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ORIGINAL ARTICLE

Takaaki Fujimoto · Hisashi Akutsu · Miki Nei
Kazuhito Kita · Makoto Kuromaru · Kazuyuki Oda

Genetic variation in wood stiffness and strength properties of hybrid larch (*Larix gmelinii* var. *japonica* × *L. kaempferi*)

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Abstract Genetic parameters for wood stiffness and strength properties were estimated in a 29-year-old hybrid larch stand (*Larix gmelinii* var. *japonica* × *Larix kaempferi*). The study included 19 full-sib larch families from Hokkaido, northern Japan. Implications of these genetic parameters in wood quality improvement are subsequently discussed. Traits included in the analyses were the dynamic modulus of elasticity of green logs (E_{log}), the modulus of elasticity (MOE), the modulus of rupture (MOR), compression strength parallel to the grain (CS) in small clear specimens, wood density (DEN), and diameter at breast height (DBH). DEN had the lowest coefficients of variation and MOE the highest. The narrow-sense heritability estimates of E_{log}, MOE, MOR, and CS were 0.61, 0.44, 0.60, and 0.43, respectively, and those of DEN and all mechanical properties increased from an inner to outer position within the stem. E_{log} and DEN had high positive phenotypic (0.52–0.83) and genetic (0.70–0.92) correlations with MOE, MOR, and CS. The mechanical properties of the inner position of the stem had rather high phenotypic and genetic correlations with those of the outer position and overall mean. The predicted gains in wood stiffness (E_{log} and MOE) were higher than those of the strength properties (MOR and CS). The predicted correlated responses in MOE, MOR, and CS when selecting for E_{log} and DEN were 72.6%–97.8% of a gain achievable from direct selection of these traits. DBH showed an insignificant correlation with all mechanical properties, although selection of this trait had a slightly negative effect on the mechanical properties.

Key words Breeding · Genetic variation · Heritability · Hybrid larch · Mechanical properties

Introduction

The hybrid between Kurile larch (*Larix gmelinii* var. *japonica*) and Japanese larch (*Larix kaempferi*) shows rapid juvenile growth and high resistance to various pests and diseases compared with Japanese larch and other hybrid larches (Hamaya and Kurahashi 1981; Takahashi and Nishiguchi 1966). Furthermore, this hybrid provides wood with desirable qualities, such as small stem crookedness, and high wood density and strength (Oshima and Nishikoori 1994; Akutsu et al. 1991), and, thus, appears to offer good potential for use under intensive forest management. However, the above findings were demonstrated through interspecies comparisons with other *Larix* species and their hybrids, and little is known about variation within the hybrid species (Kuromaru et al. 1985). Because the wood properties of this hybrid larch vary widely (Oshima and Kuromaru 1995), development of a breeding program for wood quality requires information about the genetic variation in wood properties and genetic relationships among these traits.

The mechanical properties of Japanese larch have been extensively documented. For example, Zhu et al. (2000) examined radial variation in tensile strength using full-length lumber and small clear specimens of even-aged (87-year-old) Japanese larch. Koizumi et al. (1990) investigated the growth rate, wood density, and modulus of elasticity of tree trunks of grafted clones of plus trees of Japanese larch and found that all of the above traits were significantly different between sample clones. Hashizume et al. (1997) evaluated the classification and grading method of laminae of Japanese larch lumber used for glued laminated timber by measuring strength properties.

Although Japanese larch shows outstanding strength performance, the current primary uses for its wood are pallets and packing materials, especially in Hokkaido,

T. Fujimoto (✉) · H. Akutsu · M. Nei
Hokkaido Forest Products Research Institute, 1-10 Nishikagura, Asahikawa 071-0198, Japan
Tel. +81-166-75-4233; Fax +81-166-75-3621
e-mail: tfuji@fpri.asahikawa.hokkaido.jp

K. Kita · M. Kuromaru
Hokkaido Forestry Research Institute, Bibai, Japan

K. Oda
Faculty of Agriculture, Kyushu University, Fukuoka, Japan

northern Japan. However, for the reasons mentioned above, it is believed that hybrid larch has more potential for use as construction material than Japanese larch. Despite this, few reports have documented the mechanical properties of hybrid larch wood, and little information is available on the genetic variation of these traits. The present article reports the various mechanical properties of hybrid larch in a progeny test stand in Hokkaido with the aim of estimating the genetic parameters of wood stiffness and strength and the genetic and phenotypic relationships among these traits.

Materials and methods

Plant material

Wood samples were collected from a 29-year-old *Larix gmelinii* × *Larix kaempferi* progeny test stand in Bibai, Hokkaido, northern Japan. This stand was the same one described in detail in previous articles (Fujimoto et al. 2006a, b). The progeny test consisted of 19 full-sib families derived from an incomplete factorial mating design involving four female and six male parent trees. The test was established in 1974 with 2-year-old seedlings. Families were planted in 21-tree plots at 2 × 2 m spacing according to a randomized complete block experimental design with two replicates. In 2002, one to six sample trees were harvested from each family, resulting in a total of 96 sample trees. A 1.8-m butt log was obtained from each tree and transported to the Hokkaido Forest Products Research Institute sawmill.

Sample preparation and testing

First, the dynamic modulus of elasticity of the green logs ($E_{\log}$) was measured using the longitudinal vibration method (Sobue 1986; Arima et al. 1993). The weight, log length, and diameters of both log ends were measured to calculate the wood density. $E_{\log}$ was obtained by the following formula (Arima et al. 1993):

$$E_{\log} = 4f^2l^2\rho \tag{1}$$

where f(Hz) is the fundamental vibration frequency, l(m) is the length of the sample log, and ρ (kg/m^3) is the density of green sample log.

After measuring the $E_{\log}$, a diametric flitch, 40 mm thick, was sawn from each log (Fig. 1). The flitch was then divided into two parts at 800 mm from the bottom. The upper part was dried using a conventional kiln-drying schedule; then both parts, from the bark to the pith, were successively processed into stakes with a cross-sectional size of 20 × 20 mm (Fig. 1). Small clear specimens, as free from knots as possible, were cut from the stakes for static bending and compression tests. Specimens were 20 × 20 × 320 mm and 20 × 20 × 50 mm for the static bending and compression tests, respectively. All specimens were conditioned to equilibrium in a room maintained at 20°C and 65% relative humidity. Between six and nine specimens were obtained from each tree, depending mainly on the log diameter. Annual ring width of each specimen was 5.4 mm on average (1.7–11.8 mm).

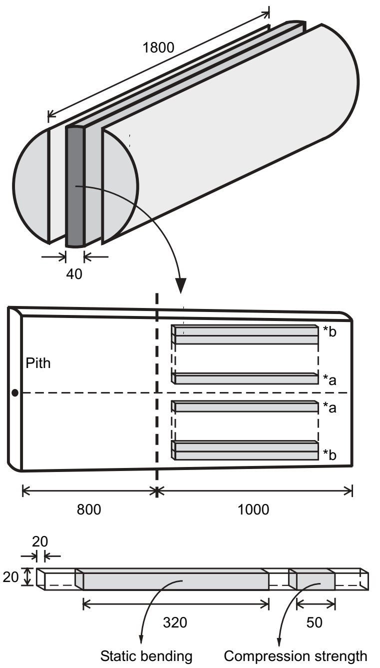

Fig. 1. Sample preparation procedure for the static bending and compression strength tests using small clear specimens. *a, innermost specimen (IN); *b, outermost specimen (OUT). Units are in millimeters

The mechanical properties of the small clear specimens were tested using an Instron universal testing machine. All testing procedures employed conformed to those of the Japan Industrial Standards Z2101 (Japanese Standards Association 1994). The specific mechanical characteristics evaluated were the modulus of elasticity (MOE) and modulus of rupture (MOR) in the bending test, the maximum crushing strength in compression parallel to grain (CS), and the wood density (DEN). Wood density was measured using the compression test specimens. The average moisture content of the small clear specimens was 13.1%.

Statistical analysis

Analyses of variance for all observed traits were performed according to the following equation using the SAS Proc GLM SS3 (SAS Institute 1990):

$$Y_{ijkl} = \mu + R_i + F_j + M_k + \mathrm{FM}_{jk} + \mathrm{RFM}_{ijk} + \varepsilon_{ijkl} \tag{2}$$

where Y_{ijkl} is the observed measurement of the lth tree of the jth female parent and kth male parent in the ith replicate, μ is the general mean, R_i is the fixed effect of replicate i, F_j is the random effect of female j with variance σ^2_{f}, M_k is the random effect of male k with variance σ^2_{m}, FM_{jk} is the random interaction effect between female j and male k with variance σ^2_{fm}, RFM_{ijk} is the between-plot error, random effect with variance σ^2_{rfm}, and ε_{ijkl} is the within-plot error, random effect with variance σ^2_{e}. Variance components for each mechanical characteristic were estimated using the

Table 1. Measured traits included in the analyses

Abbreviation	Description
$E_{\log}$	Dynamic modulus of elasticity of the green logs
MOE_IN	Clearwood modulus of elasticity of the innermost specimen
MOE_OUT	Clearwood modulus of elasticity of the outermost specimen
MOE_ALL	Average of clearwood modulus of elasticity of all specimens
MOR_IN	Clearwood modulus of rupture of the innermost specimen
MOR_OUT	Clearwood modulus of rupture of the outermost specimen
MOR_ALL	Average of clearwood modulus of rupture of all specimens
CS_IN	Clearwood compression strength of the innermost specimen
CS_OUT	Clearwood compression strength of the outermost specimen
CS_ALL	Average of clearwood compression strength of all specimens
DEN_IN	Wood density of the innermost specimen
DEN_OUT	Wood density of the outermost specimen
DEN_ALL	Average of wood density of all specimens
DBH	Diameter at breast height

restricted maximum likelihood (REML) method of the SAS VARCOMP procedure, and estimates of the covariance between these traits were obtained from MANOVA statement (SAS Institute 1990).

For analysis of the factorial mating design, the variance components for male and female plants were assumed to be equal to one fourth of the additive genetic variance ($\sigma^2_{\mathrm{A}} = 4\sigma^2_{\mathrm{f}} = 4\sigma^2_{\mathrm{m}}$); the variance component σ^2_{fm} estimated one quarter of the dominance variance ($\sigma^2_{\mathrm{D}} = 4\sigma^2_{\mathrm{fm}}$), assuming that epistatic and maternal effects were negligible and that the coefficient of inbreeding among parents was zero (Cotterill et al. 1987). The narrow-sense heritability is given by the following formula on an individual tree basis (Zobel and Talbert 1984):

$$h^2 = \frac{2\left(\sigma^2_{\mathrm{f}} + \sigma^2_{\mathrm{m}}\right)}{\sigma^2_{\mathrm{f}} + \sigma^2_{\mathrm{m}} + \sigma^2_{\mathrm{fm}} + \sigma^2_{\mathrm{rfm}} + \sigma^2_{\mathrm{e}}} \tag{3}$$

The genetic correlation was calculated as follows (Becker 1984):

$$r_{\mathrm{g}} = \frac{\mathrm{cov}_{\mathrm{f(x,y)}} + \mathrm{cov}_{\mathrm{m(x,y)}}}{\sqrt{\left(\sigma^2_{\mathrm{f(x)}} + \sigma^2_{\mathrm{m(x)}}\right) \times \left(\sigma^2_{\mathrm{f(y)}} + \sigma^2_{\mathrm{m(y)}}\right)}} \tag{4}$$

where r_{g} is the genetic correlation, $\mathrm{cov}_{(\mathrm{x,y})}$ is the covariance between traits x and y, $\sigma_{(\mathrm{x})}$ and $\sigma_{(\mathrm{y})}$ are variance components of the two traits, and subscripts f and m indicate female and male parents, respectively. Standard errors of the heritability and additive genetic correlations were calculated respectively as in Becker (1984) and Falconer and Mackay (1996).

The predicted genetic gain (ΔG) from direct selection of a single trait and the predicted correlated genetic responses of indirect selection were calculated as follows (Falconer and Mackay 1996):

$$\Delta G = ih^2_{\mathrm{F}}\sigma_{\mathrm{F}} \tag{5}$$

$$\mathrm{CR} = ih_{(\mathrm{x})}h_{(\mathrm{y})}r_{\mathrm{g}}\sigma_{(\mathrm{y})} \tag{6}$$

where i is the standardized selection intensity, h^2_{F} is family mean heritability, and σ_{F} is the standard deviation of the family mean, CR is the correlated response of trait y due to the selection of trait x, $h_{(\mathrm{x})}$ and $h_{(\mathrm{y})}$ are the square roots of family mean heritability for traits x and y, r_{g} is the genetic correlation between traits x and y, and $\sigma_{(\mathrm{y})}$ is the standard deviation of the family mean for trait y. Family mean heritability was calculated following Barnes and Schweppenhauser (1978).

The measured traits are listed in Table 1. To examine the within-tree variation, MOE, MOR, CS, and DEN were divided into inner (IN) and outer (OUT) positions representing positions nearest the pith and bark, respectively (Fig. 1).

Results

Table 2 shows the mean, range, and coefficients of variation for the various wood properties. The overall mean $E_{\log}$ was 9.7×10^3 MPa (6.4–13.1 MPa), which was nearly identical to that of MOE_ALL (9.0×10^3 MPa). The coefficient of variation ranged from 9.2% to 23.7% in all measured traits and was highest in MOE_IN. All mechanical properties and DEN were larger for IN than for OUT and the difference between the positions was highest for MOE.

Additive and dominance variance components and narrow-sense heritability estimates of the various traits are given in Table 3. The additive genetic variance components associated with both female and male parents differed significantly from zero for all measured traits, with some exceptions. Female parents had a significant effect only in the IN position and male parents were significant only in the OUT position for MOE and CS. The magnitude of the additive genetic variance component associated with the male parent effects was greater than that associated with the female parent effects for ALL mechanical properties. No dominance effect was shown with any of the traits as all dominance genetic variance components were zero. DEN_OUT showed the highest heritability estimate at 0.79 and MOE_IN was the lowest at 0.28 (Table 3). Narrow-sense heritability estimates were larger for IN than for OUT with all traits. Standard errors of the heritability estimates

Table 2. Mean, range (minimum–maximum), and coefficient of variation (CV) of all individuals for various traits

Trait		Mean	Minimum	Maximum	CV (%)
$E_{\log}$	($\times 10^3$ MPa)	9.7	6.4	13.1	14.5
MOE_IN	($\times 10^3$ MPa)	6.0	3.2	9.7	23.7
MOE_OUT	($\times 10^3$ MPa)	12.6	5.9	16.1	15.9
MOE_ALL	($\times 10^3$ MPa)	9.0	4.8	12.4	17.0
MOR_IN	(MPa)	60.6	42.2	79.3	14.8
MOR_OUT	(MPa)	95.2	64.7	126.8	12.9
MOR_ALL	(MPa)	77.0	56.9	104.0	12.4
CS_IN	(MPa)	30.9	22.9	44.4	13.2
CS_OUT	(MPa)	47.3	30.9	58.6	11.3
CS_ALL	(MPa)	39.0	28.4	49.6	10.7
DEN_IN	(kg/m^3)	481	399	587	9.2
DEN_OUT	(kg/m^3)	587	437	710	9.7
DEN_ALL	(kg/m^3)	538	418	660	9.2
DBH	(cm)	23.3	15.0	29.7	14.7

Table 3. Additive and dominance genetic variance components, and narrow-sense heritability estimates for various traits

Trait	σ_A				σ_D		h^2	SE
	$4\sigma_f$	P value	$4\sigma_m$	P value	$4\sigma_{fm}$	P value		
$E_{\log}$	1.032	0.015	1.608	0.005	0.000	0.785	0.61	0.24
MOE_IN	1.178	0.014	0.000	0.337	0.000	0.656	0.28	0.22
MOE_OUT	0.000	0.083	4.086	<0.0001	0.000	0.997	0.49	0.24
MOE_ALL	0.582	0.018	1.613	0.003	0.000	0.931	0.44	0.23
MOR_IN	51.661	0.001	21.363	0.006	0.000	0.974	0.42	0.23
MOR_OUT	0.000	0.061	183.341	<0.0001	0.000	0.985	0.61	0.24
MOR_ALL	31.264	0.002	82.444	0.000	0.000	0.984	0.60	0.24
CS_IN	9.175	0.011	4.190	0.065	0.000	0.793	0.38	0.23
CS_OUT	0.000	0.339	27.234	0.003	0.000	0.869	0.45	0.23
CS_ALL	5.396	0.026	10.310	0.010	0.000	0.888	0.43	0.23
DEN_IN	0.001	0.038	0.001	0.014	0.000	0.766	0.54	0.24
DEN_OUT	0.002	0.031	0.004	0.002	0.000	0.791	0.79	0.24
DEN_ALL	0.002	0.013	0.002	0.009	0.000	0.859	0.66	0.24
DBH	4.724	0.000	6.085	0.001	0.000	0.998	0.44	0.23

Some variance components were occasionally negative, and under these cases variance components were set to zero

σ_A, Additive genetic variance component; σ_D, dominance genetic variance component; σ_f, female variance component; σ_m, male variance component; σ_{fm}, family variance component; h^2, narrow-sense heritability estimates; SE, standard errors for h^2

Table 4. Estimated genetic (above the diagonal) and phenotypic (below the diagonal) correlations for various traits

	$E_{\log}$	MOE_ALL	MOR_ALL	CS_ALL	DEN_ALL	DBH
$E_{\log}$		0.72 (0.16)	0.70 (0.15)	0.76 (0.14)	0.79 (0.10)	–0.08 (0.32)
MOE_ALL	0.59		1.00 (0.00)	1.00 (0.00)	0.87 (0.08)	–0.15 (0.37)
MOR_ALL	0.52	0.90		0.96 (0.03)	0.88 (0.06)	–0.21 (0.31)
CS_ALL	0.54	0.84	0.85		0.92 (0.05)	–0.06 (0.38)
DEN_ALL	0.52	0.65	0.78	0.83		–0.30 (0.28)
DBH	0.01	0.04	–0.01	0.08	0.03	

Standard errors for genetic correlation estimates are given in parentheses

were large, ranging from 0.22 to 0.24, because of the small sample size.

Estimates of phenotypic and genetic correlations among traits are shown in Table 4. DEN_ALL had high positive phenotypic (0.52–0.83) and genetic (0.79–0.92) correlations with all mechanical properties measured in this study, and showed a stronger correlation with CS_ALL than MOE_ALL and MOR_ALL. $E_{\log}$ had high positive phenotypic (0.52–0.59) and genetic (0.70–0.76) correlations with the other strength properties. Standard errors of the genetic correlations among wood density and the mechanical properties ranged from 0.00 to 0.16. Estimated phenotypic and genetic correlations between diameter at breast height (DBH) and all wood quality traits measured in this study were weak, with high standard errors, ranging from 0.28 to 0.38. The correlation coefficients among IN, OUT, and

ALL were moderate to high, ranging from 0.37 to 0.88 for the phenotypic correlations and from 0.47 to 0.98 for the genetic correlations (Table 5).

The predicted genetic gains from direct selection of various wood properties and correlated responses in target traits (MOE_ALL, MOR_ALL, and CS_ALL) from indirect selection are listed in Table 6. Results showed that selection of the top 5% of families for each trait (giving a selection intensity of 1.844) would result in a 6.5%–12.1% gain in each trait. The predicted gains in wood stiffness ($E_{\log}$ and MOE_ALL) were higher than those of the strength properties (MOR_ALL and CS_ALL). The predicted correlated responses in MOE_ALL, MOR_ALL, and CS_ALL, while selecting for $E_{\log}$ and DEN_ALL were 72.6%–97.8% of a gain achievable from direct selection of these traits. The correlated responses in MOE_ALL, MOR_ALL, and CS_ALL from indirect selection of DBH were negative and low, ranging from –6.3 to –18.0%.

Discussion

Population variation

The values of the mechanical properties examined in this study were slightly larger than in earlier studies of hybrid larch, perhaps owing to the differences in tree age at sampling (Bendtsen 1978). By examining 17-year-old hybrid larch families, Akutsu et al. (1993) found that MOE and MOR in a static bending test using small clear specimens were 7.1×10^3 and 57.3 MPa, respectively. Iizuka et al. (2000) reported that the dynamic modulus of elasticity of green logs was 7.3×10^3 MPa (6.3–8.7×10^3 MPa, CV 15.2%) with 9-year-old hybrid larch families. The radial variation in MOE, MOR, and CS in the present study is shown in Fig. 2. MOE increased linearly with increasing distance from the pith, as did MOR and CS. These radial trends indicate that the samples assessed were juvenile wood, and, therefore, as the stand grows older their stiffness and strength should increase. DEN had the lowest coefficients of variation and MOE the highest (Table 2). This was consistent with earlier studies on *Larix kaempferi* (Koizumi et al. 1990; Takata et al. 1992), *Pinus taeda* (Pearson and Gilmore 1980), and *Pinus radiata* (Burdon et al. 2001; Kumar 2004).

Table 5. Relationships among sampling positions

Trait		IN vs OUT	IN vs ALL	OUT vs ALL
MOE	r_p	0.43	0.76	0.87
	r_g	0.63	0.84	0.95
	SE	0.26	0.13	0.03
MOR	r_p	0.37	0.74	0.84
	r_g	0.57	0.86	0.91
	SE	0.23	0.09	0.05
CS	r_p	0.45	0.81	0.85
	r_g	0.47	0.87	0.85
	SE	0.31	0.10	0.10
DEN	r_p	0.60	0.86	0.88
	r_g	0.77	0.98	0.91
	SE	0.11	0.01	0.04

r_p, Phenotypic correlation coefficient; r_g, genetic correlation coefficient; SE, standard error for genetic correlation

Variance components and heritability

No significant dominance variance was demonstrated with any trait, indicating that the genetic effects of the variables studied here are largely additive, while the specific combining ability is very limited in hybrid larch. However, as stated by Namkoong and Roberds (1974), a mating design with few full-sib families per half-sib family, as used here, is not optimal for estimating dominance variance. Further studies are therefore required to better understand the genetic structure of the mechanical properties of hybrid larch.

Narrow-sense heritability estimates of the mechanical properties ranged from 0.28 to 0.61 in this study, indicating that wood stiffness and strength are under moderate genetic control in hybrid larch. Compared with growth traits and wood density, genetic control of mechanical properties has not been well documented. Fujisawa et al. (1992) reported the estimated broad-sense heritability of the dynamic modulus of elasticity as 0.597–0.867 in *Cryptomeria japonica*. Kumar et al. (2002) investigated the wood stiffness and strength of *Pinus radiata* using various methods and found that individual-tree heritability of HITMAN and FAKOPP were 0.47 and 0.46, and MOE and MOR of

Table 6. Predicted genetic gain for direct selection and correlated genetic response from indirect selection for various traits

Trait		h^2_F	ΔG^a (%)	Indirect selection (%)^b		
				MOE_ALL	MOR_ALL	CS_ALL
$E_{\log}$	($\times 10^3$ MPa)	0.80	12.1	78.5	72.6	88.3
MOE_ALL	($\times 10^3$ MPa)	0.67	11.4	100.0	97.0	106.4
MOR_ALL	(MPa)	0.73	10.0	105.8	100.0	107.3
CS_ALL	(MPa)	0.59	6.5	93.3	86.1	100.0
DEN_ALL	(kg/m^3)	0.66	7.3	85.7	83.3	97.8
DBH	(cm)	0.55	8.5	–13.2	–18.0	–6.3

h^2_F, Family mean heritability; ΔG, predicted genetic gain for single trait from direct selection

[a] ΔG was arbitrarily calculated for selection of the top 5% of families, and selection intensity was given to be 1.844 according to Becker (1984), in this case

[b] The ratio of gain in MOE_ALL, MOR_ALL, and CS_ALL from indirect selection to that obtained from direct selection on these traits

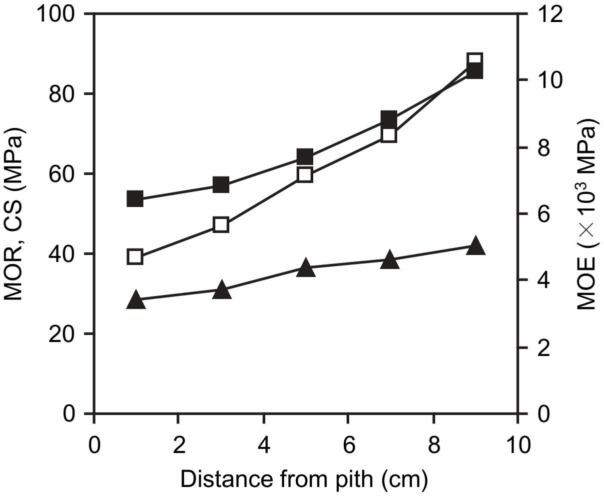

Fig. 2. Radial variation in the modulus of elasticity (*MOE*), modulus of rupture (*MOR*), and compression strength (*CS*). Each plot indicates the mean value calculated from all individuals. *Open squares*, MOE; *filled squares*, MOR; *filled triangles*, CS

small clear sticks were 0.53 and 0.54, respectively. In Norway spruce (*Picea abies*), Hannrup et al. (2004) obtained a broad-sense heritability of bending stiffness of 0.14–0.17.

Heritability estimates of wood density and mechanical properties increased from an inner to outer position, resembling the trends reported previously for wood density and tracheid length in other species (Vargas-Hernandez and Adams 1992; Hylen 1999; Hannrup and Ekberg 1998). In contrast, heritability of spiral grain angle decreases with increasing tree age (Nicholls 1967; Fujimoto et al. 2006a). These findings suggest that the genetic control of wood characters changes with age, while different characters follow different trends.

Genetic and phenotypic correlations among traits

High genetic and phenotypic correlations between DEN and $E_{\log}$ and the mechanical properties were found in this study, consistent with earlier studies. For example, Cown et al. (1999) confirmed that wood density was the most influential parameter affecting clearwood structural performance of both juvenile and mature wood of radiata pine. Due to the high correlation between $E_{\log}$ and the structural properties of sawn lumber, Arima et al. (1993) suggested that measuring $E_{\log}$ could be an effective and easy way of conducting on-site mechanical grading before transportation to the saw mill. Kumar et al. (2002) obtained high phenotypic and genetic correlations of stiffness using both nondestructive and destructive methods, namely, the acoustic methods HITMAN and FAKOPP as well as the static bending test using clearwood sticks. These results imply that nondestructive methods or surrogate traits like wood density could be used for indirect assessment of stiffness and strength in hybrid larch progeny trials.

The relationships between growth rate and wood properties are an important topic in forestry and forest products research. In this study, radial growth rate (DBH) had weak phenotypic and genetic correlations with wood density and mechanical properties. This finding suggests that some genotypes result in good growth performance as well as high wood density and stiffness characteristics. Similar results have been reported by Zhang (1995) in *Larix* species and by Kumar (2004) in *Pinus radiata*. However, it should be noted that the estimated correlations between DBH and wood properties were less precise in the present study.

Juvenile–mature and age–age correlations are important in evaluating the possibility of early selection and in determining the best selection age. In the present study, the mechanical properties and wood density of the inner part of the stem had rather high phenotypic and genetic correlations with those of the outer part and overall mean. These high correlations between inner and outer traits suggest that the inner (younger age) traits are a good genetic indicator of the outer (older age) traits and that there will be more gain per unit time with selection at an earlier age (Vargas-Hernandez and Adams 1992).

Implications for breeding

Wood stiffness (MOE) showed high predicted genetic gain from direct selection in the present study. This is because of the relatively high phenotypic variation in MOE (Table 2), although the heritability estimate of this trait was slightly lower than those of the other wood properties (Table 3). The indirect selection using $E_{\log}$ and DEN resulted in a highly positive response in wood stiffness and strength, due to the strong genetic control of $E_{\log}$ and DEN and those moderate to high genetic correlations with stiffness and strength. This finding suggests that selection using log stiffness and wood density, which are easier and cheaper to measure, should be effective in improving wood mechanical properties. These findings were in accordance with those of a previous study on *Pinus radiata* reported by Kumar et al. (2004).

Most tree breeding programs for common plantation species in Japan place major emphasis on improving growth rate. All target mechanical properties in this study, MOE, MOR and CS, showed a weak negative response with indirect selection of growth rate (DBH). This connotes that selection based solely on growth rate will simultaneously result in a slight reduction in the mechanical properties. Therefore, to achieve optimal genetic gains, index selection of multiple traits seems essential (Zhang and Morgenstern 1995). However, this negative response might be mainly due to the relatively high phenotypic variation (Table 2) and heritability (Table 3) of DBH, because the genetic correlations between DBH and the mechanical properties were low in the present study (Table 4). As mentioned above, the estimation of the genetic correlation between DBH and the mechanical properties was relatively imprecise, and, therefore, further study is required to better our understanding of the relationship among these traits.

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