

Genetic relationship between wood properties and growth traits in *Larix kaempferi* obtained from a diallel mating test

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Abstract Knowledge of the genetic relationship between growth traits and wood properties is critical for their simultaneous genetic improvement. We measured the height and diameter at breast height (DBH) and wood quality traits, including stress wave velocity (SWV) as the selection criteria for wood stiffness, wood density, and Pilodyn penetration depth as selection criteria for wood density, at a progeny test site at stand age ca. 30, which comprised of full-sib families by a full diallel mating design with eight plus *Larix kaempferi* tree clones. We estimated the genetic parameters for each trait and phenotypic, genetic and residual correlation between traits. The contribution of specific combining ability and reciprocal effects were small for all traits. Growth traits showed high positive genetic correlation with average wood density of the outermost five rings (0.912 for height, 0.826 for DBH) and with SWV (0.738 for height, 0.762 for DBH), irrespective of small phenotypic correlations between them. Wood density and SWV also showed high genetic correlation. Pilodyn penetration depth showed high selection efficiency for average wood density of the outermost five rings (79.8 %) whereas SWV showed higher

selection efficiency for wood density. Thus, simultaneous genetic improvement of growth traits and wood properties of *L. kaempferi* appears possible.

Keywords *Larix kaempferi* · Genetic correlation · Indirect selection · Stress wave velocity · Pilodyn

Introduction

In tree breeding programs, knowledge of the relationship between target traits is critically important. In almost all programs, many traits need to be improved simultaneously. When negative genetic correlation exists between two target traits, the simultaneous improvement of both traits becomes difficult; therefore, the tree breeder must grasp the degree of genetic correlation between the traits. ‘Tree improvement specialist strive to improve the forest both for better yields and better quality’ [1], and the genetic relationship between tree growth and wood quality has attracted special attention [2]. Wood stiffness is one of the most important properties of wood. Many countries have industrial standards for wood products requiring stiffness grading. For example, grading rules based on modulus of elasticity (MOE) are employed for log [3], structural lumber [4] and lamina for glulam [5] in the Japanese Agricultural Standard. Wood density is related to wood strength and stiffness [6], and is an important trait itself that strongly affects tree carbon sequestration.

Many breeding programs have focused on growth and tree form as primary selection objectives [7, 8], whereas the genetic improvement of wood quality is a major breeding objective now. In Japan, the selection of first generation plus trees has also focused on the stem volume and tree form [9].

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Larix kaempferi is naturally distributed only at the central region of Honshu Island of Japan, but is now one of the major tree species for plantation forestry in Japan, and occupied 24.4 % of newly planted forest areas in FY2011 [10]. A breeding program was launched in the 1950s [11], and selection of second generation plus trees is ongoing. Although *L. kaempferi* wood is mainly used for packing materials now, its usage as lamina for glulam is increasing [12], and genetic improvement of its wood quality for structural lumber is desired in addition to improved tree growth. To improve both tree growth and wood quality, the relationship among traits related to tree growth and wood quality must be understood.

Negative phenotypic and genetic correlations between growth traits and wood quality traits are frequently reported. Zobel and van Buijtenen [2] summarized as ‘commonly, there is a negative genetic correlation between growth rate and specific gravity, although variability is large among species and even within different geography areas and races within the same species.’ In *L. kaempferi*, there are a few reports on the genetic correlation between growth traits and wood quality traits. Koizumi et al. [13] reported no clonal correlation between MOE and diameter at breast height (DBH), negative clonal correlation between average ring width and wood density in corewood using 67 plus trees. Nakada et al. [14] reported no clonal correlation between log MOE and DBH using 199 plus trees, weak positive clonal correlation between log MOE and the average ring width in outerwood in 166 plus trees, and weak positive clonal correlation between DBH and density of outerwood in 93 plus trees. Fukatsu et al. [15] reported a positive genetic correlation between wood density and basal area. In hybrid larch, a strong negative genetic correlation between wood density and radial growth rate, and a weak negative genetic correlation between MOE and DBH were reported in *Larix gmelinii* × *L. kaempferi* hybrids [16, 17], and a strong negative genetic correlation between DBH and MOE was reported in *Larix decidua* × *L. kaempferi* hybrids [18]. To predict how the selection of a trait will affect correlated traits in the following generations of *L. kaempferi*, more research is necessary.

The direct measurement of wood density is costly, so several indirect estimation methods are utilized, such as the Pilodyn penetration depth, which has a negative correlation with wood density [19–22]. A genetic correlation of wood density and Pilodyn penetration depth has also been reported for several species [23–25], but not yet for *L. kaempferi*. For efficient selection based on wood density, knowledge of the genetic correlation between Pilodyn penetration depth and wood density is necessary.

In this study, we measured growth traits, wood density, Pilodyn penetration depth, and stress wave velocity (SWV)

at a test site comprised of full-sib families by a full diallel mating design in *L. kaempferi*. SWV on a standing tree has been used as a selection criterion for stiffness in many reports [e.g. 26, 27], and has a strong phenotypic correlation with other, more direct measurements of MOE in many species [28–30], including *L. kaempferi* [31]. We estimated the heritability for each trait and phenotypic, genetic and residual correlations between traits. We discuss the genetic relationship between traits and their effects on tree breeding strategies in *L. kaempferi*. The efficiency of indirect selection for wood density by Pilodyn penetration depth and SWV is also discussed.

Materials and methods

Study material

We measured growth traits and wood quality traits of trees in a progeny test stand located at the southern foot of Mt Asama, Nagano Prefecture, Japan (36°21′N, 138°31′E). A detailed description of the site is in Fukatsu et al. [15]. The stand was established in 1977 with 3000 stems/ha initial planting density, using a randomized block design with five replicates, and it was comprised of 56 full-sib families produced by an 8 × 8 full diallel mating design (without selfing) with eight *L. kaempferi* plus trees. Each family was planted in a quadratic plot with 20 trees in each replicate. Thinning had never been applied on the site.

Measurements

As growth-related traits, tree height and DBH were measured for each tree at age 30 years. Height was measured using a Vertex III instrument (Haglöf, Sweden). DBH was measured with a caliper. Wood quality traits measured included SWV, Pilodyn penetration depth (Pilodyn), and wood density. SWV for each tree was calculated from the average of two readings measured at a stand aged 31 years using a Fakopp stress wave timer (Fakopp Enterprise, Agfalva, Hungary) showing the time of flight of a stress wave traveling longitudinally along the stem axis between two transducers attached at heights of around 0.8 and 1.8 m (a 1 m interval) of the stem above the ground. The Pilodyn for each tree was taken as the average of two readings at breast height obtained with a 2.5 mm diameter pin without removing the bark, using a Pilodyn 6J Forest instrument (PROCEQ, Zurich, Switzerland) at a stand aged 29 years. The wood density was measured densitometrically by an X-ray technique on incremental cores of each tree [15] at a stand aged 29 years. The average wood density of the outermost five rings (RD₅) was calculated as the arithmetic mean of the

Table 1 Basic statistics, narrow sense heritability and relative genetic gain for each trait

Trait	n	n of family	Diallel set	n in plot	Average value	Heritability (standard error)	Genetic gain (%)
Height	2196	56	8×8	13.1	13.3 m	0.549 (0.226)	18.48
DBH	2196	56	8×8	13.1	14.9 cm	0.224 (0.115)	10.48
SWV	269	30	6×6	3.0	4.61 km/s	0.657 (0.305)	5.20
Pilodyn	2167	56	8×8	12.9	17.9 mm	0.500 (0.212)	7.89
RD ₅	224	30	6×6	2.8	0.514 g/cm ³	0.658 (0.313)	16.03
AWD	224	30	6×6	2.8	0.513 g/cm ³	0.572 (0.291)	12.42

DBH diameter at breast height, Pilodyn Pilodyn penetration depth, SWV stress wave velocity at the trunk, RD₅ The average wood density of outer most 5 rings at breast height, AWD area-weighted average wood density of the entire disk at breast height, n the number of measured individuals, n of family the number of measured families, n in plot the average number of measured individuals per plot. Heritability is the narrow sense heritability. The relative genetic gains were calculated under the assumption of selection of the top 10 % of individuals

ring average densities of the outermost five rings. We also used area-weighted average wood density (AWD) of the entire basal area at breast height as described in Fukatsu et al. [15]. The number of increment cores used for this research was higher than used in Fukatsu et al. [15], because the current study does not cover intra-ring structure and we raised the criterion for blurred ring boundaries to exclude a core from analysis. All 56 families in the 8×8 full diallel mating design were measured for height, DBH, and Pilodyn characters. SWV and wood density for 30 families in a 6×6 full diallel mating design selected from the 8×8 full diallel mating design were measured. The number of measured trees, families, and measured trees per plot for each trait are depicted in Table 1.

Statistical analysis

To obtain variance components of causal factors and to assess the relative ratio of the variance components for each trait, we used the following mixed linear model

$$y_{ijkl} = \mu + B_i + G_j + G_k + S_{jk} + R_{jk} + p_{ijk} + e_{ijkl} \quad (1)$$

where y_{ijkl} represents the observation of each individual for the target trait, 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), which means the average effect of a parent that appears with any partner, of female j and male k (random effect), S_{jk} represents the specific combining ability (SCA), which means an effect that appears only on with specific combination of parents j and k (random effect), R_{jk} represents the reciprocal effect (REC), which means an effect primarily caused by sex linkage and a maternal effect [32] between female j and male k (random effect), p_{ijk} represents the random effect of a plot, and e_{ijkl} represents the random residuals.

To obtain the best-fit single-trait model for each trait, we executed a model selection procedure with the Akaike Information Criteria (AIC) [33] as a measure of the fit of a

model. AIC are used to select models that have a good fit to the data with few parameters. AIC were calculated using the following equation:

$$\text{AIC} = -2\ln(L) + 2m \quad (2)$$

where $\ln(L)$ represents log-likelihood of the model obtained by the restricted maximum likelihood (REML) estimation and m represents the number of estimated parameters. We calculated AIC for each simpler model obtained by subtracting a set of arbitrary effects from the base model (Eq. 1) for each trait. We included μ , G_j , G_k and e_{ijkl} for all models compared. We adapted the model having the minimum AIC score as the best model for each trait.

We calculated narrow sense heritability of each trait as an indicator of the degree of inheritance of a trait from parents to their progeny via sexual reproduction using the following equation:

$$h^2 = \frac{4 \cdot \sigma_{\text{GCA}}^2}{2 \cdot \sigma_{\text{GCA}}^2 + \sigma_{\text{SCA}}^2 + \sigma_R^2 + \sigma_p^2 + \sigma_e^2} \quad (3)$$

where σ_{GCA}^2 , σ_{SCA}^2 , and σ_R^2 represent the variance components of the GCA, SCA, and REC effect, respectively, σ_p^2 represents the plot variance, and σ_e^2 represents the error variance.

We used a multiple trait model extended from the above single-trait model to analyze the relationship between traits. In matrix form, this is:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \sum_{k=1}^n \left(\begin{bmatrix} \mathbf{Z}_{k,1} & 0 \\ 0 & \mathbf{Z}_{k,2} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{k,1} \\ \mathbf{u}_{k,2} \end{bmatrix} \right) + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \quad (4)$$

where \mathbf{y}_1 and \mathbf{y}_2 represent the vectors of observations for trait 1 and trait 2, \mathbf{X}_1 and \mathbf{X}_2 represent the design matrices for fixed effects of trait 1 and trait 2, \mathbf{b}_1 and \mathbf{b}_2 represent the vectors of fixed effects for trait 1 and trait 2, $\mathbf{Z}_{k,1}$ and $\mathbf{Z}_{k,2}$

represent the design matrices of random effect k for trait 1 and trait 2, $\mathbf{u}_{k,1}$ and $\mathbf{u}_{k,2}$ represent vectors of random effect k for trait 1 and trait 2, \mathbf{e}_1 and \mathbf{e}_2 represent residual vectors for trait 1 and trait 2. We assumed the variance of residuals (\mathbf{R}) and the variance of random effect k (\mathbf{G}_k) as follows:

$$\mathbf{R} = \text{var}\left(\begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}\right) = \begin{bmatrix} \sigma_{e,1}^2 & \sigma_{e,12} \\ \sigma_{e,21} & \sigma_{e,2}^2 \end{bmatrix} \otimes \mathbf{I}_n \tag{5}$$

$$\mathbf{G}_k = \text{var}\left(\begin{bmatrix} \mathbf{u}_{k,1} \\ \mathbf{u}_{k,2} \end{bmatrix}\right) = \begin{bmatrix} \sigma_{k,1}^2 & \sigma_{k,12} \\ \sigma_{k,21} & \sigma_{k,2}^2 \end{bmatrix} \otimes \mathbf{I}_n \tag{6}$$

where $\sigma_{e,1}^2$ and $\sigma_{e,2}^2$ represent the variances of residuals of trait 1 and trait 2, $\sigma_{e,12}^2$ and $\sigma_{e,21}^2$ represent covariance of residuals between trait 1 and trait 2, $\sigma_{k,1}^2$ and $\sigma_{k,2}^2$ represent the variances of random effect k of trait 1 and trait 2, $\sigma_{k,12}$ and $\sigma_{k,21}$ are the covariance of random effect k between trait 1 and trait 2, \mathbf{I}_n is the identity matrix of size n , and n is the number of trees. For any two combinations of target traits, we included only fixed or random effects that were common in the adapted models obtained by model selection for each trait into the multiple trait model.

Based on the constructed multiple trait model and variance/covariance structure, we estimated variance and covariance components for GCA and the residuals.

Genetic correlations between trait 1 and trait 2 ($r_{g,12}$), which means the correlation of GCA, and residual correlation between trait 1 and trait 2 ($r_{e,12}$), which indicates the nongenetic correlation, were calculated using the following equation:

$$r_{g,12} = \frac{\sigma_{GCA,12}}{\sqrt{\sigma_{GCA,1}^2 \cdot \sigma_{GCA,2}^2}}, r_{e,12} = \frac{\sigma_{e,12}}{\sqrt{\sigma_{e,1}^2 \cdot \sigma_{e,2}^2}} \tag{7}$$

Where $\sigma_{GCA,12}$ represents the covariance parameter of GCA between trait 1 and trait 2, and $\sigma_{GCA,1}^2$ and $\sigma_{GCA,2}^2$ represent the variance components of GCA for trait 1 and trait 2, respectively. The Pearson’s product-moment correlation coefficient between traits was calculated as the phenotypic correlation (r_p).

We calculated the variance components of each random effect with the REML method using ASReml software (VSN International, Hemel Hempstead, UK). The standard error of narrow sense heritability, genetic correlation, and residual correlation were calculated by the delta method [34] from the variance of variance and covariance components using ASReml software [35].

The genetic gains by mass selection were calculated using the following equation [36]:

$$\Delta G = i \cdot h \cdot \sigma_A \tag{8}$$

where ΔG represents the genetic gain, i represents the intensity of selection, h represents the square root of heritability, and σ_A represents additive genetic standard deviation

($4 \cdot \sigma_{GCA}$). The relative genetic gain was calculated as the percentage of ΔG out of the original population mean of the target trait. The efficiency of indirect selection of individuals was calculated using the following equation [36]:

$$E = \frac{i_y \cdot h_y \cdot r_g}{i_x \cdot h_x} \tag{9}$$

where x represents the desired trait, y represents a selection trait (selection criteria), E represents the efficiency of indirect selection when selecting desired trait x using selection criterion y , i_y represents the intensity of selection of trait y , h_y represents the square root of heritability of trait y , r_g represents the genetic correlation between trait x and trait y , i_x represents the intensity of selection of trait x , h_x represents the square root of heritability of trait x . We represent E as a percentage.

Results

The narrow sense heritabilities of the measured traits are shown in Table 1. RD₅ showed highest heritability (0.657), and other traits except for DBH showed heritabilities greater than 0.5. The ratio of variance components and the results of model selection are shown in Fig. 1. The ratios of the variance of SCA were small for all traits, and the effects of SCA were not included in the adopted model after the model selection for all traits. RECs were not included in the adopted model except for height, and the ratio of the variance of REC to the total variance was small for height.

The relative genetic gain under the assumption of selection of the top 10 % of individuals (selection intensity = 1.75) is shown in Table 1. Height showed the largest relative genetic gain (18.48 %) by mass selection. Wood density and DBH showed over 10 % relative genetic gain. Pilodyn and SWV, measured as selection criteria for wood density and wood stiffness, showed smaller genetic gain than other traits. The magnitude of the genetic gain of these traits, however, has little meaning because they are selection criteria, and the gain is evaluated by the scale of objective traits when indirect selection based on these selection criteria is assumed. The indirect genetic gain of wood density using Pilodyn is described later.

The phenotypic relationships between traits are plotted in Fig. 2 and the phenotypic correlations are summarized in Table 2. Weak positive correlations were observed between height and wood quality traits with the exception of Pilodyn. The correlation was not significant between DBH and SWV, and a weak positive correlation was observed between DBH and Pilodyn. The correlations between SWV and two traits related to wood density (RD₅ and AWD) were moderately positive ($r_p = 0.428$ and

Fig. 1 The ratio of variance components and the result of model selection for each trait. The abbreviations for traits are the same as in Table 1. *GCA* general combining ability, *SCA* specific combining ability, *REC* reciprocal effect, *plot* effect of plot, *resid.* residual effect. *SCA* was not included in the models for all traits

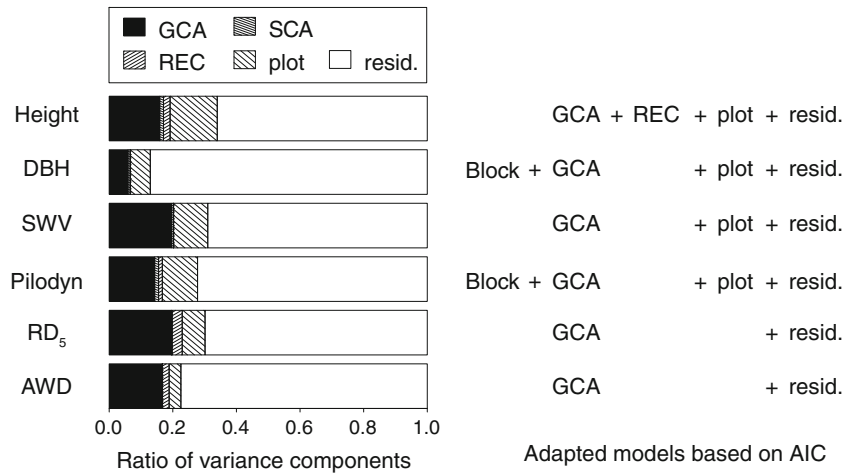
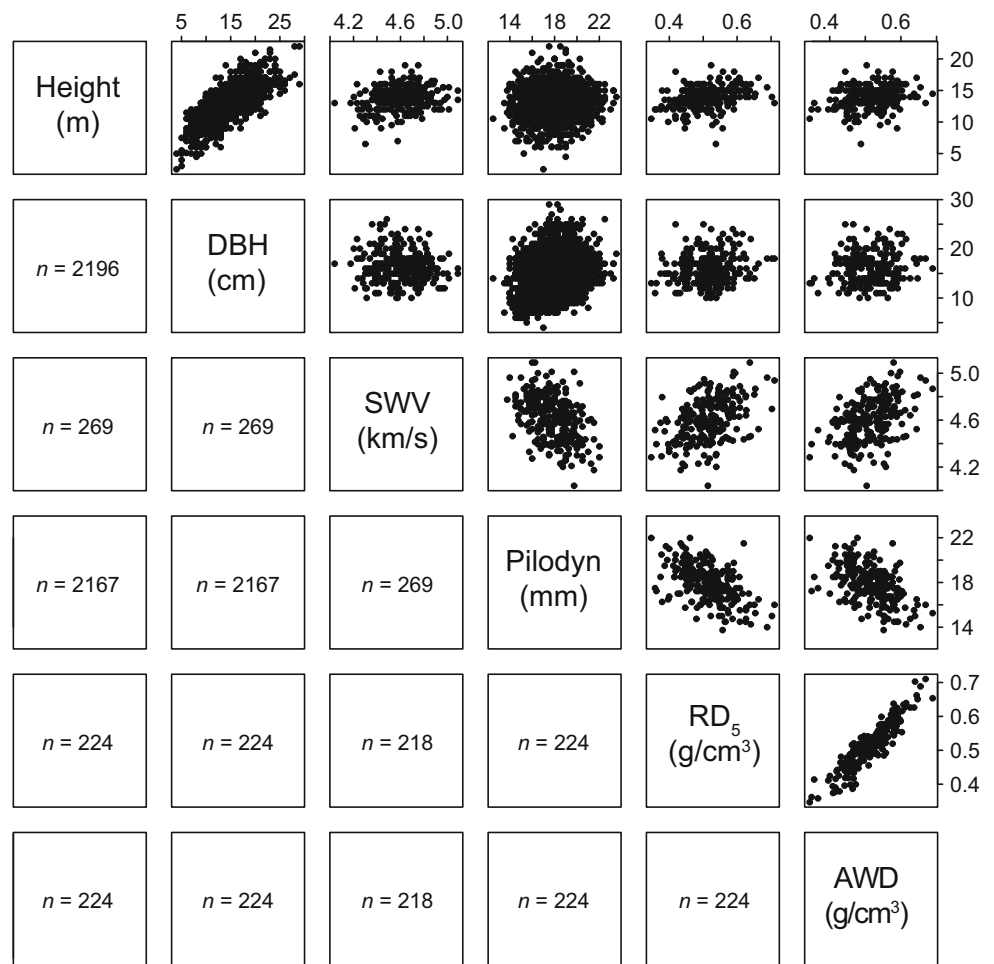


Fig. 2 Phenotypic relationships between traits. The upper-right triangular portion of the figure shows individual relationships between traits for all individuals. The abbreviations for the traits are the same as in Table 1. In the lower-left triangular portion, *n* shows the number of observations. The phenotypic correlations (Pearson’s product-moment correlation coefficient) between traits are presented in Table 2



0.435, respectively). Pilodyn, employed as an indirect measurement of wood density, showed moderate correlation with wood density ($r_p = -0.522$ with RD₅ and -0.506 with AWD).

The genetic correlations are summarized in Table 2. High genetic correlations were observed between height

and RD₅ ($r_g = 0.912$), height and AWD ($r_g = 0.804$), and height and SWV ($r_g = 0.738$). High genetic correlations were also observed between DBH and RD₅ ($r_g = 0.826$), DBH and AWD ($r_g = 0.757$), and DBH and SWV ($r_g = 0.762$). Pilodyn showed moderate genetic correlations with growth traits, $r_g = -0.432$ between Pilodyn and

Table 2 Phenotypic, genetic, and residual correlations between traits

Traits	Correlation (standard error)		
	Phenotypic	Genetic	Residual
Height vs. DBH	0.766 (0.014)***	0.903 (0.077)	0.769 (0.009)
Height vs. SWV	0.236 (0.059)***	0.738 (0.210)	−0.010 (0.072)
Height vs. Pilodyn	0.030 (0.021) ns	−0.432 (0.323)	0.187 (0.022)
Height vs. RD ₅	0.313 (0.064)***	0.912 (0.097)	0.290 (0.071)
Height vs. AWD	0.255 (0.065)***	0.804 (0.168)	0.201 (0.072)
DBH vs. SWV	−0.070 (0.061) ns	0.762 (0.205)	−0.394 (0.060)
DBH vs. Pilodyn	0.202 (0.021)**	−0.298 (0.365)	0.340 (0.020)
DBH vs. RD ₅	0.189 (0.066)**	0.826 (0.167)	0.180 (0.077)
DBH vs. AWD	0.118 (0.067) ns	0.757 (0.206)	0.071 (0.075)
SWV vs. Pilodyn	−0.429 (0.055)***	−0.750 (0.220)	−0.401 (0.057)
SWV vs. RD ₅	0.428 (0.062)***	0.947 (0.079)	0.284 (0.076)
SWV vs. AWD	0.435 (0.061)***	0.914 (0.098)	0.294 (0.064)
Pilodyn vs. RD ₅	−0.522 (0.057)***	−0.915 (0.095)	−0.409 (0.060)
Pilodyn vs. AWD	−0.506 (0.058)***	−0.823 (0.161)	−0.453 (0.052)
RD ₅ vs. AWD	0.922 (0.026)***	0.982 (0.020)	0.908 (0.012)

The abbreviations for traits are the same as in Table 1. Standard errors are given in parentheses. ** correlation estimates significantly different from 0 ($p < 0.01$); *** correlation estimates significantly different from 0 ($p < 0.001$); ns correlation estimates non-significantly different from 0 ($p > 0.05$)

height, and −0.298 between Pilodyn and DBH. Strong genetic correlations were observed between SWV and wood density ($r_g = 0.947$ for SWV and RD₅ and $r_g = 0.914$ for SWV and AWD). Strong genetic correlations were observed between Pilodyn and wood density ($r_g = -0.915$ for Pilodyn and RD₅ and $r_g = -0.823$ for Pilodyn and AWD). The absolute values of the genetic correlations between Pilodyn and wood density were smaller than between SWV and wood density.

The residual correlations are also summarized in Table 2. The residual correlation was weak between height and wood density, and none was observed between height and SWV. DBH had a weak negative residual correlation with SWV ($r_e = -0.394$), a weak positive residual correlation with Pilodyn ($r_e = 0.340$), and no residual correlation with wood density. The residual correlations between SWV and wood density were weak ($r_e = 0.284$ with RD₅; $r_e = 0.294$ with AWD). Pilodyn had a modest negative residual correlation with SWV ($r_e = -0.401$), with RD₅ ($r_e = -0.409$), and with AWD ($r_e = -0.453$).

The efficiency of indirect selection of wood density using Pilodyn was 79.8 % for RD₅ and 76.9 % for AWD. SWV had higher efficiency of indirect selection of wood density than Pilodyn, for which the efficiency was 94.6 % for RD₅ and 98.0 % for AWD.

Discussion

The objective of this research was to clarify the inheritance of traits related to growth and wood properties, and to understand the relationship between these traits from the genotypic and phenotypic perspectives.

Of all the traits investigated in this research, the variance components of SCA and REC were very small, and were not included in the selected model (Fig. 1). Low values for SCA and REC in annual ring width and intra-ring wood density parameters at the study site have already been reported [15]. We confirmed the same results for growth traits, Pilodyn and SWV. We measured SWV as an indirect indicator of MOE. As described in the introduction, a strong phenotypic correlation was reported between SWV of the trunk and direct measurement of MOE [28–31]. The small SCA and REC in SWV imply that MOE also shows small SCA and REC in *L. kaempferi*. The small ratio of variance components of SCA and REC and the large ratio of variance components of GCA mean that the genetic performance of a parent is transmitted to its progeny in any combination with the other parent. This inheritance pattern suits seed orchards, where random mating of parents is assumed. Seed production by seed orchard is cost effective and preferred to the seed production by artificial crosses. Based on these results, genetic improvement of wood stiffness, growth traits and wood density via seedling orchards is probable in *L. kaempferi*.

The phenotypic correlation between traits is a complex of genetic and nongenetic effects. The decomposition of the phenotypic correlation into genetic and other correlations is important to improve understanding the relationships among traits. The genetic correlation between SWV and wood density was very strong in this study. Nakada et al. [14] reported a modest positive correlation (0.58) in a clonal average between log MOE and outerwood density using 93 *L. kaempferi* elite tree clones. In hybrid larch (*L. gmelinii* var. *japonica* × *L. kaempferi*), Fujimoto et al. [16] reported a strong genetic correlation between average

wood density at breast height and green log MOE measured by a vibration method ($r_g = 0.79$), and between average wood density and lumber MOE obtained by a bending test ($r_g = 0.87$). The genetic relationship between wood density and SWV in our research was similar to what was found in these previous reports related to *L. kaempferi*. The residual correlation between wood density and SWV was also positive, but weak. This implies that the phenotypic relationship between wood density and SWV mainly depends on the genetic relationship. In *Cryptomeria japonica*, another major planted forest tree species in Japan, Mishima et al. [37] reported no clonal correlation between Pilodyn and SWV in a population of 745 elite trees in the Kanto region of Japan. This implies that the genetic correlation between wood density and wood stiffness is low in *C. japonica*, and therefore the genetic relationship between wood density and wood stiffness depends on species. Our results imply that the genetic improvement of wood density will result in simultaneous genetic improvement of wood stiffness in *L. kaempferi*.

The positive genetic correlation between growth traits and wood quality traits (Table 2) are favorable for genetic improvement of *L. kaempferi*. Nakada et al. [14] reported no or weak positive clonal correlation between diameter and wood quality traits, and Koizumi et al. [13] reported no clonal correlation between DBH and MOE in *Larix kaempferi*. On the other hand, negative genetic correlations between growth traits and wood quality traits (wood density and MOE) were reported in hybrid larch [16–18], and negative correlations between growth traits and wood quality traits have also been reported in several other species in *Pseudotsuga menziesii* [38–40], in *Picea sitchensis* [41], and in *Pinus radiata* [42]. Mishima et al. [37] reported a very small but positive clonal correlation between DBH and SWV in *C. japonica*. Based on our results and previous reports, the relationship between wood quality traits and growth traits also depends on species, and *L. kaempferi* in Japan might have a positive genetic relationship between wood properties and growth traits. This paper is the first report showing a genetic correlation between growth and wood properties in *L. kaempferi*. Studies on test stands established by other parental combinations will be necessary to confirm the relationships found.

Residual correlation, which means the correlation between two traits in genetically analogous individuals, was a negative between SWV and DBH. This negative residual correlation implies that wood stiffness will become low if DBH is increased by silvicultural treatment or by environmental effects. The highly positive genetic correlation, however, implies that such a decline in wood stiffness will be prevented by simultaneous genetic improvement of wood stiffness and growth in *L. kaempferi*.

Pilodyn penetration is used as an indirect measurement of wood density in many species [19, 20, 22, 23, 25, 43]. In our research, Pilodyn had a strong genetic correlation with wood density, which resulted in a high efficiency of indirect selection using Pilodyn targeting wood density. The efficiency of indirect selection using Pilodyn is higher for wood density of the outermost 5 rings than for average wood density, which is a reasonable result, because a Pilodyn pin penetrates from the surface of the trunk, and the maximum penetration depth was 23.5 mm (Fig. 2). SWV had a strong genetic correlation with wood density, and this strong genetic correlation and the high heritability resulted in a high indirect selection efficiency of SWV for wood density. Wood density is not only a selection criterion for several wood properties including wood stiffness, but also an important trait affecting carbon sequestration. Selection of individuals having higher wood density by a combination of Pilodyn and SWV would be effective in a breeding program for *L. kaempferi*, because measurements of Pilodyn penetration value and SWV using a Fakopp or similar apparatus are more rapid and lower in cost than direct measurement of wood density.

In a tree breeding strategy for *L. kaempferi*, mass selection of first generation plus trees in the past based on tree growth is unlikely to have resulted in a marked declining of wood quality, as inferred from the high positive genetic correlation between growth traits and wood quality traits in this research. For the selection of the next generation, a combination of growth traits and cost-effective selection criteria (Pilodyn penetration and/or SWV) for wood properties would be advantageous, because the high heritability of wood quality traits and their high genetic correlation with growth traits would increase the accuracy of the selection for growth traits. Silvicultural treatments are often used in commercial forests to promote growth, and the negative residual correlation between growth and wood stiffness implies that this approach will cause the decline of the phenotypic value of wood stiffness. However, the further genetic improvement of wood stiffness would likely mitigate such decline.

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