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Estimates of Genetic Parameters and Gains expected from Selection in Hoop Pine in south-east Queensland

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Summary

Genetic parameters were estimated for height, diameter, stem straightness, internode length and wood density between five and 16 years after planting in four open-pollinated progeny tests of hoop pine in south-east Queensland. All traits appear to be moderately heritable and favourably genetically correlated. Selection indices were formulated by combining the economically important traits of diameter, stem straightness and internode length. The implications of the genetic parameters estimated are discussed with reference to breeding strategies represented by these indices. It seems that substantial improvements can be made in these traits using straightforward breeding procedures such as individual selection.

Key words: Hoop pine, heritability, genetic and phenotypic correlations, selection indices.

Introduction

The natural distribution of hoop pine (*Araucaria cunnunghamii* AITON ex D. DON) is wide and extends from around latitude 7° S in Irian Jaya and Papua New Guinea down to 32° S on the east coast of Australia (FISHER, 1980). The major commercial plantings of the species are concentrated in south-east Queensland (Australia) where over 43,000 hectares of plantation have been established since the early 1920's.

As a timber species hoop pine has considerable commercial value because it produces high grade, even-density wood suitable for use as veneer, joinery, particle board and structural products. A program for genetically improving growth and form traits in the species has been undertaken in south-east Queensland with a number of first generation progeny tests being established over the last two decades. There is, however, a lack of reliable genetic information required for the efficient operation of a breeding program. The only documented estimates of genetic parame-

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Table 1. — Details of four open-pollinated progeny tests of hoop pine.

Details	Progeny test			
	A	B	C	D
Local number	394IM1	394IM2	394YR1	285IM1
Annual rainfall	1150	1150	780	1150
Soil type	brown silty loam	brown silty loam	red-brown clay loam	red-brown clay loam/ podzolic
Altitude (m a.sl)	60	60	200	60
Slope	5-15°	5-20°	5°	5-15°
Previous vegetation	transition forest *Tristania* & *Eucalyptus* spp.		rainforest	*Agathis robusta* plantation
Planting date	Dec. 1971	Dec. 1971	Dec. 1971	Dec. 1968
No. of families analysed	22	22	22	24
Percent survival	92	96	88	93
Measurements year 5			Aug. 1976	Sep. 1973
10	Sep. 1981	Sep. 1981	Oct. 1981	Aug. 1977
13	Oct. 1984	Oct. 1984	Aug. 1984	Aug. 1980
16				Feb. 1984

ters for hoop pine appear to be heritabilities for growth and form traits for 10 open-pollinated families in one progeny test analysed by Kanowski *et al.* (1985). These authors report considerable genetic variability for all traits studied. There does not seem to be any information published about the genetic associations between economically important traits in hoop pine.

The aim of this study is to provide further estimates of heritability of growth, form and wood density of hoop pine, and also to determine genetic associations between these traits. These parameters are used to estimate genetic gains expected from various selection strategies. The data used in these analyses are from four first-generation open-pollinated progeny tests in south-east Queensland.

Materials and Methods

Site, Silviculture and Field Layout

Details of the four open-pollinated progeny tests of hoop pine are given in *Table 1*. All progeny tests were planted in south-east Queensland around latitude 26° S on the east coast of Australia. This region experiences a subtropical climate with summer rainfall. The progeny tests A, B and D were established in the Imbil forest district while progeny test C occurred some two hundred kilometres west in the Yarraman district.

Table 2. — Expectations of mean squares for analyses of variance and covariance for individual progeny tests. There are b blocks, f families and n trees per plot. The variance component σ^2_b is due to blocks, σ^2_f due to families, σ^2_{fb} due to family × block interaction and σ^2_w due to within-plot error. The k coefficients relevant to heritability estimation were calculated as k_1 and k_2 = 9.13, 9.62, 8.71 and 9.26; and k_3 = 54.88, 57.76, 52.57 and 55.64 for tests A, B, C and D respectively. For density data: k_1 and k_2 = 2.88 and k_3 = 14.4.

Source of variation	d.f.	Expected mean squares
Block	(b-1)	$\sigma^2_w + k_4\,\sigma^2_{fb} + k_5\,\sigma^2_b$
Family	(f-1)	$\sigma^2_w + k_2\,\sigma^2_{fb} + k_3\,\sigma^2_f$
Block x family	(b-1)(f-1)	$\sigma^2_w + k_1\,\sigma^2_{fb}$
Error	$N-\Sigma_{ij}n_{ij}$	σ^2_w

One progeny test (D) was planted in 1968 and the other three (A, B and C) in 1971, using two-year-old tubed seedling stock raised in local nurseries. Trees were planted by hand at a spacing of 2.8 m × 3.4 m in complete randomised blocks with six replications of 10-tree row plots. Families included in the analyses were open-pollinated progeny grown from seed collected on ortets. These ortets were visually selected for superior growth and form in routine plantations.

Measurements

Height, stem diameter (over bark at 1.4 m) and stem straightness on a six-point subjective scale (1 = crooked, 6 = straight) were assessed on all surviving trees in all progeny tests at approximately 10 years after planting. Additional measurements were made in progeny tests C and D (*Table 1*). In test C, stem diameter was recorded at 13 years after planting. In test D, height was recorded at five, 13 and 16 years after planting and stem diameter at 13 and 16 years. Also in test D the height of the two uppermost branch whorls were measured at 10 years after planting and the distance between them used as an indicator of internode length. At 16 years after planting two radial 12 mm wood cores were taken from three randomly selected trees in each plot in five blocks of progeny test D. Basic density of these wood samples was determined as the ratio of oven dry weight to maximum saturated volume using the procedure of Heinrichs and Lassen (1970).

Data Analyses

Analyses of variance were carried out on individual tree data for each progeny test using the following model — (1)

$$Y_{jkl} = \mu + a_j + b_k + ab_{jk} + e_{jkl} \qquad (1)$$

where Y_{jkl} represents an individual tree observation, μ the overall mean, a_j the effect of the jth open-pollinated family, b_k the effect of the kth randomised block, ab_{jk} the effect of the family × block interaction and e_{jkl} the within-plot error.

Components of variance due to blocks (σ^2_b) families (σ^2_f), family × block interaction (σ^2_{fb}) and within-plot error (σ^2_w) were calculated from the expectations of mean squares given in *Table 2*. The open-pollinated offspring were assumed to be half-sib and individual-tree heritabilities (denoted h^2) for each progeny test were estimated as — (2)

$$h^2 = \text{additive variance/variance of individual phenotypes}$$

$$= 4\,\sigma_f^2/\,(\sigma_f^2 + \sigma_b^2 + \sigma_{fb}^2 + \sigma_w^2) \qquad (2)$$

Standard errors of individual heritabilities were estimated according to SWIGER *et al.* (1964). Genetic correlations (denoted r_a) were calculated from estimates of additive genetic variances and covariances following HAZEL *et al.* (1943) and the standard errors of these correlations according to TALLIS (1959). Phenotypic correlations (r_p) were estimated as simple correlation coefficients.

Three different selection indices were constructed using the computer program RESI (COTTERILL and JACKSON, 1981). In two of the indices stem diameter and straightness were combined using differing economic weights. In the third index stem diameter, straightness and internode length were combined. Genetic gains that might be expected in each trait following individual tree selection on the three different indices were calculated according to COTTERILL and JACKSON (1985). The intensity of selection (i) is assumed to be one tree in every 100 (i = 2.67; BECKER, 1985).

Results and Discussion

Overall means and standard deviations of all trees in each progeny test are given in *Table 3*. Individual heritabilities and their standard errors for growth at 10 years and form and wood density traits are presented in *Table 4* and correlations between these traits at 10 years are given in *Table 5*. The implications of various selection strategies for breeding hoop pine are examined in terms of genetic gains expected from selection (*Table 6*).

Table 3. — Overall means and their standard deviations for growth, form and wood density traits in hoop pine progeny tests.

Trait	Progeny test			
	A	B	C	D
Height 5[+] (m)				3.18±1.07
Height 10 (m)	12.01±1.77	8.90±2.44	10.38±1.26	8.32±2.14
Height 13 (m)				11.94±2.40
Height 16 (m)				16.01±2.70
Diameter 10 (cm)	14.86±2.44	11.97±2.75	14.98±2.26	11.85±2.83
Diameter 13 (cm)	18.59±2.90	14.53±3.09	18.59±2.55	15.07±3.04
Diameter 16 (cm)				17.64±3.47
Straightness (point)	3.35±1.45	1.54±0.63	2.86±0.79	3.52±1.31
Internode length (m)				0.85±0.37
Wood density (kg m^{-3})				459±27

+) Height 5 is height measured in the 5th year after planting, and so on for other growth traits.

Table 4. — Heritabilities and their standard deviations for growth, form and wood density traits in hoop pine progeny tests.

Trait	Progeny test			
	A	B	C	D
Height 5				0.13±0.06
Height 10	0.16±0.07	0.07±0.04	0.14±0.07	0.17±0.07
Height 13				0.23±0.09
Height 16				0.30±0.11
Diameter 10	0.12±0.06	0.14±0.06	0.12±0.06	0.18±0.07
Diameter 13	0.11±0.06	0.14±0.07	0.18±0.08	0.16±0.07
Diameter 16				0.17±0.07
Straightness	0.56±0.18	0.43±0.14	0.37±0.13	0.49±0.15
Internode length				0.74±0.20
Wood density				0.83±0.32

Table 5. — Genetic correlations (and their standard errors) and phenotypic correlations among growth and form at 10 years and wood density traits in progeny tests of hoop pine.

Trait	Correlations				
	Height	Diameter	Straightness	Internodes	Wood density
Height					
Test A		0.49±0.24[A]	0.22±0.27		
B		0.67±0.19	0.30±0.31		
C		0.60±0.21	0.37±0.27		
D		0.67±0.15	0.45±0.22	0.48±0.20	0.82±0.27
Diameter					
Test A	0.74[B]		0.41±0.26		
B	0.89		0.10±0.28		
C	0.74		0.22±0.31		
D	0.82		0.67±0.17	0.31±0.23	0.34±0.36
Straightness					
Test A	0.12	0.12			
B	0.16	0.16			
C	0.14	0.06			
D	0.19	0.09		0.02±0.24	0.19±0.35
Internodes					
Test D	0.44	0.30	0.09		0.06±0.29
Wood density					
Test D	0.12	0.04	−0.02	−0.07	

A) Genetic correlations (r_a) above the diagonal.

B) Phenotypic correlations (r_p) below the diagonal.

Table 6. — Genetic gains expected per generation following individual selection of one tree in 100 on three indices variously combining diameter, straightness and internode length with differing economic weightings. Genetic gains for each trait are expressed in actual units of measurement with the percent change in the mean in brackets below.

Weighting coefficients			Gains expected per generation		
Diameter	Straightness	Internode length	Diameter (cm)	Straightness (point)	Internode length (m)
Index One - emphasising growth					
100	1		1.1 (8)	0.9 (24)	
Index Two - growth and straightness					
2	1		1.0 (7)	1.2 (30)	
Index Three - including internode length					
2	1	4	0.8 (6)	1.0 (26)	0.3 (26)

Heritabilities

1. *Growth Traits:* The individual heritabilities of height at 10 years ranged from $h^2 = 0.07$ to 0.17 across the four progeny tests examined and all estimates had low standard errors (*Table 4*). In progeny test D, measured to 16 years, the heritability of height increased consistently over time from $h^2 = 0.13$ at 5 years to $h^2 = 0.17$ at 10 years, $h^2 = 0.23$ at 13 years and $h^2 = 0.30$ at 16 years. KANOWSKI *et al.* (1985) reported a much higher heritability of $h^2 = 0.76 \pm 0.46$ for height of hoop pine at 15 years, however, their study was based on only 200 progeny of 10 families at one site and sampling errors may be very large (as evidenced by the large standard errors associated with their estimates).

The individual heritabilities estimated for stem diameter at 10 years ranged from $h^2 = 0.12$ to 0.18 (*Table 4*) and were generally about the same magnitude as corresponding estimates for height at 10 years. In all progeny tests the heritability of diameter was fairly stable between 10 and

13 years and remained stable to 16 years in progeny test D. Kanowski *et al.* (1985) estimated a higher value of $h^2 = 0.30 \pm 0.27$ for diameter but again their estimate had a large standard error.

2. *Form and Wood Traits:* Stem straightness was found to be very highly heritable in all of the progeny tests ($h^2 = 0.37$ to 0.56; *Table 4*) with fairly low standard errors. Kanowski *et al.* (1985) also reported a very high heritability of $h^2 = 0.71 \pm 0.42$ for stem straightness.

Internode length and wood density were measured only in progeny test D where both of these traits were found to be under very strong additive genetic control. The heritability of internode length was $h^2 = 0.74 \pm 0.20$ and the heritability of wood density was $h^2 = 0.83 \pm 0.32$ (*Table 4*). The standard error for the heritability of density was larger because of the smaller number of trees sampled. A more detailed study of the wood properties of hoop pine is currently being undertaken (R. L. Eisemann, K. J. Harding and D. J. Eccles, personal communication).

Genetic and Phenotypic Correlations

Height and diameter at 10 years had fairly strong positive genetic correlations (with relatively low standard errors) in all four progeny tests ($r_a = 0.49$ to 0.67; *Table 5*) suggesting that selection for one trait should lead to strong positive indirect responses in the other. Phenotypic correlations were also positive and ranged from $r_p = 0.74$ to 0.89 (*Table 5*).

Both height and diameter were favourably associated with stem straightness in all progeny tests with genetic correlations ranging from $r_a = 0.10$ to 0.67 (*Table 5*). The standard errors, however, were large in relation to the correlation coefficients. Phenotypic correlations were small but positive in all progeny tests ($r_p = 0.06$ to 0.19; *Table 5*). Genetic and phenotypic correlations between growth traits and internode length were consistently strong and positive ($r_a = 0.48$ and 0.31, $r_p = 0.44$ and 0.30 for height and diameter respectively; *Table 5*). Selection for height or diameter should therefore lead to indirect improvement in stem straightness and also internode length. This finding for hoop pine is the opposite to results reported in *P. radiata* where Carson and Inglis (1986) found adverse genetic associations between growth and both stem straighness and internode length when breeding for clearwood production in that species.

The genetic correlations between growth traits, in particular height, and wood density were also strong and positive ($r_a = 0.82$ for height and $r_a = 0.34$ for diameter; *Table 5*). Phenotypic correlations were also favourable but much smaller in magnitude ($r_p = 0.04$ to 0.12; *Table 5*). This positive genetic association between growth and wood density certainly needs to be verified by further studies across more sites. This finding is contrary to the negative associations between growth and density reported for other plantation species such as *P. elliottii* (Allen, 1985) grown in northern Australia and *P. radiata* (Dean *et al.*, 1983) in southern Australia.

Stem straightness and internode length were poorly correlated both genetically ($r_a = 0.02$; *Table 5*) and phenotypically ($r_p = 0.09$; *Table 5*). Likewise both stem straightness and internode length had poor associations with wood density. The standard errors of these correlations were consistently large.

Gains Expected from Index Selection

Hoop pine should be a reasonably straightforward species to breed since the growth, form and wood density traits assessed here appear to be moderately heritable and are not adversely genetically associated. Indeed the existing hoop pine breeding program in Queensland has made substantial progress in improving both growth and form in the first generation (Nikles, 1980).

Table 6 presents the sort of gains which might be expected in growth and form after one generation of selection. Three selection indices have been formulated as case studies. The first two indices combined diameter and straightness at 10 years with varying emphasis being given to each trait. In the case of index 1 considerable emphasis is placed on growth. Individual tree selection on this index, at an intensity of one tree in every 100, is expected to produce a 1.1 cm (or 8% change in the mean), improvement in diameter and 0.9 point (24%) improvement in straightness (*Table 6*). Increasing the relative emphasis on straightness (index 2) led to slightly (0.1 cm) less improvement in diameter but a much greater improvement in straightness (1.2 point or 30%; *Table 6*). This second option resembles the sort of index currently used operationally in the hoop pine breeding program in Queensland.

The increasing use of hoop pine timber for veneer and associated products may lead to a situation where trees having long straight internodes (and consequently a greater proportion of clearwood) become commercially more valuable. A third index was formulated in which internode length was included with diameter and straightness. The gains expected from selection on this index (index 3) combining all three 10-year traits illustrated that substantial improvement in internode length is possible in each generation (0.3 m or 26%; *Table 6*) and would be accompanied by only small sacrifices in the improvement in diameter (0.8 cm or 6%; *Table 6*) and straightness (1.0 point or 26%; *Table 6*) at 10 years. Even though all three traits in the index are positively associated these minor reductions in expected gain come about because the selection pressure on any one trait is progressively diluted as successive traits are added to the index.

This strategy of improving growth, straightness and internode length (clearwood) is probably the best option for future improvement of hoop pine in Queensland. Trees with longer internodes are actively sought by the local timber industry and it seems that in hoop pine internode length can be easily improved with little sacrifice in other economically important traits (such as growth, form and wood density). This situation of positive genetic associations in hoop pine is in contrast to other plantation species such as *P. radiata*. In *P. radiata* there is an adverse genetic correlation between internode length and growth (Cotterill and Zed, 1980; Carson and Inglis, 1986) and it does not seem possible to breed for longer internodes without suffering a substantial decline in growth. Carson and Inglis (1986) are developing a special line of *P. radiata* with long internodes suitable for veneer, however, this special purpose line is slower growing and less desirable for other users such as pulping and sawn timber. In the case of hoop pine it seems possible to develop one breed which is generally suited to a wide range of end uses.

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Reader's Reaction and Author's Reply to " M. Huehn, J. Kleinschmit and J. Svolba: Some Experimental Results concerning Age Dependency of Different Components of Variance in Testing Norway Spruce (Picea abies (L.) Karst.) Clones", published in Silvae Genetica 36 (2), 68–71, 1987

By M. Huehn*), J. Kleinschmit**) and J. Svolba**)

(Received 4th December 1987)

Summary

Time trends in the relative importance of the variance components for "locations", "clones", "locations × clones", „blocks" and „experimental error" have been estimated in a Norway spruce clonal test for total plant-height and 10 years of measurements. In this "Short Note" these former results are completed (caused by a reader's question) by the results for the within-site clonal h^2 over time. Additionally, referring to another reader's reaction the results for annual growth are presented and discussed.

Key words: Norway spruce, clonal test, components of variance, early testing.

Zusammenfassung

Zeitliche Trends in der relativen Bedeutung der Variationsursachen „Anbauorte", „Klone", „Anbauorte × Klone", „Blöcke" und „Versuchsfehler" wurden in einer Fichten-Klonprüfung für das Merkmal „Pflanzenhöhe" bei 10 vorliegenden Messungen geschätzt. In dieser „Short Note" werden — angeregt durch eine Leserzuschrift — die früheren Resultate durch die Ergebnisse für das Verhältnis $\sigma^2_{\text{Klone}}/\sigma^2_{\text{Klone}} + \sigma^2_{\text{Fehler}}$ ergänzt. In Beantwortung einer weiteren Leseranfrage werden die Ergebnisse für das Merkmal „jährlicher Zuwachs" präsentiert und diskutiert.

Introduction

A Norway spruce clonal test, established with 5 clones on 5 extremely contrasting sites in 1967 and remeasured for total plant-height 10 times until 1981 has been used to estimate the relative importance of the components of variance for "locations", "clones", "locations × clones", "blocks" and "experimental error" dependent on the time. The results show, that in this study "blocks" and "interaction" are of minor importance, accounting to less than 5% of the total variation. "Clones" account for roughly 10% due to the limited numbers of clones included. These three sources of influence remain more or less constant over time. Considerable changes, however, occur in the components for "locations" and "experimental error". The first one increases quickly until it reaches a plateau at about 70% corresponding to the extreme sites included. The last one decreases correspondingly and ends up after few years at 15%. All values are quite stable at the end of the time of measurement.

The following question may be of general interest (Libby, personal communication): "What happens to within-site clonal h^2 over time — i.e: $\frac{\sigma^2_{\text{clone}}}{\sigma^2_{\text{clone}} + \sigma^2_{\text{error}}}$? It must go up a lot, right?"

It can be answered as follows: For this ratio $\sigma^2_{\text{clone}}/\sigma^2_{\text{clone}} + \sigma^2_{\text{error}}$ one obtains the results of *Table 1*. Two different evaluations have been performed: Evaluation I (4 sites, 5 clones, 2 blocks, 10 years of measurement) and evaluation II (5 sites, 4 clones, 2 blocks, 9 years of measurement). Both evaluations have been calculated 1) by using equal numbers of trees per plot ('orthogonal') and, additionally, 2) by using unequal numbers of trees per plot ('non-orthogonal') (see Huehn *et al.*, 1987).

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