INFLUENCE OF *CORYMBIA* HYBRIDISATION ON CROWN DAMAGE BY THREE ARTHROPOD HERBIVORES

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NAHRUNG HF, WAUGH R, HAYES RA & LEE DJ. 2011. Influence of *Corymbia* hybridisation on crown damage by three arthropod herbivores. Three common pests (eucalypt tortoise beetle *Paropsis atomaria*, leaf blister sawfly *Phylacteophaga froggatti* and eriophyid mites) of commercial spotted gum plantations were assessed for their crown damage levels on parent and hybrid *Corymbia* taxa (*Corymbia torelliana*, *C. citriodora* subsp. *variegata* and their hybrid) at three common-garden field sites. Damage levels differed significantly between sites for all three herbivore species, and between taxa for eriophyid mites and *P. atomaria*. However, herbivore response to hybridisation only differed for *P. atomaria* between sites, even where damage levels did not. Hybrids exhibited three common patterns of susceptibility relative to parent taxa, being most commonly intermediate to their parents for crown damage (additive resistance pattern), or no difference between parents and hybrids, or with one incidence of dominance for susceptibility.

Keywords: Hybrid, *Paropsis*, Eriophyidae, *Phylacteophaga*, *Eucalyptus*

NAHRUNG HF, WAUGH R, HAYES RA & LEE DJ. 2011. Kesan penghibridan *Corymbia* terhadap serangan silara oleh tiga herbivor artropod. Kumbang *Paropsis atomaria*, lalat gergaji daun *Phylacteophaga froggatti* dan hama eriofid merupakan tiga perosak utama ladang pokok gam komersial. Tahap serangan silara takson *Corymbia* induk dan hibrid (*Corymbia torelliana*, *C. citriodora* subsp. *variegata* dan hibrid kedua-duanya) dinilai di tiga tapak kebun bersama. Tahap kerosakan disebabkan ketiga-tiga herbivor di tapak berlainan berbeza dengan signifikan. Kerosakan juga berbeza antara takson untuk serangan hama eriofid dan *P. atomaria*. Namun gerak balas herbivor terhadap penghibridan hanya berbeza antara tapak untuk *P. atomaria* walaupun tahap kerosakan tidak berbeza. Hibrid mempamerkan tiga corak kerentanan utama berbanding takson induk iaitu kerosakan silara yang nilainya antara nilai induk (corak kerentanan tambahan) atau tidak berbeza dengan induk atau dengan satu insidens kedominan kerentanan.

INTRODUCTION

In Australian tropical and subtropical forestry regions, eucalypt hybrids are increasingly important hardwood taxa, enabling expansion into marginal regions and combining desirable traits from parental species (Lee 2007, Lee et al. 2009). *Corymbia torelliana* (CT) × *Corymbia citriodora* subsp. *variegata* (CCV) hybrids were developed to combine the propagation propensity, frost tolerance and disease resistance of the former species, with good growth, wood quality and tree form of the latter (Lee 2007, Lee et al. 2009, 2010). However, hybrid eucalypts are often more susceptible to herbivory (Whitham et al. 1994,

Dungey & Potts 2003, Potts & Dungey 2004) and support a more diverse herbivore assemblage than do pure species (Morrow et al. 1994, Potts & Dungey 2004).

The response of herbivores to hybrid plants can be influenced by environmental variation (Fritz et al. 1999). Preliminary studies with *Corymbia* hybrids showed that site was more important than taxon in explaining overall arthropod damage in common-garden field trials (Nahrung et al. 2010). A review of over 100 field and common-garden studies of herbivore response to hybrid and parental plants showed approximately

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equal representation of three response models: no difference between hybrids and parents (if parental species and hybrids do not differ in herbivore abundance), additive (parental species differ in their herbivore resistance and hybrids do not differ from the midparental value) and hybrid susceptibility (where susceptibility of hybrids is significantly greater than that of both parents) (Fritz et al. 1999).

We examined herbivore response to hybridisation of CCV with CT at three common-garden field sites. We chose three major folivores in which the field susceptibility and occurrence on CCV were documented (Carnegie et al. 2008 —see Table 1). Three distinct feeding outcomes on leaves were represented (chewed, mined and distorted): the eucalypt tortoise beetle *Paropsis atomaria* (Coleoptera: Chrysomelidae), leaf blister sawfly *Phylacteophaga froggatti* (Hymenoptera: Pergidae) and eriophyid mites *Rhombacus* and *Acalox* spp. (Acari: Eriophyidae) respectively. We discussed heritability patterns according to Fritz et al.'s (1999) models of hybrid resistance to pests (outlined above) and the implications of pest damage for using hybrids in forestry plantations (Lee 2007, Lee et al. 2009)

MATERIALS AND METHODS

The three major herbivores chosen as study organisms were documented pests of CCV (Carnegie et al. 2008) (Table 1). Since each herbivore caused distinct and characteristic damage symptoms on leaves we were able to score the damage.

Eucalypt tortoise beetle *P. atomaria* has a host range of around 20 species of eucalypts (CAB International 2005, Nahrung 2006). Larval and adult stages both ingest the leaf lamina, leading to distinctive scalloped edges on mature leaves and defoliating the upper crown, resulting in a characteristic broom-topped appearance to trees (Carne 1966).

Leaf blister sawfly *P. froggatti* has around 20 recorded hosts, including non-eucalypts (Thumlert & Austin 1994). Larvae feed on mesophyll tissue of older leaves and mining results in patches of dead tissue, generally restricted to the upper leaf surface of maturing foliage (Farrell & New 1980).

Eriophyid mites occur in a multispecies complex of up to seven species on CCV foliage (R Waugh & HF Nahrung, personal observation). Eriophyid mites feed by ingesting soluble nutrients from the epidermal cells of host tissue (Jeppson et al. 1975, Westphal & Manson 1996) leading to chlorosis and necrosis, distorting leaves.

The parent species, CCV and CT, were grown from open-pollinated seeds, while hybrid trees (CT × CCV) were produced by controlled cross-pollination using CT mothers artificially pollinated with CCV fathers. The CT trees were from the same mother trees as many of the hybrid trees planted in the experiments. Selection of parents for inclusion in the hybrid crossing programme was based on phenotypic selection for CCV trees with good tree form and growth that produced buds from which pollen could be collected. The CT mothers were selected on the basis that they were large trees

Table 1   Herbivore species, types of feeding and documented susceptibility and occurrence reported for CCV and CT × CCV

Herbivore species	Life stage responsible for damage	Damage symptom	Susceptibility		Occurrence	
			CCV	CT × CCV	CCV	CT × CCV
Leaf beetle (*Paropsis atomaria*)	Adult and larva	Leaf margin serrated	High	Moderate (Nahrung et al. 2009)	Uncommon	Moderate (Nahrung et al. 2009)
Leaf blister sawfly (*Phylacteophaga froggatti*)	Larva	Internal (mesophyll) damage	High	Unknown	Common	Uncommon
Eriophyid mites (*Rhombacus, Acalox* spp.)	All stages	Leaf discoloration, distortion	High	Low	Common	Uncommon

CCV = *Corymbia citriodora* subsp. *variegata*, CT = *Corymbia torelliana*

Unless indicated otherwise, the susceptibility and occurrence are from Carnegie et al. (2008).

that had sufficiently large bud crop to facilitate the cross-pollination programme. This very low selection intensity of the trees used as parents of the *Corymbia* hybrids tested in these trials was not thought to influence the findings of this study.

Three common-garden field sites located in Queensland (Table 2) each containing CCV, CT and CT × CCV were studied. As the trees were planted in a common garden, uncontrollable factors such as day length, rainfall, etc. were the same for all trees and their impacts consistent across taxa. As the trees at each site were relatively young, the entire crown was visible allowing on-ground assessments. Damage from each herbivore species was characteristic and only damage from the current season was assessed. Each site was assessed for the incidence (proportion of trees infested with each pest) and severity (proportion of crown damaged on infested trees by each pest) on one occasion in late summer/early autumn 2008. A crown damage index (CDI) score (see Stone et al. 2003) was calculated for each pest on each taxon at each site by multiplying incidence by severity. A two-way ANOVA with site and taxon as fixed factors was conducted for each herbivore species following arcsine-square root transformation of CDI scores, with a post-hoc analysis using Fisher's protected least significant difference test when significant differences were detected. Analyses were conducted using GenStat (2008). The resulting patterns were used to categorise herbivore response to hybrids using the resistance models of Fritz et al. (1999).

RESULTS

Site and taxon both significantly affected CDI score attributable to eucalypt tortoise beetle (*P. atomaria*) with a significant interaction between factors (Table 3). Site I had the lowest levels of *P. atomaria* damage; damage levels at Site II were intermediate, with highest levels at Site III (Table 3).

Table 2   Common-garden field site details for taxa trials monitored for pest incidence and severity

Site	Planting date (Months at sample)	Location (Nearest town)	Elevation (m above sea level)	Mean ± SE daily temperature (°C) (Range)	Mean ± SE daily rainfall (mm) (Total)	Original vegetation	Number of trees per taxon
I	17/5/2005 (35)	25.532° S 51.472° E (Mundubbera)	257	20.4 ± 0.3 (8.0 – 29.3)	2.0 ± 0.3 (726)	Open eucalypt forest	CCV < 123 CT × CCV < 315 CT < 186
II	24/3/2004 (46)	26.595° S 51.915° E (Kingaroy)	528	18.3 ± 0.3 (5.5 – 29)	1.8 ± 0.3 (673)	Dry subtropical rainforest	CCV < 141 CT × CCV < 192 CT < 160
III	26/3/2004 (46)	26.101° S 151.623° E (Proston)	459	19.3 ± 0.3 (6.5 – 30)	1.8 ± 0.3 (654)	Open eucalypt forest	CCV < 9 CT × CCV < 53 CT < 45

Temperature and rainfall data refer to the 12-month period prior to sampling.

Table 3   Mean ± SE CDI score for eucalypt tortoise beetle (*Paropsis atomaria*) on *Corymbia* parent and hybrid taxa

Taxon	Site I C	Site II B	Site III A
CCV	0.002 ± 0.001 a	1.825 ± 0.392 a	1.845 ± 0.569 a
CT × CCV	0.002 ± 0.001 ab	3.271 ± 0.547 a	2.117 ± 0.651 a
CT	0.000 b	0.585 ± 0.174 b	2.457 ± 0.599 a
ANOVA results	Site: $F_{2,1215}$ = 120.3, p < 0.001 Taxon: $F_{2,1215}$ = 16.4, p < 0.001 Interaction: $F_{4,1215}$ = 10.9, p < 0.001		
Hybrid pattern	Additive	Dominance–susceptibility	No difference

CCV = *Corymbia citriodora* subsp. *variegata*, CT = *Corymbia torelliana*
Different letters within columns denote means that differ significantly for taxa at each site. Differences between sites are indicated by different upper case letters within the column heading.

CDI scores attributable to leaf blister sawfly did not differ across taxa and Site II had significantly higher CDI scores than the other two sites. The site × taxa interaction was not significant (Table 4).

Site and taxon significantly influenced CDI attributed to eriophyid mites, with the interaction also significant (Table 5). All sites were significantly different from one another. Site I sustained the highest levels of mite damage, Site II, the lowest and Site III, intermediate.

DISCUSSION

Although site plasticity indicated by hybrid response to herbivores is common (Fritz et al. 1999), only one of the species examined here (*P. atomaria*) exhibited different patterns across sites. Despite CDI scores differing between sites, eriophyid mite damage on the hybrid was always intermediate to damage on parent taxa, suggesting an additive inheritance pattern of susceptibility. Leaf blister sawfly damage did not differ on parent taxa compared with the hybrid at any site.

Only *P. atomaria* showed differential response to hybridisation at each site, exhibiting an additive pattern at Site I, dominance for susceptibility at Site II and no difference at Site III: the same three patterns reported in common-garden field trials in Fritz et al.'s (1999) review. This variation in hybrid response pattern would seem not to be due to differential herbivore pressure between sites. However, *P. atomaria* populations were not high enough in this study to have forced beetles to feed upon less-preferred hosts. Indeed, despite CT supporting greater *P. atomaria* larval survival in laboratory trials (Nahrung et al. 2009), it was the least attacked host at two sites. This suggests that adult oviposition preference is not linked with larval performance in paropsine beetles (Carne 1966, de Little & Madden 1975, Baker et al. 2002, Nahrung & Allen 2003) and that *P. atomaria* adult host preference is not necessarily reflected by differential defoliation levels in the field (Henery et al. 2009). Although *P. atomaria* has a broad host range of around 20 eucalypt species (CAB International 2005), CCV, CT and CT × CCV have only become recorded hosts for *P. atomaria* recently (Nahrung 2006, Nahrung

Table 4   Mean ± SE CDI score for leaf blister sawfly (*Phylacteophaga froggatti*) on *Corymbia* parent and hybrid taxa

Taxon	Site I B	Site II A	Site III B
CCV	0.003 ± 0.002	0.476 ± 0.127	0.035 ± 0.035
CT × CCV	0.002 ± 0.001	0.645 ± 0.235	0.019 ± 0.010
CT	0.002 ± 0.001	0.462 ± 0.163	0.088 ± 0.042
ANOVA results	Site: $F_{2,1215} = 43.6$, $p < 0.001$ Taxon: $F_{2,1215} = 0.72$, $p = 0.49$ Interaction: $F_{4,1215} = 0.76$, $p = 0.55$		
Hybrid pattern	No difference	No difference	No difference

Differences between sites are indicated by different upper case letters within the column heading.

Table 5   Mean ± SE CDI score for eriophyid mites on *Corymbia* parent and hybrid taxa

Taxon	Site I A	Site II C	Site III B
CCV	4.891 ± 0.287 a	0.030 ± 0.011 a	3.084 ± 0.799 a
CT × CCV	1.381 ± 0.119 b	0.041 ± 0.032 ab	0.675 ± 0.117 b
CT	0.000 c	0.000 b	0.000 c
ANOVA results	Site: $F_{2,1215} = 246.7$, $p < 0.001$ Taxon: $F_{2,1215} = 303.0$, $p < 0.001$ Interaction: $F_{4,1215} = 127.3$, $p < 0.001$		
Hybrid pattern	Additive	Additive	Additive

Different lower case letters within columns denote means that differ significantly for taxa at each site.
Differences between sites are indicated by different upper case letters within the column heading.

et al. 2009) and hence may not yet have been subjected to selection pressure for avoidance or preference on these taxa, and this may be reflected in the variable patterns seen here.

Previous work with this *Corymbia* parent–hybrid system (Nahrung et al. 2009) demonstrated significant foliar physical and chemical differences between CT, CCV and their hybrid, which might have influenced the feeding patterns observed. For example, CT juvenile foliage (maintained on most trees throughout life) is densely hairy (Nahrung et al. 2009); leaf trichomes may influence feeding by eriophyid mites and reduce the effectiveness of their natural enemies (Duso et al. 2010). CT was resistant to eriophyid mites at all sites in this study, while CT × CCV exhibited intermediate susceptibility and intermediate leaf trichome density. Whether this directly impacted mite feeding is unknown.

Leaf blister sawfly larvae feed and pupate in the mesophyll between the upper and lower epidermis. Leaf mining was positively correlated with thinner leaves and higher specific leaf area (SLA) (Sinclair & Hughes 2008), but these traits did not influence phytophagy patterns in this study. Leaves of CCV were significantly thicker and had significantly lower SLA than the other two taxa (Nahrung et al. 2009), but leaf blister sawfly damage did not differ between the three. Leaf blister sawflies are highly polyphagous within the eucalypts, being associated with several genera and species (Mayo et al. 1997, Loch et al. 2004, Carnegie et al. 2008) which also likely differ in these foliar physical traits. Foliar chemical traits and their heritability and influence on herbivory in this system are reported elsewhere (Nahrung et al. 2011) but again show variation in response by the herbivores. Leaf blister sawfly shows no pattern with respect to chemical differences, while both the eucalypt tortoise beetle and the eriophyid mites follow monoterpenes levels (Nahrung et al. 2011).

The previous patterns of susceptibility and occurrence reported for these species by Carnegie et al. (2008) (Table 1) were generally supported here, although leaf blister sawfly did not reach as high damage scores as the other two pests on CCV. Site was more important than taxon in explaining overall damage scores in a similar study with a broader range of taxa (Nahrung et al. 2010) and this study confirmed those findings. Plant taxa also influenced crown damage scores and

the way that these scores varied was different between herbivore species. Site influence is not consistent between pest taxa with each herbivore species responding differently to site effects. The exact nature of the differences between sites is as yet unclear but appears to be unrelated to rainfall, temperature, elevation or original vegetation. Understanding these as yet undetermined factors has implications for future plantation development. The hybrid susceptibility hypothesis is generally unsupported by our results, supporting Lee's (2007) and Lee et al.'s (2009) assertion that *Corymbia* hybrids may provide germplasm that is less favoured by pests than CCV. However, the risk of pest outbreaks in even-aged, hybrid monoculture (and particularly clonal) stands may still be underestimated. To minimise the risk associated with deploying the *Corymbia* hybrids, it is therefore suggested that a minimum of six to eight unrelated *Corymbia* hybrid clones or a similar number of unrelated *Corymbia* hybrid families be deployed in commercial hardwood plantations. While this is at the lower end of the scale for both family and clonal forestry suggested by White et al. (2007), it allows for increased genetic gains to be operationalised in commercial plantations (as a result of the higher selection intensity) and should provide sufficient variation to combat the risks associated with pest and disease incursions. As the plantation area planted with *Corymbia* hybrids expands, the number of clones or families deployed can also be revised to further reduce risk.

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