohmart 1988; Nahrung et al. 2001); yet, unexpectedly, larvae were able to feed on the densely hairy CT foliage. Leaf trichomes are a deterrent to herbivory in many plant species (Kitamura et al. 2007; Bjorkman et al. 2008). *Paropsis atomaria* larval growth rate also appears unaffected by tannins and other phenolic compounds in host foliage (Fox and Macauley 1977): larvae absorb terpenoids and probably have a metabolic detoxification process for dealing with them (e.g., 86% of ingested 1,8-cineole was absorbed or converted to other compounds) (Ohmart and Larsson 1989).

Although hybrid susceptibility to herbivores is predicted in eucalypts (Dungey and Potts 2003; Potts and Dungey 2004), the hybrid taxon displayed intermediate susceptibility (field incidence) to *P. atomaria* in our study, as it did with respect to possum damage (Scott et al. 2002). Nevertheless, our results suggest a possible chemical basis for host selection behavior and that selection for potential resistance may be possible for this species (see also Henery et al. 2008). Differential resistance to a number of significant insect pests, including eucalypt weevil (Dungey and Potts 2003), sawflies (Jordan et al. 2002), leaf beetles (Raymond 1995; Rapley et al. 2004a), and autumn gum moth (Jones et al. 2002; Rapley et al. 2004b) has been found in other eucalypts.

Although we have detected useful chemical characteristics to distinguish among the taxa in this study, whether any of these are relevant to the host finding/acceptance behavior of *P. atomaria* is unclear. The next step is an examination of electroantennagraphic (EAG) responses of the beetle to the plant extracts, as a method of determining the cues used by beetles. Understanding the preferences of this insect pest will assist in the choice of parental taxa and hybrids used for forestry, as these hardwoods become an ever more important component of the industry.

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Appendix 1

Retention times, kovats retention index and tentative identities of components detected in hexane extracts of *Corymbia* leaves, and the percentage of replicates of each taxon in which the component was identified. Unidentified components are designated "?"

Ret. Time (min)	Kovats Index	Name	CCV	CT × CCV	CT
3.566	901	(*E*)-2-hexenal	0	0	100
3.614	905	*m*-xylene	100	100	0
4.339	956	α-pinene	100	100	100
5.064	999	β-pinene	80	100	100
5.398	1023	1,2,3-trimethyl benzene	80	100	100
5.87	1054	?	60	0	0
5.93	1058	limonene	80	100	0
6.146	1071	3-carene	20	100	100
6.297	1080	1,8-cineole	0	60	0
6.349	1083	?	60	0	0
6.788	1111	?	100	20	40
7.703	1176	?	20	40	0
7.974	1193	?	40	0	0
8.483	1232	?	60	0	0
9.109	1278	?	20	0	0
9.589	1314	hydrocarbon	20	100	100
9.937	1342	methyl naphthalene	80	100	100
11.109	1437	cycloisolongifolene	40	80	0
11.232	1447	4,11,11-trimethyl-8-methylenebicyclo[7,2,0]undec-4-ene	100	100	100
11.443	1465	alloaromadendrene	40	60	0
11.604	1478	α-cubebene	0	60	0
12.12	1523	β-patchoulene	0	20	0
12.16	1527	sesquiterpene	100	40	80
12.537	1561	1,2,3,4,6,8a-hexahydro-1-isopropyl-4,7-dimethylnaphthalene	80	80	0
12.846	1588	elemol	100	0	0
13.46	1646	sesquiterpene	100	100	100
13.622	1662	1,2,6-hexanetriol	60	80	80
13.737	1673	?	80	40	0
13.83	1681	?	0	20	0
13.94	1691	?	80	40	0
13.975	1695	?	80	40	0.
14.143	1711	sesquiterpene	100	0	0
14.207	1718	?	0	80	60
16.042	1906	oxygenated hydrocarbon	80	100	100
16.942	2003	? (N-containing)	60	100	100
17.377	2055	octadecanol	0	20	100
18.517	2192	? (N-containing)	0	40	80
19.171	2275	?	80	20	20
20.664	2472	?	0	40	0
20.713	2478	hydrocarbon	60	100	100
20.851	2496	hydrocarbon	60	100	100
20.885	2501	hydrocarbon	0	20	80
21.92	2633	?	0	100	100
22.253	2674	hydrocarbon	20	100	80
22.385	2690	hydrocarbon	0	100	100
23.252	2794	hydrocarbon	60	100	100

23.315	2802	hydrocarbon	40	80	100
23.524	2826	hydrocarbon	80	100	100
23.74	2851	?	0	20	80
23.834	2862	?	40	0	0
24.519	2939	hydrocarbon	100	100	100
24.833	2974	?	20	0	0
24.868	2978	?	20	0	0
25.006	2993	?	20	20	0
26.149	3115	eicosane	100	100	100
28.568	3357	?	0	0	20
28.896	3388	?	20	0	0
28.916	3390	?	20	0	0

Appendix 2

Mean ± s.e. percentage area under the peak for compounds (identified by retention time) used to distinguish between pairs of taxa (A) CCV vs. CT; (B) CCV vs. CT × CCV; (C) CT vs. CT × CCV

a

Retention time	Mean % area-CCV	Mean % area-CT	% contribution to group dissimilarity
12.846	32.3±7.89	0	6.68
3.566	0	5.51±1.07	4.34
23.252	1.30±1.10	16.6±1.62	4.17
14.143	4.34±1.07	0	4.02
5.93	12.7±5.54	0	3.81
24.519	3.37±2.07	33.8±2.47	3.59
26.149	1.50±0.61	25.0±2.02	3.47
3.614	1.93±1.14	0	2.98
22.385	0	1.03±0.18	2.87
23.524	0.43±0.19	5.14±0.75	2.49
4.339	22.5±8.18	3.33±1.24	2.42
13.46	5.60±1.20	0.21±0.05	2.39
17.377	0	0.44±0.10	2.28
21.920	0	0.38±0.03	2.25
19.171	1.14±0.72	0.01±0.01	2.18
6.146	1.14±1.14	0.34±0.11	2.15

b

Retention time	Mean % area-CCV	Mean % area-CT × CCV	% contribution to group dissimilarity
12.846	32.3±7.89	0	7.70
14.143	4.34±1.07	0	4.64
23.252	1.30±1.10	10.5±0.65	4.07
5.93	12.7±5.54	0.56±0.03	3.29
6.146	1.14±1.14	1.49±0.38	3.17
20.851	0.15±0.06	3.02±0.35	3.01
24.519	3.37±2.07	18.1±1.70	2.97
20.713	0.17±0.07	2.75±0.28	2.86
22.385	0	0.53±0.14	2.76
21.923	0	0.45±0.16	2.71
19.171	1.14±0.72	0.04±0.04	2.45
22.253	0.06±0.06	0.57±0.08	2.43

26.149	1.50±0.61	9.34±0.53	2.40
23.524	0.43±0.19	3.32±0.31	2.36
6.788	0.53±0.13	0.03±0.03	2.37
8.483	1.24±0.53	0	2.28
c			
Retention time	Mean % area-CT	Mean % area-CT × CCV	% contribution to group dissimilarity
3.566	5.51±1.07	0	7.72
3.614	0	4.08±0.59	7.18
4.339	3.33±1.24	30.5±1.24	5.46
5.93	0	0.56±0.03	4.42
13.46	0.21±0.05	4.94±0.75	4.14
17.377	0.44±0.10	0.11±0.11	3.37
23.74	0.39±0.17	0.14±0.14	2.89
12.537	0	0.21±0.07	2.84
20.851	0.38±0.09	3.02±0.35	2.76
20.885	0.24±0.07	0.13±0.13	2.70
20.713	0.39±0.11	2.75±0.28	2.63
11.109	0	0.13±0.05	2.51
26.149	25.04±2.02	9.34±0.53	2.48

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