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ORIGINAL ARTICLE

Takaaki Fujimoto · Kazuhito Kita · Kazuko Uchiyama
Makoto Kuromaru · Hisashi Akutsu · Kazuyuki Oda

Age trends in the genetic parameters of wood density and the relationship with growth rates in hybrid larch (*Larix gmelinii* var. *japonica* × *L. kaempferi*) F_1

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Abstract Age trends in variance components and heritability of overall wood density, earlywood and latewood density, and latewood proportion were investigated in 29-year-old trees of 19 full-sib families of hybrid larch (*Larix gmelinii* var. *japonica* × *Larix kaempferi*) F_1. The age–age correlation and optimum selection age for these traits were also estimated and genetic and phenotypic correlations between wood density and radial growth rate were calculated for each growth ring. Intraring wood density data were obtained using X-ray densitometry. The coefficient of additive genetic variance was stable over all ages, whereas the coefficient of environmental variances gradually decreased with increasing age, resulting in increases in heritability estimates with age for overall density. The latewood proportion had the highest heritability estimates at all ages, ranging from 0.44 to 0.66. Overall density and its various components at 28 years of age showed strong genetic correlations with their respective traits at all younger ages. Optimum selection ages for the wood density traits ranged from 8 to 14 years, at which point maximum gain efficiencies per year were obtained. There were negative correlations between wood density and radial growth rate at early ages, although these relationships tended to be weaker with increasing age. These results suggest that selection at a young age is effective for wood density, but particular care must be taken in selecting trees with an improved radial growth rate because rapid growth will result in a low-density wood product, especially in the early growth period.

Key words Age–age correlation · Heritability · Hybrid larch · Optimum selection age · Wood density

Introduction

Japanese larch (*Larix kaempferi*) is a common reforestation species in Hokkaido, Japan, because it shows rapid juvenile growth and good adaptation to even severe sites (Mikami 1988). However, this species is susceptible to various sorts of pests and diseases (Takahashi and Nishiguchi 1966; Hayashi et al. 1998). In contrast, interspecific hybrids between Kurile larch (*Larix gmelinii* var. *japonica*) and Japanese larch are superior to Japanese larch and all other hybrid larches with regard to growth and resistance to pests and diseases (Hamaya and Kurahashi 1981). Furthermore, this hybrid can maintain a moderately high wood density irrespective of rapid growth; thus; it appears to offer good potential for use under intensive forest management.

Wood density is of key importance in forest product manufacture because it is strongly correlated with the strength properties of wood and with pulp and paper quality (Zobel and van Buijtenen 1989). In addition, wood density can be altered by silvicultural and genetic manipulations (Williams and Hamilton 1961; Zobel 1961). Orita (1985) reported that broad-sense heritability of basic density in Japanese larch was 0.75 for heartwood and 0.85 for sapwood. Moreover, Oshima and Kuromaru (1995) examined 25 controlled pollinated families of 19-year-old hybrid larch and found that the narrow-sense heritability of basic density was 0.55. A major limitation of these studies, however, is that the age trends in genetic parameters and age–age correlations for wood density traits were not estimated. Knowledge of changes in the genetic parameters of traits and correlations between these traits at different ages are necessary for determination of the efficiency of early selection (Kang 1985).

The relationship between growth rate and wood density has been studied intensively, but the results reported are rather controversial. According to Zobel and van Buijtenen (1989), larch species show little or no relationship between growth rate and wood density, as in hard pine species. Zhang (1995) reported the same tendency in two larch species (*Larix gmelinii* and *Larix olgensis*); however, Koizumi et al. (1990) and Takata et al. (1992) found that wood den-

T. Fujimoto (✉) · H. Akutsu
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 · K. Uchiyama · M. Kuromaru
Hokkaido Forestry Research Institute, Bibai, Japan

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

sity is negatively correlated with growth rate in Japanese larch. Growth rates affect wood density at different ages (Zobel and Sprague 1998), and thus, ignoring the age effect can result in misinterpretation of growth rates as the causal factor of differing specific gravity (Bendtsen 1978). There is little information available about the age-associated changes in genetic and phenotypic correlations between growth rate and wood density in hybrid larch.

The objectives of the present study are to: (1) examine the age trends in genetic parameters of wood density and various components of wood density; (2) estimate the age–age correlation and optimum selection age; and (3) examine the phenotypic and genetic correlation between growth rate and wood density at different ages.

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 (43°28′N, 141°88′E; 250 m elevation). The progeny test consisted of 19 full-sib families derived from an incomplete factorial mating design involving four female and six male parent trees (Table 1). Parents were chosen from plus trees selected in Hokkaido. The test was established in 1974 with 2-year-old seedlings and the 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 of the families. As a result, the total number of sample trees was 95. A 1.8-m butt log was obtained from each tree and a diametric flitch, 40 mm thick, was then sawn from each butt log.

Wood density measurements

A 2-mm long (longitudinal direction) section including the pith was cut from the top end of each flitch free from decay and knots. This sampling position indicates a height of approximately 2 m above ground level. Resin was then extracted from these sections with a solution of benzene–ethanol (2:1) for 1 week. Thereafter, the sections were dried to an equilibrium moisture content of about 12%.

Table 1. Outline of the mating design for the progeny test stand

Females	Males (*Larix kaempferi*)					
	L1	L2	L3	L4	L5	L6
Larix gmelinii						
G1		●		●	●	
G2	●	●	●	●	●	●
G3	●	●	●	●	●	●
G4		●	●	●	●	

Filled circles indicate the sampled families

Intraring density and width information was obtained using an X-ray densitometry technique (Ohta 1970; Polge and Nicholls 1972). Each sample section was scanned from the pith toward the bark in two radial directions and density was expressed as the mean of both values. The first and last annual rings were discarded from further analysis because they were generally incomplete. For each of the remaining annual rings in the samples, earlywood density, latewood density, latewood proportion, and average ring density (overall density) were obtained based on the densitometric profiles. Demarcation between earlywood and latewood in each ring was defined as the point where the wood density in each ring was 0.55 g/cm^3 (Ohta 1970). This point was based on a detailed comparison of results obtained by X-ray analyses and the definition of latewood given by Mork (1928).

The sample sections contained 24–27 growth rings as trees reached the sampling height at different ages. To avoid a confounding effect owing to the difference in the year of wood formation, annual rings were identified and numbered starting from the bark and moving toward the pith (Vargas-Hernandez and Adams 1992). Thus, the final growth rings used in the following analyses were 7–28 in terms of tree age.

Area-weighted averages from the pith to bark were calculated for individual wood density using the following formula (Hannrup and Ekberg 1998):

$$\mathrm{AWD} = \sum a_i \cdot d_i \Big/ \sum a_i \qquad (1)$$

where AWD is the area-weighted density, a_i is the cross-sectional area of the ith growth ring assuming that each ring is perfectly circular, and d_i is the wood density of the ith growth ring. Area-weighted density for earlywood and latewood density were calculated in the same way by substituting the corresponding area and density into the formula given above. Latewood proportions of each sample section were calculated based on the total latewood width of growth rings divided by the total width of the rings. These weighted data were used in the following analyses.

Statistical analysiss

Analyses of variance for all observed values for each growth ring were performed according to the models in Eq. 2 using the SAS Proc GLM SS3 as follows (SAS Institute 1990):

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

where Y_{ijkl} is the observed value 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 parent j and male parent 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 ring were estimated using the restricted maximum likelihood (REML) method in the

SAS VARCOMP procedure and estimates of the covariance between different rings were obtained with the MANOVA statement (SAS Institute 1990). Variance components were expressed in terms of coefficients of variation to avoid potentially confounding scale effects.

The factorial mating design allowed estimation of genetic variance components: additive and dominance variances. Additive variance (σ_A^2) can be derived directly from female and male variance components, assuming that epistatic and maternal effects are negligible and that the coefficient of inbreeding among the parents is zero (Cotterill et al. 1987):

$$\sigma_A^2 = 4\sigma_f = 4\sigma_m^2 \tag{3}$$

Similarly, dominance genetic variance (σ_D^2) was estimated from:

$$\sigma_D^2 = 4\sigma_{fm}^2 \tag{4}$$

Narrow-sense heritability is given by the following formula on an individual tree basis (Zobel and Talbert 1984):

$$h^2 = \frac{2\left(\sigma_f^2 + \sigma_m^2\right)}{\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_{rfm}^2 + \sigma_e^2} \tag{5}$$

The age–age genetic correlation of each trait measured at two different ages was calculated as follows (Becker 1984):

$$r_g = \frac{\mathrm{cov}_{fi,o} + \mathrm{cov}_{mi,0}}{\sqrt{\left(\sigma_{fi}^2 + \sigma_{mi}^2\right) \times \left(\sigma_{fo}^2 + \sigma_{mo}^2\right)}} \tag{6}$$

where r_g is the genetic correlation, $\mathrm{cov}_{i,o}$ is the covariance between the ith ring and outermost ring, σ_i and σ_o are variance components of the ith ring and outermost ring, respectively, while subscripts f and m indicate female and male parents, respectively. The genetic correlation between growth rate and wood density was also estimated using Eq. 6, by substituting the corresponding variance and covariance components of ring width and wood density. Phenotypic correlation coefficients were calculated in the same way by substituting the corresponding covariance and variance components into the formula given above. Standard errors of the heritability and genetic correlations were calculated respectively as in Becker (1984) and Falconer and Mackay (1996).

The optimum age for selection was estimated using the gain efficiency per year, the ratio of the genetic gain per year of indirect selection based upon early selection relative to direct selection for the breeding goal. Assuming equal intensities of selection between mature and young ages, gain efficiency per year was calculated as (Lambeth 1980):

$$E = \frac{h_j r_g T_m}{h_m T_j} \tag{7}$$

where E is the gain efficiency, r_g is the genetic correlation between the juvenile trait and mature (assumed to be 28 years old) trait, and h_j and h_m are the square roots of individual tree heritability at juvenile and mature ages, respectively. T_j and T_m are the respective generation intervals for juvenile and mature selection. In this study, the generation interval represents the selection age plus a delay time of 5 years (Gwaze et al. 2002).

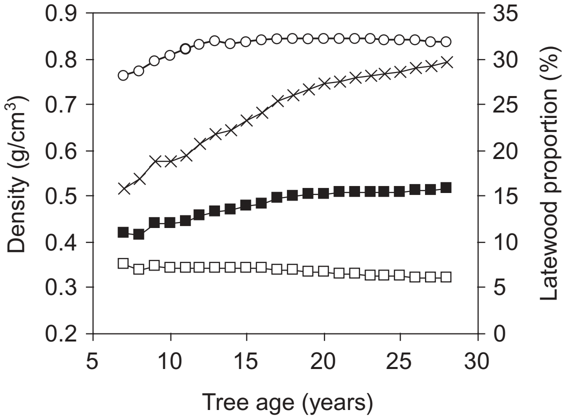

Fig. 1. Age trends in population means for wood density and its components. *Filled squares*, overall density; *open squares*, earlywood density; *circles*, latewood density; *crosses*, latewood proportion

Results and discussion

Population means

Overall density increased steadily from 0.42 g/cm^3 at 7 years of age up to 0.50 g/cm^3 at 18 years at which point it leveled off (Fig. 1). A similar tendency was observed for latewood density and latewood proportion, although the shape of the curves varied for each trait. Latewood density increased up to 12 years of age and leveled off thereafter. Latewood proportion gradually increased over time with no clear plateau region. In contrast, earlywood density decreased slightly in a linear fashion over time, ranging from 0.35 to 0.32 g/cm^3.

Age trends and magnitude of wood density and its components were consistent with those observed for the same traits in *Larix* spp. (Pearson and Fielding 1961; Nobori et al. 1990). Overall density and latewood density values leveled off at about 18 and 12 years of age, respectively; therefore, these points can be considered the transition age from juvenile to mature wood. The effect of the presence of juvenile wood on wood uniformity is one of the most important wood characteristics. Hodge and Purnell (1993) reported that in slash pine (*Pinus elliottii*), the transition age of overall density, latewood density, and latewood proportion are 9.4, 7.5 and 10.3 years, respectively. In a previous report, Fujimoto et al. (2005) examined the radial variation of tracheid length in hybrid larch and found that the transition age was 18.8 years. These results confirm that the transition age from juvenile to mature wood depends upon the species and wood characteristics examined (Zobel and Sprague 1998).

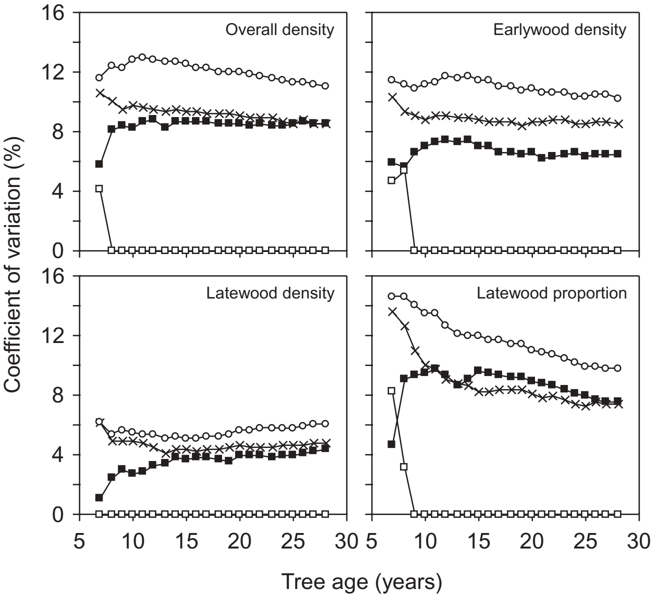

Fig. 2. Age trends of the phenotypic (*circles*), environmental (*crosses*), additive genetic (*filled squares*) and dominance genetic (*open squares*) coefficients of variation for wood density and its components

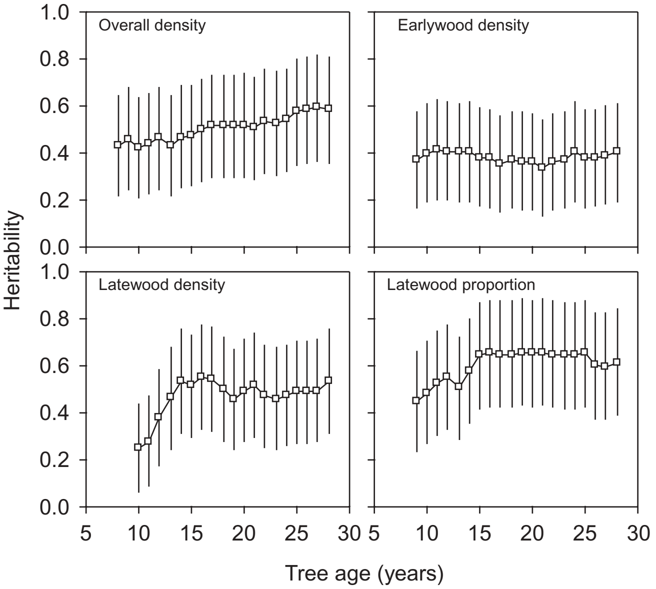

Fig. 3. Age trends in narrow-sense individual heritability estimates for wood density and its components. *Error bars* show standard error

Variance components and heritability

The effects of both female and male parents were significant at $P < 0.01$ or $P < 0.05$ for overall density and latewood proportion at all ages, except ages of 7 and 8 years. With earlywood density, the effects of the female parent were significant at $P < 0.01$ or $P < 0.05$ for all ages, except ages of 7 and 8 years, but the effects of the male parent were not significant at almost all ages. In contrast, significant effects were found only with the male parent for latewood density at all ages ($P < 0.01$). The female × male parent interaction had no significant effect on any density trait at all ages.

In general, the coefficient of phenotypic and environmental variance for all density traits declined with increasing age, except for latewood density (Fig. 2). In particular, a marked reduction was found with latewood proportion. The coefficient of additive genetic variance was stable over ages for overall density and earlywood density, although it was slightly low at an early age. Additive genetic variance for latewood density gradually increased with age. With latewood proportion, additive genetic variance increased to about 11 years of age and was then followed by a slight decrease with increasing age. The coefficient of dominance variance was zero for all density traits at all ages except an early age.

Age trends in narrow-sense heritability estimates for wood density and its components are shown in Fig. 3. Heritability estimates for each density trait were calculated only for ages that showed significant female or male parent variation. The heritability estimates for overall density steadily increased with age from 0.42 to 0.59 (Fig. 3), whereas heritability leveled off from 14 and 15 years of age for latewood density and latewood proportion, respectively. Latewood proportion had the highest heritability estimates at all ages, ranging from 0.44 to 0.66. Earlywood density had the lowest heritability estimates at nearly all ages and fluctuated around 0.38 over all ages. Standard errors of heritability estimates for all traits were high (0.15–0.23) because of the small number of progeny.

The steady decrease observed in the coefficient of environmental variance resulted in increases in heritability estimates for overall density and latewood proportion, although the heritability estimates of latewood proportion leveled off at about 15 years of age. The increase in heritability for latewood density at early ages arose from another process in which additive genetic variance increased with age while environmental variance was constant over all ages. Dominance variance was not detected for any density trait at almost all ages, indicating that the specific combining ability is very limited in hybrid larch. However, as stated by Namkoong and Roberds (1974), the used 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 wood density of hybrid larch.

The age trends in heritability estimates for wood density and its components were similar to those reported for the same traits in other studies, with some exceptions. In Douglas fir (*Pseudotsuga menziesii*), for example, Vargas-Hernandez and Adams (1992) reported that the heritability estimates increased with age for all density traits and the latewood proportion had the lowest estimates. Hylen (1999) observed a similar tendency in young Norway spruce (*Picea abies*). These results indicate that the degree of genetic control for wood density and its components change with age and that the latewood proportion is more strongly affected by environmental variation than any other wood density component. On the other hand, in this study, late-

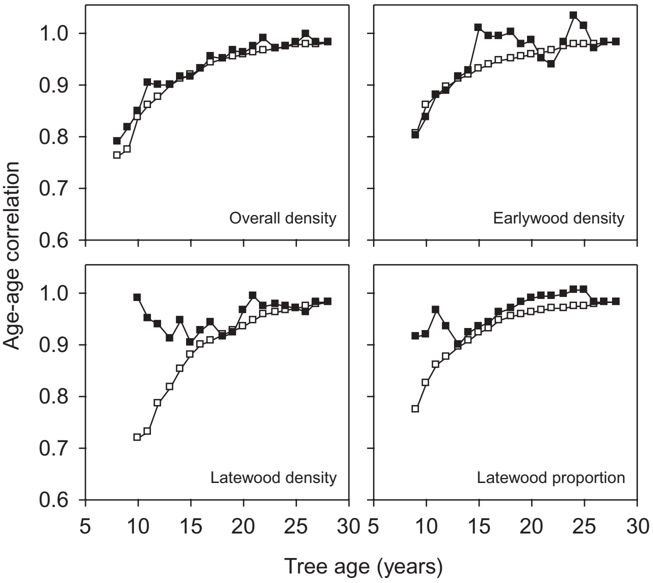

Fig. 4. Age–age genetic (*filled squares*) and phenotypic (*open squares*) correlations between wood density and its components at different ages, with their respective values at 28 years of age

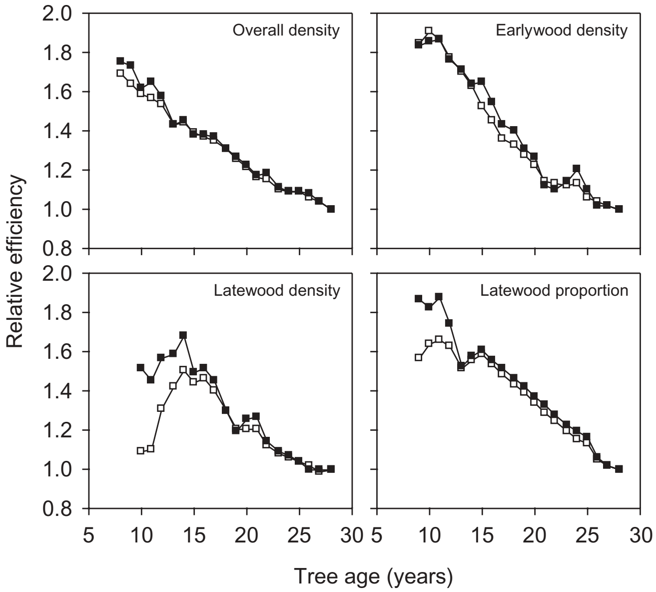

Fig. 5. Relative efficiency of selection for wood density and its components at different ages. *Filled squares*, gain efficiency per year calculated from genetic correlation; *open squares*, gain efficiency per year calculated from phenotypic correlation

wood proportion had the highest heritability estimates at all ages. As mentioned above, we obtained data from only one test stand, and thus, this might have reduced the environmental effect.

Age–age genetic and phenotypic correlations

Genetic and phenotypic correlations between wood density traits at given age and those at 28 years of age are presented in Fig. 4. High correlations were observed even at the youngest age examined here for all density traits, greater than 0.8 for genetic correlations and greater than 0.7 for phenotypic correlations. After 15–20 years of age, estimates of genetic correlation were very close to 1.0. The genetic and phenotypic correlations for overall density showed almost the same trajectories. However, with latewood density and latewood proportion, genetic correlations were higher than the corresponding phenotypic correlations, especially in the early growth stage. The standard errors of the genetic correlations were 0.05–0.10 at an early age, declining with increasing age.

The age–age genetic and phenotypic correlations were generally high at a very young age for wood density and its components, suggesting that the wood density of juvenile wood gives a good indication of mature wood density. The consistency between these high estimates implies that each density trait is directed by the same genes over time, although autocorrelations could upwardly bias these estimates from the remeasurements of the same tree per increment core (Hylen 1999; Talbert et al. 1983).

Lee et al. (2002) reported that genetic and phenotypic correlations for the weighted wood density of Sitka spruce (*Picea sitchensis*) were similar at older ages, but at younger ages, genetic correlations were much higher than their phenotypic counterparts. Similar results have been observed for the same traits in Douglas fir (Vargas-Hernandez and Adams 1992) and loblolly pine (Loo et al. 1984; Gwaze et al. 2002). These results indicate that phenotypic correlations decrease more rapidly as the age interval increases, and that using age–age phenotypic correlations rather than genetic correlations to evaluate efficiency of early selection will cause underestimates of potential gains from early selection. A similar tendency was revealed only in latewood density and latewood proportion in the present study.

Relative efficiency of early selection

The optimum selection age for overall density based on genetic correlations was estimated to be 8 years, at which point a maximum gain efficiency per year of 1.75 was obtained (Fig. 5). Gain efficiency per year for earlywood density, latewood density, and latewood proportion were maximized at a slightly older age (range: 10–14 years) than for overall density. There was no clear difference in the optimum selection age for all traits whether calculations were based on phenotypic correlations or genetic correlations, even though the gain efficiency per year was high with genetic correlations at an early age for some traits.

Few reports have addressed the optimum selection age for wood density and its components. Gwaze et al. (2002) estimated the optimum selection age for wood density in loblolly pine (*Pinus taeda*) and obtained an estimation of 5 years based on genetic and phenotypic correlations. Lee et al. (2002) reported that the recommended optimum indirect selection age and trait for wood density in Sitka spruce is the mean weighted density of the outer four rings from a 9-year-old tree. Moreover, Johnson et al. (1997) found that the optimum selection age for vigor traits in Douglas fir was

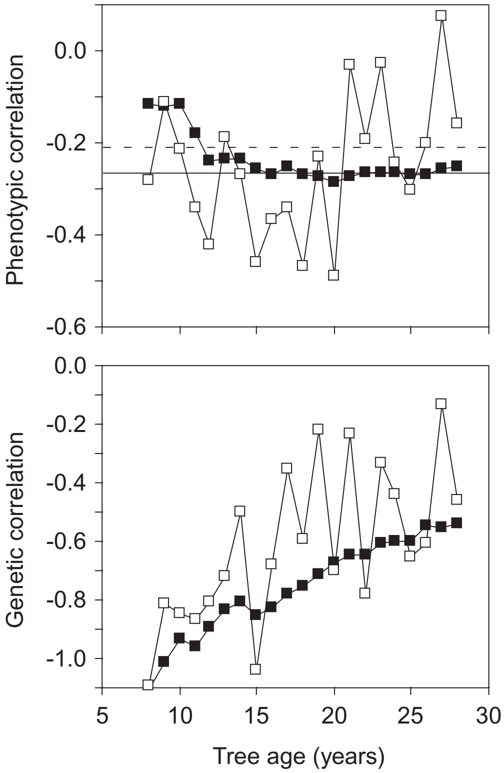

Fig. 6. Phenotypic and genetic correlations between wood density and radial growth rate over tree age. The horizontal lines in the phenotypic correlation represent the critical values at the 0.05 (*broken lines*) and 0.01 (*solid lines*) significance levels. *Filled squares*, correlation between area-weighted density and radial diameter; *open squares*, correlation between individual ring density and ring width

10 years for height and 13 years for diameter. It should be noted that sample sections in this study were taken at a height of about 2m. Figure 5 implies that the optimum selection age might be younger than 8 years old, especially for the overall density. To examine the possibility of early selection prior to 8 years of age, sampling should be made at a height below 2m.

Relationship between wood density and growth rate

Genetic and phenotypic correlations between wood density and radial growth rate at different ages are shown in Fig. 6. These correlations were calculated based on both cumulated (area-weighted) and individual ring values, between area-weighted density and radial diameter, and between individual ring density and ring width at each growth ring. Calculations were made only with regard to overall density.

In all cases there were negative correlations between wood density and radial growth rate over all ages. Based on cumulated ring values, the phenotypic correlations were slightly strong until about age 15 at which point they stabilized. Based on individual ring values, there were significant negative phenotypic correlations at an early growth stage, but these were no longer statistically significant after 20 years of age. The genetic correlations became weak with increasing tree age for both cumulated and individual ring values.

In general, the negative phenotypic and genetic correlations between wood density and radial growth rate decreased with increasing tree age, suggesting that fast growth will have a less negative effect on wood density with increasing age. This result was similar to that reported by Zhang (1998), where a reduction in the genetic and phenotypic correlations between growth rate and wood density was observed with age of black spruce (*Picea mariana*). In Japanese larch, Zhu et al. (2000) also found that wood density was negatively correlated to growth rate during the juvenile period with no correlation during the mature period.

Conclusions

The age trends of variance components and heritability observed here indicate that genetic control of wood density and its components is moderate even at a young age, increasing gradually with age in hybrid larch F_1. Genetic and phenotypic correlations between early ages and 28 years of age for wood density traits were generally high, greater than 0.7. The optimum selection age for wood density traits ranged from 8 to 14 years, assuming that the breeding goal was 28 years. Genetic and phenotypic correlations between wood density and radial growth rate decreased with age. These results suggest that early tests for wood density traits should help increase the efficiency of the hybrid larch tree-breeding program, but it should be noted that improvement of radial growth rate through selection and intensive forest management would result in a low-density wood product, especially at an early growth period.

Literature cited

Becker WA (1984) Manual of quantitative genetics 4th edn. Academic Enterprises, Pullman, WA, USA

Bendtsen BA (1978) Properties of wood from improved and intensively managed trees. Forest Prod J 28:61–72

Cotterill PP, Dean CA, van Wyk G (1987) Additive and dominance genetic effects in *Pinus pinaster*, *P. radiata* and *P. elliottii* and some implications for breeding strategy. Silvae Genet 36:221–232

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics 4th edn. Longman, Essex, UK

Fujimoto T, Akutsu H, Kita K, Uchiyama K, Kuromaru M, Oda K (2005) Genetic variation in the age of transition from juvenile to mature wood in hybrid larch (*Larix gmelinii* var. *japonica* × *L. kaempferi*) F_1 (in Japanese with English summary). Mokuzai Gakkaishi 51:85–91

Gwaze DP, Harding KJ, Purnell RC, Bridgwater FE (2002) Optimum selection age for wood density in loblolly pine. Can J Forest Res 32:1393–1399

Hamaya T, Kurahashi A (1981) Breeding of larch by species hybridization in Japan. In: Krugman SL, Katsutapp M (eds) Proceedings of the XVII IUFRO World Congress, Kyoto, 6–7 September, Division 2, pp 157–168

Hannrup B, Ekberg I (1998) Age–age correlations for tracheid length and wood density in *Pinus sylvestris*. Can J Forest Res 28:1373–1379

Hayashi E, Iizuka K, Sukeno S, Kohno K (1998) Relationship between resistance to vole browsing and content of ether extract in the bark of larch species and hybrids. J For Res 3:119–122

Hodge GR, Purnell RC (1993) Genetic parameter estimates for wood density, transition age, and radial growth in slash pine. Can J Forest Res 23:1881–1891

Hylen G (1999) Age trends in genetic parameters of wood density in young Norway spruce. Can J Forest Res 29:135–143

Johnson GR, Sniezko RA, Mandel NL (1997) Age trends in Douglas-fir genetic parameters and implications for optimum selection age. Silvae Genet 46:349–358

Kang H (1985) Juvenile selection in tree breeding: some mathematical models. Silvae Genet 34:75–84

Koizumi A, Takada K, Ueda K, Katayose T (1990) Radial growth and wood quality of plus trees of Japanese larch. Part II. Diameters at breast heights and trunk moduli of elasticity of 18-year-old offspring families (in Japanese with English summary). Mokuzai Gakkaishi 36:704–708

Lambeth CC (1980) Juvenile-mature correlations in Pinaceae and implications for early selection. Forest Sci 26:571–580

Lee SJ, Woolliams J, Samuel CJA, Malcom DC (2002) A study of population variation and inheritance in sitka spruce. Part III. Age trends in genetic parameters and optimum selection ages for wood density, and genetic correlations with vigour traits. Silvae Genet 51:143–151

Loo JA, Tauer CG, van Buijtenen JP (1984) Juvenile–mature relationships and heritability estimates of several traits in loblolly pine (*Pinus taeda*). Can J Forest Res 14:822–825

Mikami S (1988) Breeding for wood quality of Japanese larch, *Larix kaempferi* (Lamb.) Carr. (in Japanese with English summary). Bull For Tree Bree Inst 6:47–152

Mork E (1928) Die Qualität des Fichtenholzes unter besonderer Rücksichtnahme auf Schleif- und Papierholz. Papier-Fabrikant 26:741–747

Namkoong G, Roberds JH (1974) Choosing mating designs to efficiently estimate genetic variance components for trees. Silvae Genet 23:43–53

Nobori Y, Nagata Y, Chiba S (1990) The volume density analysis of *Larix leptolepis*, *L. gmelinii* var. *japonica* and *L. gmelinii* var. *koreana* by X-ray densitometric analysis (in Japanese). Trans Mtg Hokkaido Br Jpn For Soc 38:47–49

Ohta S (1970) Measurement of the wood density by the soft X-ray and densitometric technique (in Japanese). Mokuzai Kogyo 25:27–29

Orita H (1985) Estimation of genetic variance in wood quality using clonal larch – grain inclination and basic density (in Japanese). Trans Mtg Jpn For Soc 96:287–288

Oshima T, Kuromaru M (1995) Variation among families of wood properties in hybrid larch (*Larix gmelinii* var. *japonica* × *L. leptolepis*) (in Japanese). Trans Mtg Jpn For Soc 106:297–298

Pearson FGO, Fielding HA (1961) Some properties of individual growth rings in European larch and Japanese larch and their influence upon specific gravity. Holzforschung 15:82–89

Polge H, Nicholls JWP (1972) Quantitative radiography and the densitometric analysis of wood. Wood Sci 5:51–59

SAS Institute (1990) SAS/STAT user's guide, version 6, vol 2, 4th edn. SAS Institute, Cary, NC, USA

Takahashi N, Nishiguchi C (1966) Studies on the resistance of forest trees to the red-backed vole, *Clethrionomys rufocanus bedfordiae* (Thomas). Part 2. Relative feeding preference of the vole for seedlings of larch F_1 hybrids under laboratory condition (in Japanese with English summary). Bull Tokyo Univ For 62:173–188

Takata K, Koizumi A, Ueda K (1992) Variations of radial growth and wood quality among provenances in Japanese larch (in Japanese with English summary). Mokuzai Gakkaishi 38:1082–1088

Talbert JT, Jett JB, Bryant RL (1983) Inheritance of wood specific gravity in an unimproved loblolly pine population: 20 years of results. Silvae Genet 32:33–37

Vargas-Hernandez J, Adams WT (1992) Age–age correlations and early selection for wood density in young coastal Douglas-fir. Forest Sci 38:467–478

Williams RF, Hamilton JR (1961) The effect of fertilization on four wood properties of slash pine. J Forest 59:662–665

Zhang SY (1995) Effect of growth rate on wood specific gravity and selected mechanical properties in individual species from distinct wood categories. Wood Sci Technol 29:451–465

Zhang SY (1998) Effect of age on the variation, correlations and inheritance of selected wood characteristics in black spruce (*Picea mariana*). Wood Sci Technol 32:197–204

Zhu J, Nakano T, Hirakawa Y (2000) Effects of growth rate on selected indices for juvenile and mature wood of the Japanese larch. J Wood Sci 46:417–422

Zobel BJ (1961) Inheritance of wood properties in conifers. Silvae Genet 10:65–70

Zobel BJ, Sprague JR (1998) Juvenile wood in forest trees. Springer, Berlin Heidelberg New York

Zobel B, Talbert J (1984) Applied forest tree improvement. Wiley, New York

Zobel BJ, van Buijtenen JP (1989) Wood variation. Its causes and control. Springer, Berlin Heidelberg New York