

INTERNODE LENGTH OF HOOP PINE: GENETIC PARAMETERS AND PROSPECTS FOR DEVELOPING A LONG-INTERNODE BREED

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ABSTRACT

Internode length of *Araucaria cunninghamii* Ait. ex D. Don (hoop pine) is moderately to strongly inherited (average $h^2=0.48$), but shows no strong genetic correlations with vigour or stem straightness traits. Although it is feasible to develop a long-internode breed through recurrent selection and conventional multiclonal seed orchards, the addition of an extra selection criteria to those of the main breed, in the absence of favourable genetic correlations, may result in some loss of gain in growth rate and stem straightness compared to the main breed.

Keywords: internode length; heritability; genetic correlation; breeding strategy; *Araucaria cunninghamii*.

INTRODUCTION

Hoop pine is a native Australian conifer of major importance in Queensland for timber production. Large volumes of hoop pine have been harvested from natural stands in the past but presently almost the entire production comes from 44 000 ha of intensively managed plantations.

An intensive breeding programme has been maintained with hoop pine in Queensland since the 1950s. During the initial searching of plantations for first-generation plus-trees the main selection criteria were growth rate, stem straightness, and branching traits (branch diameter and branch angle). The trees selected generally had short internodes because trees with long internodes usually have a distinct kink at one or more branch nodes (in the upper crown) and larger average branch size.

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The development of a long-internode breed of hoop pine was initiated during 1986 for two main reasons. Firstly, it was recognised that long-internode trees had the potential to yield a substantial increase in the proportion of clear knot-free timber produced. Consequently, if branch nodes were cut out so as to produce clear timber, the larger branch size and kinks at branch nodes would not be serious faults, provided that the portion of stem between nodes was straight. Secondly, it was believed that an increase in the amount of knot-free timber produced would result in higher log values. As there is already a considerable premium for pruned butt logs for use in plywood production, it is reasonable to expect that long-internode trees will have an economic advantage over shorter-internode trees.

This paper reviews all available information on the genetic parameters of internode length in hoop pine in Queensland, and outlines a strategy for the development of a long-internode breed with acceptable vigour and stem straightness. The only other published estimates of the genetic parameters of internode length in hoop pine are those given by Dean *et al.* (1988), based on data from only one open-pollinated progeny test.

MATERIALS AND METHODS

The data used in this paper were drawn from seven open-pollinated progeny tests, which formed part of four separate trial series, each of which tested a different sub-set of families. The test sites were distributed throughout the main plantation areas in south-east Queensland, and are representative of the general plantation estate. Site and experimental details are summarised in Table 1 for all seven progeny tests. All tests comprised families derived from wind pollination on ortets selected in plantations of unimproved seed, and were mostly established as 10-tree row plots and six replicates in randomised complete block designs.

Measurements

Height, diameter (at 1.3 m over bark), stem straightness on a six- or eight-point scale (1 = crooked, 6 (or 8) = straight), and internode length of all surviving trees were measured at ages between 8 and 16 years in the different tests (Table 2).

Depending on circumstances and the age of the trees, three different methods were used to assess internode length.

(1) *Measuring* average length of the two uppermost internodes

The height of the uppermost branch node and the height of the third branch node from the top of the tree were measured to the nearest 0.1 m using height sticks. The average length of the two uppermost internodes was then calculated from these two heights. This value adequately predicts the average internode length in the upper third of the tree (Kanowski 1981).

(2) *Counting* the number of branch nodes

A simple count was made of the number of branch nodes in the section of stem from 6 to 12 m above ground-level. The 6- and 12-m points were identified accurately on each tree using height sticks.

(3) *Estimating* internode length visually using a six-point scale

TABLE 1—Details of seven open-pollinated hoop pine progeny tests

| Details | Progeny test | | | | | | |
|--------------------|------------------------|--------------------|--------------------|-------------------------|-------------------------|------------------------|---------------------------|
| | A | B | C | D | E | F | G |
| Local number | 285im3 | 385im | 385gl | 385kl | 394iml | 394yrl | 545im |
| Latitude | 26°31'30"S | 26°33'37"S | 26°27'37"S | 24°42'39"S | 26°33'30"S | 26°49'45"S | 26°34'14"S |
| Longitude | 152°38'E | 152°34'5"E | 152°16'40"E | 151°20'53"E | 152°42'15"E | 151°55'15"E | 152°41'9"E |
| Altitude (m a.s.l) | 150 | 140 | 520 | 400 | 250 | 560 | 170 |
| Rainfall (mm/year) | 1210 | 1210 | 920 | 900 | 1190 | 780 | 1210 |
| Soil type | Red-brown clay loam | Brown clay loam | Grey-brown loam | Grey-brown clay loam | Red-brown sandy loam | Red-brown clay loam | Dark brown clay loam |
| Planting date | Dec 1968 | Jan 1970 | Feb 1970 | Jan 1970 | Dec 1971 | Dec 1971 | Feb 1978 |
| Spacing (m) | 2.8 × 2.4 | 3.4 × 2.8 | 3.4 × 2.8 | 3.4 × 2.8 | 2.8 × 3.4 | 2.8 × 3.4 | 2.7 × 3.3 |
| Plot type | 10-tree line | 10-tree line | 10-tree line | 10-tree line | 10-tree line | 10-tree line | 8-tree non- contiguous |
| No. of families | 31 | 35 | 33 | 31 | 22 | 22 | 76 |
| No. of blocks | 6 | 6 | 6 | 4 | 6 | 6 | 6 |

TABLE 2—Over-all means and their standard deviations for diameter at breast height, height, stem straightness, and internode length

| Trait | Age (years) | Progeny test | | | | | | |
|------------------------|-------------|--------------|------------|------------|------------|------------|------------|------------|
| | | A | B | C | D | E | F | G |
| Diameter (cm) | 8 | 11.98±2.30 | 12.62±2.81 | 8.61±2.20 | 9.91±2.54 | 15.00±2.30 | | 11.76±3.11 |
| | 12 | | 16.88±3.01 | 17.51±2.75 | 17.01±2.83 | 18.76±2.74 | 18.59±2.61 | |
| | 15 | 17.84±3.20 | | | | | | |
| Height (m) | 8 | 8.39±2.08 | 9.53±2.07 | 5.16±1.29 | 7.19±1.80 | 12.35±1.60 | 10.38±1.31 | 9.34±2.30 |
| | 12 | | 14.60±2.36 | | | | | |
| | 15 | 16.19±2.46 | | | | | | |
| Straightness (0–6) | 8 | 2.94±0.72 | 2.70±0.74 | | | 1.41±0.59 | 2.88±0.63 | 4.24±1.35 |
| | 12–16 | 3.54±1.31 | 3.79±1.35 | | 3.09±0.86 | 3.37±1.44 | 3.34±0.88 | |
| Internode length* (m) | 8 | 0.86±0.37 | 0.87±0.38 | 0.63±0.23 | 0.80±0.35 | | | 0.94±0.40 |
| No. nodes† | 12–16 | | 7.34±2.38 | | 6.84±2.44 | | 6.91±2.32 | |
| Visual score‡ (points) | 12 | | | | | 2.47±0.74 | 2.86±0.83 | |

*Average length of two uppermost internodes

†Number of branch nodes in the stem section between 6 and 12 m

‡Visual assessment of internode length

The average internode length in the whole crown above 6 m was estimated visually using the following six-point objective scale:

| Score | Estimated internode length (m) | Description |
|-------|--------------------------------|------------------|
| 1 | <0.3 | Very short |
| 2 | 0.3–0.9 | Short |
| 3 | 0.9–1.5 | Short to average |
| 4 | 1.5–2.0 | Average to long |
| 5 | 2.0–2.5 | Long |
| 6 | >2.5 | Very long |

Statistical Methods

For each data set an analysis of variance was carried out using the method of least squares (Harvey 1960). The model fitted is described in Equation (1).

$$y_{ijk} = \mu + f_i + b_j + (fb)_{ij} + e_{ijk} \quad (1)$$

where y_{ijk} is the observation on tree k of family i in block j
 μ is the over-all mean
 f_i is the effect of family i
 b_j is the effect of block j
 $(fb)_{ij}$ is the interaction of family i and block j
 e_{ijk} is the normally and independently distributed random deviation of tree k in family i and block j , with a mean of zero.

Variance components were estimated by equating the appropriate mean squares to the expectations shown in Table 3, and solving for the components.

TABLE 3—Expected mean squares for the analysis of variance and covariance at single sites

| Source of variation | Degrees of freedom* | Expected mean squares |
|-----------------------|---------------------|---|
| Family | $f-1$ | $\sigma_e^2 + k_2 \sigma_{fb}^2 + k_3 \sigma_f^2$ |
| Block | $b-1$ | (of no interest)† |
| Family \times Block | $(f-1)(b-1)$ | $\sigma_e^2 + k_1 \sigma_{fb}^2$ |
| Within-plot error | $fb(n-1)$ | σ_e^2 |

where b = number of blocks (replications)
 f = number of open-pollinated families
 n = number of trees per family
 σ_f^2 = variance between families
 σ_{fb}^2 = variance of interaction of families and blocks
 σ_e^2 = variance between trees within family plots

k-coefficients relevant to the estimation of heritability using block adjusted data were calculated as:

k_1 = 9.03, 8.89, 6.41, 9.15, 8.99, 8.84, and 6.39;
 k_2 = 9.04, 9.10, 6.96, 9.27, 9.16, 9.01, and 6.62; and
 k_3 = 48.46, 52.77, 38.79, 36.43, 54.14, 53.22, and 38.59

for progeny tests A, B, C, D, E, F, and G respectively.

* The degrees of freedom as given are valid only where there are no missing families.

† Block adjusted data used.

The progeny within each family were assumed to be half-sibs and narrow-sense heritability on an individual tree basis (h^2) was estimated for each site according to Equation (2).

$$h^2 = 4\sigma_f^2 / (\sigma_e^2 + \sigma_b^2 + \sigma_f^2) \quad (2)$$

Note that the component σ_b^2 does not appear in the denominator of Equation (2), implying that the heritability estimates are appropriate for selection within blocks or on block-adjusted data. Standard errors were estimated according to Swiger *et al.* (1964). Genetic correlations were estimated from additive genetic variances and covariances according to Hazel *et al.* (1943), and the standard errors of these correlations were estimated according to Tallis (1959).

RESULTS AND DISCUSSION

The over-all means for all trees in each progeny test are presented in Table 2. Heritability estimates for internode length, growth, and stem straightness traits are presented in Table 4 and the correlations between these traits in Table 5.

Heritability of Internode Length

The heritability estimates for internode length vary from 0.18 to 0.97 (Table 4), depending on the method and age of assessment, with an over-all mean of 0.48 which is similar to the narrow-sense heritability of branch cluster frequency in *Pinus radiata* D. Don of 0.5 (Carson & Inglis 1988). Internode length in hoop pine seems to be more strongly inherited than either growth or stem straightness traits, for which estimates generally vary between 0.1 to 0.2 and 0.3 to 0.5, respectively (Table 4). Thus, it can be concluded that internode length in hoop pine is moderately to strongly heritable and there is considerable scope for genetic improvement of this trait through simple recurrent selection techniques.

Although the strong genetic correlations amongst the three different methods of assessing internode length (Table 5) suggest that each method is essentially measuring the same trait, it appears that the heritabilities estimated from the branch node count are generally higher than those estimated from the other two methods (Table 4).

Correlations

The genetic correlations of internode length with growth and stem straightness are variable in magnitude, but more often negative than positive (Table 5). The standard errors associated with these genetic correlations are generally of a size such that many of the genetic correlations will not be significantly different from zero. However, large standard errors associated with genetic correlations are not unexpected when dealing with small samples drawn from a select population because genetic correlations are normally subject to large sampling errors and are strongly influenced by gene frequencies (Falconer 1981). Where the genetic correlation is large compared to its standard error, the phenotypic correlation is often of the same magnitude and direction as the genetic correlation (Table 5).

Although there appear to be no consistent trends in the genetic correlations between internode length and height, diameter, and stem straightness, small negative correlations may exist. If this is true, selection for long internodes may lead to reduced gain in growth

TABLE 4—Narrow-sense heritability estimates (\pm standard error)

| Trait* | Age (years) | Progeny test | | | | | | |
|------------------|----------------|-----------------|-----------------|-----------------|-----------------|------------------|-----------------|-----------------|
| | | A | B | C | D | E | F | G |
| Internode length | 8 | 0.72 \pm 0.18 | 0.21 \pm 0.05 | 0.52 \pm 0.14 | 0.48 \pm 0.14 | | | 0.36 \pm 0.07 |
| Number of nodes | 12–16 | | 0.35 \pm 0.07 | | 0.97 \pm 0.22 | 0.57 \pm 0.18† | 0.64 \pm 0.18 | |
| Visual score | 12–14 | | | | | 0.18 \pm 0.09 | 0.32 \pm 0.11 | |
| Height | 8 | 0.16 \pm 0.07 | 0.15 \pm 0.06 | 0.14 \pm 0.06 | | 0.16 \pm 0.07 | 0.14 \pm 0.07 | 0.09 \pm 0.03 |
| Height | 12 | 0.25 \pm 0.09 | 0.22 \pm 0.07 | | | | | |
| Height | 15 | 0.31 \pm 0.10 | | | | | | |
| Diameter | 8 | 0.16 \pm 0.06 | 0.12 \pm 0.05 | 0.08 \pm 0.05 | | 0.11 \pm 0.06 | 0.12 \pm 0.06 | 0.06 \pm 0.03 |
| Diameter | 12 | 0.14 \pm 0.06 | 0.10 \pm 0.04 | | | 0.10 \pm 0.06 | 0.18 \pm 0.08 | |
| Diameter | 15 | 0.14 \pm 0.06 | 0.10 \pm 0.04 | 0.19 \pm 0.08 | 0.05 \pm 0.04 | | | |
| Straightness | 8 | 0.33 \pm 0.11 | 0.09 \pm 0.04 | | | 0.56 \pm 0.18 | 0.18 \pm 0.08 | 0.18 \pm 0.04 |
| Straightness | 12–16 | 0.47 \pm 0.14 | 0.15 \pm 0.06 | | 0.36 \pm 0.11 | 0.53 \pm 0.17 | 0.36 \pm 0.13 | |

*Internode length = average of two uppermost internodes

Number of nodes = count of the number of nodes between height 6 and 12 m

Visual score = visual assessment of internode using a six-point score

Height = tree height (m)

Diameter = diameter at breast height over bark (cm)

†Assessed in three blocks only.

TABLE 5—Genetic and phenotypic correlations between internode length (il, nn, vis), height (ht), diameter at breast height over bark (dbh), and stem straightness (st) (standard error of genetic correlation in parentheses)

| Test | Trait 1 | Trait 2 | r_g^* | (se) | r_p^\dagger | Test | Trait 1 | Trait 2 | r_g^* | (se) | r_p^\dagger | | |
|--|---------|---------|---------|---------|---------------|--------|---------|----------|----------|---------|---------------|---------|---------|
| A. Average length two uppermost internodes (il) | | | | | | | | | | | | | |
| A | il8yr† | ht8yr | 0.381 | (0.191) | 0.431 | C | il8yr | ht8yr | 0.853 | (0.094) | 0.615 | | |
| | | ht15yr | 0.340 | (0.186) | 0.367 | | | dbh8yr | dbh8yr | 0.565 | (0.213) | 0.445 | |
| | | dbh8yr | 0.176 | (0.213) | 0.263 | | | dbh12yr | dbh12yr | 0.443 | (0.190) | 0.400 | |
| | | dbh15yr | 0.204 | (0.210) | 0.217 | | D | dbh12yr | dbh12yr | 0.160 | (0.349) | 0.334 | |
| | | st8yr | 0.022 | (0.209) | 0.082 | | | | st16yr | st16yr | -0.288 | (0.213) | -0.074 |
| | st16yr | -0.070 | (0.203) | 0.030 | | nn16yr | | nn16yr | -1.019 | (0.064) | -0.557 | | |
| B | il8yr | ht8yr | -0.088 | (0.216) | 0.397 | G | il8yr | ht8yr | 0.301 | (0.156) | 0.492 | | |
| | | ht12yr | 0.098 | (0.205) | 0.405 | | | dbh8yr | dbh8yr | 0.230 | (0.192) | 0.388 | |
| | | dbh8yr | -0.431 | (0.195) | 0.263 | | | st8yr | st8yr | -0.021 | (0.154) | 0.041 | |
| | | dbh12yr | -0.160 | (0.233) | 0.239 | | D | dbh112yr | dbh112yr | -0.577 | (0.325) | -0.018 | |
| | | st8yr | -0.201 | (0.239) | -0.030 | | | | st16yr | st16yr | 0.399 | (0.186) | 0.121 |
| | | st16yr | -0.174 | (0.216) | -0.047 | | | F | ht8yr | ht8yr | 0.104 | (0.282) | -0.154 |
| | | nn16yr | -0.967 | (0.048) | -0.728 | | | | | dbh8yr | dbh8yr | 0.404 | (0.245) |
| B. Number of nodes between 6 and 12 m (nn) | | | | | | | | | | | | | |
| B | nn16yr | ht8yr | 0.270 | (0.202) | -0.089 | D | nn16yr | dbh112yr | -0.577 | (0.325) | -0.018 | | |
| | | ht12yr | 0.047 | (0.202) | -0.136 | | | st16yr | st16yr | 0.399 | (0.186) | 0.121 | |
| C. Visual estimate of internode length (vis) | | dbh8yr | 0.567 | (0.175) | 0.002 | F | nn12yr | ht8yr | 0.104 | (0.282) | -0.154 | | |
| | | dbh12yr | 0.302 | (0.220) | -0.005 | | | dbh8yr | dbh8yr | 0.404 | (0.245) | 0.037 | |
| | | dbh14yr | 0.073 | (0.238) | -0.007 | | | dbh12yr | dbh12yr | 0.364 | (0.243) | 0.039 | |
| | | st8yr | 0.250 | (0.230) | 0.000 | | | st8yr | st8yr | 0.290 | (0.252) | -0.046 | |
| | | st16yr | 0.317 | (0.198) | 0.076 | | | vis12yr | vis12yr | -1.026 | (0.079) | -0.797 | |
| | E | vis14yr | ht8yr | 0.564 | (0.221) | | 0.260 | F | vis12yr | ht8yr | -0.023 | (0.295) | 0.305 |
| | | | dbh8yr | -0.456 | (0.267) | | 0.137 | | | dbh8yr | dbh8yr | -0.370 | (0.262) |
| | | dbh12yr | -0.218 | (0.306) | 0.159 | | dbh12yr | | dbh12yr | -0.297 | (0.263) | 0.056 | |
| | | st8yr | -0.455 | (0.220) | -0.034 | | st8yr | | st8yr | -0.286 | (0.265) | 0.010 | |
| | | st12yr | -0.191 | (0.256) | -0.028 | | st12yr | | st12yr | 0.089 | (0.269) | 0.072 | |

* r_g = genetic correlation† r_p = phenotypic correlation

‡ Age at which the measure or assessment was performed indicated in years from planting

and straightness traits (when compared to shorter internode trees). However, genetic correlations are generally not of sufficient magnitude to allow this to be concluded with any degree of certainty. Nevertheless, there should be either no reduction, or an increase, in the over-all value of the wood produced due to the increased proportion of clear knot-free wood, as predicted by Carson (1988) for *P. radiata* under certain silvicultural systems and pricing structures.

Two selection strategies could be applied to improve internode length; either internode length could be added to the existing selection traits, or a special-purpose breed could be developed. Dean *et al.* (1988) suggested that the concurrent improvement of growth, straightness, and internode length in a single general-purpose breed may be the most appropriate strategy. However, Dean *et al.* assumed positive genetic correlations between internode length, growth, and straightness traits. The addition of another primary selection trait will reduce gain in the original selection criteria owing to the reduced selection pressure which can be applied to any one trait (Falconer 1981). In addition, the internode length of plus-trees in the current breeding population is generally quite short as reflected in the over-all means of the seven tests reported here (Table 2). Therefore, so as to not restrict gains in growth and stem straightness in the main breeding population, and to ensure large rapid gains in internode length, it was decided to develop a special-purpose long-internode breed similar to one developed with *P. radiata* in New Zealand (Shelbourne *et al.* 1986; Carson 1987, 1988).

Development of a Long-internode Strain

Of the approximately 400 first-generation hoop pine plus-trees originally selected, only 13 had sufficiently long internodes (>1.8 m) to be selected for this breed. It was necessary, therefore, to undertake a programme of phenotypic selection of plus-trees with long internodes, good relative vigour, and reasonable stem straightness.

During the 3-year period 1987–90, 58 first-generation long-internode trees were selected in mature plantations and a further 36 second-generation trees were selected in open- and control-pollinated progeny trials of the existing main breeding programme. These trees were selected for uniformly long internode length (average length exceeding 2 m) being produced from an early age. The trees selected were also required to have good relative vigour and reasonable stem straightness. It is intended to increase the total number of long-internode trees selected to around 200.

In 1989–90 the 60 long-internode plus-trees with the best phenotype were field grafted in a conventional multiclonal seed orchard. These trees are being progeny-tested for general combining ability (GCA) using a polycross mating design. Given the moderate to high heritability and the great variability of internode length, phenotypic selection should be effective in increasing internode length in hoop pine. Therefore, when progeny test data are available, it should be possible to apply a fairly heavy selection pressure on growth and straightness traits when culling the long-internode seed orchard, particularly if genetic correlations are negligible. It is expected that this orchard will be culled and producing sufficient seed to establish up to 25% of the annual planting programme by the year 2005.

Further improvement of the long-internode breed will be accomplished through selection in control-pollinated families. All the trees in the current breeding population, and any new

selections made in the future, will be single-pair-mated with one another. Selection within the progeny of these crosses to form the new breeding population will aim at improving vigour and stem straightness while maintaining internode length at between 2 and 3 m. A new clonal seed orchard will then be established using the most promising new selections and the original selections with highest GCA.

It remains uncertain as to what effect improvements in internode length in hoop pine will have on volume and straightness, but it seems likely that some genetic gain in these traits will have to be foregone.

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