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RESEARCH PAPER

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Inheritance of wood properties and their radial variations in full-sib families of 36-year-old Japanese larch (*Larix kaempferi* (Lamb.) Carr.)

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Abstract

Key message: Larger differences of maximum load among families were found in mature wood compared to juvenile wood, suggesting the possibility of improving mature wood with higher resistance to rupture and maintaining characteristics of material in *Larix kaempferi* (Lamb.) Carr. by selecting specific mating parents.

Context: Because the wood from *L. kaempferi* trees is used for construction lumber, wood properties and bending properties should be focused on as targeted traits of tree breeding programs.

Aims: We clarified the radial variation of inheritance for wood properties and bending properties and classified the features of bending properties among families in *L. kaempferi*.

Methods: Annual ring width, latewood percentage, air-dry density, microfibril angle, modulus of elasticity, modulus of rupture, and bending work at five radial positions were investigated for 15 full-sib families of 36-year-old *L. kaempferi* grown in two progeny test sites in Japan.

Results: Higher heritability at almost all radial positions was found in air-dry density. Phenotypic and genetic correlations between air-dry density and bending properties showed relatively higher values at almost all radial positions. Load-deflection curves in 15 families could be divided into three groups in juvenile and mature wood. Variation among groups for load-deflection curves in mature wood was relatively larger than that in juvenile wood.

Conclusion: Air-dry density can be used as a criterion to select trees with superior bending properties. Mature wood in *L. kaempferi* could be effectively improved by selecting individuals.

Keywords: Heritability, Air-dry density, Microfibril angle, Bending properties, Load-deflection curve

1 Introduction

Larix kaempferi (Lamb.) Carr. (*karamatsu* in Japanese and Japanese larch in English) is a deciduous conifer species that is naturally distributed in cold and high elevation areas in the central region of Honshu, Japan. It is one

of the most major softwood plantation species in Japan (Takata et al. 2005). Plantations of *L. kaempferi* are mainly distributed in Hokkaido and northern Japan, including the Tohoku and Chubu regions (Forestry Agency 2019). The trees of *L. kaempferi* and hybrids between *L. kaempferi* and other *Larix* species have been planted in Japan (Iizuka et al. 2000; Fujimoto et al. 2006a, b; Fukatsu et al. 2015), North America (Cáceres et al. 2018), China (Dong et al. 2019), and Europe (Pâques et al. 2010). This species is one of the target species for tree breeding programs managed by the Forestry Agency in Japan; it is also

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used for breeding materials in many countries (Kurinobu 2005). The tree breeding programs of *L. kaempferi* in Japan were started in the 1950s, selecting plus trees with superior growth rates and straightness as criteria in artificial and natural forests (Kurinobu 2005). Recently, the selection of second-generation plus trees crossbred by using selected first-generation plus trees has been started to improve growth rate and wood quality as target traits, with plans to establish seed orchards in each prefecture in Japan (Fukatsu et al. 2015).

Since the structural lumber in *L. kaempferi* is often subjected to bending load, bending properties—including the modulus of elasticity (MOE) and the modulus of rupture (MOR)—are important criteria for assessing wood quality. It has been reported that mechanical properties are highly heritable traits in softwood species (Fujimoto et al. 2006a; Lenz et al. 2010; Chen et al. 2014; Takahashi et al. 2021). For example, Fujimoto et al. (2006a) reported that the heritability values of MOE and MOR in hybrid larch (*L. gmelinii* × *L. kaempferi*) were 0.44 and 0.66, respectively. In addition to MOE and MOR, bending work (*W*)—which is the amount of energy absorbed until the wood is broken—is also important in bending properties because it can be used to evaluate toughness. Static bending properties are calculated from load-deflection curves obtained from a static bending test. Thus, the shape of the load-deflection curve is important for understanding the elastic and plastic properties of wood, for example, a higher proportional limit showing resistance to deformation by load and the higher maximum load and the longer deflection in the plastic region showing resistance to failure. We previously reported that the type of load-deflection curve obtained in the static bending test of juvenile wood genetically varied among 18 families of 20-year-old *Cryptomeria japonica*, and the load-deflection curves affected by mating parents could be divided into four types (Takahashi et al. 2021). However, information on the inheritance of mechanical properties, such as static bending properties, is still limited for full-sib families of *L. kaempferi*, despite being one of the important first steps to be studied for the improvement of wood quality.

Superior trees with higher mechanical properties of wood would be indirectly selected by wood density and microfibril angle (MFA) for the effective selection of trees (Alteyrac et al. 2006; Lenz et al. 2010; Pâques et al. 2010; Chen et al. 2014; Takahashi et al. 2021). Pâques et al. (2010) found higher genetic correlations between wood density and MOE for 16- and 19-year-old hybrid larch (*Larix* × *eurolepis* Henry). In 12 trees of 80-year-old *Picea mariana*, MFA was negatively correlated with MOE ($r = -0.78$) or MOR ($r = -0.53$) (Alteyrac et al. 2006). These results suggest that the selection of

trees with higher mechanical properties of wood can be achieved by the selection of wood with higher wood density and lower MFA.

For tree breeding of wood quality in *L. kaempferi*, an accumulation of information about the inheritance of static bending properties is necessary. To clarify the inheritance and relationship with wood properties in static bending properties, it is useful to understand the variation in the shapes of load-deflection curves among families. In the present study, wood properties and bending properties were measured for 15 full-sib families of 36-year-old *L. kaempferi* trees grown at two progeny test sites located in Gunma and Nagano prefectures, Japan. We aimed to clarify the inheritances of wood properties and radial variations, as well as the relationships between wood properties and bending properties. Furthermore, we tried to classify families by differences in the types of load-deflection curves in the static bending test.

2 Materials and methods

2.1 Progeny test sites

Materials were collected from two *L. kaempferi* progeny test sites (Gunma and Nagano prefectures, located in Central Japan), and two progeny test sites were defined as the Gunma and Nagano sites in the present study. The Gunma site is located 40 km north of the Nagano site (Figure 5 in Appendix). An outline of these sites is shown in Table 6 in Appendix. The two sites were established by planting the seedlings of 56 full-sib families produced with a full diallel mating design of eight common plus-tree clones without selfing, using a randomized block design with five replicates. Each family was planted in a quadratic plot with 20 trees at each replicate block. Gunma and Nagano sites were planted in 1977 at spacings of 2.2 × 2.2 m and 2.0 × 2.0 m, respectively. No thinning treatment was conducted before sampling for the present study.

2.2 Materials

From the diallel crossing of eight plus-tree clones of five replicate blocks, the complete diallel crossing of six plus-tree clones of three replicate blocks was selected for the present study. Fifteen full-sib families were pooled with reciprocal families due to the limited number of remaining trees. A total of 269 and 260 trees were used as samples at the Gunma and Nagano sites, respectively (Table 1). The stem diameter at 1.2 m above the ground and tree height were measured for each tree at the age of 30. Mean values and standard deviations of stem diameter at 1.2 m above the ground in the Gunma and Nagano sites were 15.4 cm and 15.5 cm, respectively; similarly, those of tree height were 14.0 m and 14.1 m, respectively (Table 2). For all sample trees in Gunma and

Table 1 Combination of mating parents, family ID, and number of trees in each site

Seed parent	Pollen parent					
	PL1	PL2	PL3	PL4	PL5	PL6
PL1		9/9 (1)	9/8 (2)	9/9 (3)	9/6 (4)	9/9 (5)
PL2	9/9 (1)		9/9 (6)	9/9 (7)	9/9 (8)	9/9 (9)
PL3	9/9 (2)	9/9 (6)		9/9 (10)	9/9 (11)	9/9 (12)
PL4	9/8 (3)	9/9 (7)	9/9 (10)		9/8 (13)	9/9 (14)
PL5	9/9 (4)	9/9 (8)	9/9 (11)	9/9 (13)		9/6 (15)
PL6	9/9 (5)	8/9 (9)	9/9 (12)	9/9 (14)	9/8 (15)	

Left number and right number indicate the number of trees of the Gunma and Nagano sites, respectively. Values in parentheses represent the family ID in the present study. PL1, PL2, PL3, PL4, PL5, and PL6 were mating parent codes in the present study

Table 2 Mean values of wood properties in 15 families planted in each site

Trait	Gunma site		Nagano site	
	Mean	CV (%)	Mean	CV (%)
D (cm)	15.4	4.5	15.5	5.8
TH (m)	14.0	4.3	14.1	5.0
ARW (mm)	2.3	8.7	2.6	3.8
LWP (%)	28.3	4.2	26.7	4.9
AD (g cm ⁻³)	0.506	9.5	0.448	6.5
MFA (°)	10.6	8.5	10.6	6.6
MOE (GPa)	8.98	9.1	8.75	9.5
MOR (MPa)	84.3	10.4	83.9	8.9
W (N m)	5.58	14.1	5.27	12.0

n = 15

Mean in AD, MOE, MOR, and bending work was calculated using area-weighted mean of each individual

CV Coefficient of variation, *D* Stem diameter at 1.2 m above the ground, *TH* Tree height, *ARW* Annual ring width, *LWP* Latewood percentage, *AD* Air-dry density, *MFA* Microfibril angle, *MOE* Modulus of elasticity, *MOR* Modulus of rupture, *W* Bending work

Nagano sites, 40-cm-long logs were obtained from 1.0 to 1.4 m above the ground in October and November 2013, respectively. The trees were 36 years old. Pith-to-bark radial boards of 30 mm thickness were prepared from the logs. After air-drying the boards, one radial direction of each radial board (from the pith to the bark) was used for the following experiments (Takahashi et al. 2022b).

2.3 Wood properties

Strip specimens 10 mm thick were obtained from the radial boards to measure the annual ring width (ARW) and latewood width. Cross-sectional images of strip specimens were captured using a scanner. ARW and latewood width were measured in each annual ring from the pith to the bark sides using an image analysis software, ImageJ (National Institutes of Health, Bethesda, Maryland, USA). Latewood was identified by the color difference from

earlywood. Latewood percentage (LWP) was calculated as the proportion of latewood width to ARW in each annual ring.

The MFA of the *S*₂ layer in latewood tracheids was determined using the iodine method (Senft and Bendtsen 1985). At each site, 90 trees in a replicate block were subjected to measuring the MFA. Small blocks were prepared at the 5th, 10th, 15th, 20th, and 25th annual rings from one radial direction of the pith to the bark in an obtained strip. At each radial position, the MFA of the *S*₂ layer was measured for 30 latewood tracheids on digital photomicrographs using ImageJ. The mean values were then calculated at each radial position.

2.4 Static bending properties

Radial boards from the pith to the bark sides were planned at 15 mm in thickness, and then, the boards were cut at 15 mm intervals from the pith to obtain the small-clear specimens (ca. 15 [R] × 15 [T] × 240 [L] mm). A total of 2414 specimens were obtained (1956 and 458 specimens were from juvenile wood and mature wood, respectively). The average number of specimens per individual was 4.55 specimens. When small-clear specimens were prepared, we carefully prepared the specimens without severe curvature of annual rings. The static bending test was conducted using a universal testing machine (MSC-5/200-2, Tokyo Testing Machine, Tokyo, Japan). The span and load speed were 210 mm and 4 mm/min, respectively. The MOE and MOR were calculated from the load-deflection curve after a bending test using Eqs. 1 and 2, respectively (Figure 6 in Appendix; Takahashi et al. 2021).

$$\text{MOE (GPa)} = \frac{Ppl^3}{4Ypbh^3} \quad (1)$$

$$\text{MOR (MPa)} = \frac{3Pml}{2bh^2} \quad (2)$$

where Pp is load at proportional limit, Yp is deflection at proportional limit, Pm is maximum load, l is the span, b is the width of the specimen, and h is the height of the specimen. W is calculated as an area enclosed with the OBC in Figure 6 in [Appendix](#).

Small blocks without any damage were cut from each small-clear specimen to measure moisture content and air-dry density (AD). The mean values and standard deviations of moisture content in all small-clear specimens were $9.4 \pm 0.6\%$ at testing. The MOE and MOR values were adjusted to those at 12% moisture content by the methods described by Japan Housing and Wood Technology Center (Japan Housing and Wood Technology Center [2011](#)).

2.5 Data analysis

The values of all wood properties at each radial position were calculated by averaging the values from 1st to 5th, from 6th to 10th, from 11th to 15th, from 16th to 20th, and from 21st to 36th annual rings from the pith (Figure 7 in [Appendix](#); Tanabe et al. [2014](#)). In addition, the overall mean at all radial positions in bending properties and AD was calculated by the weighted average method using the area based on the annual ring number in the center of each specimen. In *L. kaempferi*, Shiokura ([1982](#)) reported that the boundary between juvenile and mature wood was located at the 11th–19th annual rings from the pith. In the present study, the 1st–20th radial positions and the 21st–36th radial positions were regarded as juvenile and mature wood, respectively. The variance components of each trait were estimated using the restricted maximum likelihood (REML) method using ASReml-R (Butler [2021](#)). The estimation of the breeding value and variance components is expressed in the following linear mixed model (Eq. 3):

$$Y_{ijklm} = \mu + P_i + B_{ij} + G_k + G_l + S_{kl} + PG_{ikl} + BG_{ijkl} + e_{ijklm} \quad (3)$$

where Y_{ijklm} is the measurement value of the m^{th} individual of family of the k^{th} and l^{th} parents in the j^{th} block of the i^{th} site, μ is the general mean value, P_i is a fixed effect of the i^{th} site, B_{ij} is the fixed effect of the j^{th} block in the i^{th} site, G_k and G_l are random effects of genetic combining ability (GCA) of k^{th} and l^{th} parents, respectively, S_{kl} is a specific combining ability (SCA) between k^{th} and l^{th} parents, PG_{ikl} is the random interaction effect for the i^{th} site and the GCA of the k^{th} and l^{th} parents, BG_{ijkl} is the random interaction effect for j^{th} block in the i^{th} site and the GCA of the k^{th} and l^{th} parents, and e_{ijklm} is the random residual. Random factors were assumed to be distributed normally, with an expectation of zero. The random effects G_k and G_l were predicted from the variance of GCA as follows: $G_k \sim N(0, \sigma_{GCA}^2)$ and $G_l \sim N(0,$

$\sigma_{GCA}^2)$, respectively. Because the number of samples in the MFA was limited, the B_{ij} and BG_{ijklm} terms could not be included in Eq. 3 for the MFA. The random factors and breeding values of each mating parent were obtained using an “animal model” of the best linear unbiased prediction (BLUP).

The narrow-sense heritability (h^2) of each trait was estimated using Eq. 4:

$$h^2 = \frac{\sigma_{GCA}^2}{\sigma_{GCA}^2 + \sigma_{SCA}^2 + \sigma_{pg}^2 + \sigma_{bg}^2 + \sigma_e^2} \quad (4)$$

where σ_{GCA}^2 , σ_{SCA}^2 , σ_{pg}^2 , σ_{bg}^2 , and σ_e^2 are variance components of GCA, SCA, the interaction of progeny \times GCA, the interaction of block \times GCA, and the residual, respectively. These estimations were carried out using ASReml-R software (Butler [2021](#)).

The genetic correlation between trait x and trait y ($r_{g(x,y)}$) was estimated using Eq. 5:

$$r_{g(x,y)} = \frac{COV_{g(x,y)}}{\sqrt{\sigma_{g(x)}^2 \times \sigma_{g(y)}^2}} \quad (5)$$

where $COV_{g(x,y)}$ is the covariance of trait x and trait y and $\sigma_{g(x)}^2$ and $\sigma_{g(y)}^2$ are the additive genetic variances of trait x and trait y , respectively. In addition, the phenotypic correlation between trait x and trait y was estimated based on phenotypic variances.

Principal component analysis (PCA) and cluster analysis were employed to categorize the 15 families. Principal component scores were calculated by a correlation matrix with the four following variables: estimated family mean values in load and deflection at the proportional limit and maximum load and deflection. The estimated family mean for the four variables was calculated by the sum of the general mean value (μ), breeding values in each parent (G_k and G_l), and breeding values in each family (S_{kl}) (Eq. 4) to remove the effects of differences in environmental factors. Using the 1st and 2nd principal component scores from PCA as variables, cluster analysis using the Ward hierarchical clustering algorithm was performed for the categorization of 15 families. The optimal number of clusters was determined using the Jain-Dubes method (Jain and Dubes [1988](#)). These statistical analyses were performed using open-source statistical software R 4.0.3 (R Development Core Team [2020](#)).

3 Results

3.1 Mean values and radial variations of wood properties and bending properties

The mean values of the wood properties and their radial variations at each site are shown in Table 2 and Fig. 1,

respectively. The mean ARW in the two sites decreased from 1st–5th to 21st–36th radial positions, with a drastic decrease at the 11th–15th radial position (Fig. 1). The mean values of LWP, AD, MOE, MOR, and W increased drastically from 1st–5th to 11th–15th radial positions and then slightly increased or became almost stable toward the outer radial positions (Fig. 1). The AD and bending properties in the Nagano site were shown to have higher values compared with those in the Gunma site, especially in the range from the 6th–10th to the 16th–20th radial positions (Fig. 1). The site effects as fixed effects were significant at 6th–10th position in ARW and LWP, 11th–20th position in AD, 11th–36th position in MOR, 16th–20th position in W, and all positions in MOE.

The mean values of the MFA at the 5th annual ring from the pith showed the highest values in each family, being 16 to 17° (Fig. 2). Then, the mean MFA value rapidly decreased to about 7° toward the 25th annual ring

from the pith (Fig. 2). The radial variation of the MFA showed a similar pattern between the two sites (Fig. 2). The mean value of the MFA in all families was 10.6° in the two sites (Table 2).

3.2 Heritability

The heritability of ARW ranged from 0.000 at the 6th–10th radial position to 0.008 at the 11th–15th radial position (Table 3). The highest heritability in LWP ($h^2 = 0.360$), AD ($h^2 = 0.459$), and MOR ($h^2 = 0.503$) was obtained in the 21st–36th radial positions among the five radial positions. In the MFA, heritability decreased from the inner position to the outer position, with the highest heritability at the 1st–5th radial positions ($h^2 = 0.137$). The heritability of MOE and W ranged from 0.000 in the 11th–15th to 0.263 in the 6th–10th radial positions and from 0.023 in the 11th–15th to 0.199 in the 6th–10th radial positions, respectively.

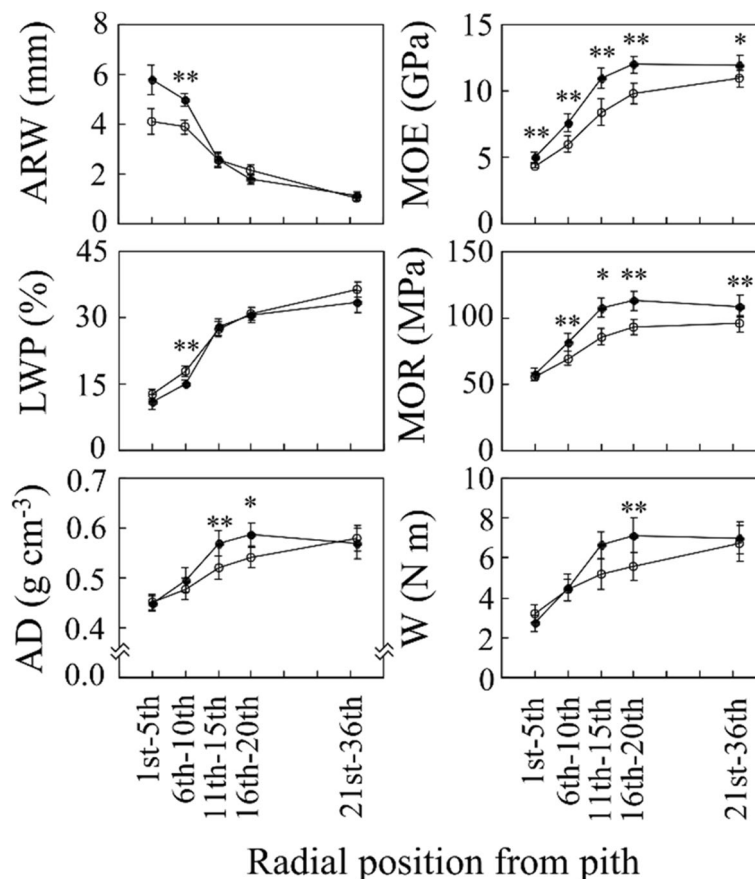


Fig. 1 Radial variations of wood properties. Note: ARW, annual ring width; LWP, latewood percentage; AD, air-dry density; MOE, modulus of elasticity; MOR, modulus of rupture; W, bending work; open circles and closed circles indicate mean values of family mean values in the Gunma and Nagano sites, respectively; bar, standard deviation. ** and * significant site effects as fixed effects at $p < 0.01$ and $p < 0.05$, respectively

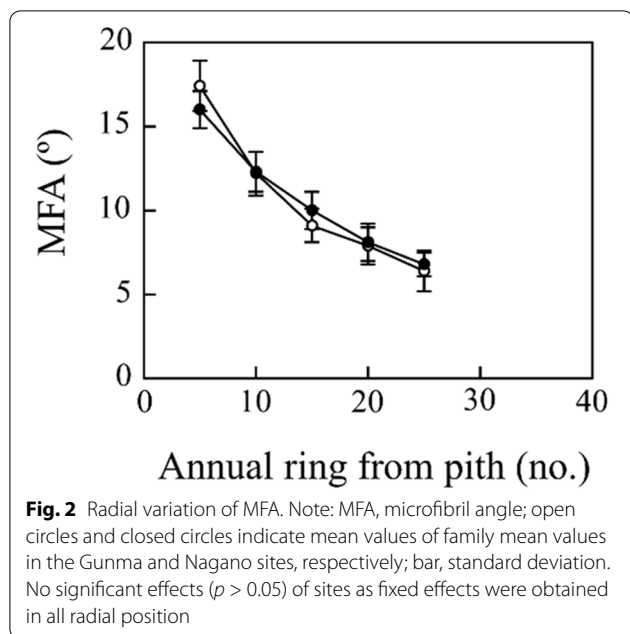


Table 3 Narrow-sense heritability of all wood properties

Trait	1st–5th	6th–10th	11th–15th	16th–20th	21st–36th
ARW	0.045 (0.093)	0.000 (0.000)	0.088 (0.105)	0.056 (0.091)	0.067 (0.061)
LWP	0.028 (0.061)	0.068 (0.091)	0.000 (0.000)	0.094 (0.117)	0.360 (0.240)
AD	0.330 (0.240)	0.383 (0.255)	0.175 (0.211)	0.381 (0.249)	0.459 (0.287)
MFA	0.137 (0.364)	0.122 (0.184)	0.000 (0.262)	0.000 (0.000)	0.000 (0.087)
MOE	0.044 (0.054)	0.260 (0.175)	0.000 (0.087)	0.085 (0.117)	0.110 (0.142)
MOR	0.030 (0.064)	0.199 (0.145)	0.011 (0.072)	0.146 (0.150)	0.422 (0.271)
W	0.035 (0.053)	0.199 (0.145)	0.023 (0.078)	0.105 (0.111)	0.120 (0.124)

Values represent narrow-sense heritability. Values in parentheses represent standard error

ARW Annual ring width, LWP Latewood percentage, AD Air-dry density, MFA Microfibril angle, MOE Modulus of elasticity, MOR Modulus of rupture, W Bending work

3.3 Genetic and phenotypic correlations between AD or MFA and bending properties

Genetic correlations with AD in all bending properties were high at almost all radial positions (Fig. 3). In addition, phenotypic correlations with AD were shown above 0.5 in MOE and MOR at 6th–36th radial positions. On the other hand, the estimated standard errors in the genetic correlations between the MFA and bending properties were larger for most radial positions (Fig. 3). As the exceptions, genetic correlations of MFA were obtained

at 1st–5th ($r_g = 0.890$) and 6th–10th ($r_g = 0.320$) radial positions. In all bending properties, phenotypic correlations with MFA were shown in the range of -0.2 to -0.4 at 16th–36th radial positions.

Table 4 shows the genetic correlations between the mean at all positions and the mean at each radial position for all wood properties. In ARW and AD, correlations were higher than 0.6 at all radial positions, while high correlations in LWP and bending properties were obtained in mainly 11th–36th radial positions.

3.4 Classification of load-deflection curves

The plot of principal components for the 15 families' scores and the loading of principal components in juvenile wood are shown in Fig. 4 and Table 5, respectively. The contributions of 1st and 2nd principal components were 52.0% and 29.1%, respectively, and, similarly, in mature wood 55.8% and 25.8%, respectively (Fig. 4). In both juvenile and mature wood, the 1st and 2nd principal components mainly contributed to loads at the proportional limit and maximum load and deflection at the proportional limit and maximum deflection, respectively (Table 5). Cluster analysis using 1st and 2nd principal components obtained from PCA as variables was conducted to classify the 15 families. Based on the Jain-Debus method (Jain and Dubes 1988), the optimal number of clusters was determined to be three groups in both juvenile and mature wood. The 15 families in juvenile wood were grouped into three groups: group I (1, 2, 3, 6, 7, 8, 9, and 10 in family ID), group II (12 in Family ID), and group III (4, 5, 11, 13, 14, and 15 in Family ID) (Fig. 4). In mature wood, the 15 families were divided into three groups by cluster analysis: group I (2, 4, 5, 11, 12, and 15 in Family ID), group II (1 in Family ID), and group III (3, 6, 7, 8, 9, 10, 13, and 14 in Family ID) (Fig. 4).

Typical load-deflection curves for the three groups in juvenile wood and mature wood are shown in Fig. 4. In juvenile wood, typical load-deflection curves differed in maximum load and load at proportional limit among groups, but there was no difference in the amount of deflection. A similar result was shown in mature wood, with a larger difference among the groups than in juvenile wood.

4 Discussion

4.1 Mean values and radial variations of wood properties and bending properties

Mean values of ARW, LWP, AD, MOE, and MOR in the present study were almost similar to those of other previous studies on larch (Table 7 in Appendix, Miyajima 1958, 1985; Kawaguchi et al. 1987; Koizumi et al. 1987; Zhu 2002; Karlman et al. 2005; Koizumi et al. 2005; Cáceres et al. 2018). These radial variations obtained in

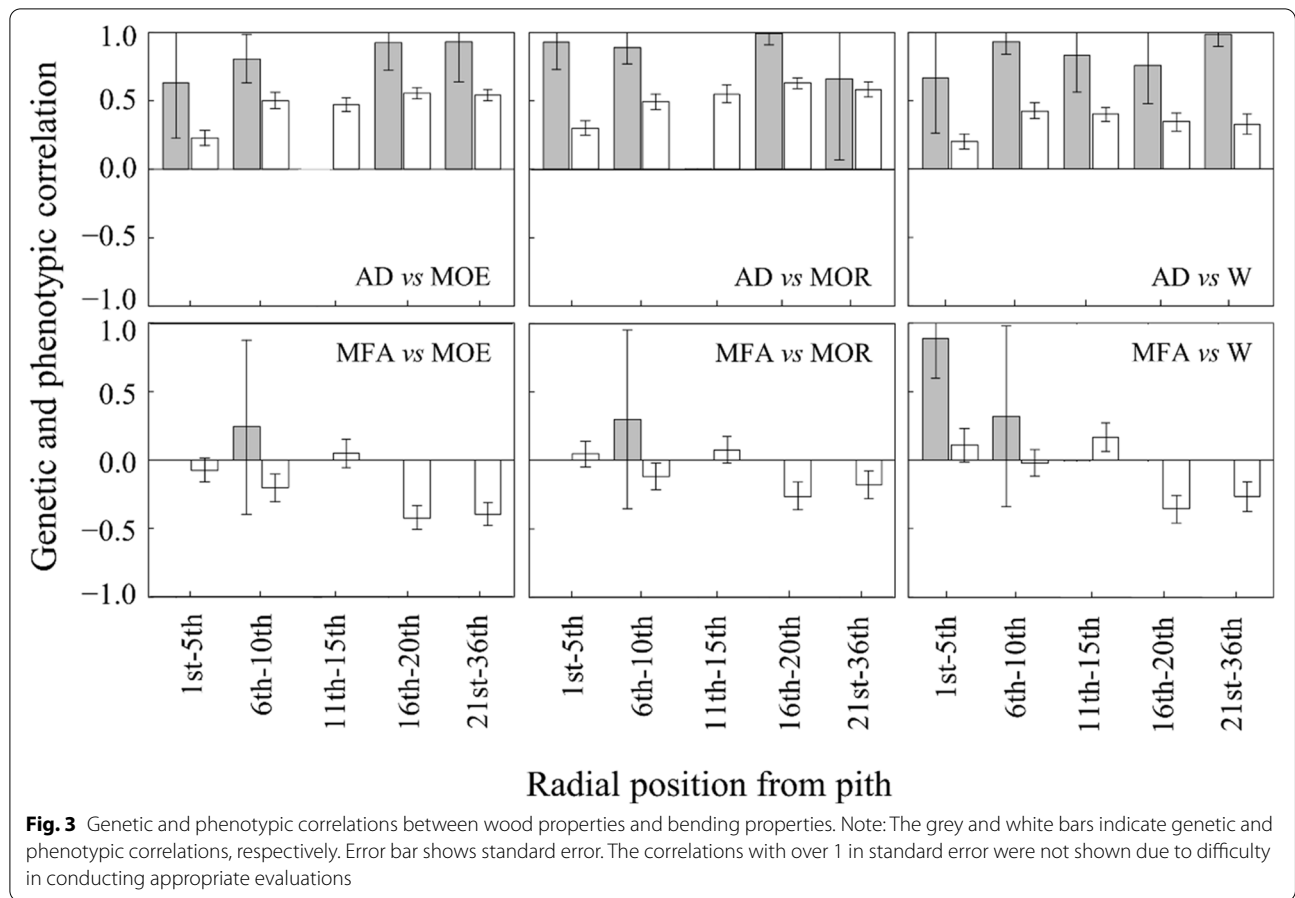


Fig. 3 Genetic and phenotypic correlations between wood properties and bending properties. Note: The grey and white bars indicate genetic and phenotypic correlations, respectively. Error bar shows standard error. The correlations with over 1 in standard error were not shown due to difficulty in conducting appropriate evaluations

Table 4 Age-age genetic correlations for age trend between area-weighted overall mean and mean at each radial position

Trait	Parameter	Radial position from pith				
		1st–5th	6th–10th	11th–15th	16th–20th	21st–36th
ARW	r_g	0.997	0.696	0.790	0.705	0.915
	s.e.	0.058	0.437	0.399	0.402	0.130
LWP	r_g	-0.618	0.909	0.356	0.954	0.946
	s.e.	0.507	0.144	0.531	0.060	0.055
AD	r_g	0.796	0.873	0.837	0.915	0.847
	s.e.	0.542	0.506	0.820	0.481	0.464
MFA	r_g	0.882	0.959	0.906	-	-
	s.e.	0.529	0.397	0.517	-	-
MOE	r_g	0.576	0.830	0.273	0.729	0.971
	s.e.	0.747	0.176	0.300	0.492	0.165
MOR	r_g	0.648	0.999	0.899	0.754	0.963
	s.e.	0.545	0.145	0.495	0.385	0.146
W	r_g	-0.184	0.992	0.838	0.984	0.733
	s.e.	0.699	0.144	0.435	0.225	0.647

Results were not shown because the standard error exceeded 1 and could not be evaluated

r_g Genetic correlation, s.e. Standard error, ARW Annual ring width, LWP Latewood percentage, AD Air-dry density, MFA Microfibril angle, MOE Modulus of elasticity, MOR Modulus of rupture, W Bending work

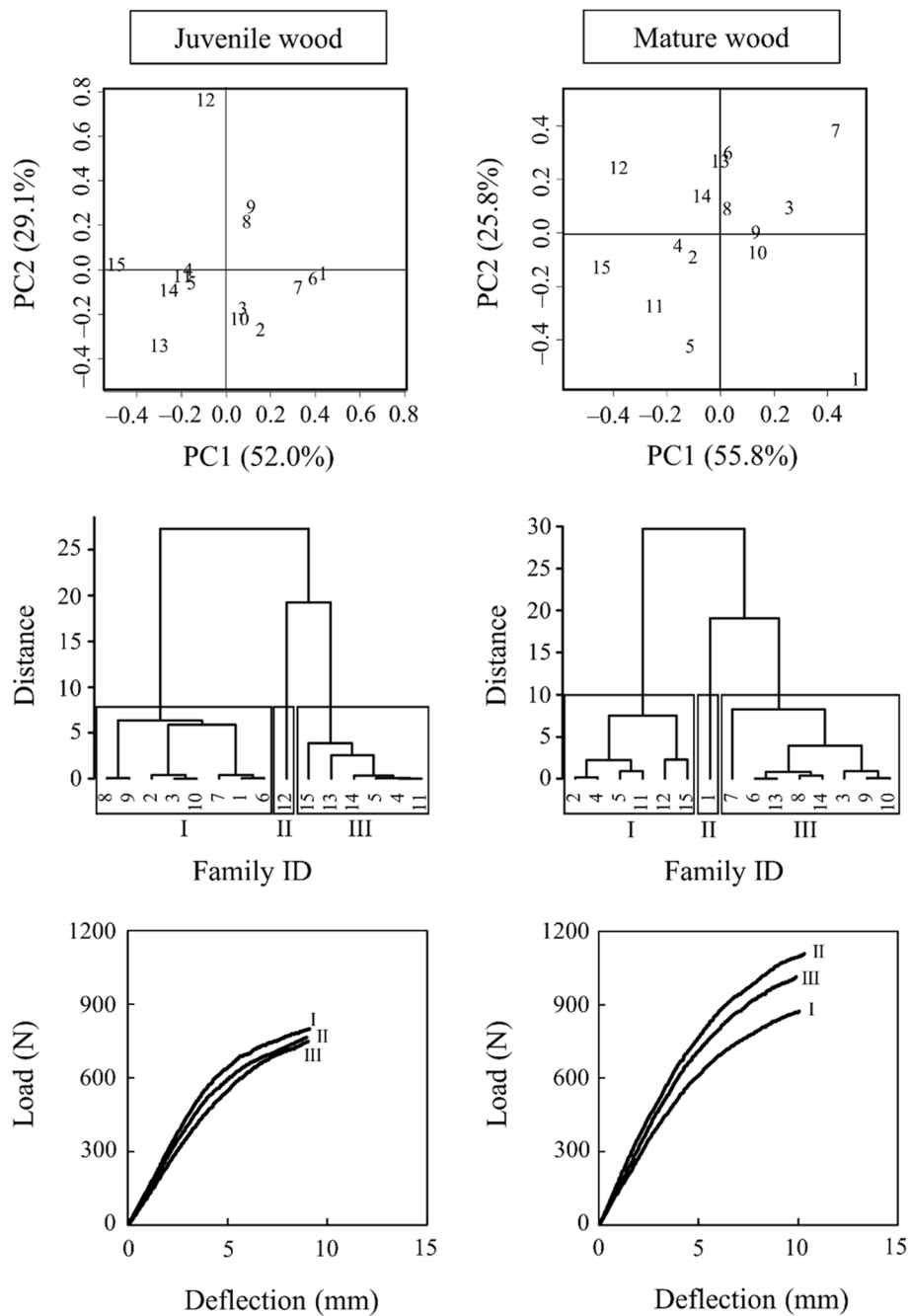


Fig. 4 A plot of principal component scores, cluster dendrogram, and typical load-deflection curves for juvenile and mature wood. Note: PC1 and PC2, first and second principal components, respectively. The plotted numbers are Family ID. The vertical axis shows the distance between families based on squared Euclidean distance using the Ward hierarchical clustering algorithm

the present study were almost similar to those reported by previous studies (Kawaguchi et al. 1987; Leban and Haines 1999; Zhu 2002; Karlman et al. 2005; Koizumi et al. 2005).

In general, the MFA in softwood species rapidly decreases from the pith to around the 20th ring from the

pith and then becomes constant (Panshin and de Zeeuw 1980). This tendency is also true for *L. kaempferi* (Takimoto et al. 2013). The mean values and radial variations of MFA obtained in the present study were almost similar to those of previous studies in *L. kaempferi* (Takimoto et al. 2013).

Table 5 Loading of principal components of PCA for 15 families

Variable	Juvenile wood		Mature wood	
	PC1	PC2	PC1	PC2
Load at proportional limit	0.671	0.091	0.621	0.349
Deflection at proportional limit	-0.131	-0.745	0.351	-0.556
Maximum load	0.687	0.005	0.638	0.284
Maximum deflection	0.246	-0.660	0.290	-0.699

PC1 and PC2 First and second principal components, respectively

Because latewood shows a higher density compared to earlywood, a higher LWP results in a higher wood density in softwood (Fukatsu et al. 2015). In the present study, AD and bending properties at the Nagano site were higher in almost all radial positions compared to those at the Gunma site (Fig. 1), although LWP did not vary among sites at all radial positions. Zamudio et al. (2005) reported that the environmental effect on latewood density was pronounced for 31 open-pollinated families planted in the *Pinus radiata* site in southern Chili. A similar result was reported in *Larix decidua* trees located at different elevations and climates (Rozenberg et al. 2020). Thus, differences in AD and bending properties between sites might occur due to differences in latewood density caused by environmental differences between sites.

4.2 Radial variations in heritability

In softwood species, wood properties differ between juvenile and mature wood (Shiokura 1982; Cown et al. 1999; Ishiguri et al. 2009; Iki et al. 2010). Therefore, to clarify differences in the inheritance of wood properties between juvenile and mature wood, radial variations in heritability have been investigated by several researchers (Fujimoto et al. 2006a; Kumar et al. 2006; Lenz et al. 2010; Chen et al. 2014). In the present study, the heritability of ARW showed low values throughout the stem (Table 3), suggesting that radial growth rate might be affected by environmental factors such as climatic conditions, soil type, and canopy closure rather than genetic factors. In half-sib families of 20-year-old *Picea glauca*, the heritability of MFA was almost constant, between 0.25 and 0.30, over the range of cambial age (Lenz et al. 2010). In half-sib families of 21-year-old *P. abies*, the heritability of MFA increased from the 1st annual ring to the 6th annual ring and then decreased up to the bark side (Chen et al. 2014). Fujimoto et al. (2006a) reported that the heritability values of MOE and MOR at the bark side ($h^2 = 0.42$ and 0.61 , respectively) for full-sib families of hybrid larch (*L. gmelinii* × *L. kaempferi*) were higher than those at the pith side ($h^2 = 0.28$ and 0.49 , respectively). The radial trend in the heritability of MFA was similar to

that reported for *P. abies* (Chen et al. 2014). Chen et al. (2014) also reported that the heritability of wood density and MOE increased from the pith to the bark sides. The higher heritability of AD, MOE, and MOR at the outer positions obtained in the present study was in accordance with those of previous studies (Fujimoto et al. 2006b; Lenz et al. 2010; Chen et al. 2014). Based on these results, it is considered that the genetic control of the MFA near the pith is larger than that at the outer radial positions. In addition, AD and bending properties in the 6th–10th radial positions were also relatively strongly genetically affected among juvenile wood positions. Because the highest heritability was obtained, it is concluded that wood properties, such as LWP, AD, and MOR in mature wood, can be effectively improved by selecting individuals.

4.3 Relationships between wood properties and bending properties

Many researchers have investigated phenotypic correlations between wood properties (AD, MFA, and others) and mechanical properties, such as bending properties in softwood species (Cown et al. 1999; Alteyrac et al. 2006; Fujimoto et al. 2006a; Kumar et al. 2006; Iki et al. 2010; Chen et al. 2014; Cáceres et al. 2018). For example, Cown et al. (1999) reported that the influence of MFA on MOE ($r = -0.76$) in 28-year-old *Pinus radiata* was larger than that of wood density ($r = 0.58$) in juvenile wood, whereas wood density showed a greater stimulus in mature wood. On the other hand, Iki et al. (2010) reported that in 43-year-old *Abies sachalinensis* masters, significant correlations between AD and MOE were found at almost all radial positions, while no significant correlations were found between MFA and MOE at almost all radial positions. The results of phenotypic correlations obtained in the present study were similar to those in hybrid larch (Fujimoto et al. 2006a) and *P. radiata* (Cown et al. 1999). With a few exceptions, correlations of MOE, MOR, and W with AD at most radial positions showed higher values of around 0.5, suggesting that bending properties in *L. kaempferi* were strongly affected by AD. The influence of MFA on bending properties is limited in outer radial positions (16th–36th).

Genetic correlations can expect the responses of a trait when selection is applied to another trait (Falconer and Mackay 1996). In 30-year-old *P. radiata*, Kumar et al. (2006) reported that genetic correlations between wood density and static MOE were moderate ($r = 0.51$) in the core wood zone (the 3rd to 4th annual ring from the pith) but high ($r = 0.78$) in the outer wood (the 9th to 10th annual ring from the pith). Chen et al. (2014) reported that genetic correlations between MFA and MOE were high negative values, and the correlations between wood

density and MOE were high positive values across all annual rings in 21-year-old Norway spruce (*Picea abies*). In the present study, high genetic correlations were found in AD with MOE and MOR at almost all radial positions. Based on the results, AD can be considered a criterion for improving the bending properties of *L. kaempferi*. On the other hand, W at 1st–10th radial positions correlated with MFA. A similar result was found for juvenile wood in *C. japonica* (Ishiguri et al. 2009). Wood properties as a criterion for selecting trees with superior bending properties should be highly heritable. Therefore, it is suggested that trees with superior bending properties can be effectively selected by the selection of trees using AD as the criterion in *L. kaempferi*.

Fujimoto et al. (2006a) reported that overall means of AD, MOE, and MOR can be estimated by mean values of those in inner wood (pith to 8th annual ring from pith) in hybrid larch (*L. gmelinii* × *L. kaempferi*). In ARW, AD, and MFA, higher correlations were obtained in the inner radial positions (Table 4), suggesting that early selection of these properties is possible in *L. kaempferi*. Based on the higher correlations in LWP and bending properties in outer radial positions (11th–36th) higher than inner positions, early selection for these wood properties is considered desirable after 11 ages.

4.4 Inheritance of load-deflection curves in 15 full-sib families

In juvenile wood of *C. japonica*, we previously investigated the types of load-deflection curves and found that they were divided into four types by the effect of the combinations of mating parents (Takahashi et al. 2021). Although the load-deflection curves in juvenile wood were not grouped distinctly compared to those in *C. japonica*, the slight differences in load-deflection curves among groups in juvenile wood of *L. kaempferi* were found in load at the proportional limit and maximum load (Fig. 4). On the other hand, it was reported that the load-deflection curves of mature wood in *Chamaecyparis obtusa* largely varied among six families compared to juvenile wood (Takahashi et al. 2022a). Similar results were obtained in the present study (Fig. 4), but there was less difference in the amount of deflection compared with mature wood in *C. obtusa* (Takahashi et al. 2022a). These results suggest that the variation of load-deflection curves, especially the amount of deflection in *L. kaempferi*, was smaller in juvenile and mature wood than in *C. japonica* and *C. obtusa*. Thus, in *L. kaempferi*, it is concluded that improving mature wood with higher bending properties while maintaining the characteristics of the materials (higher proportional limit and smaller plastic region) is possible in *L. kaempferi* by selection in tree breeding programs.

4.5 Implementation of wood quality improvement in *L. kaempferi* by tree breeding

In breeding programs for *L. kaempferi* in Japan, the selection of second-generation plus trees has been currently conducted from the breeding population in progeny test sites (Kurinobu 2005; Fukatsu et al. 2015). In the results obtained in the present study, AD was genetically strongly affected at almost all radial positions compared with other wood properties. In addition, significant genetic correlations were found between AD and MOE or MOR, especially in the outer radial positions (Fig. 3). Thus, it is concluded that in *L. kaempferi*, genetic improvement for wood density and bending properties was effective for mature wood compared to juvenile wood, and improvements in wood density resulted in improvement of bending properties, which are important traits for use as structural lumber in *L. kaempferi*. Leban and Haines (1999) reported that specific MOE (the ratio of MOE and wood density) can be used as a criterion to evaluate the strength performance of wood. In the present study, specific MOE in Nagano site (19.53) was higher value than that in Gunma site (17.74), indicating that wood produced from Nagano site was characterized by higher strength properties per unit weight compared to wood from Gunma site. Further research is needed for the evaluation of the possible application of specific MOE as a selection criterion of the superior tree for structural wood production in tree breeding.

5 Conclusions

The inheritance of wood properties (i.e., ARW, LWP, AD, and MFA) and bending properties was investigated for 15 full-sib families in 36-year-old *L. kaempferi*. In almost all wood properties, the mean values and radial variations determined in the present study were similar to those reported in previous studies. From the results of phenotypic and genetic correlations, AD can be used as a criterion by which to select trees with superior bending properties. Furthermore, significant correlations were found between the overall mean and mean values at almost all radial positions for AD, MFA, MOE, MOR, and W. MFA was genetically controlled near the pith. In contrast, the heritability of LWP, AD, and MOR was shown to have the highest values on the outer side. Although the load-deflection curves of 15 families in *L. kaempferi* could be divided into three groups in both juvenile and mature wood, similar load-deflection curves with slight differences in loading parameters were obtained in all groups for both juvenile and mature wood. Larger differences in maximum load among families were obtained in mature wood compared to juvenile wood, suggesting the possibility of improving mature wood with higher

resistance to rupture and maintaining the characteristics of materials (a higher proportional limit and smaller plastic region) in *L. kaempferi* by selection. However, because the sample trees used in the present study were small-diameter trees that were not enough size for producing the actual size of structural lumber, further study using full-size structural lumber is necessary for evaluating wood quality and that inheritance in this species.

Appendix

Table 6 Outline of two progeny test sites

Details	Gunma	Nagano
Latitude	36°30' N	36°21' N
Longitude	138°26' E	138°31' E
Above sea level (m)	1360–1380	1120
Annual temperature (°C)		
Mean	6.1	7.2
Minimum	−4.4 (Jan.)	−3.2 (Jan.)
Maximum	16.7 (Jul.)	17.9 (Jul.)
Annual precipitation (mm)		
Mean	102.8	79.8
Minimum	28.4 (Jan.)	19.8 (Jan.)
Maximum	184.1 (Sep.)	154.8 (Jul.)
Test site establishment	May 1977	April 1977
Initial planting density (seedlings/ha)	2000	2500
Number of replicated blocks	5	5
Number of families	56	56
Slope inclination (°)	5–7	0–5
Soil type	B _D	B _{D(d)}

The annual temperature and precipitation were estimated using data of the nearest meteorological station, provided by the Japan Meteorological Agency. Mean annual temperature was calculated by averaging monthly mean temperature obtained from 2008 to 2012. Mean annual precipitation was calculated by averaging total monthly precipitation obtained from 2008 to 2012

B_D Moderately moist black forest soil, B_{D(d)} Moderately moist brown forest soil

Table 7 Mean values of wood properties in *L. kaempferi* reported by several researchers

Age	Country	ARW (mm)	LWP (%)	AD (g cm ⁻³)	MOE (GPa)	MOR (MPa)	References
52	Hokkaido, Japan	3.6	-	0.40	7.64	69.5	Miyajima (1958)
53	Hokkaido, Japan	3.0	-	-	7.94	69.8	Miyajima (1985)
67	Hokkaido, Japan	-	-	0.53	8.42	83.4	Kawaguchi et al. (1987)
24	Hokkaido, Japan	3.8–6.6	-	0.47	7.94	68.8	Koizumi et al. (1987)
70	Nagano, Japan	1.67–4.13	30.7–46.1	0.50–0.58	-	-	Zhu (2002)
35	Remningstorp, Sweden	3.94	-	0.45	-	-	Karlman et al. (2005)
31	Hokkaido, Japan	-	-	0.54–0.55	8.2–9.5	93.3–97.2	Koizumi et al. (2005)
12	Quebec, Canada	-	-	0.45–0.50	-	-	Cáceres et al. (2018)

ARW Annual ring width, LWP Latewood percentage, AD Air-dry density, MOE Modulus of elasticity, MOR Modulus of rupture

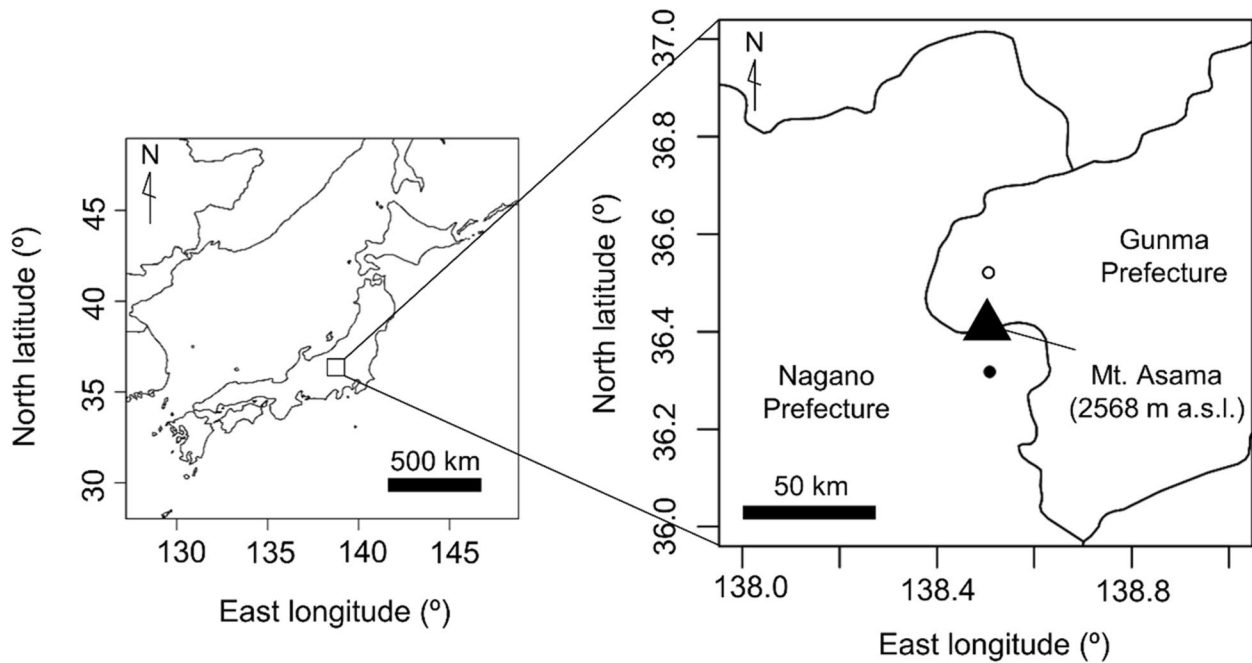


Fig. 5 Locations of two progeny trial sites. Note: a.s.l., above sea level; open and closed circles indicate progeny test sites at Tsumagoi, Gunma Prefecture, and Miyota, Nagano Prefecture, respectively.

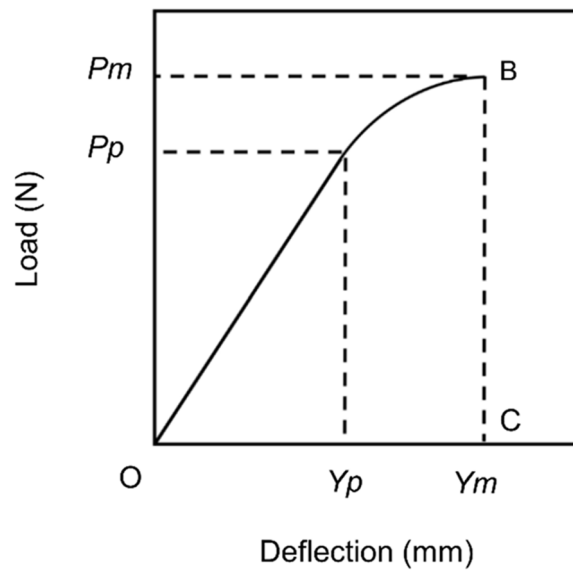


Fig. 6 Calculation of static bending properties from load-deflection curve of static bending test (Takahashi et al. 2021). Note: P_m , maximum load; P_p , load at proportional limit; Y_m , maximum deflection; Y_p , deflection at proportional limit. MOE and MOR were determined by the following equations: MOE (GPa), $P_p l^3 / 4 Y_p b h^3$; MOR (MPa), $3 P_m l / 2 b h^2$, where l is the span, b is the width of the specimen, and h is the height of the specimen. W is an area enclosed with OBC in this graph

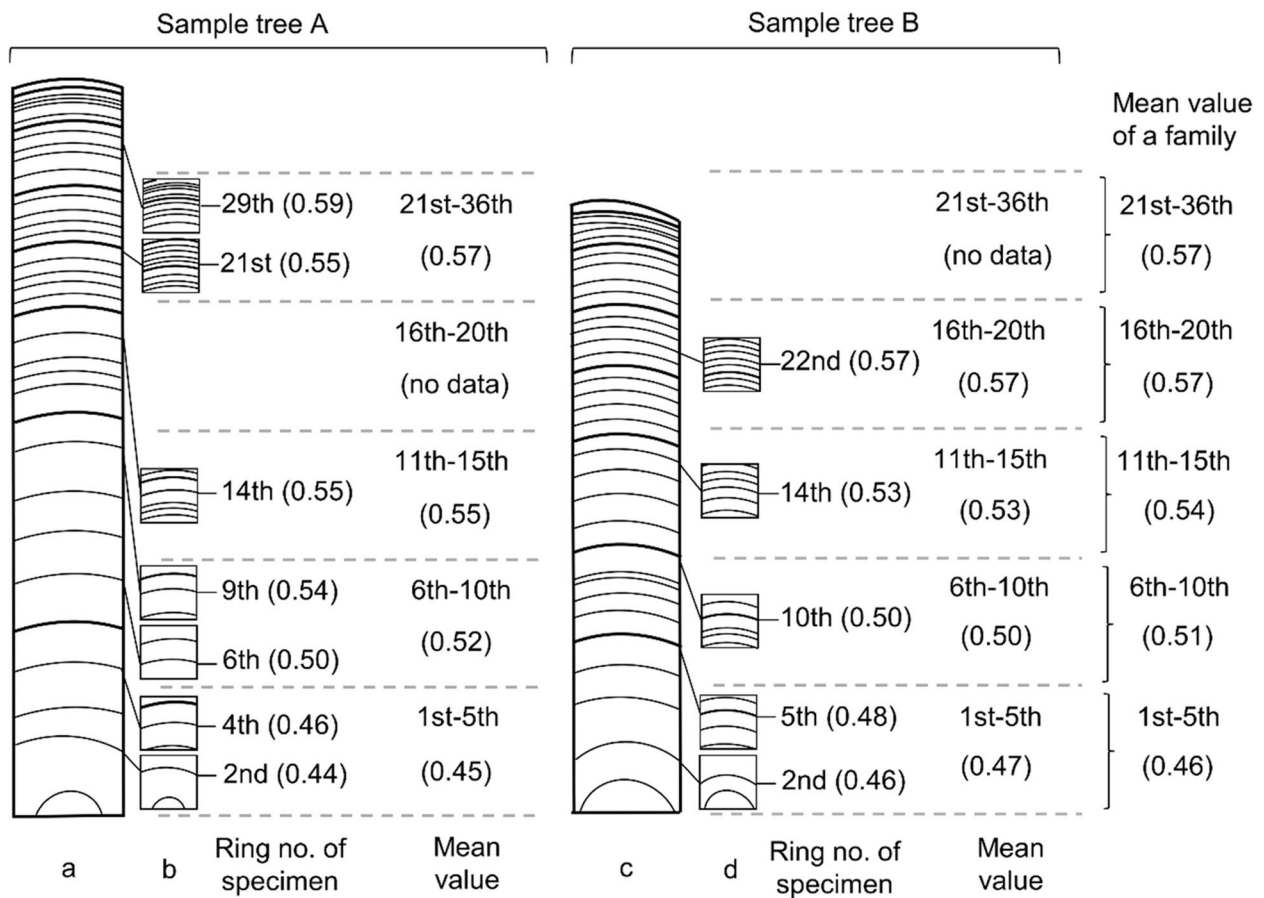


Fig. 7 Preparation of small clear specimens and calculation method of mean values at five radial positions (1st–5th, 6th–10th, 11th–15th, 16th–20th, and 21st–36th annual ring from the pith) (Tanabe et al. 2014). Note: a and c, cross-sectional images of radial board in sample trees A and B, respectively; b and d, cross-sectional images of small clear specimen in sample trees A and B, respectively. Due to sample tree size, specimen could not be obtained from all radial positions (in this Fig., specimens were not obtained from the 16th–20th annual ring positions in sample tree A and the 21st–36th annual ring positions in sample tree B). Numbers in parentheses show examples of AD value (g cm^{-3}). For example, the mean value of a family in the 1st–5th positions (0.46 g cm^{-3}) was calculated by averaging the values obtained from the same positions of sample tree A (0.45 g cm^{-3}), sample tree B (0.47 g cm^{-3}), and other sample trees

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Code availability

The code used in the current study is available from the corresponding author on reasonable request.

Authors' contributions

YT and FI designed the research layout, and YT and YH supported the statistical analysis. YT and FI collected and analyzed the data and drafted the manuscript. All authors discussed results and conclusions and contributed to writing the final manuscript. The author(s) read and approved the final manuscript.

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Availability of data and materials

The datasets have been deposited in the Figshare repository: <https://doi.org/10.6084/m9.figshare.21397674.v1>.

Declarations

Ethics approval and consent to participate

The authors declare that the study was not conducted on endangered, vulnerable, or threatened species.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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