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ORIGINAL PAPER

Genetic variation and superior provenances selection for wood properties of *Larix olgensis* at four trials

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Abstract *Larix olgensis*, one of the most important timber species in northeastern China, is used for paper making and construction. In this study, 10 wood properties (wood density, fiber length, fiber width, fiber length- to width ratio, hemicellulose content, cellulose content, holocellulose content, lignin content, ash content, and carbon content) of 10 provenances of *L. olgensis* planted at sites of CuoHai (CH), JiaGeDaQi (JGDQ), LiangShui (LS), and Mao'erShan (MES) were analyzed. The results of ANOVA showed that almost traits differed significantly among locations and provenances, with a significant interaction effect. Each trait also differed significant among provenances within sites. The phenotypic and genetic coefficient of variation (PCV and GCV) and provenance heritability (H^2) for wood properties ranged from 1.122 to 27.365%, from 0.564% to 21.113% and from 0.332 to 0.996, respectively. A correlation analysis showed that wood density was significantly negatively correlated with cellulose content and holocellulose content at sites CH, JGDQ, and LS, but were significantly positively correlated at site MES. Wood density was significantly negatively correlated with lignin content at CH and JGDQ, but not at LS and MES. Fiber width (FW) was negatively correlated with the ratio of fiber length (FL) to width across sites, and FW and FL/W were all positively correlated with FL. Lignin content was significantly positively correlated with hemicellulose content at site JGDQ and significantly negatively correlated with cellulose content and with holocellulose content at site MES. Interestingly, carbon content was positively correlated with cellulose content and holocellulose content at CH, but negatively correlated with these two traits at site MES. In a correlation analysis of wood properties with geographic, soil and climatic characteristics at the four sites, wood properties were mainly correlated with latitude and altitude of the site and affected by the average annual precipitation and temperature simultaneously. To select superior pulpwood provenances and high carbon storage provenances, we selected the two best provenances with excellent wood properties for each location based on a multi-trait comprehensive evaluation, which can be used as the preferred materials for the establishment of large-scale plantations in specific locations.

Keywords *Larix olgensis* · Wood properties · Genetic variation · Provenance selection · Carbon content

Introduction

Forests are the largest carbon sinks in terrestrial ecosystems and are important for sequestering CO_2 and mitigating the adverse effects of climate change (Peng et al. 2018). Therefore, the use of forest plantations for carbon sequestration is gaining more interest (Zhu et al. 2013). Large-scale reforestation and afforestation have significant implications for carbon sequestration (Thomas et al. 2007), so screening and

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selecting provenances, families or clones for high carbon sequestration is a critical measure to optimize plantations as carbon sinks (Wang et al. 2016). Because the carbon sequestration capacity of conifers is significantly higher than that of broad-leaved tree species, conifers should be prioritized in programs for carbon sequestration forests (Xu et al. 2013).

Wood properties are important indices to evaluate wood yield and quality and are affected by environmental factors such as temperature, precipitation, soil conditions, competition, planting density, thinning density, slope position and direction, and interactions among these factors (Guo et al. 2002a, b; Shi et al. 2011). Poor site conditions can also reduce the number and length of fibers (Wang et al. 2006). Genetic improvement of wood properties and selection of superior materials have always been an important directive for breeders and are needed to optimize timber production and carbon sequestration for afforestation projects. Long-term provenance tests are essential to determine genetic and geographic variations in tree growth and recommend appropriate seed sources for reforestation, especially in a changing climate (Weber et al. 2019). Variations in growth traits (tree height and DBH) and wood properties (wood density and carbon concentration) also need to be studied to predict the ability of trees to sequester carbon in different environments (Weber et al. 2018).

Larix olgensis, an important timber species, is mainly distributed in southeastern Heilongjiang, Liaoning, and Changbai Mountain area of Jilin, and it is also found in Korea and Russia (Hu et al. 2015). With excellent wood properties, it is not only used as wood fiber industrial raw materials, paper making raw materials and bio-fuels, but also used in industries such as construction, shipbuilding and railway (Xia et al. 2016). Because it is one of the main afforestation species in northeastern China, its genetic improvement has been a research priority. Provenance tests of *L. olgensis* in China were first started in the 1970s (Yang 1984). Superior pulpwood provenances and building timber provenances of *L. olgensis* have been identified (Yu et al. 2015a, b), and genetic variations in carbon concentration and allocation among different tissues at different sites have been reported (Jiang et al. 2019). Large interactions between genotype and environment are known affect growth of this species (Sun et al. 2018; Wang et al. 2021; Zhang et al. 2021). However, Yin et al. (2017) found that correlation coefficients among growth traits and wood properties were mostly not significant. Therefore, it is necessary to study genetic variations in wood properties in different environments.

In the present study, wood properties for 10 provenances of *L. olgensis* from four sites were measured and their variations analyzed. The objectives of this study were to (1) determine the variation and heritability of wood properties for the provenances at different sites; (2) estimate the phenotypic correlations among different traits and the relationships between traits and geographic factors at the sites; and, (3) evaluate and select superior pulpwood provenances and high carbon storage provenances within the sites.

Materials and methods

Study area

Germplasm was collected from 10 provenances of *L. olgensis* in its natural distribution area in 1980 to produce seedlings for provenance trials. Seedlings were planted in 1982 at four trial sites using a randomized complete block design. The locations and climatic characteristics of the trial sites and seedling spacing are given in Table 1.

Wood property measurements

One tree-ring core was collected three trees from each of three blocks for each provenance from each of the four sites from May to July in 2019. In total, 360 cores at breast height were obtained from south to north, and diameter at breast height (DBH) was measured. The cores were wrapped and put in paper tubes and taken to the laboratory for further analysis. All cores were placed in an oven at 80 °C for 48 h, then weighed every 2 h until the difference between the last two measurements was less than 0.5% of the total mass. Wood density was measured using the drainage method reported by Cheng (1985). Fiber length (FL) and fiber width (FW) were measured

Table 1 Geographic and climatic characteristics and spacing of *Larix olgensis* at four sites in China

No.	Site	Longitude	Latitude	Altitude (m)	Annual precipitation (mm)	Annual mean temperature (°C)	Initial spacing (m)
1	CuoHai (CH)	122°51′ E	47°27′ N	340	445.3	3.4	1×2
2	JiaGeDaQi (JGDQ)	124°07′ E	50°25′ N	427	495.0	− 1.2	3×3
3	LiangShui (LS)	128°53′ E	47°10′ N	400	676.0	− 0.3	1.5×2
4	Mao'erShan (MES)	127°57′ E	45°33′ N	300	723.0	2.8	1.5×2

Interlaced thinning as applied to the LS site in 2000. The MES site was thinned by removing one row per plot in 1997, then every other tree was removed in each remaining row in 2001 as detailed by Mu et al. (2009); the cores were divided into sapwood, heartwood, and pith, then each portion treating with nitric acid and chromic acid, and the length and width of 10 fibers in each portion were measured, then the mean FL and FW of the 30 values were calculated for each core (tree). Hemicellulose content (HEC), lignin content (LC), cellulose content (CEC), holocellulose content (HOC) and ash content (AC) of each clone were measured using a fully automatic fiber analyzer according to the national standard GB/T 2677.1 93 (A2000i; ANKOM Technology, Macedon, NY, USA) and resistance furnace and the method of Xu et al. (2016). The carbon content (CAC) of each sample was measured with a Hydrocarbon analyzer Multi EA 4000 (Analytik Jena AG, Germany).

Statistical analyses

Statistical analyses were carried out using SPSS 25.0 software (IBM, Armonk, NY, USA). The following linear model was used for joint analysis of the four sites together and *F* tests was performed to estimate the significance of ANOVA (Zhao et al. 2014):

$$y_{ijk} = \mu + S_i + P_j + SP_{ij} + \varepsilon_{ijk} \tag{1}$$

where y_{ijk} the performance of the *k*th tree of the *j*th provenance growing in the *i*th site, μ is the overall mean, S_i the random effect of the *i*th site, P_j is the random effect of the *j*th provenance, SP_{ij} the interactive effect of the *j*th provenance and *i*th site, and ε_{ijk} is the random error.

The different wood properties were subjected to analyses of variance among the provenances within sites using the following linear model (Zhang et al. 2020):

$$X_{ijk} = \mu + P_i + B_j + PB_{ij} + e_{ijk} \tag{2}$$

where X_{ijk} the performance of individual tree *k* in provenance *i* within block *j*, μ is the overall mean, P_i is the random effect of provenance *i*th, B_j is the random effect of block *j*, PB_{ij} is the interactive effect of provenance *i* and block *j*, and PB_{ij} is the random error.

The phenotypic and genotypic coefficient of variation (PCV and GCV) were calculated using the formula of Mohamed et al. (2017):

$$\mathrm{PCV} = \frac{\sqrt{\sigma_{\mathrm{p}}^2}}{X} \times 100 \tag{3}$$

$$\mathrm{GCV} = \frac{\sqrt{\sigma_{\mathrm{g}}^2}}{X} \times 100 \tag{4}$$

where σ_{p}^2 is the phenotype variance component for the trait, σ_{g}^2 is the genetic variance component for the trait, and *X* the average value for the trait.

Provenance heritability (H^2) was estimated using the formula of Razafimahatratra et al. (2016):

$$H^2 = \frac{\sigma_{\mathrm{P}}^2}{\sigma_P^2 + \frac{\sigma_{\mathrm{PB}}^2}{B} + \frac{\sigma_{\mathrm{e}}^2}{NB}} \tag{5}$$

where σ_{P}^2 the variance component of the provenance, σ_{PB}^2 the variance component of the interaction between the provenance and the block, σ_{e}^2 the variance component of the error, *B* is the number of blocks, *N* is the total number of provenances.

Equivalent latitude was adopted to reflect the real effect of latitude and eliminate any influence of altitude (Yang et al. 1991):

$$\text{Equivalent latitude} = \text{latitude} + \frac{\text{Elevation} - 300}{E} \tag{6}$$

where *E* is constant, and when the elevation is greater than 300 m, *E* is 140 or when the elevation is less than 300 m, *E* is 200.

The correlation analysis $r_{\mathrm{A}}(xy)$ among wood properties and the relationships between wood properties and environmental factors was done as described by Bi et al. (2000) using the equation:

$$r_{\mathrm{A}}(xy) = \frac{\mathrm{COV}_{\mathrm{P}(xy)}}{\sigma_{\mathrm{P}}(x)\sigma_{\mathrm{P}}(y)} \tag{7}$$

where $\mathrm{COV}_{\mathrm{P}(xy)}$ is the phenotypic covariance between index *x* and *y*, $\sigma_P(x)$ and $\sigma_P(y)$ are the phenotypic variance for index *x* and index *y* respectively.

The multiple-traits comprehensive evaluation was analyzed using the following formula (Zhao et al. 2016):

$$Qi = \sqrt{\sum_{i=1}^{n} a_i} \tag{8}$$

$$a_i = x_{ij}/x_{j\max} \tag{9}$$

where Qi the value of colligation assessment for *i*th provenance, x_{ij} the average value of *i*th provenance for trait *j*, $x_{j\max}$ is the maximum average value of different provenances for trait *j*, and *n* is number of traits.

Genetic gain was estimated using the formula of Silva et al. (2008):

$$\Delta G = H^2 S/X \tag{10}$$

where H^2, S, and X are provenance heritability, selection difference, and mean value of the given trait, respectively.

Results

Estimates of variance components

The analysis of variance showed that different wood properties reached significant difference level ($P < 0.01$) among sites and the interactions between sites and provenances during the multi-site joint analysis, while only WD, FL, and FL/W differed significantly among the different provenances (Table 2), indicating environmental effects were a predominant source of variation. Variance components among sites were all higher than those among provenances and their interactions. Therefore, it was necessary to screen for superior provenances within each site. Significant differences for different properties were detected among provenances within sites ($P < 0.01$), except for FW and FL/W, while the differences among the blocks and the interactions between provenances and blocks were mostly insignificant (Table 3), indicating high variation among provenances.

Trait means

The means for different properties of all provenances within sites are shown in Table 4. The mean DBH ranged from 17.59 to 28.51 cm across sites, and was largest at site MES and lowest at CH. The mean WD at site LS (0.576 g cm^{-3}) was significantly lower than those at the other three sites, especially compared with MES (0.645 g cm^{-3}). The mean FL, FW, and FL/W ranged from 2088.19 (MES) to 2404.27 µm (JGDQ), from 33.14 (LS) to 36.91 µm (JGDQ), and from 57.57 (MES) to 72.82 (LS), respectively. FL/W for all provenances at LS was higher than that at MES. The mean HEC, CEC, HOC, LC, and AC ranged from 9.27 (MES) to 10.601% (JGDQ), from 38.18 (MES) to 44.19% (LS), from 47.45% (MES) to 53.60% (LS), from 27.74 (JGDQ) to 30.55% (MES), and from 0.47 (JGDQ) to 0.58% (LS), respectively. HEC at CH and JGDQ was higher than at LS and MES, CEC and HOC at site MES were lower than at the other three sites, and LC at site MES was the highest. The mean CAC for sites JGDQ, LS, and MES was 456.96 g kg^{-1}, 457.42 g kg^{-1}, and 454.21 g kg^{-1} respectively, and the lowest mean was at site CH (442.48 g kg^{-1}). Across sites, WD was higher for provenances DHL and DST than for the other provenances across sites and lowest for provenance HL. Provenance LSH had the lowest values for WD at sites CH and LS, however, it was higher at sites of JGDQ and MES. FL/W for provenance DHL was lower than others at 4 sites, and higher for DST. HOC for provenance DHL was lower at sites CH, JGDQ, and LS than at site MES, but the opposite for provenance DHL. CAC differed significantly across all sites for each provenance (e.g., provenance LSH had higher CAC at CH, LS and MES than at JGDQ). Values for CAC of provenance XBH were lower across all sites, and those for provenance HL were higher across sites, except at LS. Provenance BH were the highest at site JGDQ and lowest at site LS, whereas those for provenance ML were the highest at LS and lowest at MES.

Genetic variability for wood traits

The genetic variability parameters calculated for the wood properties of the 10 provenances at each site are shown in Table 5. The PCV and GCV for AC were highest and all

Table 2 Results of ANOVA for different wood properties of *Larix olgensis* at four sites in China

Trait	Site			Provenance			Site × Provenance			Error	
	MS	df	*F*	MS	df	*F*	MS	df	*F*	MS	df
WD	0.072	3	10.937**	0.025	9	3.736**	0.007	27	1.835**	0.004	320
FL	2,027,009.468	3	12.960**	816,387.853	9	5.220**	156,405.372	27	4.410**	35,467.395	320
FW	323.333	3	9.010**	46.387	9	1.293 ns	35.886	27	4.004**	8.963	320
FL/W	3845.837	3	28.748**	315.354	9	2.357*	133.777	27	3.440**	38.892	320
HEC	0.004	3	39.069**	0.000	9	0.363 ns	0.000	27	4.595**	0.000	320
CEC	0.071	3	35.064**	0.003	9	1.251 ns	0.002	27	4.974**	0.000	320
HOC	0.099	3	37.501**	0.003	9	1.062 ns	0.003	27	5.094**	0.001	320
LC	0.015	3	8.363**	0.003	9	1.449 ns	0.002	27	7.445**	0.000	320
AC	0.000	3	3.495*	0.000	9	1.489 ns	0.000	27	10.213**	0.000	320
CAC	4413.695	3	37.646**	147.179	9	1.255 ns	117.242	27	4.879**	24.03	320

MS Mean square. *df* Degree of freedom. *WD* Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content. Significance levels: *$P < 0.05$, **$P < 0.01$; ns, not significant

Table 3 Variance components of different traits for the 10 provenances of *Larix olgensis* at four sites in China

Site	Trait	Provenance (%)	Block (%)	Provenance × Block (%)	Error (%)
CH	WD	48.74 ns	11.19 ns	23.44 ns	16.63
	FL	63.18*	12.49 ns	22.34**	1.99
	FW	36.23 ns	38.40 ns	17.40*	7.97
	FL/W	54.42 ns	6.96 ns	36.75**	1.86
	HEC	71.02**	6.14 ns	7.52 ns	15.31
	CEC	43.75*	23.91 ns	14.56 ns	17.78
	HOC	47.29**	24.17 ns	13.25 ns	15.30
	LC	61.33**	13.81 ns	13.47 ns	11.39
	AC	72.36**	2.93 ns	18.55**	6.16
	CAC	50.80**	22.08 ns	10.66 ns	16.46
JGDQ	WD	32.55 ns	16.83 ns	36.78**	13.84
	FL	72.51**	4.32 ns	19.72**	3.45
	FW	37.02 ns	36.60 ns	21.97**	4.42
	FL/W	39.04 ns	30.66 ns	25.97**	4.34
	HEC	60.61*	2.48 ns	18.60 ns	18.31
	CEC	83.70**	0.31 ns	9.75 ns	6.23
	HOC	80.22**	0.59 ns	10.75 ns	8.43
	LC	34.18 ns	24.88 ns	28.35**	12.59
	AC	75.90**	9.75 ns	9.02 ns	5.33
	CAC	43.03*	35.52 ns	12.56 ns	8.89
LS	WD	73.30**	2.60 ns	13.91 ns	10.19
	FL	56.76**	26.17 ns	15.00**	2.06
	FW	52.04 ns	19.41 ns	23.45**	5.10
	FL/W	50.78 ns	14.16 ns	31.59**	3.47
	HEC	44.59 ns	19.20 ns	19.19 ns	17.02
	CEC	50.05**	38.52*	6.60 ns	4.84
	HOC	51.34**	31.22 ns	10.37 ns	7.07
	LC	54.67*	5.80 ns	20.33 ns	19.20
	AC	80.83**	10.79 ns	3.88 ns	4.50
	CAC	61.91**	13.65 ns	9.11 ns	15.33
MES	WD	44.76 ns	2.77 ns	38.37**	14.10
	FL	41.26*	41.94 ns	14.66**	2.14
	FW	44.39 ns	18.85 ns	31.93**	4.83
	FL/W	31.61 ns	39.24 ns	27.30**	1.85
	HEC	61.39*	2.94 ns	22.68 ns	12.99
	CEC	83.03**	0.60 ns	10.41 ns	5.95
	HOC	78.47**	1.24 ns	12.46 ns	7.83
	LC	75.50**	8.53 ns	10.36*	5.62
	AC	70.33**	16.74 ns	6.75 ns	6.18
	CAC	75.33**	8.14 ns	9.40 ns	7.13

See Table 1 for site codes. *WD* Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content. Significance levels: $^{*}P < 0.05$, $^{**}P < 0.01$; ns, not significant

moderate, whereas those for CAC were the lowest. At site CH, the maximum for PCV was 19.546% and 14.430% for GCV. The maximum PCV and GCV at site JGDQ was 27.365% and 21.113%, respectively. The maximum PCV and GCV at site LS was 18.376% and 14.855%, respectively. The maximum PCV and GCV at site MES were 18.871% and 13.811%, respectively. In addition, the PCVs and GCVs for the other properties were almost always low. The H^2 for the different traits at CH ranged from 0.599 (FL/W) to 0.971 (CEC and HOC). The lowest H^2 at site JGDQ was 0.467 (LC), and the highest was 0.976 (HOC). The H^2 for the different traits at LS ranged from 0.663 (FL/W) to 0.996 (AC). The lowest H^2 at site JGDQ was 0.332 (FL/W), and the highest was 0.986 (AC). Nearly all traits had high heritability.

Inter-trait correlation analysis

The correlation coefficients between different properties within sites are shown in Table 6. There were significant correlations between traits DBH and WD at sites CH and LS, but not at other sites. DBH was significantly correlated with FL and FW at sites JGDQ and LS and negatively correlated with LC at sites CH and MES. WD was negatively correlated with CEC and HOC across all sites but MES. FW was negatively correlated with FL/W across all sites, and FW and FL/W all positively correlated with FL. HOC was positively correlated with HEC and with CEC across sites. It was interesting that CAC was positively correlated with CEC and HOC at CH, but negatively correlated with these two traits at site MES. In addition, CAC was significantly positively correlated with LC only at site MES. LC was positively correlated with HEC at site JGDQ and negatively correlated with CEC and HOC at site MES.

Geographic variations

The correlation coefficients between wood properties and geographic and climatic factors at the four sites are given in Table 7. WD was negatively correlated with elevation and positively correlated with temperature. FL was positively correlated with latitude (equivalent latitude) and elevation and negatively correlated with precipitation and temperature, while FL/W was only positively correlated with elevation. HEC, CEC and HOC were positively correlated with latitude (equivalent latitude) and elevation and negatively correlated with precipitation, but there was a significant negative correlation between HEC and longitude and between CEC and HOC with temperature. LC was negatively correlated with latitude (equivalent latitude) and elevation and positively correlated with precipitation and temperature. CAC was positively correlated with longitude, elevation, and precipitation but negatively correlated with temperature.

Table 4 Mean values for different traits for provenances of *Larix olgensis* at four sites in China

Site	Provenance	DBH (cm)	WD	FL	FW	FL/W	HEC (%)	CEC (%)	HOC (%)	LC (%)	AC (%)	CAC (g kg^{-1})
CH	BDS	18.26	0.631	2304.22	34.08	67.78	10.98	42.16	53.14	27.29	0.51	439.20
	BH	17.78	0.600	2750.91	34.17	80.64	10.40	44.33	54.74	29.04	0.41	444.62
	DHL	16.82	0.635	2044.68	33.60	60.93	10.27	41.27	51.54	28.82	0.70	436.71
	DST	17.50	0.609	2520.41	34.85	72.32	10.37	42.61	52.98	28.82	0.55	442.43
	HL	17.83	0.595	2372.98	35.00	67.89	10.60	44.00	54.60	28.84	0.54	446.01
	JX	17.72	0.643	2177.09	32.35	67.49	10.38	43.42	53.81	28.34	0.51	446.10
	LSH	17.16	0.552	2365.80	32.52	72.80	10.52	42.39	52.91	30.02	0.68	445.72
	ML	18.42	0.645	2120.14	32.19	65.91	9.78	38.93	48.71	28.49	0.58	437.67
	TQL	17.19	0.587	2328.80	36.10	65.07	10.37	42.46	52.83	29.73	0.55	443.77
	XBH	17.23	0.628	2439.30	34.39	71.55	10.41	44.17	54.58	28.68	0.64	442.58
	Mean	17.59c	0.613a	2342.43a	33.93b	69.24a	10.41a	42.57b	52.98a	28.81b	0.57a	442.48b
JGDQ	BDS	23.06	0.622	2336.09	34.12	68.78	10.04	42.67	52.71	27.56	0.54	452.49
	BH	24.04	0.601	2319.11	34.57	67.12	10.61	42.37	52.98	28.01	0.41	461.66
	DHL	24.39	0.610	2187.79	36.42	60.11	10.58	40.45	51.02	28.28	0.55	456.53
	DST	26.26	0.679	2807.27	40.52	69.65	10.57	42.20	52.77	27.71	0.47	456.76
	HL	22.58	0.589	2302.58	36.05	63.97	10.42	42.90	53.33	27.87	0.41	459.49
	JX	23.57	0.600	2425.85	38.84	63.02	10.63	44.51	55.13	26.54	0.43	456.67
	LSH	24.54	0.616	2392.74	38.34	62.62	10.68	42.26	52.94	28.29	0.34	455.86
	ML	23.16	0.605	2534.02	37.41	68.05	10.69	42.54	53.23	27.55	0.61	458.12
	TQL	24.19	0.623	2361.21	37.23	63.57	10.79	39.15	49.95	28.16	0.34	460.81
	XBH	21.62	0.594	2376.08	35.61	66.72	11.01	42.82	53.83	27.41	0.63	451.24
	Mean	23.74b	0.614a	2404.27a	36.91a	65.36b	10.60a	42.19b	52.79a	27.74c	0.47b	456.96a
LS	BDS	24.12	0.569	2288.20	30.84	74.50	8.93	44.67	53.61	28.48	0.55	458.74
	BH	22.99	0.560	2355.34	32.37	73.05	9.51	44.10	53.61	29.12	0.74	452.98
	DHL	24.23	0.596	2205.75	32.87	67.30	9.18	43.20	52.38	27.94	0.63	456.06
	DST	29.80	0.692	2936.09	37.88	78.06	9.43	44.18	53.61	28.36	0.56	457.45
	HL	24.28	0.548	2244.62	30.45	74.30	9.58	44.73	54.32	28.05	0.48	456.21
	JX	25.11	0.581	2366.95	30.15	78.93	9.59	44.56	54.15	27.79	0.52	457.31
	LSH	23.37	0.523	2392.25	35.20	67.99	9.70	45.15	54.85	29.08	0.58	460.27
	ML	25.83	0.560	2320.56	32.89	70.73	9.26	44.89	54.14	27.43	0.56	463.38
	TQL	23.76	0.558	2563.80	33.52	76.60	9.43	42.10	51.53	28.68	0.46	457.68
	XBH	24.41	0.569	2344.57	35.22	66.74	9.45	44.32	53.78	28.70	0.69	454.10
	Mean	24.79b	0.576b	2401.81a	33.14b	72.82a	9.41b	44.19a	53.60a	28.36b	0.58a	457.42a
MES	BDS	26.87	0.626	2097.55	37.22	57.45	9.59	36.63	46.22	32.91	0.55	455.07
	BH	29.67	0.664	1972.86	36.34	54.77	9.51	38.67	48.18	28.25	0.47	454.79
	DHL	29.53	0.713	2025.72	38.65	52.47	10.13	38.83	48.97	33.06	0.63	454.36
	DST	30.82	0.697	2505.64	38.69	65.33	8.66	40.98	49.63	26.42	0.42	452.80
	HL	26.62	0.589	2038.81	39.77	51.25	8.73	35.81	44.54	31.91	0.46	456.66
	JX	29.14	0.639	2113.92	35.75	59.64	9.43	38.04	47.46	30.76	0.51	459.80
	LSH	26.49	0.641	2003.39	34.43	58.63	9.08	38.64	47.72	32.93	0.46	458.49
	ML	28.73	0.633	1911.85	35.98	54.04	9.36	39.82	49.18	28.84	0.53	442.24
	TQL	28.41	0.616	1999.13	31.61	63.41	9.31	37.01	46.32	32.93	0.61	456.08
	XBH	28.77	0.631	2213.01	37.64	58.72	8.94	37.34	46.28	27.48	0.42	451.81
	Mean	28.51a	0.645a	2088.19b	36.61a	57.57c	9.27b	38.18c	47.45b	30.55a	0.51a	454.21a

DBH Diameter at breast height. *WD* Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content. The a, b, and c indicated significant differences among sites under the multiple comparisons of means

Table 5 Genetic variability parameters for different wood traits of *Larix olgensis* at four sites in China

Trait	CH			JGDQ			LS			MES		
	PCV (%)	GCV (%)	H^2	PCV (%)	GCV (%)	H^2	PCV (%)	GCV (%)	H^2	PCV (%)	GCV (%)	H^2
WD	9.384	3.923	0.862	8.710	3.147	0.575	11.419	7.291	0.962	10.846	4.784	0.398
FL	9.762	8.583	0.853	8.171	6.787	0.901	9.986	8.628	0.902	9.615	7.871	0.858
FW	6.191	3.231	0.801	7.480	5.020	0.704	9.819	6.982	0.810	8.887	6.134	0.566
FL/W	8.802	7.648	0.599	6.575	4.511	0.629	7.621	5.916	0.663	9.600	7.690	0.332
HEC	4.747	2.512	0.778	4.412	1.994	0.952	4.876	1.904	0.907	7.840	4.242	0.892
CEC	8.624	3.136	0.971	4.779	3.640	0.975	3.053	2.179	0.975	5.505	4.228	0.971
HOC	7.505	3.259	0.971	4.312	3.006	0.976	3.105	1.989	0.956	5.167	3.656	0.965
LC	4.278	2.438	0.960	3.899	1.559	0.467	4.005	1.653	0.932	11.196	8.526	0.967
AC	19.546	14.430	0.914	27.365	21.113	0.973	18.376	14.855	0.996	18.871	13.811	0.986
CAC	1.494	0.648	0.882	1.181	0.646	0.855	1.122	0.564	0.918	1.413	1.014	0.944

PCV Phenotypic coefficient of variation. *GCV* Genotypic coefficient of variation. H^2 Provenance heritability. *WD* Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content

Comprehensive evaluation and genetic gain

For the selection of superior pulpwood provenances and high carbon storage provenances, the results of the comprehensive evaluation of different wood properties and Qi values for the provenances across sites are shown in Table 8. From the perspective of pulpwood provenances, WD, FL, HEC, CEC, HOC, LC, and AC were regarded as indicators, and the values for LC and AC were calculated using negative numbers because of the negative effects of papermaking. As for high carbon storage provenances, WD, HEC, CEC, HOC, LC, AC, and CAC were used as evaluation indices, and AC was used as negative number in the calculation. Properties that had no significant effect among provenances within sites were eliminated. At site CH, the Qi value for pulpwood ranged from 1.261 (DHL) to 1.547 (BH) and for high carbon storage from 1.936 (DHL) to 2.080 (BH). At site JGDQ, Qi for pulpwood ranged from 1.642 (DHL) to 1.785 (LSH) and for high carbon storage from 1.704 (DHL) to 1.822 (LSH). At site LS, Qi for pulpwood ranged from 1.251 (BH) to 1.490 (DST) and for high carbon storage from 1.934 (BH) to 2.038 (DST). At site MES, Qi for pulpwood ranged from 1.257 (TQL) to 1.546 (DST) and for high carbon storage from 1.941 (TQL) to 2.013 (LSH). Pulpwood and high carbon storage were regarded as selected targets, with a selection rate of 20%, two superior provenances were selected at each site. The genetic gains for different traits of the superior provenances are shown in Table 9. From the view of pulpwood, the superior provenances selected at CH, JGDQ, LS, and MES were BH and BDS, LSH and JX, DST and JX, and DST and XBH, respectively. On the other hand, the superior high carbon storage provenances at 4 sites were BH and HL, LSH and JX, DST and HL, and DST and LSH, respectively. The genetic gains of different traits for superior provenances were shown in Table 9. As was shown, the genetic gain for WD at LS was ranged from 7.44 to 10.19%. Meanwhile, the genetic gains for FL at different sites were ranged from 0.19 to 11.14%. The genetic gains at the different sites ranged from −4.59 to 2.13% for HEC, from 0.40 to 4.16% for CEC, from 0.51 to 3.08% for HOC, from −11.40 to 0.44% for LC, and from −17.96 to −6.07% for AC. For CAC, the genetic gain was 0.57% at CH, −0.13% at JGDQ, −0.12% at LS, and 0.30% at MES.

Discussion

Tree growth and wood quality were affected by a variety of factors such as genotype, temperature, precipitation, soil conditions, and their interactions (Fang et al. 2020). Heritability was closely related to climatic factors. Therefore, heritability of different traits for the same provenance or family will certainly differ among the sites. Our analysis of variance for wood properties of *L. olgensis* provenances at the four sites showed that all traits differed significantly among different sites, indicating that the different conditions had vital effects on plant growth. The values for the wood traits also differed among the different provenances within each site, indicating that the evaluation and selection of provenances within sites were effective. The phenotypic and genotypic coefficients of variation for almost all properties at the different sites were lower than those reported for 26-year-old clones of *L. olgensis* (Yin et al. 2017); however, the provenance heritability in the present study was higher than that found by Yin et al. (2017).

Wood density is a strong determinant of mechanical strength, which affects wood quality and potential uses (Lundqvist et al. 2018) and is considered the main physical

Table 6 Correlation coefficients for wood properties of *Larix olgensis* at four sites in China

Site	CH	DBH	WD	FL	FW	FL/W	HEC	CEC	HOC	LC	AC
CH	WD	0.231*									
	FL	–0.058	–0.121								
	FW	0.168	–0.093	0.228*							
	FL/W	–0.149	–0.055	0.839**	–0.333**						
	HEC	0.061	–0.153	0.221*	0.152	0.124					
	CEC	–0.149	–0.413**	0.281**	0.141	0.188	0.118				
	HOC	–0.137	–0.424**	0.305**	0.158	0.201	0.253*	0.991**			
	LC	–0.208*	–0.304**	0.204	0.085	0.147	–0.100	0.106	0.089		
	AC	–0.057	–0.004	–0.289**	–0.114	–0.215*	–0.059	–0.153	–0.157	0.116	
	CAC	0.049	–0.303**	0.276**	0.170	0.182	0.144	0.338**	0.349**	0.091	–0.126
JGDQ	WD	0.204									
	FL	0.231*	0.136								
	FW	0.284**	0.088	0.592**							
	FL/W	–0.067	0.035	0.440**	–0.458**						
	HEC	–0.024	–0.146	0.065	0.002	0.052					
	CEC	–0.144	–0.259*	0.204	0.101	0.133	0.076				
	HOC	–0.143	–0.282**	0.210*	0.096	0.139	0.312**	0.971**			
	LC	0.013	–0.256*	–0.037	–0.025	–0.039	0.237*	–0.108	–0.046		
	AC	–0.140	–0.124	0.084	0.017	0.069	–0.114	0.106	0.074	–0.057	
	CAC	–0.007	0.061	0.053	0.113	–0.076	0.009	–0.145	–0.136	0.033	–0.205
LS	WD	0.239*									
	FL	0.522**	0.342**								
	FW	0.400**	0.252*	0.656**							
	FL/W	0.144	0.087	0.398**	–0.426**						
	HEC	–0.034	–0.250*	0.047	0.002	0.069					
	CEC	–0.159	–0.241*	–0.202	–0.204	0.016	0.281**				
	HOC	–0.148	–0.287**	–0.159	–0.176	0.035	0.560**	0.953**			
	LC	–0.163	–0.152	0.085	0.159	–0.087	0.026	0.116	0.108		
	AC	–0.041	–0.069	–0.104	0.152	–0.292**	0.009	0.057	0.052	0.089	
	CAC	0.122	–0.069	0.025	–0.113	0.161	0.082	0.009	0.034	–0.197	–0.268*
MES	WD	0.160									
	FL	0.115	0.061								
	FW	0.181	0.307**	0.279**							
	FL/W	–0.056	–0.215*	0.597**	–0.598**						
	HEC	0.031	0.055	–0.172	–0.096	–0.071					
	CEC	0.163	0.266*	0.186	–0.035	0.168	0.119				
	HOC	0.157	0.258*	0.108	–0.064	0.126	0.453**	0.939**			
	LC	–0.356**	–0.136	–0.292**	–0.149	–0.088	0.121	–0.446**	–0.358**		
	AC	0.039	0.086	–0.290**	–0.066	–0.169	0.313**	–0.171	–0.045	0.376**	
	CAC	–0.164	–0.062	–0.087	–0.099	–0.003	–0.003	–0.274**	–0.247*	0.329**	–0.051

Correlation significance: *$P<0.05$, **$P<0.01$ (2-tailed). *WD* Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content

variable and key index for evaluating wood quality and pulp yield (Ortega Rodriguez and Tomazello-Filho 2019). An increase in wood density has an important effect on the efficiency of pulp production (Niemczyk and Thomas 2020). Site is also an important factor with a strong effect on wood density (Dias et al. 2018). In the present study, the average wood density of *L. olgensis* provenances at all sites was 0.612 g cm^{-3}, with the maximum of 0.645 g cm^{-3} found at MES and the minimum of 0.576 g cm^{-3} at LS, both significantly higher than obtained by Li and Lian (2017a). This difference might be due to differing afforestation densities. In addition, the wood density of the DHL and DST provenances

Table 7 Correlation coefficients of wood traits of *Larix olgensis* and geographic and climatic factors at four sites in China

Trait	Longitude	Latitude	Equivalent latitude	Elevation	Precipitation	Temperature
WD	–0.111	–0.159	–0.204	–0.401*	0.050	0.320*
FL	–0.200	0.434**	0.458**	0.514**	–0.340*	–0.373*
FW	–0.093	0.168	0.134	–0.050	0.026	–0.078
FL/W	–0.080	0.242	0.287	0.472**	–0.283	–0.271
HEC	–0.833**	0.732**	0.693**	0.412**	–0.858**	–0.159
CEC	–0.128	0.406**	0.453**	0.629**	–0.351*	–0.424**
HOC	–0.309	0.538**	0.572**	0.667**	–0.518**	–0.422**
LC	0.243	–0.540**	–0.559**	–0.582**	0.375*	0.455**
AC	0.077	–0.198	–0.179	–0.059	0.014	0.142
CAC	0.574**	0.170	0.217	0.420**	0.511**	–0.678**

Correlation significance: $*P<0.05$, $**P<0.01$ level (2-tailed). *WD* Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content

was greater than 0.600 g cm^{-3} at all the sites, and less than 0.600 g cm^{-3} for provenance HL at all the sites, indicating that although the same provenances had certain differences in the different site conditions, the provenances had certain commonalities in their site responses.

Pulp properties and paper quality are mainly influenced by wood fiber traits (fiber length and fiber length to width ratio) (Liu et al. 2020). The greater the fiber length to width ratio, the more times the fibers can be mixed and the better the combinability of the fibers, which gives the paper greater strength (Bai et al. 2009). In this study, the average fiber length was 2266.602 μm, considered as a long fiber. The average fiber length and fiber width were similar to previous findings (Shi et al. 2011). The average fiber length to width ratio was 65.68, higher than reported for *Populus deltoids* by Wu et al. (2011); therefore, *L. olgensis* is categorized as high-quality material for papermaking.

In the process of genetic improvement of forest trees, multiple traits are increasingly expected to be improved simultaneously (Lin 2010); thus, correlation analyses can provide a reference guide for joint breeding of multiple traits (Jia et al. 2016). However, genetic correlations between growth and wood traits are likely to depend on the trial site (Li et al. 2017). In the present study, DBH and WD were significantly correlated, which disagrees with a report for *Pinus taeda* (Xu et al. 2000). However, the WD of *Larix kaempferi* is negatively related to growth rate of juveniles and was not correlated with growth rate at maturity (Zhu et al. 2000). Similarly, Stackpole et al. (2010) found a significant negative genetic correlation for *Eucalyptus globulus* between basic wood density and diameter at the selection age (4–5 years); however, at the harvest age, the genetic correlation was not significant and slightly positive. Zhang et al. (2014) found a weak positive correlation between DBH and WD for triploid hybrid clones of *Populus tomentosa*. Here, we found that wood density was negatively correlated with cellulose content at all sites except MES, whereas Guo et al. (2014) found a significant positive correlation between these traits for *Salix suchowensis* and a negative correlation between WD and hemicellulose content; these differences might be related to the tree species. The correlation between fiber length and fiber width was extremely significant and positive, similar to the results of Liang et al. (2016) for *Pinus koraiensis*. For *L. olgensis*, fiber length was significantly correlated with hemicellulose content, which indicates that fiber qualities were closely related to chemical composition. Interestingly, CAC was positively correlated with CEC and HOC at CH, but they were negatively correlated at MES, which might be due to CAC was significantly positively correlated with LC at MES, and lignin contains more carbon than cellulose does (Weber et al. 2018).

The results of the correlation analysis between wood traits and geographic factors of the trial sites showed a significant negative correlation between wood density and altitude, agreeing with finding that the wood density of *Pinus nigra* decreased with an increase in altitude (Dias et al. 2018). Similarly, growing *Alnus formosana* at lower latitudes increased the wood density (Yang et al. 2012). Although wood density is a heritable trait, it interacts with the meteorological variables (Rocha et al. 2020). Here we found a significant positive correlation between wood density and temperature; the higher the temperature, the earlier cambial activity can begin, and as cell division accelerates, more wood cells are produced, which can increase wood density (Xu et al. 2011). The correlations between wood fiber length and latitude, equivalent latitude and altitude were extremely significant, contrary to the results of Yang et al. (2009). This finding might be due to the fact that JGDQ is at a high latitude with appropriate temperature and precipitation for *L. olgensis*, positively influencing growth. At the same time, fiber length was significantly negatively correlated with the annual average precipitation and temperature, consistent

Table 8 Qi values of different provenances of *Larix olgensis* at four sites in China

Site	Provenance	Pulpwood	High C storage
CH	BDS	1.456	2.021
	BH	1.547	2.080
	DHL	1.261	1.936
	DST	1.430	2.010
	HL	1.444	2.035
	JX	1.422	2.029
	LSH	1.332	1.978
	ML	1.283	1.938
	TQL	1.392	2.017
	XBH	1.401	1.995
LS	BDS	1.359	2.004
	BH	1.251	1.934
	DHL	1.309	1.966
	DST	1.490	2.038
	HL	1.386	2.017
	JX	1.401	2.013
	LSH	1.337	1.991
	ML	1.371	1.993
	TQL	1.396	2.008
	XBH	1.289	1.953
JGDQ	BDS	1.676	1.720
	BH	1.746	1.795
	DHL	1.642	1.704
	DST	1.767	1.764
	HL	1.744	1.793
	JX	1.775	1.809
	LSH	1.785	1.822
	ML	1.681	1.708
	TQL	1.750	1.795
	XBH	1.669	1.708
MES	BDS	1.316	1.968
	BH	1.427	1.987
	DHL	1.320	1.980
	DST	1.546	1.993
	HL	1.324	1.965
	JX	1.386	1.984
	LSH	1.364	2.013
	ML	1.392	1.970
	TQL	1.257	1.941
	XBH	1.449	1.965

with the results of Zhang et al. (2011) for cotton; appropriate precipitation was conducive to an increase in cotton fiber length, whereas excessive precipitation resulted in shorter fibers. Our correlation analysis showed that carbon content was significantly positively correlated with longitude, altitude and annual precipitation and significantly negatively correlated with annual average temperature, similar to the results of Zhou (2015) on *Fraxinus mandshurica*; temperature decreases as altitude increases, plant growth rate slows, which increases the degree of lignification, and resulting in greater carbon content.

The best provenance must be selected for a given site or region to achieve maximum plantation productivity (Loha et al. 2009). In the past, growth traits, wood quality, and disease resistance have been the main criteria for selecting suitable reproductive material for tree species (Buras et al. 2020). Our correlation analysis of numerous wood traits at four sites allowed us to select superior pulpwood provenances and high carbon storage provenances for the sites, although the genetic gains were lower than for the elites selected by Yin et al. (2017), probably due to the different tree ages or the number of materials (provenances and clones).

Conclusions

Our results on genetic and geographic variations in the wood properties of 10 *L. olgensis* provenances at four sites showed a significant difference in wood properties among the sites, provenances, and their interactions. Wood traits were mainly related to the latitude and altitude of the site and were also affected by annual precipitation and temperature. Superior pulpwood provenances and high carbon storage provenances within sites could be selected separately for use as the preferred afforestation material for a particular site.

Table 9 Genetic gains of different wood traits of *Larix olgensis* within four sites in China

Site	Function	WD	FL	HEC	CEC	HOC	LC	AC	CAC
CH	Pulpwood		6.74%	2.13%	1.53%	1.75%	–2.14%	–17.08%	
	High C storage			0.70%	3.62%	3.08%	0.44%	–14.67%	0.57%
JGDQ	Pulpwood		0.19%	0.48%	2.76%	2.31%		–17.96%	
	High C storage			0.48%	2.76%	2.31%		–17.96%	–0.13%
LS	Pulpwood	10.19%	9.38%	0.98%	0.40%	0.51%	–0.95%	–6.07%	
	High C storage	7.44%		0.96%	0.59%	0.65%	–0.53%	–9.32%	–0.12%
MES	Pulpwood		11.14%	–4.59%	2.50%	1.03%	–11.40%	–16.50%	
	High C storage			–3.91%	4.16%	2.50%	–2.77%	–12.62%	0.30%

WD Wood density. *FL* Fiber length. *FW* Fiber width. *FL/W* Fiber length to width ratio. *HEC* Hemicellulose content. *CEC* Cellulose content. *HOC* Holocellulose content. *LC* Lignin content. *AC* Ash content. *CAC* Carbon content

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