日本落叶松木材性状与生长曲线参数的关系及其种源变异对降水的响应

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摘　要:【目的】了解木材性状的遗传变异及其与生长性状和环境变量的关系对林木复杂性状的遗传改良至关重要。本研究的目的是调查木材性状的变异及其与生长曲线参数的关系，并确定影响木材性状的主要气候因子。【方法】测定了来自6 个种源 450 株日本落叶松的 15 个木材解剖和木材化学性状及生长性状。采用线性混合模型和 Pearson 相关分析估计这些性状的遗传参数以及木材性状与树高和胸径生长曲线参数的相关性。采用线性回归分析和 Mantel 检验来检验气候变量与木材性状之间的关系及相关强度。【结果】大部分木材解剖性状在不同种源间差异显著，其遗传力($\hat{h}_i^2$=0.07-0.65)普遍高于木材化学和生长性状($\hat{h}_i^2$=0.01-0.17)。早材解剖性状($\hat{h}_i^2$=0.09-0.65)的遗传力高于晚材解剖性状($\hat{h}_i^2$=0.08-0.45)。在种源效应显著的性状中，木材纤维长度与树高极大值呈正相关，木材纤维宽度与胸径的极大值及生长速率呈正相关。降水类变量（年平均降雨，降雪，春季、夏季、秋季、冬季平均降雨）与大部分性状显著相关，包括早晚材纤维宽、早材纤维长宽比、晚材率和木材基本密度。空间类变量（经度，纬度，海拔）与早材纤维长、早材纤维长宽比和晚材率显著相关。温度类变量（年平均温度，年热，无霜期，春季、夏季、秋季、冬季的平均温度，最高温度及最低温度）与早材纤维长宽比和晚材率显著相关。早材纤维宽度与春季降水、晚材纤维宽度与夏秋季降水均表现出较强的相关性和预测趋势。【结论】相较于晚材解剖性状、木材化学性状及生长性状，早材解剖性状表现出较高的遗传力。树高的极大值、生长速率参数与木纤维长度，胸径的极大值参数与木纤维宽度之间存在显著的遗传相关。因此，早材木纤维长度和宽度是日本落叶松育种和选择的重要参考表型。早材纤维的纤维宽度和长宽比以及木材基本密度与降水变量具有较强的预测关系。在长期适应不同环境的过程中，不同种源地的降水强度影响木材纤维宽度和长度的遗传组成和表型。本研究为不同育种目的的日本落叶松引种提供了降水范围的参考，为当前气候变化背景下的日本落叶松育种计划提供了更有价值的育种指标和实证支持。

关键词：木材性状，遗传力，近红外光谱，种源变异，生长曲线参数，气候因子

Provenance variations in wood traits of Larix kaempferi and their relationships to growth curve parameters and precipitation

Abstract:【Objective】Understanding the genetic variation in wood traits and their relationships to growth traits and environmental variables is essential for the genetic improvement of forest tree species. The aims of this study were to investigate the variation in wood traits and their relationships with growth curve parameters and to identify the main climatic factors affecting wood traits. 【Method】Fifteen wood anatomical and wood chemical traits and annual growth traits were measured in 450 Larix kaempferi (Lamb.) Carr. (Japanese larch) individuals from six provenances. Linear mixed models and Pearson correlation analysis were used to estimate the genetic parameters of these traits as well as the correlations between wood traits and growth curve parameters of tree height and diameter at breast height. Linear regression analysis and the Mantel test were used to examine the relationships and the correlation strength between climatic variables and wood traits. 【Result】Most wood anatomical traits varied significantly among different provenances, with heritabilities ($\hat{h}_i^2$ = 0.07 to 0.65) generally higher than those of wood chemical and growth traits ($\hat{h}_i^2$ = 0.01 to 0.17); the $\hat{h}_i^2$ of earlywood anatomical traits (0.09 to 0.65) were higher than those of latewood anatomical traits (0.08 to 0.45). Among the traits with significant provenance variation, wood fiber length was positively correlated with the maximum growth value of tree height,

基金项目：公益林业科学研究专项资金（201504104）、国家自然科学基金面上项目（31971652）

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and wood fiber width was positively correlated with the diameter at breast height. Precipitation variables were significantly correlated with most of the traits, including EWFW, LWFW, EWFL_W, LWP and BD (Figure 2a). Spatial variables showed significant correlations with EWFL, EWFL_W, and LWP. Temperature variables showed significant correlations with EWFL_W and LWP. Strong correlations and predictive trends were observed between earlywood fiber width and spring precipitation (R2 = 0.45 and 0.78), as well as latewood fiber width and summer and fall precipitation (R2 = 0.55 to 0.80). Wood anatomical traits of earlywood presented high heritability values with high selective accuracies. Significant genetic correlations were found between maximum value, growth rate of tree height and wood fiber length, and between maximum value of diameter at breast height and wood fiber width. Hence, earlywood fiber dimension is an important reference phenotype for breeding and recurrent selection of L. kaempferi. Fiber width and length-to-width ratio of earlywood fiber and wood basic density had strong predictive relationships with precipitation variables. In the process of long-term adaptation to different environments, the genetic composition and phenotype of the fiber width and length could be shaped by precipitation in different provenances. 【Conclusion】For the introduction of L. kaempferi with different breeding purposes, we provided a reference of precipitation range. These findings provide guidance and empirical support for L. kaempferi breeding programs in the context of current climate change.

Key words: wood traits, heritability, near-infrared spectroscopy, provenance variation, growth curve parameters, climatic variables

1. Introduction

Genetic improvement of extensive wood traits has been incorporated into breeding objectives with the development of wood trait determination technology, especially nondestructive testing techniques. These wood traits, including mechanical properties (e.g., density, stiffness), anatomical properties (e.g., fiber dimensions, microfibril angle), and chemical properties (e.g., lignin, cellulose), have essential effects on different end-use products and are often regarded as important breeding targets for industrial plantations (Gallo et al., 2018; Rashidi-Jouybari et al., 2022a; Santos et al., 2012; Soro et al., 2021; Wimmer et al., 2002).

The source of wood trait variation has been a focus of research in conifer selection and breeding. All wood traits are determined by genetics, the environment and their interaction (Zobel and Van Buijten, 1989). It has been shown that most wood trait variation derives from provenance variation (Mickaël et al., 2007; Santos et al., 2021). Moreover, provenance variation can be divided into family and individual sampling, as well as environmental differences (Moura et al., 1998). There is interest in the responses of genetic variation of wood traits to environmental gradients and in the identification of the most important environmental variables. For example, wood density and latewood ratio of *Picea abies* were strongly correlated with the environmental variables in the natural range (Letitia et al., 2021; Sandak et al., 2015); radial growth has been found to be strongly correlated with temperature and precipitation in most conifers, such as *Picea schrenkiana*, *Pinus armandii* and *Larix sibirica* (Dulamsuren et al., 2011; Jiao et al., 2022, 2019; Peng et al., 2018; Wang et al., 2022). The establishment of provenance trials has provided common environmental conditions to eliminate the influence of other factors, such as environmental heterogeneity. Thus, it is feasible to study the relationships between geoclimatic variables and traits to obtain a general pattern of the specific climate variables affecting the genetic variation of wood traits (Mckown et al., 2014).

Wood traits are often negatively correlated or can be independently improved with growth traits in different tree species. In conifers, one variable is the relationship between tree growth and different wood traits. For example, growth traits have been reported to have positive genetic correlations with cellulose content in *Larix kaempferi* (Fukatsu et al., 2015; Pan et al., 2020); in contrast, selection and breeding for growth traits might adversely affect wood quality traits, such as diameter at breast height, which is often negatively related to MoE and wood density (Baltunis et al., 2010; Gapare et al., 2009). In addition, most studies have focused only on the relationship between age-specific growth traits and wood traits (Rashidi-Jouybari et al., 2022b). Ignoring the growth trend may lose some information on genetic variation and decrease the selection efficiency. Growth curves can better represent tree growth trajectories and patterns (Boris, 1993) and are important in ecology because their parameters characterize the evolutionary changes in morphology during ontogeny. Due to the difficulty of obtaining continuous observational data over many years, there are few studies of genetic variation in tree growth curve parameters. Early studies of the growth curves in maritime pine showed that the heritabilities for the growth curve parameters (maximal growth rate and asymptote) were similar to the heritabilities of the cumulative heights (Danjon, 1994). Therefore, it is preferable to estimate correlations between growth curve parameters and wood traits rather than conventional age-specific multivariate analyses.

Larix kaempferi (Lamb.) Carr. (Japanese larch) is naturally distributed in the high mountains of central Japan and is one of the most successfully introduced tree species for timber, pulp and paper production in Europe, Asia, and North America (Hoshi, 2004). In a previous study, we fitted the growth curve and estimated the three parameters for each tree using 22 years growth investigated data from provenance trials (Y. Zhang et al., 2022). Here, fifteen wood traits, including wood anatomical, wood chemical and four growth traits, were measured on 450 individual trees from 84 families of six natural *L. kaempferi* provenances. The objectives of this study were to (1) estimate the variation and genetic parameters for the extensively collected wood traits, (2) determine the genetic correlations between the wood traits and growth curve parameters of tree height and diameter at breast height, and (3) assess the relationships between trait variation and geoclimatic variables of the different provenances.

2.Materials and methods

2.1 Material sources and trial design

Seeds were collected from 84 open pollination families from six natural provenances along the mountains of central Japan covering the complete native distribution of *L. kaempferi* (Table 1) based on a Japan International Cooperation project. In March 1996, the seeds were germinated, raised to two-year-old seedlings and planted at the Jianshi trial site in Hubei Province, China (30. 08° N, 110.05° E). The trial design was a randomized complete block design with six blocks of eight-tree two-row plots, each block contained 84 families. We selected 4-6 individual tree samples from each family.

Table 1 Sampling and geographical information for *Larix kaempferi* provenances

Provenance	Number of Families	Selected number	Latitude (N)	Longitude (E)	Elevation (m)
Kusatsu	20	97	36°35′	138°30′	1374
Asama	6	54	36°20′	138°30′	927
Fuji	16	80	35°30′	138°45′	844
Ina	15	75	35°45′	138°10′	1726
Nikko	18	90	36°45′	139°25′	1444
Matsumoto	9	54	36°20′	139°45′	1620
Total	84	450			

***2.1.1** Collection of growth traits and wood cores*

A total of 450 trees were sampled from the provenance trial, including all provenances and families, the number of samples from each provenance was shown in Table 1. The height (HGT, m), diameter at breast height (DBH, cm), crown length (CL, m) and crown diameter (CD, m) data for each sampled tree were collected at tree age 17. Wood cores were extracted from bark to bark through the pith at breast height (1.3 m) using a 12 mm diameter increment borer at tree age 14.

***2.1.2** Measurement of wood anatomical and chemical traits*

The 5th, 9th and 13th annual growth rings were taken from the 450 wood cores to measure wood basic density (BD) and wood anatomical traits. The BD was measured by the drainage method, and was calculated according to the national standard (Standardization Administration of the People's Republic of China 2009). The widths of the growth ring and latewood were recorded by a micrometer with an accuracy of 0.01 mm and then used to calculate the latewood proportion (LWP). The wall-to-lumen ratios of earlywood (EWT_D) and latewood (LWT_D) cells, fiber width of earlywood (EWFW) and latewood (LWFW) were measured 50 times in the three growth rings by observing the resin section scanned by color image computer analysis system (TDY-5.2, Northeast Forestry University, China), TDY-5.2 has been developed for rapid analysis on the binary images according to the different coloring of wood cell lumen and cell wall, according to the characteristic values of pixel gray value, size, number and location, using automated and microscopy measurements, image and data analyses (Zhang et al., 2014). The fiber length of earlywood (EWFL) and latewood (LWFL) were measured 50 times in the three growth rings by observing the 12mm ×2mm×2mm strips treated by the Jeffrey segregation process (nitric acid-chromic acid separation process). The segregation solution consisted of 1:1 aqueous nitric acid and aqueous chromic acid (10% each; Jeffrey, 1917). The microfibril angles of earlywood (EMAF) and latewood (LMAF) were measured 20 times in the three growth rings by observing the iodine-stained slices (Donaldson and Frankland, 2004).

The 450 wood cores were dried for 24 h at 25 °C to constant weight, ground, and filtered through a 60-mesh sieve. Near infrared (NIR) spectra were collected using a near-infrared spectrometer (LabSpec®Pro, ASD company, USA). Each spectral output was an average of thirty scans. The final spectral data for each sample were an average of three replicates. The contents of three wood chemical properties, including lignin, hemi-cellulose and holo-cellulose, were predicted using NIR models developed for *L. kaempferi* (Zhang et al., 2022). The model determination coefficients between NIR predicted and measured values of lignin, hemi-cellulose and holo-cellulose in this study were 0.95, 0.95 and 0.90, respectively.

2.1.3 Geoclimatic variables

Based on published studies, 16 geoclimatic variables that are relevant to growth and wood traits were selected to characterize the climate of each provenance (Chen et al., 2012; Takahashi et al., 2011). Mean values of provenance climate variables from 1961 to 2000 were obtained by ClimateAP v2.30 (Wang et al., 2017). We divided all geographical and climatic variables into three categories.

Table 2 Geoclimatic variables for *Larix kaempferi* provenances

category	abbreviation (units)	geoclimate variable
Spatial	Alt (m)	altitude
	Lat (°)	latitude
	Lon (°)	longitude
Temperature	MAT (℃)	mean annual temperature
	AHM	annual heat: moisture index
	NFFD (day)	the number of frost-free days
	Tmax/min_DJF (°C)	December, January and February mean maximum/minimum temperatures
	Tmax/min_MAM (°C)	March, April and May mean maximum/minimum temperatures
	Tmax/min_JJA (°C)	June, July and August mean maximum/minimum temperatures
	Tmax/min_SON (°C)	September, October and November mean maximum/minimum temperatures
Precipitation	MAP (mm)	mean annual precipitation
	PAS (mm)	precipitation as snow (mm) between August in previous year and July in current year
	PPT_DJF (mm)	December, January and February precipitation
	PPT_MAM (mm)	March, April and May precipitation
	PPT_JJA (mm)	June, July and August precipitation

PPT_SON (mm)	September, October and November precipitation

Variables derived from 1961–2000 weather data using ClimateAP

2.2 Statistical analysis

2.2.1 Variance and genetic parameter estimation

The ASReml current mixed linear model and restricted maximum likelihood (REML) algorithm were used to estimate variance components for each trait. All calculations were performed using the statistical software ASReml-R (v. 3.0) package in R 3.1.0 (Butler et al., 2009; R Core Team, 2022).

$$y = Xb + Z_1p + Z_2pb + Z_3f + Z_4fb + e \quad (1)$$

where *y* is the observation vector for growth and wood traits; *b* is the fixed block effect, X is the incidence matrix for *b*; *p*, *pb*, *f*, *fb* and *e* represent vectors of random effect of provenances, provenance by block, family, family by block and random error, respectively, which are assumed to follow normal distribution p~N(0, $\hat{\sigma}_p^2$), pb~N(0, $\hat{\sigma}_{pb}^2$), f~N(0, $\hat{\sigma}_f^2$), fb~N($\hat{\sigma}_{fb}^2$) and *e*~N(0, $\hat{\sigma}_e^2$), respectively, where $\hat{\sigma}_p^2$ is provenance variance, $\hat{\sigma}_{pb}^2$ is provenance by block variance, $\hat{\sigma}_f^2$ is family variance, $\hat{\sigma}_{fb}^2$ is family by block variance, $\hat{\sigma}_e^2$ is random effect variance, and Z_1~Z_4 represent incidence matrices of the random effects.

Approximate standard errors of estimated parameters were estimated using a standard Taylor series expansion method (Gilmour et al., 2009). The statistical significance of the variance components for each trait was determined using a two-tailed likelihood ratio test (Self and Liang, 1987).

The phenotypic coefficient of variance ($\widehat{CV}_P$) and genetic variation coefficient ($\widehat{CV}_G$) were calculated using the following equations:

$$\widehat{CV}_P = \frac{\sqrt{\hat{\sigma}_{phen}^2}}{\overline{X}} \times 100\% \quad (2)$$

$$\widehat{CV}_G = \frac{\sqrt{\hat{\sigma}_a^2}}{\overline{X}} \times 100\% \quad (3)$$

where $\hat{\sigma}_{phen}^2$ is phenotypic variance. $\overline{X}$ is the overall mean.

The individual tree heritability ($\hat{h}_i^2$) was calculated as follows:

$$\hat{h}_i^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_e^2} \quad (4)$$

where $\hat{\sigma}_a^2$ is the variance of the additive effect, calculated as $\hat{\sigma}_a^2 = 4\,\hat{\sigma}_f^2$. In diploids, the covariance among open-pollinated families would be one-fourth of the additive genetic variance.

We characterized the growth pattern of each tree with growth curve parameters (*a*, *r*) and analyzed the Pearson's correlation and genetic correlation between growth curve parameters and wood traits. Since the initial growth parameter *b* had no significant difference among provenances, *b* was discarded in the analysis.

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The growth curve parameters *a* and *r* of individual tree were calculated as:

$$P(t) = a/(1 + be^{-rt}) \quad (5)$$

Where t is the age, $P(t)$ represented the average phenotype value at the provenance level at age t; a is the maximum value of the HGT and DBH; b is the initial growth parameter, r is the relative growth rate.

The genetic correlation coefficients (R_g) between wood traits and growth curve parameters were calculated as follows:

$$R_g = \frac{\hat{\sigma}_{g(xy)}}{\sqrt{\hat{\sigma}^2_{g(x)} \times \hat{\sigma}^2_{g(y)}}} \quad (6)$$

where $\hat{\sigma}^2_{g(x)}$ represented genetic variance components of x, $\hat{\sigma}^2_{g(y)}$ represented genetic variance components of y, respectively. $\hat{\sigma}_{g(xy)}$ represented genetic covariance components between x with y. In this study, x refers to the growth curve parameters (a and r) of HGT and DBH; y refers to all wood traits. The complex model does not converge when calculating partial genetic correlation relationship, coupled with the large error. Therefore, the results of R_g were used as reference.

2.2.2 Climate association analyses

Wood traits with significant provenance effects (p < 0.05) were selected for linear regression analysis with geoclimatic variables. The Mantel test was used to assess the overall association of different classes of geoclimatic variables with wood traits based on euclidean distance matrices of temperature variables, precipitation variables, spatial variables and bray-curits distance matrix of traits with significant provenance effects and implemented in ape v. 5.7 (Houyun, 2020) in R 4.1.0 (R Core Team, 2022). Graphic drawing and data analysis were performed using ggplot2 v. 3.3.6 (Villanueva and Chen, 2019).

3. Results

3.1 Genetic parameters of wood traits

Means, variance components of random effects and genetic parameters for all measured traits are shown in Table 3. The $\widehat{CV}_P$ of wood anatomical traits and growth traits were greater than the $\widehat{CV}_P$ of wood chemical traits; the $\widehat{CV}_G$ were mostly greater for wood anatomical traits. Among the wood anatomical traits, except for fiber width, the $\widehat{CV}_P$ and $\widehat{CV}_G$ of the earlywood anatomical trait were greater than those of the latewood; the $\widehat{CV}_P$ and $\widehat{CV}_G$ of EWT_D (33.73% and 8.68%) were the highest among all traits. Most of the traits with significant provenance effects were concentrated in wood anatomical traits, especially earlywood traits, including EWT_D, EWFL, EWFW, LWFW, EWFL_W, LWP and BD. Family had significant effects on three categories of traits, especially for latewood-related traits, lignin and holocellulose. The estimates of $\hat{h}^2_i$ for wood anatomical traits ranged from 0.08 for LWFL to 0.65 for EWFL_W, which were also higher than those of other traits (0.01 to 0.17); the $\hat{h}^2_i$ of earlywood anatomical traits (0.09 to 0.65) were higher than those of latewood anatomical traits (0.08 to 0.45), indicating the higher additive effect of earlywood anatomical traits in *L. kaempferi*. The potential for selection and breeding for anatomical traits, especially earlywood anatomical traits, was higher than that for wood chemical and growth traits.

Table 3 Means, the variance components with standard error (SE) in parentheses, including the variance components of provenance ($\hat{\sigma}_p^2$), provenance by block interaction ($\hat{\sigma}_{pb}^2$), family ($\hat{\sigma}_f^2$), family by block interaction ($\hat{\sigma}_{fb}^2$) and random effect ($\hat{\sigma}_e^2$). $\hat{h}_i^2$, $\widehat{CV}_p$ and $\widehat{CV}_g$ represent the heritability, phenotypic variation coefficient and genetic variation coefficient for growth, wood anatomical and chemical traits average value measured in *Larix kaempferi*.

Category	Trait (units)	Mean value (SD)	$\hat{\sigma}_p^2$	$\hat{\sigma}_{pb}^2$	$\hat{\sigma}_f^2$	$\hat{\sigma}_{fb}^2$	$\hat{\sigma}_e^2$	$\hat{h}_i^2$	$\widehat{CV}_p$	$\widehat{CV}_g$
	EWT_D	0.17 (0.01)	0.77 (1.17) **	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	0.01 (0.01)	0.32 (0.16)	33.73%	8.68%
	LWT_D	0.52 (0.01)	0.83 (1.60)	<0.01 (<0.01) **	<0.01 (<0.01) *	<0.01 (<0.01)	0.01 (0.01)	0.30 (0.17)	23.54%	6.03%
	EWFL (μm)	2287.00 (13.12)	0.70 (0.50) **	0.01 (<0.01)	0.14 (0.22)	0.01 (<0.01)	71415.55 (4793.68)	0.09 (0.14)	12.15%	1.65%
	LWFL (μm)	2742.00 (12.68)	0.85 (0.61)	0.01 (0.16) **	0.02 (0.19) **	<0.01 (<0.01)	67411.82 (4524.73)	0.08 (0.14)	9.80%	0.54%
	EWFW (μm)	55.90 (0.26)	0.03 (0.01) **	0.72 (0.77) **	2.95 (1.25)	0.07 (2.04)	27.98 (1.87)	0.47 (0.19)	9.68%	3.08%
anatomical traits	LWFW (μm)	29.89 (0.16)	0.01 (0.01) **	0.89 (0.47) **	1.11 (0.45) **	0.01 (0.01)	11.23 (0.75)	0.45 (0.17)	11.40%	3.53%
	EWFL_W	41.19 (0.27)	3.59(2.91) **	0.46 (0.03)	1.18 (1.76)	0.03 (0.01)	28.68 (1.92)	0.65 (0.19)	13.71%	5.12%
	LWFL_W	92.63 (0.55)	2.14 (0.14)	22.40 (9.77)	9.75 (5.63) **	11.80 (10.70)	133.79 (8.98)	0.32 (0.18)	12.68%	3.37%
	EMAF (°)	21.78 (0.18)	<0.01(<0.01)	0.41 (0.36) *	0.81 (0.49)	<0.01 (<0.01)	13.77 (0.92)	0.27 (0.16)	17.24%	4.14%
	LMAF (°)	18.00 (0.14)	0.07(0.16)	0.09 (0.19) *	0.55 (0.34)	<0.01 (<0.01)	8.29 (0.56)	0.27 (0.16)	16.09%	4.10%
	LWP (%)	32.28 (0.42)	8.78(7.75) *	2.43 (2.18)	<0.01 (<0.01) **	<0.01 (<0.01)	72.78 (4.88)	0.22 (0.13)	27.53%	0.02%
	BD (g/cm^3)	0.38 (0.01)	0.11 (0.23) **	0.01 (0.03)	<0.01 (<0.01) *	<0.01 (<0.01)	0.01 (0.01)	0.23 (0.18)	10.74%	2.39%
	Lignin (%)	28.68 (0.04)	0.08(0.06)	<0.01 (<0.01)	0.03 (0.03) **	0.04 (0.07)	0.86 (0.06)	0.13 (0.16) [1]	3.29%	0.56%
chemical traits	Holo (%)	70.02(0.15)	0.73(0.59)	0.29 (0.25)	0.27 (0.25) **	<0.01 (<0.01)	7.80 (0.52)	0.17 (0.15) [1]	4.08%	0.75%
	Hemi (%)	28.58(0.11)	0.11(0.14)	0.07 (0.14)	0.12 (0.20)	0.33 (0.45)	5.04 (0.34)	0.10 (0.16) [1]	7.87%	1.23%
	HGT(m)	11.95(0.11)	0.15(0.21)	0.28 (0.25)	<0.01 (<0.01) *	2.22 (0.47)	3.29 (0.37)	0.01 (0.01) [1]	20.37%	0.01%
	DBH (cm)	16.75(0.17)	0.20(0.33)	0.44 (0.46)	<0.01 (<0.01)	1.98 (1.04)	10.30 (1.12)	0.01 (0.01) [1]	21.18%	0.01%
growth traits	CL(m)	10.06(0.11)	0.22(0.19)	<0.01 (<0.01)	0.23 (0.20) **	0.04 (0.01) ***	0.08 (0.01)	0.16 (0.13)	23.44%	4.74%
	CD(m)	4.283(0.04)	0.01(0.01)	0.01 (0.01)	<0.01 (<0.01)	0.21(0.04)	0.31 (0.04)	0.01(0.01)	17.88%	0.01%

Notes: ** P < 0.01, *P < 0.05; [1] study reported. Wood anatomical traits: wall-to-lumen ratio of earlywood (EWT_D), wall-to-lumen ratio of latewood (LWT_D), fiber length of earlywood (EWFL), fiber length of latewood (LWFL), length-to-width of earlywood fiber (EWFL_W), length-to-width of latewood fiber (LWFL_W), fiber width of earlywood (EWFW), fiber width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), wood basic density (BD). Wood chemical traits: Holo-cellulose (Holo), Hemi-cellulose (Hemi). Growth traits: height (HGT) and diameter at breast height (DBH).

***3.2** Correlations between wood traits and growth curve parameters of HGT and DBH*

Four wood anatomical traits were significantly correlated with growth curve parameters (Figure 1). The EWT_D (*R* = 0.19/-0.19), EWFL (*R* = 0.25/-0.23), LWFL (*R* = 0.27/-0.28) and EWFW (*R* = 0.31/-0.29) were significantly related to the *a* and *r* of height. The EWFW and LWFL were also positively correlated with the *a* of DBH, and the EWFW was negatively correlated with the *r* of DBH. The highest positive correlations were estimated between EWFW and DBHa (*R* = 0.33). It was worth noting that the BD of 5-year-old juvenile wood was positively correlated with the HGTr, and the BD of 9-year-old and 13-year-old was significantly negatively correlated with the DBHr. The genetic correlation between BD of three ages rings and growth curve parameters also showed the same results (Table A2). However, there was no correlation between wood chemical traits and growth curve parameters. Many traits had strong intercorrelations within wood anatomical traits, particularly EWFL and LWFL, EMAF and LMAF.

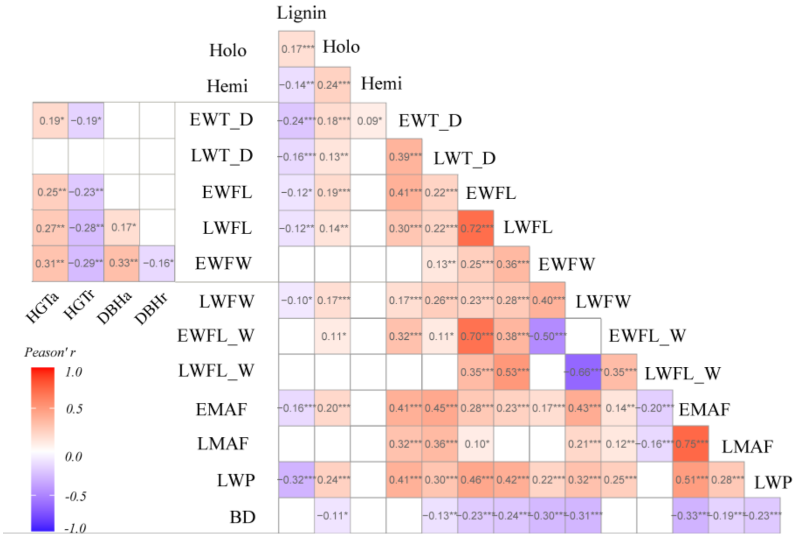

Figure 1: Significant Pearson correlation coefficient among average value of wood traits and growth curve parameters. ** and * denote significance for $P < 0.01$ and $P < 0.05$, respectively. HGTa, maximum value of height; HGTr, relative growth rate of height; DBHa, maximum value of diameter at breast height; DBHr, relative growth rate of diameter at breast height. Wood anatomical traits: wall-to-lumen ratio of earlywood (EWT_D), wall-to-lumen ratio of latewood (LWT_D), fiber length of earlywood (EWFL), fiber length of latewood (LWFL), length-to-width of earlywood fiber (EWFL_W), length-to-width of latewood fiber (LWFL_W), fiber width of earlywood (EWFW), fiber width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), wood basic density (BD). Wood chemical traits: Holo-cellulose (Holo), Hemi-cellulose (Hemi).

The genetic correlation coefficients (R_g) for average value of wood traits and growth curve parameters are shown in Table A1. EWFL and LWFL also showed significant genetic correlations with *a* of HGT (R_g = 0.58/0.61) and with r of HGT (R_g = -0.57/-0.52). EWFW and LWFW were significantly and positively correlated with *a* of DBH (R_g = 0.61/0.65). However, there was no statistically significant relationship between wood chemical properties and growth curve parameters.

***3.3** Relationships between wood traits and geoclimatic variables*

Precipitation variables were significantly correlated with most of the traits, including EWFW, LWFW, EWFL_W, LWP and BD (Figure 2a). Spatial variables showed significant correlations with EWFL, EWFL_W, and LWP. Temperature variables showed significant correlations with EWFL_W and LWP. The linear regressions of wood anatomical traits with significant provenance effects on each geoclimatic variable yielded four significant predictive relationships (Figure 2b), including EWFL_W with MAP, EWFW with PPT_MAM and MAP, LWFW and BD with PPT_SON and PPT_JJA. The EWFW was negatively correlated with EWFL_W (R = -0.5, $P < 0.001$) and BD (R = -0.31, $P < 0.001$) and positively correlated with LWFW (R = 0.4, $P < 0.001$; Figure 2a). And with the growth of juvenile wood, the correlation coefficient of functional relationship between MAP and EWFW and EWFL_W was getting higher. These results indicated that fiber width and basic density were significantly affected by precipitation variables, among which PPT_MAM was a key climatic factor influencing the EWFW of *L. kaempferi*. The genetic adaptation of fiber width to precipitation might be one of the reasons for the significant provenance effect of seven wood traits.

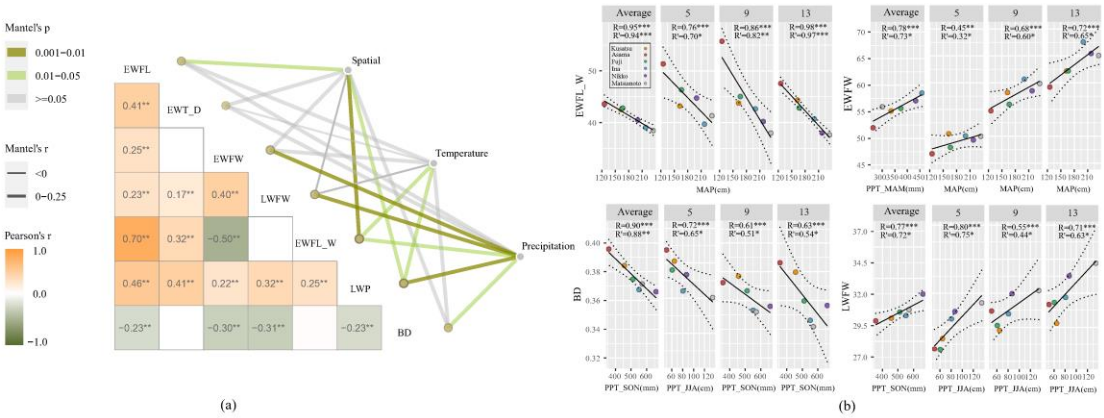

Figure 2: Association of wood anatomical traits, wood basic density and climatic factors in *Larix kaempferi*. (a) Mantel correlation coefficients (Mantel's r) between seven anatomical traits with significant provenance effects and three geoclimatic variable matrices. Top right: Spatial, temperature and precipitation represent spatial variables, temperature variables and precipitation variables, respectively. Thick lines indicate that the Mantel correlation coefficient is 0-0.25, and the thin lines indicate that the Mantel correlation coefficient is lower than 0; the dark green line indicates 0.001 > Mantel's P > 0.01, the light green line indicates 0.01 > Mantel's P > 0.05, and the gray line indicates Mantel's P > = 0.05. Bottom left: Pearson correlation coefficient matrix of seven wood anatomical traits with significant provenance effects. In addition, 1 is indicated by orange and -1 by green. '**' indicates P < 0.01, '*' indicates P< 0.05. (b) Regression analysis of four anatomical traits and precipitation variables. Each trait included the average value of the 5th, 9th, and 13th-year-old growth rings and the total average value of each provenance. The abscissa indicates the precipitation variable with the strongest correlation with the trait; note that one precipitation variable may be associated with traits at multiple ages. Precipitation variables: mean annual precipitation (MAP); March, April and May precipitation (PPT_MAM); June, July and August precipitation (PPT_JJA); and September, October and November precipitation (PPT_SON).

4. Discussion

4.1 Wood anatomical traits have higher variation and breeding potential

Provenance variation occurred in most wood anatomical traits (EWT_D, EWFL, EWFW, LWFW, EWFL_W, LWP, BD), among which the $\hat{h}_i^2$, $\widehat{CV}_p$ and $\widehat{CV}_g$ of earlywood anatomical traits were mostly greater than those of the corresponding latewood anatomical traits. Heritability estimates for wood fiber width in this study were similar to those for over 10-year-old Scots pine ($\hat{h}_i^2$ =0.42) and Norway spruce ($\hat{h}_i^2$ =0.34 to 0.48; Chen et al., 2016; Hong et al., 2015). The highest heritability estimates for EWFL_W may also indicate that fiber width was strongly inherited in *L. kaempferi*. Therefore, more attention should be paid to wood anatomical traits in *L. kampferi* breeding program, and it is expected that considerable genetic gains would be captured by recurrent selection. In addition, it is worth noting that the heritability of wood chemical traits was low, which may be because these traits (e.g., lignin content) were controlled to some extent by a significant dominance effect (Dong et al., 2018). However, the family variation in wood chemical traits cannot be ignored, and families can be used as an important source of variation for clone selection.

4.2 Asymptotic parameters of the growth curve correlated with fiber dimensions

Genetic improvement of growth traits is complex and challenging due to both the polygenic effect of genetic control and low heritability (Hodge and Dvorak, 2015; Lin et al., 2013). Genetically associated traits play an important role in the multitrait improvement of wood traits and indirect selection. In the present study, the growth maximum (asymptotic parameter) of HGT and DBH were positively correlated with fiber length and fiber width, respectively, which was also confirmed by Pearson correlation. The correlation between the average value of juvenile wood traits and the growth curve parameters lacks some key information. As wood grows, the genetic correlation between DBHa and BD, LWFL, and EWFW become stronger and stronger, and interannual variations in the strength of association are critical for early selection. Wood traits that were always associated with HGTa, such as EWFL and LWFL, provided an easily measurable and predictable indicator of recurrent selection in *L. kaempferi*. The *a* of DBH could be improved by improving EWFW, coupled with improving EWT_D. The correlation trends of these traits could be verified by the trait correlations in other conifers. For instance, the genetic and phenotypic correlations between radial fiber diameter and fiber wall thickness in *Picea glauca* were negative (Lenz et al., 2011). And Ina provenance can be planted with high yield in both two environments in the previous study, and the Ina has the highest EWFW among all provenances (Table A4). The growth and fiber dimensions could be improved jointly; the genetic correlations between the three wood chemical traits and growth curve parameters were not significant, implying that growth and wood chemical traits could be improved independently.

4.3 Seasonal rainfall affects wood fiber width

Phenotype or genetic adaptation to the environment is the mechanism of evolution. When *L. kaempferi* was transplanted into another environment, it carries the ‘memory’ caused by previous environmental pressure. This ‘memory’ may be epigenetic variation or genetic variation, which in turn affects the response intensity of gene response elements to a certain environmental factor. The original habitat of *L.kaempferi* is distributed on the mountains along the altitude gradient. It limits the range of native habitat variation and the environmental variation more regular than other widely distributed tree species. Our research suggested that precipitation factors of provenance were closely related to wood anatomical traits, which was consistent with the conclusion that precipitation limits the growth of *L. kaempferi* in previous studies (Guo et al., 2022; Chen et al., 2012; Kharuk et al., 2006). The EWFW was greatly affected by precipitation, which could address more general issues related to the genetic improvement of traits or introduction of *L. kaempferi* populations. From the results of the four traits significantly correlated with the rainfall variables, the positive correlation between EWFW and rainfall seemed to be the primary cause of the correlation between the four traits and precipitation, which deepened our research interest in the genetic improvement of the EWFW.

5. Conclusions

Wood anatomical traits of earlywood presented high heritability values with high selective accuracies. Significant genetic correlations were found between maximum value, growth rate of tree height and wood fiber length, and between maximum value of diameter at breast height and wood fiber width. Hence, earlywood fiber dimension is an important reference phenotype for breeding and recurrent selection of *L. kaempferi*. It is more valuable for family selection and breeding within the Ina provenance, based on its wide adaptability, high fiber width, moderate fiber length-width ratio and the current high yield.

Fiber width and length-to-width ratio of earlywood fiber and wood basic density had strong predictive relationships with precipitation variables. Thus, in the process of long-term adaptation to different environments, the genetic composition and phenotype of the fiber width and length could be shaped by precipitation in different provenances. For the introduction of *L. kaempferi* with different breeding purposes, we provided a reference of precipitation range.

Appendices

Table A1 Genetic correlation between wood traits and growth curve parameters in *Larix kaempferi*

Wood traits	HGTa	HGTr	DBHa	DBHr
Lignin	0.67 (0.64)	0.51 (6.31)	0.67 (1.13)	-0.09 (4.21)

Holo	0.67 (1.15)	0.67 (26.29)	0.49 (8.24)	0.67 (5.65)
Hemi	-0.8 (2.56)	0.67 (2.40)	0.89 (1.23)	0.67 (8.7)
EWT_D	0.64 (0.65)	0.04 (4.72)	0.68 (0.65)	-0.45 (2.05)
LWT_D	0.63 (0.45)	0.99 (0.86)	0.67 (0.68)	0.47 (0.11)**
EWFL	0.58 (0.26)*	-0.57 (0.26)*	-0.54 (0.66)	0.53 (0.68)
LWFL	0.61 (0.31)*	-0.52 (0.20)*	-0.67 (3.10)	0.67 (3.09)
EWFW	0.57 (0.39)	0.62 (0.56)	0.61 (0.03)**	0.38 (0.21)*
LWFW	0.47 (0.82)	0.60 (0.57)	0.65 (0.33)*	0.67 (3.86)
EWFL_W	0.55 (0.24)*	0.61 (0.26)**	0.59 (0.17)**	0.61 (0.25)**
LWFL_W	0.65 (0.37)*	0.55 (0.87)	0.52 (1.04)	0.67 (0.36)*
EWMA	0.57 (0.30)*	-0.80 (9.11)	0.53 (0.25)*	0.67 (50.36)
LWMA	0.58 (0.22)**	0.67 (9.96)	0.59 (0.17)**	0.67 (9.93)
LWP	0.50 (0.37)	0.50 (1.01)	0.67 (0.15)**	0.71 (0.28)**
BD	0.62 (0.46)	-0.17 (9.06)	-0.14 (0.01)*	-0.47 (2.09)

Notes: ** P < 0.01, *P < 0.05. Wood anatomical traits: wall-to-lumen ratio of earlywood (EWT_D), wall-to-lumen ratio of latewood (LWT_D), fiber length of earlywood (EWFL), fiber length of latewood (LWFL), length-to-width of earlywood fiber (EWFL_W), length-to-width of latewood fiber (LWFL_W), fiber width of earlywood (EWFW), fiber width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), wood basic density (BD). Wood chemical traits: Holo-cellulose (Holo), Hemi-cellulose (Hemi). HGTa, maximum value of height; HGTr, relative growth rate of height; DBHa, maximum value of diameter at breast height; DBHr, relative growth rate of diameter at breast height.

Table A2 Pearson correlation between wood traits of age 5, 9, 13 and growth curve parameters in *Larix kaempferi*

Traits	growth curve parameter			
	HGTa	HGTr	DBHa	DBHr
EWT_D5	0.11*	-0.10*	-0.05	0.07
EWT_D9	0.13*	-0.12*	0.04	-0.04
EWT_D13	0.25*	-0.20*	0.05	-0.06
LWT_D5	-0.02	0.04	0.11	0.04
LWT_D9	-0.18	0.21	-0.10	0.09
LWT_D13	0.08	-0.10	0.19	-0.30**
EWFL5	0.31**	-0.25**	0.22*	-0.08
EWFL9	0.24*	-0.20*	0.23*	-0.12
EWFL13	0.20*	-0.13	0.07	-0.02
LWFL5	0.37**	-0.35**	0.25*	-0.02
LWFL9	0.30**	-0.30**	0.31**	-0.12
LWFL13	0.29**	-0.27**	0.36***	-0.12
EWFW5	0.22*	-0.22*	0.21*	-0.20*
EWFW9	0.21*	-0.14	0.25**	0.03
EWFW13	0.23*	-0.16.	0.33**	0.03
LWFW5	0.04	-0.06	0.07	-0.05
LWFW9	0.08	-0.09	0.07	0.03

LWFW13	0.01	-0.02	0.13	-0.08
EWFL_W5	0.07	-0.03	0.01	0.09
EWFL_W9	0.07	-0.08	0.03	-0.14
EWFL_W13	-0.01	0.01	-0.15	-0.08
LWFL_W5	0.25**	-0.22*	0.14	0.01
LWFL_W9	0.13	-0.14	0.13	-0.10
LWFL_W13	0.19	-0.16	0.11	-0.03
EWMA5	-0.01	-0.04	0.04	0.03
EWMA9	-0.09	0.07	-0.01	0.08
EWMA13	-0.13	0.09	-0.05	0.16
LWMA5	-0.04	0.01	0.01	0.03
LWMA9	-0.04	0.01	-0.01	-0.01
LWMA13	-0.16	0.14	-0.03	0.11
LWP5	0.02	-0.02	0.07	-0.10
LWP9	0.01	-0.01	-0.11	-0.07
LWP13	0.05	-0.06	-0.01	0.05
BD5	-0.19	0.20*	-0.08	-0.07
BD9	-0.07	0.04	0.02	-0.20*
BD13	-0.06	0.09	-0.04	-0.25**
Lignin	-0.01	0.05	-0.04	0.07
Holo	0.19	-0.17	-0.10	-0.04
Hemi	0.11	-0.04	0.06	0.05

Notes: ** P < 0.01, *P < 0.05. Wood anatomical traits: wall-to-lumen ratio of earlywood (EWT_D), wall-to-lumen ratio of latewood (LWT_D), fiber length of earlywood (EWFL), fiber length of latewood (LWFL), length-to-width of earlywood fiber (EWFL_W), length-to-width of latewood fiber (LWFL_W), fiber width of earlywood (EWFW), fiber width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), wood basic density (BD). Wood chemical traits: Holo-cellulose (Holo), Hemi-cellulose (Hemi). HGTa, maximum value of height; HGTr, relative growth rate of height; DBHa, maximum value of diameter at breast height; DBHr, relative growth rate of diameter at breast height.

Table A3 Genetic correlation between wood traits of age 5, 9, 13 and growth curve parameters in *Larix kaempferi*

Trait	growth curve parameters			
	HGTa	HGTr	DBHa	DBHr
EWT_D5	0.57 (0.31)*	-0.54 (0.30)*	0.68 (0.50)	-0.05 (0.25)
EWT_D9	0.64 (0.31)**	-0.68 (0.31)**	0.70 (0.45)	-0.14 (0.23)
EWT_D13	0.69 (0.82)**	-0.97 (0.41)**	0.69 (0.46)	-0.27 (0.32)
LWT_D5	0.10 (1.27)	-0.58 (0.05)**	0.07 (2.07)	-0.33 (0.09)**
LWT_D9	0.17 (0.79)	-0.55 (0.08)**	0.14 (0.65)	-0.68 (3.09)
LWT_D13	0.13 (0.98)	0.61 (0.75)	0.11 (1.25)	-0.56 (0.07)**
EWFW5	0.84 (0.04)**	0.37 (0.35)	0.57 (0.51)	0.39 (0.39)
EWFW9	0.49 (0.08)**	-0.38 (0.19)*	0.61 (0.03)***	-0.38 (0.21)*
EWFW13	0.43 (0.1)**	0.31 (0.38)	0.54 (0.06)***	0.37 (0.37)
LWFW5	0.54 (0.29)*	0.49 (0.47)	0.57 (0.23)**	-0.66 (0.12)**
LWFW9	0.55 (0.25)*	0.57 (1.61)	0.60 (0.17)**	-0.64 (0.12)**
LWFW13	0.54 (0.23)**	0.52 (0.38)	0.65 (0.33)*	-0.63 (0.10)**

EWFL5	0.42 (0.18)**	-0.42 (0.18)**	0.37 (0.25)	0.37 (0.26)
EWFL9	0.48 (0.07)**	-0.48 (0.07)**	0.35 (0.14)**	-0.34 (0.15)*
EWFL13	0.38 (0.22)*	0.37 (0.23)	0.34 (0.31)	0.34 (0.32)
LWFL5	0.46 (0.15)**	0.46 (0.16)**	0.26 (0.45)	0.26 (0.46)
LWFL9	0.34 (0.35)	0.34 (0.36)	0.36 (0.39)	0.36 (0.43)
LWFL13	0.61 (0.31)*	-0.52 (0.31)	0.18 (0.39)	0.01 (0.30)
EWFL_W5	0.58 (0.04)**	-0.50 (0.06)**	0.63 (0.02)**	-0.47 (0.08)**
EWFL_W9	0.59 (0.03)**	-0.94 (0.02)**	0.63 (0.02)**	-0.42 (0.05)**
EWFL_W13	0.54 (0.05)**	-0.39 (0.14)**	0.62 (0.02)**	-0.43 (0.13)**
LWFL_W5	0.65 (0.37) *	-0.51 (0.49)	0.39 (0.54)	-0.45 (5.23)
LWFL_W9	0.55 (0.25) *	-0.49 (0.47)	-0.80 (1.27)	-0.53 (0.90)
LWFL_W13	0.71 (0.31) *	-0.60 (0.49)	0.40 (0.32)	-0.67 (0.36)*
EMAF5	0.63 (0.02)**	-0.38 (0.19)*	0.75 (0.33)*	-0.37 (0.22)*
EMAF9	0.64 (0.02)**	-0.46 (0.11)**	0.83 (0.2)**	-0.40 (0.16)**
EMAF13	0.64 (0.02)**	-0.43 (0.1)**	1.52 (3.65)	-0.37 (0.15)**
LMAF5	0.60 (0.26)*	-0.61 (0.20)**	0.65 (0.23)**	0.67 (0.97)
LMAF9	0.67 (0.31)*	-0.66 (0.22)**	0.62 (0.17)**	-0.80 (0.67)
LMAF13	0.96 (0.60)	-0.72 (0.32)*	0.57 (0.13)**	0.72 (0.53)
LWP5	0.62 (0.03)**	0.98 (0.02)**	0.63 (0.02)**	0.33 (0.07)**
LWP9	0.61 (0.02)**	0.86 (0.02)**	0.64 (0.02)**	0.42 (0.03)**
LWP13	0.59 (0.03)**	0.47 (0.04)**	0.64 (0.02)**	0.45 (0.04)**
BD5	-0.69 (0.08)**	0.54 (0.11)**	0.64 (0.50)	-0.52 (0.07)**
BD9	-0.69 (0.74)	0.34 (2.09)	0.65 (0.49)	-0.35 (0.10)**
BD13	-0.69 (0.82)	0.40 (1.09)	0.65 (0.49)	-0.51 (0.07)**
Lignin	0.39 (1.22)	-0.51 (1.29)	-0.08 (9.73)	0.67 (178.79)
Holo	0.35 (0.41)	-0.41 (0.40)	0.07 (5.14)	0.67 (31.53)
Hemi	0.38 (0.41)	-0.37 (0.40)	-0.08 (6.80)	0.67 (41.64)

Notes: ** $P < 0.01$, *$P < 0.05$. Wood anatomical traits: wall-to-lumen ratio of earlywood (EWT_D), wall-to-lumen ratio of latewood (LWT_D), fiber length of earlywood (EWFL), fiber length of latewood (LWFL), length-to-width of earlywood fiber (EWFL_W), length-to-width of latewood fiber (LWFL_W), fiber width of earlywood (EWFW), fiber width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), wood basic density (BD). Wood chemical traits: Holo-cellulose (Holo), Hemi-cellulose (Hemi). HGTa, maximum value of height; HGTr, relative growth rate of height; DBHa, maximum value of diameter at breast height; DBHr, relative growth rate of diameter at breast height.

Table A4 The average value of wood traits with significant provenance effect in 6 provenances.

Provenance	EWT_D	EWFL (μm)	EWFW (μm)	LWFW (μm)	EWFL_W	LWP (%)	BD (g/cm3)
Kusatsu	0.20	2327.70	55.16	29.33	42.52	33.43	0.38
Asama	0.17	2256.19	52.00	29.12	43.61	27.41	0.40
Fuji	0.17	2370.83	55.63	29.82	42.81	36.38	0.37
Ina	0.18	2350.94	58.53	29.54	40.49	33.00	0.37
Nikko	0.15	2219.20	57.07	31.25	39.05	33.28	0.37
Matsumoto	0.14	2144.70	55.94	30.00	38.47	26.40	0.37

Notes: Wood anatomical traits: wall-to-lumen ratio of earlywood (EWT_D), fiber length of earlywood (EWFL), length-to-width of earlywood fiber (EWFL_W), fiber width of earlywood (EWFW), fiber width of latewood (LWFW), latewood proportion (LWP), wood basic density (BD).

References

Baltunis, B.S., Gapare, W.J., Wu, H.X., 2010. Genetic parameters and genotype by environment interaction in radiata pine for growth and wood quality traits in Australia. Silvae Genet. 59, 113–124. https://doi.org/10.1515/sg-2010-0014

Boris, Z., 1993. Analysis of Growth Equations. For. Sci. 3, 594–616.

Butler, D., Cullis, B., Gilmour, A., Gogel, B., 2009. ASReml-R reference manual (Version 3). Queensland Department of Primary Industries and Fisheries, Brisbane, Australia.

Chen, F., Yuan, Y.J., Wei, W.S., Fan, Z.A., Zhang, T.W., Shang, H.M., Zhang, R.B., Yu, S.L., Ji, C.R., Qin, L., 2012. Climatic response of ring width and maximum latewood density of Larix sibirica in the Altay Mountains, reveals recent warming trends. Ann. For. Sci. 69, 723–733. https://doi.org/10.1007/s13595-012-0187-2

Chen, Z.Q., Karlsson, B., Mörling, T., Olsson, L., Mellerowicz, E.J., Wu, H.X., Lundqvist, S.O., Gil, M.R.G., 2016. Genetic analysis of fiber dimensions and their correlation with stem diameter and solid-wood properties in Norway spruce. Tree Genet. Genomes 12. https://doi.org/10.1007/s11295-016-1065-0

Danjon, E., 1994. Heritabilities and genetic correlations for estimated growth curve parameters in maritime pine 911–921.

Donaldson, L., Frankland, A., 2004. Ultrastructure of iodine treated wood. Holzforschung 58, 219–225. https://doi.org/10.1515/HF.2004.034

Dong, L.M., Zhang, S.G., Sun, X.M., 2018. Application of Pedigree Reconstruction in Open-pollinated Progeny Testing of Japanese Larch. For. Res. 31, 27–35. https://doi.org/10.13275/j.cnki.lykxyj.2018.01.003

Dulamsuren, C., Hauck, M., Leuschner, H.H., Leuschner, C., 2011. Climate response of tree-ring width in Larix sibirica growing in the drought-stressed forest-steppe ecotone of northern Mongolia. Ann. For. Sci. 68, 275–282. https://doi.org/10.1007/s13595-011-0043-9

Fukatsu, E., Hiraoka, Y., Matsunaga, K., Tsubomura, M., Nakada, R., 2015. Genetic relationship between wood properties and growth traits in Larix kaempferi obtained from a diallel mating test. J. Wood Sci. 61, 10–18. https://doi.org/10.1007/s10086-014-1436-9

Gallo, R., Pantuza, I.B., Santos, G.A. dos, Resende, M.D.V. de, Xavier, A., Simiqueli, G.F., Baldin, T., Santos, O.P. dos, Valente, B.M. dos R.T., 2018. Growth and wood quality traits in the genetic selection of potential Eucalyptus dunnii Maiden clones for pulp production. Ind. Crops Prod. 123, 434–441. https://doi.org/10.1016/j.indcrop.2018.07.016

Gapare, W.J., Baltunis, B.S., Ivković, M., Wu, H.X., 2009. Genetic correlations among juvenile wood quality and growth traits and implications for selection strategy in Pinus radiata D. Don. Ann. For. Sci. 66, 606–606. https://doi.org/10.1051/forest/2009044

Gilmour, A., Gogel, B., Cullis, B., Thompson, R., 2009. ASReml User Guide Release 3.0 VSN Hemel Hempstead: International Ltd. Hemel Hempstead. Hemel Hempstead, UK.

Guo, H., Xiangdong, L., Lei, Y., Weisheng, Z., Pumei, L., Yuancai, L., 2022. Climate-sensitive diameter distribution models of larch plantations in north and northeast China. For. Ecol. Manage.

Hodge, G.R., Dvorak, W.S., 2015. Provenance variation and within-provenance genetic parameters in Eucalyptus urophylla across 125 test sites in Brazil, Colombia, Mexico, South Africa and Venezuela. Tree Genet. Genomes 11. https://doi.org/10.1007/s11295-015-0889-3

Hong, Z., Anders, F., Harry X., W., 2015. Age trend of heritability, genetic correlation and efficiency of early selection for wood quality traits in Scots pine. Can. J. For. Res. 45(7), 817–825.

Hoshi, H., 2004. Forest Tree Genetic Resources Conservation Stands of Japanese Larch (Larix kaempferi (Lamb .) Carr .). For. Tree Genet. Resour. Inf. Special Is.

Houyun, 2020. ggcor.

Jeffrey, E.C., 1917. The Anatomy of Woody Plantse. University of Chicago Press, Chicago.

Jiao, L., Jiang, Y., Zhang, W., Wang, M., Wang, S., Liu, X., 2019. Assessing the stability of radial growth responses to climate change by two dominant conifer trees species in the Tianshan Mountains, northwest China. For. Ecol. Manage. 433, 667–677. https://doi.org/10.1016/j.foreco.2018.11.046

Jiao, L., Wang, S., Chen, K., Liu, X., 2022. Dynamic response to climate change in the radial growth of Picea schrenkiana in western Tien Shan, China. J. For. Res. 33, 147–157. https://doi.org/10.1007/s11676-021-01336-6

Kharuk, V.I., Ranson, K.J., Im, S.T., Naurzbaev, M.M., 2006. Forest-tundra larch forests and climatic trends. Russ. J. Ecol. 37, 291–298. https://doi.org/10.1134/S1067413606050018

Lenz, P., MacKay, J., Rainville, A., Cloutier, A., Beaulieu, J., 2011. The influence of cambial age on breeding for wood properties in Picea glauca. Tree Genet. Genomes 7, 641–653. https://doi.org/10.1007/s11295-011-0364-8

Lin, Y., Yang, H., Ivković, M., Gapare, W.J., Colin Matheson, A., Wu, H.X., 2013. Effect of genotype by spacing interaction on radiata pine genetic parameters for height and diameter growth. For. Ecol. Manage. 304, 204–211. https://doi.org/10.1016/j.foreco.2013.05.015

Mckown, A.D., Guy, R.D., Klápště, J., Geraldes, A., Friedmann, M., Cronk, Q.C.B., El-Kassaby, Y.A., Mansfield, S.D., Douglas, C.J., 2014. Geographical and environmental gradients shape phenotypic trait variation and genetic structure in Populus trichocarpa. New Phytol. 201, 1263–1276. https://doi.org/10.1111/nph.12601

Mickaël, H., Michaël, A., Fabrice, B., Pierre, M., Thibaud, D., 2007. Soil detritivore macro-invertebrate assemblages throughout a managed beech rotation. Ann. For. Sci. 64, 219–228. https://doi.org/10.1051/forest

Pan, Y., Jiang, L., Xu, G., Li, J., Wang, B., Li, Y., Zhao, X., 2020. Evaluation and selection analyses of 60 Larix kaempferi clones in four provenances based on growth traits and wood properties. Tree Genet. Genomes 16. https://doi.org/10.1007/s11295-020-1420-z

Peng, J., Peng, K., Li, J., 2018. Climate-growth response of Chinese white pine (Pinus armandii) at different age groups in the Baiyunshan National Nature Reserve, central China. Dendrochronologia 49, 102–109. https://doi.org/10.1016/j.dendro.2018.02.004

R Core Team, 2022. R: A language and environment for statistical computing [WWW Document]. R Found. Stat. Comput. Vienna, Austria. URL https://www.r-project.org/

Rashidi-Jouybari, I., Lenz, P., Beaulieu, J., Nadeau, S., Bousquet, J., Achim, A., 2022a. Multi-trait selection for improved solid wood physical and flexural properties in white spruce. For. An Int. J. For. Res. 1–12. https://doi.org/10.1093/forestry/cpac006

Rashidi-Jouybari, I., Lenz, P., Beaulieu, J., Nadeau, S., Bousquet, J., Achim, A., 2022b. Multi-trait selection for improved solid wood physical and flexural properties in white spruce. Forestry 95, 492–503. https://doi.org/10.1093/forestry/cpac006

Sandak, J., Sandak, A., Cantini, C., Autino, A., 2015. Differences in wood properties of Picea abies L. Karst. in relation to site of provenance and population genetics. Holzforschung 69, 385–397. https://doi.org/10.1515/hf-2014-0061

Santos, A., Anjos, O., Amaral, M.E., Gil, N., Pereira, H., Simões, R., 2012. Influence on pulping yield and pulp properties of wood density of Acacia melanoxylon. J. Wood Sci. 58, 479–486. https://doi.org/10.1007/s10086-012-1286-2

Santos, T.S., Martins, K., Aguiar, A. V., Baptista Filho, M.J., Menucelli, J.R., Faria, R.F.P., Moura, R.D., MacHado, J.A.R., Longui, E.L., 2021. Growth and Wood Quality Traits in a Dipteryx alata Vog. (Fabaceae) Progeny and Provenance Test. For. Sci. 67, 468–477. https://doi.org/10.1093/forsci/fxab010

Self, S.G., Liang, K.Y., 1987. Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. J. Am. Stat. Assoc. 82, 605–610. https://doi.org/10.1080/01621459.1987.10478472

Soro, A., Lenz, P., Hassegawa, M., Roussel, J.-R., Bousquet, J., Achim, A., 2021. Genetic influence on components of wood density variation in white spruce. For. An Int. J. For. Res. 1–13. https://doi.org/10.1093/forestry/cpab044

Takahashi, K., Okuhara, I., Tokumitsu, Y., Yasue, K., 2011. Responses to climate by tree-ring widths and maximum latewood densities of two Abies species at upper and lower altitudinal distribution limits in central Japan. Trees - Struct. Funct. 25, 745–753. https://doi.org/10.1007/s00468-011-0552-z

Villanueva, R.A.M., Chen, Z.J., 2019. ggplot2: Elegant Graphics for Data Analysis (2nd ed.). Meas. Interdiscip. Res. Perspect. 17, 160–167. https://doi.org/10.1080/15366367.2019.1565254

Wang, H., Zhu, A., Duan, A., Wu, H., Zhang, J., 2022. Responses to subtropical climate in radial growth and wood density of Chinese fir provenances, southern China. For. Ecol. Manage. 521, 120428. https://doi.org/10.1016/j.foreco.2022.120428

Wang, T., Wang, G., Innes, J., Seely, B., Chen, B., 2017. ClimateAP: an application for dynamic local downscaling of historical and future climate data in Asia Pacific. Front Agr Sci Eng 4(4), 448–458.

Wimmer, R., Downes, G.M., Evans, R., Rasmussen, G., French, J., 2002. Direct effects of wood characteristics on pulp and

handsheet properties of Eucalyptus globulus. Holzforschung 56, 244–252. https://doi.org/10.1515/HF.2002.040
Yang, K., Hazenberg, G., 1987. Geographical variation in wood properties of Larix laricina juvenile wood in northern Ontario. Can. J. For. Res. 17, 648–653.
Zhang, C., 2014. Spatial Variation of Vessel characteristics in Quercus mongolica. Henan University of Science and Technology. https://doi.org/10.7666/d.D01142245
Zhang, S., Sun, X., Chen, D., Xie, Y., Liu, C., 2022. Method for detecting wood chemical properties of Japanese Larch. LU501423
Zhang, Y., Dong, L., Xie, Y., Chen, D., Sun, X., 2022. Altitude shape genetic and phenotypic variations in growth curve parameters of Larix kaempferi. J. For. Res. https://doi.org/10.1007/s11676-022-01483-4
Zobel, B.J., Van Buijten, J.P., 1989. Wood Variation, Journal of Chemical Information and Modeling.