

Susceptibility of some *Eucalyptus* species and their hybrids to possum damage

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Summary

Common brushtail possums (*Trichosurus vulpecula*) are a significant vertebrate pest of eucalypt plantations in Tasmania; their browsing damage can cause loss in growth, reduced seedling survival and deformities. Possum damage could therefore become a serious problem in Australia's rapidly expanding eucalypt plantations. In addition, expansion of plantation areas is projected to include drier zones, where inter-specific eucalypt hybrids may play an important role. However, hybrids are currently being developed with little knowledge of their resistance to pests. This study examined the susceptibility to browsing by common brushtail possums of a range of eucalypts (*Eucalyptus bicostata*, *E. globulus*, *E. gunnii*, *E. nitens*, *E. morrisbyi* and *E. ovata*) and their F₁ hybrids in four separate field trials in Tasmania.

The Tasmanian endemics *E. gunnii* and *E. morrisbyi* were extremely susceptible to browsing whereas the other four species were relatively resistant. Within *E. globulus*, significant differences in damage between provenances were also detected. Field damage on interspecific F₁ hybrids was generally intermediate in crosses between susceptible and resistant eucalypt species. While the exact degree of susceptibility varied, crossing a relatively resistant species with a highly susceptible species resulted in a significant increase in the susceptibility of the F₁ hybrid compared with that of the resistant species. Only the hybrids between the two major plantation species *E. nitens* and *E. globulus* were significantly more susceptible to browsing than either the *E. nitens* or *E. globulus* controls, which were both relatively resistant. In practical terms, the present study indicated that possum susceptibility is an important factor to consider when investigating the potential of pure species and their hybrids for commercial use.

Keywords: wildlife; damage; *Eucalyptus*; inter-specific hybrids; possums; *Trichosurus vulpecula*; Tasmania

Introduction

Common brushtail possums (*Trichosurus vulpecula*) are widely distributed in Tasmania (Statham 1983; Kerle 1984) where they

have been reported damaging managed native eucalypt forests (Cremer 1960; Mollison 1960; Gilbert 1961; Cremer 1969) and eucalypt plantations (Bulinski 1999; Bulinski and McArthur 1999; Scott *et al.* 2002). Possums have also become a serious pest of native forests and exotic plantations following their introduction into New Zealand (Fitzgerald 1978, 1981, 1984; Fitzgerald and Wardle 1979). Browsing damage from possums may not only impact on seedling survival and growth (Bulinski and McArthur 1999; Scott *et al.* 2002), but also branch breakage in mature trees may result in poor stem form (Volker and Orme 1988). Such form deformities may have little economic impact on logs harvested for pulpwood, but may have a significant effect on timber recovery.

With the increase in plantation forestry in Australia, there is increasing interest in understanding the patterns of susceptibility of eucalypts to the common brushtail possum (McArthur and Turner 1997; Scott *et al.* 2002). Tree and stand susceptibility to browsing by these mammals may be affected by environmental and silvicultural factors, such as plant nutritional status (Landsberg 1987; McArthur and Turner 1997). However, large genetically-based differences in susceptibility have also been reported between (McArthur and Turner 1997; Scott *et al.* 2002) and within (Volker and Orme 1988; Cannon 1993; O'Reilly-Wapstra *et al.* 2001) eucalypt species. Such differences have been demonstrated from uncontrolled browsing in experimental field trials as well as from feeding trials with captive animals (e.g. Scott *et al.* 2002).

In addition to possum damage on pure species, the response to brushtail possums by hybrid eucalypts has recently come under increased scrutiny (Scott *et al.* 2002). Eucalypt hybrids have been widely used in other countries (see Dungey 1999; Dungey *et al.* 2000a), and there has been renewed interest in the use of eucalypt hybrids in Australian plantations (Dale *et al.* 2000; Robson 2000; cf. Potts *et al.* 2000; Tibbits 2000). However, Australian plantations are subject to invasion by pests and diseases from native eucalypt forests, and the susceptibility of eucalypt hybrids to such pests and diseases is a key issue (reviewed in Fritz *et al.* 1999; Whitham *et al.* 1999). For example, natural and artificial hybrids between *E. amygdalina* and *E. risdonii* supported greater numbers of insect taxa than either of the pure host species (Whitham *et al.* 1994; Dungey *et al.* 2000b). Although the responses of individual insect taxa varied between these man-

made F_1 eucalypts hybrids (Dungey *et al.* 2000b), there was a trend for insect species that were specific to one or other host species to occur on the hybrids at levels that were intermediate or comparable to those on the more susceptible host. In contrast, generalist insect taxa that were found in equal numbers on the host species either exhibited no response to the hybrid hosts or occurred in numbers that surpassed the populations observed on either pure host species (Dungey *et al.* 2000b). Whether these trends, determined to be significant by Dungey *et al.* (2000b), are ubiquitous and extend to other eucalypt pests and hybrid systems is unclear at present.

The present study investigated the browsing damage caused by the common brushtail possum to determine whether such trends were also significant in vertebrates. The host preferences of this possum in Tasmania were investigated through determining the genetic differences in possum browsing susceptibility in six *Eucalyptus* species and their F_1 hybrids from four experimental field trials. These species included the two most important plantation eucalypts in temperate Australia, *E. globulus* and *E. nitens* (Tibbits *et al.* 1997), the closely related *E. bicostata*, and three Tasmanian native species, *E. ovata*, *E. gunnii* and *E. morrisbyi*. Differences in host preference between and within these species will also indicate whether more resistant genotypes of these major plantation species can be selected for deployment into high-risk areas.

Methods

Four experimental field trials were assessed for possum damage. Three (Trials 1, 3 and 4) were located near Ridgley, in north-western Tasmania (latitude 41°09'S, longitude 145°46'E); the other near Tyenna (latitude 146°39'42"S, longitude 42°43'35"E) in southern Tasmania. The trials were established to study the relative growth of hybrids compared with pure species controls and differed in their designs. The assessment of possum damage was opportunistic and followed the uncontrolled browsing of these trials by wild possums.

Trial 1

Trial 1 was established by CSIRO Division of Forestry and North Forest Products, at West Ridgley in north-western Tasmania. In brief, the trial contained progeny from an incomplete 8×26 *E. globulus* factorial mating design, an incomplete 10×10 *E. nitens* half-diallel mating design, an incomplete 6×14 *E. nitens* \times *E. globulus* F_1 hybrid factorial mating design and open-pollinated progeny (Table 1, for full details see Volker *et al.* 1994; Hodge *et al.* 1996; Dungey *et al.* 1997). The *E. globulus* parents were from the Taranna (T) and King Island (K) provenances (see Dutkowski and Potts 1999). The factorial included both intra- (T, K) and inter-provenance (T \times K, K \times T) crosses. All the *E. nitens* parents were from the Toorongoo provenance (Pederick 1979) and were growing in seed orchards or in plantations in north-western Tasmania. Open-pollinated (OP) progeny of all the males (native stand OP) and females (seed orchard OP) were also included. The *E. nitens* \times *E. globulus* F_1 hybrids included *E. globulus* males from both the King Island and Taranna provenances. All males used in the *E. nitens* \times *E. globulus* hybrid factorial were also used in the *E. globulus* factorial and all females were used in the

Table 1. The number of full-sib families (common female and male) and individuals of each cross-type planted in field Trial 1 near West Ridgley. Provenances are in brackets following species names. *E. globulus* pooled contains the *E. globulus* inter- and intra-provenance crosses between Taranna (T) and King Island (K); (T, K, T \times K and K \times T).

Cross-type	Number of families	Number of individuals
<i>E. globulus</i> pooled	168	3486
<i>E. globulus</i> (King Island)	28	579
<i>E. globulus</i> (Taranna)	55	1096
<i>E. nitens</i> (Toorongoo)	36	714
<i>E. nitens</i> \times <i>E. globulus</i>	43	665

Table 2. The number of full-sib families (common female and male) and number of individuals planted per family for each cross-type in Trial 2 at Tyenna, south-eastern Tasmania.

Cross-type	Number of families	Number of individuals
$F_1 \times F_1$ (F_2)	22	169
$F_1 \times E. globulus$	23	158
$F_1 \times E. nitens$	12	85
<i>E. globulus</i> \times F_1	3	23
<i>E. globulus</i> \times <i>E. globulus</i>	20	127
<i>E. nitens</i> \times F_1	15	107
<i>E. nitens</i> \times <i>E. globulus</i>	19	77
<i>E. nitens</i> \times <i>E. nitens</i>	19	107
Grand total	133	853

E. nitens half-diallel. In addition to the control-cross and open-pollinated material, some unpedigreed *E. bicostata* and *E. bicostata* \times *E. globulus* F_1 hybrids were included in the trial (four and six full-sib families respectively). The trial originally contained 6000 trees and was based on an alpha lattice design (Patterson and Williams 1976). Each of the four replicates of 1500 trees comprised 15 incomplete blocks, with the *E. nitens*, *E. globulus* and the hybrids allocated to separate sub-blocks to avoid direct competition between cross-types. The small number of *E. bicostata* progeny (four families) were included with *E. globulus* and the *E. bicostata* \times *E. globulus* hybrids (six families) with the *E. nitens* \times *E. globulus* F_1 hybrids. Each incomplete block comprised 20 line plots of five trees and the spacing between trees was 3 m \times 4 m.

Trial 2

The Tyenna trial contained pure *E. globulus* (G), *E. nitens* (N), and F_1 and advanced-generation *E. nitens* \times *E. globulus* full-sib families (Table 2). The advanced-generation hybrids included F_2 progeny derived from crossing unrelated F_1 s and backcrosses to *E. globulus* (BCG) and to *E. nitens* (BCN). These crosses were undertaken using parents selected only for flower abundance and accessibility in Trial 1. Each female was crossed with several random samples of *E. nitens*, *E. globulus* or F_1 pollen unrelated to the female to generate populations of single paired-crosses with pedigree links maintained both within and between cross-types. The F_1 and *E. globulus* cross-types were supplemented with additional families of the same cross-type provided by North Forest Products, derived by crossing parents selected for growth and wood properties.

Table 3. Full-sib crosses included in Trial 3. Numbers indicate the number of individuals of each cross-type planted within the trial. The numbers of parents involved are detailed in the text.

Female	Male			
	<i>E. globulus</i>	<i>E. gunnii</i>	<i>E. morrisbyi</i>	<i>E. ovata</i>
<i>E. globulus</i>	360	6		
<i>E. gunnii</i>	37	52		
<i>E. morrisbyi</i>	54	10	33	46
<i>E. ovata</i>	143		21	114

Trial 2 was planted in October 1995 and consisted of seven replicates, with families planted in single-tree plots that were completely randomised within replicates. Spacing was 2.5 m between plants within a row and 3 m between rows.

Trial 3

Progeny from intra- and inter-specific hybrid crosses of *Eucalyptus* were established in an experimental field trial near West Ridgely in September 1988. The main species incorporated in this trial were *E. globulus* (parents originating from Hobart, Tinderbox, King Island and Bruny Island), *E. ovata* (12 parents from near Cygnet and south of Hobart), *E. gunnii* (eight parents from Shannon Lagoon and Snug Plains) and *E. morrisbyi* (two parents from Calverts Hill). The crosses within and between these species are given in Table 3. Pure species controls comprised a mixture of open-pollinated progeny and controlled crosses.

The trial was divided into five replicates, each divided into five blocks to avoid competition between species differing markedly in growth rates. Each block contained three-tree linear plots of each family. The *E. globulus* controlled cross and open-pollinated families comprised one block, and those of *E. ovata* another. The F_1 hybrids and other parental controls were allocated to a third block. The remaining two blocks contained self-pollinated progeny of either species that were not included in this study. The arrangement of the blocks, within replicate and families within blocks was random. Spacing between trees was 3 × 3 m. Further details are given in Lopez *et al.* (2000). At the time of assessment the trees were about four years old.

Trial 4

This trial was planted adjacent to Trial 3 and was established by North Forest Products in May 1988. The trial contained eight replicates, with families arranged in five-tree linear plots and spacing between trees of 3 m × 3 m. Within each replicate, families were randomised, except for the fact that all the *E. nitens* families were grouped into a sub-block within each replicate to avoid problems of competition with the hybrids and open-pollinated controls of the pollen parents. The trial contained *E. nitens* × *E. globulus* (eight families and 64 individuals) and *E. nitens* × *E. gunnii* (nine families and 129 individuals) F_1 hybrids derived from crossings amongst five *E. globulus* males and five *E. gunnii* males and seven *E. nitens* females. The pure species controls included open-pollinated progeny from four of the five *E. globulus* parents ($n = 42$) and six *E. gunnii* parents ($n = 113$). The *E. nitens* controls were eight full-sib families ($n = 164$) derived from crossings amongst the same *E. nitens* parents used to produce the F_1 hybrids. Six of the *E. nitens* parents used in the crossings were

from the Toorongo, Northern New South Wales, Southern New South Wales, Errinundra and Macalister provenances and five parents were from an unknown provenance. One of each of the four *E. globulus* parents used originated from the provenances Geeveston, Leprena, Otways and North Flinders Island (see Volker and Orme 1988). The *E. gunnii* parents represented included two parents from Pensford, and four from near Great Lake on the Central Plateau, Tasmania. About 1300 trees were planted within the trial, although a number of deaths had occurred at the time of assessment.

Damage assessment

Following the observation of possum damage in Trials 1, 3 and 4, damage on individual trees was assessed using a six-point ordered scale: (1) no damage or very little damage visible; (2) some damage, a few eaten leaves and/or scratch marks on trunk; (3) damage immediately obvious, 20% < damage < 50% of crown foliage removed, scratch marks evident on trunk; (4) damage immediately obvious, but >50% and <65% damage to crown, scratch marks evident on trunk; (5) damage fairly serious, at least 65% of leaf material lost, but less than 80%, leaf material still obvious in the crown and scratch marks present on trunk, some broken branches may be present; (6) serious damage, with at least 80% of leaf material lost, scratch marks on trunk very obvious and branches usually broken in the canopy. Examination of scats demonstrated that the possum species responsible for the damage was *T. vulpecula*. No scats resembling those of the common ringtail possum (*Pseudocheirus peregrinus*) were found. Possum damage is quite distinctive and easily recognised by broken branches, scratches on the trunk and the way the leaf material is removed (Landsberg 1987). Possum damage was scored in Trial 1 and Trial 4 in September 1993 and in Trial 3 in November 1992.

The advanced generation hybrid trial at Tyenna (Trial 2) was scored for possum damage in August 1998 and July 1999, approximately three and four years after planting. Damage at Tyenna was based on the classes 0, 5, 10, 20, 40, 60, 80 and 100 percent defoliation in the top 1.5 m of the canopy. Due to the presence of some insect defoliation in the trial, damage in the lower classes (5% and 10%) was difficult to assess, and insect and possum damage scores at this low level may be confounded.

Data analysis

Due to the lack of normality of all the possum damage data for Trials 1, 3 and 4 ($P < 0.001$, Shapiro–Wilk statistic), arithmetic means of cross-types were determined for graphical presentation only, using the MEANS procedure in SAS (SAS Institute 1990). Testing for differences between cross-types was undertaken using the CATMOD procedure in SAS (SAS Institute 1990) using the number of trees in each damage category (1 to 6) within each cross-type. Cumulative logits were chosen, as the data were an ordered response. Contrasts between cross-types are given as chi-squared values (Wald statistic) and their probabilities. All 94 individuals of *E. bicostata* in Trial 1 had possum damage scores of 1. This lack of variation meant that cross-type comparisons involving *E. bicostata* in CATMOD were not possible and differences were therefore tested using pair-wise contrasts in the NPAR1WAY procedure (SAS Institute 1990).

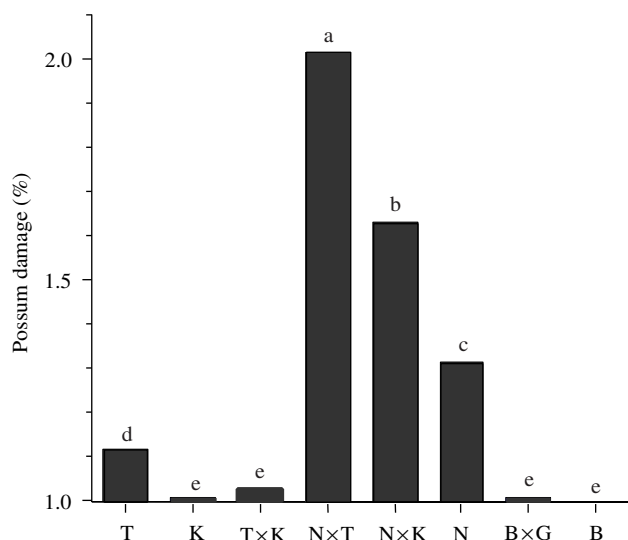


Figure 1. Mean possum damage score on the different cross-types within experimental field Trial 1. Damage was assessed on a 1 to 6 scale with the highest damage being 6. Cross-types included the Taranna (T) and King Island (K) provenances of *E. globulus*, inter-provenance crosses within *E. globulus* (T x K, incorporating both T x K and K x T crosses), *E. nitens* (N), interspecific F₁ hybrids between *E. nitens* and *E. globulus* (N x T and N x K), *E. bicostata* (B) and interspecific F₁ hybrids between *E. bicostata* and *E. globulus* (B x G). Different letters above the cross-types (except *E. bicostata*) represent significant differences at the 0.05 level of probability, given by the chi-squared test (Wald statistic) using the CATMOD procedure of SAS (SAS Institute 1990). Cross-type comparisons involving *E. bicostata* were determined using the NPAR1WAY procedure of SAS (SAS Institute 1990).

Data residuals from the Tyenna trial (Trial 2) were normalised after transformation (square-root) and therefore a one-way model was fitted to test the effect of the six cross-types (G, BCG, F1, F2, BCN and N) using PROC MIXED of SAS (SAS Institute 1990). Least-squares family means were also determined for percentage of foliage lost through possum feeding and the significance of the difference between transformed means was tested using the Tukey–Kramer adjustment.

Results

Host preference

Trial 1

Despite relatively low overall levels of possum damage in Trial 1, significant differences in susceptibility between cross-types were still detected (Fig. 1). The Taranna (T) provenance of *E. globulus* had significantly higher possum damage than the King Island (K) provenance. The mean damage level on the inter-provenance hybrids (T x K and K x T) was intermediate, but they were not significantly more damaged than the less susceptible provenance. The Toorongoo *E. nitens* was more damaged than the *E. globulus* provenances. In contrast to the inter-provenance hybrids, however, the inter-specific *E. nitens* x *E. globulus* F₁ hybrids (N x T and N x K) clearly had greater possum damage than either of the parental taxa. Consistent with the ranking in pure species combination, the interspecific F₁ hybrids involving *E. globulus*

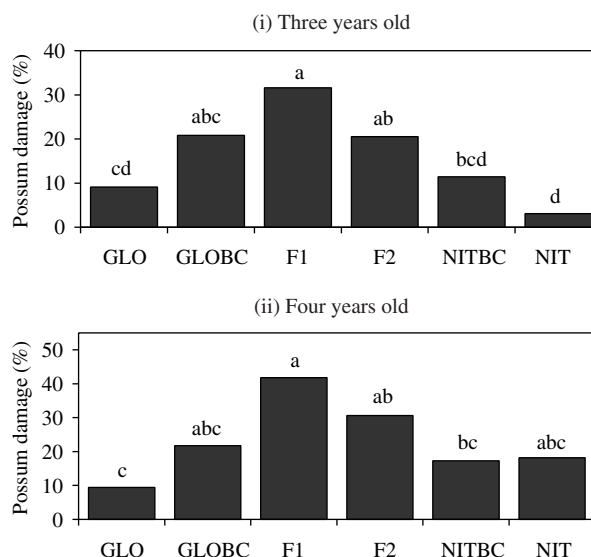


Figure 2. The mean percentage of the new season's foliage in the upper canopy lost through possum browsing for the different cross-types in Trial 2, at three (i) and four (ii) years of age. Means were calculated from untransformed data, and different letters above the cross-types represent significant Tukey–Kramer differences at the 0.05 level of probability based on transformed data. F₁ and F₂ represent the first and second generation *E. nitens* x *E. globulus* hybrids respectively. NIT represents *E. nitens*, GLO *E. globulus*, GLOBC F₁ hybrids backcrossed to *E. globulus*, and NITBC F₁ hybrids backcrossed to *E. nitens*.

males from the Taranna provenance (N x T) were significantly more susceptible than those involving males from King Island. Damage was low on *E. bicostata* and the *E. bicostata* x *E. globulus* F₁ hybrids and was not significantly different from damage on the King Island provenance of *E. globulus* or the *E. globulus* inter-provenance hybrids (T x K).

Trial 2

The hybrids in the Tyenna trial were nearly always more damaged than the pure parent taxa, at both three and four years of age (Fig. 2). The F₁ hybrid between *E. globulus* and *E. nitens* was the most damaged in both years of browsing. The F₂ progeny was more damaged than all taxa but the F₁ at age four years, and equivalent to the backcross to *E. globulus* at age three years. The backcross to *E. globulus* was always more damaged than the *E. nitens* backcross, although this difference was not significant. The pure taxa *E. nitens* and *E. globulus* were always among the least damaged host cross-type in the trial at both ages of assessment and did not differ significantly in their susceptibility.

Trial 3

Of the four species examined in Trial 3, *E. globulus* had significantly lower damage than all other cross-types, whereas the two Tasmanian endemics, *E. gunnii* and *E. morrisbyi*, were highly susceptible (Fig. 3). The general order of damage levels recorded was: *E. gunnii* = *E. morrisbyi* > *E. ovata* > *E. globulus*. All hybrids but one had intermediate damage levels when compared with their two parent species. Only the F₁ hybrids between the least susceptible species *E. globulus* and *E. ovata*

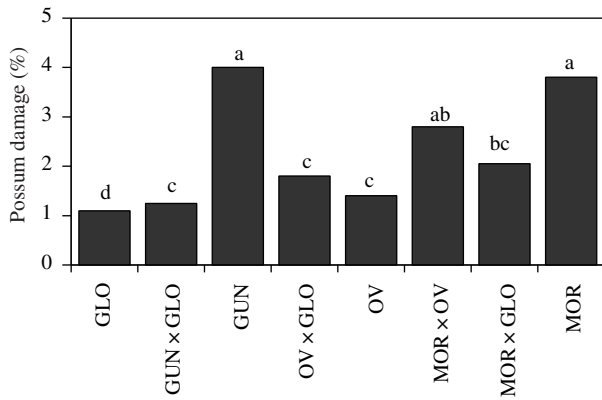


Figure 3. Mean possum damage on the cross-types well represented in Trial 3. Different letters above the cross-types represent significant differences at the 0.05 level of probability. The pure species controls comprised both open and controlled-cross progenies and reciprocal crosses have been combined in the *E. gunnii* × *E. globulus* and *E. morrisbyi* × *E. ovata* cross-types. GLO represents *E. globulus*, GUN × GLO *E. gunnii* × *E. globulus* hybrids, GUN *E. gunnii*, OV × GLO *E. ovata* × *E. globulus* hybrids, OV *E. ovata*, MOR × OV *E. morrisbyi* × *E. ovata* hybrids, MOR × GLO *E. morrisbyi* × *E. globulus* hybrids, MOR *E. morrisbyi*. Differences between cross-types that appear large but are not statistically significant are probably due to the sample size of the cross-types involved (see Table 3).

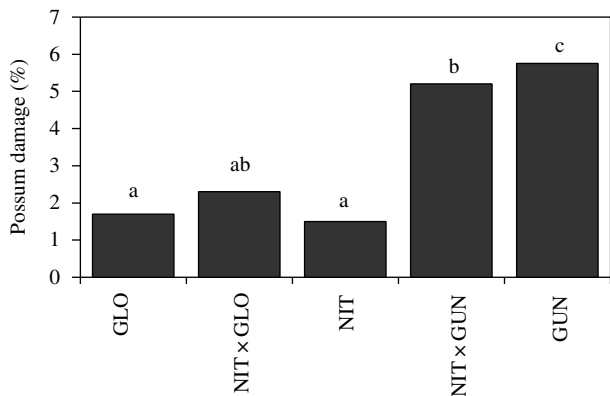


Figure 4. Mean possum damage on the cross-types well represented in experimental Trial 4, *E. globulus* (GLO), *E. nitens* × *E. globulus* (NIT × GLO), *E. nitens* (NIT), *E. nitens* × *E. gunnii* (NIT × GUN) hybrids and *E. gunnii* (GUN). Different letters above the different cross-types represent significant differences at the 0.05 level of probability (chi-squared test, Wald statistic).

had an average damage level higher than both parents, but they were not significantly more damaged than *E. ovata*.

Trial 4

As with Trial 3, *E. gunnii* was the taxon most damaged by possums in Trial 4 (Fig. 4). The *E. nitens* × *E. gunnii* F₁ hybrids had intermediate levels of possum damage and were significantly different from both parental controls. There was no significant difference in the damage on the pure species *E. nitens* and *E. globulus* in this trial. The *E. nitens* × *E. globulus* F₁ hybrids were again more damaged than either parent, but, in contrast to both Trials 1 and 2, the difference was not significant.

Discussion

The two Tasmanian endemics *E. morrisbyi* and *E. gunnii* were found to be extremely susceptible to browsing by brushtail possums. This confirmed prior observations that the susceptibility to possum damage of the rare and endangered *E. morrisbyi* is a major problem in establishment of *ex situ* conservation plantings (Potts unpub. data). The major plantation species *E. nitens* and *E. globulus* were relatively resistant to browsing damage by comparison. *E. ovata* similarly had low levels of possum damage. Differences between the two commercial species *E. globulus* and *E. nitens* were small, although *E. nitens* appeared to be more susceptible than *E. globulus* in one trial. Such a difference was not detected in the other field trials nor in other studies (McArthur and Turner 1997; Scott *et al.* 2002). As both species exhibit significant genetic variation in susceptibility, the trial results may simply be a reflection of the families represented in the trial.

Within the species *E. globulus*, we also detected significant differences in damage between provenances. While the difference was relatively subtle between the two provenances represented (Taranna and King Island) this difference was evident in both the pure species and hybrid progeny. In addition, because this difference was detected in a fully randomised field trial, it must also have a genetic basis. Other *E. globulus* provenances have been shown to have greater possum susceptibility than the provenances represented here (Volker and Orme 1988; O’Reilly-Wapstra *et al.* 2001). Therefore, genetic diversity in susceptibility to possum damage clearly exists within this species and could be further exploited. Variation within *E. nitens* also occurs at the provenance (O’Reilly-Wapstra *et al.* 2001) and family level (Cannon 1993; Dungey 1996). However, this variation appears minor compared to the variation induced by hybridisation of either of these plantation species with more susceptible eucalypt species.

Damage on interspecific F₁ hybrids was generally intermediate in crosses between susceptible and resistant eucalypts (e.g. *E. morrisbyi* × *E. ovata*, Fig. 3). However, while remaining intermediate, hybrids were also damaged at a similar level to the most resistant parent (e.g. *E. gunnii* × *E. globulus*, Fig. 3) or not significantly different from damage incurred by the more susceptible parent (e.g. *E. nitens* × *E. gunnii*, Fig. 4). However the relative susceptibility of the parent taxa and hybrids may vary between different field trials. For example, in the study of Scott *et al.* (2002), the F₁ hybrids between *E. globulus* and *E. gunnii* were found to have intermediate levels of field damage, but in choice and non-choice laboratory feeding trials, foliage browsing was more similar to the more susceptible *E. gunnii*. In the present study, the average browsing damage on the *E. gunnii* × *E. globulus* F₁ was more similar to the resistant *E. globulus* than to *E. gunnii*. Such differences in field browsing may well be a reflection of the magnitude and period over which browsing occurs and the quantity and quality of alternate food sources. Possums may initially feed on the more susceptible species, moving to taxa that are less preferred as the supply of foliage of the more susceptible species is exhausted. In such cases, trial design and adjacent alternative food sources may affect the relative browsing levels observed in the field. For example, the *E. gunnii* × *E. globulus* hybrids in Trial 3 were grown in the same block, within each replicate, as the highly susceptible *E. gunnii* and

E. morrisbyi controls, whereas each cross-type was confined to a separate block in the trials assessed by Scott *et al.* (2002). Furthermore, Trial 3 was also surrounded by pasture, whereas those trials assessed by Scott *et al.* (2002) were surrounded by plantation *E. nitens*. Nevertheless, regardless of the exact degree of intermediacy observed in the field, in all cases where a resistant species was crossed with a highly susceptible species, this resulted in an F_1 hybrid with greater susceptibility than the resistant species.

There were two cross-types where the F_1 hybrid had greater damage than both parent species: *E. nitens* × *E. globulus* and *E. ovata* × *E. globulus*. In these cases the parental taxa were relatively resistant to browsing. It was only in the case of the *E. nitens* × *E. globulus* hybrid, however, that this difference was significant, i.e. Trial 1 and both seasons of assessment in Trial 2. It was initially thought that the susceptibility of the F_1 hybrids in Trial 1 could simply be a consequence of their higher early mortality and thus the increased space between trees in the F_1 sub-block. This was negated, however, by the fact that the hybrids exhibited consistent susceptibility across two years in Trial 2, where cross-types were growing as single-tree plots in a completely randomised block design. Not only was the pattern consistent when the cross-types were fully randomised in the trial design (Trial 2), but it was consistent across years (Fig. 2). Therefore, although these trials were not specifically designed to test the difference in possum browsing, the consistent browsing of the *E. nitens* × *E. globulus* hybrids across trials with different designs would argue that this result is a reflection of true susceptibility. Hence it appears that crossing two relatively resistant species *E. nitens* and *E. globulus* resulted in a hybrid that was genetically more susceptible to possum damage than either parent taxa. This hybrid susceptibility diminished in the F_2 and backcross generations, but they nevertheless tended to remain more susceptible than the parent species *E. nitens* or *E. globulus*. However, in order to exclude conclusively any other causes for browsing preferences, multiple-choice feeding experiments are required and are planned.

The patterns of average response of the brushtail possums to hybrid eucalypt hosts observed in the present study conforms to the general trends reviewed by Fritz *et al.* (1999) and observed by Dungey *et al.* (2000b) for a range of insect taxa occurring on eucalypts. Their results indicated that when susceptible and resistant hosts were crossed, the susceptibility of the F_1 hybrids tended to be intermediate to varying degrees or similar to the more susceptible parent. In contrast, crossing host taxa that were equally susceptible or resistant resulted in F_1 hybrids that were either as susceptible as the parental taxa or more susceptible. When hybrids were tested as a group rather than as individual trees, no cases were found where the hybrids were more resistant than either pure species controls (Dungey *et al.* 2000b) and such reports are rare in the literature (Fritz *et al.* 1999). This does not exclude the possibility, however, that a specific hybrid individual may exhibit resistance to a pest.

There are several genetic mechanisms that could explain cases, such as the possum susceptibility of the *E. nitens* × *E. globulus* hybrid, where crossing two resistant species results in a susceptible hybrid (reviewed in Fritz *et al.* 1999; Whitham *et al.* 1999). Recombination and the breakup of genetic-based resistance

mechanisms, or advanced generation hybrid breakdown, have been suggested as a cause of hybrid susceptibility in *Populus* (Whitham 1989). Such genetic recombination, however, occurs only after meiosis and would not explain the susceptibility observed in the first-generation (F_1) hybrids. Such susceptibility would strongly argue for the two species having independent mechanisms of resistance and/or host recognition. In the latter case, greater susceptibility of the F_1 hybrid than all other hybrid types (F_2 and backcrosses) and pure species classes could arise through (i) recessive inheritance of independent genes affecting resistance (Fritz *et al.* 1999) or (ii) additive inheritance of independent resistance mechanisms, each requiring threshold levels to confer resistance (Fritz *et al.* 1999; Dungey *et al.* 2000b). A combination of both mechanisms may be occurring and a similar argument would apply to host recognition but involve dominance. Although such mechanisms are possible, since pest–host relationships can be closely associated (e.g. with pathogens; Burdon 2001), the exact mechanisms conferring resistance to possum browsing in both *E. globulus* and *E. nitens* remain to be determined.

In practical terms, the present study clearly indicates that pest susceptibility is an important factor to consider when developing hybrids for commercial deployment. In Tasmania, species combinations currently being tested have been aimed at improving the frost resistance of *E. globulus* (Tibbitts 1986; Scott *et al.* 2002). Any gain in frost resistance in these cases, however, may be offset by reduced resistance to pests (see Dungey 1996), including possums. As a direct consequence, the *E. nitens* × *E. globulus* hybrid combination may be unusable in Australian plantations (Scott *et al.* 2002). Further, it appears that susceptibility to possum damage is sometimes difficult to predict. Host species and hybrids investigated in this paper indicate that hybrid resistance to possum damage is not always predicted by the susceptibility of the parent species. Therefore, new hybrid combinations should be tested carefully before they are considered for deployment.

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