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Provenance variations in wood traits of *Larix kaempferi* (Lamb.) Carr. and their relationships with growth parameters

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Abstract

Understanding genetic variation in wood traits and their relationships with dynamic growth is essential for the genetic improvement of forest tree species. This study investigated genetic control of 15 wood traits and their associations with dynamic growth patterns in Japanese larch (*Larix kaempferi* (Lamb.) Carr.), using a 22-year-old common garden experiment in Hubei Province, China. Through analysis of 450 trees from 84 families across six provenances, we demonstrate that growth parameters derived from logistic nonlinear models effectively capture temporal growth dynamics. Linear mixed model was used to estimate the genetic parameters of traits. The bivariate mixture model and Pearson correlation analysis were used to estimate genetic correlations of wood traits and growth parameters. Tracheid dimensions showed high genetic regulation and exhibited positive correlations with asymptotic growth parameters of tree height and diameter at breast height, height growth rate displayed negative correlations with earlywood tracheid width. These findings establish that growth parameters effectively characterize ontogenetic growth patterns while tracheid size is closely linked to these developmental processes. The demonstrated connections between tracheid size and growth parameters provide new breeding objectives in *L. kaempferi* breeding programs.

Keywords: wood traits, heritability, provenance variation, growth parameters, *Larix kaempferi*

1.Introduction

Larix kaempferi (Lamb.) Carr. (Japanese larch) is naturally distributed in the high mountains of central Japan [1] and is one of the most successfully introduced fast-growing tree species for timber, pulp and paper production in Europe, Asia, and North America [2-4]. In China, its rapid juvenile growth makes it superior to the native *Larix* species when compared to *L. gmelinii* and *L. olgensis*, making it the most suitable conifer for timber and pulp production [4, 5]. Early-stage

selection and improvement of wood and growth traits during the optimal rotation period are critical for enhancing biomass accumulation and pulp productivity in this species.

Wood properties can be classified into three principal categories: wood chemical traits (e.g., lignin and cellulose), wood physical traits (e.g., density and stiffness) and wood anatomical traits (e.g., cell dimensions and microfibril angle). Zobel and Van Buijtenen [6] suggested that the basic density is the most strongly correlated with wood properties. Lignin, hemicellulose and cellulose content are doubtlessly the key factors affecting the efficiency of pulp extraction [7]. The genetic variation for growth traits and wood chemical and physical traits in Japanese larch and its hybrid has been well documented through a variety of trials [8-11]. The anatomical traits of wood, such as tracheid radial and tangential growth, microfibril angle, tracheid wall thickness, and fibre coarseness, are of significant importance to the pulp and paper industry [12-15]. However, the inheritance of wood anatomical traits has received limited attention. The incorporation of wood traits into tree improvement programs has been facilitated by the advent of wood trait determination technology, particularly the rapid field-type nondestructive methods [15-17].

The assessment of growth traits, such as height and diameter at breast height, has been a primary objective of numerous tree improvement programmes due to the relative ease of their assessment and their significant impact on log value [18]. Growth curve modeling provides an innovative framework for characterizing dynamic growth processes in trees, particularly through parameters that capture ontogenetic developmental patterns [19]. The logistic curve with its three biologically interpretable parameters (asymptotic value, initial value and relative rate of growth) has demonstrated exceptional efficacy in quantifying age-specific growth trajectories across multiple tree species [20-23]. This dynamic approach overcomes the limitations of static trait

67 measurements (e.g., single-timepoint tree height), enabling the identification of critical growth
68 phases and genetic regulation mechanisms during developmental transitions.

69 The relationships between growth dynamics and wood quality constitutes as a major concern
70 in tree breeding [24, 25]. Although positive genetic correlations between growth rates and cellulose
71 content suggest joint selection potential [26, 27], well-documented trade-offs between diameter at
72 breast height and wood density [28-30] underscore the risks of unilateral selection. For pulping and
73 papermaking species like *L.kaempferi*, it's important to balance growth rate and timber output with
74 wood quality and quantify correlations between growth parameters and key wood traits becomes
75 imperative.

76 The present study collected data on growth and fifteen wood traits from 450 individual natural
77 trees from 84 families of six *L. kaempferi* provenances in a long-term observed provenance test. The
78 main objectives of this study were to (1) quantify the provenance and family variation and
79 heritability for the wood traits, (2) select the best nonlinear growth model suitable for this population
80 and examine the correlations between the wood traits and growth parameters of tree height and
81 diameter at breast height.

82 2.Materials and methods

83 *2.1 Material sources and trial design*

84 Seeds were collected from 84 open pollination families from six natural provenances along the
85 mountains of central Japan covering the complete native distribution of *L. kaempferi* (Table 1) based
86 on a Japan International Cooperation project (JICA, Forestry Project Phase I (8), 1996-2000). The
87 seeds were germinated in March 1996, and two-year-old seedlings were transplanted from nursery
88 to the Jianshi trial site in Hubei Province, China (30.08° N, 110.05° E, 1700 m), where exhibits a

cool and humid subtropical alpine climate. The trial design was a randomized complete block with six replications. Families were planted in a double row plot of eight seedlings and randomized within each replication.

Table 1. Sampling and geographical information for *Larix. kaempferi* provenances and the Hubei trial site.

Provenance/ trial site	Family	Sample size	Mean annual temperature (℃)	Mean annual precipitation (mm)	Latitude (°)	Longitude (°)	Elevation (m)
Kusatsu	20	97	6.0	1627	36.58	138.50	1374
Asama	6	54	9.3	1254	36.33	138.50	927
Fuji	16	80	10.5	1665	35.50	138.75	844
Ina	15	75	4.8	1875	35.75	138.17	1726
Nikko	18	90	5.7	2176	36.75	139.42	1444
Matsumoto	9	54	13.5	1445	36.33	139.75	1620
Hubei	84	450	11.4	1650	30.80	110.05	1700

Note: the name of provenance from the prefix of the local state-owned forest farms' name in 1996-2000.

2.1.1 Collection of growth traits and wood cores

Four to six trees per family were randomly selected across the blocks, and a total of 450 trees were sampled from the trial. The numbers of families and sampled trees from each provenance are

shown in Table 1. For each sampled tree, height (*HGT*, m) and diameter at breast height (1.3 m, *DBH*, cm) were measured at ages 3-5, 7-10, 12, 13, 17, 18, 22 and 7-10, 12, 13, 17, 18, 22, respectively; and wood cores were extracted from the bark to the bark through the pith at breast height using a 12 mm diameter increment borer at age 14.

2.1.2 Measurement of wood anatomical and chemical traits

Three growth rings, the 5th, 9th and 13th from the pith were selected from each wood core to measure average wood basic density (BD) and wood anatomical characteristics for 450 individual trees. The water displacement method was employed to ascertain the basic density (BD) of the wood samples [31]. The widths of the growth ring and the latewood were measured with a micrometer, with an accuracy of 0.01 mm, and subsequently employed in the calculation of the latewood proportion (LWP). For each growth ring, a tangential section 20 um thick and a transverse section 4 um thick were continuously cut from the earlywood to the latewood. The specific method of resin-embedded and sectioning is illustrated in the method described by Liu [32]. A color image computer analysis system with a microscope (TDY-5.2, Northeast Forestry University, China) was used to measure the wall-to-lumen ratio of earlywood (EWW_L) and latewood (LWW_L) cells, the tracheid width of earlywood (EWFW) and latewood (LWFW), the tracheid length of earlywood (EWFL) and latewood (LWFL), and the microfibril angles of earlywood (EMAF) and latewood (LMAF). The TDY-5.2 system has been developed for the rapid analysis of binary images according to the different colors of the wood cell lumen and cell wall, according to the characteristic values of pixel gray value, size, number, and location. The data is obtained by utilizing microscopic measurements and image and data analysis. The EWW_L, LWW_L, EWFW, and LWFW values were obtained through the observation of the average cell size from the bark to the pith, with measurements taken 10 to 20 times

per ring. The EMAF and LMAF were measured randomly in 20 different tracheids (earlywood and latewood) by observing the iodine-stained slices [33]. The EWFL and LWFL were measured 50 times by observing the wood strips treated by the defibration solution. The defibration solution consisted of 1:1 aqueous nitric acid and aqueous chromic acid (10% each; method in Appendix).

The 450 wood cores were dried for 24 h at 25 °C to a constant weight, ground, and filtered through a 60-mesh sieve. Near infrared (NIR) spectra were collected using a near-infrared spectrometer (LabSpec®Pro, ASD, Inc., USA). Each spectral output was an average of 30 scans. The final spectral data for each sample were an average of three replicates. The three wood chemical properties, namely, lignin, holo-cellulose and cellulose, were predicted using NIR models developed for *L. kaempferi* [34], with determination coefficients of 0.96, 0.95 and 0.96 for lignin, holocellulose and cellulose, respectively. The final hemicellulose content is obtained by subtracting the cellulose content from the holocellulose content.

2.2 Statistical analysis

2.2.1 Variance and genetic parameter estimation

The ASReml linear mixed 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 software [35, 36].

$$y = Xb + Z_1p + Z_2pb + Z_3f(p) + Z_4f(p)b + e, \quad (1)$$

where y is the observation vector for growth and wood traits; b is the fixed block effect; p, pb, f, fb and e represent vectors of the random effect of provenances, interaction between provenance and block, family within provenance, interaction between family within provenance and block and random error, respectively, which are assumed to follow a normal distribution $p \sim N(0, \hat{\sigma}_p^2)$,

pb~N(0, $\hat{\sigma}^2_{pb}$), $f(p)$~N(0, $\hat{\sigma}^2_{f(p)}$), $f(p)b$~N($\hat{\sigma}^2_{f(p)b}$) and e~N(0, $\hat{\sigma}^2_e$), respectively. $\hat{\sigma}^2_p$, $\hat{\sigma}^2_{pb}$, $\hat{\sigma}^2_{f(p)}$, $\hat{\sigma}^2_{f(p)b}$, and $\hat{\sigma}^2_e$ are the variances of four random effects and residual effects, respectively. X is the incidence matrix for b, 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 [37]. The statistical significance of the variance components for each trait was determined using a two-tailed likelihood ratio test [38].

The coefficients of phenotypic (CVP) and genetic (CVG) variation were calculated using the following equations:

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

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

where $\hat{\sigma}^2_{phen}$ is the phenotypic variance $\hat{\sigma}^2_{phen} = \hat{\sigma}^2_{f(p)} + \hat{\sigma}^2_{f(p)b} + \hat{\sigma}^2_e$; $\hat{\sigma}^2_a$ is the additive genetic variance $\hat{\sigma}^2_a = 4\,\hat{\sigma}^2_{f(p)}$, assuming the open-pollinated mating produced true half-sibs, so the genetic variation would be a quarter of the total additive genetic variance; $\overline{X}$ is the overall mean.

The narrow-sense heritability ($\hat{h}^2_i$) was calculated as follows:

$$\hat{h}^2_i = \frac{\hat{\sigma}^2_a}{\hat{\sigma}^2_{f(p)} + \hat{\sigma}^2_{f(p)b} + \hat{\sigma}^2_e}, \quad (4)$$

The Logistic growth curve, as a biological law, was chosen to capture the age-specific change in growth due to its simplicity and can be described mathematically by [39, 40]:

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

where $P(t)$ represents the average phenotypic value at the provenance level at age t, a is the upper asymptotic value of the *HGT* or *DBH* (*HGTa*, *DBHa*), b is the initial growth parameter of the *HGT* or *DBH* (*HGTb*, *DBHb*), and r is the relative growth rate of *HGT* and *DBH* (*HGTr*, *DBHr*).

The genetic correlation coefficients (R_g) between wood traits and growth 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 $\hat{\sigma}^2_{g(x)}$ and $\hat{\sigma}^2_{g(y)}$ represent the genetic variance components of x and y, respectively. $\hat{\sigma}_{g(xy)}$ represents the genetic covariance components between *x* and *y*. In this study, x refers to the growth parameters (*a*, *b* and *r*) of *HGT* and *DBH*, and y refers to all wood traits.

To determine whether the age effect of wood traits is significant, the aov and LSD.test function in R were used for multiple comparisons to determine whether the effect of age factor is significant [41].

2.2.2 Association analyses of growth parameters

The accuracy of the growth parameters for each tree was evaluated using Pearson's correlation coefficient between the fitted and measured values for *HGT* and *DBH*. Pearson's correlation coefficient (R_p) was also used to determine the relationships between the wood traits and the growth parameters (*a*, *b*, and *r*). Regression analysis was used to quantify the relationships between wood traits with significant provenance effects and growth parameters.

Results

3.1 Genetic parameters and provenance variation in wood traits and growth parameters

The means, variance components, heritability, and coefficients of variation for wood traits are shown in Table 2. The coefficients of phenotypic (CVP) and genetic (CVG) variation were generally higher for wood anatomical traits than for chemical traits. For most wood anatomical traits, both phenotypic (CVP) and genetic (CVG) variation coefficients were higher in earlywood compared to latewood. EWW_L displayed the highest variability (CVP = 33.73%, CVG = 19.73%) among wood anatomical traits, underscoring its sensitivity to genetic and environmental interactions.

Table 2. Descriptive statistics (with standard deviation values in parentheses) and genetic parameters (with standard error values in parentheses) for wood traits and growth parameters.

Trait (units)	Mean (sd)	$\hat{\sigma}_p^2$ (se)	$\hat{\sigma}_{pb}^2$ (se)	$\hat{\sigma}_{f(p)}^2$ (se)	$\hat{\sigma}_{f(p)b}^2$ (se)	$\hat{\sigma}_e^2$ (se)	$\hat{h}_i^2$ (se)	CVP (%)	CVG (%)
EWW_L	0.17 (0.06)	1.56 (0.60) **	7.39 (2.87)	0.28 (<0.01) **	4.46 (0.01)	2.01 (<0.01)	0.17 (0.02)	33.73	19.73
LWW_L	0.52 (0.12)	0.68 (<0.01)	2.01 (1.17)	1.20 (<0.01)	3.02 (1.17)	13.44 (<0.01)	0.27 (0.24)	23.54	13.75
EWFL (μm)	2287.00 (277.91)	0.05 (<0.01) **	<0.01 (<0.01)	0.19 (0.29) **	<0.01 (<0.01)	12.05 (<0.01)	0.06 (0.14)	12.15	5.10
LWFL (μm)	2742.00 (268.72)	0.06 (0.07)	<0.01 (<0.01)	0.29 (<0.01) *	<0.01 (<0.01)	10.00 (<0.01)	0.11 (0.05)	9.80	6.18
EWFW (μm)	55.90 (5.41)	4.12 (1.60) *	9.26 (0.08) **	4.12 (<0.01) **	1.03 (<0.01)	40.01 (<0.01)	0.36 (0.03)	9.68	7.84

LWFW (μm)	29.89 (3.41)	1.64 (6.36) **	<0.01 (<0.01)	1.95 (0.02) **	1.64 (0.06)	16.19 (0.63)	0.39 (0.02)	11.40	7.25
EWFL_W	41.19 (5.65)	5.51 (2.14) **	5.51 (2.14)	5.93 (0.05) **	5.51 (<0.01)	35.44 (2.11)	0.51 (<0.01)	13.71	10.35
LWFL_W	92.63 (11.73)	4.01(1.55)	8.01 (1.55)	3.07 (0.09) **	4.00 (<0.01)	13.96 (<0.01)	0.58 (0.09)	12.68	8.09
EMAF (°)	21.78 (3.76)	1.17 (0.04)	1.17 (<0.01)	2.69 (0.03) **	1.17 (<0.01)	22.15 (0.04)	0.41 (<0.01)	17.24	8.80
LMAF (°)	18.00 (2.90)	1.26 (0.04)	1.26 (<0.01)	9.62 (1.32) **	1.26 (<0.01)	56.46 (0.48)	0.57 (<0.01)	16.09	8.59
LWP (%)	32.28 (8.89)	5.98 (0.08) *	6.82 (<0.01)	6.01 (<0.01) **	6.60 (<0.01)	36.52 (2.53)	0.49 (0.17)	27.53	15.92
BD (g/cm^3)	0.38 (0.04)	2.15 (8.33) *	2.13 (<0.01) **	0.79 (1.13) **	2.15 (<0.01)	21.21 (0.82)	0.13 (<0.01)	10.74	5.49

Lignin (%)	28.68 (0.95)	0.08 (0.06)	<0.01 (<0.01)	0.03 (0.03) **	0.04 (0.07)	0.86 (0.06)	0.40 (0.18)	3.29	2.08
Cellouse (%)	41.43 (3.19)	0.73 (0.59)	0.29 (0.25)	0.27 (0.25)	<0.01 (<0.01)	7.80 (0.52)	0.48 (0.17)	4.08	2.67
Hemi (%)	28.58 (2.25)	0.11 (0.14)	0.07 (0.14)	0.12 (0.20)	0.33 (0.45)	5.04 (0.34)	0.20 (0.16)	7.87	3.48

Notes: **, $p < 0.01$, *, $p < 0.05$; Wall-to-lumen ratio of earlywood (EWW_L); wall-to-lumen ratio of latewood (LWW_L); tracheid length of earlywood (EWFL), tracheid length of latewood (LWFL), length-to-width of earlywood tracheid (EWFL_W), length-to-width of latewood tracheid (LWFL_W), tracheid width of earlywood (EWFW), tracheid width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), and wood basic density (BD). Wood chemical traits: hemi-cellulose (Hemi). *HGTa*, maximum height; *HGTr,* relative growth rate of height; *HGTb*, initial growth parameter of tree height; *DBHa,* maximum diameter at breast height; *DBHr*, relative growth rate of diameter at breast height; *DBHb*, initial growth parameter of diameter at breast height. The variance components included provenance ($\hat{\sigma}_p^2$), interaction between provenance and block ($\hat{\sigma}_{pb}^2$), family ($\hat{\sigma}_{f(p)}^2$), interaction between family and block ($\hat{\sigma}_{f(p)b}^2$) and random effect ($\hat{\sigma}_e^2$). $\hat{h}_i^2$, CVP and CVG represent the heritability, phenotypic variation coefficient and genetic variation coefficient, respectively.

Provenance had a significant effect on seven traits ($P < 0.05$): EWW_L, EWFL, EWFW, LWFW, EWFL_W, LWP, and BD, five of which were associated with earlywood. Family effects were significant for all traits except LWW_L, cellulose, and hemicellulose, indicating strong within-family genetic control for most traits.

High narrow-sense heritability ($\hat{h}_i^2 > 0.35$) was detected for tracheid dimensions (EWFW and LWFW), tracheid shape indices (EWFL_W and LWFL_W), microfibril angles (EMAF and LMAF), LWP, and chemical constituents (lignin and cellulose). Notably, the age-stable heritability of EWFW did not decline with increasing tree age (Table S1), highlighting its potential as a robust selection trait for long-term breeding programs.

Multiple comparisons and age-related trends of wood traits are presented in Figure 1. EWFW increased significantly with age. In contrast, BD remained relatively stable in young *L. kaempferi* provenances. No significant age-related variation was observed for the other traits.

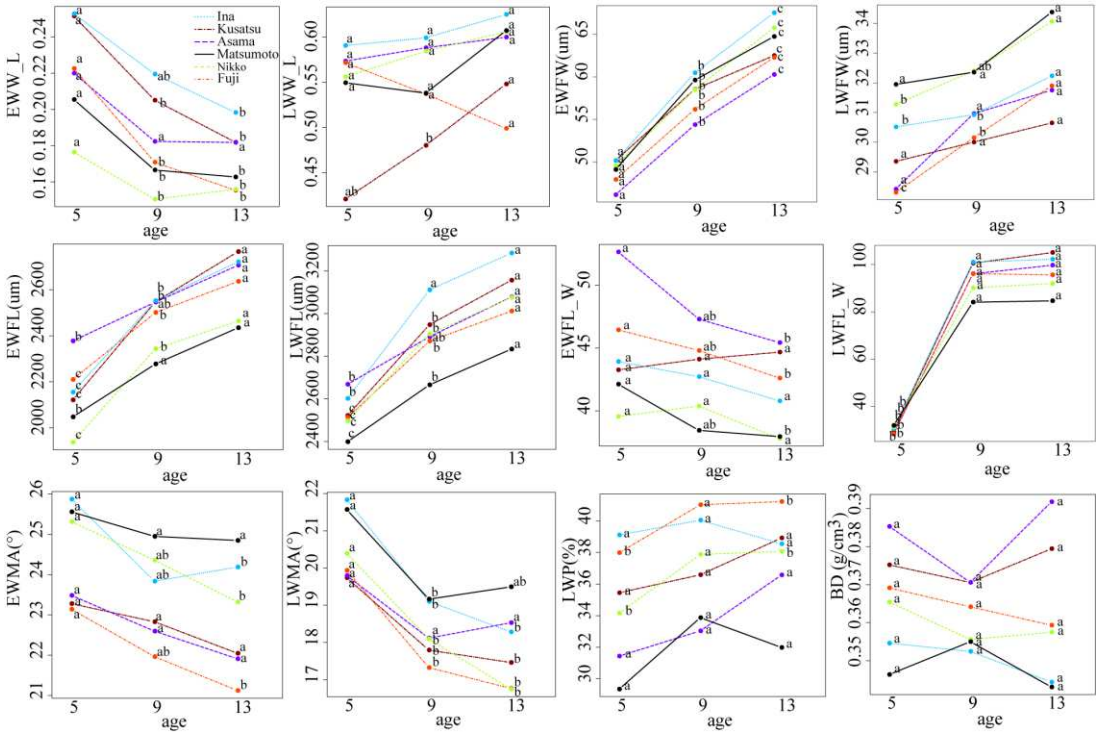

Figure 1. The provenance differences of wood traits with significant provenance effect in the 5th,

9th, 13th years. The letters 'a', 'b' and 'c' indicate that the age difference was statistically significant by one-way ANOVA. Wall-to-lumen ratio of earlywood (EWW_L); wall-to-lumen ratio of latewood (LWW_L); tracheid length of earlywood (EWFL), tracheid length of latewood (LWFL), length-to-width of earlywood tracheid (EWFL_W), length-to-width of latewood tracheid (LWFL_W), tracheid width of earlywood (EWFW), tracheid width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), and wood basic density (BD).

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

Following a comparative evaluation of five commonly used growth models in forestry, the Logistic model was selected to describe height growth (*HGT*) and diameter at breast height (*DBH*) due to its superior fitting performance (Table 3). The model achieved high convergence success rates (100% for *HGT* and 99.8% for *DBH*) and exhibited strong goodness of fit, with coefficients of determination (R^2) of 0.986 for *HGT* and 0.995 for *DBH*.

The Logistic growth function is expressed as:

$$P(t) = a/(1 + be^{-rt}) \quad (7)$$

where $P(t)$ represents the predicted value of the growth trait at age *t*. For height growth, a (*HGTa*) denotes the asymptotic maximum tree height, *b* (*HGTb*) is a scaling parameter related to the initial growth condition, and r (*HGTr*) represents the growth rate of height development. Similarly, for diameter growth, a (*DBHa*) corresponds to the asymptotic maximum diameter at breast height, b (*DBHb*) reflects the initial growth status, and r (*DBHr*) indicates the growth rate of *DBH* over time.

Table 3. Comparison of five nonlinear growth models fitted to tree height (*HGT*) and diameter at

breast height (*DBH*) growth of *Larix kaempferi* provenance populations, including model formulations, parameter estimates, convergence success rates (CSR), coefficients of determination (R^2), and root mean square errors (RMSE).

Model	Growth trait	Model form	CSR (%)	R^2	RMSE
Logistic	*HGT*	$P(t) = \frac{a}{1 + be^{-rt}}$	100.0	0.986	0.405
	DBH		99.8	0.995	0.527
Chapman–Richards	*HGT*	$P(t) = a(1 - e^{-rt})^b$	91.7	0.987	0.411
	DBH		90.1	0.993	0.372
Gompertz	*HGT*	$P(t) = ae^{-be^{-rt}}$	100.0	0.984	0.475
	DBH		99.7	0.991	0.410
Bertalanffy	*HGT*	$P(t) = a(1 - be^{-rt})^3$	99.7	0.986	0.435
	DBH		99.7	0.992	0.373
Korf	*HGT*	$P(t) = ae^{-\frac{b}{t^r}}$	3.2	0.973	0.386
	DBH		33.4	0.995	0.323

Significant Pearson correlations were detected between 12 out of 15 wood traits and growth parameters (Table 4). Among wood chemical traits, cellulose and hemicellulose showed positive correlations with *HGTa* (R_p= 0.18 and 0.14, respectively), while cellulose exhibited a negative correlation with *HGTr* (R_p= −0.18).

Among anatomical traits, EWFL, LWFL and EWFW were found to be positively correlated to *HGTa* (R_p= 0.24, 0.28, 0.35). EWFW and LWFL were positively correlated with *DBHa* (R_p= 0.31 and 0.15). EWW_L, EWFL_W, EWMA, LWMA and LWP were negatively correlated with *DBHa* (R_p= −0.14 to −0.22). EWFL, LWFL, and EWFW showed negative correlations with *HGTr* (R_p=

243 −0.22 to −0.34), *DBHr* (R_p = −0.14 to −0.16), and *DBHb* (R_p = −0.18 to −0.30), respectively.
244 LWFL_W was positively correlated with *HGTa* (R_p= 0.16) while negatively correlated with *HGTr*
245 (R_p= -0.15).

246 The observed correlation trends between wood anatomical traits and growth parameters
247 supported by phenotypic (Pearson's *r*) and genetic correlation (R_g) analyses using three consecutive
248 years of wood trait and growth parameter data (Tables S2 and Table 5).

249 **Table 4.** Pearson's correlation coefficients (with *t* values in parentheses) between wood traits and growth parameters

Traits	*HGTa*	*HGTr*	*HGTb*	*DBHa*	*DBHr*	*DBHb*
Lignin	0.09 (1.30)	-0.03 (-0.46)	0.07 (1.09)	0.11 (1.99)	0.01 (0.06)	0.07 (1.31)
Cellouse	0.18 (2.67) *	-0.18 (-2.68) *	0.04 (0.56)	-0.05 (-0.94)	-0.11 (-1.94)	-0.11 (-2.03)
Hemi	0.14 (2.10) *	-0.12 (-1.75)	0.01 (0.17)	0.02 (0.29)	0.01 (0.23)	-0.06 (-1.07)
EWW_L[#]	0.13 (1.93)	-0.12 (-1.78)	0.02 (0.36)	-0.12 (-2.17) *	-0.05 (-0.87)	-0.08 (-1.41)
LWW_L	0.02 (0.34)	-0.01 (-0.21)	-0.01 (-0.17)	-0.05 (-0.89)	-0.04 (-0.67)	-0.08 (-1.49)
EWFL[#]	0.24 (3.76) **	-0.22 (-3.36) *	0.01 (-0.05)	0.07 (1.31)	-0.16 (-2.90) *	-0.27 (-4.95) **
LWFL	0.28 (4.38) **	-0.30 (-4.70) **	-0.07 (-1.01)	0.15 (2.63) *	-0.16 (-2.90) *	-0.30 (-5.63) **
EWFW[#]	0.35 (5.52) **	-0.34 (-5.50) **	-0.05 (-0.71)	0.31 (5.87) **	-0.14 (-2.46) *	-0.18 (-3.21) *
LWFW[#]	0.08 (1.24)	-0.11 (-1.64)	-0.06 (-0.92)	0.09 (1.61)	-0.11 (-1.99)	-0.17 (-3.17) *
EWFL_W[#]	-0.03 (-0.46)	0.05 (0.79)	0.03 (0.50)	-0.15 (-2.78) *	-0.06 (-1.06)	-0.12 (-2.20) *
LWFL_W	0.16 (2.41) *	-0.15 (-2.23) *	0.01 (-0.05)	0.04 (0.73)	-0.03 (-0.53)	-0.09 (-1.53)

EMAF	-0.10 (-1.48)	0.07 (1.05)	0.04 (0.64)	-0.17 (-2.99) *	0.06 (1.06)	0.01 (0.13)
LMAF[#]	-0.12 (-1.75)	0.11 (1.67)	0.07 (0.99)	-0.12 (-2.09) *	0.07 (1.21)	0.05 (0.93)
LWP	0.03 (0.40)	-0.04 (-0.62)	-0.03 (-0.47)	-0.22 (-3.93) **	-0.08 (-1.39)	-0.17 (-2.99) *
BD[#]	0.06 (0.91)	-0.11 (-1.65)	0.01 (0.22)	-0.03 (-0.48)	-0.03 (-0.59)	0.09 (1.63)

Notes: ** $p < 0.001$, * $p < 0.05$. [#] wood traits with significant provenance effect. Wall-to-lumen ratio of earlywood (EWW_L); wall-to-lumen ratio of latewood (LWW_L); tracheid length of earlywood (EWFL), tracheid length of latewood (LWFL), length-to-width of earlywood tracheid (EWFL_W), length-to-width of latewood tracheid (LWFL_W), tracheid width of earlywood (EWFW), tracheid width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), and wood basic density (BD). Wood chemical traits: hemi-cellulose (Hemi). *HGTa*, maximum height; *HGTr,* relative growth rate of height; *HGTb*, initial growth parameter of tree height; *DBHa,* maximum diameter at breast height; *DBHr*, relative growth rate of diameter at breast height; *DBHb*, initial growth parameter of diameter at breast height.

Table 5. Genetic correlation coefficients (with se value in parentheses) between wood traits and growth parameters in *Larix kaempferi*

Wood traits	*HGTa*	*HGTr*	*HGTb*	*DBHa*	*DBHr*	*DBHb*
Lignin	0.39 (1.22)	-0.51 (1.29)	0.58 (1.26)	-0.08 (9.73)	0.06 (8.79)	0.04 (0.20)

Cellulose	0.35 (0.41)	-0.41 (0.40)	0.47 (0.92)	0.07 (5.14)	0.06 (3.53)	0.07 (0.59)
Hemicelluloses	0.38 (0.41)	-0.37 (0.40)	0.36 (0.36)	-0.08 (6.80)	0.06 (4.64)	0.04 (0.47)
EWW_L	0.04 (0.65)	0.04 (4.72)	-0.43 (0.22) *	0.08 (0.65)	-0.45 (2.05)	0.05 (1.08)
LWW_L	0.03 (0.45)	0.09 (0.86)	-0.67 (0.22) *	0.67 (0.68)	0.47 (0.11) *	0.20 (0.04)
EWFL	0.58 (0.26) *	-0.57 (0.26) *	-0.77 (0.16) *	-0.54 (0.66)	0.53 (0.68)	-0.67 (0.15) *
LWFL	0.61 (0.31) *	-0.52 (0.20) *	-0.67 (0.32) *	-0.17 (3.10)	0.07 (3.09)	-0.67 (0.23) *
EWFW	0.57 (0.39) *	-0.62 (0.56) *	-0.67 (0.05) *	0.61 (0.03) *	-0.38 (0.21) *	0.26 (0.44)
LWFW	0.47 (0.82)	-0.60 (0.57) *	-0.08 (0.32)	0.65 (0.33) *	0.07 (3.86)	0.08 (0.27)
EWFL_W	0.55 (0.24) *	-0.61 (0.26) *	0.07 (0.35)	0.59 (0.17) **	-0.61 (0.25) *	0.07 (0.70)
LWFL_W	0.65 (0.37) *	-0.55 (0.87)	-0.67 (0.13) *	0.52 (1.04)	-0.67 (0.36) *	0.08 (0.20)
EWMA	0.57 (0.30) *	-0.08 (1.11)	0.06 (0.35)	-0.53 (0.25) *	0.07 (5.36)	0.06 (0.29)
LWMA	0.58 (0.22) *	0.07 (1.96)	0.07 (0.22)	-0.59 (0.17) *	0.07 (9.93)	0.07 (0.42)
LWP	0.50 (0.37) *	0.05 (1.01)	0.06 (0.16) *	-0.67 (0.15) *	-0.71 (0.28) *	0.08 (0.28)

BD	0.62 (0.46) *	-0.17 (1.06)	0.05 (0.37)	-0.14 (0.01) *	-0.47 (2.09)	-0.08 (0.33)

Notes: * $p < 0.05$. Wood traits: wall-to-lumen ratio of earlywood (EWW_L); wall-to-lumen ratio of latewood (LWW_L); tracheid length of earlywood (EWFL), tracheid length of latewood (LWFL), length-to-width of earlywood tracheid (EWFL_W), length-to-width of latewood tracheid (LWFL_W), tracheid width of earlywood (EWFW), tracheid width of latewood (LWFW), microfibril angle of earlywood (EMAF), microfibril angle of latewood (LMAF), latewood proportion (LWP), and wood basic density (BD).

Linear regression analyses between growth parameters and wood traits are illustrated in Figure 3. EWFW exhibited significant positive linear relationships with *DBHa* and *HGTa*, and a negative linear relationship with *HGTr*, explaining 10–30% of the variance (R^2 = 0.10–0.30). EWFL showed a significant negative linear relationship with *DBHb*, accounting for 20–30% of the observed variance (R^2 = 0.20–0.30).

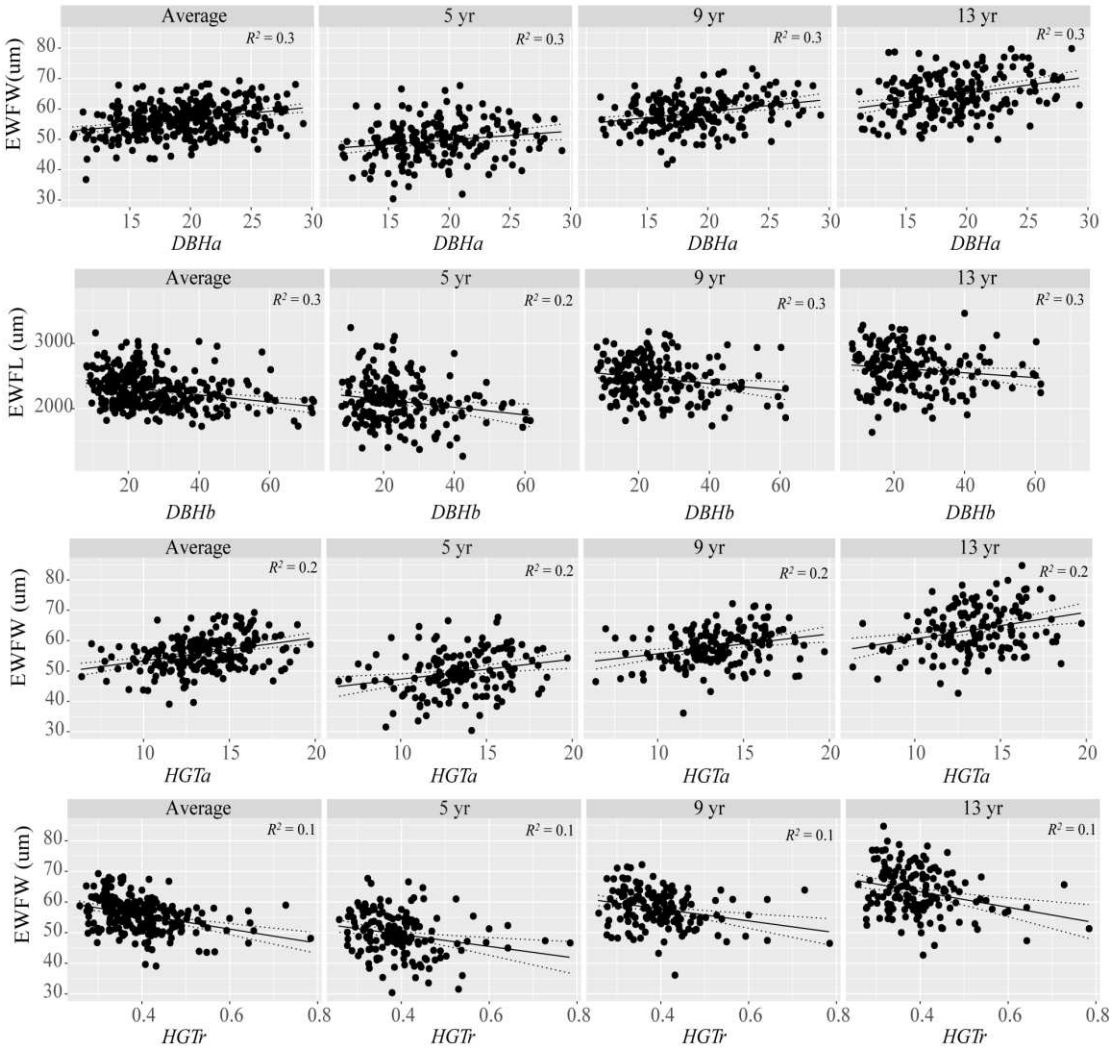

Figure 3. Relationships among Tracheid length of earlywood and tracheid width of earlywood of the 3-year average and the growth rings of the 5th, 9th and 13th years and *DBHb*, *HGTa*, *DBHa* and *HGTr*, with 95% confidence intervals (dotted line) on the regression line (solid line). Tracheid length of earlywood (EWFL), tracheid width of earlywood (EWFW), *HGTa*, maximum height; *HGTr,*

271 relative growth rate of height; *DBHa,* maximum diameter at breast height; *DBHb*, initial growth
272 parameter of diameter at breast height.

273 4. Discussion

274 Genetic variation is a primary concern for breeders, as it directly governs the scope of genetic
275 gain achievable through selection. However, variability in genetic material, stand age, and
276 experimental conditions (e.g., test site heterogeneity) may introduce substantial fluctuations in key
277 genetic parameters, including heritability estimates, coefficients of genetic variation, and genetic
278 correlations between wood properties and growth traits. To mitigate these uncertainties, breeding
279 strategies must adopt a context-specific approach: correlation patterns should be rigorously analyzed
280 by aligning statistical frameworks with distinct breeding objectives, validating hypotheses against
281 localized experimental data, or expanding the geographic scope of trials to capture environmental
282 gradients. The genetic parameters for wood traits and their relationships with growth process, as
283 quantified in this study, provide actionable insights for early-stage selection and long-term breeding
284 programs. Specifically, these findings enable the prioritization of traits with high heritability and
285 stable genetic correlations, thereby streamlining resource allocation and informing adaptive forest
286 management practices. Future efforts could further refine predictive models by integrating multi-
287 site datasets or incorporating molecular markers to disentangle genotype-environment interactions.

288 In this study, we estimated the genetic variation in 15 wood traits and growth parameters for
289 growth traits in a 22-year-old common garden experiment. The coefficients of genetic variation
290 (CVG) were moderate for growth traits (6.98-36.20) but low for wood traits (2.08-19.73). For growth
291 traits, the estimates of CVG were comparable to those (5.48-9.30) from a trial of 128 families from
292 seven seed orchards in Japan [42] and greater than those (2.51-3.70) from a progeny test of full-sib

293 families derived from plantations in the northeastern China [10]. Significant provenance effects
294 were observed for nearly half of the wood traits (Table 2). In addition, our previous microsatellite
295 markers revealed that the mean expected heterozygosity of this testing was moderate to high at 0.64
296 [43]. Thus, the genetic improvement for growth and wood traits is feasible through provenance and
297 family selection in *L. kaempferi*, although its natural range is restricted to a narrow mountainous
298 area [1].

299 There are a variety of growth models, such as the Logistic, Gompertz, Bertalanffy and
300 Chapman-Richard equations, which are frequently used to describe biological processes of tree. It
301 should be noted that the tree growth process cannot be fully characterized by a single or a few
302 separate values. The simplicity of the growth equation and the accuracy of the estimated parameters
303 were the main considerations in this study. The three parameters in the Chapman-Richard or other
304 Logistic equations are not significantly different from one another, particularly when the growth
305 pattern is the primary consideration. The Logistic equation proposed by Boris [40] was selected for
306 use in this study due to its higher convergence success rate (Table 3). Conversely, the Chapman-
307 Richard equation was failed to converge in more cases. It should be noted that the Logistic equation
308 is quite efficient for fast-growing conifers that have a short business objective, but is not suggested
309 for species that require accurate inflection point information, e.g., the establishment of a site index
310 model [44-47]. It is likely that considering the growth parameters as the result of dynamic biological
311 processes and integrating them into breeding and cultivation represents an efficient way of
312 understanding the relationship between wood traits and growth patterns and of making joint or
313 independent improvements.

314 Tree breeders have long tried to reduce the negative effects of improved growth on wood

properties [15, 24, 25]. Although the multi-year growth data are relatively easily accessible and amenable to perform year-to-year genetic analysis, breeders recognize that growth traits are controlled by a large number of minor genes. Consequently, it is challenging to achieve a balance between these two factors through the improvement of growth traits. The development of MAS and traditional breeding is oriented towards traits with higher genetic control and joint selection. However, this in turn involves clarifying the relationship between these relatively easy-to-improve wood traits and growth. The estimated heritability for wood tracheid width, tracheid length-to-width ratio, microfibrillar angle and LWP was found to be high, exceeding 0.35. Furthermore, EWFW was found to be correlated with the growth parameter, with both the genetic correlation and Pearson correlation yielding identical results (see Tables 3 and 4). Therefore, it is reasonable to prioritize EWFW for selection. Similar results have been reported for other tree species. For instance, the $\hat{h}_i^2$ of radial tracheid width was 0.48, and stem diameter demonstrated a moderate and positive genetic correlation with radial tracheid width (0.49) in a 21-year-old Norway spruce progeny trial [48, 49]; the $\hat{h}_i^2$ of radial tracheid width was 0.45, and growth traits exhibited positive and weak genetic correlations with tracheid width in a 40-year-old Scots pine progeny trial [50]. Nevertheless, no distinction was observed between earlywood and latewood tracheid width in the two conifer species. These results demonstrated that radial tracheid width is strongly inherited in conifers. Together with advances in non-destructive methods, for example Trephor micro growth cones can detect radial tracheid width for at least 3 years [51, 52], more attention should be paid to tracheid width in conifer and other tree breeding programs. In particular, it is expected that considerable genetic gains would be captured by selection of trees with greater tracheid width in *L. kaempferi*.

5. Conclusion

Tracheid width exhibited high heritability over 5-, 9-, and 13-year periods, highlighting the reliability of selection and improvement. Moreover, the tracheid width and length of the earlywood is significantly correlated with the asymptote parameters and growth rate, which further substantiates the value of breeding and selection for tracheid cell size in the future.

Authors' contributions

Zhang YL wrote the manuscript, L Dong, Y Xie conducted the statistical analysis, X Sun and D Chen collected the data and carried out the critical reading and grammatical correction of manuscript. Dong LM and Sun XM participated in discussions and helped to draft the manuscript. All authors read and approved the final manuscript.

Conflicts of interest

The authors declare that they have no conflict of interest.

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Availability of data and material (data transparency)

The datasets generated during and/or analysed and additional tables and figures during the current study are available in the https://doi.org/10.17605/OSF.IO/8DYJRd

Declarations

Ethics, Consent to Participate, and Consent to Publish declarations: Not applicable.

Appendix

Method: Observation of tracheid length by defibration of wood

(1) Defibration. Place strips samples (about 5mm × 1mm × 1mm) in a water bath. Boil hot to eliminate air, add nitric acid and chromic acid (10 %), boil for 24-48 hours, rinse with water several times until no acid remains.

(2) Oscillation and staining. Shake the test tube until the sample becomes wood pulp. Add 1-2 drops of saffron staining reagent.

(3) Sectioning. Take out the wood pulp with an anatomical needle and place it on the microscope slide. Add a drop of water to separate the wood cells and cover the glass slide. Absorb excess water on the coverslip, and observe under the microscope (Carl Zeiss Microimaging GmbH37081, Oberkochen, Germany).

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