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The Genetics of Resistance to *Phoracantha semipunctata* Attack in *Eucalyptus globulus* in Spain

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Abstract

A study of the inheritance of resistance to *Phoracantha semipunctata* (eucalypt longhorn borer) was conducted in a progeny trial established in southern Spain, from a large *Eucalyptus globulus* base population, a commercial control seedlot and 2 previously selected clones. The results showed small race effects and a low heritability ($h^2 = 0.19$) for resistance to PHORACANTHA attack. The commercial seedlot was not significantly different from the mean of the Australian seedlots, but the 2 selected clones were significantly more resistant and faster growing. The level of PHORACANTHA attack was positively correlated with growth at the race ($r = 0.17$) but not at the genetic within race level ($r = 0.05$).

Key words: Heritability, genetic correlation, drought, Eucalypt longhorn borer, Spain.

FDC: 165.3; 165.53; 232.1; 450; 453; 145.7 x 19.88 *Phoracantha semipunctata*; 176.1 *Eucalyptus globulus*; (46).

Introduction

In many areas of Iberia and the Mediterranean Basin, which is characterized by low rainfall and extended dry summers, the productivity of eucalypt plantation can be considerably reduced because low survival following attack by *Phoracantha semipunctata*, a cerambycid beetle native from Australia.

So far the main control measure used has been burning of trap log piles, but this is costly and only partially effective. There has been differences reported in resistance to *Phoracantha* attack between different eucalypt species (HANKS et al., 1993, 1995), but the magnitude of genetic variation within *Eucalyptus globulus*, the most important eucalypt species in Spain, has not been previously described. This paper looks at the level of genetic control of resistance to *Phoracantha* attack and its relationship with growth on a large *E. globulus* base population trial established in a severely infected area of the

planting of Empresa Nacional de Celulosa (ENCE), in the South of Spain.

Material and Methods

Genetic material

The study includes a range-wide collection of 256 open-pollinated families covering the entire natural range of *Eucalyptus globulus* ssp. *globulus* in Australia. Collection details are given in GARDINER and CRAWFORD (1988) and published in JORDAN et al. (1994). Cuttings of 2 plus-trees from ENCE breeding program, and 1 commercial seedlot were also included in the trial. The plus-trees were selected for their superior growth and health and were amongst the very few survivors in highly affected plantations.

Trial site and design

The trial is located in the SW of Spain, in the province of Andaluzia, near Huelva (latitude 37° 34'N; longitude 6° 50'W; altitude 70 m). Climatic conditions are typically Mediterranean: mean annual rainfall of 500 mm, a mean annual temperature of 17.5°C, and less than 10 days per year of frost. However, the climatic conditions prevalent during most of the life of the trial were generally drier than average: the total rainfall in the second year of the trial, was a record low of 250 mm. The soil is a distric cambisol, with a hard-pan horizon at around 50 cm of depth. The soil was cultivated prior to planting to 60 cm using a mul-board plough. Plants were established at a 3 m x 3.5 m spacing, and fertilized at planting. For the commercial seedlings, a slow release fertiliser was also applied to the paper-pot medium. Weeds were controlled one year after planting by disc ploughing.

Families were nested in 5 sub-lines, but allowing for some crossover of races across different sublines (Table 1). The 2 clones, propagated from stem cuttings, and the commercial seedlot were included in all blocks across the 5 sublines. There were 4 blocks per subline. Each family or clone were represented in each block by 3 non-contiguous plots, each plot having 2 trees, which were randomly allocated within a block. DUTKOWSKI et al. (1998) race classification was used as a basis

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Table 1. – Distribution of races across the 5 sublines (SL1 to SL5), and total number of families and trees per race in the trial.

Race	Subline					No. Fam	No. Trees
	1	2	3	4	5		
Commercial + clones	X	X	X	X	X	3	328
W. Otways	X					5	64
Cape Patton	X			X		41	588
E. Otways		X				28	382
Strzelecki			X			32	531
S.Gippsland	X					5	30
Lighthouse	X					1	9
Flinders Island	X	X			X	35	477
S. Furneaux Group		X		X		28	422
St. Helens				X		3	42
NE Tasmania			X			3	54
Interior NE Tasmania			X			5	84
Dromedary	X					5	48
SE Tasmania			X		X	26	470
South Tasmania					X	4	47
Tasman Peninsula				X		5	88
West Tasmania		X				9	121
King Island		X				4	43
No families	41	60	52	46	49	248	3992
No trees	635	742	922	823	870		

to group the different families into native races. The 2 clones and the commercial seedlot were included in separate genetic groups (Table 1).

Measurements

The trial was measured at age 5 for diameter and damage, with a putative cause of damage assigned (Table 2). Trees which were sick or dead because of *Phoracantha* (Status 02 and 03 and Cause 04 and 08) were assigned a resistance score of 0, whereas those which showed no sign of attack or recovered from previous attacks were given a score of 1. Trees affected or killed by other causes (frost, wind, animals, broken tops, leaning), were excluded from the analysis. Of the 3992 records in the final dataset, 3834 were scored (either 0 or 1) for *Phoracantha*, but only 1854 were measured for diameter. Of these, only 220 had a *Phoracantha* score of 0.

Statistical analysis

Estimates of variance and covariance for diameter and resistance were obtained by Restricted Maximum Likelihood

(REML), using an Average Information algorithm (GILMOUR, et al., 1995). For estimation of variance components, the commercial controls and clones were removed from the data. The analysis was carried out using the reduced dataset based on the following linear model:

$$y = u + sub + sub/b/k + race + fam + plot + res \quad [1]$$

where y is the vector of observations for diameter and resistance, u is the overall trial mean, sub is the effects due to subline (fixed), sub/blk is the effects due to blocks within sublines (fixed), fam is the effect due to open pollinated families (random), race is the effect due to races (random), plot is the effects due to family by replicate interaction (random) and res are the residual effects. Standard errors for variance ratios were obtained directly from the inverse of the mixed model equations. Given the binary nature of resistance, genetic and phenotypic parameters estimates were on a binomial scale and were converted to a liability scale according to the methods of OLAUSSON and RONNINGEN (1975).

Table 2. – Classification of the Damage and Cause of Damage in the trial.

Damage	01	Broken top
	02	Sick
	03	Dead
	04	Leaning
	99	None of the above
Cause of damage	01	Water runoff
	02	Waterlogging
	03	Frost
	04	Drought (in association with <i>Phoracantha</i>)
	05	Cattle
	06	Rats
	07	Wind
	08	<i>Phoracantha</i>
	09	Fungus
	10	Machines
99	None of the above	

Table 3. – Estimated means for diameter and resistance to *Phoracantha* (as proportion of trees with no visible damage) at 5 years for the Australian races, commercial seedlot and 2 clones from ENCE breeding program. The best 5 families in the native collection for each trait is also listed. The LSD, at 1% level, was approximated as twice the average estimated prediction errors of the estimates for diameter and resistance.

Race	Diam Cm	Phor (%)
Land race		
Clone A	6.53	0.86
Clone B	6.31	0.81
Commercial	5.87	0.57
W. Otways	6.06	0.53
Cape Patton	5.92	0.44
E. Otways	5.63	0.58
Strzelecki	6.02	0.64
S.Gippsland	5.83	0.56
Lighthouse	4.23	0.37
Flinders Island	5.52	0.63
S. Furneaux Group	5.31	0.67
St. Helens	6.21	0.59
NE Tasmania	5.82	0.48
Interior NE Tasmania	5.56	0.49
Dromedary	5.37	0.51
SE Tasmania	5.81	0.48
South Tasmania	6.06	0.48
Tasman Peninsula	5.72	0.50
West Tasmania	5.48	0.41
King Island	5.74	0.36
Best 5 Aust. Families	6.46	0.81
LSD (1% level)	0.10	0.12

To estimate race and tree genetic merit of races and all trees across sublimes, the data included not only the Australian open pollinated families, but also the unimproved seedlings and the 2 clones were added to the dataset and an individual tree model was used:

$$y = u + blk + race + tree + plot + error \quad [2]$$

where tree is the effect due to additive genetic effects and error the effect due to environments. Variances and covariances for all random effects were taken from the previous analysis, with additive variance assumed to be equal to 2.5 the family variance. All control trees and clones were assumed unrelated.

Results and Discussion

The trial had poor growth and survival. Around 10% have been killed or were badly affected by frost. Of the remaining trees, only 49% survived to *Phoracantha* attack. Such level is not uncommon in many dry areas of Spain and Portugal (LENCART E SILVA, 1994), particularly following a number of dry years. The resistance to PHORACANTHA varied across the trial,

with resistance per block ranging between 26% and 72%. Diameter at 5 years was 6.2 cm. This growth rate is lower than that reported in progeny trials of similar origin and age in higher rainfall areas in central and southern Portugal (BORRALHO et al., 1992a and b; ARAÚJO et al., 1996), and the north of Spain (SORIA et al., 1997). It is also amongst the lowest productivities recorded in forest inventory in Portugal (TOMÉ, 1994). This reflected the particularly poor years experienced by this trial prior to the 5 year assessment.

Race effects

The means for diameter and resistance to *Phoracantha* are listed in table 3. The local land race was not significantly better than the mean of all Australian races, excluding Lighthouse (Table 3). The best native races for diameter growth were St. Helens (Tasmania), Strzelecki (Victoria), West Otway Ranges (Victoria) and South Tasmania, all significantly better (at 1% level) than the commercial seedlot.

A few native races were also more resistant to *Phoracantha* than the commercial seedlot. The most resistant races were South Furneaux Group and Flinders Island, in the Bass Straight, with 67% and 63%, respectively. King Island, West Coast Tasmania and Lighthouse were the least resistant (with 36%, 41% and 37%, respectively).

However, the 2 clones, which were phenotypically selected for growth and health in *Phoracantha* affected areas in South of Spain, had better growth and resistance than the trial mean. The clones were 15% better than commercial seedlings for diameter, and had a resistance to *Phoracantha* of 81%, a substantial improvement from the 57% in the commercial seedlings.

Genetic parameters

Variances for race, family, plot and residual effects are listed in table 4, for diameter and resistance to *Phoracantha* attack. Race effects were significant (at 1% level), accounting for 12% of the total variation in diameter and 5% in resistance to *Phoracantha*. Within-race heritability for diameter was 0.14, somewhat lower but within one standard error of previous estimates in the same population in Australia (MACDONALD et al., 1997). However, they agree well with results in Portugal (BORRALHO et al., 1992a and b; ARAÚJO et al., 1996) and Spain (SORIA et al., 1997). The results suggests that growth in Mediterranean conditions may be less heritable than on less water limiting conditions, although the poor connectedness between the 5 sublimes and the large block sizes could also have played a role. The heritability of resistance to *Phoracantha* on the underlying scale, was also low ($h^2 = 0.19$). To our knowledge, this is the first reported heritability estimate for *Phoracantha* resistance in eucalypts.

The race and genetic correlations between diameter and resistance to *Phoracantha* were positive but low and not significantly different from zero at the 1% level (Table 5).

It is possible that these correlations may have been affected by unbalance in the data; as most trees scored as affected did

Table 4. – Variance components and heritability estimates based on an intraclass correlation amongst open pollinated sibs of 0.4.

Trait	Variance components				h^2 (s.e.)
	Race	Fam	Plot	Error	
Diameter	0.464	0.194	0.220	3.027	0.14 (0.048)
Phoracantha	0.012	0.011	0.006	0.210	0.19 (0.022) ¹

¹) Heritability adjusted to the liability scale.

Table 5. – Genetic (above diagonal) and race correlations (below diagonal) between diameter and resistance to *Phoracantha*.

	Diameter	Phoracantha
Diameter		0.17 ± 0.22
Phoracantha	0.05 ± 0.37	

not have growth measurements. If the 2 traits are genetically correlated, this would have resulted in an indirect selection for growth due to the mortality caused by *Phoracantha*. In theory, this problem is expected to reduce in absolute terms, albeit only marginally, the estimated covariance between the 2 traits (VILLANUEVA and KENNEDY, 1990), so the magnitudes of the correlations reported here should be seen as a lower limit for the true estimates. Given the near zero value of the correlations, however, any bias due to unbalance in the data is not expected to alter our conclusions.

Implications for breeding

In terms of identifying more resistant populations, the material from the Furneaux Group of Islands was the most resistant to *Phoracantha*, but was below average for growth. St. Helens, from one of the driest parts of the species range, had the fastest growth rate, a result also found in dry conditions in Western Australia (KUBE et al., 1995; DUTKOWSKI, 1995), but it was only average in resistance to *Phoracantha*. On the other extreme, West Tasmania and King Island had poor growth and were less resistant to *Phoracantha*. The 2 are genetically close (JORDAN et al., 1994; DUTKOWSKI et al., 1997) and come from the wettest part of the range of *E. globulus* distribution. The poor relationship between growth and resistance to *Phoracantha* does support only partially the hypothesis advanced by HANKS et al. (1995) that drought and insect resistance may share the same mechanism.

There was also substantial genetic variation between families within a race. For example, selecting the 5 best Australian families on the basis of progeny information alone is expected to increase growth (by 6.5 cm, an increase of 15%) and resistance to 81%. These gains are similar to those already achieved by the 2 clones in the trial (15% better growth and a 83% resistance). Expected gains from family selection seem therefore to be of the same magnitude to observed gains from mass selection and propagation. Mass selection is less accurate than family selection but can use a much higher selection intensities. This is likely to have been the case because the clones have been previously selected for their superior growth and health in highly borer affected plantations. The result confirm the effectiveness of ENCE's plus-tree selection and subsequent propagation program to improve growth and borer resistance under local conditions.

Unfortunately, the binary nature of the trait restricts further improvements from within family selection; this would require having several ramets per genotype or establishing large family blocks in highly infested areas, both hard to achieve in practice. As it is, at least 50% of the trees within each family were scored as 1, resulting in a very low within family selection intensity (less than 1 in 2). These are important operational limitations for forward selection schemes when considering the breeding for resistance to *Phoracantha* attack. Although CHAMBERS and BORRALHO (1997) have recently showed that when survival is reduced to 50% of its optimum level, as observed in our trial, it becomes 4 times more important than growth of the survivors when improving volume per hectare, effective within family selection for *Phoracantha*, will be a challenge for tree breeders.

Conclusions

To date, *E. globulus* breeding programs have concentrated mainly on volume per tree and, in some cases, wood density (BORRALHO, et al., 1993; GREAVES et al., 1997; VERGARA and GRIFFIN, 1997). However, given the large impact of *Phoracantha* in the productivity of plantations in southern Spain, breeding programs should consider including resistance as a major selection criteria. Our results showed important gains in survival and growth of the survivors have already been achieved from mass selection, and similar improvements can be made from family selection in the breeding population. However, resistance to *Phoracantha* attack seems to be poorly correlated with growth, so selection programs relying on growth alone are not expected to improve resistance.

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Genetic Variation Among Clones of *Picea abies* in Resistance to Growth of *Heterobasidion annosum*

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Summary

An inoculation experiment with *Heterobasidion annosum* on 98 four-year-old *Picea abies* clones was conducted on rooted cuttings under greenhouse conditions. One isolate of *H. annosum* and 10 ramets of each clone were used. After 34 days of incubation, fungal growth in sapwood and lesion length in the inner bark were measured. There were significant differences among clones in lesion length in the inner bark and in fungal growth in sapwood. Broad sense heritability was 0.35 for fungal growth and 0.27 for lesion length in the inner bark. Fungal growth and lesion length showed strong genotypic correlation. Bud-flushing index of the clones was correlated with mean fungal growth, whereas the growth termination index was not. Fungal growth in sapwood and lesion length in the inner bark of cuttings were not correlated with the mean height and provenance of 15-year-old ramets of the same clones in previously conducted field tests.

Key words: *Heterobasidion annosum*, *Picea abies* clones, Root rot, Norway spruce, resistance, genetic variation.

FDC: 165.53; 443; 416.3; 172.8 *Heterobasidion annosum*; 174.7 *Picea abies*.

Introduction

Investigations of genetic variation among Norway spruce (*Picea abies* (L.) KARST.) clones have revealed that several characters vary significantly. Results of an investigation by ERIKSSON *et al.* (1978) suggest that the photoperiod and temperature responses of Norway spruce are determined and influenced by a number of genes and/or alleles with small additive effects. SKRÖPPA and DIETRICHSON (1986) found that between-clone variation in height growth during a 7 year period accounted for 35% of the total variation in that particular character. Tree size, the wood specific gravity of *Picea sitchensis* (BONG) CARR. and height growth of *P. abies* were found to vary significantly between clones (CANNELL *et al.*, 1983; ROULUND *et al.*, 1985; SHAW *et al.*, 1988). DIMITRI (1974 and 1976), VON WEISSENBERG (1975) and SWEDJEMARK and STENLID (1994 and 1996) showed significant between-clone

variation in the growth of *Heterobasidion annosum* (FR.) BREF. in clones of Norway spruce.

Norway spruce has proved to be a good species for large-scale clonal tree improvement programs (BENTZER, 1993). Cuttings showed, on average, a 25% higher growth rate compared with seedlings in a Danish investigation (ROULUND and Bergstedt, 1982). Clonal selection is a good means of improving genetic gain (KLEINSCHMIDT, 1983), and the mass propagation of clones is an efficient way of exploiting genetically improved material. If resistance factors could be included in existing selection programmes for clonal production, the advantage of using cuttings for reforestation would be even greater since less resistant clones could be excluded.

H. annosum is the most serious of the pathogens attacking Norway spruce in Scandinavia. It causes root and butt-rot to conifers and broadleaf trees throughout the boreal and temperate zones of the Northern Hemisphere. Primary spread of the fungus is via spores that settle and germinate on freshly cut stumps or wounds on stems and roots to form a mycelium. The mycelium colonizes the stump, extends throughout the roots and infects healthy trees via root contacts between stumps and trees. Decay may spread up to 12 m in infected stems (STENLID and WASTERLUND, 1986).

The results of inoculation experiments under greenhouse conditions, used in several studies to test large amounts of plant material in a short period, correlate well with observations and inoculation studies in the field (KUHLMAN, 1970; BUTCHER *et al.*, 1984; STENLID and SWEDJEMARK, 1988; CHASE *et al.*, 1989; CAPRETTI *et al.*, 1994; SWEDJEMARK and STENLID, 1995). DIMITRI and SCHUMANN (1989), showed that the rankings of *P. abies* clones in terms of *H. annosum* growth in sapwood was the same on cuttings as well as on 15-year old trees. However, negative results have also been reported by KUHLMAN (1972). He tested 185 families including some 10 000 seedlings of *Pinus taeda* and found no difference among the 6 provenances studied. Likewise, no difference was detected between two series of *Pinus elliottii* progenies.

The purpose of our study was to estimate the genetic variation in *H. annosum* growth in sapwood and lesion length in the

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