842–9 (1997). — GAIOTTO, F. A. and GRATTAPAGLIA, D.: Estimation of genetic variability in a breeding population of *Eucalyptus urophylla* using AFLP (Amplified fragment length polymorphism) markers. IUFRO Conference on Silviculture and Improvement of Eucalyptus, Salvador, Brazil, **2**, 46–51 (1997). — GRATTAPAGLIA, D., BERTOLUCCI, F. L. and SEDEROFF, R.: Genetic mapping of QTLs controlling vegetative propagation in *Eucalyptus grandis* and *E. urophylla* using a pseudo-testcross strategy and RAPD markers. Theor. Appl. Genet. **90**: 7–8, 933–47 (1995). — GRATTAPAGLIA, D. and SEDEROFF, R.: Genetic linkage maps of *Eucalyptus grandis* and *Eucalyptus urophylla* using a pseudo-testcross: mapping strategy and RAPD markers. Genetics **137**: 4, 1121–37 (1994). — HOUSE, A. P. N. and BELL, J. C.: Isozyme variation and mating system in *Eucalyptus urophylla* S.T. Blake. Silvae Genet. **43**, 167–76 (1994). — ISABEL, N., BEAULIEU, J. and BOUSQUET, J.: Complete congruence between gene diversity estimates derived from genotypic data at enzyme and random amplified polymorphic DNA loci in black spruce. Proc. Natl Acad Sci USA **92**, 6369–73 (1995). — KEIL, M. and GRIFFIN, A. R.: Use of random amplified polymorphic DNA (RAPD) markers in the discrimination and verification of genotypes in *Eucalyptus*. Theor. Appl. Genet. **89**, 442–50 (1994). — LANGE, W. J. DE, WINGFIELD, B. D. and VILJOEN, C. D.: RAPD-fingerprinting to identify *Eucalyptus grandis* clones. South African Forestry Journal. **167**, 47–50 (1993). — MARTINS-CORDER, M. P.: Caracterização isoenzimática de híbridos de *Eucalyptus ssp*. Botucatu, 90p. Tese (Doutorado em Ciências Biológicas/Genética) Instituto de Biociências – Universidade Estadual Paulista (1994). — MILLER, M. P.: Tools for population genetic analyses (TFPGA) 1.3: A Windows program for the analysis of allozyme and molecular population genetic data. Computer software distributed by author. (1997). — MORI, E. S. and KAGEYAMA, P. Y.: Genetic variability in selected sub populations of *Eucalyptus grandis* HILL ex MAIDEN by isoenzymes. In: IUFRO International Symposium, proceedings, Valdivia, Chile, 10–15 September, 2001). — MULLIS, K. and FALOONA, F.: Specific synthesis of DNA *in vitro* via a polymerase catalyzed chain reaction. Meth. Enzym. **55**, 335–50 (1987). — NEI, M.: Genetic distance between populations. American Naturalist **106**, 283–92 (1972). — NEI, M.: Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583–90 (1978). — NESBITT, K. A., POTTS, B. M., VAILLANCOURT, R. E., WEST, A. K. and REID, J. B.: Partitioning and distribution of RAPD variation in a forest tree species, *Eucalyptus* globulus (Myrtaceae). Heredity **74**, 628–37 (1995). — NEWBURY, H. J. and FORD-LLOYD, B. V.: The use of RAPD for assessing variation in plants. Plant Growth Regulator **12**, 43–51 (1993). — PHILLIPS, T. D., MURPHY, J. P. and GOODMAN, M. M.: Isozymes variation in germplasm accession of the wild oat *Avena sterilis* L.. Theor. Appl. Genet. **86**, 54–64 (1993). — ROHLF, F. J.: Relative warp analysis and an example of its application to mosquito wings. n Contributions to Morphometrics, (MARCUS, L. F., BELLO, E., GARCIA-VALDECASAS, A. eds.). Museo Nacional de Ciências Naturales (CSIC) **8**. Madrid, Spain (1993). — WILLIAMS, J. G. K., KUBELIK, A. R., LIVAK, K., RAFALSKI, J. A. and TINGEY, S. V.: DNA polymorfisms ampliefield by arbitrary primers are useful as genetics marker. Nucleid Acids Res. **18**, 6531–5 (1990). — WRIGHT, S.: Evolution and the Genetics of Populations, Vol. 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago (1978).

Direct and Indirect Measures of Stiffness and Strength Show High Heritability in a Wind-Pollinated Radiata Pine Progeny Test in New Zealand

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Abstract

Seventy-two first-generation open-pollinated (OP) families grown in a 12-year-old radiata pine progeny test were sampled to evaluate the effectiveness of several destructive and non-destructive measures of stiffness. The test was located in Kinleith forest, in the central North Island of New Zealand. Five to seven trees from each of 72 OP families were sampled for assessing various wood properties. Indirect (FAKOPP), non-destructive (clearwood sticks), destructive (HITMAN) and surrogate (density) traits were compared with each other. The measurements using FAKOPP were recorded on the standing trees; stiffness (MOE) and strength (MOR) were measured on clearwood sticks taken from standing trees; HITMAN on felled trees, and wood density (DEN) was also measured on each tree using discs. Diameter (DBH), branching cluster frequency (BR) and straightness (STR) were measured on all 32 replications of all 224 wind-pollinated families available in this trial.

The narrow-sense heritability estimates for HITMAN, MOE, MOR, FAKOPP and DEN were 0.47, 0.53, 0.54, 0.46 and 0.70, respectively. The genetic correlations for HITMAN: MOE, FAKOPP: MOE, DEN: MOE, MOR: DEN and clearwood MOE: MOR were 0.84, –0.69, 0.72, 0.88 and 0.98, respectively. The narrow-sense heritability estimate for DBH, STR and BR were 0.10, 0.17 and 0.06, respectively. Assuming clearwood MOE as the target trait for improving stiffness, HITMAN and DEN were found to be best indirect traits for selection. Predicted genetic gain from indirect selection of parents based on HITMAN and DEN was 80 and 78 percent, respectively, of that predicted from direct selection on MOE. There was some indication that density was a better predictor of strength than of stiffness.

Key words: Stiffness, strength, wood density, heritability, breeding strategy, *Pinus radiata*

Introduction

Wood stiffness, measured in terms of its modulus of elasticity (MOE), is the most important property of structural timber. Low stiffness is an important limitation of timber from radiata pine (*Pinus radiata* D. DON), particularly under short rotations favoured in the interests of reducing growing costs; such rotations result in a high proportion of juvenile wood and an associated reduction in wood quality (COWN, 1999; COWN *et al.*, 1999).

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New Zealand has had a longstanding genetic improvement program for radiata pine; this program has been described in several publications (e.g. SHELBOURNE *et al.*, 1986; JAYAWICKRAMA and CARSON, 2000). New Zealand radiata pine breeders have been proactive in trying to improve wood quality. Wood density was the first trait to be given emphasis (being considered a predictor of many important properties including stiffness), and a big effort made as far back as 1975 when nearly 6,000 trees were cored in two "268" series progeny test sites (JAYAWICKRAMA, 2001a). A High Wood Density Breed was formed in 1986. Stiffness was further elevated in the breeding programme, with a Structural Timber Breed included in the advanced-generation breeding population (JAYAWICKRAMA and CARSON, 2000).

Preliminary studies on small numbers of entries have shown high heritabilities of wood stiffness, for radiata pine (e.g. SHELBOURNE, 1997; MATHESON *et al.*, 1997) and other conifer species (e.g. SHI *et al.*, 1987; KOIZUMI *et al.*, 1990; FUJISAWA *et al.*, 1992). There are two main reasons for further work on stiffness of radiata pine. First, stronger estimates of genetic parameters for stiffness, based on more entries and a broader sample, are needed. Second, ranking highly-ranked progenies used by the New Zealand Radiata Pine Breeding Cooperative (NZRPBC) for stiffness was chosen as a priority in 1997 (SORENSSON, 1997) and continues to be of high priority as expressed at a NZRPBC Wood Quality workshop held in November 2000.

Various direct, indirect and surrogate tests can be used to estimate wood stiffness and strength (reviewed by JAYAWICKRAMA, 2001b). First, measuring stiffness directly on large boards would clearly give the best estimates of stiffness; however this would be very expensive for ranking genotypes, and trees cut down for testing would no longer be available for breeding or other work unless clonally replicated. Second, small clear wood specimens are another option, and specimens of 300 x 20 x 20 mm have been used routinely in New Zealand (e.g. BIER and BRITTON, 1999). *Forest Research*, with funding from the NZRPBC developed a tool ("Sticksaw") to cut clearwood sticks of 300 x 20 x 20 mm from standing trees (JAYAWICKRAMA, 2001b). Third, we can measure stiffness indirectly using ultrasonic sound velocity; several researchers and companies have taken this approach.

Carter Holt Harvey Forests Ltd and Fletcher Challenge Forests Ltd, two New Zealand companies, have both developed acoustic measurement systems for log evaluation, these being the HITMAN and SWAT respectively (ANONYMOUS, 1999; PARKER, 1999). In terms of progeny evaluation, both are destructive methods since they can only be applied on cut ends of logs. One of the few options currently available for use on standing trees is FAKOPP, a device developed in Hungary. This device measures the transit time of a stress wave between two transducers (BOOKER and SORENSSON, 1999; ANONYMOUS, 2000). *Forest Research* data suggests that sound velocity, measured by the FAKOPP technique on standing trees, is correlated with the stiffness of clearwood sticks (BOOKER and SORENSSON, 1999). Fourth, density has long been advocated as a good predictor of stiffness in radiata pine (e.g. COWN, 1999; COWN *et al.*, 1999).

Breeders need to test the various options available and choose a strategy, to measure MOE, that is (i) relatively inexpensive, (ii) usable on standing trees (iii) gives repeatable results and good heritability, and (iv) gives reading well correlated with end-product value. This paper documents a study on stiffness testing using acoustics, clearwood sticks and density on 72 families taken from an open-pollinated first-generation radiata pine progeny test in New Zealand. The main objective of this study was to evaluate the effectiveness of various acoustic tools (FAKOPP and HITMAN) for indirect assessment of stiffness, and compare it with direct assessment (clearwood MOE) for improving stiffness. Inter-relationships between wood quality traits and growth and form traits were also investigated.

Materials and Methods

Study material

An open-pollinated (OP) progeny trial of 224 first-generation families from the "887" series was planted in 1988 on three sites. Parent trees for this series were selected from the New Zealand landrace of radiata pine, growing in the central North Island, at a selection intensity of about 1 tree per 2 ha. The main emphasis was on growth rate, followed by stem form and to a slight extent by tree health. The trial in Kinleith Forest in the central North Island of New Zealand (Trial no. FR 38/2) was chosen for this wood quality sampling; this site had moderate individual-tree heritability for diameter (0.18) and was relatively close to the main *Forest Research* office. The experimental design was of randomised complete blocks with each family represented as single-tree plots in 32 replicates. Some details on the "887" series are given in JAYAWICKRAMA *et al.* (1997) and JAYAWICKRAMA (2001a).

Direct assessment of clearwood stiffness involves three labor-intensive steps: cutting the sticks in the field, machining in the laboratory and the static-bending test. It is therefore costly to sample many families and lots of trees per family. However genetic parameter estimates need to be based on an adequate sample of families to be meaningful. Funding was available to sample about 450 trees. Assuming a heritability of 0.5 for two traits and a genetic correlation (between the traits) of 0.6, a simple simulation showed that sampling 70 families at seven trees per family would provide a better (less biased) estimate of genetic correlation than sampling 40 families at 12 trees per family. A subset of 72 (out of 224) families was thus selected to assess for stiffness using destructive and acoustic tools. These 72 OP families covered the following ranges for the following traits (with 1 being the highest ranked of 224 progenies): DBH: 2 to 224, STR: 1 to 224, BR: 3 to 224, malformation score: 6 to 207, acceptability score: 1 to 224 and needle retention score 5 to 224.

Measurements

As a part of routine assessment at age 8-years, growth and form traits, namely, diameter at breast height (DBH), branching cluster frequency score (BR) and straightness score (STR) were measured on all 32 replications of all 224 OP families available in this trial.

Information on FAKOPP, HITMAN, MOE, MOR and DEN was obtained from 5 to 7 offspring from each of 72 OP families. The trees were 12 years from planting at the time of assessment of these wood properties. Details on FAKOPP procedure are given in the FAKOPP user guide (ANONYMOUS, 2000). In brief, two transducers were driven a few cm. into the stem and 1-meter apart, with the lower transducer about 1-meter above the ground level. The start transducer was then tapped gently and a reading recorded. What is measured, by use of an amplification device, is the time for the sound wave to travel from the start transducer to the stop transducer.

Sticks were cut from the standing trees using the "Sticksaw" built at *Forest Research*. Wherever possible, the slabs were taken from the same part of the tree used for the FAKOPP assessment. After cutting the slabs from the trees, sticks were machined to the standard dimension of 300 x 20 x 20 mm. To the extent possible, the sticks were taken to include the same growth rings in each tree, nominally centred on ring eight from the pith. Rings six to eight have been selected as a good place to sample wood properties, given the emphasis on improving juvenile wood quality (SORENSSON *et al.*, 1997). These sticks were tested using the static bending technique (MACK, 1979) at the *Forest Research* Timber Engineering laboratory.

The measurements using the HITMAN tool were taken on the first log (5-meter length) after cutting down all the trees that had been previously assessed for FAKOPP and clear-wood sticks. The HITMAN tool measures the sound velocity produced by tapping the log end with a hammer. Density was measured by taking discs at breast height. The following variables were considered for analysis:

HITMAN	(velocity measurements (km per second) taken using HITMAN tool)
MOE	(stiffness (MPa) measurements on Small-clear sticks)
MOR	(strength (MPa) measurements on Small-clear sticks)
FAKOPP	(transit time between two transducers using FAKOPP tool)
DEN	(wood density (kg/m^3) measurements using disc)
DBH	(diameter (mm) at breast height)
STR	(straightness score on 1–9 scale, 1 = very crooked, 9 = very straight)
BR	(branching frequency score on 1–9 scale, 1 = one whorl per year, 9 = several whorl per year).

Data analysis

The following linear model was used for analysis of each trait:

Phenotype = mean + replication + family + error (1)

In this model, replication, family and the error effects were assumed as random effects. For multivariate analysis, there are assumed to be *f* groups (OP families) each of size *n* (number of offspring per half-sib family), and *p* traits are recorded on each individual. It was further assumed that the observations are multivariate normally distributed with among- and within-group effects independent of each other. REML estimates of genetic and environmental variance-covariance were obtained through iterative process using multivariate analysis in ASREML software (GILMOUR *et al.*, 1997). Estimates of individual-tree heritability ($\hat{h}^2$) and genetic correlation ($\hat{r}_g$) were obtained as:

$$\hat{h}^2 = 4\,\hat{\sigma}^2_f / (\hat{\sigma}^2_f + \hat{\sigma}^2_e) \qquad (2)$$

$$\hat{r}_g = \hat{\sigma}_{xy} / \sqrt{\hat{\sigma}^2_x \times \hat{\sigma}^2_y} \qquad (3)$$

where $\hat{\sigma}^2_f$ and $\hat{\sigma}^2_e$ are the estimated among-family and within-family variance components, respectively, for a given trait; $\hat{\sigma}_{xy}$ is estimated additive genetic covariance between two traits; $\hat{\sigma}^2_x$ and $\hat{\sigma}^2_y$ are estimated additive genetic variance for two traits. Estimates of genetic correlation among all traits (HITMAN, FAKOPP, MOE, MOR, DEN, DBH, STR, and BR) were obtained using information from 72 open-pollinated families with 5 to 7 offspring each, measured for all these traits. As the information on DBH, STR and BR was available on all families in this trial (224 families with 32 offspring each), estimates of genetic parameters for these three traits were also obtained using complete data set. Estimates of standard errors of heritability and genetic correlation estimates were obtained using ASREML software. Significance of the differences among family effects (assumed random) was tested using likelihood ratio test. Best linear unbiased predictions (BLUP) of family-means were also obtained for each trait. The correlated response in the target trait (MOE) from indirect family selection based on acoustic measures (FAKOPP and HITMAN) was calculated following FALCONDER and MACKAY (1996). Estimates of phenotypic correlations at the individual-tree level were obtained by using SAS PROC CORR (SAS INSTITUTE INC., 1988).

Results

The summary statistics of predicted (BLUP) family means for all traits are shown in *Table 1*. The average MOE, MOR and DEN were 6334.26 MPa, 62.53 MPa and 351.99 kg/m^3 with coefficient of variation 6.55, 4.43 and 2.07 percent, respectively. The coefficient of variation for HITMAN, FAKOPP, DBH, STR and BR were 2.44, 2.93, 2.21, 5.19 and 6.48 percent respectively. Predicted range of MOE and MOR, at the family-mean level, were 5272.38 to 7369.02 MPa and 56.11 to 69.75 MPa respectively. The variation (e.g. range and coefficient of variation) in predicted family-means was lesser than the observed family-means (results not shown) for all traits. It could be because BLUP of family means are regressed or shrunken towards the mean and also because part of the variation in the observed family means is due to sampling and environmental variances (WHITE and HODGE, 1989). The variation among BLUP of individual tree values was almost twice (results not shown) of that among BLUP of family-means for all traits.

Table 1. – Summary statistics of BLUP of family-means obtained from a sample size of 72 open-pollinated families for different traits.

Trait	Mean	Minimum	Maximum	CV (%)
HITMAN	2.26	2.13	2.37	2.44
FAKOPP	422.17	391.63	447.53	2.93
MOE (MPa)	6334.26	5272.38	7369.02	6.55
MOR (MPa)	62.53	56.11	69.75	4.43
DEN (kg/m^3)	351.99	333.97	370.63	2.07
DBH (mm)	220.86	210.45	231.42	2.21
STR (1 – 9 scale)	5.18	4.48	5.70	5.19
BR (1 – 9 scale)	4.67	3.95	5.47	6.48

Estimates of phenotypic correlations among all traits, at the individual-tree level, are given in *Table 2*. The correlation coefficients of MOE with FAKOPP, MOR, HITMAN and DEN were –0.47, 0.89, 0.59 and 0.35, respectively. The extent of correlation between density (DEN) and MOE (0.35) was lesser than that between DEN and HITMAN (0.48). Estimated correlation between DEN and MOR was 0.51 (*Table 2*). In general, growth and form traits showed weak phenotypic correlations with all wood quality traits measured in this study. Estimated phenotypic correlation between DBH and DEN was –0.21. The correlation coefficient of DBH with STR and BR was 0.11 and 0.25 respectively.

Estimates of genetic correlation, along with their estimated standard error are shown in *Table 3*. In general, very high genetic correlations were observed among direct, acoustic and surrogate measures of stiffness. Wood density was found highly correlated with various measures of stiffness and strength.

Table 2. – Observed phenotypic correlations at the individual-tree level.

Trait	FAKOPP	MOE	MOR	DEN	DBH	STR	BR
HITMAN	-0.59	0.59	0.54	0.48	-0.30	0.10	-0.07
FAKOPP		-0.47	-0.40	-0.27	0.16	-0.13	0.00
MOE			0.89	0.35	0.02	0.18	0.05
MOR				0.51	-0.05	0.15	0.01
DEN					-0.21	0.04	0.00
DBH						0.11	0.25
STR							0.20

Table 3. – Estimates of genetic correlations between pairs of variables, based on a sample size of 72 half-sib families. Estimates of standard errors are given in parentheses.

Trait	FAKOPP	MOE	MOR	DEN	DBH	STR	BR
HITMAN	-0.39 (0.22)	0.84 (0.12)	0.85 (0.13)	0.84 (0.13)	-0.81 (0.49)	0.13 (0.40)	-0.96 (0.99)
FAKOPP		-0.69 (0.17)	-0.68 (0.18)	-0.26 (0.23)	0.74 (0.54)	0.10 (0.42)	0.73 (0.90)
MOE			0.98 (0.03)	0.72 (0.15)	-0.41 (0.53)	-0.22 (0.42)	-0.54 (0.78)
MOR				0.88 (0.11)	-0.49 (0.53)	-0.19 (0.41)	-0.24 (0.64)
DEN					-0.97 (0.60)	-0.21 (0.37)	-0.36 (0.64)
DBH						0.26 (0.75)	-0.62 (1.58)
STR							-0.86 (1.44)

Estimated genetic correlation of MOE with HITMAN, FAKOPP, DEN and MOR was 0.84, –0.69, 0.72 and 0.98 respectively. DEN showed high positive genetic correlation with MOE (0.72) and MOR (0.88). Estimates of standard errors of correlations among various wood property traits varied from 0.03 (for MOE and MOR) to 0.23 (for DEN and FAKOPP).

Estimated genetic correlations among wood property traits and growth and form traits (*Table 3*) were generally higher than the corresponding phenotypic correlations among these traits. Estimated genetic correlation between DBH and STR, DBH and BR, and STR and BR were 0.26, –0.62 and –0.86 with standard error of 0.75, 1.58 and 1.44 respectively. The corresponding estimates of genetic correlations among DBH, STR and BR obtained from complete data set (224 families with 32 replications each) were 0.03, 0.28 and 0.24 respectively.

Results from the test of significance for family effects (assumed random) obtained using likelihood ratio test are shown in *Table 4*. A significant ($p \leq 0.0005$) difference among family effects was found for all traits except DBH, STR and BR. This shows the ability of direct and acoustic methods to differentiate among families for stiffness. Estimates of individual-tree heritability, along with estimated standard error, are also shown in *Table 4*. Individual-tree heritability estimates for HITMAN, FAKOPP, MOR, MOE and DEN were 0.47, 0.46, 0.54, 0.53 and 0.70, respectively. Heritability estimates for DBH, STR and BR were 0.10, 0.17 and 0.06 with standard error of 0.13, 0.14 and 0.13 respectively. Analysis of complete data set (224 families with 32 offspring each) revealed heritability estimates as 0.18, 0.22 and 0.29 with standard error of 0.03, 0.03 and 0.04 for DBH, STR and BR respectively.

Table 4. – Estimates of individual-tree heritabilities (h^2) and their standard errors (SE). Test of significance for h^2 is shown using p-values from likelihood ratio test.

Trait	p-value	h^2	SE
HITMAN	0.0004	0.47	0.17
FAKOPP	0.0005	0.46	0.17
MOE	0.0001	0.53	0.17
MOR	0.0001	0.54	0.17
DEN	0.0000	0.70	0.19
DBH	0.4028	0.10	0.13
STR	0.1797	0.17	0.14
BR	0.5839	0.06	0.13

Discussion

The high correlations between MOE and MOR are consistent with previous studies (e.g. COWN *et al.*, 1999). There was some indication that density was a better predictor of strength (MOR) than of stiffness (MOE). The same was reported for radiata pine by COWN *et al.* (1999), at both the within-tree and between-tree level, for juvenile and for mature wood. Genetic correlation of HITMAN and FAKOPP with stiffness (MOE) was 0.84 and –0.69 respectively. This suggests that these acoustic tools could be used for indirect assessment of stiffness in radiata pine progeny trials.

There is little information reported on genetic correlations between some wood properties (like, MOE and MOR) and growth and form traits (like, DBH, STR and BR). In this study, some of the estimated genetic correlations, for example: correlation between DBH and DEN (–0.97) was much higher than previously reported (e.g. BURDON and LOW, 1992; JAYAWICKRAMA, 2001a). High standard error estimates of genetic correlations indicated the poor precision of some estimated correlations in this study. Genetic correlations among growth and form traits obtained from a sub-sample (72 open-pollinated families with 5 to 7 offspring each) were quite different from those obtained from complete data set (224 open-pollinated with 32 offspring each). Estimated genetic correlations among DBH, STR and BR obtained from complete data set from this trial were similar to those reported from a synthesis of results from a number of progeny trials (JAYAWICKRAMA, 2001a).

Results obtained in this study indicated that small sample size, particularly within-family size (for example, 5 to 7 offspring per family), might not provide reliable estimates of genetic correlations among growth and form traits and wood quality traits in radiata pine. Further studies would be required for better understanding of inter-relationship of various wood properties and growth and form traits. Negative genetic correlation among stiffness and growth suggests that large simultaneous gain cannot be achieved in these traits. However, various index selection procedures can be used to maximise genetic gain in wood quality traits while avoiding loss in growth and form traits.

Table 5. – Predicted genetic gain in target trait (MOE) via indirect family selection on HITMAN, DEN, and FAKOPP. Genetic correlation (r_g) of MOE with other traits, family-mean repeatability (h^2_f) for each trait is also shown. Selection intensity was assumed to be 1.

Trait	h^2_f	r_g	Gain	Gain (%)
MOE	0.48	1	383	100
HITMAN	0.45	0.83	308	80
DEN	0.56	0.72	298	78
FAKOPP	0.44	-0.69	-253	66

Individual-tree heritability estimate obtained for wood density in this study compare favourably to that previously reported (e.g. Burdon and Low, 1992; Jayawickrama, 2001a). Individual-tree heritability estimates for MOE and MOR (0.53 and 0.54, respectively) also compare favourably to those reported by Matheson *et al.* (1997). Estimates of heritability in this study may be upwardly biased because measurements were taken on a single test site and family-site interaction, if any, was not taken into account. Before drawing any definite conclusion, however, the sensitivity of heritability estimates to within-family sample size and the test environment should be evaluated.

Significant family differences along with high heritability of MOE indicated the extent of genetic variation and the possibility of improving stiffness by making family selections based on MOE. Some forest growers in New Zealand are using HITMAN to segregate logs for stiffness. Genetic correlation of HITMAN with MOE was 0.84, which was higher than that of FAKOPP and DEN with MOE (–0.69 and 0.72 respectively). Thus, acoustic tool like HITMAN or a surrogate trait like DEN could successfully be used as indirect traits for improving MOE in radiata pine. The need to cut the trees down is a disadvantage for HITMAN unless the test needs to be thinned or unless extra replicates were planted to allow felling. Both DEN and FAKOPP would also offer non-destructive indirect measures for ranking families for MOE, but DEN might be more attractive as it is less costly to measure and also is a highly heritable trait.

Predicted genetic gain in target trait (MOE) from indirect selection of parents based on HITMAN, DEN and FAKOPP are shown in *Table 5*. Results showed that indirect family selection based on HITMAN and DEN would give 80 and 78 percent, respectively, of the gain that predicted from direct selection on the target trait. FAKOPP was found to be least effective tool for indirect selection. This is because of the relatively poor genetic correlation of FAKOPP with the target trait. DEN can also be shown as best indirect trait for improving MOR as it has very high genetic correlation with MOR.

Some important future questions are: (i) how clearwood MOE, FAKOPP, HITMAN and DEN correlate with whole-tree stiffness, or overall juvenile-wood stiffness (whichever is the final goal of selection); (ii) site × family interaction for these traits; (iii) the relative economic weights to attach to stiffness, density, growth and form, both in the breeding and production populations.

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Forest Research is not promoting or advertising either the HITMAN or the FAKOPP tool.

References

Anonymous: Tool for timber expected to be a hit in the forest. INNOVATE Issue 33, September 1999. Industrial Research Ltd., PO Box 31–310, Lower Hutt, New Zealand (1999). — Anonymous: FAKOPP User's Guide. ALNUS Bt., H-9400 Sopron, Feher D. u. 22, Hungary (2000). — Bier, H. and Britton, R. A. J.: Strength properties of small clear specimens of New Zealand-grown timbers. *Forest Research* Bulletin No. 41, *Forest Research*, Rotorua, New Zealand, 27p (1999). — Booker, R. and Sorensson, C.: New tools and techniques to determine mechanical wood properties. In: Proc. 3rd Wood Quality Symposium: "Emerging Technologies for evaluating wood quality for wood processing". 30th November, 1999, Rotorua, New Zealand. Forest Industry Engineering Association, PO Box 6150, Rotorua (1999). — Burdon, R. D. and Low, C. B.: Genetic survey of *Pinus radiata* 6: wood properties: variation, heritabilites, and interrelationship with other traits. N. Z. J. For. Sci. **22**: 228–245 (1992). — Cave, I. D. and Walker, J. C. F.: Stiffness of wood in fast-grown plantation softwood: the influence of microfibril angle. For. Prod. J. **44**: 43–48 (1994). — Cown, D. J.: New Zealand Pine and Douglas-fir: Suitability for processing. *Forest Research* Bulletin No 216, *Forest Research*, Rotorua, New Zealand (1999). — Cown, D. J, Hebert, J. and Ball, R.: Modelling *Pinus radiata* lumber characteristics. Part 1: Mechanical properties of small clears. N.Z. J. For. Sci. **29**: 203–213 (1999). — Falconer, D. S. and Mackay, T. F. C.: Introduction to Quantitative Genetics. 4th Edition. Addison Wesley Longman Ltd., Essex, UK. 464pp. (1996). — Fujisawa, Y., Ohta, S., Nishimura, K. and Tajima, M.: Wood characteristics and genetic variations in sugi (*Cryptomeria japonica*). Clonal differences and correlations between locations of dynamic growths in plus-tree clones. Mokuzai Gakkaishi **38**: 638–644 (1992). — Gilmour, A. R., Thompson, R., Cullis, B. R. and Welham, S. J.: ASREML User's manual, New South Wales Agriculture, Orange, Australia (1997). — Jayawickrama, K. J. S.: Genetic parameter estimates for radiata pine in New Zealand and New South Wales: A synthesis of results. Silvae Genet. **50**: 45–53 (2001a). — Jayawickrama, K. J. S.: Breeding radiata pine for wood stiffness: review and analysis. Aust. For. **64**: 51–56 (2001b). — Jayawickrama, K. J. S. and Carson, M. J.: A breeding strategy for the New Zealand radiata pine breeding cooperative. Silvae Genet. **49**: 82–90 (2000). — Jayawickrama, K. J. S., Carson, M. J., Jefferson, P. A. and Firth, A.: Development of the New Zealand radiata pine breeding population. Pp. 217–225 *in* Burdon, R. D.; Moore, J. M. (Ed.) "IUFRO '97 Genetics of Radiata Pine". Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. FRI Bulletin No. 203 (1997). — Koizumi, A., Takada, K., Ueda, K. and Katayose, T.: Radial growth and wood quality of Japanese larch. I. Radial growth, density and trunk modulus of elasticity of grafted clones. Mokuzai Gakkaishi **36**: 98–102 (1990). — Mack, J. J.: Australian method for mechanically testing small clear specimens of timber. Building Research Technical Paper (Second Series) No. 31, CSIRO, Australia (1979). — Matheson, A. C., Spencer, D. J., Nyakuengama, J. G., Yang, J. and Evans, R.: Breeding for wood properties in radiata pine. Pp. 169–179 *in* Burdon, R.D.; Moore, J.M. (Ed.) "IUFRO '97 Genetics of Radiata Pine". Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. FRI Bulletin No. 203 (1997). — Parker, J.: Cut plan determination by individual stem testing. *In:* Proc. 3rd Wood Quality Symposium: "Emerging Technologies for evaluating wood quality for wood processing". 30th November, 1999, Rotorua, New Zealand. Forest Industry Engineering Association, PO Box 6150, Rotorua (1999). — SAS Institute Inc.: SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute Inc., Cary, NC, USA (1988). — Shelbourne, C. J. A.: Genetics of adding value to the end-products of radiata pine. Pp. 129–141 *in* Burdon, R. D.; Moore, J. M. (Ed.) "IUFRO '97 Genetics of Radiata Pine". Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. FRI Bulletin No. 203 (1997). — Shelbourne, C. J. A., Burdon, R. D., Carson, S. D., Firth, A. and Vincent, T. G.: Development plan for radiata pine breeding. *Forest Research* Institute, Rotorua, New Zealand (1986). — SHI, J. S., YE, Z. H. and CHENG, Y. W.: Inheritance and variation of the wood properties of Chinese fir (*Cunnighamia lanceolata*). II. The genetic variation among open-pollinated progenies from a seed orchard of Chinese fir and the correlations between several traits. Journal of Nanjing Forestry University **4**: 15–25 (1987). — SORENSSON, C. T.: NZRPBC Five-year R&D Plan: Radiata Pine Wood Properties (1997–2001). New Zealand Radiata Pine Breeding Cooperative Report No. 69 (1997). — SORENSSON, C. T., BURDON, R. D., COWN, D. J., JEFFERSON, P. A. and SHELBOURNE, C. J. A.: Incorporating spiral grain into New Zealand's radiata pine breeding programme. Pp. 180–191 *in* BURDON, R. D.; MOORE, J. M. (Ed.) "IUFRO '97 Genetics of Radiata Pine". Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. FRI Bulletin No. 203 (1997). — WHITE, T. L. and HODGE, G. R.: Predicting Breeding Values with Applications in Forest Tree Improvement. Kluwer Academic Pub., Dordrecht, The Netherlands. 367pp., (1989).

Study of Early Selection in Tree Breeding

4. Efficiency of Marker-Aided Early Selection (MAES)

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Abstract

One of the main attractions of Marker-Aided Selection (MAS) in tree breeding is its potential for early selection through juvenile traits as Marker-Aided Early Selection (MAES). The theoretical advantages of incorporating molecular markers into early selection in tree breeding are examined. Equations were derived to answer the following questions: (1) how effective is the use of markers for early selection relative to conventional late (mature) selection? (2) what is the efficiency of using markers for early selection relative to early selection based on morphological traits? (3) how effective is incorporating markers into an early selection index relative to an early selection index based on morphological traits alone? (4) what are the efficiencies when MAS is used only for within-family selection in the combined family and within family selection approach, relative to selection using combined family and within family phenotypic information alone? and (5) how effective is selection when MAES is used for within-family selection only in the combined family and within family early selection approach, relative to early selection using combined family and within family phenotypic information alone? These equations could be used to compare relative efficiencies of MAES and QAES (QTL-Aided Early Selection) relative to traditional phenotypic selection in breeding programs. For Marker-Aided Early Selection or QTL-Aided Early Selection to be applicable in tree breeding populations, it may be necessary to demonstrate that efficiency from MAES or QAES is higher than efficiency of early selection using less expensive early phenotypic traits. Furthermore, the relative efficiency of MAES or QAES is higher when genetic correlation of early-mature trait and/or heritability of the early trait is lower and is less for full-sib family than for half-sib family selection.

Key words: Marker-Aided Selection, Marker-Aided Early Selection, Early Selection, Genetic Gain, Index Selection.

Introduction

The construction of genetic linkage maps using molecular markers and detection of quantitative trait loci (QTL) has been an exciting research area in forest genetics in recent years. Following the publication of restriction fragment length polymorphism (RFLP) linkage map in humans (BOSTEIN *et al.,* 1980) and tomato (BERNATZKY and TANKSLEY, 1986), genetic linkage maps based on RFLP markers were published for loblolly pine, *Pinus taeda* (DEVEY *et al.,* 1994), and based on random amplified polymorphism DNA (RAPD) markers in eucalypts (GRATTAPAGLIA and SEDEROFF, 1994). Since then, molecular (DNA) linkage maps have been constructed or are under construction for many important timber and pulping species (NEALE and SEDEROFF, 1991; NEALE and HARRY, 1994; SEWELL and NEALE, 2000; TEMESGEN *et al.,* 2001). Major QTLs in crops have been identified using molecular markers, first in maize (EDWARDS *et al.,* 1987 and STUBER *et al.,* 1987) and tomato (PATERSON *et al.,* 1988), followed by numerous other crop species (O'BRIEN, 1993; TANKSLEY, 1993) and for virtually all agronomically important traits (e.g. drought and salt resistance, seed hardness and size, plant biomass, size, and maturity, disease resistance, oil and protein content, fecundity, *et al.*) (YOUNG, 1999). In forest tree species, significant QTLs have been detected in vegetative propagation traits (GRATTAPAGLIA *et al.,* 1995; MARQUES *et al.,* 1999), crown form (HARFOUCHE *et al.,* 2000), early growth (BRADSHAW and STETTLER, 1995; VERHAEGEN *et al.,* 1997; EMEBIRI *et al.,* 1998), wood quality traits (GROVER *et al.,* 1994; GRATTAPAGLIA *et al.,* 1996; KNOTT *et al.,* 1997; NEALE *et al.,* 1997; SEWELL *et al.,* 2000; KURANMOTO *et al.,* 2000), biotic and abiotic resistance (KUBISIAK *et al.,* 2000; SKOV and WELLENDORF, 2000).

With potentially unlimited DNA markers available to tree species, forest geneticists soon began to believe that marker-aided selection (MAS) may become a reality (STRAUSS *et al.,* 1992). The possibility of selecting desirable trees based on genotypes rather than phenotypes and to select elite breeding trees in the seedling stage (very early selection) was extremely

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