The Heritability of Fibre Characteristics and its Application to Wood Quality Improvement in Forest Trees[1]

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Introduction

The primary objectives of this paper are to summarize available data on the heritability of fibre characteristics in both conifers and arboraceous Angiosperms[3], to evaluate it with a view to assessing its present worth in wood quality improvement Programmes, and to draw attention to any deficiencies in present knowledge or practice which may be restricting a wider application of the results of heritability studies.

The fibre characteristics to be considered are cell length, cross-sectional dimensions and cell wall organization. Where pertinent, reference will be made to other features, the inheritance of which is known or believed to influence these.

Qualitative or quantitative evidence for the heritability of such traits in forest trees has been deduced, with varying degrees of validity, from numerous studies showing variation between taxonomic sections of genera, species, races, and trees; between F, hybrids and parents in inter-species crosses, diploids and polyploids, clones, and open- and control-pollinated progenies.

Although earlier work had justified the conclusion that certain fibre characteristics such as cell length were heritable, there was, as recently as 5 years ago, a real need for a quantitative indication of the degree to which these features are transmissible from parent to progeny and the gain to be excepted from selection for them (64).

Some such quantitative data are now available for all fibre characteristics mentioned previously. Unfortunately, the number of species covered is not large and, understandably, the amount of work done on the conifers has far exceeded that on hardwoods.

The available evidence is presented and evaluated in the first section of this paper. In the second section, the use of this information in wood quality improvement programmes is considered, factors influencing the heritability of fibre characteristics discussed, and attention drawn to apparent deficiencies affecting its application on a wider scale.

Evidence for the Inheritance of Fibre Characteristics

Fibre *Length*

Hardwoods. – Meyer-Uhlenried (37) found distinct differences in fibre length between sections of the genus *Populus*.

Pryor and Dadswell (47) reported that, in 11-year old F, hybrids from a *Eucalyptus* maideni X E. *rubida* cross, the fibre length was intermediate between that of the parents. with a degree of segregation evident in the F,.

Bamber and Humphreys (1) obtained some indication that seed source had an effect on fibre length in 5-year old *Eucalyptus* grandis (Hill) Maiden, but between-source differences were not statistically significant in their rather small sampling from six different seed-sources. In Tectona grandis L. f., there was significant between-tree variation in at least one of the four seed-sources studied by Kedharnath et al. (30).

The most conclusive proof of genetic influence on cell length in hardwoods has stemmed from the discovery that natural *Populus* triploids had superior fibre length to normal diploids, with remarkably similar increases recorded from different continents, *viz.*, 26 per cent. in American work (61), and 21 per cent. in a Russian report (28).

Van Buijtenen et al. (60) and Boyce and Kaeiser (6) have independently estimated gross heritability for average fibre length at breast height from clonal studies on normal Populus *tremuloides* Michx. and P. *deltoides* Bartr. respectively as 0.35 maximum and 0.30. From studies on triploid clonal material, Einspahr et *al.* (14) concluded that fibre length *and strength* therein appear to be under "moderate" genetic control.

In view of the obvious advantages of polyploids for fibre-length improvement in Populus, it is most encouraging to note that the triploids can be quite fertile and, since they are capable of transmitting certain of their superior morphological features to open-pollinated progeny (28), it seems reasonable to assume that similar transmission of additive genetic differences in respect of fibre length is also possible.

Conifers. – Differences between geographic races of *Pinus* pinaster Ait. in tracheid length in the last-formed late wood of individual rings aged from 1 to 23 years from pith have been reported by Nicholls et al. (43), but it was concluded that the differences between the four races they studied, although significant, were so small that racial selection would have little effect on progeny values in this case. Echols (13) found highly significant differences between fifteen provenances of 17-year old Pinus *sylvestris* L. grown in the same area for mid-band early wood and late wood tracheid length in the five last-formed rings.

Significant between-tree variation in tracheid length, generally interpreted as probably due to genetic influence, has been reported for quite a wide range of coniferc, including:

Tsuga *heterophylla* (Rafn.) Sarg. – 5th and later rings (63);

Pinus *radiata* D. Don – up to 25 per cent. improvement on the mean population curve for length in last-formed late wood at breast height possible in preselected morphologically "superior" trees from four populations (41);

P. radiata D. Don – initial and final length in seedlings less than 1-year old from one open-pollinated parent (23);

Pinus serotina – mean length for the late wood of rings 20 to 30 inclusive (35);

Araucaria cunninghamii Ait. – initial length, "final" length at 28 years from pith, and rate of increase in length from pith outwards (53);

Pinus *caribaea* Morelet – initial length, mean length for the pith to bark radial strip, average length at "maturity",

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[3] Hereafter referred to as hardwoods in this paper.

age and distance from pith at which mature length was attained, in 26-year old morphologically superior stems (51);

Pinus elliottii Engelm. — length in the first ring from pith in branches from the top whorl (29);

P. taeda L. — (29, 69); and

P. pinaster Ait. — last-formed late wood of rings 1 to 23 within a race (43).

Other examples are quoted in an excellent review by Goggans (17).

Greene and Carmon (21) demonstrated significant differences between clones of *Pinus echinata* Mill. for early wood tracheid length of first-order branches from the current year's growth and, from a study of seven parents and 8-year old open- and control-pollinated *P. elliottii* progenies, Echols (12) concluded that late wood tracheid length appears to be under rigid genetic control, governed by a multiple gene series. Further work on *P. elliottii* and *P. taeda* by Jackson and Greene (29), using progenies from open pollination and intra- and inter-species crosses, led them to infer that tracheid length was influenced more by the female than the male parent.

Quantitative gross heritability estimates (H^2) derived from clonal material, and narrow-sense estimates (h^2) are now available for the following species:

	H^2	h^2
Pinus radiata D. Don. —		
Using two trees from twenty-two 12-year old clones and twenty-nine adjacent 12-year old seedling trees of unknown seed-source to obtain two estimates; samples at approximately breast height (9):		
average tracheid length, last-formed late wood —		
combined values rings 2—8, clones	0.73**	
combined values rings 6—8, clones	0.81**	
combined values rings 2—8, clones and seedlings	0.83	
combined values rings 6—8, clones and seedlings	0.86	
Using 10-year old open-pollinated progenies of thirty-three morphologically preselected parents × five blocks × three trees (=495 trees), samples approximately breast height (42):		
tracheid length, last-formed late wood, 7th ring (± 1 year), one radius		0.28* (SE/0.13)
Pinus elliottii Engelm. —		
Using thirty-nine 4 to 6-year old clones × 5 to 10 ramets = 258 grafts (67):		
tracheid length, late wood, 3rd ring	0.56	
Using 11-year old open-pollinated progenies of sixteen morphologically preselected parents × four blocks × two trees = 128 trees; equal number of rings (10 in all samples (over 2 ft. 6 in. to 4 ft. 6 in. level); 'A' radius is that estimated to contain least compression wood, 'B' the opposite radius (54):		
average initial tracheid length (first-formed secondary xylem), A+B radii		0.00
mean length, whole of ring 1, A+B radii		0.60* (SE/0.35)
tracheid length, last-formed late wood, ring 3, A radius only		0.48* (SE/0.33)
tracheid length, last-formed late wood, ring 5, A radius		0.38** (SE/0.30)
tracheid length, last-formed late wood, ring 7, A radius		0.46* (SE/0.32)
tracheid length, last-formed late wood, ring 9, A radius		0.43^{ns} (SE/0.32)
average length, last-formed late wood, rings 3, 5, 7 and 9A		0.60** (SE/0.35)
average length, last-formed late wood, rings 3−9A + mean length ring 1A+B		0.59** (SE/0.35)
mean tracheid length for first 5 rings (composite strip maceration whole-rings 1—5A+B)		0.13^{ns} (SE/0.24)
mean length for first 10 rings, same basis		0.16^{ns} (SE/0.25)
Pinus taeda L. —		
From two open-pollinated trials in different areas; one (L) using 7-year old progenies of six morphologically preselected parents × two reps. × two plots × five trees = 120 trees; the other (G) using 8-year old progenies of eight parents × two reps. × two plots × eight trees = 256 trees; sampled at breast height (18, 19):		
tracheid length, late wood, last (5th) ring, area L		0.97
tracheid length, late wood last (6th) ring, area G		0.85
tracheid length, early wood, last (5th) ring, area L		0.54
tracheid length, early wood, last (6th) ring, area G		0.77

* = significant at the 95 per cent. level
** = significant at the 99 per cent. level.
ns = non-significant at the 95 per cent. level.
SE = magnitude of standard error of the estimate.

Fibre Cross-Sectional Dimensions

Hardwoods. — The only direct evidence known to the author for genetic influence on fibre cross-sectional dimensions in hardwoods is that presented by van Buijtenen *et al.* (61), who found that, in *Populus tremuloides* Michx., the fibre-tracheid diameter was 10 per cent. greater in triploids (3n) than diploids (2n). They detected little or no difference in fibre-tracheid wall thickness between 3n and 2n material.

However, indirect indications of inheritance of such characteristics could be inferred from basic density data, since basic density is determined by cell diameter and wall thickness to a considerable degree, although the proportion of fibrous to non-fibrous elements, chemical composition of the cell wall, and deposits in conductive and storage elements undoubtedly make such an inference much less valid in hardwoods than conifers.

Basic density has been found to be intermediate between the parents and subject to genetic control in inter-species hybrid crosses (46, 47); and significantly different between seed-sources within a species (1) in *Eucalyptus.* Although clonal variation has been noted in triploid *Populus,* it was considered to be under weaker genetic control than fibre length in one study (14).

Conifers. — As in the case of hardwoods, inheritance of fibre cross-sectional dimensions has, until quite recently been generally assumed rather than demonstrated, admittedly with more justification in this instance because of the obvious causal relationship between cell cross-sectional geometry and percentage late wood and the strong influence of both as determinants of basic density with relative freedom from other confounding factors as compared with hardwoods.

Variation between races, seed-sources, clones, progenies and trees in percentage late wood and/or basic density must be indicative of some accompanying degree of variation in cell transverse dimensions. The documented evidence for heritability of basic density and percentage late wood is fairly convincing (9, 13, 17, 19, 24, 35, 42, 43, 51, 56, 59, 67, 70), despite a great range in magnitude of any quantitative estimates reported.

The earliest direct evidence of genetic control of transverse dimensions seems to be that of CHOWDHURY (8), who found the tracheid tangential diameter and wall thickness of a hybrid larch to be intermediate between those of the parents.

ZOBEL *et al.* (69) reported considerable between-tree variation in tracheid width and wall thickness in *Pinus taeda* L. In unpublished work, the present author has observed appreciable between-tree variation in mean radial diameter of the early wood, late wood, and "whole-ring" tracheids in the last-formed ring of even-aged 29 to 31-year old *P. elliottii* ENGELM. and *P. taeda* L. over three successive years on the same site.

GOGGANS (17) states that a very large amount of between-tree variation has been found in the pattern of variation in cell cross-sectional dimensions and, in the most comprehensive study yet seen on the inheritance of wood properties, presents the only quantitative estimates of heritability of transverse dimensions located. The following narrow-sense estimates were derived for *Pinus taeda* L. from the two open-pollinated trials (L and G) from which tracheid-length data were quoted previously in this paper (18, 19). As in that case, *estimates are for the last ring,* rings 5 and 6 from pith respectively from areas L and G.

Characteristic		h^2	
		Area L	Area G
Double-wall thickness	late wood	0.84	NC
	early wood	0.13	NC
Radial lumen diameter	late wood	0.44	0.31
	early wood	0.59	0.68
Tracheid radial width	late wood	0.81	NC
	early wood	0.76	0.65
Tracheid tangential width	late wood	0.59	0.27
	early wood	0.80	0.49
Ratio of double-wall thickness to cell radial width	late wood	NC	0.72
	early wood	0.15	0.67

NC = not calculable.

Cell Wall Organization

Fibrillar and microfibrillar (micellar) angle of orientation in the middle layer of the secondary wall of coniferous fibres seems to be the only cell wall structural feature considered in relation to possible genetic control of fibre characteristics and very little work has been done on this, despite the conclusions of PILLOW *et al.* (45) and ZOBEL (66) that there is a need for such information.

So far as is known, no evidence for inheritance of fibrillar orientation in hardwoods has been reported.

HILLER (25) inferred that genetic factors may directly or indirectly influence fibril angle in *Pinus elliottii.* ZOBEL (64) quotes CALLAHAM (7) as having reported that its heritability is fairly high.

SMITH (53) found significant between-tree variation in (i) "final" micellar angle, (ii) rate of decrease in angle with distance from pith, and (iii) the relationship between micellar angle and cell length, but not in "initial" angle in even-aged 28-year old *Araucaria cunninghamii* from the same area.

In even-aged 26-year old *Pinus caribaea* MORELET, SCHMIDT and SMITH (51) determined significant differences between trees in mean micellar angle for a radius and in the micellar angle/tracheid length relationship, but again not in "initial" angle.

As far as is known, the only quantitative estimates of heritability of micellar angle calculated are the following, derived by SMITH and MOORE (54) for *Pinus elliottii* ENGELM., using the 11-year old open-pollinated progenies of sixteen parents for which tracheid length estimates were quoted previously. These are, of course, narrow-sense estimates. The data were derived from X-ray diffraction analysis of the *last-formed late wood of spaced rings* across two opposite radii A and B, except for "initial" angle, which was for the first-formed secondary xylem in ring 1: —

	h^2	
Initial micellar angle		
A radius (that estimated to contain least compression wood)	0.11ns	(±0.23)
B radius (opposite to 'A').	0.00	
Average initial angle, A+B radii	0.00	
Micellar angle ring 1A	0.09ns	(±0.23)
ring 1B	0.00	
Average angle, ring 1A+B	0.00	
Micellar angle ring 3A	0.66*	(±0.36)
ring 5A	0.93**	(±0.41)
ring 7A	0.69**	(±0.37)
ring 9A	0.88***	(±0.40)
Average angle		
first 5 rings A (1, 3, 5)	0.54**	(±0.34)
first 5 rings B (1, 3, 5)	0.00	
first 5 rings A+B (1, 3, 5)	0.48*	(±0.33)
second 5 rings A (7, 9, 10)	0.85***	(±0.40)
second 5 rings B (7, 9, 10)	0.49*	(±0.33)
second 5 rings A+B (7, 9, 10)	0.90***	(±0.40)
rings 3—9A (3, 5, 7, 9)	1.02***	(±0.42)
first 10 rings A (1, 3, 5, 7, 9, 10)	0.86***	(±0.40)
first 10 rings B (1, 3, 5, 7, 9, 10)	0.36ns	(±0.30)
first 10 rings A+B (1, 3, 5, 7, 9, 10)	0.88**	(±0.42)

* = significant at the 95 per cent. level.
** = significant at the 99 per cent. level.
*** = significant at the 99.9 per cent. level.
ns = non-significant.
± = the magnitude of the standard error of the estimate.

Evaluation of the Evidence

Hardwoods. — Despite the meagre information available, it seems reasonable to infer for hardwoods in general that at least fibre length and diameter are under genetic control. Improvement in these characteristics can be expected from controlled crosses between compatible species, from selection of "superior" seed-sources and individual parents, and, in *Populus*, by the selection of superior triploids and diploids for use in breeding programmes.

Data on the heritability of wall thickness are inconclusive since, although one diploid/triploid comparison in *Populus* showed little or no difference for this trait, some indication of possible genetic control could be inferred from indirect evidence for transmission of the complex phenotypic characteristic, basic density.

The gross heritability of fibre length in normal diploid *Populus* seems to be of the order of 30 to 35 per cent. but, since this includes an unestimated non-additive genetic component, the amount of additive genetic variance, from which expected gains through breeding are computable, would be less than this. Higher gains should be attainable by the use of triploid material in this genus, as (i) this has an apparent 20 to 25 per cent. advantage over diploids in fibre length, (ii) the trait is still under "moderate" genetic control within 3n stock, and (iii) the triploids can be quite fertile and, by inference from data on morphological features, capable of transmitting additive genetic components of variance to pollinated progenies.

No quantitative heritability estimates for cross-sectional dimension have been seen, but, in *Populus*, fibre diameter has been stated to be 10 per cent. greater in triploids than in normal diploids. On this slender basis, selection for fibre diameter could, perhaps, be expected to be about one-half as effective as for fibre length.

To the author's knowledge, the inheritance of cell wall organization in hardwoods has not yet been investigated.

Conifers. — Tracheid Length: Considerable progress has been made in establishing the heritability of tracheid length but the proposition of a generalized conclusion is complicated by the wide range of phenotypic expressions of this basic characteristic investigated.

The results of numerous studies suggest genetic control of tracheid length in the first ring of first-order branches; initial length in the first-formed secondary xylem of stems; length in segments of individual rings of varying age, such as last-formed late wood, mid-band or whole-band early wood or late wood; mean length for whole rings; and average or mean length for multiple-ring series. The rate of increase in tracheid length, "mature" length, and age and distance from pith for attainment of "mature" length also appear subject to genetic influence.

However, the degree of heritability of these characteristics has, in several cases, not been demonstrated at all and, in others, has been shown to be quite variable within and between species. Quantitative estimates, in a few cases, have not sustained the earlier promise of qualitative studies. Although initial length in the first-formed secondary xylem has been found to differ significantly between trees in several species, its narrow-sense heritability (h^2) has been calculated as 0.00 in one study on *Pinus elliottii* (54), suggesting possible predominance of intra- and/or extra-tree environmental factors over any genetic influence on this characteristic. At the same time, mean length for the first ring in the same study seems to be quite heritable ($h^2 = 0.60$*).

Late wood cell length in individual rings 3, 5, 6, 7, and 9 appears to be moderately to highly heritable (0.28* to 0.97) from h^2 estimates for *P. radiata, P. elliottii* and *P. taeda.* Between-species differences in the degree of additive genetic control could possibly be construed here and there is some suggestion of stronger influence on late wood than early wood length in Goggan's results (18, 19) even though the latter is still quite highly heritable.

The effect of averaging individual ring data and composite maceration of whole strips to determine the heritability of average or mean length from single values for a multiple-ring series is most interesting. Averaging data from a series of rings gave a higher estimate (0.60**), compared with inidividual ring estimates from the same data ranging from 0.38** to 0.48* for the ring-series 3 to 9 in *P. elliottii* (54). The high gross estimates (0.73** to 0.86) for the ring series 2 to 8 and 6 to 8 in *P. radiata* (9) were also determined in this manner. On the other hand, the use of single mean values from composite maceration of thin diametral strips gave greatly reduced estimates in *P. elliottii* (54) of 0.13^{ns} and 0.16^{ns} for the first five and first ten rings respectively, using exactly the same specimens and a method of measurement which had a calculated accuracy of ± 4 per cent. This tends to complicate evaluation of the available information in terms of the degree of improvement to be expected in *mean* tracheid length through selection and this problem will be further discussed in the second Section.

However, the weight of evidence indicates that the prospects for modification of late wood and early wood tracheid length within individual rings over at least the first 9 years' growth and mean length for the first whole ring should be moderately to quite good, through selection of superior provenances or trees, on the basis of Zobel's (65) statement that h^2 values of 0.50 or more would yield rapid gains. Prospects for improvement in initial (first-formed secondary xylem) cell length seem poor. The potentiality for modification of mean cell length for a multiple-ring series should be quite high, but this last assessment for a most important feature requires checking in further studies in which composite-strip and averaged-segmental data are used to derive comparative estimates.

Conifers. — Tracheid Cross-Sectional Dimensions: Although much less work has been done to investigate the inheritance of cross-sectional dimensions other than by an indirect approach through studies on percentage late wood and basic density, there is sufficient information available to justify the conclusion that individual geometrical components and the pattern of variation in transverse dimensions are under genetic control and capable of modification through racial and superior-tree selection in a number of species.

From the only study seen in which quantitative estimates of additive genetic variance have been computed for specific dimensions (18, 19), it seems that the prospects for modification within individual early rings through selection could be relatively good for early wood radial and tangential cell width and radial lumen diameter; moderate for late wood radial and tangential cell width and wall thickness, and early wood and late wood wall thickness/radial cell width ratio; promising for late wood radial lumen diameter; and relatively poor for early wood wall thickness. h^2 values for the individual characteristics were extremely variable but quite high in many cases, ranging up to 0.84.

No estimates are available for characteristics in rings older than 6 years and any assumption that calculated heritabilities and relative assessments of prospects for modification will be similar in later rings or for multiple-ring strips, is as yet unjustified.

Conifers. — Cell-Wall Organization: In spite of the very small amount of information on the inheritance of cell wall organization, it appears that genetic factors operate to influence micellar angle and the rate of decrease in angle with age or distance from pith.

Narrow-sense heritability estimates recently calculated for micellar angle in *Pinus elliottii* (54) confirm an earlier report (7) that its heritability is fairly high. Results of the former study indicate that moderate to rapid improvement in last-formed late wood micellar angle in individual rings aged 3 to 9 years from pith and average angle for the first 5 and 10 years can be expected from the selection of superior trees for use in breeding. h^2 values were, in general, higher than for most other wood characteristics studied simultaneously and ranged from 0.48* to 1.02**.

Little or no improvement in micellar angle in first-formed secondary xylem or first-ring late wood seems feasible.

The heritability of micellar angle is reduced, often to a very large degree, by relatively higher incidence of compression wood if only one radius is sampled, but the presence of compression wood in study material has no significant effect on estimates if pooled data from two opposite radii are used.

There is some indication of increase in heritability of average micellar angle with age from pith, from 0.00 in the first ring to 0.48* for the first five and 0.88** for the first ten, but any such inference should be drawn with caution because the inflatory effect of averaging individual ring values to derive single mean values for calculation of estimates, is again apparent. Attention has already been drawn to this peculiarity in relation to tracheid length.

The Application of Fibre Characteristic Heritability in Wood Quality Improvement

Tree improvement programmes have now been actively pursued in several countries for many years but, in the author's opinion, knowledge gained concerning the heritability of wood features in general, and fibre characteristics in particular, has been capable of only limited application in many current breeding programmes. Quantitative information is needed on the heritability of (i) all fibre characteristics in hardwoods to supplement the available data on fibre length in *Populus,* and (ii) mature tracheid length and age to maturity in conifers. More data are required to check existing evidence for the heritability of initial, whole-ring and strip-mean tracheid length, cross-sectional dimensions and cell-wall organization.

In concurrence with Zobel's (64) and Larson's (33) recommendations, it is agreed that economic factors justify stressing improvement in vigour, stem form, branching characteristics and disease resistance, and the acceptance of wood quality factors as secondary selection criteria. This is apparently almost universal practice in forest tree breeding and is considered the most prudent approach.

Consequently, it is fortunate that the variation in wood properties between preselected, morphologically superior trees at least approaches that of the species in general and that high-rating wood types are represented in the former (64). Much of the quantitative heritability information presented in the first Section was derived from clones or progenies from preselected parents and is, thus, especially valuable when wood quality improvement has to be effected by selection from this very small proportion of the original population.

The establishment of clonal seed orchards is the most popular approach to tree improvement and, where wood quality has been considered with other selection criteria, involves assessment and ranking on the basis of wood properties known or believed to influence it.

Comparative Sampling

Non-destructive testing of selected trees is highly desirable and probably essential as a safeguard against possible loss of superior breeding stock through initial or delayed failure of grafts. Single-level sampling has been considered a necessity for economic reasons and breast-height level generally accepted as satisfactorily representing the whole stem on the basis of numerous studies showing highly significant correlations between lower-stem and whole-stem values for several wood characteristics (15, 16, 58, 62). Nevertheless, the magnitude of the correlation coefficients indicates that, in some cases, a relatively small proportion of whole-stem variation may be accounted for by breast-high variation; in one study (15), as little as 25 per cent. for fibre length and not much over 50 per cent. for percentage late wood and basic density (transverse cell dimension constructs).

Furthermore, the method of sampling must be considered. For most characteristics it is considered that single-radius core or strip data are inadequate to compensate for circumferential variation but pooled data from two samples from opposite radii should yield sufficient information to represent the breast-high disc (18).

Consequently, unless or until higher degrees of relationship between lower-stem and whole-stem values are demonstrated, use of the former in the selection of trees with superior fibre characteristics should be regarded as giving a preliminary assessment to be checked by later sampling from higher levels and using pooled within-stem data in reassessment of tree ratings. However, extended check sampling is proposed merely as a desirable precautionary measure and should not delay the use of fibre or other wood characteristics as selection criteria in seed orchard establishment. There is at present no reason to believe that initial ratings would be altered.

Selection of Superior Phenotypes

The author has no detailed knowledge of the actual methods used in other countries in selection for superior fibre traits or other wood quality indicators or of the weight given to particular features. In Australia, some workers (*e. g.* 40) have used the preselected population mean pith to bark trend line as a general basic standard, which usually results in acceptance of about 50 per cent. of the candidate trees. In such cases, above average fibre length and above- or below-average basic density (depending on desired modification) have been the main criteria used, with certain others being similarly evaluated in subjective summations of overall quality and with excessive grain deviation, in particular, being considered as a disqualifying feature.

An objective ranking technique using a combination of trend lines and strip means, advocated and demonstrated by Schmidt and Smith (51), has been modified and is now used in Queensland. It sets minimum desired scores for each characteristic and summation generally within the upper two-thirds of the preselected population points range and is aimed, for the present, at ensuring that heritable wood characteristics in initial seed orchard representatives shall be of satisfactory, rather than superior, standard. High mean tracheid length, low average micellar angle, early maturity of both length and angle, maximum cell length and minimum angle have been awarded points for summation with those for other wood characteristics. The ultimate objective is to continue selection until seed orchards can be established using morphologically superior trees all with all wood characteristics and summations scoring in the upper third of the population range. In *Araucaria cunninghamii,* only 7 per cent. of the trees examined to date fall in this category, 16 per cent. in the upper half of that range, and 33 per cent. in the upper two-thirds.

All basic characteristics have been given equivalent weight except for "spiral grain" and the relatively low percentage of candidates rated by this method in the upper half of the range compared with the previous method quoted, confirms the well-known fact that selection becomes easier as the number of traits in which simultaneous improvement is attempted, is decreased. Nevertheless, it is believed that maintenance of initial acceptable standards for all characteristics with progressive improvement in each in subsequent orchards, as superior trees are located, is safer than selection for superiority in some traits with the attendant risk of introducing stock markedly inferior in other features and possibly reducing general wood quality standards, especially in the absence of workable information on genetic correlations between characteristics in the population under consideration.

The only application of genetics in selections by either method has been the knowledge that the characteristics used are heritable. Lack of authoritative information as to relative degrees of heritability and possible genetic correlations within and between wood and morphological features have precluded weighting and/or elimination of certain criteria to develop a more satisfactory selection index.

This essential information is now being obtained for some species in certain areas and will undoubtedly be applied as it becomes available, but it is of local value only, except in so far as it stimulates workers elsewhere to test the material on which they are working for comparable results. Estimates of genetic variance and correlation are applicable only to specific populations and environmental conditions and must be calculated for each population and environment within which improvement is attempted.

Interrelation of Morphological and Wood Quality Selection Criteria

It is important to know whether preselection of parental stock on other bases has had an effect on fibre or other wood characteristics in which modification may be desired. A comparison of selected parent and unselected population means gives some indication, but estimation and evaluation of genetic correlations between the preselected features and wood properties is a much more useful means of ascertaining whether there is genetic antagonism between two desired traits and to what degree. Regrettably, little authoritative work seems to have been done in either field.

DYSON (11) in "plus"/norm-tree comparisons in *Pinus radiata* and *P. patula,* found no significant differences for last-formed late wood tracheid length but consistently lower whole-ring basic density (and, by inference, modified cell cross-sectional dimensions) in the more vigorous preselected trees; despite the latter, the "plus" trees yielded more wood by weight over the same period of growth.

NICHOLLS *et al.* (42) suggested, from non-significance of genetic correlations calculated for 7th ring characteristics in *Pinus radiata,* that selection for late wood tracheid length and basic density might be carried out independently and without prejudice to growth rate. On the other hand, ZOBEL *et al.* (70) predicted slow progress if improvement in both growth rate and tracheid length were attempted in *Pinus taeda.* These proposals may not be contradictory because of possible differences between species and could serve to emphasize the necessity for local testing.

GOGGANS' (18, 19) recent work has done much to indicate the phenotypic and genotypic relationships between tracheid length, cross-sectional dimensions, percentage late wood and basic density in young *Pinus taeda* and to illustrate how these can vary in sign and magnitude between areas. Detailed examination of his results is strongly recommended. He has been cautious in interpreting his data and emphasizes that undue precision be not accorded to the figures reported. However, they may be more meaningful than his cautionary remarks suggest because it seems a remarkable coincidence that calculated phenotypic and genotypic correlations for 10-year old *Pinus elliottii* (38) are surprisingly similar in sign and magnitude to those for comparable pairs of characteristics reported by him.

Of possibly even greater importance in the use of morphological preselections for breeding, is the necessity to establish the effects of changes in vigour and stem or branch characteristics on desired changes in wood features. Genetic correlations may show that certain external and internal objectives will not permit simultaneous movement in the desired direction and a compromise may be necessary. They could be of great value in locating external indicators of internal features which, if sufficiently highly correlated genetically in the required direction, could safely permit less easily measured wood characteristics to be deleted in assessments.

The amount of work done in this field is negligible and information is badly needed. MOORE and SMITH (38) expect to present phenotypic, genotypic and environmental correlations between morphological and wood (including fibre) selection criteria in 11-year old *Pinus elliottii* shortly.

It is evident from GOGGANS' work that modification of a particular feature may affect selection for several other genotypically correlated characteristics and it should be possible to segregate the quantitative effect selection for the primary trait would have on each of the others, through calculation of multiple genotypic correlations. So far as is known, this has not yet been attempted and would be a profitable objective in future work.

Determination and Interpretation of Heritability Estimates

Close examination of the information presented in the first Section of this paper also points to the necessity for critical consideration of methods used in the calculation of heritability estimates and their interpretation for use in improvement programmes.

Many of the estimates derived have been for characteristics in individual rings or segments thereof. While these are useful in indicating which wood quality indicators may be heritable and to what degree, those responsible for forest management must be convinced that selection for any trait is justifiable in terms of improvement on an economic basis. For example, it is obviously of little advantage to know that fibre characteristics can be modified in the desired direction in the last-formed late wood of particular rings if the stem-mean values for those characteristics are unalterable. Logically, it must be demonstrated that fibre and other traits influencing wood quality can be improved in the whole marketable product, not just portions thereof which it is impossible to market separately.

Consequently, either significant genotypic correlations of appreciable magnitude must be determined between segmental values and at least whole-diameter strip values or, alternatively, heritability of the latter separately estimated for practical application. Phenotypic correlations, however high, are not considered good enough for breeding work because of the unknown environmental component involved.

Larson (32) has pointed out the necessity to distinguish between short-term and long-term environmental effects on fibre cross-sectional dimension constructs such as percentage late wood and has also indicated that physiological crown genotypic variants obviously exist (31) whose auxins regulate tracheid diameter and the photosynthates that contribute to cell wall development (34) through probably heritable differences in length of growing season or more subtle physiological processes associated with crown growth (27, 32, 48, 52). Bannan (4) has also found wide between-tree differences in the rate of pseudo-transverse anticlinal division in the cambium. His earlier work has clearly shown the influence of this on fibre length and, since he and other workers referred to in his publication (4) have provided evidence that unidirectional pseudo-transverse divisions are involved in the development of spiral grain, inheritance of this micro-characteristic could be a fundamental factor influencing the heritability of grosser wood characteristics.

Larson (33) has previously drawn attention to the pitfalls in deducing general information from small fractions of a ring or other sample because, as he rightly cautions, the finer one subdivides growth increment for analysis, the less satisfactory is the relationship with environmental factors which strongly influence fibre dimensions within a tree within the limitations of its genetic potential. The primary influence of crown development on activity of the cambium and the characteristics of its derivatives, and the existence of crown and physiological genotypic variants with variable responses to a given set of environmental conditions on short-term and long-term bases, make it essential to measure fibre and other wood characteristics over growth periods long enough to allow full interaction of genotype and environment if heritability estimates are to be of practical value.

Fibre length has most commonly been measured in "last-formed late wood". This has been stated (41) to be justified by small variation within late wood, ease of duplication in other rings for comparison and inferred representation of whole-ring values. Close examination of published data for hardwoods and conifers *(e. g.* 5, 41) does not confirm its representative value nor even that it consistently gives a measure of maximum length within individual rings; the latter depends on within-ring variation in anticlinal division rate and is influenced by age and growth rate (2, 3, 4). Inchbold-Stevens (26) concluded there are so many inexplicable variations that it is better to take a mixed sample from the whole ring.

The so-called last-formed late wood constitutes an extremely variable proportion of each late wood band or ring in a pith to bark series. When related to published within-ring trends, this sheds doubt on its whole-ring or maximum-length representative value. For a 23-ring series in *Pinus elliottii,* it has been found (55) that last-formed late wood values may be higher or lower than mean ring values, "residue of late wood" consistently higher and early wood consistently lower, particularly for individual rings beyond 10 years, and that the mean of the differences (ignoring sign) between last-formed late wood and whole-ring values differs significantly from zero.

This recent work indicates that, in order to segregate genetic and environmental components contributing to between-tree variation in fibre length on a long-term basis, it would be most desirable to use mixed samples from multiple whole-ring series. Multiple-ring mean values are not difficult to determine for a single composite sample for tracheid length, percentage late wood, ring width and basic density but, by present methods, it seems mean cell cross-sectional dimensions, micellar angle and spiral grain may be obtainable only by averaging segmental values. with the attendant risk of inflating heritability estimates, as indicated earlier. Further investigation may result in the derivation of correction factors or the development of new measurement techniques which would overcome this problem, and seems warranted.

Richardson (49) stresses the desirability of using specimens containing the same number of rings from even-aged trees to avoid possibly erroneous interpretation of variability as due to direct genetic control. In concurring with this, Dinwoodie (10) suggests sampling at a percentage of height as the next best alternative rather than the use of a fixed height. Application of these methods in heritability studies would be advantageous but fixed-level sampling may be unavoidable in comparisons between trees of uneven age for selection purposes.

If it is accepted that the heritability of desired traits should be determined from strip rather than segmental data, then consideration must be given to Grafius' (20) warning that certain traits can be mental constructs rather than genetic entities and heritability values for the trait spurious if individual characteristics constituting the trait are not correlated. Mean fibre length and basic density are both constructs of several fibre characteristics (51, 66) and, while correlation of at least some of their constituents suggests they are heritable entities, further investigation may be desirable. Should they prove to be mental constructs, selection for individual components would be necessary to improve the compound traits.

It should also be emphasized that the heritability of certain fibre characteristics may be influenced by age (66). Evidence for maturity of late wood fibre length and early wood cell radial diameter has been reported (33, 51) and estimates for such features could be relatively low in young material but increase towards rotation age. However, it is encouraging to note, from work in other fields, that selection on early measurements could be effective if the degree of genotypic correlation between these and later measurements is sufficiently high (39). A possible effect of age on micellar angle heritability could be inferred from data in the first Section of this paper.

There seems to be undue caution in accepting heritability estimates calculated for open-pollinated progenies by the usual half-sib analysis technique *(e. g.* 42, 56, 59), because of the likely presence of a proportion of full-sibs within progeny groups. Almost certainly the estimate of additive genetic variance used in calculations should be something lower than the calculated value, but to reduce it by one-half, as has been done in some publications, is an extreme which invalidly assumes the groups consist entirely of full-sibs. Hattemer (24) states that open-pollinated progeny can be considered half-sibs with a certain degree of security by assuming the number of viable "selfings" to be close to 0 and pollen sources at least 4. Natural selfing, at least in several conifers, has been found to be of a very low order (57), with as little as 20 per cent. of these viable in some cases (22, 24), and between-tree variability in pollen-fly and receptivity periods could reasonably be expected to ensure the availability of pollen from a number of sources to a particular female parent. At worst, reduction of calculated half-sib h^2 estimates by no more than one-quarter seems a reasonable precaution.

It may be a matter of concern to some workers that narrow-sense heritability estimates in excess of 1.00 are sometimes calculated. Theoretically, of course, h^2 cannot be greater than 1.00 but estimated h^2 can (36). The reasons for this are not fully obvious to the author. Averaging segmental values to determine strip mean heritability has an inflatory effect on h^2 estimates also for reasons as yet not explicable (see data in first Section), but this is relatable to the previous phenomenon only in a secondary way.

Elucidation of these observations in relation to statistical techniques used in calculating narrow-sense heritability would be most useful and may result in the development of models and/or correction factors which could allow heritability estimates to be used with a higher degree of confidence as to their precision.

Many published estimates could also be applied with greater confidence if accompanied by some indication of their calculated precision in the form of the standard error or fiducial limits.

Major Factors Affecting Wider Application of Heritability Information

It is obvious from the published work reported in the first Section that, while basic knowledge of the heritability of fibre characteristics influencing wood quality has been accumulating fairly rapidly in recent years, this still requires expansion and its wider application in breeding programmes is being hindered to an appreciable degree, firstly by the unavailability of material of advanced age in experimental layouts of ideal design, and secondly by lack of standardization in the experimental procedures used in the determination of basic characteristics of economic significance for which heritability estimates are required.

The first problem is one which can be solved either by the passage of time or by the consideration of other approaches to derivation of estimates such as that proposed by Sakai and Hatakeyama (50), which is stated to allow estimation of heritability and genetic correlation from even-aged forest populations by a method requiring neither clonal material nor progeny-groups of known percentage. This appears promising and further investigation seems highly desirable.

The second problem is one which warrants early and earnest consideration and is probably only capable of solution by discussion in conference and wide-spread publication of recommended standard procedures.

In the meantime, the available knowledge on heritability of fibre characteristics is considerable and useful for application in conjunction with selection for improvement in vigour and morphological features, and Zobel's (64) recommendation that it be applied, with recognition of its limitations while expanding the information, is undoubtedly sound procedure.

Summary

The available evidence for the heritability of several fibre characteristics in conifers and hardwoods is presented and evaluated, its application to wood quality improvement programmes discussed, and attention is drawn to apparent deficiencies in present knowledge or practice restricting wider use of the results of studies on fibre trait heritability.

Gross and narrow-sense estimates are reported.

In hardwoods, on the basis of relatively limited data, moderate improvement in fibre length and diameter can be expected from inter-species crosses and superior-tree selection for breeding purposes. Fibre length seems more highly heritable than diameter and, in *Populus*, even higher gains in length should be attainable by the use of triploids. Possible genetic control of wall thickness is inferred but data on its heritability are inconclusive. The inheritance of cell wall structural features has apparently not yet been investigated.

In conifers, heritability of the basic phenotypic characteristic, tracheid length has been investigated in several forms of expression and, in most cases, found to be moderately to highly heritable in at least the first 9-year increment. Between-species differences in the degree of genetic control of late wood tracheid length could be construed and late wood tracheid length appears to be somewhat more highly heritable than early wood tracheid length. Tracheid length in the first ring of first-order branches, "mature" tracheid length, the rate of increase in tracheid length, and age and distance from pith for attainment of "mature" tracheid length also appear subject to genetic influence.

The heritability of certain tracheid cross-sectional dimensions is apparently quite high within individual early rings. The pattern of variation in transverse tracheid dimensions is also apparently under genetic control.

Last-formed late wood micellar angle heritability also seems quite high in the third and subsequent rings, as does average latewood micellar angle for the first 10-year increment. There is some indication of increase in heritability of micellar angle with age.

The prospects for improvement of the various tracheid length, transverse dimensional and micellar angle characteristics in conifers are evaluated.

Present knowledge of the heritability of fibre characteristics has been capable of only limited application in current breeding programmes. Supplementary quantitative information is needed on the heritability of all fibre characteristics in hardwoods and several traits, particularly in older material, in conifers.

When fibre and other wood quality characteristics are used as secondary selection criteria in tree improvement programmes, improvement of these traits is feasible using stock preselected for vigour and morphological features.

Comparative sampling methods, superior phenotype selection techniques, the interrelation of morphological and wood quality selection criteria, and their effect on the derivation and interpretation of estimates of heritability which are economically meaningful, in terms of improvement in the whole marketable product, are considered. Matters requiring further investigation are indicated.

Major factors hindering the wider application of heritability information are considered to be the unavailability of older material in ideally designed experimental lay-outs and lack of standardization in experimental procedures used in the determination of basic characteristics of economic significance. Consideration of other approaches to the derivation of estimates and the adoption of standard experimental procedures are advocated.

It is concluded that, despite its limitations, the available information on fibre characteristic heritability is useful and should be applied in tree improvement programmes.

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The Correspondence Between Genetic, Morphological, and Climatic Variation Patterns in Scotch Pine

I. Variations in Parental Characters[1]

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The native range of Scotch pine (*Pinus sylvestris* L.) includes most of Europe and northern and west-central Asia. The relatively recent glaciation in these areas and the activities of man have resulted in changing environments. Consequently displaced origins, genetic differentiation and new genetic combinations have developed among the continuous populations as well as in the isolated populations of southern Europe and west-central Asia. Mirov (1961) considered Scotch pine as a complex of pines. Carlisle (1958) listed 144 named variants.

The annual planting of millions of Scotch pine seedlings in north-eastern and north-central United States has resulted in a practical demonstration of the great amount of variability. It has also shown the economic necessity to obtain the proper seed. A comprehensive study of the performance of trees from 176 different places is being conducted in north-central United States as part of the NC-51 project (Wright, 1963; Wright and Bull, 1963). Early results based on juvenile characteristics of the seedlings have shown genetic differences between seed origins.

My study was made to determine the variability present within native stands and between regions within the natural range of Scotch pine in Europe and Asia, and to compare this variability with genetic differences determined through Wright's and Bull's study of seedling origins grown under a common environment.

The parental-stand specimens were obtained from the same stands or stand areas from which Wright and Bull collected their Scotch pine seed for the NC-51 origin test. Therefore wherever reference is made in this study to a stand or to a region the designations given by Wright and Bull are used.

The choice of parental characters used in this study was influenced by four factors: review of literature, estimated influence of environment, availability and transportability of materials, and ease and rapidity of measurements.

Literature Review

Vidaković (1958, 1960) studied the significance of seed, cone and cone scale characters as taxonomic determinants in European black pine (*Pinus nigra* Arn.). He found that seed color, seed mottling and the form of the seed and cones were most useful in differentiating between populations.

Staszkiewicz (1960, 1961, 1962) used 10 characteristics of the cone of Scotch pine to divide his population samples from Poland, Czechoslovakia, Switzerland, France, Scotland, Sweden and Finland into 6 morphological types of cones, each type distinguished by some characteristic feature.

Gerhold (1959) studied the chloroplast pigments and nutrient elements in the needles of 6 geographic origins of Scotch pine growing in the New Hampshire IUFRO plantings. He found significant differences in needle color, total chlorophyll, magnesium, nitrogen, iron and calcium.

Cvrkal (1958) determined differences in the essential oils of Scotch pine from several European countries.

The results of King (1965 a, 1965 b), Pauley *et al.* (1965) and Steinbeck (1965) corroborated and strengthened the genetic differences reported by Wright (1963) and Wright and Bull (1963) on the NC-51 Scotch pine project.

Fielding (1953), Critchfield (1957), Schoenike *et al.* (1959) and Thor (1961) used seed, cone and cone scale differences to determine variation patterns in Monterey pine (*P. radiata* D. Don), lodgepole pine (*P. contorta* Dougl.) jack pine (*P. banksiana* Lamb.), and loblolly pine (*P. taeda* L.) respectively.

Methods

The characters studied in the parental populations (*Table 1*) were principally those of the cone and seed since these have proven to be of value. Needle length and twist were also studied because they could be analyzed in the juvenile progenies grown under a common environment by Wright. In all, 19 different characters were studied on each individual.

Thirty-nine stands from 13 countries were sampled. In each stand one cone and one needle fascicle was collected from each of a number of young trees growing in full sunlight. The location of the sample on each tree was standardized. The number of trees sampled per stand was usually 20 but in a few cases was as few as 10 and as many as 34. The period of collection for all countries except Spain was August, 1960, to March, 1961. Spanish collections were made during the period December, 1961, to February, 1962.

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