haploid number of chromosomes (2n and 4n) and these were viable.

4. Pollen grains with more than the haploid number of chromosomes (2n and 4n) did not germinate on the media normally used for pines. Their viability was expressed on a medium consisting of 1% agar + 2% of saccharose and 0.01% of boric acid, at a temperature of 30° C and relative humidity of 96%.

5. Pollen tubes with 2n and 4n chromosomes reached "giant" sizes.

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Preliminary Observations on the Change With Age of the Heritability of Certain Wood Characters in Pinus radiata Clones

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Introduction

Wood characters have come to be regarded as important and necessary selection factors in tree improvement programmes and therefore it is essential to know how they are transmitted from parent to progeny. ,Qualitative descriptions of inheritance are far from adequate for this purpose and information may be more precisely presented by some unambiguous measure of the intensity of genetic control.

The most commonly used measure utilizes a ratio called heritability (LUSH, 1937), employed in either a broad or a narrow sense. Broad sense or gross heritabilities can be estimated following the examination of vegetatively propagated material since the genotypes of individuals are transmitted unchanged. Narrow sense heritabilities are determined using seedling material where non-additive genetic effects cannot be transferred from the parents to the progenies. Besides being used to measure expected progress resulting from selection, heritability has also been used to describe the "degree of rigidity of genetic control" of characters (MERGEN, 1960).

Several methods have been proposed for estimating heritabilities, but a commonly used approach separates the variance of a character into components attributable to different causes. The calculations may be based either on progeny means or on individual tree observations. However, few existing experiments are suitable for heritability studies and less than ideal material has had to be used in many of the studies conducted to date.

The heritability of wood characters changes with the age of the experimental material and different characters follow different trends (STERN, 1958, 1960; ZOBEL, 1964). It is useful to establish the form of the relationship of heritability with age for important wood characters. Heritabilities of wood characteristics derived from young trees might then be extrapolated to obtain estimates appropriate to harvest age. In addition, such patterns may assist towards an understanding of the mechanism of genetic control as applied to wood characters. Data used to calculate heritabilities could also be submitted to analyses of covariance to determine genetic correlations between selected pairs of characters. These correlations provide some indication of the change in one character due to a change in another as a result of selection.

The experimental material used for such an investigation should be old enough to provide a clear picture of any worth-while trends of heritability, and individual determinations s'hould not be subject to large standard errors. There are at least two clonal plantations in Australia which would satisfy the requirementc regarding age, and vegetatively propagated material eliminates any uncertainty in the relationship between progenies from a given parent group.

Mature clonal material of *Pinus radiata* was used to determine gross heritabilities at successive growth rings from the pith for ring width, percentage late wood, average tracheid length, basic density, and incidence of grain deviation from the tree axis.

Material

The specimens were obtained from a clonal plantation of Pinus *radiata* which had been established at Mt. Burr, South Australia, in 1940. The clones were planted in adjacent rows, or, in some instances pairs of rows, without replication, at a spacing of 2% m. between rows, and $2^{1}/_{8}$ m. between trees. They were propagated from cuttings taken from the same location within the parents and raised under the same methods and conditions, so that all the trees were of the same physiological age. The stand was silviculturally untreated apart from the pruning of dead limbs to a height of 2% m. The site was without appreciable slope, of practically uniform quality and located on a transitional, volcanic soil described as a coarse, sandy, valley type.

Originally 20 clones were planted, but 1 died and the remainder are represented by 12—30 trees in each case. From each of the 19 clones, 3 trees were chosen at random, within the limits imposed by avoiding trees of low vigour (resulting from early dead tops and competition).

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Experimental Procedure

The wood specimens were obtained by means of a modified plug-cutter (PAWSEY, unpublished, 1964), the particular cutter in use producing 35 mm. diameter cores extending from bark to bark and including the pith. Sampling was carried out midway between whorls of branches in the plane of the lean of the trees. It has been pointed out that sampling in even-aged stands should be carried out at such heights as to show the same number of growth rings in each specimen (RICHARDSON, 1961). In the present case a convenient sampling height resulted when this was chosen to be 22 complete rings. Before removal from the tree, the ends of each specimen were marked to show the direction of the tree axis. Specimens were stored in a refrigerator until required for examination.

The cores were divided into strips extending from bark to bark as follows. With the pith direction vertical, a strip, 7 mm. thick, was sawn from the top of each core and planed for use in the determination of ring width and percentage late wood. Vertical saw cuts were made through the remainder to separate a piece, 12 mm. wide, and containing the pith, for use in the measurement of grain deviation. One of the transverse surfaces of this piece was planed to serve as a datum relative to the marks showing the direction of the tree axis, so that angles of grain deviation were referred to this direction. The remains of the core provided material for the determination of basic density and average tracheid length.

Ring width, late wood width, average tracheid length and basic density were determined using material from the shorter of the two radii of each core, as this would normally be expected to contain the least amount of compression wood. Angles of grain deviation for individual growth rings in each specimen were expressed as the mean of values from both radii.

The procedure for the examination of the above-mentioned strips was similar to that outlined by NICHOLLS *et al.* (1963). The number of growth rings examined was deemed sufficient to enable representative trends of heritability to be established, *viz.* rings 2, 3, 5, 7, 9, 11, 14, 17 and 21 for each character, and additionally rings 4, 6 and 8 for grain inclination and rings 4, 6, 8, 10, 12, 13, 15, 16, 18 and 19 for basic density.

Results and Discussion

The mathematical model assumed for the analyses of data is: —

$$X_{ijk} = \mu + r_i + c_j + t_{jk} + (rc)_{ij} + (rt)_{ijk}$$

where X_{ijk} is the value for the i^{th} ring from the k^{th} tree of the j^{th} clone for a characteristic X,

μ is the population mean,

r_i is the effect of the i^{th} ring,

c_j is the effect of the j^{th} clone,

t_{jk} is the effect of the k^{th} tree in the j^{th} clone,

$(rc)_{ij}$ is the interaction effect of the i^{th} ring with the j^{th} clone,

$(rt)_{ijk}$ is the interaction effect of the i^{th} ring with the k^{th} tree in the j^{th} clone, and

c_j, $(rc)_{ji}$ and $(rt)_{ijk}$ are all assumed to be normally and independently distributed with means zero and variances σ_c^2, σ_t^2, σ_{rc}^2 and σ_{rt}^2 respectively.

Ring effects are assumed fixed, and therefore $\sum_i r_i = 0$; also $\sum_i (rc)_{ij} = 0$ and $\sum_i (rt)_{ijk} = 0$.

The sample contains n clones, q trees per clone and m rings per tree.

The analysis of variance for this mixed model is as follows:

Source of Variation	*D. F.*	*Expected Value of Mean Square*
Between clones	n-l	$m\sigma_t^2 + mq\sigma_c^2$
Trees within clones	n(q-l)	$m\sigma_t^2$
Rings	m-l	$\frac{m}{m-l}\sigma_{rt}^2 + \frac{mq}{m-l}\sigma_{rc}^2 + \frac{mq}{m-l}\sum_i r_i^2$
Rings × clones	(n-l) (m-l)	$\frac{m}{m-l}\sigma_{rt}^2 + \frac{mq}{m-l}\sigma_{rc}^2$
Rings × trees	n(m-l) (q-l)	$\frac{m}{m-l}\sigma_{rt}^2$

When each ring is considered separately, the analysis of variance becomes:

Between clones	n	$\sigma_t^2 + \sigma_{rt}^2 + q(\sigma_c^2 + \sigma_{rc}^2)$
Trees within clones	n(q-l)	$\sigma_t^2 + \sigma_{rt}^2$

The estimate of intra-class correlation is:

$$\frac{\sigma_c^2 + \sigma_{rc}^2}{\sigma_c^2 + \sigma_{rc}^2 + \sigma_t^2 + \sigma_{rt}^2}$$

In the case of the clonal material this is equivalent to gross heritability. This model may also be used to estimate components of covariance and hence the genetic correlation between two characters.

Figure 1 shows the trend of heritability with age for tracheid length, basic density and grain deviation.

It should be noted that the trends obtained using the estimates of variance components will apply only to the

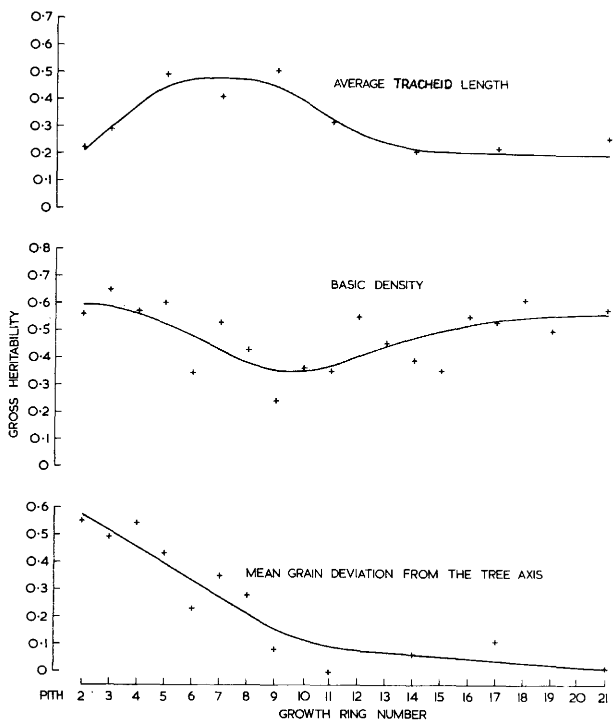

Figure 1. — Estimates of gross heritability for mean grain deviation from the tree axis, basic density, and average tracheid length for successive growth rings from the pith in *Pinus radiata* clonal material.

population under review, according to the conditions of the experiment, and for other populations and circumstances, different patterns of change might be found.

The five characters under review have shown markedly different behaviour patterns in the heritability estimates obtained with increasing age of material.

For ring width heritability values are small and are subject to comparatively large standard errors and no clear relationship with age is evident. Heritability estimates for percentage late wood are generally not significant, and again no trend with age is discernible. However, the great difficulty associated with accurately locating the early wood-late wood interface in growth rings of the present material detracts from the possibility of obtaining precise results for this character.

In the case of mean grain deviation, it can be seen from *Figure 1* that values follow a consistent pattern. Maximum heritability of 0.55 (S. E. 0.13) occurs close to the pith and is followed by a steady decrease with increasing age until estimates become insignificant at the ninth growth ring from the pith where a value of 0.08 (S. E. 0.15) was recorded. These results are consistent with the trend suggested by Zobel (1964).

Figure 1 also shows that heritability values for tracheid length are subject to a pattern of change with increasing age. Heritability increases from the pith outwards until a broad maximum of 0.5 (S. E. 0.13) is reached at about the fifth to the ninth ring from the pith and then declines to a value of 0.2 (S. E. 0.15) in subsequent growth rings.

The trend for the heritability of basic density shown in *Figure 1* is one of a decrease from a maximum of 0.6 (S. E. 0.11) near the pith until a minimum of 0.24 (S. E. 0.15) is reached at about the ninth growth ring from the pith followed by an increase in heritability to 0.6 (S. E. 0.12) with further increase in age.

None of the estimates depicted in *Figure 1* were subject to standard errors exceeding 0.15.

It is likely that several factors have been responsible for the observed trends in heritability.

During the period of time in which the wood for examination was being formed, the trees involved would have been subjected to both random and patterned environmental variation as a result of climatic conditions and of changing competition with other trees in the stand. Such changes could affect the variance components, and hence the heritability estimates.

It has been suggested (see, for example, Larson, 1964) that environment influences wood formation indirectly by affecting the vegetative growth of the crown, thus modifying the production of auxins which in turn regulate cell development. Therefore, results derived from radial specimens taken from a single level in the tree, may be affected by the changing relationship between the crown and the wood formed in successive years.

However, there is also the possibility of an inherent age factor. If it is assumed that continuously varying characters, such as those under review in the present study, are subject to polygenic control, it is possible that the expression of the genes will change with age. This could be due to the relative importance of different genes at different times, or due to a change in the dominance relations of the same genes at different times.

The sampling errors of genetic correlation coefficients calculated from analyses of variance and covariance have been discussed by Tallis (1959). He contends that the variance of the genetic correlation coefficient may be estimated from such analyses provided that the components of variance and covariance are bounded away from zero. In the present experiment, it can be shown that in only a few cases do the genetic components of variance fulfil this condition, and, for some of these, the genetic component of covariance between two characters is not significantly different from zero. Under these circumstances, and since the aim of this study is to discuss patterns of change with age, it is considered that there is little point in reporting the few genetic correlation coefficients where sampling errors can be estimated. On the other hand, to list all estimates of genetic correlation without regard to these errors could be misleading, especially since in some instances the estimate is greater than unity due to the large sampling errors of the variance or covariance components.

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Summary

Heritability estimates for ring width, percentage late wood, basic density, average tracheid length and incidence of grain inclination were obtained for selected growth rings from pith to bark following the examination of specimens from a 25-year-old clonal plantation of *Pinus radiata*. Systematic change with age was observed in the estimates for grain inclination, average tracheid length and basic density. The genetic correlation between characters is briefly discussed.

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