GENETIC PARAMETERS FOR GROWTH, FORM, AND CANKER RESISTANCE OF CUPRESSUS MACROCARPA IN NEW ZEALAND

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ABSTRACT

In two *Cupressus macrocarpa* Gordon progeny tests planted at Strathallan (South Island) and Gwavas (North Island), with 76 New Zealand land race families and 76 Californian families, the land race progenies performed better than the Californian progenies. Among Californian populations Point Lobos showed flatter branch angles than Cypress Point.

Most traits were highly variable and the narrow-sense heritabilities for branching (0.5) and straightness (0.3) were high to moderate. Due to micro-site variability, diameter growth and height showed smaller heritabilities.

Thirty individuals were selected as seed orchard clones, with a maximum of one tree selected per open-pollinated family. Those clones were grafted and planted, initially, in a clonal archive at the New Zealand Forest Research Institute, and will form the basis of any commercial seed orchard planted in the future. Cypress canker is a serious problem for the species and canker resistance has been emphasised in the orchard selections.

Keywords: progeny trials; genetic parameters; cypress canker; Cupressus macrocarpa.

INTRODUCTION

Cupressus macrocarpa has been identified by smaller forest owners in New Zealand as a species with considerable potential for plantation forestry. *Cupressus macrocarpa* comes from a very small area of two separate groves of less than 100 ha on the shores of Carmel Bay on the Monterey Peninsula in California. It is believed to have been introduced into New Zealand about 130 years ago, planted initially in private arboreta but soon used quite extensively for shelterbelts because of its fast growth and wind resistance, particularly when trimmed (Franklin 1994).

A breeding programme for *C. macrocarpa* was started in New Zealand in the early 1980s (C.J.A.Shelbourne & J.T.Miller unpubl. data). In the best-quality stands available, superior trees were selected for stem straightness, above-average growth rate, minimal stem-fluting, and good health. The breeding programme was enhanced with the importation of seed from over 100 open-pollinated families from the natural stands in California (Kafton 1976).

Open-pollinated progeny tests were planted at Strathallan in the South Island and Gwavas in the North Island in 1985. They were intended as a breeding population and as a source of future seed orchard clones for *C. macrocarpa*. The new generation's breeding population will be composed of selections of the best individual per family, with open-pollinated seed collected from those individuals, and used to plant a further progeny test/breeding population (Shelbourne & Miller unpubl. data).

Cypress canker is the major threat to growing *C. macrocarpa* in New Zealand. The canker invades the cambium through small wounds, killing the cambium as it spreads and frequently ring-barking the stems of young trees. The effect ranges from foliage loss, slowing growth, to inducing stem fluting and often the death of the tree. Cypress canker is caused by infection of either of two fungi, *Seiridium unicorne* (Cooke & Ellis) Sutton and *S. cardinale* (Wagener) Sutton & Gibson. The current view (N.M.Self pers. comm.) is that *S. unicorne* is more easily spread but less damaging than *S. cardinale*. The latter produces toxins which cause a bronze coloration and frequently death of most of the crown. Both fungi were identified within the stands at Strathallan and Gwavas.

MATERIAL AND METHODS Seedlots

New Zealand and Californian families were planted in a combined sets-in-reps design. Seedlings of 76 open-pollinated plus-tree seedlots from 29 different stands from both North and South Islands were raised with another 76 open-pollinated families from Californian trees (Table 1) and planted at Gwavas and Strathallan with 24 and 25 trees per family, respectively.

Progenies were segregated according to their New Zealand or Californian origin into separate sets of 19 families, plus a control seedlot. It was expected that these would differ due to the evolution of the New Zealand land race. *Cupressus macrocarpa* hybridises readily with a number of other cypresses, and it is likely that some of the New Zealand land race progenies represent advanced-generation inter-specific hybrids, which may have advantages in form and growth rate. The control seedlot from Longwoods seed-stand was thought to have a mixture of *C. sempervirens* L., and some individuals resembles *C. lusitanica* Miller.

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Provenance	Number of seedlots					
Progenies of plus-trees selected in New Zealand	76 families	26 from the North Island 50 from the South Island				
Progenies of Californian selections.	47 families Cypress Point 29 families Point Lobos	7 subpopulations 6 subpopulations				

TABLE 1–Genetic ma

* Additional Californian families, where stock was insufficient for planting at the pair of sites, were planted in a third site, Mahinapua, which was not assessed.

Assessment

Progenies were assessed at Strathallan and Gwavas in 1992, and again in 1995/96.

The assessments at Strathallan included the following traits:

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- diameter (mm) by tape at ages 7 and 10 years
- height (cm) by poles at age 7
- canker infection, by subjective rating on the following scales at age 7: 1 (no canker) to 4 at age 10: canker infection 1 (no infection) to 7 (heavy infection) and
 - canker severity 1 (nil) to 7 (severe)
- cone production at age 10: 1 (none) to 3 (abundant)
- straightness at age 7: 1 (poor) to 9 (good)
- form at ages 7 and 10: 1 (good) to 9 (malformed)
- branch angle at age 10: 1 (steep) to 9 (flat)
- malformation at age 10: 1 (multi-leader) to 9 (single leader).

Form had been scored in 1992 as a combination of traits, including branch angle, branch diameter, and stem malformation. In 1996 these traits were scored separately, with form then being scored purely on size and regularity of branching. Because growth in the stand was not uniform, the better-grown trees overtopped their competitors and tended to have larger and more vigorous branches. Branch angle was considered an important trait for *C. macrocarpa*, as acute-angled branching (a low score) is thought to be correlated with the stem fluting of older trees and also could provide a better site for canker infection. The greatest benefit of scoring it separately may be to lessen its interference with form and branch angle scoring, and also to document malformation at the individual tree level for computer selections.

At Gwavas only height, form (1-9 scale), and acceptability (0 not acceptable to 1 acceptable) were assessed. A preliminary analysis of the Strathallan canker scoring showed no advantage of the two-trait canker-scoring system, and so it was decided to use the simpler 1 to 4 scale developed in 1992. Because the levels of infection were much higher at Gwavas, the scale was extended to give a separate score of 5 (stem girdled by canker), 6 (recently killed), and 7 (killed in 1992).

Statistical Analysis

The analysis of variance was done for each trait at each site according to the following model:

(1) for the individual-site analysis

$$y_{ijk} = \mu + R_i + P_j + R_i P_j + C_{k(P_j)} + e_{ijk}$$

where

- μ = overall mean,
- R_i = random effect of the ith replicate,
- P_i = random effect of the jth provenance,

 $R_i P_i$ = interaction between the ith replicate and the jth provenance,

 $C_{k(P_i)}$ = random effect of the kth family nested in provenance,

 e_{iik} = random error of the tree.

(2) for the combined-site analysis

 $y_{ijk} = \mu + S_i + P_{j(S_i)} + F_k + S_i F_k + e_{ijk}$

where in addition to the factors assumed before there is a random effect of the site (S_i) and the interaction between family and site (S_iF_k) .

Sums of cross products were generated from the data for each site using the MANOVA option of PROC GLM and covariance components were derived from these using SAS/IML. Variance components per site were calculated using PROC MIXED. Genetic correlations were derived from covariance components and phenotypic family mean correlations were generated by the SAS procedure PROC CORR.

The across-site analysis was performed on four traits at age 7 (height, form, cone production, and canker infection) in order to estimate levels of genotype \times environment interaction.

Heritabilities, of individual trees and families, were calculated for each site and for each provenance within site as:

$$h_{ns}^{2} = \frac{4 \times \sigma_{f}^{2}}{\sigma_{f}^{2} + \sigma_{e}^{2}}$$
$$h_{F}^{2} = \frac{\sigma_{f}^{2}}{\sigma_{f}^{2} + \frac{\sigma_{e}^{2}}{n}}$$

where: h_{ns}^2

 h_F^2 = heritability of family means

= narrow-sense heritability of individual trees

 σ_f^2 = family variance component

 r_e^2 = error variance component

n = mean number of replications

Heritabilities were calculated using variance components for family-in-provenance and the interaction between family and site. Heritabilities for the across-site analysis were calculated as:

$$h_{ns}^{2} = \frac{4 \times \sigma_{f}^{2}}{\sigma_{f}^{2} + \sigma_{fs}^{2} + \sigma_{e}^{2}}$$
$$h_{F}^{2} = \frac{\sigma_{f}^{2}}{\sigma_{f}^{2} + \frac{\sigma_{fs}^{2}}{2} + \frac{\sigma_{e}^{2}}{n}}$$

where σ_{fs}^2 = family within-provenance × site interaction variance component

A selection index (Falconer 1989) for the best families and the best individuals per family was constructed to identify the best candidates for the breeding population and seed orchards.

RESULTS

Provenance Differences, Variance Components, and Heritabilities

There were appreciable differences between provenances, with the New Zealand land race material generally performing better for most traits at both sites and Californian populations significantly inferior in growth rate and more affected by canker (Table 2). The poorer growth performance of the Californian progenies presumably reflects a degree of neighbourhood inbreeding which can be expected in natural stands. The better straightness and canker resistance would be expected as a result of phenotypic selection of the New Zealand parents. The differences among the Californian populations (Cypress Point *v*. Point Lobos) and local populations (North Island *v*. South Island selections) were also tested in the

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Trait / age	New Zealand	Californian provenances		
C C	provenances			
Strathallan				
Form / 7	4.92a	5.34b		
Canker / 7	1.15a	1.14a		
Cones / 7	1.14a	1.03b		
Height / 7	43.19a	39.36b		
Diameter / 7	82.15a	70.04b		
Straightness / 7	6.35a	5.94b		
Diameter / 10	159.36a	146.66b		
Branching / 10	5.45a	5.53a		
Form / 10	5.9a	5.36b		
Malformation / 10	8.38a	8.31b		
Cones / 10	0.97a	0.41b		
Canker infection /10	2.03a	3.41b		
Canker severity / 10	0.22a	0.36b		
Gwavas				
Form / 7	4.49a	4.20b		
Canker / 7	2.3a	2.45b		
Cones / 7	1.16a	1.09b		
Height / 7	40.97a	36.5b		
Acceptability / 11	3.94a	4.68b		
Canker / 11	0.57a	0.32b		

TABLE 2-Family means by provenances at both sites. Significant differences using Bonferoni's test with Alpha=0.05 are shown next to the mean values

analysis of variance. There were no differences for any trait on any site between North and South Island progenies; however, there were statistically significant differences among the Point Lobos and Cypress Point populations for branching characteristics, with the Point Lobos population presenting flatter branch angles at age 10 (5.74) than Cypress Point (5.39) (data not included in tables).

Variance components and heritability estimates for New Zealand and Californian progenies at both sites are shown in Table 3. There was an overall trend of higher heritabilities for the New Zealand than the Californian populations, except for branching at Strathallan and height and acceptability at Gwavas.

Analysis of variance for Gwavas and Strathallan (Table 3) showed a wide variability among families for all traits assessed. Canker assessments at Strathallan at age 11 showed low heritabilities. The scoring method for canker used at Strathallan was chosen with the aim of quantifying damage to the crown and potential severity, with separate scores for each category. It was disappointing that it did not differentiate family means well, although it would be useful for describing the status of the stand. The Gwavas expanded scale gave good heritabilities and much better information on family performance, both as family means and as frequency distributions of individual values within each family.

The across-site analysis of variance showed a significant level of genotype × environment interaction only for canker infection; this was the consequence of the patchy incidence of infection at Strathallan, mostly associated with areas of poor growth that introduced too much environmental variation. Variance component and across-site heritability estimates

Trait / age		New Zealand	d provenances		Californian populations					
	Family variance	Error variance	Individual h ²	Family h ²	Family variance	Error variance	Individual h ²	Family h ²		
Strathallan										
Form / 7	0.091***	1.347	0.25	0.59	0.052***	1.205	0.17	0.51		
Canker / 7	0.045	0.223	0.67	0.81	0.002	0.203	0.04	0.19		
Cones / 7	0.009***	0.140	0.24	0.58	0.002***	0.030	0.19	0.55		
Height / 7	2.706***	49.930	0.21	0.54	1.137***	46.300	0.10	0.37		
Diameter / 7	28.950***	793.210	0.14	0.44	11.600***	761.060	0.06	0.27		
Straightness / 7	0.131***	1.940	0.25	0.59	0.198***	2.250	0.32	0.68		
Diameter / 10	64.207*	1327.500	0.18	0.50	14.550*	1362.250	0.04	0.20		
Branching / 10	0.316***	2.400	0.47	0.73	0.350***	2.310	0.53	0.78		
Form / 10	0.200***	3.160	0.24	0.56	0.264***	3.260	0.30	0.66		
Malformation / 10	0.067***	2.089	0.12	0.39	0.040***	2.320	0.07	0.29		
Cones / 10	0.126***	1.030	0.44	0.71	0.047***	0.660	0.27	0.63		
Canker infection / 10	0.190*	53.880	0.01	0.07	2.094*	89.480	0.09	0.36		
Canker severity / 10	0.006*	0.419	0.06	0.23	0.035*	0.670	0.20	0.56		
Gwavas										
Form / 7	0.052***	0.713	0.27	0.54	0.036***	0.577	0.23	0.50		
Canker / 7	0.047***	1.103	0.16	0.43	0.020***	1.449	0.06	0.20		
Cones / 7	0.013***	0.127	0.36	0.62	0.005***	0.080	0.23	0.49		
Height / 7	4.265***	70.439	0.23	0.49	3.985***	53.612	0.28	0.54		
Acceptability / 11	0.019***	0.367	0.19	0.36	0.016***	0.219	0.27	0.45		
Canker / 11	0.201***	1.815	0.40	0.65	0.041***	1.582	0.10	0.31		

TABLE 3-Variance component estimates, individual heritabilities, and family mean heritabilities by provenances at both sites. Significant difference	s for
the ANOVA are shown next to the values.	

(Table 4) were poor for canker infection (0.02) but moderate for height (0.2) and form (0.17). Cone production showed the highest values (0.22).

Trait /age	Family within provenance	Family within provenance × site interaction	Error	h ² _{ns}	$h_{\rm F}^2$
Height age 7	2.41ns	0.37ns	55.57	0.16	0.43
Form age 7	0.046ns	0.013ns	1.012	0.17	0.43
Cone age 7	0.006ns	0.0004ns	0.100	0.22	0.52
Canker age 7	0.005**	0.015***	0.708	0.02	0.10

TABLE 4-Variance components, individual heritabilities, and family mean heritabilities for the across-site analysis. Significant differences for the ANOVA are shown next to the values.

Phenotypic Correlations of Family Means, and Genetic Correlations

There were strong significant phenotypic correlations between family mean for height at Gwavas (age 7) with height at Strathallan (age 7) (0.88), and between height at Gwavas with diameter at each Strathallan assessment (age 7 = 0.90, and age 10 = 0.80) (Table 5). Withinand across-site genetic correlations for growth traits (height and diameter) were also high. Negative phenotypic and genetic correlations among canker resistance with form and acceptability at both sites could be explained because the canker often causes malformation and loss of apical dominance due to leader damage and adverse effects of toxins. Cone production for both sites and assessments has shown very high family mean phenotypic and genetic correlations.

Selection Index

It was anticipated that there would be difficulties in arriving at an ideal index for selecting superior individuals because of some negative correlations between traits (e.g., canker – height). This guaranteed dilution of gain in any one trait for each of the other traits which were also chosen. The first attempt included all traits at both sites, and was unsatisfactory. Strathallan was then chosen as the best site to select candidate trees for the breeding population and seed orchard clones because it showed the better estimates of heritabilities and genetic parameters. The final index was constructed using family information on canker (age 11) at Gwavas, and height, straightness (age 7), branching, and form (age 10) at Strathallan, as gains in these traits were considered the most valuable. The index weighted these traits in equal proportions except for canker where the economic weight was trebled due to the importance of the trait, its moderate heritability, and its slightly negative correlation with height.

The top 30 families were identified for seed orchard purposes. Some Californian families from outside this group were also identified, especially those from Point Lobos, because their family means might have been disadvantaged by inbreeding and also there is a possibility of heterosis with the inclusion of fresh genes. Groups of selected progenies were compared with the mean of all selected families, and the mean of the control seedlot (Table 6). The seedlot from the Longwoods seed stand, used as the control, produced values for branching similar to those of the selected families, but lower scores for form, canker resistance, and height.

	Gwavas / 7				Gwava	as / 11	Strathallan / 7				Strathallan / 10								
	Height	Form	Canker	Cones	Canker	Accept.	Diameter	Height	Straight.	Form	Canker	Cones	Diameter	Ca	nker	Branch.	Form	Malform.	Cones
				1									1	Infectior	n Severity				
Gwavas	/7												 						
Height		0.68	0.25	0.35	-0.16	0.61	0.90	0.88	-0.06	0.41	-0.04	0.64	0.80	0.22	-0.22	-0.02	0.42	-0.08	0.58
Form	0.52		-0.06	0.33	-0.16	0.57	0.80	0.88	0.16	0.77	0.18	0.61	0.74	0.04	-0.39	0.45	0.65	0.24	0.48
Canker	-0.12	-0.17		0.32	0.44	-0.13	0.20	0.05	-0.21	-0.08	0.24	0.04	0.26	0.61	0.45	0.08	-0.19	-0.01	0.06
Cones	0.29	0.21	-0.03		0.15	0.04	0.40	0.34	-0.11	0.24	0.20	1.26	0.39	0.07	-0.09	0.39	0.32	-0.12	0.72
Gwavas	/ 11												 I						
Canker	-0.35	-0.22	0.69	-0.07	I	-0.76	-0.31	-0.36	-0.27	-0.21	-0.03	-0.12	0.22	0.65	0.42	0.01	-0.27	-0.59	-0.17
Accept.	0.56	0.45	-0.35	0.07	-0.64		0.54	0.59	0.40	0.28	0.00	0.22	0.48	-0.05	-0.28	-0.98	0.52	0.19	0.46
Strathal	lan / 7				1								1						_
Diameter	0.58	0.33	-0.10	0.31	. –0.28	0.34		0.84	0.30	0.47	0.37	0.48	0.94	-0.06	-0.13	-0.14	0.61	-0.04	0.57
Height	0.64	0.45	-0.14	0.28	-0.32	0.40	0.84		0.37	0.73	0.33	0.52	0.75	-0.20	-0.21	0.01	0.54	0.14	0.54
Straight.	0.12	0.11	-0.02	-0.04	-0.11	0.25	0.18	0.25		0.41	-0.10	0.14	0.20	-0.39	-0.36	-0.22	0.65	0.42	0.19
Form	0.27	0.49	-0.13	0.16	-0.15	0.21	0.32	0.58	0.40		0.02	0.41	0.41	-0.56	-0.37	0.59	0.77	0.52	0.35
Canker	0.02	-0.07	0.12	-0.10	0.12	-0.05	0.09	0.08	0.10	-0.11		0.03	0.44	0.75	0.33	0.03	-0.08	0.00	0.08
Cones	0.33	0.32	-0.16	0.56	-0.26	0.23	0.31	0.37	0.07	0.24	-0.06		0.38	-0.25	-0.21	0.13	0.30	0.15	0.90
Strathal	 lan / 10				· 								+ · 						
Diameter	0.57	0.31	-0.11	0.30	-0.24	0.32	0.91	0.75	0.15	0.30	0.08	0.20	I	0.01	-0.06	-0.12	0.20	-0.07	0.56
Canker	_0.17	_0.10	0.23	_0 14	0.36	-0.17	_0.25	-0.23	_0.20	0.15	0.26	_0 19	-0.18		1 22	-0.18	-0.62	-0.23	-0.25
Canker	-0.17	0.10	0.25	0.14	0.50	0.17	0.25	0.25	0.20	0.15	0.20	0.17	0.10		1.22	0.10	0.02	0.20	0.20
severity	-0.19	-0.19	0.22	-0.16	0.37	-0.22	-0.21	-0.24	-0.24	-0.21	0.28	-0.19	i —0.16	0.89		-0.04	-0.40	-0.24	-0.24
Branch.	-0.11	0.28	-0.04	0.04	0.08	-0.10	-0.20	-0.08	-0.19	0.46	-0.06	0.09	-0.17	0.09	0.05		0.33	0.46	-0.01
Form	0.24	0.35	-0.09	0.09	-0.18	0.28	-0.05	0.24	0.50	0.57	-0.13	0.17	-0.08	-0.20	-0.27	0.34		0.89	0.31
Malform.	-0.12	0.11	-0.01	-0.10	I0.10	0.11	-0.17	0.05	0.28	0.37	-0.21	0.04	-0.16	-0.05	-0.12	0.25	0.56		0.31
Cones	0.47	0.38	-0.22	0.47	-0.35	0.36	0.49	0.50	0.16	0.24	-0.04	0.70	0.45	-0.20	-0.23	-06	0.17	0.11	

TABLE 5-Phenotypic (below) and genetic (above) correlations of family means within and among sites

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Variable	Control means (Longwood)	Mean of 153 families	Mean of top 30 selected families	Mean of top 10 selected families
Canker score	3.92	4.30	3.31	2.93
Height	42.78	41.34	43.81	43.86
Straightness	6.17	6.15	6.44	6.50
Branching	5.80	5.48	5.70	5.75
Form	5.87	5.66	6.27	6.30

TABLE 6-Comparison of mean values for the control and selected families

The means for the 76 New Zealand selected families show gains over the control for all traits except branching, with high gains on canker resistance. The group of the top 30 selected families included one Californian family from Cypress Point. The group of the top 10 families showed gains over the control for all traits. It can be seen from these figures that selecting families for canker resistance has resulted in improvement in stem form.

CONCLUSIONS

The assessment of the *C. macrocarpa* progeny tests revealed a wide variability between and within families in most traits. The narrow-sense heritabilities for branching (0.5) and straightness (0.3) were high to moderate. Due to micro-site variability, growth measured by either diameter and height showed lower heritabilities. Canker resistance scores used at Gwavas showed a higher narrow-sense heritability (0.4 to 0.1) than those generated by the two-trait canker assessment at Strathallan (0.2 to 0.01).

New Zealand progenies grew faster than the Californian progenies, they had higher heritabilities for many traits and were less susceptible to canker. The progenies of Longwood selections had flat branch angles and very good form but these advantages were offset by below-average canker resistance.

Kafton (1976) postulated that no domesticated *C. macrocarpa* has been derived from the Point Lobos population because access to this area was difficult; the seaward side of the stand is bounded by steep cliffs, and, until recently, access from the eastern side was prohibited by an inhospitable landowner. This population therefore represents a source of genes not previously sampled in the New Zealand land race. Furthermore, a new round of selection and breeding should create additional gains in growth rate from outcrossing.

Thirty individuals were identified as seed orchard candidates, with a maximum of one tree selected per open-pollinated family. Those clones were grafted and planted, initially, in a clonal archive at New Zealand Forest Research Institute, and will form the basis of any commercial seed orchard planted in the future, with the possibility of some added genetic gain from roguing based on further assessment of the progeny tests. The development of flower stimulation and controlled-pollination techniques (D.Franklin & P.Milne pers. comm.), and a vegetative multiplication system for *C. macrocarpa* will have an impact on any decisions for seed orchard establishment. It is probable that the current requirement for 100–200 kg *C. macrocarpa* seed could be much reduced if controlled-pollinated seedlings were multiplied vegetatively. If production of *C. macrocarpa* × *C. lusitanica* hybrids is advocated, a clonal forestry strategy would be necessary to select, multiply, and deploy good hybrid clones.

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Canker caused by *S. unicorne* and *S. cardinale* is a major problem and resistance to canker was heavily weighted in the selection index.

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