Susceptibility of *Eucalyptus globulus* ssp. *globulus* to sawfly (*Perga affinis* ssp. *insularis*) attack and its potential impact on plantation productivity

Gregory J. Jordan[a,b], Bradley M. Potts[a,b,*], Anthony R. Clarke[a,c,1]

[a]*Cooperative Research Centre for Sustainable Production Forestry, Australia*
[b]*School of Plant Science, University of Tasmania, G.P.O. Box 252-55, Hobart 7001, Australia*
[c]*School for Agricultural Science, University of Tasmania, G.P.O. Box 252-54, Hobart 7001, Australia*

Abstract

Sawflies (*Perga* species) are leaf-damaging pests of the major plantation tree species *Eucalyptus globulus* ssp. *globulus*. This work describes the patterns of quantitative genetic variation in susceptibility to attack by *Perga affinis* ssp. *insularis*, based on data from a large open-pollinated trial containing genetic material from throughout the geographic range of *E. globulus* ssp. *globulus*. Forty three per cent of the trees in the trial exhibited damage from sawflies in either their sixth or seventh growth seasons. The incidence of damage was genetically based, with significant variation between geographic races of *E. globulus* ssp. *globulus* and highly heritable ($h^2 = 0.43 \pm 0.05$) variation in damage incidence within races. Susceptibility to sawfly damage significantly affects plant fitness with both genetic and environmental correlations demonstrating that sawfly damage causes slow growth and increased mortality of trees. Mild and severe sawfly damage resulted in 16 and 31% reduction in the basal area of surviving trees, and the effect was consistent across races and families. Based on this data, we propose a model predicting relative plantation productivity of races of different susceptibility under different infestation regimes.
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1. Introduction

A world-wide expansion of *Eucalyptus* pulpwood plantations over the last two decades has been associated with an expansion in genetic research to assist breeding programmes. While much of this research has focused on the use of field trials to quantify genetic variation in growth and wood property traits, there is an increasing recognition that herbivory can limit production (Candy et al., 1992; Coleman et al., 1997). Eucalypts are prone to intense insect herbivory (Ohmart and Edwards, 1991; Elliott et al., 1998) which can cause significant decreases in growth in both plantations and naturally regenerating forests (Carne et al., 1974; Elliot et al., 1993; Stone et al., 1998). While integrated pest management programmes have been formulated for major insect pests (e.g. Elliot et al., 1992), the nature of eucalypt forestry

* Corresponding author. Tel.: +61-3-62262641; fax: +61-3-62262698.
E-mail address: b.m.potts@utas.edu.au (B.M. Potts).
[1] Current address: Australian School of Environmental Studies, Griffith University, Nathan Campus, Nathan 4111, Qld, Australia.

in Australia limits any management strategy relying on insecticides (Clarke, 1995). As a result, a variety of alternatives have been proposed (Stone and Clarke, 1998), including the use of less susceptible genotypes (Floyd and Farrow, 1994). Many tree genera, including eucalypts (e.g. Farrow et al., 1994; Floyd et al., 1994; Raymond, 1995), show variable resistance to key pests. As a result, the use of natural tree resistance to manage forest insects may become economically viable, where post-planting intervention is expensive or difficult, or where environmental concerns restrict the use of pesticides.

Sawflies (*Perga* species: Hymenoptera, suborder Symphyta, family Pergidae) are one of the more dramatic groups of eucalypt defoliating insects. Adults lay batches of up to 65 eggs into host foliage, and the external foliage feeding larvae that hatch from these batches remain together. Neighbouring cohorts often aggregate to form groups of several hundred individuals (Macdonald and Ohmart, 1993). As the final instar larvae are quite large ($\sim$70–80 mm long), these aggregations are not only conspicuous, but also can cause extreme defoliation (Carne, 1965; Elliott et al., 1998).

This study was initiated when damaging populations of the large-green sawfly, *Perga affinis* ssp. *insularis* Riek, were observed in a *Eucalyptus globulus* Labill. ssp. *globulus* trial in northwestern Tasmania. *P. affinis* ssp. *insularis* is the Tasmanian subspecies of *P. affinis*, a common eucalypt pest species widely distributed in eastern Australia (Elliot and Bashford, 1996; Elliott et al., 1998). Although eight subspecies of *P. affinis* are recognised (Macdonald and Ohmart, 1993), the differences between them are poorly understood and it is not clear if, or how, *P. affinis* ssp. *insularis* differs from the others. Field observations (A.R. Clarke, personal observation) and published records (Elliot and Bashford, 1996; Elliott et al., 1998) for *P. affinis* ssp. *insularis* differ little from the available information for other subspecies, particularly the well-known *P. affinis* ssp. *affinis* (Carne, 1962, 1965, 1969). Information concerning any subspecies of *P. affinis* is, therefore, likely to be valid for the entire species.

While quite detailed information is known for some aspects of the behaviour and ecology of *P. affinis*, little information is available on host plant resistance and larval impact on hosts, and this information is contradictory. For example, Carne (1965) states that "sawflies (*P. affinis affinis*) do not find all individuals of the same (tree) species equally attractive", while Farrow (1996) states that "there is little evidence that there are any populations of trees or individual trees within a susceptible eucalypt host species that are more resistant to attack by sawfly than other trees". These contradictions may be the result of genetically based variation in resistance being masked by factors such as local environment, herbivore density and defoliation history, and emphasises the need for studies under uniform environments.

The present work investigates the quantitative genetic control and impact of sawfly susceptibility in the major temperate hardwood plantation taxon, *E. globulus* ssp. *globulus* and populations morphologically intermediate between ssp. *globulus* and other subspecies. This subspecies is used for pulpwood production in many parts of the world (Eldredge et al., 1993; Tibbits et al., 1997), and the quantitative genetics of its growth, reproduction, development and survival are quite well known (see Dutkowski and Potts, 1999). The effects of sawfly damage on growth are investigated, including the proposal of a preliminary model of the effects of sawfly damage on wood production.

2. Trial site, genetic material and traits measured

The present work is based on data from the North Forests Products' *E. globulus* ssp. *globulus* trial at Massy Greene in northwestern Tasmania. This large trial contained plants grown from open-pollinated seed collected by CSIRO Tree Seed Centre (Gardiner and Crawford, 1987, 1988). The genetic material in the trial includes 594 families, and provides a representative sample of the whole subspecies and its intergrades with other subspecies, although some populations and regions are better represented than others (Gardiner and Crawford, 1987, 1988; Jordan et al., 1993; Dutkowski and Potts, 1999). The collections have been classified into 13 races and 49 locations (Dutkowski and Potts, 1999). Two races and five locations were excluded from analyses (as in Jordan et al., 1999) because they are either aberrant or represented by only one family. The trial was laid out in a randomised incomplete block design and

occupies a fertile site in a mild climate (see Jordan et al. (1994) for further details).

The Massy Greene trial was damaged by sawflies early in each of the several growing seasons. Damage was most severe in the sixth and seventh growing seasons, and was scored in January and November 1995, respectively. Noticeable sawfly damage was present in 18.3% of plants in the sixth season and 39.9% in the seventh. To simplify the analytical procedures, scores from the sixth and seventh growing seasons were pooled, resulting in a single variable: presence/absence of damage in either season. This variable, referred to as *damage* in this work, showed an overall incidence of 43.1%. The pooling of this information resulted in a minimal loss of information content, because damage in the sixth and seventh seasons was almost perfectly correlated. A three-state variable called *severity of damage* also was created, with levels of undamaged, mildly damaged or severely damaged. Severely damaged was defined as removal of all or nearly all foliage in the canopy in either year, and mildly damaged as noticeable foliage loss in either year, but with the retention of the basic canopy shape.

Three growth measurements also were used. Basal area at 4 years of age represented the total growth before the main infestations. Basal area at 8 years represented the total growth after the main infestations. The increment in basal area between 4 and 8 years represented net growth after infestation.

3. Analyses

3.1. Analyses of genetic variation

Analyses of mixed models were performed using ASReml (Gilmour et al., 1995, 1999). This uses the average information algorithm and sparse matrix technology to provide restricted maximum likelihood solutions for a wide range of mixed models, including univariate and multivariate models. It can be used to estimate variance components for traits and correlations between traits at any level of the hierarchy of random effects in the models.

Univariate analyses of damage treated this presence/absence trait as binary with a probit link function, which assumes that the trait reflects a threshold value in an underlying, normally distributed quantitative genetic trait (Gilmour et al., 1999). The analysis followed model 1, where random effects are shown in italics and nesting is indicated by brackets:

$$y = \mu + \text{replicate} + race + locality(race)$$
$$+ family(locality) + incomplete\ block(replicate)$$
$$+ residual \tag{1}$$

The difference of the variance components from zero for this and other models were tested using the likelihood ratio test, that is assuming a $\chi^2_{0.5}$ distribution for $-2\log(\text{likelihood})$ for the difference between models including and excluding the relevant component (Shaw, 1991; Stram and Lee, 1994). Heritabilities were calculated as 2.5 times the family within race variance divided by the sum of the family within locality and residual variances. This assumes an outcrossing rate of 30%, and is commonly used for tree species (Griffin and Cotterill, 1988; Potts and Jordan, 1994b).

The size of the effect of sawfly infestation on growth rates was assessed by fitting model 2:

$$\text{increment} = \mu + \text{severity of damage} + \text{race}$$
$$+ \text{race.damage} + \text{replicate}$$
$$+ \text{4-year basal area}$$
$$+ incomplete\ block(replicate)$$
$$+ family(race) + family(race).damage$$
$$+ residual \tag{2}$$

where increment is the increment in basal area from 4 to 8 years, damage was a three-level factor (0: no damage, 1: moderate damage, 2: severe damage) and 4-year basal area was a covariate. Note the inclusion of interaction effects (race.damage and *family(race).-damage*) to test whether the impact of sawfly damage on growth varied among genotypes.

The impact of damage on individual races was assessed by fitting model 3:

$$\text{increment} = \mu + \text{severity of damage} + \text{replicate}$$
$$+ \text{severity of damage.race}$$
$$+ \text{4-year basal area} + incomplete\ block$$
$$+ family(race) + residual \tag{3}$$

Other interaction effects among fixed effects were not included because they were not significant.

3.2. Correlations between sawfly damage, growth and survival

Genetic and environmental correlations were calculated from bivariate and trivariate models fitted with ASReml. These correlations are uniquely attributable to the relevant design stratum in the models. As a result, race correlations reflect only genetic associations among races, family within race correlations reflect only genetic associations within races (and therefore are genetic correlations in the narrow-sense), and incomplete block correlations reflect only associations at the meso-environmental scale (and hence are called environmental correlations; see Jordan et al. (2000) for more details). The significance of the difference of each correlation from zero was tested by a likelihood ratio test assuming a χ_1^2 distribution for the difference in $-2\log(\text{likelihood})$ between a model in which the correlation was constrained to be zero and the unconstrained model (Shaw, 1991). Differences among correlations within the same stratum in the trivariate model were tested with a likelihood ratio test in which the relevant correlations were equal in the constrained model.

Correlations between sawfly damage and 8-year survival assumed a binomial distribution and a probit link function, and were calculated by simultaneously fitting model 4 for each trait, and allowing unconstrained covariances at the race, family within race and incomplete block levels.

$$y = \mu + \text{replicate} + \textit{incomplete block}(\textit{replicate}) \\ + \textit{race} + \textit{family}(\textit{race}) + \textit{residual} \quad (4)$$

Correlations between sawfly damage, 4-year basal area and the increment in basal area from 4 to 8 years were estimated by fitting a trivariate model where each trait followed model 4 and all covariances were unconstrained. All three traits were treated as continuous, normally distributed variables in this analysis. Although this creates a bias in the variance components, correlations are not biased (Olausson and Ronningen, 1975).

3.3. Modelling sawfly damage on trial productivity

The presence of strong genetic differences among races in susceptibility to sawfly attack, and of marked differences in the intensity of attack within the trial, allowed the construction of a model of the effect of sawfly infestation on plantation production (as measured by increment in basal area) for different races. The model treated the five replicates in the trial as replicate sites, since infestation of the different replicates ranged from 28 to 59% of trees. Within each replicate, the actual mean growth increment for that race could be compared with an estimated mean growth increment with no infestation. This was possible because the effect of a given level of sawfly damage on growth was independent of genotype (see Section 4), i.e., the genetic variation in the effect of sawfly damage on growth is due to variation in host susceptibility, rather than given levels of damage affecting growth differently for different genotypes.

Since mortality was genetically associated with sawfly damage (see Section 4), the model needs to allow for differential survival. Thus, the following model was fitted for each combination of race and replicate to estimate least squares means for each level of sawfly damage:

$$\text{survival} = \mu + \text{severity of damage} + \textit{residual} \quad (5)$$

The estimated mean growth increment (basal area (cm^2)) including sawfly damage for each combination of replicate and race was calculated as

$$\text{increment}_{\text{actual}} = \text{inc}_0 \times \text{surv}_0 \times p_0 + \text{inc}_1 \times \text{surv}_1 \\ \times p_1 + \text{inc}_2 \times \text{surv}_2 \times p_2 \quad (6)$$

where inc_0, inc_1 and inc_2 are the least squares mean for growth increment for trees with no damage, moderate and severe damage, respectively (from analyses of model 3), surv_0, surv_1 and surv_2 the corresponding incidences of survival (from model 5), p_0, p_1 and p_2 the incidences of each damage class for the combination of race and replicate.

Similarly, the estimated mean growth increment (including the mortality effect) without sawfly damage for each combination of replicate and race was calculated as

$$\text{increment}_{\text{no sawfly}} = \text{inc}_0 \times \text{surv}_0 \quad (7)$$

The relative performance of races under different intensities of sawfly damage was then modelled as follows. For each race and replicate, the net loss in growth increment was calculated as the difference

between increment$_{actual}$ and increment$_{no\ sawfly}$. This was then regressed (linear regression with a zero intercept) on the total incidence of sawfly attack in that replicate. There was no evidence of non-linearity in the regressions. The relative performances of the races were estimated by adding the estimated growth increment without damage (least squares means from model 2).

4. Results

4.1. Genetic control of susceptibility to sawfly damage

There were large differences between races in sawfly susceptibility (Table 1, Fig. 1): Southern Gippsland, Southern Tasmania, Recherche Bay and King Island were the least susceptible (<30% of trees damaged). Western Tasmania, Strzelecki Ranges and South-eastern Tasmania showed moderate susceptibility (39–43%). The Northeastern Tasmania, Furneaux Group and the Western Otways races showed high susceptibility (49–52%), but the Eastern Otways Race was clearly the most susceptible (66%). No significant differences were observed between localities within races; however, there were large, and significant genetic differences among *E. globulus* families within localities (Table 1). As a result, the heritability of the incidence of damage within localities was high (0.43 ± 0.05).

4.2. Genetic and environmental correlations between damage, growth and survival

Highly significant ($P < 0.001$) negative environmental (incomplete block within replicate) and within race genetic correlations between survival to 8 years and sawfly attack (Table 2) imply that increased sawfly damage was associated with increased tree mortality. The correlation among race effects was not significantly different from zero (Table 2). The within race genetic and environmental correlations of incidence of sawfly damage with basal area before the main sawfly infestation (age 4 years) were weakly negative, but these negative correlations significantly strengthened after the main infestation at age 8 years, with the 4–8-year basal area increments highly correlated with sawfly damage (Table 2).

4.3. Differences in growth rate

Undamaged, damaged and severely damaged trees had markedly different growth rates. At the race level, sawfly damaged plants after infestation grew slower than undamaged plants during the same time (Fig. 2). The reductions for the different races in the increment basal area of surviving plants ranged from 10 to 29% for moderate damage, and from 12 to 67% for severe damage. However, there were no significant differences among races or among families in response to sawfly damage ($F_{291,385} = 1.32$ for the race by damage interaction effect, $P > 0.05$, and $\sigma^2 = 0.0017$ or 0.00002% of the total variance for the family within race interaction effect). Thus, the best summary of damage is the overall effect. After taking early growth, genetic and environmental differences into account, the mean increment in basal area of trees with mild and severe sawfly damage was reduced by 16 and 31%, respectively (least squares means of 233 ± 3, 196 ± 4 and 160 ± 4 cm^2 for undamaged, mildly damaged and severely damaged plants, respectively). These differences were very highly significant ($F_{21,385} = 171$, $P < 0.0001$).

Table 1
Partition of the variation in the incidence of sawfly damage in *E. globulus* ssp. *globulus*, with significance levels of likelihood ratio tests of the variance components[a]

	Race	Locality within race	Family within locality	Incomplete block
Variance (±S.E.)	0.18 ± 0.09	0.04 ± 0.19	0.20 ± 0.03	0.13 ± 0.24
% of total variance	11.5%[*]	2.3% NS[b]	13.1%[***]	8.6% NS

[a] The incidence of sawfly attack varied very highly significant among the replicates ($F_{4,120} = 16.2$; $P < 0.001$).

[b] NS: $P > 0.05$.

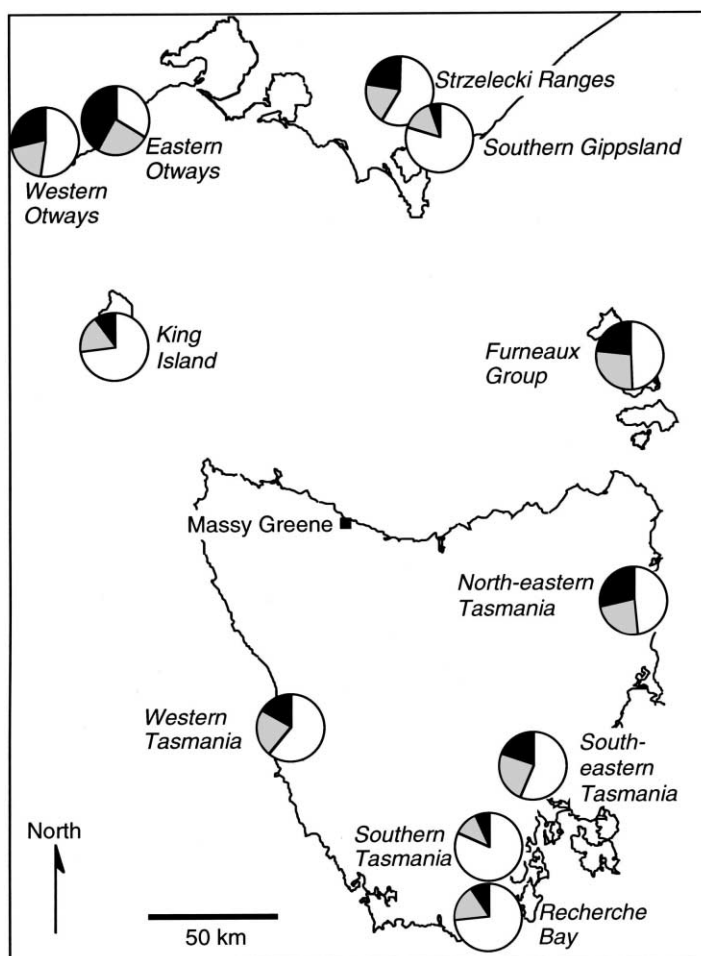[*] $P < 0.05$.

[***] $P < 0.001$.

Fig. 1. Impact of *P. affinis* ssp. *insularis* on geographic races of *E. globulus* ssp. *globulus*. Small squares indicate the location of trial site and pie charts show the proportions for each race of trees severely damaged by sawflies (black), mildly damaged (stippled) and undamaged (white).

Table 2
Correlations of damage with 8-year survival, 4- and 8-year basal area, and the increment in basal area from 4 to 8 years[a]

	8-year survival	4-year basal area	Increment	Difference	8-year basal area
Race	0.44 ± 0.31 NS[b]	0.46 ± 0.28 NS	-0.37 ± 0.25 NS	***	-0.29 ± 0.32 NS
Family within race	-0.33 ± 0.10***	-0.20 ± 0.08*	-0.66 ± 0.06***	***	-0.56 ± 0.06***
Incomplete block	-0.99 ± 0.20***	-0.38 ± 0.12*	-0.92 ± 0.11***	***	-0.82 ± 0.12***

[a] The significance of each correlation, and of the difference between the correlation of damage with 4-year basal area and that with the increment are given.

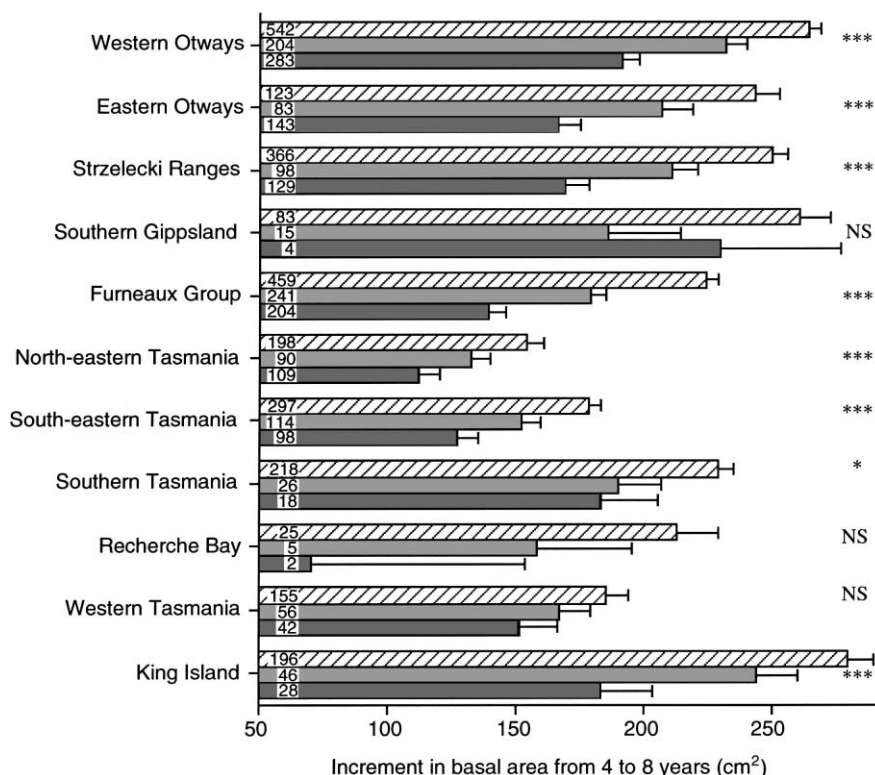[b] NS: $P > 0.05$.

* $P < 0.05$.

*** $P < 0.001$.

Fig. 2. Race least squares means (with standard errors) of increment in basal area of surviving plants for undamaged (cross hatching), damaged (lightly stipple) and severely damaged plants (dark stipple). The number of plants are given at the base of each column. The significance levels of F-tests of the damage level are shown (NS: $P > 0.05$; *: $P < 0.05$; ***: $P < 0.001$).

4.4. Mortality in damaged plants

The incidence of mortality in undamaged plants was 2.4% ($n = 2662$), in moderately damaged plants was 1.9% ($n = 978$), and 3.4% in severely damaged plants ($n = 1061$). Mortality of moderately damaged plants ranged between 0 and 12.5% depending on race, and the mortality of severely damaged plants ranged between 0 and 16.6%. The greatest mortality occurred in the small South Gippsland race.

4.5. The modelled effect of sawfly damage on growth

The markedly different susceptibility of the races to sawfly attack is reflected in the modelled loss of productivity (Fig. 3). Most races showed significant regressions of growth increment versus intensity of sawfly infestation, with the only exceptions in races with low susceptibilities. Under the model, severe

sawfly damage changed the rank order of races for mean growth increments significantly. Thus, under the conditions prevailing at Massy Greene, the King Island race remained the fastest growing regardless of damage, but Southern Gippsland, Southern Tasmania and Recherche Bay improved their rankings, whereas Western Otways, Eastern Otways, Furneaux Group and Strzelecki Ranges slipped at least one rank. Under more severe attack, the model predicts more extreme ranking changes, with very poor performance of Eastern Otways and Furneaux Group races.

5. Discussion

5.1. Genetic variation in susceptibility

Both races and families within races of *E. globulus* ssp. *globulus* exhibit genetically based variation in
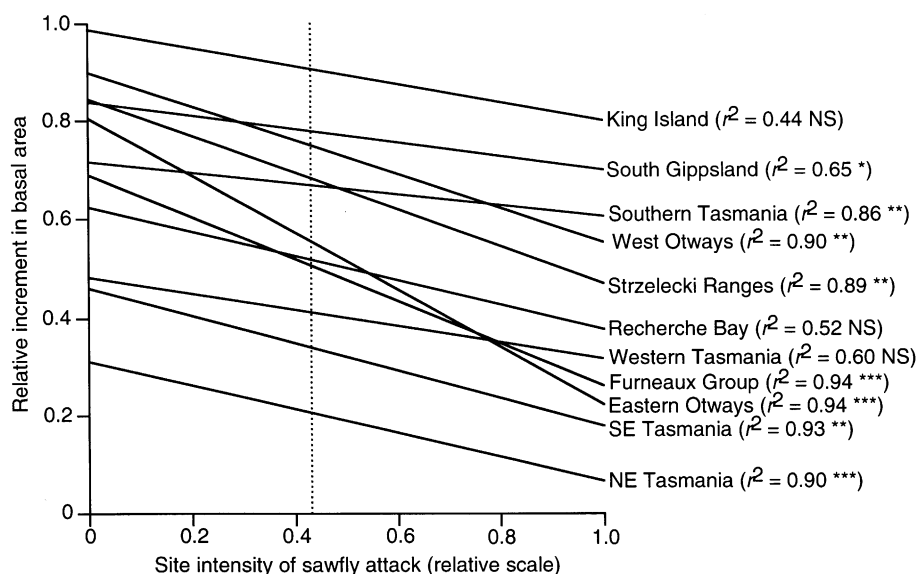
Fig. 3. Modelled loss of productivity due to sawfly damage. The increment in basal area is based on 4–8 year growth at Massy Greene. The vertical line is the overall incidence of attack (damage or severe damage) in the Massy Greene trial.

their susceptibility to sawfly damage. Severe damage shows very similar geographic patterns (Fig. 1) and partition of variation to the damage trait reported here (G.J. Jordan, unpublished data). Mild and severe damage may, therefore, represent different thresholds of the same underlying genetic trait. This is, however, difficult to test more formally because these two variables are not arithmetically independent of each other. Even though this work shows strong quantitative genetic control of susceptibility to sawfly damage, there may, in fact, be even stronger genetic control because the damage appeared to follow a spatial pattern within the trial that was difficult to identify analytically (G. Dutkowski, personal communication).

The strong variation among races and even greater variation within races is typical of more highly heritable traits in ssp. *globulus* (G.J. Jordan, unpublished data). Furthermore, the geographic pattern of racial variation is quite consistent with many other traits and overall racial classification of ssp. *globulus* (Dutkowski and Potts, 1999), with King Island and the southern and western regions of Tasmania showing low susceptibility, and Victoria, Furneaux Group and North-eastern Tasmania showing high susceptibility. The only exception to this trend is the low susceptibility in the Southern Gippsland race in Victoria. This

race is represented by only 16 families in this trial, so it is possible that the low average susceptibility may be a sampling effect.

The mechanisms underlying the genetically based variation to sawfly susceptibility are unknown, but, apart from chemical defences, bark and leaf morphology may be involved. Sawfly susceptibility is positively associated with the relative thickness of the bark at the locality level (Dutkowski and Potts, 1999), and at both the race and family within race genetic levels ($r_{race} = 0.61 \pm 0.22$; $r_g = 0.28 \pm 0.09$; $P < 0.01$ for both; G.J. Jordan, unpublished data). One possible reason for this would be that the smoother surface of thinner barked trees might inhibit the movement of sawfly larvae. Carne (1965) suggested that leaf width and the level of leaf glaucousness affected oviposition behaviour in *P. affinis affinis* and thus genetic variation in adult leaves may affect susceptibility. However, the genetic patterns of variation in adult leaves of ssp. *globulus* are not known, although significant variation in juvenile leaves occurs both within and among populations (Potts and Jordan, 1994a). Carne (1962, 1965) also noted that trees attacked in 1 year tended to be attacked the following year, a trend that resulted from a combination of how females search for oviposition sites and changes in leaf quality following

re-growth. Thus, strong correlations of tree damage across years may not only be due to patterns of susceptibility, but also to insect behaviour.

5.2. The association of sawfly damage with mortality and reduced growth

Sawfly damage almost certainly caused significant reduction in growth rates at Massy Greene. The correlations at the race, family within race and environmental levels of sawfly damage with the increment in basal area from 4 to 8 years are significantly lower than the corresponding correlations with 4-year basal area. The fact that the correlations with growth increment are negative adds further support to this proposal. The alternative explanation that the correlations are due to preferential attack of slow growing plants is unlikely for the following reasons. The weak associations between growth and sawfly damage prior to the first major attack suggests that attack by sawflies is not strongly determined by the size of the trees, or by genes which favour fast or slow growth. In fact, the presence of weakly negative genetic and environmental correlations between 4-year growth and sawfly damage may have been due to the documented sawfly infestation prior to 1993. Although sawflies show preference for the less glaucous adult foliage (Carne, 1965), this cannot explain the correlations observed here because fast growing plants reach phase change sooner, which would result in positive correlations between growth and sawfly damage (Jordan et al., 2000).

Sawfly damage is also almost certainly a significant cause of mortality within the trial, as shown by the significant negative genetic and environmental associations between sawfly damage and survival. An alternative explanation would be sawflies preferentially attacking plants and genotypes that were not vigorous, but this seems unlikely considering the relatively weak association between sawfly attack and early growth. At least some of the mortality due to sawfly damage may be the result of reduced growth rates in the competitive environment of the Massy Greene trial, since growth dependent mortality occurs in such environments (Chambers et al., 1995). In this competitive environment, the strong reduction in growth shown below is likely to cause further mortality.

5.3. The impact of sawfly damage on productivity

The strong genetic association between sawfly damage and both mortality and growth of surviving trees clearly shows that sawflies affect plant fitness. Furthermore, the strongly negative association between damage and 8-year basal area and similar impacts reported by Raymond (1995) imply that genetic susceptibility to insect damage is incorporated in later age growth measurements. As a result, selection for growth will incorporate responses to pests and other aspects of the biotic environment.

The weakness of the interaction effects between sawfly damage and either race or family for the increment in basal area implies that, although there is considerable variation among races and families in the susceptibility to infestation, the impact on growth of an infestation is independent of genotype. This is significant because it means that the simple linear model of the impact of sawfly damage proposed here on productivity is likely to be valid. This model is uncalibrated at present. Firstly, the site propensity for sawfly attack is based on the levels of attack among the five replicates in the Massy Greene trial, but at present there is no quantitative way of assessing how this relates to the propensity of other locations to sawfly attack. Although the distribution of sawfly damage is not well documented, significant damage has been documented in other locations (Carne, 1965; Ohmart, 1990; Stone, 1993; Farrow, 1996), indicating that infestation is a potential problem and that a survey of damage is possible. At present, the scale is not only dependent on site propensity but also on the genetic composition of the Massy Greene trial, because the genetic makeup of a trial should affect the overall incidence of damage. The second way that the model is uncalibrated is that the growth rates only reflect conditions at Massy Greene, which is a highly productive site.

Although uncalibrated, the model demonstrates a major reduction in growth due to sawfly attack and that sawfly attack can alter the rankings of races. This work has two implications for the selection of genetic material for use in plantations. Firstly, susceptible families will grow poorly in infested trials. This may result in suboptimal selections for plantations where insect damage is unlikely unless breeding values are adjusted to allow for this. Secondly, in environments

with significant risks of sawfly damage, a model such as the one proposed here may help selections and predicting yields. This leads to two obvious paths of further research. Firstly, studies of the distribution of potential sawfly attack may help identify susceptible sites. Secondly, the accumulation of more data on the effects of sawfly damage would assist in calibrating and refining the proposed model. In particular, the model could be refined to make family level predictions, since the bulk of the genetic variation for sawfly resistance occurs among families within races.

Acknowledgements

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