

Genetic improvement of wood density and radial growth in *Larix kaempferi*: results from a diallel mating test

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Abstract

• **Context** Wood density is an important component of wood quality, and it is therefore important to assess whether it can be subject to genetic improvement.

• **Aim and methods** We assessed the potential for genetic improvement of wood density in *Larix kaempferi* by recording components of annual growth rings. A full diallel mating test based on six plus *L. kaempferi* trees was used. Trees were 29 years old. Wood density was recorded by soft X-ray densitometry, and genetic parameters and genetic gains were computed.

• **Results** Wood density of mature wood was highly heritable, and the largest heritability (0.78) was reached at age 25. Specific combining ability and reciprocal effects displayed very low variance. The age–age correlation of overall wood density was very high (>0.94). The genetic correlation between overall wood density and basal cross-sectional area was positive after age 10. Early selection at age 6 would account for 69 % of the genetic gain from direct selection at age 28 in terms of wood density.

• **Conclusion** Genetic improvement of wood density could be achieved by mass selection and a simultaneous selection for radial increment in *L. kaempferi*; early selection for wood density can be achieved in this species.

Keywords Genetic parameters · Wood density · *Larix kaempferi* · Japanese larch · Heritability · Genetic correlation

1 Introduction

Larix kaempferi (Lambert) Carrière (Japanese larch) is a relict species that is naturally distributed only in cold and high elevation areas in the central regions of Honshu Island, Japan (Hayashi 1960). *L. kaempferi* is one of the major species used in the forestry industry in northern Japan where it accounts for approximately 20 % of all newly planted forest in the country (Forest Tree Breeding Center, Forestry and Forestry Product Research Institute 2011). Outside Japan, *L. kaempferi* has been used as breeding material in many countries. The earliest foreign planting of *L. kaempferi* was recorded in 1885 in Europe (Bergstedt and Lyck 2007). A hybrid between *L. kaempferi* and other *Larix* species has been used in Europe (Matyssek and Schulze 1987; Pâques 2004), North America (Li and Wyckoff 1994; Baltunis et al. 1998), and in Hokkaido Island, Japan (Fujimoto et al. 2006; Kita et al. 2009). In Japanese *L. kaempferi* breeding programs, first-generation plus trees were selected on the basis of their growth characteristics and tree stem form during the 1950s and 1960s. The selection of second-generation trees and the evaluation of the wood properties of first-generation plus tree clones are currently being undertaken (Kurinobu 2005).

Wood density is a particularly important trait because it affects other traits such as the mechanical properties of wood (Zobel and van Buijtenen 1989). Takata and Hirakawa (1996)

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identified a tight correlation between the bending stiffness and wood density in *L. kaempferi*. Pâques et al. (2010) reported a tight genetic correlation between the wood density and modulus of elasticity in hybrid larch. Apiolaza (2009) detected a positive correlation between the wood density and the modulus of elasticity in *Pinus radiata* aged >15 years, whereas the correlation remained weak in younger trees. They also claimed that the importance of wood density for wood quality was overemphasized. Wood density is also an important component of carbon sequestration in trees. The amount of C stored in trees depends on the biomass as well as the C content of the wood and other tissues. Because the C content varies very little in *L. kaempferi* (Fukatsu et al. 2008), wood density and stem volume alone may control C storage at the tree level.

Large genetic variation in wood density has been reported for *L. kaempferi* and hybrids with other *Larix* species. A large clonal variation was detected in plus tree clones from populations in Honshu (Nakada et al. 2005) and Hokkaido Island (Koizumi et al. 1990). No geographical cline in wood density was detected in provenance trials (Takata et al. 1992). Wood density was determined mainly by the characteristics of the parental European larch in the hybrid larch (*L. decidua* × *L. kaempferi*, Pâques 2004). Large narrow sense heritabilities (0.57–0.83 depending on the position on the trunk) and low specific combining abilities affected wood density in a half diallel mating system comprising six parents (Oshima 1998). Unfortunately, wood density was only assessed at a tree level or at best averaged over five successive growth rings, and age-related trends in more detailed growth ring components, such as earlywood and latewood, were not taken into account. Potential age-related changes in heritability were also not assessed in the studies summarized above.

Examination of age-related trends of inheritance in wood density and their correlation with growth traits are necessary to estimate an appropriate selection age. Age-related trends in the heritability of wood density in a hybrid larch (*Larix gmelinii* × *L. kaempferi*) were elucidated, and an appropriate age for the selection of wood density was inferred (Fujimoto et al. 2006), although this has not yet been achieved for *L. kaempferi*.

Clarifying the modes of inheritance of growth ring components, including growth rings, the average densities of earlywood and latewood, and the percentage of latewood, are necessary for understanding the inheritance of wood density characteristics in detail. The mode of inheritance of growth ring components in hybrid larches has already been reported (Pâques 2004; Fujimoto et al. 2006), whereas the inheritance mode in *L. kaempferi* is not well understood (Oshima 1998).

In the present study, we measured the wood density and other growth ring parameters in a 29-year-old test site that comprised full-sib families from a full diallel mating design. We estimated age-related trends in the genetic parameters for each trait, genetic correlations among traits, and genetic gain from early selection. We discuss possible breeding

strategies for promoting genetic improvement of wood density in *L. kaempferi*.

2 Materials and methods

This study used a progeny test stand that comprised 56 full-sib families produced by a full diallel mating design (8 × 8 full diallel, without selfing) with eight plus trees. *L. kaempferi* plus trees were selected for their fast growth and stem straightness in the Japanese forest tree breeding program during the 1950s and 1960s. The test stand (test stand code, 496) was established in 1977 using a randomized block design with five replicates, and it is located at the southern foot of Mt Asama, Nagano Prefecture, Japan (36°21' N, 138°31' E, Fig. 1). Each family was planted in a quadratic plot with 20 trees in each replicate. The initial planting density was 3,000 stem/ha, and thinning had never been applied. The survival rates of trees were 92, 92, 88, 80, and 73 % at stand ages 10, 15, 20, 25, and 30, respectively. At stand age 30, the mean height and diameter at breast height (DBH) were 13.2 and 14.8 cm, respectively.

In March 2007, increment cores of 5.15 mm diameter were sampled from 30 families. The families were selected after full diallel mating of six plus trees. Three out of five replicates were used in this study. From each quadratic plot, we selected three trees that were not suppressed (in some plots, this was only two trees). An increment core was collected from one tree. The average number of individuals in each family across all replicates was 8.9. The stand age at the time of collection was 29 years. DBH of the sampled trees during core sampling was 16.1 cm on average.

Sampled cores were cut into transverse 2.2-mm-thick sections using a Dendrocut table saw (Walesch Electronic GmbH, Zurich, Switzerland). The sections were extracted using

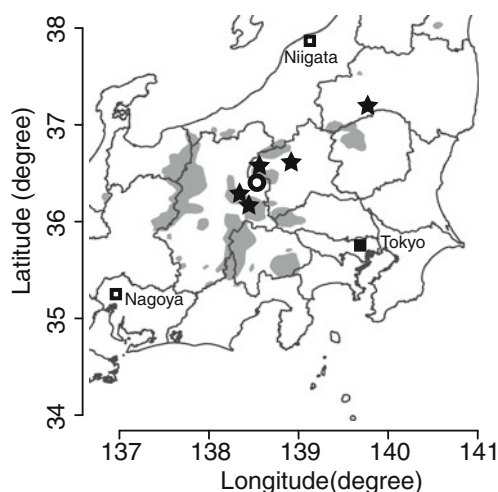


Fig. 1 Location of the test site (circle) and locations where the plus trees used in the present study were selected (stars). Shaded regions indicate the natural distribution range of *L. kaempferi*

acetone in a glass beaker for a period of 7 days where acetone was replaced each day. The sections were conditioned in a room with a constant temperature (20 °C) and humidity (60 %) for 1 month. The sections were then placed on an X-ray sensitive film (Industrial X-Ray film Enveropak IX-FR, Fujifilm Co., Tokyo, Japan) and irradiated using a soft X-ray apparatus (Softex Co., Tokyo, Japan). The processed films were digitized at a resolution of 2,400 dpi using a film scanner (GT-X900, Seiko Epson Co., Suwa, Japan). The growth ring components, including the ring width (RW), average wood density (RD), proportion of latewood (LWR), average density of earlywood (earlywood density, ED), and average density of latewood (latewood density, LD), were calculated for each ring using a software package (WinDENDRO, Regent Instruments Inc., Quebec City, Canada) using a 200- μm path width in the tangential direction and a resolution of approximately 10 μm in the radial direction. A density of 0.55 g/cm^3 was the demarcation between earlywood and latewood in each ring (Ohta 1970). Growth rings with inclined borders against the X-ray irradiation direction and those with blurred borders between the latewood and the next year's earlywood in the X-ray films were excluded from the LWR, ED, and LD analyses. Finally, 65 % of the total number of rings was used in the analysis of the three traits (the average number of rings per family per year was 4.7). In the present study, the analyses of each ring component were based on the stand age rather than the cambial age because not all of the sample cores included the piths that are required to estimate the cambial age. This "stand age-based analysis" had the advantage of excluding the effects of annual weather differences. The arithmetic mean of each trait was calculated on the basis of the arbitrary ages of each individual to determine the average genetic properties of each trait. The area-weighted average wood density at age i (AWD_i) was also calculated using the following equation to estimate the overall wood density at breast height:

$$\text{AWD}_i = \left(\sum_{k=m}^i \text{RA}_k \cdot \text{RD}_k \right) / \text{CRA}_i,$$

where RA_k represents the ring area at age k , RD_k represents RD at age k , CRA_i represents the cumulative ring area at age i , and m represents the innermost available ring number. RA was calculated as follows:

$$\text{RA}_i = \pi(\text{CRW}_i^2 - \text{CRW}_{i-1}^2),$$

where CRW_i represents the cumulative ring width at age i . CRW was calculated as follows:

$$\text{CRW}_i = D_n/2 - \sum_{k=i+1}^n \text{RW}_k,$$

where D_n represents DBH at the time of sampling (age n), and RW_k represents the ring width at age k . CRWs were not calculated using the sum of RWs because the cores did not always include pith. The basal area at age i (BA_i) was calculated as follows.

$$\text{BA}_i = \sum_{k=m}^i \text{RA}_k$$

Genetic analysis was performed using the following mixed linear model:

$$Y_{ijkl} = \mu + B_i + G_j + G_k + S_{jk} + R_{jk} + p_{ijk} + e_{ijkl},$$

where μ represents the general mean, B_i represents the fixed effect of replicate i , G_j and G_k represent the general combining ability (GCA) of female j and male k (random effect), S_{jk} represents the specific combining ability (SCA) of parents j and k (random effect), R_{jk} represents the random effect of the specific cross (reciprocal effect) between female j and male k , p_{ijk} represents the random effect of plot, and e_{ijkl} represents the random residuals. The variance components of each random effect, covariance components between random effects, and their standard errors were estimated using REML methods with ASReml (Gilmour et al. 2009). The narrow sense heritability of each trait was calculated using the following equation:

$$h^2 = \frac{4\sigma_{\text{GCA}}^2}{2\sigma_{\text{GCA}}^2 + \sigma_{\text{SCA}}^2 + \sigma_{\text{R}}^2 + \sigma_{\text{p}}^2 + \sigma_{\text{e}}^2},$$

where σ_{GCA}^2 , σ_{SCA}^2 , and σ_{R}^2 represent variance components of GCA, SCA, and the reciprocal effect, respectively, σ_{p}^2 represents the plot variance, and σ_{e}^2 represents the error variance. Genetic correlations between trait i and trait j [$r_{g,(i,j)}$] were calculated using the following equation:

$$r_{g,(i,j)} = \text{COV}_{\text{GCA},(i,j)} / \sqrt{\sigma_{\text{GCA},(i)}^2 \sigma_{\text{GCA},(j)}^2},$$

where $\text{COV}_{\text{GCA},(i,j)}$ represents the covariance parameter of GCA between trait i and trait j , and $\sigma_{\text{GCA},(i)}^2$ and $\sigma_{\text{GCA},(j)}^2$ represent the variance components of GCA for trait i and trait j , respectively. Age-age genetic correlations were also calculated using the same equation where traits in different years were treated as independent traits. The residual correlations

between trait i and trait j [$r_{e,(i,j)}$] were calculated using the following equation:

$$r_{e,(i,j)} = \text{COV}_{e,(i,j)} / \sqrt{\sigma_{e,(i)}^2 \sigma_{e,(j)}^2},$$

where $\text{COV}_{e,(i,j)}$ represents the covariance parameter of the residuals between trait i and trait j , and $\sigma_{e,(i)}^2$ and $\sigma_{e,(j)}^2$ represent the variance components of residuals of trait i and trait j . The standard errors of heritabilities and genetic correlations were calculated on the basis of the method described by Gilmour et al. (2009) using ASReml. The genetic gains from early selection of individuals were calculated using the following equation, similar to the genetic gains from indirect selection (Falconer and Mackay 1989):

$$\text{GG}_{(t/m)} = ih(t)r_{g(t,m)}\sigma_{A(m)},$$

where $\text{GG}_{(t/m)}$ represents the genetic gain from early selection (predicted genetic gain at objective age m , selected at younger age t), i represents the intensity of selection, $r_{g(t,m)}$ represents the genetic correlation between ages t and m , and $\sigma_{A(m)}$ represents the square root of the additive genetic variance at age m , which was calculated as the square root of four times σ_{GCA}^2 . The genetic gain was expressed as the ratio (percentage) of the average value of a target trait in an objective year. The efficiency of early selection, where the rotation age used in tree breeding was taken into consideration, was calculated as follows (Lambeth 1980):

$$E_{(t/m)} = \frac{h(t)r_{g(t,m)} / [S(t) + I]}{h(m) / [S(m) + I]},$$

where $E_{(t/m)}$ represents the selection efficiency of the time-based genetic gain from early selection at age t to mature age m , $S_{(m)}$ represents the selection age (year) for a normal selection cycle, $S_{(t)}$ represents the selection age (year) of early selection, and I represents a period of time, which included vegetative regeneration and the time spent waiting for flowering, crossing, and seedling production. A period of 15 years was used for I on the basis of the current situation for tree breeding using *L. kaempferi* in Japan.

3 Results

The phenotypic values of the growth ring components are shown in Fig. 2a. RD increased with age and subsequently

leveled off around age 12. RW decreased steeply prior to age 13, after which the reduction in RW became much more gradual. LWR and LD exhibited patterns similar to those of RD. ED decreased gradually with the stand age. Age-related trends changed at around age 15; therefore, we divided the duration investigated into two stages at around age 15, i.e., the young stage and elder stage, in the following section.

The narrow sense heritabilities of the growth ring components are shown in Fig. 2b. The narrow sense heritabilities of RD were higher at elder stage. After age 20, high RD values were maintained and the RD heritability peaked at a value of 0.78 [standard error (SE)=0.35] at age 25. RW heritability was highest at age 14, i.e., 0.55 (SE=0.30). RW was lower at the elder stage. The age-related trends in LWR and LD were similar to that in RD, with higher heritabilities at the elder stage. ED heritabilities were relatively high at the young stage but low at the elder stage.

The ratios of the variance components for each trait at each stand age are shown in Fig. 2c. For RD and LD, the GCA variance was the highest of the three genetic variances (GCA, SCA, and reciprocal effects) at most stand ages. For LWR, the SCA variance had specific ratios at the elder stage. For RW, the ratios of the genetic variances were low. For ED, the variance of reciprocal effects had a higher ratio at around age 25 than at other stand ages.

The genetic correlations between RD and the other traits are shown in Fig. 2d. LWR and LD had a high positive genetic correlation with RD at most stand ages. LD had a high positive genetic correlation with RD, with few exceptions, and it had high correlations at the elder stage. RW had high positive genetic correlations with RD at the young stage, although the values had large SEs. At the elder stage, the correlation between RD and RW was not strong. The genetic correlations between ED and RD were generally high, but they tended to vary at the elder stage. The residual correlation between RD and RW (not shown in the figures) were negative at all stand ages from 6 to 15, with the exception of age 14, although the absolute values were not high (from -0.31 to 0.06 and -0.14 on average). From ages 16 to 28, the residual correlations between RD and RW were positive (from 0.02 to 0.32 and 0.15 on average).

The genetic gains in the average RD of mature wood (average value of the 10 outermost rings, $\text{RD}_{\text{outer10}}$) with direct selection and indirect early selection are shown in Table 1. Selection was simulated using a selection intensity of 1.0 (selection of the top 38.1 % of individuals) with indirect early selection using the average growth ring parameters of the young stage (average of trait X between ages 6 and 10, X_{6-10}). ED_{6-10} had the largest gain for $\text{RD}_{\text{outer10}}$ (5.5 %), and it accounted for 58.1 % of the gain obtained by direct selection. The gain in $\text{RD}_{\text{outer10}}$ by selection using ED_{6-10} was higher than that obtained by selection using RD_{6-10} . Indirect early selection with LD_{6-10} or LWR_{6-10}

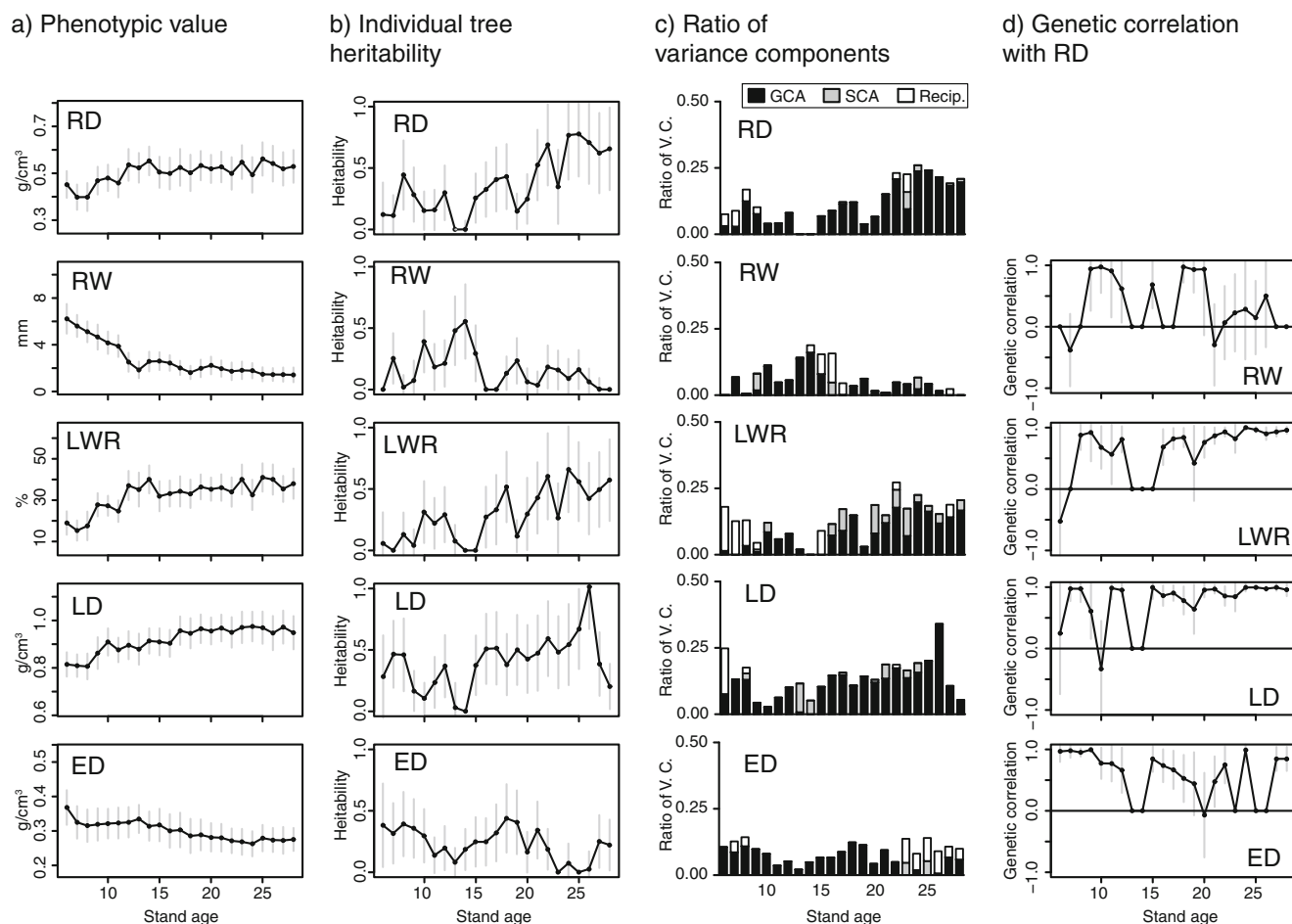


Fig. 2 Age-related trends of the phenotypic values (a), individual tree heritabilities (b), ratios of variance components (c), and genetic correlations between the investigated growth ring parameters and the ring density (d). *RD* the average wood density of a ring, *RW* ring width,

LWR the proportion of latewood, *LD* latewood density, *ED* earlywood density. *X*-axis indicates stand age. Vertical lines in a indicate standard deviations, while the lines in (b) and (d) indicate standard errors

had low relative genetic gains in $RD_{\text{outer}10}$. The efficiency of early indirect selection was highest for ED_{6-10} (0.99), and this value exceeded the early selection of RD_{6-10} , whereas it did not exceed direct selection.

Figure 3a shows the narrow sense heritabilities of AWD and BA, and the genetic correlation between them at each age. The narrow sense heritability increased gradually for AWD and reached a value of 0.46 (SE=0.25) at age 28. BA

Table 1 Genetic parameters, genetic gains, and selection efficiency of indirect early selection targeting the average wood density of mature wood (outermost 10 rings) using the averages of the growth ring components at the young stage as the selection traits

Selection trait	Narrow sense heritability	Genetic correlation with $RD_{\text{outer}10}$	Genetic gain in $RD_{\text{outer}10}$ (%)	Indirect/direct (%)	Selection efficiency in $RD_{\text{outer}10}$
RW_{6-10}	0.22	0.69	3.4	37.0	0.64
LWR_{6-10}	0.02	0.79	1.0	11.0	0.19
RD_{6-10}	0.19	≈ 1.00	4.6	49.0	0.84
ED_{6-10}	0.36	0.84	5.5	58.1	≈ 1.00
LD_{6-10}	0.35	0.29	1.9	19.7	0.34
$RD_{\text{outer}10}$	0.76	1.00	9.4	100.0	1.00

The selection traits are the averages of the growth ring components between ages 6 and 10. Indirect/direct indicates the ratio of indirect selection to direct selection with respect to the genetic gain. The objective trait is the average wood density of the 10 outermost rings ($RD_{\text{outer}10}$). The selection intensity is 1.0 (selection of the top 38.1 % of individuals)

RW_{6-10} ring width, LWR_{6-10} percentage of latewood, RD_{6-10} ring density, ED_{6-10} earlywood density, LD_{6-10} latewood density

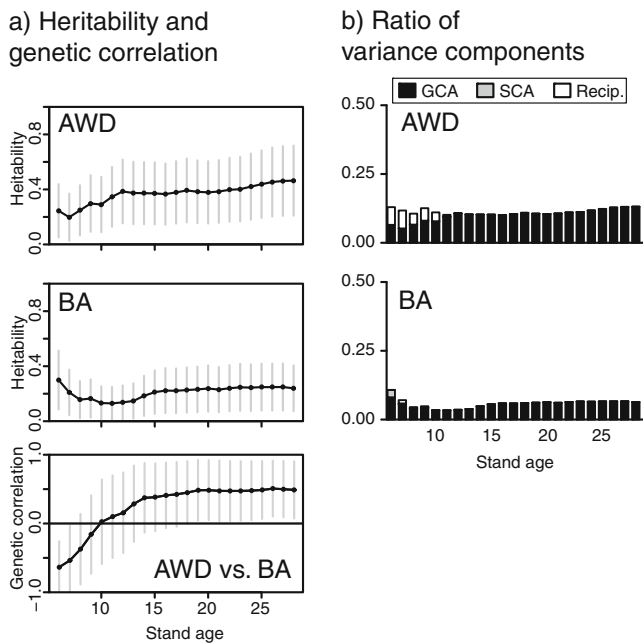


Fig. 3 Age trends in the heritability of overall wood density (*AWD*) and basal area (*BA*), genetic correlations between *AWD* and *BA* (a), and ratios of the variance components of *AWD* and *BA* (b). The *X*-axis indicates the stand age. The vertical bars shown in (a) are the same as those in Fig. 2

heritability leveled off after age 15 and reached a value of 0.23 (SE=0.17) at age 28. The genetic correlations between *AWD* and *BA* were negative at the young stage (−0.73 at age 6). However, they increased with age after age 6 and became positive at age 10, before leveling off after age 20. The genetic correlation at age 28 was 0.49 (SE=0.43). Figure 3b shows the ratios of the variance components for *AWD* and for *BA* at each stand age. The ratio of the variance components of GCAs increased with age while that of the reciprocal effects were observed for *AWD* at the young stage but they disappeared as the age increased. The ratios of the variance components of GCAs were lower for *BA* than for *AWD*. The ratios of the variance components of SCAs and reciprocal effects were very low for *BA*.

The age–age genetic correlations between arbitrary ages and age 28 for *AWD* and *BA* are shown in Fig. 4a. The age–age genetic correlations were considerably higher for *AWD* than for *BA*. The age–age correlations between ages 6 and 28 were 0.95 (SE=0.10) and 0.59 (SE=0.39) for *AWD* and *BA*, respectively. For *AWD*, the correlations between age 28 and previous ages had consistently high values (>0.94). The age–age genetic correlations with *BA* increased rapidly until age 12, before reaching the maximum and stabilizing toward the final age measured. Figure 4b shows the genetic gains at age 28 due to early selection with a selection intensity of 1.0 (top 38.1 % individuals) at arbitrary ages for *AWD* and *BA*. The genetic gains from direct selection (selection at age 28) were 5.4 and 8.8 % for *AWD* and *BA*, respectively. The genetic

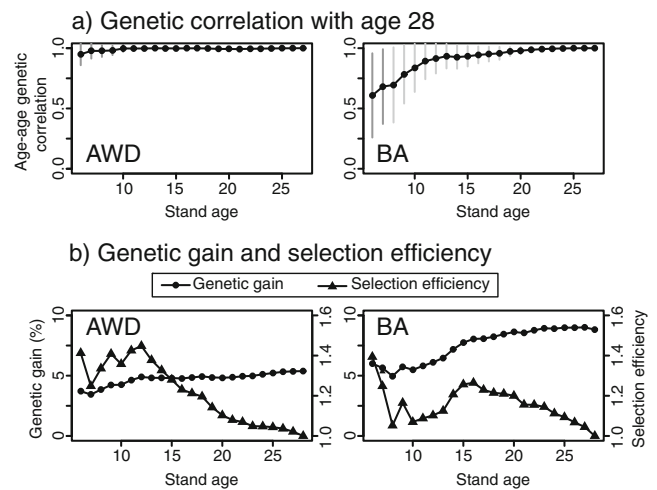


Fig. 4 Age–age genetic correlations of overall wood density (*AWD*) and basal area (*BA*) compared with values at age 28 (a), genetic gains (%) at a selection intensity of 1.0 (top 38.1 % individuals), and the selection efficiencies of early selection (b)

gains from early selection (selection at age 6) were 3.7 and 6.0 %, which accounted for 69.0 and 68.1 % of the genetic gains at age 28 for *AWD* and *BA*, respectively. The genetic gains resulting from early selection generally increased with age where the rate of increase leveled off earlier for *AWD* than for *BA*. Genetic gains that equaled 90 % of the total observed at age 28 were observed at ages 12 and 16 for *AWD* and *BA*, respectively (Fig. 4b). The selection efficiencies are also shown in Fig. 4b. The selection efficiencies had stable and high values, where the selection for *AWD* at the young stage was approximately 1.4 times that of the normal selection at age 28. The selection efficiencies for *BA* decreased until around age 10, before they increased and reached a local maximum at age 15.

4 Discussion

The present study elucidated the relatively large GCA effects, small SCA and reciprocal effects, and high heritabilities of RD (Fig. 2) and *AWD* (Fig. 3). These results suggest that the supply of genetically improved planting materials via mass selection and seed orchards may be promising for improving the wood density of *L. kaempferi*. Large clonal effects on wood density (Koizumi et al. 1990; Nakada et al. 2005) and the high narrow sense heritability of wood density (Oshima 1998) have already been reported in *L. kaempferi*. A hybrid of *L. gmelinii* and *L. kaempferi* had age-dependent narrow sense heritabilities of RD (0.42–0.59, Fujimoto et al. 2006) and a narrow sense heritability of 0.28 for area-weighted wood density (Kita et al. 2009). For a hybrid of *L. decidua* and *L. kaempferi*, the full-sib family heritability was 0.40 for wood density and there was only a small contribution of *L.*

kaempferi as the male parent (Pâques 2004). In general, wood density has high heritability in conifers and hardwoods (Zobel and van Buijtenen 1989). This was confirmed for *L. kaempferi* in the present study by a detailed genetic analysis using a progeny test with a diallel mating design.

RD heritability varied widely across ages but tended to increase with age (Fig. 2b). AWD heritability also increased with age. The observed increase in heritability with age was consistent with previous studies (Fujimoto et al. 2006 using hybrid larch; Vargas-Hernandez and Adams 1992 using *Pseudotsuga menziesii*). At the young stage (stand age approximately <15 years), RD heritabilities were low and fluctuated widely compared with that in previous studies. At this stage, trees were producing juvenile wood, as demonstrated by the increase in wood density with age (Fig. 2a). The cause of the unstable heritability of wood density from age 6 to around age 15 was not clear. This instability was prominent at stand ages 13 and 14 where the age RW decreased locally (Fig. 2a), whereas the RW heritability was maximal. Different responses of traits to the temporal annual weather may explain the different responses of the heritabilities.

The genetic relationship between the growth characteristics and wood density is important because the primary aim of most tree breeding programs is to obtain fast-growing trees in many cases (Zobel and Talbert 1984). The genetic correlations between RD and RW in the present study were generally positive between ages 10 and 20, with the exception of ages 13–14 and 16–17, when the insufficient size of the additive genetic variance for either or both traits interrupted the calculation of the genetic correlation (Fig. 2d). These correlations resulted in generally positive and increasing genetic correlations between BA and AWD (Fig. 3a). In previous reports, negative genetic correlations have been detected more often, especially at the young stage. Fujimoto et al. (2006) reported a negative genetic correlation (around -1.0 to -0.6) between the ring width and average wood density in a larch hybrid between *L. kaempferi* and *L. gmelinii*. *L. gmelinii* is a species with a higher wood density and lower growth rate than *L. kaempferi* (Kurahashi 1989), and these differences may have resulted in the negative correlations. Zhu and Nakano (1998) detected a negative correlation between the ring width and average wood density in the corewood (formed before cambial age 15), but no correlation in the outerwood in *L. kaempferi*, although they did not consider any genetic effects. Loo and Fowler (1982) reported a weak but significant negative correlation between the mean wood density and tree diameter in *L. kaempferi* at age 20 using the trees from 17 seed sources. Zobel and van Buijtenen (1989) found little or no correlation between the ring width and wood density in hard pines, where *Larix* species were similar to hard pines. However, negative genetic correlations have been reported for hard pine species, including *Pinus taeda* (Atwood et al. 2002),

Pinus sylvestris (Fries and Ericsson 2006), and *Pinus radiata* (Li and Wu 2005). Furthermore, intensive silvicultural management (i.e., fertilization, irrigation, and cultivation) have inverse effects on diameter growth and wood density (Isebrands and Hunt 1975). Thus, the relationship between ring width and wood density is dependent on the species, environmental, and silvicultural conditions, as well as the genetic composition of the population sampled. Further studies are required to reach a general conclusion about *L. kaempferi*.

Different growth ring components differed with respect to their age-related heritability trends and genetic correlations with wood density. Tight genetic correlations with RD were observed for LWR and LD at the elder stage, which had heritability patterns similar to those of RD (Fig. 2b, d). ED differed from LWR and LD with respect to the pattern of heritability and correlations with RD, and it had high heritabilities before age 20. The patterns of age-related trends with respect to heritability and genetic correlations with RD suggested that the genetic variation in ED contributed to the variation in RD at the young stage, whereas variations in LWR and LD contributed to the variation in RD at the elder stage.

The prediction of the efficiency of early selection for the genetic improvement of density of mature wood is important for the use of larch wood as solid construction lumber or lamina for glulam. Of the growth ring components, ED had the largest effect on early indirect selection of wood density in mature wood (Table 1). This was due to the high ED heritabilities at the young stage and tight genetic correlations between ED and mature wood density. However, the selection efficiency of ED did not exceed the efficiency of direct selection for RD in mature wood. Few studies have examined the early indirect selection of traits at the young stage to improve mature wood density. Future studies should address this lack of knowledge.

Genetic improvement of the average wood density in the entire trunk is a key factor for improving biomass accumulation and carbon sequestration in trees, unless the improvement has negative effect on growth characteristics. In the present study, AWD was used as a representative value of the average wood density of the entire trunk. The genetic gain through early selection accounted for a high proportion of the gain at the elder stage for AWD and BA (Fig. 4b) because of the high age–age genetic correlation between AWD (Fig. 4a) and the high BA heritabilities at the young stage (Fig. 3a). The selection efficiency was highest at age 6, which was the youngest stand age analyzed with respect to AWD in this study. The selection of hybrid larch was most efficient at cambial age 8, which was the analyzed innermost ring (Fujimoto et al. 2006). In other species, the optimum selection age reported for wood density was 5 years for *P. taeda* (Gwaze et al. 2002) and 4 and 6 years for *P. radiata*

(Li and Wu 2005). Thus, our results were consistent with those of previous studies. Ages ranging from 10 to 15 years should be selected for the simultaneous genetic improvement of both traits by early selection because BA had a second peak in the selection efficiency and the genetic correlation between wood density and basal area was positive at these ages.

The present study had several limitations because of the population size, sample size, and specific site environment, to elucidate general conclusions about the inheritance mode of wood density in *L. kaempferi*. The effects of population and sample sizes on the estimation of genetic parameters have been reported (Apiolaza et al. 1999; Perron et al. 2012; Apiolaza 2012). Compared with those studies, our sample size was small. The number of parents in our study was small compared with the 232 *L. kaempferi* plus trees in the corresponding breeding region at this site. In addition, the site had not been thinned and self-thinning would have started between stand ages 15 and 20. We sampled only unsuppressed trees, but our results were not a direct consequence of properly thinned stands. Further studies are necessary using larger populations and sample sizes under different environmental conditions.

In conclusion, the genetic improvement of wood density is promising through mass selection in *L. kaempferi*. It may also be possible to improve wood density and growth traits simultaneously. The planting materials used for forestation can also be genetically improved by supply from seed orchards using the improved parental materials.

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References

- Apiolaza LA (2009) Very early selection for solid wood quality: screening for early winners. *Ann For Sci* 66:601. doi:10.1051/forest/2009047
- Apiolaza LA (2012) Basic density of radiata pine in New Zealand: genetic and environmental factors. *Tree Genet Genomes* 8:87–96
- Apiolaza LA, Burdon RD, Garrick DJ (1999) Effect of univariate subsampling on the efficiency of bivariate parameter estimation and selection using half-sib progeny tests. *For Genet* 6:79–87
- Atwood R, White T, Huber D (2002) Genetic parameters and gains for growth and wood properties in Florida source loblolly pine in the southeastern United States. *Can J For Res* 32:1025–1038
- Baltunis BS, Greenwood MS, Eysteinnsson T (1998) Hybrid vigor in *Larix*: growth of intra- and interspecific hybrids of *Larix decidua*, *L. laricina*, and *L. kaempferi* after 5-years. *Silvae Genet* 47:288–293
- Bergstedt A, Lyck C (2007) Larch wood – a literature review. Forest & Landscape Working Papers no. 23–2007. Forest & Landscape Denmark
- Falconer DS, Mackay TFC (1989) Introduction to quantitative genetics, 4th edn. Pearson Education Ltd, Harlow
- Forest Tree Breeding Center, Forestry and Forestry Product Research Institute (2011) The current states and statistics in forest tree breeding in Japan. Forest Tree Breeding Center, Forestry and Forestry Product Research Institute, Hitachi (in Japanese)
- Fries A, Ericsson T (2006) Estimating genetic parameters for wood density of Scots pine (*Pinus sylvestris* L.). *Silvae Genet* 55:84–92
- Fujimoto T, Kita K, Uchiyama K, Kuromaru M, Akutsu H, Oda K (2006) Age trends in the genetic parameters of wood density and the relationship with growth rates in hybrid larch (*Larix gmelinii* var. *japonica* x *L. kaempferi*) F₁. *J For Res* 11:157–163
- Fukatsu E, Fukuda Y, Takahashi M, Nakada R (2008) Clonal variation of carbon content in wood of *Larix kaempferi* (Japanese larch). *J Wood Sci* 54:247–251
- Gilmour AR, Gogel BJ, Cullis BR, Thompson R (2009) ASReml user guide. VSN International Ltd., Hemel Hempstead
- Gwaze D, Harding K, Purnell R, Bridgwater F (2002) Optimum selection age for wood density in loblolly pine. *Can J For Res* 32:1393–1399
- Hayashi Y (1960) Taxonomical and phytogeographical study of Japanese conifers. Norin-Shuppan, Tokyo (in Japanese)
- Isebrands J, Hunt C (1975) Growth and wood properties of rapid-grown Japanese larch. *Wood Fiber Sci* 7:119–128
- Kita K, Fujimoto T, Uchiyama K, Kuromaru M, Akutsu H (2009) Estimated amount of carbon accumulation of hybrid larch in three 31-year-old progeny test plantations. *J Wood Sci* 55:425–434
- Koizumi A, Takata T, Ueda K, Katayose T (1990) Radial growth and wood quality of plus trees of Japanese larch I. Radial growth, density, and trunk modulus of elasticity of grafted clones. *Mokuzai Gakkaishi* 36:98–102 (Japanese with English summary)
- Kurahashi A (1989) The tree breeding of F₁ hybrid between *Larix gmelinii* and *L. kaempferi*. *For Tree Breed Hokkaido* 32:7–12 (in Japanese)
- Kurinobu S (2005) Forest tree breeding for Japanese larch. *Eurasian J For Res* 8:127–134
- Lambeth CC (1980) Juvenile-mature correlations in *Pinaceae* and implications for early selection. *Forest Sci* 26:571–580
- Li L, Wu HX (2005) Efficiency of early selection for rotation-aged growth and wood density traits in *Pinus radiata*. *Can J For Res* 35:2019–2029
- Li B, Wyckoff GW (1994) Breeding strategies for *Larix decidua*, *L. leptolepis* and their hybrids in the United States. *For Genet* 1:65–72
- Loo J, Fowler DP (1982) Geographic variation in specific gravity among Japanese larch from different provenances. *Wood Fiber Sci* 14:281–286
- Matyssek R, Schulze E (1987) Heterosis in hybrid larch (*Larix decidua* x *leptolepis*). I. The role of leaf characteristics. *Trees* 1:219–224
- Nakada R, Fujisawa Y, Taniguchi T (2005) Variations of wood properties between plus-tree clones in *Larix kaempferi* (Lamb.) Carrière. *Bull For Tree Breed Cent* 21:85–105 (Japanese with English summary)
- Ohta S (1970) Measurement of the wood density by the soft X-ray and densitometric technique. *Wood Ind* 25:27–29 (In Japanese)
- Oshima T (1998) The age trends in the combining ability and heritabilities in the wood density in Japanese larch. *Trans Meet Hokkaido Branch Jpn For Soc* 46:157–159 (In Japanese)
- Pâques LE (2004) Roles of European and Japanese larch in the genetic control of growth, architecture and wood quality traits in interspecific hybrids (*Larix* x *eurolepis* Henry). *Ann For Sci* 61:25–33

- Pâques LE, Millier F, Rozenberg P (2010) Selection perspectives for genetic improvement of wood stiffness in hybrid larch (*Larix x eurolepis* Henry). *Tree Genet Genomes* 6:83–92
- Perron M, DeBlois J, Despons M (2012) Use of resampling to assess optimal subgroup composition for estimating genetic parameters from progeny trials. *Tree Genet Genomes*. doi:10.1007/s11295-012-0540-5
- Takata K, Hirakawa Y (1996) Variation in growth ring parameters among Japanese larch from different provenances. In: Donaldson LA, Singh AP, Butterfield BG, Whitehouse LJ (eds) Recent advances in wood anatomy. NZ Forest Research Institute Ltd, Roturua, pp 351–356
- Takata K, Koizumi A, Ueda K (1992) Variations of radial growth and wood quality among provenances in Japanese larch. *Mokuzai Gakkaishi* 38:1082–1088 (Japanese with English Summary)
- 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
- Zhu J, Nakano T (1998) Effect of growth on wood properties for Japanese larch (*Larix kaempferi*): differences of annual ring structure between corewood and outerwood. *J Wood Sci* 44:392–396
- Zobel BJ, Talbert J (1984) Applied forest tree improvement. The Blackburn Press, Caldwell
- Zobel BJ, van Buijtenen JP (1989) Wood variation - its causes and control. Springer-Verlag, Berlin