GENETIC SELECTION CRITERIA IN *PINUS RADIATA* BASED ON CROWN CHARACTERS

by

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ORIGINALITY OF THESIS

The progeny trial information used in this thesis was made available to me by the Forest Research Institute, Canberra. The analysis, interpretation and presentation of the data are my own original work.

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SUMMARY

The potentials of crown variables for increasing productivity are investigated for *Pinus radiata*. Genetic data are based on a twelve-year-old progeny trial containing twelve controlled-crossed families. Sampling is restricted to the dominant and codominant crown classes to minimize competitional effects. Heritability estimates and genotypic and phenotypic correlations are derived for eleven crown characteristics and four productivity variables. The crown traits are branch diameter, branch length, branch angle, number of branches per foot, number of branches per whorl, number of whorls per foot, crown length, crown radius, crown length-to-width ratio, crown surface area, and crown volume. The productivity variables are diameter at breast height, total volume, basal area increment, and volume per acre.

Selection indices for productivity per acre are constructed from these data. One series of indices are based on genetic information alone, and another series include 'reasonable' estimates of economic values for crown traits. The efficiency of the selection indices is assessed from the expected genetic gain in productivity which is compared with the gain anticipated from selection for productivity alone. The indices are tested on the family means to detect which type of tree the indices favour.

Narrow sense heritability estimates indicate branch and whorl frequency variables have high breeding values, unit branch characters are moderately genetically controlled, and crown dimension traits have low heritabilities. Productivity variables have the lowest breeding values.

Genotypic and phenotypic correlations derived from components of variance and covariance show that most crown traits are strongly related to productivity per acre. Improving productivity through correlated response to selection for crown traits is genetically feasible.

Selection indices based on volume per acre and crown traits such as number of whorls per foot, number of branches per whorl, crown length-to-width ratio, and crown radius estimate a three- to four-fold improvement in productivity per acre can be achieved in comparison with selection for volume per acre alone. Incorporating economic values in the index does not greatly alter the relative index weights or expected advance.

Testing the indices on the family means shows the majority select the type of trees having narrow, multinodal crowns with a good length-to-width ratio combined with a moderate stem volume.

Crown traits are shown to play a significant role in the whole tree concept. Breeding programmes must place more emphasis on evaluation of crown attributes to achieve a maximum yield of useable wood.

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INTRODUCTION

THE CROWN IN TREE IMPROVEMENT RESEARCH

1. Increasing Emphasis

The tree crown is receiving increasing attention by tree improvement workers in their search for indicators of genetic capacity. The Second World Consultation on Forest Tree Breeding (1969) recommended that crown traits "which influence many economic and technical aspects of timber use, and which have been shown to be heritable should receive greater attention than in the past". Faulkner (1969) presented a paper to this meeting reviewing published research on the genetic variability of branch and crown characters, most of which has been carried out during the last decade. It is notable that in Hattemer's (1963) summary of published heritability estimates presented to the First World Consultation no values for crown traits were given. Crown traits are now being assessed in most selection programmes and progeny trials, where once these parameters were considered unimportant and too expensive to measure.

2. The Whole-Tree Concept

This increased emphasis on crown research is the result of changing attitudes towards breeding objectives.

The goal of breeding only for increased growth rate is being superseded by the whole-tree concept which is defined by Stonecypher (1969) as "the goal of the tree breeder to produce a maximum of economically useable wood per tree and per acre". The term 'economically useable wood' implies not only volume must be considered, but also the manner in which this volume is produced. The crown exerts a sizeable influence on economically useable wood both directly and indirectly, and has become a recognized factor in the whole tree concept.

2.1 Direct effects of the crown

Unlike the agriculturalist who has the advantage of small plant size, tree improvers cannot hope to measure photosynthesis directly under forest conditions. Indeed, the non-destructive collection of leaf area or leaf weight data so as not to affect the value of a candidate plus tree or long-established progeny trial is a formidable problem in itself. Consequently, the improvement worker must relate crown attributes to wood increment in order to assess the photosynthetic process.

However, a simple relationship between crown and stem is improbable because of the inherent complexity of the photosynthetic process and the multitude of factors which affect it. For example, the amount of bole wood produced by a particular crown is a function of the efficiency of the photosynthetic tissue, the total photosynthetic area contributing to the production of carbohydrates, the duration of photosynthetic activity both daily and annually, and the propensity of the tree to store its photosynthetic product in the bole in preference to branches, roots, or more leaf tissue (Kramer and Kozlowski, 1960).

Measurements of the crown largely reflect the size of the photosynthetic system. Stiell (1962) assessed crown structure of _Pinus densiflora_ and found an excellent correlation between foliage weight and crown volume. Crown surface area was also found to be highly correlated with needle weight. Loomis _et al_. (1966) found highly significant correlations between foliage weight and branch diameter for shortleaf pine. Attiwill (1962) detected similar association for _Eucalyptus obliqua_. Senda _et al_. (1952) and Senda and Satoo (1956) studied density effects on crown and stem parameters for _Pinus densiflora_ and _Pinus strobus_ respectively. Both studies found a decrease in crown size and live crown ratio are associated with a decrease in the amount of needles per tree when stand density increases.

Through their relationship to size of the photosynthetic system, crown traits have been shown to be related to productivity (Wareing, 1964). Total and incremental values of productivity have been reported to be significantly correlated with the absolute size of the crown, as assessed by such variables as crown volume, crown surface area, and crown projection area. Brown and Goddard (1961) demonstrated that crown surface area, volume, radius, and projection area are significantly related to ten-year basal area increment for *Pinus taeda*. Berlyn (1962) found that stem volume of *Populus deltoides* was highly related to the surface and volume of the tree crown. He postulated that crown volume and surface area are reflections of both stem volume and basal area increment. Hamilton (1969) detected highly significant correlations between the crown parameters of volume, surface area, projection area, and length, and the productivity variables stem volume, girth, and height. His study material was a twenty-three year old *Picea sitchensis* stand.

Crown traits independent of the absolute size of the crown have also been related to productivity. Wedel *et al.* (1967) found number of branches per whorl to be highly correlated with stem diameter for *Pinus taeda*. Branch size and length were likewise associated with bole volume. Number of whorls per tree is shown to be related to stem diameter (Fielding, 1960), and to tree height (Bannister, 1962; Fielding, 1967). Grano (1957) shows that *Pinus taeda* seed-trees visually classed as having dense crowns grew faster in diameter than those with less foliage.

All crown variables that estimate the amount of photosynthetic tissue present on a tree will be associated with productivity. They will thus have a direct bearing on the optimization of useable wood per tree and per acre.

2.2 Indirect effects of the crown

The effect of crown traits on wood quality are well-known. Branch size and frequency, number of whorls, and branch angle are all associated with percentage of knotwood. The strength properties of saw timber are affected by knots, as are the peeling properties and appearance of veneer (Faulkner, 1969). Knotwood affects pulping costs, and the associated reaction wood changes the quality of the pulp (Nicholls, 1967; Wedel *et al*., 1967). These branch and whorl characteristics are also related to pruning costs (Jacobs, 1938), limbing expenses, and mechanical debarking costs. Self-pruning ability influences the quantity of sound wood and the products that can be derived from it (Fenton, 1967).

2.3 The role of the crown in the 'ideal' tree

What emerges is a picture of the 'ideal' tree towards which breeding must progress to maximize useable wood. Such a tree could be visualized as having a large, straight bole of good wood quality combined with a narrow, long, vigorous crown consisting of small branches at a near-horizontal angle. In effect, the ideal tree is one that will produce the greatest quantity of useable wood for the space it occupies (Matthews, 1963). The relative importance of the crown is seen to be great. It must be manipulated in order to control tree growth and quality for maximum economic yield (Smith and Ker, 1960; Smith, 1963).

MULTIPLE-TRAIT SELECTION

1. Methods

The fact that crown traits as well as productivity variables must be considered together implies multiple-trait selection. There are three basic methods available for applying multiple-trait selection. These are tandem, independent culling level, and selection index (Hazel and Lush, 1942).

1.1 Tandem selection

Tandem selection involves the improvement for one trait at a time over successive breeding generations. Because of the long generation interval of most tree species, this method is of limited use to forest tree breeders.

1.2 Independent culling level

Independent culling level is based on the establishment of a level of merit for each trait below which a candidate is rejected regardless of its acceptability for all other traits. If the level of acceptance for each trait is set high the selection differential becomes increasingly difficult to achieve as the number of tree characters under consideration rises (Pederick, 1967). For example, if the standard of selection is the best one per cent of the population for each of three traits, the chance of obtaining an individual up to standard with respect to all three characters is one in one million trees. This system is obviously of limited use.

1.3 Selection index

The selection index is the most efficient in terms of providing an objective method whereby the characters are weighed in a systematic manner. It takes into account the relative economic value of each trait, the genotypic and phenotypic variances of these traits, and the genotypic and phenotypic covariances (or correlations) between each pair of characters. With the proper information an index can be constructed which has no peer for assigning weights (Brim *et al.*, 1959).

The widely used point-score system of selection is an attempt by breeders to construct an index with inadequate information. It assigns values to each trait based on an arbitrarily chosen scale. This scale is determined by the relative economic importance of each trait, but it has no genetic basis. Woessner (1965) points out many grading systems are derived "with little knowledge of the heritabilities or genetic correlations between the characters for which the trees are being selected". The point-score system has proved adequate for selection during the period of tree improvement when genetic information on most species has been limited. However, with the increasing maturity of many progeny trials the data required to construct proper selection indices are becoming available and should be so used.

2. Construction of a Selection Index

The data required to construct a selection index are: genotypic and phenotypic variances of each trait, genotypic and phenotypic covariances between each pair of traits, and the relative economic values of each trait.

2.1 Reliability of input information

Emphasis must be placed on the reliability of genetic information used to construct an index. Ehrenberg (1969) points out "when genetic variances are being estimated, many assumptions have to be made which are never fully realized in the material investigated. This fact lends a varying degree of unreliability to the calculated values". Williams (1962) cautions that an index derived from poorly estimated parameters is likely to be poor, "and may even have an expected negative correlation with the optimum index". Namkoong (1969) directs attention to the fact that the error of estimate for the genetic parameters is usually high because sampling of the population is restricted to small numbers of relatives and very few environments. The usual material from which we derive our parameters is a progeny trial not specifically designed for the purpose of estimating genetic variances (Stonecypher, 1966). In general, progeny trials are representative of a small sample of the population biased through initial selection, and are restricted to a single environment. The experimental designs in which they are laid out were developed to test differences between means rather than variances (Stonecypher, 1966). These factors present a formidable deterrent to the construction of an accurate index, but as long as it is derived from the best available data it can be expected to be better than no index at all.

2.2 Genotypic and phenotypic variances

There is an ever-increasing store of knowledge about the genetic and phenotypic variation of most economically important traits. This information is usually presented in the form of heritability estimates. Essentially, heritability expresses the degree of correspondence between the phenotypic value and breeding value of a character. It quantifies the concept of whether progress from selection for a character is relatively easy or difficult to make in a breeding program (Hanson, 1963). Unfortunately, the misuse of the term has vitiated the usefulness of a large number of the published values. The FAO/IUFRO Meeting on Forest Genetics (1964) recommended "the genetic structure of populations should be investigated as thoroughly and defined as precisely as possible to permit realistic estimates of genetic parameters...used in developing breeding programmes". Too often the estimate has not been qualified with the nature of the genetic variability, the experimental units, or the inference population, and therefore its implications cannot be interpreted by geneticists (Hanson, 1963). Many researchers consider publication of the variances conjointly with the heritabilities would prevent much confusion. However, the relative amounts of variation in a trait attributable to genetic and phenotypic sources can usually be inferred from heritability estimates.

2.3 Genotypic and phenotypic covariances and correlations

Genetic and phenotypic covariances and correlations are derived in conjunction with variances. Although there is a fair knowledge of the phenotypic relationships between variables for many species, little is known about the genetic correlations. Many researchers have assessed two or more traits in a progeny trial, but have failed to publish the genetic associations between characters. This deficiency is now recognized, and the Second World Consultation on Forest Tree Breeding has recommended that genotypic covariance should be included in reports.

A genetic correlation coefficient measures the degree of association between the genetic variances of two quantitative characters in a given population (Reeve, 1955). Its meaning can best be understood from its relation to phenotypic correlation. The association between two characters which can be observed directly is the correlation of phenotypic values (Falconer, 1964). This observational correlation results from two main causes; genetic and environmental. It is assumed these causes are uncorrelated. The genetic component is chiefly determined by pleiotropy which is the property of a gene to affect more than one character. If the gene is segregating it causes simultaneous variation in all characters it affects. Environmental correlation results from the effect the same environment has on several characters; it also includes all non-additive genetic components. Hence, the genetic and environmental correlations correspond to the partitioning of the phenotypic covariance into the additive genetic component versus all remaining components.

The degree of heritability, or breeding value, of the correlated traits play an important part in establishing which of the two components is the chief determinant of the observational correlation. Falconer (1964) points out that the phenotypic correlation is equivalent to

$$r_P = \frac{COV_A + COV_E}{\sqrt{(VAR_{AX}+VAR_{EX})(VAR_{AY}+VAR_{EY})}} = h_X h_Y r_A + e_X e_Y r_E \ , \quad (1)$$

where P, A, and E denote phenotypic, additive genetic, and environmental parameters respectively; X and Y symbolize the two traits; h the square root of heritability, and e its complement; r is the correlation coefficient. If the characters have low heritability values, the environmental rather than the genetic correlation will determine the observational correlation. The dual nature of the phenotypic relationship makes it clear that the magnitude and even the sign of the genetic correlation cannot be derived from the phenotypic correlation alone.

The selection index uses the information contained in the variances and covariances to show the expected genetic response in a character through selection for correlated traits. Genetic gain in one particular character that can be achieved through multiple-trait selection will depend on both the heritability of the character being considered and those of correlated characters. If the heritabilities of these correlated characters are high in relation to that of the desired trait, correlated response to selection for the highly breedable attributes will increase the possibility of gain in the desired trait. Characters that are not genetically correlated will have little effect on the progress of the trait in question.

2.4 Economic evaluation

Economic evaluation of the traits is the final information required to construct a selection index. This presents a special difficulty to the tree breeder. However, the problem of economic evaluation is by no means limited to selection index technique alone; any method of multiple-trait selection, and particularly the point-score system, requires identical subjective valuation of the relative importance of each trait.

The breeder is not in a particularly favourable position to collect data from which he can assess the importance of traits. Silviculturists, procurers, processors and marketers all evaluate a trait differently according to its effect on their particular discipline, and there is no special body to collate information from all sectors of the wood industry. Even the economic importance of traits within one small segment of the industry is not fully understood. Namkoong _et al_. (1967) illustrate the problem of defining breeding objectives in the Southeast United States. They remark "the relative value of tree and wood traits in pulp production...are but vaguely known now, dimly foreseeable in the future, and perhaps only definable in terms of limits to relative values".

The importance of a trait is not likely to remain static over time. Technical improvements tend to change the significance of a trait. Changing product markets similarly influence the economic importance of wood characteristics, and since breeding takes many years to yield results, the tree improver must compromise in predicting the future importance of tree characters.

Namkoong (1969) points out one other difficulty in evaluating traits. Because of differing product potential and the common practice of grading and marketing by classes, a character's value function is generally discontinuous rather than linear over the size range. Selection indices require linear functions since they show the relative improvement in the unit of selection which is caused by a change of one unit of the correlated character. However, this problem may be over-emphasized since linearity can generally be assumed over the size range being considered for the traits.

The problem of collecting reliable information does not preclude the exploitation of the selection index as a method of multiple trait selection. Like any other facet of genetic research, there is a lack of 'suitable' material, but use must be made of existing data. Efforts to derive a satisfactory index will certainly result in better selection criteria than are currently used in most improvement programmes.

PROJECT OBJECTIVES

The goal of this thesis is to study the genetic variability of several crown traits, and to assess their implications for the production of economically useable wood per tree and per acre. Each trait will be viewed in relation to its genetic and economic impact on productivity. Selection indices will be constructed using those variables which maximize economically useable wood. The efficiency of these indices will be compared with selection for productivity alone. Genetic data will be provided by a twelve-year-old progeny trial of *Pinus radiata*.

DATA COLLECTION

THE PROGENY TRIAL

The genetical data used in this study were obtained from a controlled pollinated progeny trial located in Uriarra Forest, A.C.T. It was established by the Forest Research Institute in 1953 to test the superiority of progeny derived from controlled pollination of trees selected from surrounding plantations. Its designation, Progeny Test No. 3, indicates that it is one of the oldest trials in the area. Permission was obtained to use the Institute's 1966 measurements of the trial, and, combined with additional measurements carried out by the author in 1969, these constitute the data used for analysis.

1. History and Environmental Factors

The trial was originally established with twenty different full-sib families. However, not all families were fully replicated in the experimental design, and in order to simplify computation and interpretation only the twelve fully replicated families were used in the analyses. The parentage and number code for these families are shown in Table I.

In all, fourteen parent trees were used in combinations as male and female to produce the twelve

Table I

Parentage and Code of Twelve Full-Sib Families Analyzed in Progeny Trial

Code Number	Parents Female		Male	Code Number	Parents Female		Male
1	443	x	942	7	985	x	994
2	440	x	944	8	991	x	935
3	941	x	942	9	982	x	990
4	937	x	991	10	937	x	935
5	443	x	994	11	984	x	991
6	855	x	985	12	482	x	991

progeny groups. These parents were selected primarily for their vigor and branching habits. Table II gives the original notes recorded for these trees. The age at time of selection is not given, but most parents would have been between fifteen and eighteen years old considering the average age of A.C.T. plantations at that time. The lack of quantitative data on parent-tree characteristics prevents any statistical analysis of parent-offspring relationships or genetic advance.

The trial is planted at eight-foot square spacing, and occupies an area of 1.2 acres situated on a well-drained, gentle slope having a south-west aspect. The area receives about thirty-five inches of rain a year, and the soil is porous sandy-loam. The previous forest type was dry sclerophyll which was felled and broadcast-burned prior to

Table II

Characteristics of Parent Trees as Recorded at Time of Selection

Plus-Tree Designation	Characteristics
440	Dominant. Average vigor. Wide-angled branch type - a good branching type.
443	Very vigorous. Some heavy and acute-angled branches.
482	Medium vigor. Very small and evenly spaced branches. A good type.
855	Dominant. Vigorous. Branch angle fairly wide. Branches slightly heavy. Whorls of uneven size.
935	Fair vigor. Branches very small. Multinodal.
937	Vigorous. Small branched tree. Only fault was two whorls of cones.
941	Very good tree of medium vigor.
942	Very good tree of medium vigor.
944	Medium vigor. Narrow crown. Small, wide-angled branches.
982	Good branching type.
984	Good branching type.
985	Very vigorous. Badly branched.
990	Vigorous. Multinodal. Branches slightly acute.
991	Very vigorous.

planting. There are still partially burnt logs remaining in the area, but these did not greatly disturb the regularity of spacing. The trial was pruned to six feet at ten years, but no other silvicultural treatment has been applied to the area. The site class for pine is seventy feet at age twenty which is good quality for this area. There are no obvious diseases or problems in the trial or surrounding stand, and growth can be said to be progressing normally for this environment. Plate 1 shows a view looking downslope through the trial.

The twelve families form a randomized complete block replicated five times. The unit plot originally contained ten trees, but sampling was restricted to the dominant and codominant individuals only. A total of 371 trees were selected. Table III gives a breakdown of the sampling distribution in the trial.

Plate 1

View of Trial at Age Fifteen
Average diameter is eight inches. Note regular spacing.

Table III

Sampling Distribution of Progeny Trial

Family	Block 1	2	3	4	5	
1	8	4	5	7	5	29
2	8	6	3	8	6	31
3	8	8	8	7	6	37
4	5	3	7	6	6	27
5	7	9	6	5	9	36
6	5	3	3	4	4	19
7	6	6	7	7	3	29
8	4	5	6	8	7	30
9	7	7	9	10	7	40
10	5	6	4	7	4	26
11	6	7	8	7	9	37
12	7	6	6	5	6	30
	76	70	72	81	72	371

Plot arithmetic mean 6.18
Plot harmonic mean 5.64

2. Rejection of Unrepresentative Data

The validity of rejecting the suppressed and intermediate portions of the trial can be challenged. The obvious disadvantage of removing any tree from progeny analysis is that information is lost, and the ability to test for significant differences between means is reduced through loss of degrees of freedom. However, in genetical research the emphasis is on the relationship of genotypic and phenotypic variances rather than means. Stonecypher

(1966) points out that practically all experimental designs, especially those used in progeny tests, were developed for precise comparison of means and not for estimating variances and their components. Wright and Freeland (1960) and Wright (1963) claim that statistical efficiency is at a maximum when environmental differences among plots belonging to the same replicate are small. This leads to the suggestion that removal of individuals from a plot that are largely the product of environmental and competitional stresses would improve the efficiency of the trial.

The removal of suppressed trees is a crude way of accounting for competitional effects. With special experimental designs variances resulting from competition between different genotypes can be explained (Stern, 1965; Sakai, 1961). However, the design used for this trial and, indeed, most progeny designs do not permit interpretation of competitive effects. If competition is not accounted for in some way, the within- and between-plot variances will be increased (Singh, 1967) resulting in unrealistically low heritability estimates. The effectiveness of removing competitional influences in this manner remains to be seen.

Curtin (1968) gives strong support for removing the suppressed portion of a stand. He found a bimodal size distribution in Eucalyptus obliqua stands corresponding to the suppressed and codominant classes. Over fifty per cent of the stand did not play a significant role in stand growth, and contributed only twenty per cent of the total basal area. He found that suppressed individuals may greatly change the mean of a population yet contribute little of growth. Curtin emphasizes that the two sub-populations behave in different ways, and should be considered separately in growth analysis.

Figures 1 and 2 show that the Pinus radiata stand conforms with Curtin's results. Although the young age of the stand prevents a clear distinction between the two sub-populations, Figure 1 indicates the distribution of diameters is decidedly skewed to the left by the suppressed stems. This portion of the stand remains alive, although no significant increment occurs. This may be due to exchange of assimilates through root grafts which keeps this portion of the stand alive (Will, 1966; Wood, 1969). The suppressed trees remain relatively static in size, whereas the dominant trees continue to grow causing the means of the two sub-populations to draw apart.

Figure 2 demonstrates the negligible amount of growth contributed by the suppressed trees. When the trees were arranged according to diameter, the smallest fifty per cent of the stand accounted for only 24.6 per cent of basal area

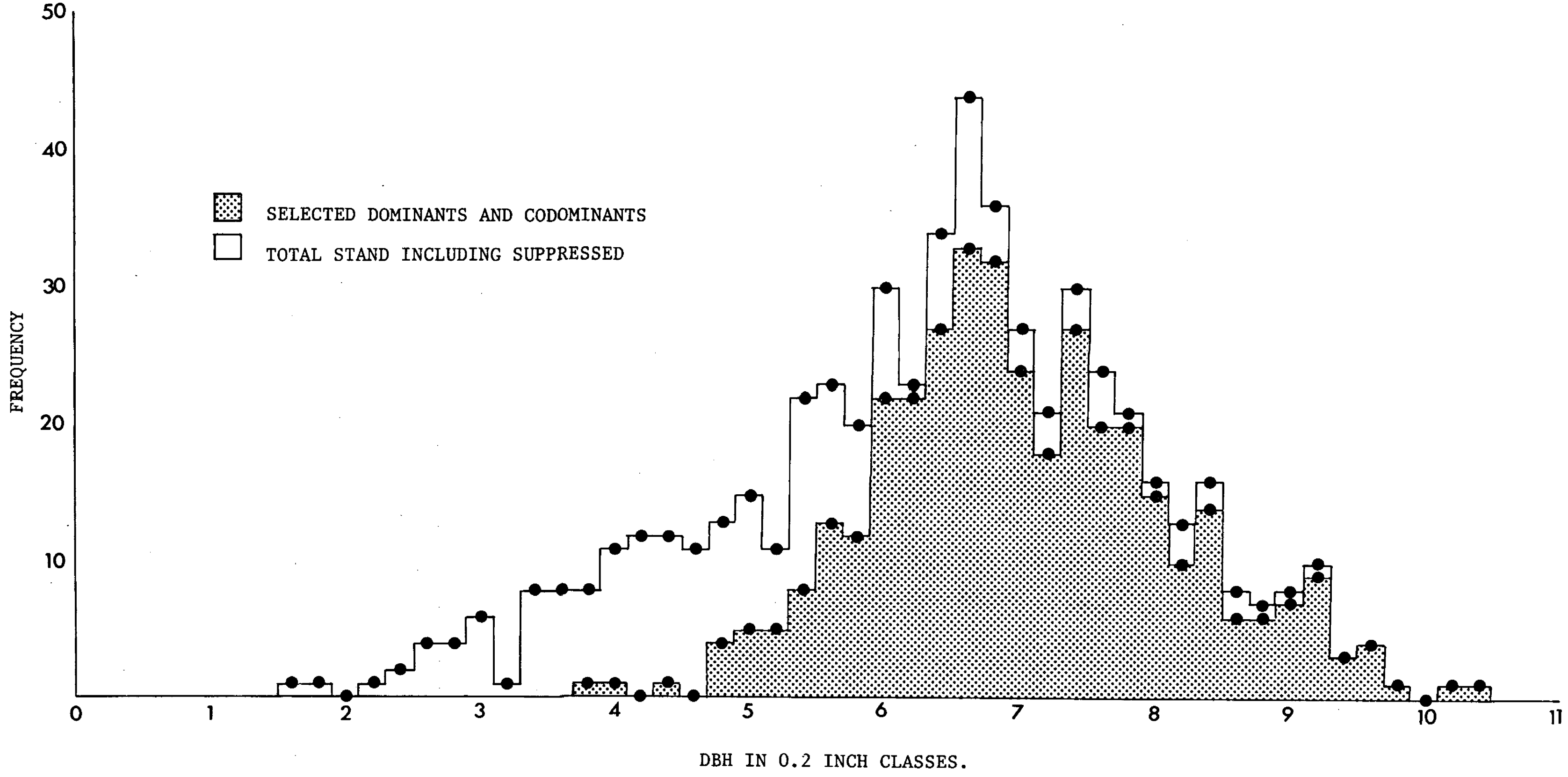

Figure 1. Diameter Distribution of Trial Before and After Removing Suppressed, Intermediate, and Forked Trees.

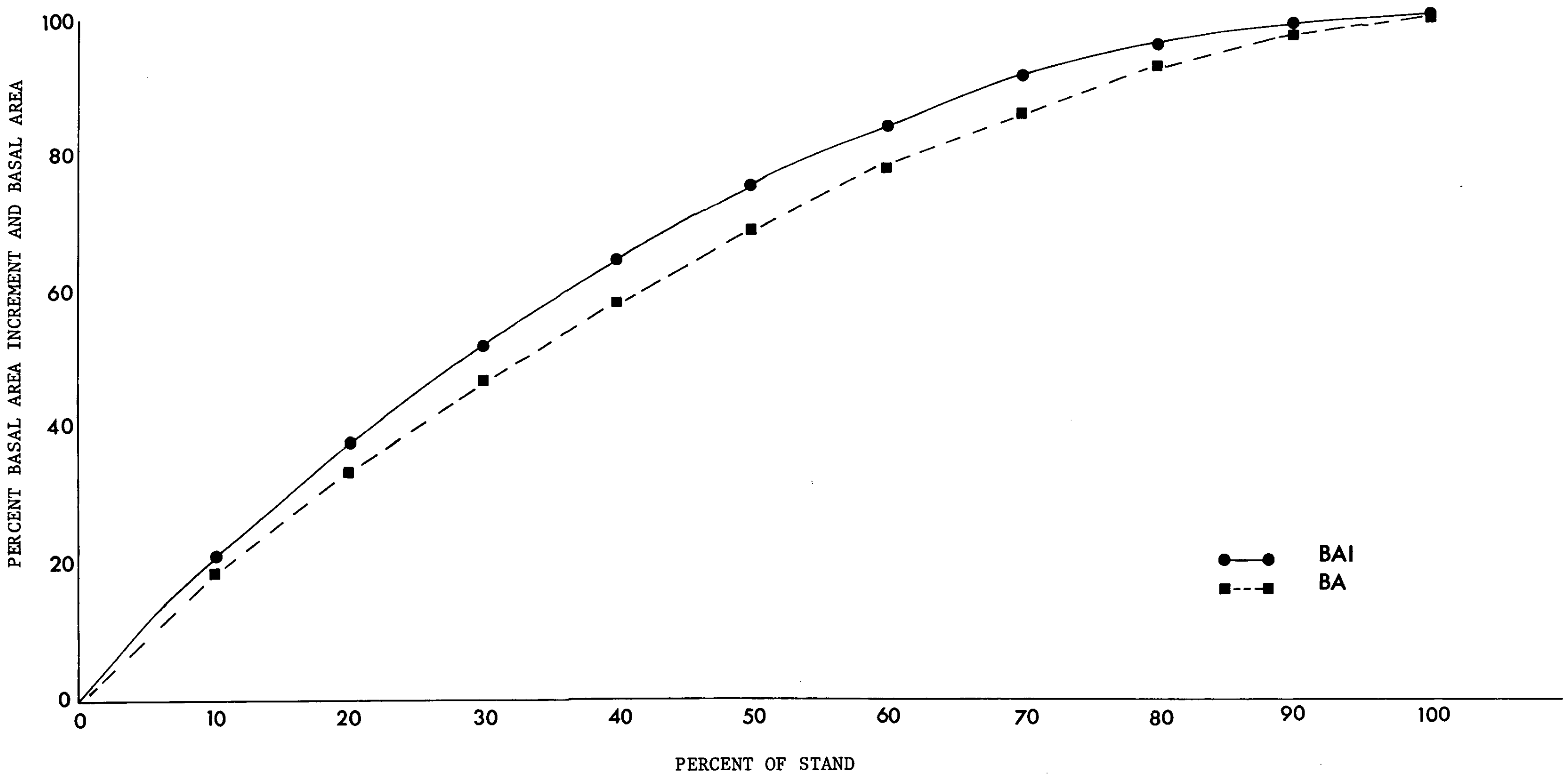

Figure 2. Percentage of Trial Contributing Total Basal Area and Basal Area Increment.

increment and 31.7 per cent of total basal area. Ten per cent of the stand produced no increment at all. The portion of the stand that was actually rejected from analysis amounted to thirty-five per cent, and produced 16.4 per cent of the increment and 23.4 per cent of basal area. This is a higher proportion than the graph indicates because fifteen per cent of the rejected individuals were from the dominant and codominant classes. These were considered unrepresentative because of forks or broken tops. Plate 2 depicts an example of a suppressed tree that was not included in analysis.

CROWN VARIABLES

The crown can be quantified in various ways. Van Slyke (1964) and Marden and Conover (1959) give excellent descriptions of crown measurements. But rather than test all possible variables that can be assessed on a crown we can select those which are most applicable to the experimental material - immature *Pinus radiata* grown in plantation conditions.

1. Description of the Crown

The crown of immature *Pinus radiata* grown in plantations has certain characteristics. Its shape can be described as paraboloid or conical depending on the growing

Plate 2

Typical Suppressed Tree Removed from Analysis

This tree has added no increment in three years, yet the crown is still green. The tree must be classed as 'alive'.

space available to the individual (Brown and Hall, 1968). The lowermost branches curve upwards, but once crown closure has occurred newly produced branches fail to curve as much and are shorter than the initial laterals. Two theories attempt to explain this: Rawlings (1961) has suggested that the beating of branch primordia by adjacent crowns limits branch elongation, and Fielding (1960) contends that apical dominance increases with physiological age. He offers as evidence the fact that clones exhibit greater apical dominance than seedlings.

Needle persistence is closely related to light intensity. Needles live for two to three years on both the main stem and laterals. They die from the branch base upwards as new growth added each year reduces the amount of light reaching the older needles. The photosynthetically effective crown thus forms as a sheath which moves upwards with age as light is excluded from the lower portion by competing trees. The rate of ascent of the green crown and the age at which it initially moves has been shown to be linearly related to spacing (Beekhuis, 1965).

P. radiata is multinodal; in any given year zero to five or more whorls of branches may be produced (Bannister, 1962). There is large variation within the species for this character, but an individual tends to have limited variation from year to year. This suggests strong genetic control. The internodal length varies both within a year and from year to year. The variation between years can be accounted for by annual shoot elongation; as a tree ages height increment declines, and so internodal length is reduced.

Size of branches on a given whorl varies from small epicorms to large, acute-angled ramicorms that have at one time competed with the main shoot. There is also large variation in average branch size from whorl to whorl. Some whorls have mainly small branches, and others carry chiefly large ones. The number of branches on a whorl is also highly variable ranging from one to ten or more.

Branch angle varies from acute to horizontal both within a whorl and between whorls. Angle generally widens with age due to the increased weight of the branch (Fielding, 1960).

Fielding (1960, 1967) has detected several phenotypic relationships between crown traits in P. radiata. Branch diameter is positively correlated with branch length and negatively associated with branch angle, number of whorls per foot, and number of whorls per tree. Number of whorls is positively related to branch angle, dbh, tree height, and number of branches per foot.

Plates 3 to 6 illustrate the variation found in several crown characters in the progeny trial.

Plate 3

Variation in Crown Cover

Three different families have heavy, intermediate, and light crowns. The heavier crowns are associated with fewer large branches, whereas the light crowns have numerous fine branches.

Plate 4

Variation in Branch Size
Three different families point out the relationship of branch size and whorl frequency. The large-branched crowns are associated with fewer whorls per foot and less compact foliage.

Plate 5

Variation in Number of Whorls per Foot

Whorl frequency of two families show greater whorl frequency is associated with smaller, more horizontal branches.

Plate 6

Variation in Branch Angle
Branch angle for two families illustrates this variable is under strong genetic control.

2. Measurement of Variables

Variables which best describe the immature *Pinus radiata* crown are unit branch characteristics, branch and whorl frequency traits, and crown dimensions.

2.1 Unit branch characteristics

Unit branch characteristics represent an average of the three largest diameter branches found in the two-foot section above the pruned stem. The average sampling position was thus six to eight feet above ground. Branch characteristics therefore approximate the mean maximum values for the tree. The following measurements were taken:

Branch diameter (BD) - measured to the nearest tenth of an inch two inches from junction with bole,

Branch length (BL) - measured to nearest tenth of a foot from tip to butt in a straight line, and

Branch angle (ANG) - measured to nearest degree with a special protractor developed by the Forest Research Institute (Brown, 1967). The protractor measures the angle between branch and stem at approximately six inches from the axis.

2.2 Branch and whorl frequency characteristics

Branch and whorl frequency characteristics were measured on the ten-foot stem section above the pruned base. To be counted a branch had to be more than one-half inch in diameter two inches from the base. A whorl had to consist of two or more branches of one-fifth inch or larger to be included in the count. Estimates of branch size were made by eye from the ground.

These specifications were laid down to give some biological significance to the variables. The size restriction for branches was arrived at after a preliminary analysis showed the variation was almost wholly random and uncorrelated to productivity if all branches greater than one-fifth inch were included in the count. It was felt that unless a branch contributed to growth for a significant portion of the life of the sample portion of the crown the branch should not be included in the count. The size restriction of one-half inch was derived from the distribution of mean maximum branch diameters for the stand.

Whorls, on the other hand, could contribute to productivity even if all branches are under one-half inch. A whorl of several small branches could be as effective as one of a few large branches. Hence, the specification of one-fifth inch for branch size was established only to exclude epicormic branches from the count.

The following counts were taken:

Number of whorls per foot (NOW) - average for the ten-foot section,

Number of branches per foot (NOB) - average for the ten-foot section, and

Number of branches per whorl (B/W) - ratio.

2.3 Crown dimension characteristics

Crown dimension variables were computed as products and ratios of crown radius and crown length which were themselves derived from other measurements. Crown radius was calculated as the horizontal projection of branch length at the measured angle. It is equivalent to the mean maximum radius for the crown. Crown length was derived as the difference between total tree height and pruned length which averaged six feet. This is analagous with establishing the lower limit of green crown at the lowermost whorl with one or more green branches. The crown dimension variables were derived in the following manner:

Crown radius (CR) - BL x sin(ANG),

Crown length (CL) - Tree height less six feet,

Crown surface area (CSA) - $CR\pi\sqrt{CR^2+CL^2}$, Crown volume (CV) - $\frac{1}{3}\pi CR^2 CL$, and

Crown length-to-width ratio (L/W) - CL/CR.

2.4 Productivity characteristics

Productivity variables were derived from diameter and height measurements. Diameter at breast height over bark (DBH) was recorded to the nearest tenth of an inch, and height (HT) was measured to the nearest foot with height sticks. Total volume per tree (VOL) was calculated over bark as one-third the volume of a cylinder of this diameter and height. Volume per acre (V/A) was defined as the summation of all trees of a given volume and crown radius that could be fitted on an acre. It is essentially a measure of productivity per unit area of land, and the acre was chosen as the unit to facilitate computation of economic values for the selection index. The variable was calculated in units of 100 cubic feet according to the formula $43560 \times VOL/(100\pi CR^2)$.

DBH was remeasured in 1969, and the three-year basal area increment (BAI) was computed from the gain in diameter.

Table IV gives a summary of the crown and productivity variables assessed for the trial.

Table IV

Statistical Summary of Variables

Variable	Units	Min.	Max.	Mean	S.D.	C.V.
V/A	100 cu.ft	4.51	93.98	20.48	13.84	0.67
DBH	inches	3.70	10.19	6.87	1.10	0.16
BAI	sq.ft	0.01	0.23	0.09	0.04	0.40
VOL	cu.ft	0.87	12.71	4.87	1.93	0.39
BD	inches	0.27	1.37	0.73	0.21	0.29
BL	feet	2.30	13.50	7.09	1.87	0.26
ANG	degrees	38.00	89.00	63.35	10.19	0.16
NOB	number	0.0	4.20	1.54	0.86	0.55
B/W	number	0.0	11.43	3.47	2.23	0.64
NOW	number	0.25	1.37	0.49	0.11	0.24
CL	feet	29.00	64.00	48.12	5.76	0.12
CR	feet	2.20	11.40	6.19	1.55	0.25
L/W	ratio	4.12	20.00	8.29	2.46	0.29
CSA	sq.ft/10	26.30	175.10	94.91	27.63	0.29
CV	cu.ft/100	1.90	64.48	20.67	10.85	0.52

ECONOMIC DATA

The effects of economic weights on selection indices are stressed rather than their accuracy. The values should be considered 'reasonable' rather than precise. The influence that economic values have on the indices will be investigated so that the impact of economic evaluation on the construction of selection indices can be judged. Brim *et al*. (1959) found that for one population of soybean the economic weights could be varied within a wide range without significantly altering the relative values of the index weights. The applicability of this conclusion will be tested for *P. radiata* by comparison of indices constructed with and without economic values.

1. Basis of Evaluation

No effort is made to assess the economic significance of a trait in terms of anything other than royalty. This absolves the problem of considering the implications of a trait in different sectors of the wood industry. Prediction of future values is not attempted. The economic evaluation of the variables is restricted to trait ranges at a first thinning, and discontinuities or non-linear functions are therefore somewhat modified. With the reduced range the assumption that functions are linear can more readily be accepted. Figure 3 gives the average

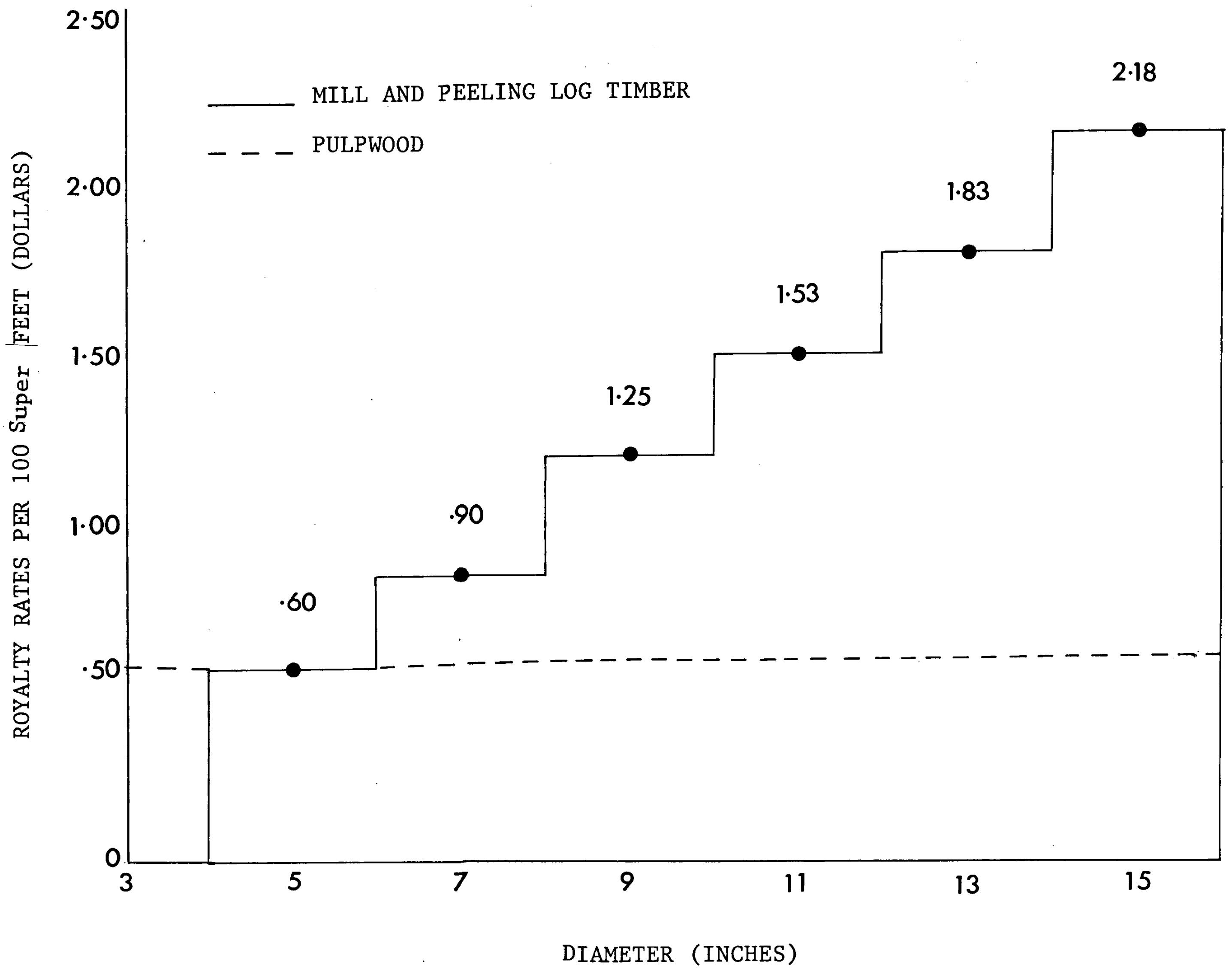

Figure 3. Royalty Rates for Mill and Peeling Log Timber and Pulpwood for

stumpage value of P. radiata for the Mount Gambier area, South Australia. It is based on diameter classes which imply discontinuities, but the fit of points to a linear regression is excellent.

The major discordancy in the economic data is caused by pulpwood values which are constant over the diameter ranges. No premium is paid for a larger-sized pulpwood log as for mill and peeling logs. Rather than ignore this problem a separate index will be constructed for pulpwood and sawlog regimes.

1.1 Maximizing volume per acre

The objective of pulpwood regimes is to maximize volume production per acre. The size of the individual tree is immaterial provided it is above a minimum diameter, and the quality of the stems is also unimportant within broad limits. Wood characteristics are economically relevant, but consideration of such variables is beyond the scope of the thesis. Hence, of all the crown and stem traits considered none has an economic value for pulpwood, and each trait will receive an economic weight of zero. Volume per acre will have a weight of one.

1.2 Maximizing economically useable wood per acre

The objective of a sawlog regime is to maximize production of economically useable wood, and log quality and size must be considered along with volume per acre.

Royalty rates usually increase with increases in log size and decrease with defects in log quality such as excessive sweep, knot size, and branch frequency. Although the trend is linear for log size (Figure 3), there are marked discontinuities in the royalty scales for defects. In fact, most Pinus radiata log royalty rates do not have grade limits, but concessions are given for certain classes of logs and in certain circumstances (Conservator of Forests, South Australia, personal communication). These discontinuities result from the dependence of the seriousness of the defect on log size; a larger log will sustain a more serious defect before it is degraded. However, the range of log sizes and quality traits is limited for the age of the stand under consideration, and the problem can be simplified by estimating the seriousness of defects on a log of average dimensions. We can assume that at a certain limit a defect will reduce the value of the average log to that of pulp quality, and that the value function for each variable is independent and linear over this limited range. We can then estimate the economic weight of a character under these restrictions.

Given that these assumptions are valid for the limited conditions of a first thinning, we can establish the limits at which a quality trait is likely to reduce the value of an average-sized tree. Let us assume that if we double the average size and frequency of knots degrade will occur. If branch diameter is increased to one and one-half inches, number of branches per foot to three, number of whorls per foot to one, and number of branches per whorl to seven, reduction in value per one hundred cubic feet of volume for the average-sized log will be from $0.90 to $0.58 (Figure 3) or thirty-five per cent. The economic weight attached to each variable relative to the selection unit for volume per acre will be; branch diameter -0.45, number of branches per foot -0.23, number of whorls per foot -0.70, and number of branches per whorl -0.35. These values are derived from the relationship between the increase in units of the variable from the mean to the established limit and the relative decrease in value for the unit of selection. For example, branch diameter increased 0.77 inches (units) from the mean value, 0.73 inches (Table IV), to the predetermined limit, 1.50 inches. This is related to a relative decrease in value of the selection unit of -0.35; thus, an increase in branch diameter of 1.0 unit will result in a decrease in value of -0.45 relative to the unit of selection which is one hundred cubic feet of volume. A weight for branch angle can likewise be derived if we set the limit at which the average log is degraded at 50 degrees. The weight will be positive because the direction of increase is favorable to wood quality. It is calculated at 0.03 for each unit of change.

Increasing diameter of the average log by one inch adds a value of $1.50 to the selection unit (Figure 3). For the average tree this would indicate an economic value of 0.17 for diameter measured in one-inch units.

Varying the area occupied by the crown will also influence volume per acre. Cromer and Pawsey (1957) show that total volume per acre is inversely related to spacing for immature Pinus radiata. Their values at age ten over a range of spacing from six to eleven feet indicate a reduction in volume per acre of 140 cubic feet for an increase in spacing of one foot. Average crown radius is consequently increased by one-half a foot. Hence, a one-foot increase in crown radius equivalent to a two-foot increase in spacing results in a reduction in volume of 280 cubic feet per acre. The appropriate economic weight for crown radius and its component branch length will be -2.8 relative to the selection unit of 100 cubic feet.

An economic value of zero is given all other traits that have no direct influence on the value of wood produced. They will be incorporated into the index, nevertheless, because their genetic and phenotypic relationships to other variables, and particularly to volume per acre, will be of value for correlated response and increase in genetic gains. Table V summarizes the economic values for both regimes.

Table V

Relative Economic Values for Traits in Pulpwood and Sawlog Regimes

Variable	Relative Economic Value	
	Pulpwood	Sawlog
V/A	1.0	1.00
DBH	0	0.17
BAI	0	0
VOL	0	0
BD	0	-0.45
BL	0	-2.80
ANG	0	0.03
NOB	0	-0.23
B/W	0	-0.35
NOW	0	-0.70
CL	0	0
CR	0	-2.80
L/W	0	0
CSA	0	0
CV	0	0

Although the economic weights have been derived in an extremely crude manner and can be challenged on several counts, they will serve to illustrate the effects of economic data on a selection index. Arbitrarily chosen values could just as easily serve this purpose, but the use of 'realistic' figures will make interpretation more understandable.

STATISTICAL PROCEDURES

ANALYSIS OF VARIANCE AND COVARIANCE

1. Model of Variation

Analyses of variance were performed on each of the traits assessed. The experimental design allowed analysis to be carried out on both an individual-tree and plot-mean basis. The models on which analyses were based are:

$$Y_{ijk} = u + B_i + F_j + W_{ij} + E_{ijk} \quad ,$$

where Y_{ijk} is the measured value of an individual tree,

u is the population mean,

B_i is the effect of the ith block,

F_j is the genotypic effect of the jth family,

W_{ij} is the interaction effect of the jth family in the ith block, and

E_{ijk} is the residual error effect.

$$Y_{ij} = u + B_i + F_j + E_{ij} \quad ,$$

where Y_{ij} is the mean value of a plot,

u, B_i, and F_j are the same as above, and

E_{ij} is the residual error including interactions.

The appropriate forms of analysis of variance are shown in Tables VI(a) and VI(b). Analysis of covariance follows the same procedure except that mean square values become mean products.

Table VI

Forms of Analysis of Variance

(a) INDIVIDUAL-TREE BASIS

Source	df	Mean Square	Components
BLOCK	(b-1)	MS_B	$\sigma_E^2 + n\sigma_W^2 + nf\sigma_B^2$
FAMILY	(f-1)	MS_F	$\sigma_E^2 + n\sigma_W^2 + nb\sigma_F^2$
INTERACTION	(b-1)(f-1)	MS_W	$\sigma_E^2 + n\sigma_W^2$
ERROR	bf(n-1)	MS_E	σ_E^2

(b) PLOT-MEAN BASIS

Source	df	Mean Square	Components
BLOCK	(b-1)	MS_B	$\sigma_E^2 + f\sigma_B^2$
FAMILY	(f-1)	MS_F	$\sigma_E^2 + b\sigma_F^2$
ERROR	(b-1)(f-1)	MS_E	σ_E^2

2. Estimation of Components

The estimation of the components of these models requires certain assumptions concerning both the experimental and mating designs.

2.1 Assumptions concerning the experimental design

The purpose of an experimental design is to obtain unbiased estimates of treatment means, differences, and experimental errors. How well the design performs these functions can be inferred from the results of analysis of variance and covariance, and it is the assumptions underlying these analyses with which we are concerned. These are:

(1) family and environmental factors are additive,

(2) errors are independent from family to family,

(3) errors are normally distributed, and

(4) errors have common variance from progeny to progeny, and have zero mean.

If the data meet these criteria we can interpret the effects of environment on the variable, and can say that the estimated components of block, interaction, and error effects are unbiased. If, however, these assumptions are not met, corrective measures can be taken such as transformation of data. Statistical tests such as Tukey's test of additivity, Bartlett's test for homogeneity of variance, and Kilmogorov-Smirnov's test for goodness of fit will show how well the data comply with these assumptions. Descriptions of these tests can be found in statistical texts such as Snedecor (1965) and Sokal and Rohlf (1969).

2.2 Assumptions concerning the mating design

The purpose of the mating design is to interpret the genetic component of the model. The assumptions concerning the mating design as noted by Stonecypher (1966) are:

(1) regular diploid and mendelian inheritance,

(2) the population is in linkage equilibrium,

(3) no epistasis or dominance is present,

(4) there are no maternal effects,

(5) the relations are not inbred,

(6) the relatives are full-sib, and

(7) the relatives are random members of a non-inbred population.

A number of these assumptions must be accepted as correct. Assumptions one to three may be considered valid if _Pinus radiata_ follows normal genetic patterns, and no published information would lead us to believe otherwise. Assumption four could be substantiated if records had been kept of seed size, storage conditions, and nursery procedures, but these data are not available. We must accept the assumption as valid. The next two assumptions are satisfied by the records of parents and matings. The last assumption is correct insofar as the randomness of selection is concerned, but the degree of inbreeding is unknown. The chances of choosing an inbred tree are remote, however, because selection was for superior material, and inbreeding usually results in depression. Such trees would not be selected. It is also assumed that environmental and genetic effects are uncorrelated (Reeve, 1953).

Given the above assumptions, the genetic component of variation estimates one-half the additive genetic variance.

2.3 Statistics related to variance estimates

The standard errors of the components gives some idea of the sampling variation in the components. Snedecor (1965) gives the formula as

$$S_{(\sigma^2)} = \sqrt{\frac{1}{b^2}\sum_i \frac{2M_i^2}{f_i+2}} \quad , \qquad (2)$$

where b is the number of replicates, M_i denotes each of i mean squares used to derive the component, and f_i is the corresponding degrees of freedom for the mean squares.

Duncan's New Multipe Range Test was employed to test for significant differences between family means for each variable.

3. Estimation of Heritability

Heritabilities were derived for each trait measured according to the full-sib model given by Falconer (1964). Since the family component of variance was assumed to estimate one-half of the additive genetic variance, the narrow-sense heritability on an individual-tree basis was determined to be

$$h^2_{NS} = \frac{2\sigma^2_F}{\sigma^2_E+\sigma^2_W+\sigma^2_F} \quad . \tag{3}$$

A standard error can be derived to show whether the estimates calculated from this trial are greater than zero. The error is an approximation given by Falconer (1964, p.181) modified[1] to take into account the variance due to trees within plots. The formula is

$$S_{(h^2)} = \sqrt{\frac{8b^2}{A^4}\{\frac{n-1}{bf}MS^2_E(MS_F-MS_W)^2 + \frac{1}{(b-1)(f-1)}MS^2_W(MS_F+(n-1)MS_E)^2 + \frac{1}{(f-1)}MS^2_F(MS_W+(n-1)MS_E)^2\}} \quad , \tag{4}$$

where $A = MS_F + (b-1)MS_W + b(n-1)MS_E$. The symbols represent the analysis of variance mean squares, and are derived from Table VI(a).

4. Correlations Based on Components of Variance

Correlations take the general form

$$r = \frac{COV_{XY}}{\sqrt{VAR_X VAR_Y}} \tag{5}$$

where X and Y are the two characters being correlated, COV_{XY} is the mean product of these characters, and VAR_X and

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[1] E.J. Williams, Dept. of Statistics, Univ. of Melbourne.

VAR_Y are the mean squares. The value of the correlation coefficient, r, will lie within the limits $-1 \leq r \leq +1$, and the hypothesis that the calculated value is significantly different from zero can be tested by critical limits based on degrees of freedom.

When a coefficient is derived from components of variance rather than mean squares it cannot be tested for significance in this manner, the reason being that the distribution of the components is unknown. Hence, the correlation coefficient has no established limits. This presents a difficulty to the forest geneticist concerned mainly with the correlation between components.

4.1 Testing the significance of correlation

A practical method for testing if the correlation is different from zero is to compare the value with its standard error. This system was employed by Brown *et al.* (1969) for interpreting genetic correlations in sugar cane. If the correlation is greater than twice its standard error, we can assume the true value is different from zero. Although this is not an accurate statistical test it places emphasis on the variation of the components, and reduces the importance of absolute size of the coefficient. A correlation based on components can be large by chance, and unless the standard error is considered too much emphasis may be placed on the high value.

4.2 Genotypic correlations

The genotypic correlations were estimated with the family components of variance and covariance,

$$r_A = \frac{\sigma^2_{FXY}}{\sqrt{\sigma^2_{FXX}\sigma^2_{FYY}}} \quad . \tag{6}$$

The standard error was derived according to the method of Mode and Robinson (1959). They show that when a parameter is a function of moments an approximate expression for its sampling variance can be derived. For a particular parameter

$$r = \frac{M_{XY}}{\sqrt{M_{XX}M_{YY}}} \quad , \tag{7}$$

where M denotes any variance, covariance or component thereof, the formula is

$$S_{(r)} = \sqrt{r^2\{\frac{VAR(M_{XY})}{M^2_{XY}} + \frac{VAR(M_{XX})}{4M_{XX}} + \frac{VAR(M_{YY})}{4M_{YY}} - \frac{COV(M_{XY},M_{XX})}{M_{XY}M_{XX}} - \frac{COV(M_{XY},M_{YY})}{M_{XY}M_{YY}} + \frac{COV(M_{XX},M_{YY})}{M_{XX}M_{YY}}\}} \quad . \tag{8}$$

When the component σ^2_F takes the place of M, the variances and covariances of the component are derived from the general formula given in equation (2).

4.3 Phenotypic correlations

The phenotypic correlation coefficients are estimated from a combination of progeny and error components on a unit-plot basis. The phenotypic variances and covariances are constructed from twice the genotypic component plus the error term after Robinson *et al*. (1951). This is equivalent to the additive genetic effect together with all unaccounted for environmental and random effects. The formula is

$$\sigma_P^2 = 2\sigma_F^2 + \sigma_E^2 \quad . \tag{9}$$

The coefficient is calculated as

$$r_P = \frac{\sigma_{PXY}^2}{\sqrt{\sigma_{PXX}^2 \sigma_{PYY}^2}} \quad , \tag{10}$$

and its standard error is computed in a similar manner to the genotypic counterpart taking into account the dual nature of the phenotypic component.

THE SELECTION INDEX

Smith (1937) was the first to use the concept of discriminant functions to derive a linear equation based on observable characteristics as the best available guide to the genetic value of animal lines. Hazel (1943) developed the principles of constructing and using economically weighted selection indices which allow maximum genetic progress to be made. With increasing knowledge of genetic principles Robinson *et al*. (1951), Johnson *et al*. (1955a), and Brim *et al*. (1959) refined the method of deriving genotypic and phenotypic correlations from full-sib mating designs, and applied the selection index technique to plant species.

1. Construction of the Index

The statistical procedures for constructing a selection index are described most comprehensively by Brim *et al*. (1959).

The index is of the general form

$$I = \beta_1 X_1 + \beta_2 X_2 + \ldots\ldots \beta_n X_n \quad , \qquad (11)$$

where the β's are weights given to the traits, X's, in computing the index value, I. The appropriate β's which maximize the advance from selection are derived from the simultaneous equations

$$\begin{array}{l} \beta_1 P_{11} + \beta_2 P_{12} + \ldots\ldots \beta_n P_{1n} = \alpha_1 G_{11} + \alpha_2 G_{12} + \ldots\ldots \alpha_n G_{1n} \\ \beta_1 P_{21} + \beta_2 P_{22} + \ldots\ldots \beta_n P_{2n} = \alpha_2 G_{21} + \alpha_2 G_{22} + \ldots\ldots \alpha_n G_{2n} \\ \quad\vdots \qquad\qquad\qquad\qquad \vdots \qquad\qquad \vdots \qquad\qquad\qquad \vdots \\ \beta_1 P_{n1} + \beta_2 P_{n2} + \ldots\ldots \beta_n P_{nn} = \alpha_1 G_{n1} + \alpha_2 G_{n2} + \ldots\ldots \alpha_n G_{nn} \quad , \end{array} \qquad (12)$$

where $P_{ij} = P_{ji}$ is the phenotypic covariance (variance if i=j), $G_{ij} = G_{ji}$ is the genotypic covariance (variance if i=j), and α_i is the economic weight defined as the relative net income expected to accrue if the i^{th} trait is increased by one unit. The values of α can assume any number negative or positive, but must be relative to each other. If the unit on which selection is based is set at 1 (i.e. an increment of one unit of that variable will increase the economic worth of the product by 1), then all other economic values should be established relative to 1. If a trait has no economic importance but is included in the index for its correlated response to the variable being improved, its economic value may be set at zero. It should be stressed that the units in which variables are measured is most important since the economic evaluation is based on increments of that particular unit. In general, a trait should be measured in small enough units so that increments of that unit will reflect gradually changing economic worth of the trait. If the unit is large, a single increment may completely alter the value of the trait so that a linear economic function cannot be fitted to the units.

The right hand side of the equation is equivalent to

$$G_i = \Sigma\alpha_i G_{ij} \quad . \tag{13}$$

Even though the index may not include the economically important variables, the genotypic covariance between the traits used in the index and the traits of economic importance are essential to compute the value of G_i.

The β values which are the solutions to the simultaneous equations form the basis for constructing the index (equation 11). This index determines the relative value of an individual or line as parental material for breeding in terms of the unit on which selection is based. The larger the index the more productive the material will be for the trait being improved.

2. Estimation of Genetic Advance

The β values can also be used to determine the advance expected from selection with the index. The formula for selection advance is

$$A = K\sqrt{\sum_i \beta_i G_i} \quad , \tag{14}$$

where A is the advance in units on which selection is based, and K is the selection differential in standard deviations. It is an indirect function of the number of trees from which selection is made (Wright, 1962). The functions under the square root are the optimum weights, β_i, and the right hand side of the equation, G_i, summed for the number of variables, i, included in the index. The advance expected for a particular index can be compared with the advance predicted by any other index regardless of the number or type of variables used to construct the indices. They are all measured in similar units.

RESULTS AND DISCUSSION

All statistical analyses were performed on the University's IBM360 model 50H computer. Programmes required in the analyses were written and edited by the author.

TOTAL VARIATION WITHIN THE TRIAL

The crown and productivity characteristics chosen for analyses are listed in Table IV. Each variable was assessed on 371 trees belonging to the dominant and codominant crown classes. Their minimum and maximum values, means, standard deviations, and coefficients of variation are shown. The dispersion parameters indicate the large amount of variation present in most traits. The variables all conform to a normal distribution as determined by the Kilmogorov-Smirnov test for goodness of fit. The removal of the suppressed portion of the stand from analysis has substantially reduced skewness to the left. The normalcy of the distribution allows analysis of variance to be carried out on untransformed data.

ANALYSIS OF VARIANCE AND COVARIANCE

Analyses of variance and covariance were effected on each variable or combination of variables. Both individual-tree and plot-mean models were used. Tables VII and VIII give the mean squares and products for the models. These values form the basis for all further statistics.

1. Analysis of Variance for each Individual Trait

Let us first investigate the analysis of variance for each trait. The individual-tree model will give the most information concerning the causes of variation. It will indicate if the design is adequate, and will yield a more accurate estimate of narrow-sense heritability.

For many traits the experimental design is not adequate. The interaction or experimental error term is shown to be significantly greater than zero in six variables and highly significant in one other. There does not seem to be any connection between the types of variables for which the design is inappropriate; productivity, branching frequency, and crown dimension attributes all have significant interaction terms. Although the trial was not initially established for the purpose of testing as wide a range of variables as were assessed in this thesis, the design did not achieve the purpose for which it was intended. Diameter, height and volume all have significant

Table VII

Mean Squares and Mean Products Derived from Individual-Tree Model

	DBH	BAI	VOL	V/A	BD	BL	ANG	NOB	B/W	NOW	CL	CR	L/W	CSA	CV
DBH	10.221 2.615 1.614 0.986														
BAI	-0.0151 0.0636 0.0167 0.0235	0.0003 0.0036 0.0009 0.0012													
VOL	22.315 4.369 2.718 1.632	-0.034 0.101 0.027 0.038	49.157 7.843 4.818 2.846												
V/A	112.96 21.02 5.18 2.55	-0.30 1.17 -0.01 0.08	254.82 37.19 9.78 5.32	1506.98 665.00 127.14 166.64											
BD	0.2704 -0.1446 0.1379 0.1148	0.0015 -0.0197 0.0018 0.0026	0.5626 -0.3597 0.2224 0.1769	1.6724 -10.1399 -0.5181 -1.2063	0.0220 0.2334 0.0333 0.0431										
BL	3.809 -0.771 1.275 0.888	0.006 -0.152 0.014 0.021	7.146 -2.195 2.094 1.359	8.884 -85.748 -6.636 -12.496	0.263 1.897 0.264 0.339	6.136 16.776 2.899 3.070									
ANG	-124.91 9.18 -4.15 -1.22	0.21 0.53 0.02 -0.02	-272.03 27.52 -8.18 -1.96	-1320.23 130.35 -42.04 -15.60	-3.07 -6.97 -0.55 -0.60	-52.02 -51.44 -5.11 -4.16	1608.06 621.77 83.31 68.94								
NOB	-1.643 -0.176 0.715 0.504	-0.004 -0.059 0.012 0.012	-3.804 -0.869 1.099 0.805	-20.598 -37.688 0.045 -1.268	-0.073 0.931 0.113 0.097	-0.154 7.560 0.786 0.836	17.857 -28.068 -1.828 -0.700	0.541 4.162 0.994 0.594							
B/W	3.293 -2.332 1.664 1.046	-0.032 -0.266 0.018 0.025	6.887 -6.036 2.544 1.659	39.441 -144.029 0.107 -4.112	-0.077 3.470 0.252 0.229	1.237 27.427 2.083 2.026	-46.867 -118.186 -5.581 -1.898	0.295 14.742 2.077 1.256	4.018 55.054 5.191 3.220						
NOW	-0.8396 0.2067 -0.0312 -0.0013	0.0033 0.0169 0.0005 -0.0004	-1.8781 0.4571 -0.0551 -0.0018	-10.9511 7.2605 -0.1245 0.2106	-0.0057 -0.1805 -0.0030 -0.0036	-0.1000 -1.4218 -0.0616 -0.0355	10.4850 7.3985 0.4429 0.0743	0.1121 -0.7184 -0.0068 -0.0057	-0.4312 -2.8261 -0.0876 -0.0509	0.0880 0.1584 0.0135 0.0082					
CL	111.03 9.07 7.70 2.36	-0.15 0.17 0.02 0.06	243.22 19.22 14.03 4.52	1223.63 115.34 37.73 12.00	3.00 -2.02 0.52 0.22	40.85 -14.93 6.42 1.63	-1368.32 144.35 -40.23 -1.22	-18.51 -8.94 1.64 1.14	33.84 -37.91 5.20 2.26	-9.08 2.12 -0.30 -0.01	1211.11 77.70 58.18 12.92				
CR	-2.970 -0.248 0.973 0.703	0.017 -0.106 0.014 0.017	-7.508 -0.594 1.549 1.064	-60.540 -66.740 -7.879 -12.048	0.082 1.273 0.204 0.260	2.979 11.768 2.357 2.432	35.054 -13.902 -0.661 0.418	0.786 5.051 0.609 0.701	-1.281 17.436 1.600 1.672	0.451 -0.840 -0.034 -0.027	-33.143 -5.495 4.306 1.245	4.562 9.359 2.136 2.189			
L/W	21.873 2.142 0.082 -0.485	-0.050 0.177 -0.017 -0.009	49.118 4.355 0.404 -0.569	281.981 118.474 21.894 25.194	0.363 -2.114 -0.200 -0.326	2.508 -18.385 -2.112 -3.156	-261.498 36.335 -7.116 -1.264	-3.952 -8.553 -0.572 -0.742	7.443 -31.036 -1.259 -1.809	-2.073 1.505 -0.007 0.037	237.977 21.806 4.950 0.611	-11.283 -13.816 -2.197 -2.899	53.617 23.686 4.734 5.040		
CSA	154.31 13.94 29.34 15.32	-0.00 -1.28 0.29 0.37	323.48 29.34 50.26 25.15	1271.53 -811.44 -53.99 -169.62	6.66 15.53 4.14 4.46	118.85 152.54 47.92 40.96	-1939.40 91.24 -76.05 3.97	-21.51 60.39 12.84 12.95	40.79 192.69 34.65 30.26	-9.48 -8.60 -0.95 -0.46	1677.20 68.03 171.58 42.80	9.35 134.97 41.00 36.39	255.58 -172.52 -24.89 -44.15	3163.54 2247.11 954.68 651.24	
CV	18.094 2.686 9.216 5.702	0.049 -0.584 0.114 0.137	33.743 5.250 15.511 9.111	28.899 -372.386 -32.109 -66.541	1.464 7.131 1.513 1.788	31.949 69.705 17.492 16.624	-236.039 -24.757 -16.710 1.432	-1.171 28.185 4.677 5.043	3.523 92.654 12.369 12.086	-0.236 -4.334 -0.261 -0.189	193.857 -0.516 49.002 13.240	17.323 58.481 15.434 14.794	8.246 -79.055 -11.189 -17.385	612.292 915.268 333.457 257.892	172.543 385.815 123.314 106.395

NOTE**VARIANCES AND COVARIANCES IN ORDER OF BLOCK,FAMILY,INTERACTION,AND ERROR SOURCES

Table VIII

Mean Squares and Mean Products Derived from Plot-Mean Model

	DBH	BAI	VOL	V/A	BD	BL	ANG	NOB	B/W	NOW	CL	CR	L/W	CSA	CV
DBH	1.813 0.464 0.286														
BAI	-0.0027 0.0113 0.0030	0.0001 0.0006 0.0002													
VOL	3.959 0.775 0.482	-0.006 0.018 0.005	8.721 1.391 0.355												
V/A	20.039 3.730 0.918	-0.052 0.207 -0.001	45.207 6.598 1.734	267.349 117.977 22.556											
BD	0.0480 -0.0257 0.0245	0.0003 -0.0035 0.0003	0.0358 -0.0638 0.0394	0.2967 -1.7989 -0.0919	0.0039 0.0414 0.0059										
BL	0.6757 -0.1369 0.2261	0.0011 -0.0269 0.0024	1.2677 -0.3394 0.3715	1.5762 -15.2124 -1.1772	0.0466 0.3366 0.0469	1.0885 2.9762 0.5142									
ANG	-22.160 1.628 -0.736	0.038 0.094 0.004	-48.260 4.882 -1.451	-234.219 23.125 -7.459	-0.545 -1.236 -0.097	-9.229 -9.126 -0.906	285.281 110.307 14.780								
NOB	-0.2915 -0.0312 0.1269	-0.0007 -0.0104 0.0021	-0.6748 -0.1543 0.1950	-3.6543 -6.6861 0.0079	-0.0129 0.1652 0.0201	-0.0273 1.3412 0.1395	3.1680 -4.9794 -0.3242	0.0960 0.7384 0.1763							
B/W	0.5842 -0.4138 0.2951	-0.0056 -0.0472 0.0032	1.2217 -1.0709 0.4514	6.9971 -25.5517 0.0189	-0.0137 0.6157 0.0447	0.2194 4.8657 0.3696	-8.3145 -20.9670 -0.9901	0.0523 2.6154 0.3685	0.7128 9.7670 0.9210						
NOW	-0.1489 0.0367 -0.0055	0.0006 0.0030 0.0001	-0.3332 0.0311 -0.0098	-1.9428 1.2381 -0.0221	-0.0010 -0.0320 -0.0005	-0.0177 -0.2522 -0.0109	1.8601 1.3125 0.0786	0.0199 -0.1274 -0.0012	-0.0765 -0.5014 -0.0155	0.0156 0.0281 0.0024					
CL	19.698 1.608 1.365	-0.026 0.030 0.004	43.149 3.409 2.489	217.081 20.461 6.693	0.533 -0.358 0.092	7.247 -2.649 1.138	-242.750 25.608 -7.138	-3.283 -1.586 0.291	6.004 -6.726 0.922	-1.611 0.376 -0.052	214.859 13.784 10.321				
CR	-0.5269 -0.0441 0.1726	0.0029 -0.0187 0.0025	-1.3320 -0.1053 0.2748	-10.7402 -11.3402 -1.3977	0.0145 0.2259 0.0363	0.5285 2.0878 0.4181	6.2188 -2.4663 -0.1173	0.1395 0.8960 0.1081	-0.2272 3.0933 0.2838	0.0800 -0.1490 -0.0061	-5.8799 -0.9746 0.7639	0.8094 1.6603 0.3793			
L/W	3.880 0.380 0.015	-0.009 0.031 -0.003	8.714 0.773 0.072	50.025 21.018 3.884	0.064 -0.375 -0.036	0.445 -3.262 -0.375	-46.392 6.446 -1.262	-0.701 -1.517 -0.102	1.320 -5.506 -0.223	-0.368 0.267 -0.001	42.219 3.869 0.878	-2.002 -2.451 -0.390	9.512 4.202 0.840		
CSA	27.375 2.473 5.206	-0.001 -0.227 0.051	57.388 5.206 8.917	225.578 -143.955 -9.578	1.191 2.754 0.735	21.085 27.062 8.502	-344.063 16.188 -13.491	-3.816 10.714 2.278	7.237 34.185 6.148	-1.682 -1.525 -0.168	297.547 12.068 30.439	1.658 23.944 7.274	45.342 -30.607 -4.416	561.234 398.653 169.366	
CV	3.210 0.477 1.635	0.009 -0.104 0.020	5.986 0.931 2.752	5.127 -66.064 -5.696	0.260 1.265 0.268	5.668 12.366 3.103	-41.875 -4.392 -2.964	-0.208 5.000 0.830	0.625 16.438 2.194	-0.042 -0.769 -0.046	34.392 -0.092 8.693	3.073 10.375 2.738	1.463 -14.025 -1.985	108.625 162.375 59.158	30.610 68.446 21.877

NOTE**VARIANCES AND COVARIANCES IN ORDER OF BLOCK,FAMILY,AND ERROR SOURCES interaction terms. It is clear that a better design is required.

1.1 Productivity variables

The analyses of variance for the four productivity variables are given in Table IX. The cumulative productivity variables of diameter, volume, and volume per acre have highly significant portions of their variation accounted for by blocks, but the increment trait, basal area increment, has non-significant block effects. The tree up to age twelve is influenced in its growth by a set of environmental factors which will be modified in many ways during the next three years from age twelve to fifteen. Therefore the variation attributable to blocks will have a different meaning for certain variables depending on the age when observations were made. The trial was largely free-growing to age twelve, but came under intensified competitive conditions during the following three years. It is likely that the initial limiting factors such as moisture and weed competition would have been modified by the closure of the canopy, and other influences due mainly to mutual competition between trees would supplant these in importance. Competitive stresses are randomly distributed throughout the stand. Singh (1967) showed theoretically that in progeny tests variance components within and between plots are strongly

Table IX

Statistical Analysis of Productivity Variables

```
              *****ANALYSIS OF DBH*****

               ANALYSIS OF  VARIANCE                MULTIPLE RANGE TEST
 SOURCE        DF     M.S.        F     COMPONENT    NO.  MEAN   RANGE

BLOCK.....      4   10.2214  10.37**      0.1272      11   7.452  I
                                                      12   7.115  II
FAMILY....     11    2.6153   2.65**      0.0355       9   7.048  III
                                        ( 0.0383)      8   6.980  III
BL X FA...     44    1.6144   1.64*       0.1115       1   6.919  III
                                                      10   6.830  III
ERROR.....311        0.9857               0.9857       4   6.777  III
                                                       3   6.677  III
              NARROW-SENSE HERITABILITY = 0.063        6   6.660  III
                                         (0.080)       5   6.650   II
                                                       2   6.551   II
                                                       7   6.280    I
```

```
              *****ANALYSIS OF BAI*****

               ANALYSIS OF  VARIANCE                MULTIPLE RANGE TEST
 SOURCE        DF     M.S.        F     COMPONENT    NO.  MEAN   RANGE

BLOCK.....      4    0.0003   0.25        0.0          9   0.107  I
                                                      11   0.102  II
FAMILY....     11    0.0036   2.86**      0.0001       8   0.099  III
                                        ( 0.0001)     10   0.090  IIII
BL X FA...     44    0.0009   0.75        0.0          2   0.090  IIII
                                                       4   0.089   III
ERROR.....311        0.0012               0.0012       3   0.087   IIII
                                                       5   0.085   IIII
              NARROW-SENSE HERITABILITY = 0.140       12   0.082    III
                                         (0.089)       1   0.077     II
                                                       6   0.076     II
                                                       7   0.069      I
```

```
              *****ANALYSIS OF VOL*****

               ANALYSIS OF  VARIANCE                MULTIPLE RANGE TEST
 SOURCE        DF     M.S.        F     COMPONENT    NO.  MEAN   RANGE

BLOCK.....      4   49.1568  17.27**      0.6555      11   5.785  I
                                                      12   5.512  II
FAMILY....     11    7.8431   2.76**      0.1073       8   5.182  III
                                        ( 0.1148)      9   5.056  III
BL X FA...     44    4.8180   1.69*       0.3498       4   4.857  III
                                                      10   4.842  III
ERROR.....311        2.8463               2.8463       1   4.764  III
                                                       6   4.511  III
              NARROW-SENSE HERITABILITY = 0.065        5   4.499  III
                                         (0.082)       3   4.317   II
                                                       2   4.298   II
                                                       7   3.960    I
```

Table IX (continued)

```
                    *****ANALYSIS OF V/A*****

             ANALYSIS OF VARIANCE                        MULTIPLE RANGE TEST
  SOURCE      DF       M.S.        F       COMPONENT       NO. MEAN     RANGE

BLOCK.....   4 1506.9785   9.04**     20.3994            9   28.288 I
                                                         5   24.810 II
FAMILY.... 11   665.0049   3.99**     19.0841            8   24.343 II
                                     ( 9.3025)          12   22.674 III
BL X FA... 44   127.1427   0.76        0.0              10   21.973 IIII
                                                         2   21.555 IIII
ERROR.....311   166.6438             166.6438           11   20.678  III
                                                         4   16.544   III
      NARROW-SENSE HERITABILITY = 0.206                  1   16.099   III
                                 (0.113)                 3   15.780   III
                                                         6   15.515    II
                                                         7   11.644     I
```

affected by competition. This would explain the large portion of random variation unaccounted for by blocks.

The family components of variance for productivity traits are generally small in relation to the unaccounted for components. Their heritability estimates are consequently low. Diameter, volume, and basal area increment all have narrow-sense estimates less than 0.1, and judged not significantly greater than zero by their standard errors. Volume per acre, on the other hand, has a heritability of 0.21 which is approximately twice its standard error. However, a cautious approach to the interpretation of this value is necessary. This variable reflects the relationship between volume and area occupied by the crown which produced this volume. It will be shown later how this variable is more closely related to crown spread traits than to volume of the tree. It is actually the influence of the area component which results in a moderate heritability estimate.

The weak genetic control shown for most productivity variables indicates breeding for these traits will yield little improvement unless the intensity of selection is increased beyond practical levels.

1.2 Unit branch characteristics

The analyses of variance for unit branch characters given in Table X shows blocks account for a significant

Table X

Statistical Analysis of Unit Branch Variables

```
                      *****ANALYSIS OF  BD*****

             ANALYSIS OF VARIANCE                     MULTIPLE RANGE TEST
  SOURCE      DF      M.S.    ,  F       COMPONENT      NO. MEAN    RANGE

BLOCK.....   4     0.0220   0.51         0.0            1   0.871 I
                                                        6   0.870 I
FAMILY.... 11      0.2334   5.42**       0.0071         7   0.825 I I
                                       ( 0.0033)        3   0.820 I I
BL X FA... 44      0.0333   0.77         0.0           11   0.755   I I
                                                       12   0.720   I I I
ERROR.....311      0.0431                0.0431         4   0.712     I I
                                                        5   0.682     I I
        NARROW-SENSE HERITABILITY =  0.283             10   0.667     I I
                                    (0.139)             8   0.649     I I
                                                        9   0.636       I
                                                        2   0.621       I
```

```
                      *****ANALYSIS OF  BL*****

             ANALYSIS OF VARIANCE                     MULTIPLE RANGE TEST
  SOURCE      DF      M.S.       F       COMPONENT      NO. MEAN    RANGE

BLOCK.....   4      6.1356   2.00        0.0479         7   8.208 I
                                                        1   8.189 I
FAMILY.... 11     16.7760   5.46**       0.4924         6   7.733 I I
                                       ( 0.2345)        3   7.720 I I
BL X FA... 44      2.8986   0.94         0.0           11   7.552 I I
                                                       12   7.045   I I
ERROR.....311      3.0704                3.0704         4   6.888   I I
                                                        5   6.457     I
        NARROW-SENSE HERITABILITY =  0.276             10   6.438     I
                                    (0.138)             9   6.388     I
                                                        8   6.294     I
                                                        2   6.058     I
```

```
                      *****ANALYSIS OF ANG*****

             ANALYSIS OF VARIANCE                     MULTIPLE RANGE TEST
  SOURCE      DF      M.S.       F       COMPONENT      NO. MEAN    RANGE

BLOCK.....   4 1608.0603 23.32**        22.5418         4  70.427 I
                                                        8  69.553 I
FAMILY.... 11   621.7722   9.02**       19.1054        11  67.222 I I
                                       ( 8.6751)        2  66.708 I I I
BL X FA... 44    83.3103   1.21          2.5486        10  66.029 I I I
                                                       12  65.732 I I I
ERROR.....311    68.9443                68.9443         7  62.095   I I I
                                                        5  61.480     I I I
        NARROW-SENSE HERITABILITY =  0.422              3  59.406       I I
                                    (0.179)             9  58.679       I I
                                                        6  58.363       I I
                                                        1  56.423         I
```

portion of the total variation for branch angle, but for little of the total variation in branch diameter or length. The implications are that the environmental forces which affect branch angle differ from those that influence branch length and diameter.

The factors which influence angle are those which are present at branch initiation. The angle of a branch does not change appreciably over time. It is true that weight of the branch tends to depress the overall angle from tip to butt (Fielding, 1960), but the angle measured at the base does not change much. Plate 7 illustrates this point. Branch length and diameter are dependent on the amount of available growing space. This becomes limiting over time, but is not an environmental influence at the time of branch initiation. Whereas moisture or nutrient availability may have been the environmental factors removed by blocks for branch angle, competitive stress would be likely to determine branch elongation and growth.

The genetic control of branch traits is moderate. All heritability estimates are greater than twice their standard errors. Both branch diameter and length have values of 0.28, and branch angle has an even higher estimate of 0.42.

Plate 7

Bending of Branch by Weight
Angle changes from tip to base of branch, but angle near stem remains the same.

1.3 Branch and whorl frequency characteristics

Table XI gives the results of analysis of variance for frequency traits.

Number of branches per foot and number of branches per whorl have non-significant block effects, whereas number of whorls per foot has a significant portion of its total variation explained by blocks. This dissimilarity is not incongruous when the derivation of these variables is considered. Branch count is restricted to those branches which have contributed to the production of carbohydrates for a significant portion of the life of that part of the crown. The amount of contribution is related to the size of the branch; the larger a branch is, the longer it has carried on photosynthesis. A size restriction of one-half inch based on the distribution of branch diameters in the stand was chosen to reflect a count having some biological significance. The number of branches is closely related to the branch size variable since a tree with a large mean maximum branch diameter will have a greater number of branches over one-half inch. Hence, the number of branches per foot and per whorl will be influenced bv similar environmental factors as branch size. The major influence is competition, a cause of variation not removed by blocks.

Number of whorls per foot is not similarly influenced. All whorls with two or more branches greater than one-fifth

Table XI

Statistical Analysis of Branch and Whorl Frequency Variables

```
                    *****ANALYSIS OF NOB*****

             ANALYSIS OF  VARIANCE                          MULTIPLE RANGE TEST
  SOURCE       DF      M.S.        F         COMPONENT       NO.  MEAN     RANGE

BLOCK.....   4       0.5411   0.91          0.0              6    2.262  I
                                                             3    1.930  II
FAMILY.... 11       4.1623   7.01**        0.1124            1    1.903  II
                                          ( 0.0584)         11    1.876  II
BL X FA... 44       0.9936   1.67*         0.0710            7    1.845  III
                                                            12    1.395   III
ERROR.....311       0.5936                 0.5936            4    1.368   III
                                                             9    1.273    II
          NARROW-SENSE HERITABILITY =  0.289                 5    1.263    II
                                       (0.154)              10    1.226     I
                                                             8    1.214     I
                                                             2    1.080     I



                    *****ANALYSIS OF B/W*****

             ANALYSIS OF  VARIANCE                          MULTIPLE RANGE TEST
  SOURCE       DF      M.S.        F         COMPONENT       NO.  MEAN     RANGE

BLOCK.....   4       4.0180   1.25          0.0              6    6.236  I
                                                             1    5.274  II
FAMILY.... 11      55.0539  17.10**        1.7692            7    4.786   II
                                          ( 0.7671)          3    4.614   II
BL X FA... 44       5.1913   1.61*         0.3498           11    3.919    II
                                                             4    2.767     II
ERROR.....311       3.2196                 3.2196           12    2.726     II
                                                             5    2.611     II
          NARROW-SENSE HERITABILITY =  0.663                10    2.566     II
                                       (0.221)               9    2.468      I
                                                             8    2.301      I
                                                             2    1.923      I



                    *****ANALYSIS OF NOW*****

             ANALYSIS OF  VARIANCE                          MULTIPLE RANGE TEST
  SOURCE       DF      M.S.        F         COMPONENT       NO.  MEAN     RANGE

BLOCK.....   4       0.0880  10.77**        0.0011           2    0.582  I
                                                             4    0.558  II
FAMILY.... 11       0.1584  19.39**        0.0051            8    0.557  II
                                          ( 0.0022)          9    0.543  II
BL X FA... 44       0.0135   1.65*         0.0009           12    0.526  II
                                                            10    0.521  II
ERROR.....311       0.0082                 0.0082           11    0.509   I
                                                             5    0.505   I
          NARROW-SENSE HERITABILITY =  0.721                 3    0.439    I
                                       (0.226)               7    0.401    II
                                                             1    0.379    II
                                                             6    0.365     I
```

inch were counted. Competition would not affect branch growth to this size because a 'countable' whorl will be formed before mutual competition occurs. The environmental factors affecting whorl frequency, then, are those present at whorl initiation. These factors have been accounted for by the design.

Breeding values of branch and whorl frequency characteristics are high. All heritability estimates are greater than twice their errors. These values are substantial when contrasted with those derived for productivity variables.

1.4 Crown dimension variables

Crown dimension variables show differing reactions to the experimental design. The analyses are shown in Table XII. Crown length, length-to-width ratio and crown surface area have significant block effects, whereas crown radius and crown volume have not. Crown length and radius are the primary dimension variables from which the others are derived, and factors which influence these traits also affect the derived traits. Crown length is relatively more important in length-to-width ratio and surface area, and the environmental factors which affect it are accounted for by blocks in these variables. Crown volume is more closely related to radius because of the effect of squaring this

Table XII

Statistical Analysis of Crown Dimension Variables

```
                   *****ANALYSIS OF  CL*****

            ANALYSIS OF  VARIANCE                      MULTIPLE RANGE TEST
  SOURCE     DF     M.S.       F       COMPONENT         NO. MEAN    RANGE

BLOCK.....    4  1211.1096  93.75**      17.0448         12   51.376 I
                                                         11   49.390 II
FAMILY....   11    77.6975   6.01**       0.6926          8   49.280 II
                                        ( 1.1638)        10   48.590 II
BL X FA...   44    58.1771   4.50**       8.0292          4   48.496 II
                                                          5   48.293 II
ERROR.....311      12.9184               12.9184          2   47.650 II
                                                          1   47.219 II
             NARROW-SENSE HERITABILITY = 0.064            9   46.930 II
                                        (0.123)           6   46.083  I
                                                          7   45.986  I
                                                          3   45.744  I
```

```
                   *****ANALYSIS OF  CR*****

            ANALYSIS OF  VARIANCE                      MULTIPLE RANGE TEST
  SOURCE     DF     M.S.       F       COMPONENT         NO. MEAN    RANGE

BLOCK.....    4     4.5623     2.08       0.0358          7    7.065 I
                                                          1    6.764 I
FAMILY....   11     9.3586   4.28**       0.2562         11    6.763 I
                                        ( 0.1312)         3    6.560 II
BL X FA...   44     2.1382     0.98       0.0             6    6.477 II
                                                          4    6.351 III
ERROR.....311       2.1888                2.1888         12    6.326 III
                                                          8    5.746  III
             NARROW-SENSE HERITABILITY = 0.210           10    5.704  III
                                        (0.117)           5    5.568   II
                                                          2    5.531   II
                                                          9    5.351    I
```

```
                   *****ANALYSIS OF L/W*****

            ANALYSIS OF  VARIANCE                      MULTIPLE RANGE TEST
  SOURCE     DF     M.S.       F       COMPONENT         NO. MEAN    RANGE

BLOCK.....    4    53.6166  10.64**       0.7227          9    9.360 I
                                                          5    9.353 I
FAMILY....   11    23.6865   4.70**       0.6725          2    9.050 II
                                        ( 0.3315)         8    8.951 II
BL X FA...   44     4.7339     0.94       0.0            10    8.911 II
                                                         12    8.796 II
ERROR.....311       5.0400                5.0400         11    7.803  II
                                                          4    7.797  II
             NARROW-SENSE HERITABILITY = 0.235            3    7.387   I
                                        (0.125)           1    7.339   I
                                                          6    7.310   I
                                                          7    6.816   I
```

Table XII (continued)

```
                    *****ANALYSIS OF CSA*****

            ANALYSIS OF VARIANCE                         MULTIPLE RANGE TEST
  SOURCE     DF      M.S.       F        COMPONENT        NO.  MEAN    RANGE

BLOCK.....   4  3163.5405   4.86**     32.6557           11  106.882  I
                                                          7  104.797  II
FAMILY....  11  2247.1111   3.45**     45.8573           12  103.207  II
                                      (32.0606)           1  101.145  III
BL X FA...  44   954.6772   1.47*      53.8325            4   98.865  IIII
                                                          3   95.417  IIII
ERROR.....311    651.2366             651.2366            6   95.189  IIII
                                                          8   89.691  IIII
      NARROW-SENSE HERITABILITY = 0.122                  10   88.112  IIII
                                  (0.098)                 5   85.581   III
                                                          2   83.583    II
                                                          9   79.878     I
```

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                    *****ANALYSIS OF  CV*****

            ANALYSIS OF VARIANCE                         MULTIPLE RANGE TEST
  SOURCE     DF      M.S.       F        COMPONENT        NO.  MEAN    RANGE

BLOCK.....   4   172.5430   1.62        0.7278            7   25.908  I
                                                         11   25.437  I
FAMILY....  11   385.8152   3.63**      9.3139            1   23.583  II
                                      ( 5.4463)          12   23.023  III
BL X FA...  44   123.3145   1.16        3.0016            3   21.750  IIII
                                                          4   21.679  IIII
ERROR.....311    106.3955             106.3955            6   20.987  IIII
                                                          8   17.790   III
      NARROW-SENSE HERITABILITY = 0.157                  10   17.365   III
                                  (0.103)                 5   16.845   III
                                                          2   16.196    II
                                                          9   15.132     I
```

value. These two variables are influenced by competitive forces, and block effects are non-significant.

Dimension variables are under limited genetic control. Crown length has a very low heritability, and crown surface area and volume have breeding values under 0.2. Crown radius and length-to-width ratio have heritability estimates above 0.2, but these are not greater than twice their errors.

1.5 General comments on variation in traits

In general, the environmental variation in crown traits is not adequately removed by the experimental design. The relationship of genetic to unexplained variation is consequently biased, and heritabilities are lower than one would expect for several variables. The inadequacy of the design is understandable since it was not specifically employed to assess crown traits. These appear to be influenced by competition rather than by static environmental factors which the design attempts to remove. The method of removing suppressed trees to account for competition has not proved adequate. A more sophisticated procedure for evaluating these effects is necessary, particularly for crown traits which are strongly influenced by competition. A design which allows for a range of competitive pressures within a trial, such as the Nelder arrangement, may prove more successful in detecting competitive effects (Nelder, 1962).

The analyses of variance indicate crown variables are under stronger genetic control than productivity traits, and simple crown characters are more heritable than complex ones. Assessment of specific branch characters will lead to more definite improvement than assessment of the total crown in terms of surface area or volume. Branch and whorl frequency variables which reflect the density of the crown are highly heritable, and would be easy to improve. However, the repercussions on productivity of breeding for crown traits must be determined. The whole-tree concept implies that improvement in several traits rather than a single character must be undertaken in an improvement programme.

2. Observational Correlations

Before we investigate further the genetic variability and covariability of crown traits let us look at the observational correlations based on individual-tree data. Table XIII gives the correlation matrix for all variables. With 369 degrees of freedom the critical values are 0.10 at the five per cent level and 0.13 at the one per cent level of significance. It can be seen how most pairs of variables are highly correlated, although the amount of

Table XIII

Observational Correlations Based on Individual-Tree Data

	DBH	BAI	VOL	V/A	BD	BL	ANG	NOB	B/W	NOW	CL	CR	L/W	CSA	CV
DBH	1.000														
BAI	0.598	1.000													
VOL	0.973	0.555	1.000												
V/A	0.303	0.199	0.355	1.000											
BD	0.466	0.233	0.406	-0.452	1.000										
BL	0.446	0.228	0.389	-0.532	0.923	1.000									
ANG	-0.231	0.015	-0.241	-0.202	-0.365	-0.326	1.000								
NOB	0.511	0.303	0.444	-0.201	0.650	0.631	-0.164	1.000							
B/W	0.424	0.191	0.369	-0.236	0.666	0.665	-0.275	0.902	1.000						
NOW	-0.059	0.070	-0.064	0.158	-0.340	-0.362	0.370	-0.250	-0.533	1.000					
CL	0.689	0.273	0.779	0.392	0.172	0.198	-0.278	0.138	0.137	-0.116	1.000				
CR	0.390	0.237	0.326	-0.637	0.831	0.931	0.015	0.610	0.603	-0.253	0.116	1.000			
L/W	-0.036	-0.055	0.048	0.890	-0.665	-0.743	-0.145	-0.464	-0.455	0.180	0.304	-0.842	1.000		
CSA	0.608	0.311	0.591	-0.418	0.795	0.891	-0.085	0.586	0.579	-0.260	0.481	0.921	-0.624	1.000	
CV	0.517	0.291	0.479	-0.471	0.810	0.912	-0.037	0.600	0.595	-0.249	0.305	0.960	-0.681	0.970	1.000

variation in the dependent variable explained by the independent one is not great even though the values are significant.

When discussing the correlations between crown and productivity variables the productivity traits will be the dependent variables and crown traits the independent ones, as crown components are the cause of wood production. When considering the correlations among crown attributes there is no such ready distinction, and there will be no totally dependent and independent variables.

2.1 Sample correlation coefficients

Let us review some of the more important associations among crown variables which are found in this sample.

The correlations between unit branch characteristics are similar to those detected by Fielding (1960, 1967), Forestry and Timber Bureau (1959), Barber (1969) and others. Branch diameter and length are both negatively related to branch angle, and are highly positively correlated with each other. Because of this latter correlation branch diameter and length are similarly related to all other variables, and either variable could be used to assess the absolute size of the branch.

Both branch length and diameter are positively associated with branch frequency and crown dimension characters. They are negatively correlated with number of whorls per foot and with crown length-to-width ratio. These correlations indicate a large unit branch will be a component of a crown consisting of numerous, large, acutely-angled branches distributed on few whorls. The crown will have a large absolute size but a poor form as assessed by its length-to-width ratio.

Number of branches per foot and number of branches per whorl are highly related to each other, and are negatively correlated with number of whorls per foot.

The negative correlation between branch frequency characters and number of whorls per foot requires some explanation. As the number of whorls increases the size of branches becomes smaller, and the number of branches larger than one-half inch is reduced. Both branch frequency traits are similarly related to other variables which suggests either variable would serve equally well as an indicator of branch frequency. The relationship of branch frequency variables with branch size has previously been discussed, and is confirmed by the significant correlations between branch frequency and size. The relationships of branch frequency to other crown variables are also similar to those of branch size though slightly less significant. This indicates either size or frequency variables could be used in breeding for correlated response.

Number of whorls per foot has some interesting associations with other crown variables. Besides those correlations with branch size and frequency it is negatively related to all other crown dimension variables except length-to-width ratio. It is also positively correlated with branch angle. The type of tree having a multinodal habit, then, would have small, wide-angled branches and a crown of small absolute size with a good length-to-width ratio.

Crown dimension variables are highly correlated with each other. Crown radius dominates crown length in their respective relationships with the dimension variables of which they are components. Crown radius is much more highly correlated with crown surface area, crown volume, and length-to-width ratio than crown length. Crown length-to-width ratio is negatively related to all dimension variables except crown length. Again this indicates the influence of crown radius on the dimension variables.

2.2 Partial correlation coefficients removing the effect of tree size

Discussion concerning the correlation of crown attributes to productivity has been purposely neglected. Table XIII shows how, in general, a large crown component is associated with a large individual-tree productivity variable. This suggests that the correlations may be due to their common relation to tree size, since a correlation between two variables may be, wholly or in part, due to their common association with other factors. If we assess the size of the tree by diameter, and hold this variable constant, the relationships between other traits will be freed from the effects of tree size. Table XIV gives the partial correlation coefficients after removing the effect of diameter.

This table confirms the impression that many crown variables are largely dependent on the size of the tree for their relationships with productivity. Branch diameter and length, number of branches per foot and per whorl, crown radius, crown surface area, and crown volume which are shown to be positively correlated with volume in Table XIII are negatively or non-significantly related to this productivity variable when the effect of tree size has been removed.

The correlation of volume with branch angle, number of whorls per foot, and crown length remain largely unaffected, and crown length-to-width ratio has its coefficient changed from non-significant to positive. This suggests that crown attributes measuring the absolute size of the crown are positively related to volume through common size, whereas traits not assessing size of the crown are not dependent on tree size. In effect, for trees of equal diameter, volume

Table XIV

Partial Correlations Removing Effect of Tree Size

	DBH	BAI	VOL	V/A	BD	BL	ANG	NOB	B/W	NOW	CL	CR	L/W	CSA	CV
DBH	0.0														
BAI	0.0	1.000													
VOL	0.0	-0.145	1.000												
V/A	0.0	0.023	0.277	1.000											
BD	0.0	-0.064	-0.234	-0.703	1.000										
BL	0.0	-0.055	-0.219	-0.782	0.904	1.000									
ANG	0.0	0.197	-0.070	-0.143	-0.299	-0.255	1.000								
NOB	0.0	-0.004	-0.269	-0.434	0.542	0.524	-0.055	1.000							
B/W	0.0	-0.087	-0.212	-0.422	0.585	0.587	-0.201	0.881	1.000						
NOW	0.0	0.132	-0.030	0.185	-0.353	-0.376	0.367	-0.257	-0.562	1.000					
CL	0.0	-0.241	0.647	0.265	-0.233	-0.170	-0.168	-0.345	-0.237	-0.104	1.000				
CR	0.0	0.005	-0.252	-0.860	0.796	0.918	0.118	0.519	0.525	-0.250	-0.230	1.000			
L/W	0.0	-0.042	0.362	0.946	-0.733	-0.813	-0.158	-0.518	-0.486	0.178	0.454	-0.899	1.000		
CSA	0.0	-0.083	-0.006	-0.795	0.728	0.872	0.072	0.404	0.446	-0.283	0.108	0.936	-0.758	1.000	
CV	0.0	-0.027	-0.125	-0.769	0.751	0.890	0.100	0.457	0.485	-0.256	-0.083	0.963	-0.775	0.965	1.000

is primarily a function of tree height, and increased volume is related to narrower crowns with smaller branches and a better length-to-width ratio. The more productive trees are those which have a greater propensity to store carbohydrates in their boles than in their crowns.

The correlations between crown variables and productivity, as measured by basal area increment and volume per acre, are largely unchanged after removing the effect of tree size. The relationships with increment become non-significant, but the change is slight. The correlations of crown attributes and volume per acre become slightly larger indicating that the highly significant relationships are founded on the growing-area factor rather than the volume component in the productivity variable, volume per acre. This is supported by the similar increase in the correlations between crown radius and other crown dimension variables once the effect of tree size is removed.

In general, removing the effect of tree size has little influence on the correlations among crown variables, and the relationships discussed in the previous section are valid. The associations between most crown components remain relatively stable over the range of tree sizes encountered in this trial. However, the relationships between crown length and other crown variables is radically altered by the removal of size effect. The partial correlations indicate a long crown is associated with a narrow radius and small branches. Observational correlations suggest the reverse is true. Because crown length and total tree height are equivalent in immature stands of Pinus radiata which have just begun to compete, this variable is a function of productivity as well as crown size. Its reaction to the removal of the effect of tree size is similar to that of other measures of productivity. The meaning of this variable should be interpreted in terms of tree height rather than crown length. Until the crown has begun to rise, the assessment of crown length cannot be considered only as a component of the crown, but must also be classified as a measure of productivity. Hence, the interpretation of the significance of green crown length in immature stands must be treated with some caution.

The observational correlations have pointed out that certain crown measures, notably branch diameter and length, are similarly correlated with other variables, and one would be as good as the other for assessing branch size. Either one of the two branch frequency variables would be adequate for assessing branch number. Crown radius is a better estimator of crown dimension than surface area or volume, and crown length is a poor measure of the crown in an immature stand.

Most crown variables are correlated with productivity through their common relationships with tree size. Variables that show significant positive relationships with volume and basal area increment become negatively or non-significantly correlated when the effect of tree size is removed. Thus trees with narrower, longer, more finely-branched crowns will be better volume producers.

The relationships between crown traits and volume per unit area are unaffected by tree size. These correlations are largely influenced by the growing space component rather than the volume factor.

3. Genotypic and Phenotypic Correlations

We have seen the observational associations between crown variables. Let us now investigate the genotypic and phenotypic correlations derived from components of variance and covariance. Table XV gives the genotypic and phenotypic correlation coefficients together with their standard errors. The asterisks designate the coefficients which are greater than twice their standard errors, the criterion by which significance is judged. For this particular set of data the size of the correlation which is detected as 'significant' is within the range 0.39 to 1.03. Non-significant values are as high as 1.80.

The phenotypic correlations differ from the observational relationships in that only the additive

Table XV

Genotypic and Phenotypic Correlations Derived from Components of Variance and Covariance and Their Standard Errors

GENOTYPIC AND PHENOTYPIC CORRELATION COEFFICIENTS WITH STANDARD ERRORS

	DBH	BAI	VOL	V/A	BC	BL	ANG	NCB	B/W	NOW	CL	CR	L/W	CSA	CV
DBH	0.0 0.0	0.304 0.132	0.065 0.012	0.368 0.156	0.536 0.207	0.557 0.204	0.494 0.201	0.598 0.200	0.499 0.205	0.443 0.193	0.822 0.096	0.581 0.200	0.472 0.189	0.793 0.172	0.668 0.188
BAI	0.915* 0.560*	0.0 0.0	0.327 0.141	0.138 0.148	0.170 0.176	0.199 0.183	0.298 0.201	0.271 0.206	0.198 0.180	0.149 0.141	0.647 0.181	0.228 0.193	0.209 0.185	0.343 0.202	0.285 0.202
VOL	0.949* 0.969*	0.833* 0.517*	0.0 0.0	0.360 0.153	0.522 0.207	0.548 0.206	0.481 0.200	0.583 0.204	0.480 0.203	0.425 0.188	0.450 0.067	0.570 0.200	0.453 0.185	0.764 0.168	0.655 0.187
V/A	0.683 0.438*	0.985* 0.560*	0.680 0.457*	0.0 0.0	0.095 0.110	0.098 0.106	0.315 0.229	0.151 0.152	0.122 0.136	0.142 0.150	0.517 0.148	0.084 0.090	0.034 0.028	0.212 0.152	0.151 0.132
BC	-0.631 0.052	-0.937* -0.450*	-0.743 -0.013	-0.927* -0.701*	0.0 0.0	0.022 0.026	0.208 0.164	0.037 0.052	0.021 0.038	0.041 0.074	0.918 0.193	0.081 0.064	0.053 0.071	0.209 0.112	0.153 0.096
BL	-0.549 0.111	-0.866* -0.404*	-0.662 0.053	-0.916* -0.712*	0.980* 0.937*	0.0 0.0	0.241 0.177	0.058 0.077	0.049 0.064	0.063 0.086	0.988 0.202	0.041 0.026	0.043 0.061	0.156 0.074	0.093 0.051
ANG	0.574 0.048	0.426 0.293	0.384 0.144	0.320 0.084	-0.619* -0.535*	-0.536* -0.471*	0.0 0.0	0.226 0.170	0.177 0.153	0.130 0.118	1.254 0.198	0.328 0.219	0.256 0.221	0.395 0.211	0.363 0.216
NCB	-0.500 0.168	-0.769* -0.244	-0.636 0.084	-0.914* -0.541*	1.027* 0.870*	1.021* 0.800*	-0.635* -0.474*	0.0 0.0	0.018 0.020	0.075 0.104	0.948 0.190	0.106 0.104	0.085 0.105	0.239 0.139	0.176 0.126
B/W	-0.566 0.009	-0.785* -0.427*	-0.699 -0.072	-0.380* -0.520*	1.019* 0.912*	0.963* 0.839*	-0.687* -0.584*	1.008* 0.948*	0.0 0.0	0.025 0.051	0.912 0.178	0.123 0.109	0.071 0.096	0.259 0.153	0.200 0.140
NOW	0.625 0.168	0.838* 0.590*	0.774 0.223	0.836* 0.572*	-1.043* -0.922*	-0.959* -0.779*	0.787* 0.698*	-1.050* -0.725*	-1.019* -0.883*	0.0 0.0	0.942 0.177	0.157 0.142	0.110 0.131	0.293 0.176	0.230 0.168
CL	0.310 0.715*	0.641 0.222	0.675 0.807*	0.757 0.458*	-1.284 -0.132	-1.297 -0.090	1.800 0.239	-1.345 -0.212	-1.382 -0.296	1.435 0.303	0.0 0.0	0.841 0.198	0.578 0.156	1.161 0.170	0.970 0.190
CR	-0.454 0.152	-0.867* -0.337	-0.458 0.126	-0.945* -0.753*	0.889* 0.837*	0.940* 0.939*	-0.212 -0.154	0.929* 0.709*	0.835* 0.706*	-0.788* -0.595*	-0.826 0.021	0.0 0.0	0.040 0.051	0.050 0.032	0.017 0.014
L/W	0.473 0.182	0.865* 0.387*	0.522 0.230	0.957* 0.932*	-0.982* -0.317*	-1.003* -0.845*	0.430 0.169	-1.030* -0.713*	-0.969* -0.749*	0.913* 0.637*	0.876 0.410*	-0.992* -0.870*	0.0 0.0	0.165 0.123	0.102 0.098
CSA	-0.428 0.426*	-0.847* -0.199	-0.335 0.445*	-0.908* -0.503*	0.708* 0.673*	0.781* 0.805*	0.201 -0.014	0.743* 0.552*	0.623* 0.509*	-0.559 -0.391*	-0.652 0.418*	0.973* 0.914*	-0.943* -0.624*	0.0 0.0	0.014 0.009
CV	-0.403 0.308	-0.839* -0.244	-0.364 0.307	-0.966* -0.602*	0.775* 0.739*	0.865* 0.874*	-0.021 -0.076	0.815* 0.620*	0.702* 0.587*	-0.660* -0.468*	-0.692 0.238	0.989* 0.964*	-0.962* -0.723*	0.999* 0.977*	0.0 0.0

NOTE**GENOTYPIC CORRELATIONS ABOVE PHENOTYPIC CORRELATIONS ON LOWER LEFT.
CORRESPONDING STANDARD ERRORS ON UPPER RIGHT

genetic component and the unaccounted for error variation are considered. All portions of variation attributable to blocks have been removed. This method follows the one used by Robinson _et al_. (1951). An alternate system of using family mean squares and mean products to calculate phenotypic correlations (Johnson _et al_., 1955b) was tried and was found to yield similar results. However, Robinson's method was used for the sake of consistency.

In general, there is close agreement between genotypic and phenotypic correlations, particularly when both values are judged significantly greater than zero. The genotypic correlations are usually larger than the corresponding phenotypic values, a fact noted by Berry _et al_. (1969) and Johnson _et al_. (1955b).

3.1 Significant genotypic and phenotypic correlations

Most relationships follow the general pattern noted for observational correlations.

Branch diameter and length are similarly related to other crown attributes. They are negatively correlated with branch angle, number of whorls, and crown length-to-width ratio, and positively associated with number of branches per foot and per whorl, crown radius, crown surface area, and crown volume. Branch angle is negatively correlated with branch frequency, and positively related to number of whorls. Branch angle is not significantly correlated with any productivity variables, but branch length and angle are negatively related to both basal area increment and volume per acre.

Number of branches per foot and number of branches per whorl are both similarly related to other variables, and give almost identical genotypic correlations as branch diameter and length. Number of whorls per foot is positively correlated with basal area increment and volume per acre. It is negatively related to branch size and frequency, crown radius, and crown volume. Its association with crown length-to-width ratio is positive.

Crown length is not significantly related genotypically to any other variable, although there are several significant phenotypic relationships, notably with diameter, volume, and volume per acre. It is also phenotypically correlated with crown length-to-width ratio and crown surface area.

Crown radius, on the other hand, is negatively related to basal area increment and volume per acre. It is negatively correlated with number of whorls and crown length-to-width ratio, and is positively associated with other crown dimension variables.

Crown length-to-width ratio is correlated with the same variables as crown radius, but in the reverse. This shows the importance of crown radius in this ratio.

3.2 Implication of genotypic correlations

The genotypic correlations indicate the type of crown which will result from selection pressure. If selection is for increased productivity per unit area, the most efficient genotype will have a small crown radius, good length-to-width ratio, small branch size, near-horizontal branch angle, and numerous whorls. The volume of this genotype will not necessarily be larger than a less efficient type, but a greater amount of basal area increment will be produced. This suggests that a narrow crown is a better producer of increment under competitive conditions. It is not necessarily the better producer in the free growing state before crown closure occurs.

Explanations for this difference can be deduced from other genetic relationships. The negative correlation between crown radius and length-to-width ratio indicates that a narrow-crowned genotype has a more favourable shape for exposure to sunlight in stand conditions relative to trees with wide crowns. Ability of the crown to photosynthesize is less impaired by surrounding crowns. Jahnke and Lawrence (1965) showed on a mathematical basis how a larger crown length-to-width ratio is more productive per unit area of land. Although their model avoids "consideration of complexities arising from close spacing and mutual shading", the positive correlations with both volume per acre and basal area increment indicate the model is applicable to competitive conditions. The narrow crown is also associated with a greater number of whorls which will increase the genotype's foliage density. Photosynthetic capacity will be increased and, consequently, so will productivity. Prior to crown closure in the stand the factors of shape and density would not be as important as the absolute size of the crown. One would expect the vigorous, heavily branched genotype to develop best in a free growing state. But once crown competition begins the narrow, denser-crowned genotype is better able to retain its photosynthetic capacity and increase its productivity relative to a wider-crowned genotype.

Hamilton (1969) reached a similar conclusion from studies of a twenty-three year old Sitka spruce stand. He found the partial regression coefficient of crown projection area on volume increment is negative while that of crown surface area is positive. He interprets this as indicating a narrow crown is a better producer of increment in stand conditions, and suggests the cause could be genotypic.

If the cumulative productivity variables of diameter and volume assessed at age twelve accurately represent growth in a non-competitive environment, and basal area increment for the three year period to age fifteen reflects growth under competitive stress, the genotypic correlations imply early testing of progeny may be impractical if based on stem size alone. The initial vigour of a genotype with a wide crown may be lost once competition has begun. The ability of a tree to withstand competitive pressure must be evaluated at an early age to accurately predict a progeny's growth potential. Closer spacing of trials would cause rapid commencement of competition, and would allow early assessment of competitive ability of genotypes. An alternative would be to establish supplementary trials at very close spacing to test competitive effects within the first few years. The competitive ability of genotypes in the normally spaced trials could then be predicted. The genetic correlations with basal area increment indicate crown variables such as length-to-width ratio and whorl frequency could be used to evaluate the competitive ability of genotypes.

The genetic relationships between productivity per unit area and crown variables result primarily from the association of crown traits with the area factor rather than their relation with volume. Improvement in volume production per acre should be attacked by way of reducing the growing space rather than by selection for volume *per se*. Crown radius, a measure of growing space, is genetically correlated with the highly heritable crown traits of branch and whorl frequency, and is itself a moderately heritable character. Volume per tree, on the other hand, is not associated with any crown traits, and has a very low breeding value. It will thus be difficult to substantially improve volume per tree either through direct selection or by correlated response.

Increasing volume per acre can best be accomplished by selecting narrow-crowned, multinodal genotypes and growing them at closer spacing. The greater basal area increment anticipated for these genotypes would compensate for the expected decrease in volume per tree when adopting greater stocking density. It is probable that density of the narrow-crowned genotypes could be increased to the point where a crown cover comparable to that for an unimproved stand at eight-foot spacing is attained before a significant reduction in individual tree productivity occurs.

Although genetic correlations do not show any significant relationships between the crown and diameter or volume per tree, the idea of increasing individual-tree volume should not be abandoned. The correlations with basal area increment show that crown traits are related to some measure of productivity. As the stand gets older an increasing portion of the total volume will be formed under competitive conditions, and the correlations with cumulative productivity variables will become significant. The trend towards significance is evident from the similar genetic correlations between crown traits and both volume per tree and basal area increment. The correlations for volume per tree are very nearly significant in several instances, particularly in its relationship to number of whorls per foot.

When stem diameter at age fifteen is used as a measure of productivity, the following significant genetic correlations with crown variables are found:

BD	BL	NOB	B/W	NOW	L/W
-0.767*	-0.691*	-0.618*	-0.665*	0.720*	0.651*

Diameter at age fifteen reflects cumulative growth under several years of competitive stress, and the correlations with crown traits verify the genetic link between individual-tree productivity and the crown. A crown formed in a competitive regime will be associated genetically with volume produced under these same conditions.

4. Assessment of the Variables for Selection Criteria

Selection for 'efficient' crowns as envisaged by Brown and Goddard (1961) and Douglass (1961) is highly feasible. However, the method of rating the efficiency of the crown through the assessment of crown surface area or crown volume will not lead to a ready increase in wood production. The low heritabilities (less than 0.2) of these dimension variables indicate parents having favourable crown size will not necessarily pass the characteristic to their progeny. Branch and whorl frequency variables may prove better estimators of the efficiency of the crown. The branch is the basic structural unit of the crown, and it regulates the amount of photosynthetic tissue that can be displayed. By increasing the number of branches the density of the crown is increased. In a species like Pinus radiata which has its branches arranged in whorls, the frequency of whorl production is very important. The density of the crown is largely a function of whorl frequency. Multinodality ensures photosynthetic material is more efficiently and compactly distributed.

Traits which assess the size or shape of the crown do not take into account density values. Two crowns may have identical surface areas or volumes, yet one can have far fewer branches or whorls. The denser crown will have a larger photosynthetic area, and, assuming equal photosynthetic efficiency, it will be more productive. Both density and size must be considered in assessing the efficiency of the crown.

No crown trait is solely responsible for productivity. Each trait estimates the photosynthetic capacity of the crown in some manner, and is thus related to productivity. These variables are highly inter-related genotypically and phenotypically. The traits that reflect the absolute size of the crown have the disadvantage of low breeding values. Improving these traits would be difficult. The shape of the crown, as assessed by length-to-width ratio, is moderately heritable and is free from the influence of tree size. It measures the ability of a tree to utilize the photosynthetic capacity of all crown size characters. Crown attributes that measure the density of the crown have high heritabilities, and are genetically correlated with productivity variables. Branch and whorl frequency would be relatively simple to improve, and would yield excellent correlated improvement in productivity. These crown traits are the most suitable candidates for construction of selection indices.

Another aspect of the applicability of crown traits in tree improvement programmes is their practicality. Unless a trait can be easily measured it will not receive wide approval for selection purposes. Of all crown traits dimension variables are most difficult to assess in stand conditions. Curtin (1968) has pointed out the problems associated with measuring green crown length and crown radius. Counting whorl and branch frequencies is much easier, and could be readily incorporated into any selection programme.

THE SELECTION INDICES

The selection indices presented in this thesis have been chosen from all possible combinations of traits for one-, two-, and three-variable indices. The criterion for choosing an index is the size of the expected genetic advance, and only the best indices are shown.

Advances are measured in units of 100 cubic feet, and indicate the gain in volume per acre to be expected at age twelve from selection using the index. The selection differential used to determine genetic advance is 2.06, which corresponds to selection of the best five per cent of the population. 'Best' refers to that part of the population which receives the largest selection scores for the particular index.

The standard for comparison of the indices is the expected advance of the index based on selection for volume per acre alone. Any index showing a genetic advance greater than this value will be more efficient for improving volume per acre.

1. Single-Variable Indices

Table XVI gives the relative weights and expected genetic advances in terms of volume per acre for selection indices based on single variables. The pulpwood regime is shown together with the sawlog regime. The economic values

Table XVI

Selection Indices Based on Single Variables

Variable	Pulpwood			Sawlog		
	Economic value	Index weight	Advance	Economic value	Index weight	Advance
V/A	1.00	0.096	2.8	1.00	0.096	2.8
DBH	0.0	0.481	1.1	0.17	0.486	1.1
BAI	0.0	30.177	2.3	0.0	30.177	2.3
VOL	0.0	0.285	1.1	0.0	0.285	1.1
BD	0.0	-6.145	3.0	-0.45	-6.202	3.0
BL	0.0	-0.697	2.9	-2.80	-1.064	4.4
ANG	0.0	0.056	1.2	0.03	0.061	1.3
NOB	0.0	-1.505	2.9	-0.23	-1.534	3.0
B/W	0.0	-0.720	4.0	-0.35	-0.807	4.4
NOW	0.0	13.507	3.9	-0.40	13.401	3.8
CL	0.0	0.123	1.2	0.0	0.123	1.2
CR	0.0	-0.776	2.6	-3.00	-1.061	3.6
L/W	0.0	0.541	2.8	0.0	0.541	2.8
CSA	0.0	-0.034	2.0	0.0	-0.034	2.0
CV	0.0	-0.094	2.2	0.0	-0.094	2.2

given the traits in the respective regimes are shown in Table V, and are repeated in this table. Several important points are illustrated in this table.

The index weights indicate the direction selection must take in order to improve volume per acre. Example 1 shows number of whorls per foot must be increased and crown radius must be reduced to yield correlated improvement in volume per acre. The genotypic and phenotypic correlations have indicated these trends.

Example 1

Variable	Index Weight
NOW	13.507
CR	-0.776

Several indices indicate greater expected advances in volume per acre than selection for that trait alone. Example 2 shows some of these indices. For the pulpwood regime the indices showing larger gains are those with higher heritabilities and a high genotypic correlation with volume per acre. The advances for the sawlog regime indices are also dependent on these factors, but the economic values play an important role. If the direction of economic improvement (i.e. the sign of the economic value) coincides with the direction of genetic improvement (i.e. the sign of the genotypic correlation between volume per acre and the trait), the advance predicted for an index will be greater than if no economic value is applied.

Example 2

Variable	Advance Pulpwood	Advance Sawlog	Per cent change
V/A	2.79	2.79	0.0
B/W	3.95	4.43	+12.0
NOW	3.87	3.84	-0.1
BL	2.88	4.90	+70.0

Example 2 shows how branch length has a larger expected advance for the sawlog regime. The economic value for this trait is negative, and the genetic correlation with volume per acre is also negative. The variable, number of whorls per foot, demonstrates what will occur if the directions of economic and genetic improvement are opposed. Number of whorls is positively correlated genetically with volume per acre, but has a negative economic weight. The expected advance for the index selecting for number of whorls is smaller in the sawlog regime. This illustrates breeding objectives are not always in line with what is genetically possible. Decreasing whorl frequency may be economically desirable but genetically impractical.

Including 'reasonable' economic values in the indices does not greatly alter most of the single variable index weights. Number of whorls has an economic value of -0.70, but its index weight differs little between sawlog and pulpwood regimes (Example 3).

Example 3

Variable	Economic value		Index weight	
	Pulpwood	Sawlog	Pulpwood	Sawlog
NOW	0	-0.70	13.506	13.400
BD	0	-0.35	-6.144	-6.202
BL	0	-2.80	-0.697	-1.064

Branch diameter is another example. A more dramatic change occurs for branch length where a fifty per cent difference in the weight is caused by inclusion of the economic value. Wherever the economic value is of the same sign as the genotypic and phenotypic correlations the index weight and genetic advance for a particular index will be larger for the sawlog regime.

2. Two-Variable Indices

A selection of ten indices constructed from two variables which predict the largest genetic advances are shown in Table XVII. Pulpwood and sawlog indices are shown separately.

Several points are evident from comparison of the two regimes. Volume per acre is an important variable to include in the two-variable indices. This trait is incorporated in half the indices for both regimes. This suggests that improvement in volume per acre can best be achieved through selection for this trait and another genetically correlated character.

Table XVII

Selection Indices Based on Two Variables

PULPWOOD REGIME

Variables		Index weights		Advance
V/A	B/W	-0.002	-1.444	7.9
V/A	NOW	0.004	26.844	7.7
V/A	L/W	-0.361	2.878	7.3
V/A	BD	-0.018	-12.879	5.9
V/A	NOB	0.043	-2.829	5.9
V/A	BL	-0.037	-1.554	5.8
B/W	NOB	-1.426	2.184	4.3
B/W	NOW	-0.446	7.716	4.2
NOW	BAI	12.441	21.515	4.1
NOW	L/W	11.432	0.294	4.1

SAWLOG REGIME

Variables		Index weights		Advance
V/A	B/W	0.000	-1.524	8.3
V/A	BL	-0.020	-1.848	7.2
V/A	NOW	0.004	26.745	7.7
V/A	L/W	-0.361	2.878	7.3
V/A	NOB	0.044	-2.854	6.0
V/A	BD	-0.018	-12.925	6.0
BL	BAI	-1.166	49.940	5.8
CR	B/W	-0.092	-1.007	5.7
CR	NOW	-0.571	15.306	5.4
BL	CL	-1.129	0.273	5.1

Another similarity between the indices is the importance of branch and whorl frequency variables. These attributes are included in more than half the indices, and sometimes in conjunction with each other. The high heritabilities and significant genetic correlations of these variables make them attractive for improving productivity through correlated response.

In the sawlog regime branch length and the closely related variable crown radius assume greater importance. Of the indices that do not incorporate volume per acre, one or the other of these variables is included. The economic values placed on these traits accentuate the genetic relationship with volume per acre. However, the changes in the index weight and genetic advance are not as dramatic as for the comparable single-variable indices. A twenty per cent change in the index weight is caused by including the economic value for branch length in the index. Example 4 illustrates this point. Similar results are obtained when branch length or crown radius is combined with other variables in an index.

Example 4

Index variables	Index weight for BL		Per cent change
	Pulpwood	Sawlog	
BL	-0.697	-1.064	52
V/A BL	-1.555	-1.849	19

The index weights of a two-variable index show the relative importance attached to each variable. If, for example, the index containing the variables volume per acre and number of whorls is applied to a candidate tree, the emphasis for selection will be placed on number of whorls rather than volume per acre. Volume per acre assessed in units of 100 cubic feet will be multiplied by a factor of 0.005, whereas number of whorls measured on a unit-foot basis will be multiplied by 26.845 (see Example 5). If the tree being assessed has a volume-per-acre equivalent of 21.55 hundred cubic feet and a whorl frequency of 0.582 whorls per foot, the respective index scores will be 0.108 for volume per acre and 15.624 for number of whorls for a total score of 15.732. By far the most influential variable is number of whorls. The second index shown in Example 5 has a more equitable relationship between the variables.

Example 5

Index values	Index scores using values in volume per acre equivalents		Aggregate score
0.005 x V/A + 26.845NOW	+0.108	+15.624	15.732
11.432 x NOW + 0.295xL/W	+6.654	+2.667	9.320

Values for variables: V/A = 21.5; NOW = 0.582; L/W = 9.05

Number of whorls accounts for seventy per cent of the aggregate score in this instance. However, a tree with fewer whorls but a more favourable length-to-width ratio could receive a high selection score because of its large length-to-width ratio.

The proportionately larger genetic advances shown for the sawlog indices is attributable to the magnifying influence of economic values. The reasons have previously been discussed. However, the relative differences in expected advances between the same indices for pulpwood and sawlog regimes are smaller than those shown in Example 2. Example 6 demonstrates that the economic values have less effect on two-variable indices.

Example 6

Variables	Advance		Per cent change
	Pulpwood	Sawlog	
V/A B/W	7.90	8.38	+6.1
V/A NOW	7.75	7.72	-0.0
V/A BL	5.83	7.30	+25.0

3. Three-variable indices

Let us finally review the best indices constructed from three variables. Table XVIII gives the ten most efficient indices for pulpwood and sawlog regimes. The results and trends inferred from one- and two-variable indices also apply to these indices.

All indices for both regimes include volume per acre as a variable. The two-variable indices were noted to be

Table XVIII

Selection Indices Based on Three Variables

PULPWOOD REGIME

Variables	Index weights			Advance
V/A BAI L/W	-0.779	132.071	4.888	11.2
V/A CR DBH	-0.483	-5.806	5.978	9.6
V/A NOW L/W	-0.359	22.787	2.377	9.5
V/A B/W DBH	-0.096	-1.963	2.769	9.5
V/A BAI B/W	-0.068	72.129	-1.608	9.4
V/A VOL B/W	-0.089	1.438	-1.854	9.2
V/A VOL CR	-0.450	3.195	-5.329	9.1
V/A BL DBH	-0.319	-3.689	4.658	9.1
V/A BD DBH	-0.224	-26.555	4.005	8.8
V/A NOB B/W	-0.020	4.467	-2.924	8.6

SAWLOG REGIME

Variables	Index weights			Advance
V/A BL DBH	-0.345	-4.313	5.375	10.9
V/A CR DBH	-0.498	-6.293	6.426	10.6
V/A BL B/W	0.023	0.066	-1.896	10.4
V/A BL NOW	-0.043	-0.948	29.185	10.2
V/A VOL CR	-0.461	3.411	-5.755	10.1
V/A B/W DBH	-0.097	-2.070	2.899	10.0
V/A VOL B/W	-0.090	1.506	-1.954	9.7
V/A B/W CR	0.015	-1.714	-0.047	9.6
V/A NOW L/W	-0.359	22.690	2.376	9.4
V/A BL CL	-0.145	-2.523	0.601	8.8

more efficient if they contained this variable, and a similar result is evident for the three-variable indices. The importance of branch and whorl frequency variables is likewise apparent in these indices. Branch length and crown radius play a more prominent role in sawlog indices, but the expected genetic gains are not much greater for these indices than for the same ones excluding economic values. Example 7 shows the advance predicted for the index containing volume per acre, branch length, and stem diameter. The advance is only 19% greater for the sawlog regime than for the pulpwood. This shows how the effect of economic values is reduced as the number of variables in an index increases. This example also shows the respective index weights are very similar for both regimes.

Example 7

Variables	Index weights			Advance
	V/A	BL	DBH	
Pulpwood	-0.319	-3.689	+4.658	9.2
Sawlog	-0.345	-4.313	+5.375	10.9

Approximately the same emphasis is placed on each variable by both indices, and the type of tree which will receive the highest selection score will be the same for both regimes.

Indices with a greater number of variables could readily be derived. However, Stonecypher (1969) emphasizes that the success of multiple-trait breeding is dependent on the breeder's ability to select for only the most important traits. Adding more variables will only increase the probability of error in an index.

4. Applying the Indices

We now have a series of indices based on one, two, and three variables which can be applied to selection for volume per acre and economically useable wood per acre. Their effectiveness is estimated by the genetic advance predicted from the use of the indices. The pulpwood index constructed from volume per acre, number of whorls, and crown length-to-width ratio estimates the per generation gain in volume per acre at age twelve to be 9.50 hundred cubic feet. Selection based on volume per acre alone will improve volume by only 2.80 hundred cubic feet. The advantage of applying selection indices is readily seen.

The indices can be used to select superior individuals or families. Their use is restricted to selection from the population used in their construction. If the progeny trial is representative of the species, the indices have a wide application. However, let us confine their use to the families contained in the trial, and discover what sort of family the indices favour for the purpose of improving volume per acre. The variable means for each family will provide the observational data on which the indices will be tested.

Table XIX rates the families from best to worst depending on the selection score received from the use of each particular index. The actual values of the index scores are unimportant since they serve only to rank the candidate families; the larger the score is, the more appropriate the family for improvement of volume per acre and economically useable volume per acre.

The rankings for single-variable indices are not given because the index weights are merely constants and will rate the families by the size of the variable means. This data is already available as range tests in Tables IX to XII. However, if the single index weight is negative, such as for crown radius, the positions will be reversed, and those families with the smallest variable means will receive the highest score.

All indices, both for pulpwood and sawlog regimes, rank the families very similarly. Families 2, 8 and 9 rank in the highest three scores in practically every index. Families 6 and 7 are found in the lowest three almost without exception. Other families tend to retain their relative position in most indices. For example, family 10 always ranks in the upper half, and families 1 and 3 always remain in the bottom positions.

The reasons for this constant ranking are found in the construction of the majority of indices. In most instances the indices are a combination of the variables volume per acre, whorl and branch frequencies, length-to-width ratio, branch length, and crown radius. The genotypic and phenotypic correlations are such that families with narrow crowns, large number of whorls, a good length-to-width ratio, and few large branches are associated with greater volume per acre. The families having this favourable combination of attributes will receive high selection scores. Families 2, 8, and 9 are shown by the range tests in Tables IX to XII to be very similar for these attributes. Families 6 and 7 are unfavourably endowed with respect to these critical variables.

The consistent ranking of families indicates the selection index does provide a method of objective selection. If constructed with reliable information the index can be applied to evaluation of progeny within a trial, or it can be used for plus-tree selection in unimproved plantations. It could serve as a screening system for final evaluation of plus phenotypes. This would enable a large number of potential candidates to be selected at a low intensity, and final assessment would be made by the index.

Table XIX

Order Ranking of Families by Selection Indices

PULPWOOD REGIME

Index variables			Rank											
	V/A	B/W	2	8	9	10	5	12	4	11	3	7	1	6
	V/A	NOW	2	8	4	9	12	10	11	5	3	7	1	6
	V/A	L/W	2	5	10	12	8	9	4	3	6	7	1	11
	V/A	BD	2	9	8	10	5	4	12	11	7	3	6	1
	V/A	NOB	2	9	8	5	10	12	4	11	1	7	3	6
	V/A	BL	2	8	10	5	9	4	12	11	3	6	7	1
	B/W	NOB	2	8	9	12	4	5	10	11	3	7	1	6
	B/W	NOW	2	8	9	4	10	12	5	11	3	7	1	6
	NOW	BAI	2	9	8	4	11	10	12	5	3	7	1	6
	NOW	L/W	2	8	9	4	12	10	5	11	3	7	1	6
V/A	BAI	L/W	2	10	9	8	5	4	12	11	3	6	1	7
V/A	CR	DBH	9	10	2	8	4	5	11	12	6	1	3	7
V/A	NOW	L/W	2	4	8	10	5	12	9	11	3	7	1	6
V/A	B/W	DBH	8	2	12	9	10	4	11	5	3	1	7	6
V/A	BAI	B/W	2	9	8	10	4	5	12	11	3	7	1	6
V/A	VOL	B/W	8	12	2	4	10	9	5	11	3	7	1	6
V/A	VOL	CR	10	8	9	2	4	12	5	11	6	1	3	7
V/A	BL	DBH	8	2	10	4	11	9	12	5	3	6	1	7
V/A	BD	DBH	8	11	9	2	10	4	12	5	3	1	7	6
V/A	NOB	B/W	2	8	9	12	4	10	5	11	3	7	1	6

continued

Table XIX (continued)

SAWLOG REGIME

Index variables			Rank											
	V/A	B/W	2	8	9	10	5	12	4	11	3	7	1	6
	V/A	BL	2	8	10	9	5	4	12	11	3	6	7	1
	V/A	NOW	2	8	4	9	12	10	11	5	3	7	1	6
	V/A	L/W	2	5	10	12	8	9	4	3	6	7	1	11
	V/A	NOB	2	9	8	5	10	12	4	11	1	7	3	6
	V/A	BD	2	9	8	10	5	4	12	11	7	3	6	1
	BL	BAI	9	8	2	10	5	4	11	12	3	6	1	7
	CR	B/W	2	8	9	10	5	12	4	11	3	7	1	6
	CR	NOW	2	9	8	4	10	5	12	11	3	7	1	6
	BL	CL	8	2	12	10	5	9	4	11	6	3	1	7
V/A	BL	DBH	8	2	10	4	9	11	12	5	3	6	1	7
V/A	CR	DBH	9	10	8	2	4	5	11	12	6	1	3	7
V/A	BL	B/W	2	8	9	10	5	12	4	11	3	7	1	6
V/A	BL	NOW	2	8	4	9	10	12	5	11	3	7	6	1
V/A	VOL	CR	10	9	8	2	4	12	5	11	6	1	3	7
V/A	B/W	DBH	8	2	12	9	10	4	11	5	3	1	7	6
V/A	VOL	B/W	8	12	2	4	10	9	5	11	3	7	1	6
V/A	B/W	CR	2	8	9	10	5	12	4	11	3	7	1	6
V/A	NOW	L/W	2	4	8	10	5	12	9	11	3	7	1	6
V/A	BL	CL	2	8	12	10	4	5	9	11	6	3	1	7

CONCLUSIONS

The progeny trial of Pinus radiata analyzed is twelve years old, and is therefore immature. It represents a stand environment established on a good site. The twelve families contained in the trial are the progeny of fourteen selected parents which are samples of the superior portion of the population rather than the entire population. Only the dominant and codominant individuals are included in analyses.

Analysis of variance has shown productivity variables to be under weak genetic control. Narrow-sense heritabilities are of a low order. Crown traits, on the other hand, have reasonably high heritabilities. Whorl and branch frequency traits have relatively high breeding values, and branch angle is under strong genetic control. Of all crown attributes those which assess the absolute size of the crown have the lowest heritability estimates.

The results of variance analysis are as might be expected. Productivity variables are influenced by a multitude of physiological processes each of which is controlled by unique gene complexes. These physiological processes are in turn affected by many environmental factors. Productivity traits reflect the complex reactions and interactions of these diverse physiological processes and environmental influences. It is, therefore, understandable that productivity variables are under weak genetic control.

Crown traits are less complex variables and are probably subject to less complex control by polygenes than productivity traits. However, dimension variables are a combination of crown traits, and are also subject to different environmental factors over time. They are under only weak to moderate genetic control. Competition is the major environmental influence acting on these variables. Crown traits which are affected by environment mainly at the time of initiation, such as whorl frequency and branch angle, are likely to be most highly heritable. This certainly is so for the present study.

The analyses emphasize the need for new methods to allow for variation due to competition in progeny trials. The effect of competition must be accounted for at some stage in analysis. The method of removing obviously suppressed individuals is not wholly effective, and better solutions are required. Possible methods are to improve the experimental design and so remove some competitive effect, or to incorporate a competitional component in the variance model which estimates the competitive ability of a genotype. It may be practical to plant progeny trials at a closer spacing to assess competitive effects at an early age, and to specifically design experiments to explore competitive ability of genotypes.

The heritability values derived from this progeny trial indicate there is little opportunity for achieving rapid improvement in productivity by selecting and breeding for size alone. A better response would be obtained by breeding for highly heritable crown characters which are shown to be genetically correlated with productivity. Improvement in the crown trait would result in correlated improvement in yield.

The most efficient way of selecting for multiple traits is the selection index. Analysis shows selection for increased productivity per unit area can best be achieved by using an index consisting of the variables volume per acre and combinations of the crown traits number of whorls per foot, number of branches per whorl, length-to-width ratio, and crown radius. Basal area increment and diameter at breast height are also valuable variables to include in an index.

The most efficient index derived from analysis of this single progeny trial is based on the variables volume per acre, basal area increment, and crown length-to-width ratio. Expected gain from one generation of selection at age twelve will be 11.2 hundred cubic feet. This represents approximately fifty-five per cent improvement in volume yield, and an improvement of 0.81 standard deviations. Selection for volume per acre alone will give an improvement of only 2.8 hundred cubic feet, which is equivalent to thirteen per cent increase in yield and 0.20 standard deviations. Other selection indices based on crown variables predict substantial genetic gains of volume per acre, far in excess of that expected for volume alone.

Introducing economic criteria does not greatly modify either the index weights for the variables or the expected genetic advances. The weights and advances are slightly increased in most instances. This indicates genetic response is in an economically desirable direction. Economic objectives as determined in this thesis are therefore genetically practical. However, there is a need to develop better economic criteria for crown traits before they can be incorporated into an index.

The authenticity of the results is verified by the consistency of ranking of the families when the indices are tested on the trial. The families having narrow, multinodal crowns and moderate individual volume are ranked highest by all indices. Those with wide, heavily-branched crowns are ranked lowest even though they have moderate-to-high volume. The indices place greater emphasis on crown traits than on individual volume variables.

The selection index would be most useful for evaluating either family means or individual trees of a progeny trial. They could also be used for routine selection in the open plantation. The genetic and economic data would have to be more representative of the total population for general use. However, the use of the selection index should be encouraged. An index is soundly based on genetic information, and its application is easy and totally objective. It would require little effort on the part of tree breeders to build up a pool of information from a number of progeny trials, and from these data construct an accurate index applicable to a fairly wide range of selection conditions.

Crown traits are seen to play a significant part in the whole-tree concept. Their relatively high heritabilities will ensure rapid improvement in these traits which will result in higher quality wood. Their strong genetic correlations with productivity formed under competitive conditions and with productivity per unit area will produce a correlated improvement in yield. The ease with which crown traits can be measured in an immature stand makes these variables attractive parameters to assess in progeny trials. Breeding programmes must place more emphasis on evaluation of crown attributes to achieve maximum production of useable wood per tree and per acre.

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