

1985), but if this is the case, then the relationship is not straightforward. The monoterpenes of all the *P. radiata* provenances are similar, being composed mainly of α -pinene and β -pinene (BANNISTER and McDONALD, 1983). In *P. muricata* there is wide variation in monoterpene composition. Oleoresin of the Trinidad Head population is largely α -pinene. For the other northern populations it is mainly 3-carene, while for the southern populations, mainly sabinene (MIROV *et al.*, 1966). This variation is not related to susceptibility to either aphid species in any simple way.

It is more likely that resistance involves various active resistance responses (ROHFRIE, 1988) as well as anatomical, chemical and nutritional characteristics of the host (HANOVER, 1975) and if so would be polygenetically inherited. BARNES *et al.* (1976) reported genetic variation in susceptibility to *P. pini* in several *Pinus* species in Zimbabwe (then Rhodesia) and estimated narrow sense heritability as 0.65 for severity of infestation of *P. elliottii*. They also suggested that maladaptation to the planting site was an important factor predisposing trees to attack. This could explain why their local population of *Pinus patula* was less susceptible to *P. pini* than provenances from natural populations in Mexico, even though the pest had only recently been introduced to southern Africa and there could have been no direct selection for resistance.

In the trials reported here, the rankings of the provenances for susceptibility to both species of aphid were stable over both sites, suggesting that there is minimal genotype x site interaction, even though the soils had very different nutritional status. However, infestation of *P. muricata* by *E. thunbergii* was much greater at site one, the less fertile site which is deficient in nitrogen, phosphorus, calcium and magnesium (SIMPSON and ADES, unpubl. data), suggesting that physiological stress may increase susceptibility to that species also.

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Genetic Parameters and Predicted Selection Responses for Growth and Wood Properties in a Population of *Araucaria cunninghamii*

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Summary

Growth traits, stem straightness and wood properties were assessed in a hoop pine (*Araucaria cunninghamii*)

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progeny trial in south-eastern Queensland at 15 years of age. Estimates of narrow-sense heritability for height, diameter and straightness were 0.19, 0.22 and 0.61 respectively. For wood properties, the estimates for spiral grain angle, compression wood percentage and basic density were 0.33, 0.44 and 0.83 respectively. These estimates

indicated that a range of responses to phenotypic selection for single traits would occur, with substantial response expected for basic density. Heritability of spiral grain angle assessed in wood segments of different ages up to 15 years reached a maximum value of 0.35 near the pith where phenotypic expression of spiral grain was largest.

Genetic correlations between traits were generally favourable and ranged from small to medium. The correlations led generally to small or moderately favourable predicted indirect responses to selection when compared with direct responses for individual traits. The strongest adverse genetic correlation (0.16) was estimated for basic density and spiral grain angle, but only resulted in small adverse predicted indirect responses for two traits. A selection index combining growth, straightness and wood properties was more efficient in selecting for improved growth, and was not strongly detrimental to other traits. A strategy of restricting genetic change in basic density to zero still allowed substantial gains in other traits without exacerbating the effects of compression wood or spiral grain. Therefore, it appeared the assessed population of hoop pine would respond favourably to selection to improve growth and stem straightness without adverse effects on wood properties. Implications for the genetic improvement of hoop pine in Queensland are discussed.

Key words: *Araucaria*, heritability, correlation, genetic gain, growth, straightness, wood properties.

Introduction

In order to improve the productivity of plantation forests, tree-breeding programmes exploit, genetically variable populations to develop superior trees. A basic knowledge of the genetic characteristics of the populations is necessary to conduct effective breeding and selection. Quantitative information is required about the size of genetic variances, the type of gene action, and the heritability and genetic correlations for economically important traits. This enables the outcome of selection, particularly genetic gains, to be predicted. It also helps to determine likely difficulties in selection and the strategies to overcome such problems. In a wider context, it broadens knowledge of the genetics and breeding behaviour of the species involved.

In Queensland, the Department of Forestry conducts a tree-breeding programme to improve plantation-grown hoop pine (*Araucaria cunninghamii* ARTON ex D. DON). The main objectives are to improve the growth rate and quality of the species (NIKLES, 1980). Most emphasis in breeding and selection has been placed on vigour, and on quality characteristics such as bole straightness. Wood properties were not considered in initial selection. Subsequently, candidate trees for inclusion in wind-pollinated seed orchards were screened and trees with unsatisfactory wood properties, such as excessive spiral grain, were rejected (SMITH, 1980). Wood density in hoop pine is considered satisfactory for its current range of end uses and there is no plan at present to change density by selection.

Very little genetic information about hoop pine populations is available, particularly for wood properties (SMITH, 1980). Such information is required to guide breeding strategy and to evaluate the likely results of selection. However, measurement of wood properties is time-consuming and expensive, and usually cannot be undertaken on young trees which may be suitable for assessments of growth and form. In Queensland, progeny tests of hoop pine suitable for studying wood properties have only

recently become available. The aim of this paper is to present a genetic analysis for a population of hoop pine to help overcome the general lack of quantitative genetic information. The genetic analysis will enable preliminary conclusions to be drawn about the extent to which wood properties can be improved by selection, the effectiveness of phenotypic selection for growth and wood properties, and the likely effects on wood properties of selection for improved growth and bole straightness.

Materials and Methods

Experimental details

Data for the study came from a progeny trial growing near Imbil in south-eastern Queensland (latitude 26° 28' S). The trial site, on a brown and red-brown clay loam, with a 10° to 15° slope, originally carried rainforest which was cleared in 1937 and planted with kauri pine (*Agathis robusta* (C. MOORE ex F. MUELL.) BAILEY). Poor survival of the kauri pine led to re-clearing of the site and planting of the progeny trial. The hoop pine seedlings were raised in a nursery under uniform, intensively managed conditions. Seedlots, sown in February 1967, were maintained in nursery beds until four months prior to planting in the field, when the most vigorous seedlings in each seedlot were transferred to individual planting tubes.

The experimental design used in the field was a randomized complete block with six replications of a single row plot per treatment. There were 10 trees per row plot. Seedlings were planted by hand at a spacing of 3.0 m × 2.4 m in December 1968. Hot, dry conditions at planting resulted in a 4% loss of seedlings. Losses were replaced four months after the initial planting. At the time of this study, after 15 years, survival was better than 95%.

Of the 27 treatments in the trial, 25 were progeny lots (half-sib families) grown from wind-pollinated seeds collected from phenotypically superior ortets standing in plantations around Imbil. The ortets were selected for high growth rate and good bole straightness. The two remaining treatments were seedlots of different origin and their data were excluded. Differences in the flowering behaviour of the ortets whose progeny were included in the trial suggested that they originated from at least two different provenances in south-eastern Queensland. Therefore, differences between provenances may have contributed to the genetic variability measured in this study. However, for the purposes of this study provenance differences were ignored because the hoop pine programme has been based on a single breeding population of trees from different provenances and this study was seeking to determine parameter estimates applicable to that population.

Measurements

One replication containing trees damaged by wind was excluded from this study. Three trees per family were sampled at random from each plot in the remaining five replications after excluding unrepresentatively small, damaged and mis-shapen trees. Data recorded included diameter over bark at breast height (1.3 m above ground), tree total height, and bole straightness scored on a points scale from 1 (crooked) to 6 (straight).

To assess wood properties of the sampled trees, a 12 mm diameter core of wood was taken from the inter-whorl closest to 1.2 m above ground level using an increment borer. This wood sample was obtained as either a single core taken straight through the tree to include the pith, or as two bark-to-pith cores, one taken at 180° to the

other. Core sampling was at right angles to the lean of the tree, or to the prevailing wind direction if no lean was detectable. This sampling strategy was adopted to avoid confounding the assessment of basic density in core samples with large and variable amounts of compression wood caused by basal sweep. Some trees showed a pronounced basal sweep, attributable to severe wind damage at 3.25 years of age. Generally this sweep was below the sampling point and was therefore avoided.

Wood samples were sealed in plastic bags and frozen until processed in the laboratory. Grain angle for the cambial layer was recorded in the field on both sides of each tree adjacent to the core sampling point using the methods and equipment described by HARRIS (1984). The cambial measurement provided a reference angle for adjusting grain angles measured on inner core segments.

For laboratory measurements of grain angle and compression wood, the moist wood core from each radius was machined with an electric planer to give a transverse section approximately seven millimetres thick. To assess compression wood, a sector was drawn on the machined surface from pith to cambium and the section illuminated from below. The proportion of the sector containing compression wood was obtained by counting dots on an overlying grid. Results from the two cores for each tree were averaged to give the percentage of compression wood in the tree.

Grain angles were measured at six equally spaced points along each radial core section using a projection microscope. As detailed in HARRIS (1984), these were adjusted to actual grain angles in the tree using field and laboratory measurements available for the cambial layer. The final grain angle for each core segment in each tree was expressed as the arithmetic mean of the angles for corresponding segments from opposite radii in the tree. Mean grain angle for the whole tree was calculated as the arithmetic mean of the angles for the six core segments, ignoring differences in sign. Variation in grain angle occurring in each tree was quantified by the standard deviation of angles across the six core segments.

Basic density was measured as the ratio of oven dry mass to maximum saturated volume for individual cores. Volume was determined by the method of HEINRICHS and LASSEN (1970). Data for the two radial cores from each tree were averaged to give a mean value for the tree. Resin was not extracted before basic density was determined because hoop pine lacks resin canals and therefore generally gives a low yield of extractives.

Analysis

A linear model containing random block, family and error effects was used for analysis of variance to estimate variance components for all traits. Standard errors were calculated using formulae given by BECKER (1975). Narrow-sense heritability (h^2) for each trait, expressed on the basis of selecting an individual tree, was calculated as:

$$(1) \quad h^2 = 4\sigma_f^2 / \sigma_p^2$$

with the phenotypic variance (σ_p^2) obtained as:

$$(2) \quad \sigma_p^2 = \sigma_b^2 + \sigma_f^2 + \sigma_e^2 + \sigma_w^2$$

where σ_b^2 is the variance component for blocks;
 σ_f^2 is the variance component for families;
 σ_e^2 is the variance component for plots;
 and σ_w^2 is the variance component for trees.

Standard errors on h^2 were estimated using formulae detailed by GORDON *et al.*, (1972).

Genetic correlations between traits were estimated from analysis of covariance, and the phenotypic correlations were estimated by obtaining simple correlation coefficients of individual tree values. Standard errors for estimates of genetic correlations were calculated using the method of TALLIS (1959), while those for phenotypic correlations were obtained using a formula given by STEEL and TORRIE (1960). Predicted response to selection for each trait under mass selection was estimated (BECKER, 1975) as:

$$(3) \quad PR = i\sigma_p h^2$$

where i is the selection intensity.

Predicted responses to indirect selection for pairs of traits were also calculated. The indirect response expected in trait y through selection for trait x was calculated (FALCONER, 1960) as:

$$(4) \quad IR_{(x,y)} = ih_{(x)} h_{(y)} r_g \sigma_p(y)$$

where r_g is the genetic correlation between traits x and y .

The relative selection efficiency of indirect selection for trait y through trait x was expressed (SEARLE, 1965) as:

$$(5) \quad RSE_{(x,y)} = r_g h_{(x)} / h_{(y)}$$

To examine simultaneously the combined effects of selection on all traits, several multi-trait selection indices were calculated. These were constructed primarily to help assess the likely effects of selection in this population of hoop pine. Standard Smith-Hazel indices, combining six traits (diameter, height, straightness, basic density, compression wood and mean spiral grain angle), were derived using the computer program RESI (COTTERILL and JACKSON, 1981). Sets of economic weights were varied to give equal emphasis weighting (COTTERILL and JACKSON, 1985), and a 100-fold emphasis on either growth traits alone or on growth and straightness traits. A restricted index (COTTERILL and JACKSON, 1981) which constrained genetic change in basic density to zero was also derived for each set of economic weights. The effects of selection using these indices were assessed by examining the correlated responses predicted to occur in individual traits. As for indirect selection involving pairs of traits, the relative selection efficiency of index selection was calculated as the proportion of the direct single-trait response for each trait achieved by index selection.

Results and Discussion

Heritabilities

Estimates of means, variance components, heritabilities and their standard errors for growth, straightness and wood traits are given in Table 1. Also included is spiral grain deviation, expressed as the standard deviation of grain angles across the six core segments. Of the wood

Table 1. — Estimates of overall means ($\hat{\mu}$), variance components ($\hat{\sigma}^2$), and heritabilities (\hat{h}^2) for growth, form and wood properties.

Estimate	Trait							
	Diameter (cm)	Height (m)	Straightness (1-6)	Basic density (kg m ⁻³)	Compression wood (%)	Mean spiral grain angle (°)	Spiral grain deviation (°)	
$\hat{\mu}$	17.43 ± 0.15 ^c	15.92 ± 0.12	2.21 ± 0.04	459.6 ± 1.38	8.09 ± 0.39	3.59 ± 0.08	1.465 ± 0.039	
$\hat{\sigma}_b^2$	1.151 ± 0.730	2.170 ± 1.289	0.014 ± 0.011	46.72 ± 30.94	2.160 ± 1.700	0.232 ± 0.147	0.0041 ± 0.0054	
$\hat{\sigma}_f^2$	0.474 ± 0.300	0.257 ± 0.164	0.073 ± 0.028	147.03 ± 50.51	6.332 ± 2.888	0.198 ± 0.087	0.0257 ± 0.0148	
$\hat{\sigma}_e^2$	0.757 ± 0.445	0.794 ± 0.234	0.006 ± 0.023	-1.28 ± 28.89	4.901 ± 3.065	-0.089 ± 0.098	-0.0481 ± 0.0243	
$\hat{\sigma}_w^2$	6.224 ± 0.554	2.315 ± 0.206	0.389 ± 0.035	517.56 ± 46.11	43.622 ± 3.886	1.937 ± 0.173	0.5329 ± 0.0470	
\hat{h}^2	0.22 ± 0.14	0.19 ± 0.12	0.61 ± 0.20	0.83 ± 0.24	0.44 ± 0.19	0.33 ± 0.14	0.18 ± 0.10	

a) $\hat{\sigma}_b^2$, $\hat{\sigma}_f^2$, $\hat{\sigma}_e^2$, $\hat{\sigma}_w^2$ are variance components for blocks, families, plots and trees within plots, respectively.

b) Standard deviation of pith to cambium spiral grain values.

c) Standard error of the estimate.

properties, mean basic density and spiral grain angle are comparable to those found previously in plantation grown hoop pine of similar age in south-eastern Queensland (SMITH, 1980). The mean compression wood percentage under-estimates the expression of this character because sampling perpendicular to tree lean avoided its worst occurrence. The extent of the downward bias in estimating the level of compression wood is likely to be substantial, but realistic estimates of basic density were considered more important.

Family variance components in *Table 1* were significantly greater than zero for all traits, as were the block components except for spiral grain deviation. Thus genetic variation was expressed for all traits measured in the assessed hoop pine population despite initial phenotypic selection for growth and straightness. The variance among trees within plots represented the largest component of variation for all traits, however, ranging from about 42% of the total phenotypic variance for height to 95% for spiral grain.

The heritabilities for different traits in *Table 1* vary widely. However, for mass selection of individual trees, all fall within a range of intermediate to high in terms of the likely response to selection. The estimates are conservative because block variance was included in the phenotypic variance for each trait. Ignoring block variance in calculating heritabilities for individual tree selection may considerably over-estimate the heritability, particularly where block variance is relatively large, as for height in this study (*Table 1*). Diameter and height had moderate heritabilities of 0.22 and 0.19 respectively. The heritabilities are similar to estimates for other plantation-grown species in Australia, including *P. caribaea* var. *hondurensis* (DEAN *et al.*, 1986) and *P. radiata* (DEAN *et al.*, 1983). No comparable estimates are available for hoop pine, although recent studies of other Queensland hoop pine populations gave similar results (DEAN *et al.*, 1988). Stem straightness had a higher heritability than the growth traits (0.61, *Table 1*), which contrasts with lower estimates for exotic pines in Australia of around 0.3 or less (DEAN *et al.*, 1983; DEAN *et al.*, 1986).

The heritability of 0.83 for basic density is very high, while those for compression wood (0.44) and mean spiral grain (0.33) are also relatively high (*Table 1*). Therefore, these three traits, and in particular basic density, appear quite amenable to phenotypic selection. Furthermore, it could be anticipated that the traits will show less genetic-environmental interaction than the growth traits over a broader range of environments, given their stronger inheritance (*Table 1*). These factors simplify the breeding and selection procedures necessary to manipulate wood properties in hoop pine.

Published heritabilities for wood density in other species vary greatly (NICHOLLS *et al.*, 1964; SHELBORNE *et al.*, 1969; ZOBEL, 1964). Estimates are often high (>0.7) and comparable with the results obtained in this study. Twenty-one of the 25 parents were screened for wood properties prior to this study by sampling the ortets. Parent-offspring regression using ortet whole core values and progeny data gave a heritability of 0.66 for basic density, in reasonable agreement with the main study estimate. The high heritability of basic density may result from the slow growth rate of hoop pine. The characteristic uniformity of its wood and the small pith to bark density gradient also suggest that wood production is insensitive

to micro-environmental conditions. Such insensitivity would enhance the expression of genetic differences.

Compression wood is a significant feature of wood quality in hoop pine because the species is used extensively in veneer and joinery production. Although wind damage was expected to influence phenotypic expression of compression wood rather strongly, the heritability estimate of 0.44 was reasonably high (*Table 1*). It is not clear how sampling strategy affected the expression of genetic differences. However, since the strategy attempted to minimise the sampling of compression wood in each tree, it is surmised that this reduced the environmental variance for this trait, making the heritability higher than would be expected from random sampling of wood cores from each tree.

For spiral grain, the means, variance components and heritabilities for separate core segments are given in *Table 2*. Mean grain angles across the six segments show a typical trend, with an early peak in the juvenile wood and a gradual decline in later-formed wood (NICHOLLS, 1967). Heritability estimates vary from 0.12 for segment 2 to 0.35 for segment 3. Apart from the aberrant value for segment 2, the estimates show a high to low trend from pith to bark corresponding to that for the segmental grain angles. This trend has also been found in other coniferous species (NICHOLLS *et al.*, 1964). Heritability for spiral grain appeared to peak at the time of its maximum phenotypic expression (*Table 2*). The decline in heritabilities in later-formed segments resulted from a large loss of genetic variance and also a reduction in phenotypic variance for grain angle. Results for segment 2 deviate from the general pattern, and may be attributable to the substantial disorientation of trees resulting from the wind damage mentioned previously. Such disturbance may have altered patterns of growth sufficiently to mask the expression of genetic differences until the trees recovered, although the mean grain angle for this segment does not seem anomalous when compared to that for other segments (*Table 2*).

Spiral grain heritabilities suggest that responses to selection should occur for mean pith to bark grain angle (*Table 1*), and also for grain angle in juvenile wood close to the pith where maximum phenotypic expression of grain spirality occurs (*Table 2*). However, genetic variance in juvenile segments close to the pith is much larger, and larger responses to selection would be expected there for spiral grain angle. Genetic variation in both mean spiral grain angle and the standard deviation of angles across segments (*Table 1*) indicated there were genetic differences in the characteristic pattern of grain angles from pith to bark. Therefore, selection to alter the pattern of expression of spiral grain would be possible by combining these two traits in selection to reduce both the level and variability of spiral grain from pith to bark.

However, a simple alternative strategy would be to select for reduced juvenile grain angle close to the pith. This would reduce the strongest expression of spiral grain, and would also indirectly influence the variability of grain angles from pith to bark. Such a strategy could simplify sampling to assess spiral grain by confining it to a single measurement *in situ* on juvenile trees, thus avoiding more time-consuming laboratory analysis.

Genetic and Phenotypic Correlations

Table 3 shows the correlations estimated in this study. Phenotypic correlations varied from small negative to

Table 2. — Estimates of overall means ($\hat{\mu}$), variance components ($\hat{\sigma}^2$), and heritabilities (\hat{h}^2) for spiral grain angle measured in pith-to-bark wood cores segmented into six equal lengths.

Estimate	Core segment numbered from pith					
	Segment 1 (°)	Segment 2 (°)	Segment 3 (°)	Segment 4 (°)	Segment 5 (°)	Segment 6 (°)
$\hat{\mu}$	3.85 ± 0.12 ^b	3.92 ± 0.12	4.15 ± 0.12	3.83 ± 0.10	3.49 ± 0.10	2.31 ± 0.08
$\hat{\sigma}_b^2$	0.20 ± 0.14	0.16 ± 0.13	0.54 ± 0.35	0.28 ± 0.18	0.20 ± 0.14	0.31 ± 0.09
$\hat{\sigma}_f^2$	0.41 ± 0.18	0.15 ± 0.12	0.46 ± 0.21	0.18 ± 0.11	0.17 ± 0.11	0.08 ± 0.06
$\hat{\sigma}_e^2$	-0.58 ± 0.21	-0.18 ± 0.24	0.08 ± 0.25	-0.15 ± 0.18	0.08 ± 0.18	0.03 ± 0.11
$\hat{\sigma}_w^2$	5.00 ± 0.45	4.67 ± 0.42	4.24 ± 0.38	3.61 ± 0.32	3.12 ± 0.28	1.94 ± 0.17
\hat{h}^2	0.29 ± 0.12	0.12 ± 0.10	0.35 ± 0.15	0.17 ± 0.11	0.19 ± 0.12	0.15 ± 0.11

a) $\hat{\sigma}_b^2$, $\hat{\sigma}_f^2$, $\hat{\sigma}_e^2$, $\hat{\sigma}_w^2$ are variance components for blocks, families, plots and trees within plots, respectively.

b) Standard error of the estimate.

large positive values, while genetic correlations also varied widely from moderate negative to large positive values. In some cases, standard errors were large relative to the estimated values. Consequently, the estimates, particularly those for genetic correlations, can only be used as a general guide. Most phenotypic correlations were small,

apart from those for diameter and height (0.77) and mean spiral grain angle and spiral grain deviation (0.41). The morphological traits showed stronger and positive genetic correlations, and were also positively genetically correlated with basic density (Table 3). Compression wood and mean spiral grain angle showed generally negative and slightly

Table 3. — Genetic and phenotypic correlations a) among growth, form and wood properties.

Trait	Diameter	Height	Straightness	Basic Density	Compression Wood	Mean Spiral Grain Angle	Spiral Grain Deviation
Diameter		0.77 ± 0.18	0.63 ± 0.26	0.32 ± 0.32	-0.16 ± 0.38	-0.46 ± 0.38	-0.15 ± 0.46
Height	0.77 ± 0.03		0.46 ± 0.32	0.69 ± 0.29	-0.41 ± 0.36	-0.23 ± 0.40	0.01 ± 0.51
Straightness	0.25 ± 0.05	0.15 ± 0.05		0.48 ± 0.22	0.03 ± 0.30	-0.53 ± 0.24	-0.42 ± 0.36
Basic density	0.09 ± 0.05	0.15 ± 0.05	-0.02 ± 0.05		-0.29 ± 0.27	0.16 ± 0.30	0.09 ± 0.33
Compression wood	0.09 ± 0.05	0.02 ± 0.05	-0.02 ± 0.05	0.02 ± 0.05		0.27 ± 0.31	-0.10 ± 0.39
Mean spiral grain angle	0.14 ± 0.05	0.12 ± 0.05	-0.18 ± 0.05	0.12 ± 0.05	0.11 ± 0.05		0.60 ± 0.35
Spiral grain deviation ^b	-0.11 ± 0.05	-0.10 ± 0.05	-0.13 ± 0.05	0.12 ± 0.05	0.02 ± 0.05	0.41 ± 0.05	

a) Genetic correlations above diagonal; phenotypic correlations below diagonal.

b) Standard deviation of pith to cambium spiral grain values.

smaller genetic correlations with diameter and height. Straightness showed moderate negative correlations with grain angle and deviation, but not with compression wood. Genetic correlations for wood traits ranged from -0.29

for basic density and compression wood to 0.60 for grain angle and deviation (Table 3). Overall, genetic correlations were very favourable. Selection to increase growth rate and stem straightness and to reduce compression wood

Table 4. — Predicted direct responses and correlated responses to selection for growth, form and wood properties resulting from mass selection of one in 10 trees.

Trait directly selected	Direct response ^a	Correlated responses ^b for indirectly selected traits							Spiral grain deviation
		Diameter	Height	Straightness	Basic density	Compression wood	Mean spiral grain angle	Spiral grain	
Diameter (cm)	1.13 (6.5)	1.13 (1.00)	0.65 (0.83)	0.28 (0.38)	6.39 (0.16)	-0.66 (0.11)	-0.33 (0.38)	-0.04 (0.17)	
Height (m)	0.78 (4.9)	0.81 (0.72)	0.78 (1.00)	0.19 (0.26)	12.81 (0.33)	-1.57 (0.27)	-0.16 (0.17)	0.00 (-0.01)	
Straightness (1-6)	0.74 (33.6)	1.19 (1.05)	0.65 (0.82)	0.74 (1.00)	15.97 (0.41)	0.21 (0.04)	-0.64 (0.72)	-0.18 (0.77)	
Basic density (kg m ⁻³)	38.80 (8.4)	0.70 (0.62)	1.13 (1.44)	0.42 (0.56)	38.80 (1.00)	-2.32 (0.40)	0.23 (-0.25)	0.05 (-0.19)	
Compression wood (%)	-5.82 (-71.9)	0.26 (0.23)	0.49 (0.62)	-0.02 (-0.03)	8.19 (0.21)	-5.82 (1.00)	-0.28 (0.31)	0.04 (-0.16)	
Mean spiral grain angle (°)	-0.89 (-24.8)	0.64 (0.56)	0.24 (0.30)	0.29 (0.39)	-3.91 (-0.10)	-1.36 (0.23)	-0.89 (1.00)	-0.19 (0.81)	
Spiral grain deviation (°) ^c	-0.24 (-16.2)	0.15 (0.14)	-0.01 (-0.01)	0.17 (0.23)	-1.63 (-0.04)	0.37 (-0.06)	-0.39 (0.44)	-0.24 (1.00)	

a) Absolute value of the direct response with percentage of mean in parentheses.

b) The response to indirect selection as a proportion of that for direct selection for each trait at the same intensity of selection, i.e. the relative selection efficiency, is given in parentheses.

c) Standard deviation of pith to cambium spiral grain values.

Table 5. — Predicted genetic gains for individual traits obtained using several different selection indices for mass selection of one in 10 trees.

Economic weights ¹	Index ²	Predicted genetic gains ³										
		Diameter	Height	Straightness	Basic density	Compression wood	Mean spiral grain angle					
Equal emphasis												
10	10	40	1	-3	-20	A	1.46 (1.87)	0.80 (1.08)	36.83 (0.95)	-3.78 (0.65)	-0.60 (0.68)	
						B	1.33 (1.18)	0.51 (0.69)	0.00 (0.00)	-2.03 (0.35)	-1.09 (1.22)	
Growth emphasis												
1000	1000	40	1	-3	-20	A	1.70 (1.50)	1.45 (1.87)	0.77 (1.04)	33.89 (0.87)	-3.53 (0.61)	-0.63 (0.71)
						B	1.40 (1.24)	0.62 (0.79)	0.46 (0.62)	0.00 (0.00)	-1.68 (0.29)	-0.98 (1.10)
Growth and form emphasis												
1000	1000	4000	1	-3	-20	A	1.68 (1.49)	1.35 (1.73)	0.86 (1.17)	33.36 (0.86)	-2.36 (0.41)	-0.66 (0.74)
						B	1.37 (1.21)	0.47 (0.60)	0.60 (0.81)	0.00 (0.00)	0.08 (0.00)	-1.01 (1.13)

¹) Relative economic weights in order are: diameter, height, straightness, basic density, compression wood and mean spiral grain angle, respectively.

²) Index A is an unrestricted index; B is an index restricting the genetic gain in basic density to zero.

³) The predicted genetic gain for each trait achieved by index selection as a proportion of that for direct selection for each trait at the same intensity of selection, i.e. the relative selection efficiency, is given in parentheses.

and mean spiral grain angle in this hoop pine population would not appear to be limited by strongly adverse genetic correlations. It would also lead to only a small increase

in basic density, which would probably have few undesirable consequences. Furthermore, the phenotypic correlation between basic density and both diameter and height

is much lower than the genetic correlation, indicating that environmental effects acting on these traits are negatively correlated. This implies that silvicultural changes applied to improve the growth of hoop pine may reduce basic density and a small increase through selection may be necessary to maintain wood density.

Phenotypic correlations for individual segment spiral grain angles and the other traits (not shown) were similar to those for mean spiral grain angle given in *Table 3*. Genetic correlations between the grain angles in individual segments and other traits were variable in magnitude, but similar in sign relative to those in *Table 3* for mean spiral grain angle. Thus the consideration of spiral grain angle in an individual segment rather than the mean over all segments would not appreciably alter the direction of selection responses although it could affect the general size of changes resulting from indirect selection.

Expected Gains from Selection

Predicted gains from direct selection for individual traits and the associated effects of indirect selection on other traits are shown in *Table 4*. The selection rate of one in 10 trees chosen for the predictions is arbitrary. It is likely to be realistic in selection for wood properties, but not for growth and straightness. However, changing the intensity of selection for different traits affects only the size of, and not the relation between, predicted responses for different traits. Responses to selection for wood properties other than basic density are negative because selection would normally be applied to reduce their expression. The direct responses in *Table 4* show that even a mild mass selection intensity (10% retained) would effect substantial improvements in straightness and wood defects. An increase in basic density of about 40 kg/m³ (8.4% of the population mean) is also predicted, should an increase be required.

Indirect selection is generally predicted to be less efficient than direct selection, except for height when directly selecting for basic density, a result of the higher heritability for basic density (0.83, *Table 1*) and the strong positive genetic correlation between the two traits (0.69, *Table 3*). There is little scope for selecting efficiently for wood properties using either diameter, height or stem straightness. Indirect responses in wood properties are generally favourable, but the changes are small relative to direct selection (*Table 4*). The exception is for straightness and spiral grain, where stronger genetic associations lead to more substantial reductions in adverse spiral grain properties.

Selection efficiencies indicate no strongly adverse effects of indirect selection. The worst case is selection for basic density which would give a concomitant increase in mean spiral grain angle and spiral grain deviation estimated at about 20% to 25% of the direct response to selection for these traits (*Table 4*). However, the genetic correlations are so weak that in practice this could easily be avoided in selection.

Relative selection efficiencies for individual traits estimated for selection using multi-trait indices are given in *Table 5*. Equal emphasis economic weights were applied by using the inverse of the phenotypic standard deviation for each trait (COTTERILL and JACKSON, 1985). Weights for compression wood and spiral grain angle were negative to account for selection to decrease the levels of these two traits. Other economic weights were varied from the

equal emphasis weightings (*Table 5*). We emphasize that the purpose in applying these indices was to assist in assessing the effects of selection, rather than to investigate optimal strategies for multi-trait selection in hoop pine. No attempt was made to evaluate methods of index selection as this was beyond the scope of this study.

Even with heavy weighting for diameter, height and straightness, the unrestricted index still predicted a selection efficiency of 0.41 for compression wood, which was the lowest predicted for unrestricted index selection. The efficiencies were generally larger than those for indirect selection in *Table 4*, and in the case of growth and straightness indicated substantial improvements in predicted gains beyond those expected for direct selection of individual traits (*Table 5*). The improvements highlighted the favourable nature of the genetic correlations in this study, and reinforced the value of index selection in capitalising on favourable associations to maximise genetic gains.

Restricted selection indices which avoided genetic change in basic density gave reduced efficiencies for all traits except mean spiral grain angle, relative to unrestricted index selection (*Table 5*). However, no trait was adversely affected, and only compression wood failed to respond positively to index selection using a restricted index with heavy emphasis on growth and straightness. In contrast, response in diameter and spiral grain angle was better than that predicted for direct selection, while height and straightness also showed moderately high selection efficiencies (*Table 5*).

Conclusions

The work reported here has demonstrated that the studied population of hoop pine has considerable potential value for breeding and selection. Although the data came from progeny of trees subjected to prior selection for growth and straightness, they sample current hoop pine breeding populations, and results should provide valid inferences for those populations. However, the inferences may not apply more generally to hoop pine. From the levels of genetic variances, heritabilities and genetic correlations estimated, it is apparent that substantial genetic gains for growth and straightness are possible without adversely affecting wood quality. Furthermore, there is considerable flexibility and scope for simultaneous improvement of wood properties. While there is no need to alter the basic density of plantation hoop pine at present, its high heritability indicates that phenotypic screening to maintain existing density standards should be highly effective. Also, breeding and selection should be capable of arresting any detrimental changes in density that might be caused by new silvicultural and management practices.

In selecting for wood properties, it may be possible to limit the assessment of spiral grain angle to a single measurement on juvenile trees. The effect would be to reduce the cost and complexity of collecting spiral grain data for breeding purposes. Furthermore, simultaneous selection for several traits (growth, straightness and wood quality) would best be pursued by an appropriate form of index selection, which should offer the most effective method of maximising genetic gains in this population. Further genetic studies to consolidate the reported findings are warranted.

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Giemsa C-Banded Karyotype in *Quercus L.* (Oak)

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Abstract

A detailed karyotypic investigation by Giemsa C-banding in three species of *Quercus*: *Q. robur*, *Q. petraea* and *Q. rubra* has revealed a general interspecific uniformity with respect to C-banded patterns and karyomorphology. However, the different chromosomes can be identified and paired on the basis of C-bands. A similar constancy in nuclear DNA amounts is also noticed. One B-chromosome has been found in all the three species of oak investigated.

Key words: *Quercus*, oak Fagaceae, Giemsa C-banding, Karyotype analysis, nuclear DNA, B-chromosome.

Introduction

Quercus belongs to the family Fagaceae which represents the most important source of timber among the broad-leaved species of the northern hemisphere. Oak wood is specially known for its strength, durability and all-round usefulness. A good amount of work has been done in population genetics, hybridization and speciation in North America and Europe. However, cytological studies are restricted to only chromosome numbers. No

thorough karyological studies using modern banding methods are available for *Quercus*. Proper identification of chromosomes with the help of C-bands, on the one hand, is essential in the systematics of the species and, on the other hand, for a clear understanding of the chromosomal basis of somaclonal variation in the micropropagated plants. Micropropagation is being increasingly carried out in oak for clonal propagation and conservation of elite genotypes (AHUJA, 1986). The present study deals with a detailed karyotypic analysis of three oak species.

Materials and Methods

Three species of oak, viz, *Q. robur* L., *Q. petraea* LIEBL., and *Q. rubra* L. were employed for cytological studies. Root tips were taken from potted plants grown at the Institute of Forest Genetics and Forest Tree Breeding at Grosshansdorf. These were pretreated in 0.002 M aqueous solution of 8-hydroxy-quinoline at 15° to 16° C for three hours and fixed in 1:3 acetic alcohol overnight. After washing twice for 30 minutes each in 0.1 M citrate buffer pH 4.7, root tips were macerated in 1% w/v pectinase at 37° C for two hours, and subsequently in 0.25% w/v cellulase for 15 minutes, again washed in 0.1 M citrate buffer (pH 4.7) for 10 minutes and squashed in 45% acetic

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