able reagent, causing complete spindle inhibition and repeatable chromosome contraction.


### Summary

Karyotypes were determined for six species of Abies using female gametophyte tissue. No specific differences were observad and it is felt that these rnay be obscured by differences due to position in the mitotic cycle and to method of measurement.

The Abies karyotype is characterized by having three chromosomes that are distinctly heterobrachial. Two additional chromosomes rnay or rnay not be heterobrachial.

Solutions of 1% and 0.5% colchicine and 0.002 M 8-hydroxyquinoline were compared for their effects on spindle inhibition and chromosome contraction in root tips. 8-hydroxyquinoline alone and in combination with colchicine proved unsuitable for use with Abies chromosomes. The optimum treatment appeared to be five hours in 1% colchicine. This resulted in complete inhibition of spindle formation and in 37% and 39% contraction of the shortest and longest chromosomes.

### Zusammenfassung

Titel der Arbeit: Karyotyp-*Analyse* bei Abies.

Von 6 Abies-Species wurden die Karyotypen am Gewebe des weiblichen Gametophyten festgestellt. Es wurden keine arteigenen Unterschiede beobachtet. Diese können aber auch infolge von Besonderheiten verborgen bleiben, die vom Mitosezyklus und der Meßmethode herrühren.

Der Abies-Karyotyp wird durch 3 Chromosomen charakterisiert, die distinkt heterdbrachial sind. Zwei weitere Chromosomen können zusätzlich manchmal heterobrachial sein.

Verglichen wurden nun die Effekte von 1% und 0,5% Colchicin und von 0,002 M 8-Hydroxychinolin auf die Spindelhemmung und auf die Chromosomenkontraktion in Wurzelspitzen. 8-Hydroxychinolin allein und in Kombination mit Colchicin war nicht geeignet für Abies-Chromosomen. Dagegen war eine 5stündige Behandlung mit 1% Colchicin optimal. Dabei ergab sich eine komplette Hemmung der Spindelbildung und eine Kontraktion von 37% bzw. 39% der kürzesten bzw. längsten Chromosomen.

### Résumé

Titre de l'article: Analyse des karyotypes de sapins.

On a déterminé les karyotypes de six espèces de sapins a partir des tissus du gametophyte femelle. On n'a remarqué aucune différence spécifique, mais on pense que celles-ci peuvent être masquees par des differences dues a la position dans le cycle mitotique et a la méthode de mesure.

Le karyotype du sapin est caractérisé par trois chromosomes qui sont nettement hétérobrachiaux. Deux autres chromosomes peuvent être hétérobrachiaux, mais pas toujours.

On a comparé les effets de solutions de colchicine a 1% et 0,5% et de l'hydroxyquinoline 0,002 M 8 sur l'inhibition du fuseau et la contraction des chromosomes dans les extrémités des racines. L'hydroxyquinoline 8, seule et combinée a la colchicine s'est révélée impropre pour les chromosomes de sapins. Le traitement optimum semble être cinq heures dans la colchicine à 1%. Ceci a entraîné l'inhibition totale de la formation du fuseau et une contraction a 37% et 39% des chromosomes les plus courts et les plus longs.


### Literature Cited


(1) KANEZAWA, R.: Polyploids appeared in twin seedlings of forest trees. *(Japanese with English Summary.)* Jour. Jap. For. Soc. 31: 22–24 (1949). — (2) KLAEHN, F. U., and WINIESKI, J. A.: Interspecific hybridization in the genus *Abies*. Silvae Genetica 11: 130–142 (1962). — (3) MEHRA, P. N., and KHOSHOO, T. N.: Cytology of conifers. I. Jour. Genet. 54: 155–180 (1956). — (4) MERGEN, F., and LESTER, D. T.: Microsporogenesis in *Abies*. Silvae Genetica 10: 146–156 (1961a). — (5) MERGEN, F., and LESTER, D. T.: Colchicine-induced polyploidy in *Abies*. For. Sci. 7: 314–319 (1961b). — (6) MERGEN, F., and NOVOTNY, H. M.: Squash technique for chromosome studies in pine needles and root tips of slash pine. For. Sci. 3: 56–60 (1957). — (7) SAX, K., and SAX, H. J.: Chromosome number and morphology in the conifers. Jour. Arnold Arb. 14: 356–375 (1933). — (8) SAYLOR, L. C.: A karyotypic analysis of selected species of *Pinus*. Silvae Genetica 10: 77–84 (1961). — (9) STÅLFELT, M. G.: The effect of oxyquinoline on protoplasmic viscosity. Appendix to TJIO and LEVAN, 1950. — (10) TJIO, J. H., and LEVAN, A.: Use of oxyquinoline in chromosome analysis. Anal. Estac. Exp. Aula Dei 2: 21-64 (1950).


# The Heritability of Wood Characteristics of Pinus radiata


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### Introduction

Selection for wood characteristics in tree improvement Programmes has been a feature of forest research during recent years and has stimulated widespread interest in the inheritance of woud properties.

Most of the studies have been based on species of the genus Pinus and this information has recently been summarized by ZOBEL (1961). He has warned of the confusion which rnay arise from quoting heritability results without indicating the methodused in the calculation, the age of trees examined and the eonditions of environment for which the estimates were obtained.

It is useful to report estimates of gains as well as heritabilities from an inheritance study, but values of expected improvement rnay be of little significance if the results are derived from experimental material which is young compared with the harvest age. This follows because of the changes in heritability of a wood property with age (ZOBEL, 1961), but it is not implied that inheritance studies conducted on young trees are not of great importance; in fact they rnay be the only ones available until they can be supplemented by results from more mature subjects. Furthermore it is prefenable to investigate a variety of properties in the material for examination so that genetic correlations between features rnay be calculated, as these too are of great interest in tree improvement work.


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## Material and Methods

The present investigation follows an earlier one in which gross or broad sense heritability values were determined on samples from clones and seedlings of *Pinus radiata* (Dadswell *et al.*, 1961). In it, estimates of narrow sense heritability have been derived by analysis of variance among open-pollinated groups of progeny of this same species. Some 495 trees from a 1952 planting have been examined, and determinations carried out for such wood characteristics as ring width, percentage late wood, percentage longitudinal shrinkage, average fibre length, basic density and spiral grain.

Sampling procedure in relation to between-tree comparison has been discussed recently for average fibre length (Nicholls and Dadswell, 1962) and spiral grain (Nicholls, 1963). For the precise comparison of wood properties in the case of an even-aged population, such as in the present study, it has been suggested that individual sampling heights be adjusted so that all specimens contain the same number of growth rings (Richardson, 1961). This requirement is complicated by the difficulty of establishing ring identification, but for the specimens involved it was met to the extent that ring counts between specimens varied only by one.

To carry out determinations of six wood features on 495 specimens was a time consuming task so that it was only practicable to examine one growth ring. For this the 1960-61 growth ring (seventh growth ring from the pith in most cases) was chosen because it was the last completely formed growth ring. However, in view of the large variation in heritability for ring width and spiral grain reported between rings 2—8 inclusive and rings 6, 7, 8 (Dadswell *et al.*, 1961), extra determinations for these two features were carried out on the 1957—58 growth ring (fourth ring from the pith). Thus heritability estimates and genetic correlations could be calculated for six features on the 1960—61 increment and for spiral grain and ring width in the case of the 1957—58 growth ring.

The specimens for examination were obtained from *Pinus radiata* trees growing in the Australian Capital Territory. The trees were sampled by the method of Brown (1958) at the mid-point of the internode closest to a nominal breast height, the actual height being varied so that each specimen contained seven or eight growth rings. Each specimen was approximately 2 cm wide and 7 cm deep, and extended from bark to bark through the pith in a north-south direction. However, if the tree was crooked at the point of sampling then the specimen was taken in the direction of the bend. As soon as it was removed from the tree, each piece was placed in water and kept immersed until needed for examination.

The stand which was sampled was planted in 1952, to test the rate of growth of open-pollinated seedling progenies from trees which had been selected on the basis of vigour, form and branching characteristics. With the exception of one, a hybrid between *P. radiata* and *P. attenuata*, the selected parent trees are typical examples of plantation-grown *P. radiata* and, as far as is known, are unrelated. The seed from the parent trees was obtained from open-pollinated cones belonging in almost all cases to two or more different crops.

The experimental plantation contains progeny from thirty-three of these selected trees. In each of five blocks the thirty-three progeny groups were randomly allocated to thirty-three plots or rows, the progeny from one parent being confined to a single twenty-tree row in each block. Specimens were taken from the first three trees in every plot, providing in all 495 specimens for examination. Though every effort is made in an experimental design of this nature to keep environmental variation to a minimum, small differences are often unavoidable. In the present case, after the plantation was laid out, one of the blocks was found to be noticeably moister than the other four.

## Determination of Wood Characteristics

The following measurements were carried out on green material from the 1960—61 increment in the shorter of the two radii of each specimen.

*Ring Width.* — This was measured using a low power lens in association with an engraved scale reading to 0.1 mm. The 1957—58 ring in the shorter radius was also measured.

*Percentage of Late Wood.* — The width of the late wood was measured using the above lens and scale, disregarding dense material in false rings.

*Longitudinal Shrinkage.* — This was determined on pieces 25 mm long and 6 mm wide with the grain direction parallel to the 25 mm side, taken from the late wood in each specimen. Shrinkage was referred to the oven-dry condition.

*Average Fibre Length.* — The last-formed late wood from the growth ring for examination was macerated in a mixture of equal quantities of 100 volume hydrogen peroxide and glacial acetic acid by heating in a boiling water bath for 2 hours. Freed fibres were washed well and sampled. In each case approximately fifty *whole* fibres taken at random were measured, using a projection microscope and a magnification of 40 diameters.

*Basic Density.* — This property (the ratio of oven-dry weight to green volume) was determined on the whole growth ring which had previously been treated with an alcohol-benzene mixture to remove the resinous infiltrates.

*Spiral Grain.* — The grain direction in the late wood of the 1960—61 and 1957—58 growth rings of each specimen was measured with respect to the pith direction.

## Results

The results of the various determinations were tabulated separately for the 1957—58 and 1960—61 growth rings. Care was taken to ensure the correct matching of growth rings using easily identifiable features in the 1955—56 and 1959—60 rings.

All results were submitted to statistical analysis to separate components of variance. For material which is propagated by sexual means, such as the progenies for examination in the present study, non-additive genetic variance caused by dominance and epistasis cannot be passed on to the next generation, so that the term heritability is used in the narrow sense. This is defined by Lush (1937) as the ratio of the additive genetic variance to the total phenotypic variance in the population:

*i. e.* narrow sense heritability $h^2 = \frac{\sigma_A^2}{\sigma_P^2}$

Variance components have been estimated from analyses of variance of the following form:

| Source | Degrees of Freedom | Expectation of Mean Squares |
|---|---|---|
| Between blocks (b) | 4 | |
| Between progeny groups (p) | 32 | $\sigma_w^2 + 3\sigma_{bp}^2 + 15\sigma_p^2$ |
| Interaction (b × p) | 128 | $\sigma_v^2 + 3\sigma_{bp}^2$ |
| Within plots (w) | 330 | $\sigma_w^2$ |

The environmental variance includes plot and block components and so is defined as $\sigma_w^2 + \sigma_{bp}^2$; the genetic component is $\sigma_p^2$. The method of estimating heritability for wind-pollinated progeny, however, will depend on the relationship between members of a progeny group. Attention has been drawn to this point by SQUILLACE *et al.* (1962) and VAN BUIJTENEN (1962). If the relationship is assumed to be half-sib, the estimate of heritability is given by:

$$h^2 = \frac{4\sigma_p^2}{\sigma_p^2 + \sigma_w^2 + \sigma_{bp}^2}$$

where $4\sigma_p^2$ is the estimate of the additive genetic variance, and $\sigma_p^2 + \sigma_w^2 + \sigma_{bp}^2$ is the estimate of phenotypic variance. However, consideration of pollen distribution patterns such as that obtained by COLWELL (1951) would indicate that the estimate of additive genetic variance should be modified because of the probability that a proportion of the within-group relationship will be full sib. The estimate of the additive genetic variance should be revised therefore, and will lie between $2\sigma_p^2$ and $4\sigma_p^2$.

Estimates of narrow sense heritability for the 1957—58 and 1960—61 growth rings are set out in *Table 1*. The values quoted are on the assumption of a half-sib relationship and will accordingly be reduced to some value between these figures and one half of them.

*Table 1* also tabulates gross heritability estimates previously obtained for the means of growth rings 6, 7, 8 from the pith (DADSWELL *et al.*, 1961) for comparison with the narrow sense heritabilities obtained for the 1960—61 growth ring (ring 7 from the pith).

*Table 2* sets out mean squares used in the analyses, and it is apparent from the variance ratios that there is a significant difference between blocks. This has already been mentioned and is explained on the grounds that one block was moister than the others. This has had some small effect on the results in that the interaction mean square is slightly larger than the within plot mean square, tending to increase the estimate of environmental variance compared to a uniform environment.

Analyses of covariance between the following pairs of properties were calculated:

Spiral grain — ring width,
Percentage late wood — basic density,
Ring width — basic density,
Fibre length — basic density.

From these, and the corresponding analyses of variance, estimates of genetic correlations were obtained but in no case was the correlation found to be significant.

*Table 1.* — Narrow sense heritability estimates for 1957—58 and 1960—61 growth rings together with gross heritability estimates reported by DADSWELL *et al.* (1961).

| Feature | Narrow Sense Heritability Estimates*) | | Gross Heritability Estimates | |
|---|---|---|---|---|
| | 1957-58 Growth Ring | 1960-61 Growth Ring | Based on Specimens from Clones | Based on Specimens from Seedlings |
| Ring width | 0.00 | 0.05 ns | .63** | .50 |
| Percentage late wood | | 0.14 ns | .72** | .45 |
| Average fibre length | | 0.28* | .81** | .86 |
| Basic density | | 0.16 ns | .75** | .53 |
| Longitudinal shrinkage | | 0.00 | .74** | NE |
| Spiral grain | 0.44** | 0.24** | .28 ns | NE |

*) calculated on the basis of half sib relationship within progeny groups
ns not significant
* significant at 5 per cent. level
** significant at 1 per cent. level
NE no estimate made

## Discussion of Results

It is to be stressed that heritability is a property of a population and of the environmental conditions pertaining to the individuals of that population. Therefore, the results are strictly speaking applicable only to the *P. radiata* trees which have been examined. However, some inferences may be drawn from these results which have a wider application, especially when viewed in conjunction with the results previously obtained from clones and seedlings grown in the same area (DADSWELL *et al.*, 1961).

Though it is known that the heritability of a wood property will change with age of tree (ZOBEL, 1961), the pattern of change for all characteristics is not known. ZOBEL surmised that spiral grain may show a decreasing heritability with increasing age of tree, and in fact this conjecture is supported by the present results, where the estimate for this feature has decreased from 0.44 (fourth ring from pith) to 0.24 (growth ring 7 from pith). This trend was also noticeable in the earlier work (DADSWELL *et al.*, 1961).

The value of 0.16 for the narrow sense heritability of basic density is of the same order as that previously recorded by FIELDING and BROWN (1960) who reported an estimate of 0.20 for determinations carried out on 6 year old open-pollinated *P. radiata* trees grown in the Australian Capital Territory.

The heritability estimate of 0.28 for average fibre length is low compared to the values obtained by GOGGANS (1962). He reported narrow sense estimates of 0.54 and 0.77 in the case of early wood fibre length and 0.97 and 0.85 for the heritability of late wood fibre length. His material for study was obtained from 8 year old open-pollinated *P. taeda* progenies which were laid out in a block layout rather than in rows and GOGGANS has referred to the fact that there were only two replications in his experimental design and the progenies were "growing under rather uni-

*Table 2.* — Mean squares for five wood features for two growth rings.

| Source | D.F. | Ring Width | | Per Cent. Late-wood | Average Fibre Length | Basic Density | Spiral Grain | |
|---|---|---|---|---|---|---|---|---|
| | | 1957-58 ring | 1960-61 ring | 1960-61 ring | 1960-61 ring | 1960-61 ring | 1957-58 ring | 1960-61 ring |
| Between blocks | 4 | 42.92 | 57.31 | 57.75 | 0.6106 | $16620 \times 10^{-6}$ | 29.98 | 20.16 |
| Between progeny groups | 32 | 4.17 | 5.38 | 11.68 | 0.2109 | $1980 \times 10^{-6}$ | 25.90 | 21.63 |
| Interaction | 128 | 4.36 | 4.68 | 7.82 | 0.1173 | $1291 \times 10^{-6}$ | 9.94 | 11.75 |
| Within plots | 330 | 2.92 | 2.90 | 6.34 | 0.0673 | $997 \times 10^{-6}$ | 8.05 | 9.53 |

form conditions". This tends to reduce the estimate of the environmental variance and inflate the estimate of heritability compared to conditions encountered in practice. The same arguments already presented in respect of relationships within progeny groups also apply to GOGGANS' results so that the true estimate of heritability may be reduced to one half the reported values.

The lack of significant genetic correlations between the pairs of features which were tested is also relevant to tree improvement work. Indications from this investigation suggest that selection for desirable features such as basic density and fibre length may be carried out independently of one another and without prejudice to rate of growth as expressed by ring width.

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**Summary**

Determinations of a number of wood characteristics have been carried out on specimens taken at approximately breast height from 10 year old open-pollinated progenies of *P. radiata*. Ring width, percentage late wood, fibre length, longitudinal shrinkage, basic density and spiral grain were determined for the seventh growth ring from the pith; ring width and spiral grain for the fourth growth ring.

From the results estimates of heritability in the narrow sense were derived by analysis of variance. Significant values were obtained for fibre length and spiral grain but estimates from open-pollinated progenies cannot be precisely evaluated. Genetic correlations between selected pairs of features were not found to be significant.

**Zusammenfassung**

Titel der Arbeit: *Die Heritabilität von Holzeigenschaften von Pinus radiata.*

An zufällig aus 10jährigen windbestäubten Nachkommenschaften genommenen Bäumen von *Pinus radiata* wurde etwa in Brusthöhe eine Reihe von Holzmerkmalen bestimmt. Ringbreite, Spätholzprozent, Faserlänge, Längsschwindung, Raumdichte und Drehwuchs wurden für den siebten Jahrring vom Mark bestimmt, Ringbreite und Drehwuchs auch für den vierten Jahrring.

Aus den Ergebnissen wurden mit der Varianzanalyse Schätzwerte für Heritabilitäten i. e. S. abgeleitet. Signifikante Werte für Faserlänge und Drehwuchs konnten erhalten werden, aber Schätzungen an windbestäubten Nachkommenschaften können nicht genau bewertet werden. Genetische Merkmalskorrelationen in herausgegriffenen Merkmalspaaren wurden als nicht signifikant befunden.

**Résumé**

Titre de l'article: *L'héritabilité des caractères du bois de Pinus radiata.*

La détermination d'un certain nombre de caractères du bois a été réalisée sur des échantillons prélevés approximativement à hauteur d'homme sur des descendances individuelles de *Pinus radiata* agées de 10 ans et obtenues par pollinisation libre. La largeur du cerne, le pourcentage de bois d'été, la longueur des fibres, le retrait longitudinal, la densité et la fibre torse ont été déterminés pour le septième cerne de croissance à partir du coeur, (la largeur des cernes et la fibre torse pour le quatrième cerne).

De ces résultats, on a tiré des estimations de l'héritabilité au sens strict par analyse de variance. On a obtenu des valeurs significatives pour la longueur des fibres et la fibre torse, mais on ne peut faire d'estimations précises pour les descendances obtenues par pollinisation libre. Les corrélations génétiques entre les couples de caractères choisis ne se sont pas révélées significatives.

**References**

BROWN, A. G.: The extraction of large samples from living trees. J. For. 56 (10): 764 (1958). — COLWELL, R. N.: The use of radioactive isotopes in determining spore distribution patterns. Amer. J. Bot. 38: 511—523 (1951). — DADSWELL, H. E., FIELDING, J. M., NICHOLLS, J. W. P., and BROWN, A. G.: Tree-to-tree variations and the gross heritability of wood characteristics of *Pinus radiata*. Tappi 44 (3): 174—179 (1961). — FIELDING, J. M., and BROWN, A. G.: Variations in the density of the wood of Monterey pine from tree to tree. For. and Timber Bur. Aust. Leaflet No. 77 (1960). — GOGGANS, J. F.: The correlation, variation and inheritance of wood properties in loblolly pine (*Pinus taeda* L.). Tech. Rept. 14, School of Forestry, N. C. State College, Raleigh (1962). — LARSON, P. R.: Effect of environment on the percentage of summer wood and specific gravity of slash pine. Yale Univ. School of For. Bull. No. 63 (1957). — LUSH, J. L.: Animal breeding plans. Iowa State College Press, Ames (1937). — NICHOLLS, J. W. P.: The relation of spiral grain to wood quality. Paper prepared for the Working Group on wood quality, IUFRO (1963). — NICHOLLS, J. W. P., and DADSWELL, H. E.: Tracheid length in *Pinus radiata* D. DON. C. S. I. R.O ., Aust., Div. For. Prod., Technol. Pap. No. 24 (1962). — RICHARDSON, S. D.: A biological basis for sampling in studies of wood properties. Tappi 44 (3): 170—173 (1961). — SQUILLACE, A. E., ECHOLS, R. M., and DORMAN, K. W.: Heritability of specific gravity and summerwood per cent. and relation to other factors in slash pine. Tappi 45 (7): 599—601 (1962). — VAN BUIJTENEN, J. P.: Heritability estimates of wood density in loblolly pines. Tappi 45 (7): 602—605 (1962). — ZOBEL, B.: Inheritance of wood properties in conifers. Silvae Genetica 10 (5): 65—96 (1961).