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Comparison of genetic impact on growth and wood traits between seedlings and clones from the same plus trees of *Pinus koraiensis*

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Abstract To evaluate the relationships among clones and open pollinated families from the same plus trees and to select elite breeding materials, growth, and wood characteristics of 33-year-old *Pinus koraiensis* clones and families were measured and analyzed. The results show that growth and wood characters varied significantly. The variation due to clonal effects was higher than that of family effects. The ratio of genetic to phenotypic coefficient of variation of clones in growth and wood traits was above 90%, and the repeatability of these characteristics was more than 0.8, whereas the ratio of genetic to phenotypic coefficient of variation of families was above 90%. The broad-sense heritability of all characteristics exceeded 0.4, and the narrow-sense family heritability of growth traits was less than 0.3. Growth characteristics were positively correlated with each other, but most wood properties were weakly correlated in both clones and families. Fiber length and width were positively correlated between clones and families. Using the membership function method, eleven clones and four families were selected as superior material for improved diameter growth and wood production, and two families from clonal and open-pollinated trees showed consistently better performance. Generally, selection of the best clones is an effective alternative to deployment of families as the repeatability estimates from clonal trees were higher than narrow-sense heritability estimates from open pollinated families. The results provide valuable insight for improving *P. koraiensis* breeding programs and subsequent genetic improvement.

Keywords *Pinus koraiensis* · Korean pine · Clonal parents · Progeny testing · Repeatability · Broad-sense heritability · Narrow-sense heritability

Introduction

The relationship between parents and offspring in numerous tree species has been studied and research shows that many growth and wood traits can be stably inherited, which provides important opportunities for early selection and genetic improvement (Li et al. 2020; Zhang et al. 2020,

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2021, 2022). The evaluation and selection of elite families is therefore important for genetic improvement of *Pinus koraiensis* (Sieb. et Zucc). Consequently, the establishment of *P. koraiensis* seed orchards began since the 1980s (Zhang et al. 2015), and more than 20 seed orchards have been established according to the provenance (Liang 2021). Previous research mainly focused on the establishment of seed orchards (Sun 2006), molecular markers (Li et al. 2021), the evaluation of superior material (Kaviriri et al. 2021), hybridization technology (Mo et al. 2017), seed nutrition (Wang et al. 2019a) and other aspects. Because of the slow growth of *P. koraiensis* and weak breeding technology, seed orchards of *P. koraiensis* are still in primary stages. In the evaluation of these orchards, most have parents for upgrading through the evaluation of progeny. However, the parents themselves are also superior individuals selected from the natural forest, and the evaluation and selection of parents are equally important.

P. koraiensis is an economically valuable species of the cold-temperate mixed forest (Ding et al. 1981) and belongs to the Pinaceae family (Zhou et al. 2020). It usually forms a mixed forest with broad-leaved species and is mainly distributed in China, Russia, the Korean Peninsula and Japan, among which the largest cover is in northeast China (Ma et al. 1992). *P. koraiensis* has ecological and economic values (Liang et al. 2016). In northeast China, it is an important native economic species. It is widely used in construction, shipbuilding, furniture, for planks and timber (Zhao et al. 2018; Liu et al. 2020) owing to its dense, straight trunk, beautiful texture, convenient processing, and is not easily damaged or deformed. Because of their rich fats, proteins, carbohydrates and other components, the seeds are extracted for oil or used as food (Zhang et al. 2017, 2019). In addition, pine seed oil regulates blood lipids (Wang et al. 2019b). Finally, *P. koraiensis* forests positively influence the environment such as temperature, humidity, water regulation, and wind speed, and root systems stabilize the soil, conserve water, and control erosion (Wang et al. 2019c), so its ecological value is particularly important.

In the past several decades, *P. koraiensis* forests have been seriously degraded due to over-logging. With the expansion of development of the economy in China, *P. koraiensis* is often used for afforestation in the construction of the Three-North Shelterbelt program and in the conversion of abandoned farmland to forest. Due to its slow growth, its breeding cycle is lengthy, and therefore, it is important to plan an effective breeding strategy to achieve maximum gain. Forward and backward selection can obtain the highest genetic gain in the short term while reducing costs. Backward selection is a method of selecting superior parents according to their breeding value based on progeny measurement. At present, there have been reports on backward selection of good parents (Zhou et al. 2020). However, the genetic impact on growth and wood traits between seedlings and clones from the same plus trees is not well known and such a study would be important to select the best material for establishing seed orchards. Thus, this research was carried out with the following objectives: (1) to compare the effects of additive and non-additive effects on seedling traits by estimating the broad-sense heritability and narrow-sense heritability of each trait in open-pollinated families and the repeatability of each trait in the clones; (2) to compare the coefficients of variation and correlation between seedlings and grafted plants, and the genetic variation of growth and wood characters between parents and offspring; and, (3) to select the best clones and open-pollinated families in terms of growth and wood properties so as to provide the basis for breeding improvement. To achieve these objectives, the variations in growth traits and wood properties among 35 *P. koraiensis* parental clones and open- pollinated families were examined and elite clones and families selected.

Materials and methods

Study site

The research was carried out in a *P. koraiensis* seed orchard in Lushuihe, Fusong County (127°29′ E, 42°29′ N), Baishan City, Jilin province. The seed orchard is located in the north temperate East Asian monsoon climate, with an average altitude of 780 m, average annual and maximum temperatures of 2.7 °C and 32.5 °C, respectively, a minimum temperature of − 44.4 °C, annual average precipitation of 871 mm, and annual average evaporation of 1166.44 mm. Annual sunshine hours are 2117 and the annual frost-free period is 115 days.

Plant materials

Thirty-five *P. koraiensis* clones and open- pollinated families were used as experimental materials. The plus trees were selected from the natural forest of Lushuihe Forestry Bureau of Jilin province in 1984, and seeds and scions collected in the autumn of the same year. The scions were grafted on local 4-year-old *P. koraiensis* rootstock for establishment of the seed orchard in the spring of 1985 in a randomized complete block design, with 10 blocks of 10 single plants of the same clone, each block containing one plant at 3 m × 3 m spacing. The seeds were germinated in the following year. The soil conditions used for seedlings and grafted materials were similar. In 1989, 4-year-old seedlings were used for the establishment of the progeny trail in a randomized complete block design with four blocks containing 24 single seedlings of the same family, each block containing 6 plants at 2 m × 2 m spacing.

Measurement of growth characteristics

In the autumn of 2017, the growth properties of 35 clones and 35 open- pollinated families were measured, including height (H) and diameter at breast height (DBH) for clones, and for open-pollinated families, ground diameter (GD), DBH, diameter at 3 m height (D_3), crown width (CR), stem straightness (SS), branch angle (BA), height to 1st branch whorl l from the ground (1BH), and height of the 6th branch whorl (6BH) from the ground for open pollinated families. Due to the high density of the seed orchard, height of individuals of open- pollinated families was not recorded. Height (H) was measured using the Vertex IV ultrasonic height range finder, and DBH, GD and D3 by a tape and volumes were calculated. Crown widths in the east–west and north–south directions were measured by tape. The 1BH and 6BH were measured by a sliding staff. The SS and BA were determined following the methods of Zhao (2010) and Liang et al. (2018a).

Measurement of wood properties

In the same year, wood cores from 35 clones in the first five blocks were taken at a height of 1.3 m in the north–south direction of each tree. Wood cores from the 35 open-pollinated families in the first block were also taken in the same pattern from each tree. The cores were marked, put in paper bags, and brought to the laboratory for determining wood traits. Wood density (WD) was determined by the drainage method (Yin et al. 2017) using five cores for each clone and six per family. Fiber lengths (FL) and widths (FW) were measured on five and six cores per clone and family, respectively, according to Yin (2017). Each clone and family consisted of 30 FLs and 30 FWs.

Statistical analysis

For each tree, volume (V) was calculated following Zhao et al. (2013) as follow:

$$V = 0.19328321D^2H + 0.007734354DH + 0.82141915D^2 \tag{1}$$

where V is volume, D is diameter at breast height, and H is tree height.

Analysis of variance (ANOVA) was used to examine the variations in growth and wood properties among clones and open- pollinated families (Liang et al. 2019) using the following model:

$$X_{ij} = \mu + C_i(F_i) + e_{ij} \tag{2}$$

$$X_{ij} = \mu + F_i + B_j + FB_{ij} + e_{ij} \tag{3}$$

where μ is the overall mean, C_i (F_i) the clone (family) effect, B_j the block effect, FB_{ij} the effect of family i within block j, and e_{ij} is the random residual. Clones, families and interactions between blocks and families were treated as random factors and blocks as fixed factors. For each growth and wood trait, variance components were estimated for each source of variation based on the maximum likelihood method, and broad-sense heritability was estimated according to Xu (2006) as follows:

$$H^2 = 1 - \frac{1}{F} \tag{4}$$

where F value is from analysis of variance.

The estimation of narrow-sense heritability (h^2) of a characteristic for the families was calculated according to Xu (2006) as follows:

$$h^2 = \frac{4\sigma_F^2}{\sigma_F^2 + \sigma_{FB}^2 + \sigma_e^2} \tag{5}$$

where σ_F^2 and σ_e^2 are the family and residual variances, and σ_{FB}^2 the variance component of interaction between family and block. Since the wood cores in the same block were used for sampling, there was no block effect, the effect of environmental differences is small, and the results of narrow-sense heritability are unsatisfactory. Therefore, the narrow-sense heritability of wood traits was not analyzed. The repeatability (R) of clones of all investigated characteristics was calculated as follows (Zhao et al. 2015):

$$R = \frac{\sigma_d^2}{\sigma_d^2 + \sigma_e^2} \tag{6}$$

where σ_d^2 is the genetic variance component between clones and σ_e^2 is the residual variance component.

The phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) were calculated using the following formula (Zhang et al. 2019):

$$PCV = \frac{\sqrt{\sigma_p^2}}{\overline{X}} \times 100 \tag{7}$$

$$GCV = \frac{\sqrt{\sigma_g^2}}{\overline{X}} \times 100 \tag{8}$$

where σ_p^2 and σ_g^2 are the phenotypic variance and genetic variance of a character, respectively, $\overline{X}$ is the phenotypic mean of a character.

The phenotype correlation r_{p12} of characters x and y was calculated as follows (Guerra et al. 2016):

$$r_{p12} = \frac{Cov_{p12}}{\sqrt{\sigma_{p1}^2 \cdot \sigma_{P2}^2}} \tag{9}$$

where Cov_{p12} denotes the phenotypic covariance between characters of x and y, and σ_{p1}^2 and σ_{P2}^2 denote the phenotypic variance of a character x and y, respectively.

The general combining ability was calculated as follows (Wang et al. 2016):

$$g = xu \tag{10}$$

where g is the general combining ability of the parent, x is the average value of the offspring of a certain mating combination of a parent in a certain trait, u is the total mean value of all combinations of this trait.

For selection of the best clones and families in growth and in wood production, the membership function of different clones (families) was calculated using DBH, WD and FL as selection indexes. As fiber length and fiber width were positively correlated, only fiber length was considered in the evaluation. The membership function was calculated as follows (Liu et al. 2017):

$$X_i = (X_{ij}X_{j\min})/(X_{j\max}X_{j\min}) \tag{11}$$

When the trait was negatively correlated with wood physical properties:

$$X_i = 1(X_{ij}X_{j\min})/(X_{j\max}X_{j\min}) \tag{12}$$

where Xij is the measured value for the j character of clone (family) i, X_{jmax} is the maximum value of the character, X_{jmin} is the minimum value of the character. All data were analyzed using SPSS 19.0 software (IBM Corp., Armonk, NY, USA).

Results

Variations in growth traits

Highly significant variations were detected among parental clones and open- pollinated families (Table 1). Estimates of variance show that the clonal effect was substantially higher than family effects (Table 2). They also show that family variation in growth traits was very low compared to the interaction between families and blocks as well as clonal effects. Descriptive statistics for each trait are shown in Table 3. Among clones, height ranged from 5.6 m to 13.2 m, DBH from 10.7 cm to 24.8 cm, and volume from 0.03 m³ to 0.19 m³. Among open-pollinated families, GD (ground diameters) ranged from 15.4 cm to 24.6 cm, DBH 12.4 cm to 20.4 cm, the D3 (diameter at 3 m) from 11.2 cm to 18.6 cm, the BA (branch angle) from 130.8° to 157.1°, the CR (crown

width) from 3.2 m to 5.2 m, SS (stem straightness) from 3.9 to 4.7, the 1BH (1st branch whorl) from 1.7 m to 1.9 m, and the 6BH (6th branch whorl) from 3.8 m to 4.4 m.

The phenotypic coefficient of variation (PCV) and the genotypic coefficient variation (GCV) were higher for clones than for open-pollinated families. Values of PCV and GCV among clones were closer as compared to values for open-pollinated families, suggesting that most of the variations in growth traits were genetically controlled. This is further evidenced from the high repeatability of each trait ($R > 0.90$) compared to the low narrow-sense heritability ($h^2 < 0.3$). However, family broad-sense heritability was high ($H^2 \geq 0.66$) for all traits except stem straightness and height at the 1st branch whorl for which heritability was less than 50% (Table 3). Due to the high planting density of the materials in this study, the heritability and coefficient of variation of 1BH were not considered.

Variations in wood properties

Significant variations in wood properties were observed among parental clones and open- pollinated families (Table 1). Estimates of variance showed that clonal variations in wood properties was very high (78.6% − 86.2%) compared to family variations (20.0% − 53.0%; Table 2). The average FL ranged from 1855.47 μm to 2583.41 μm, the average FW from 29.47 μm to 41.93 μm, the average WD from 0.44 g cm⁻³ to 0.62 g cm⁻³ among parental clones (Table 3). Among open-pollinated families, the average FL ranged from 1314.86 μm to 2112.12 μm, the average FW from 34.76 μm to 50.43 μm, and the average WD from 0.47 g cm⁻³ to 0.57 g cm⁻³.

The phenotypic coefficient of variation (PCV) and the genotypic coefficient of variation (GCV) were slightly higher for open-pollinated families than for clones, particularly for fiber length (FL) and fiber width (FW). The repeatability of FL and FW was slightly lower ($R = 0.79 − 0.86$) for clones than for family broad-sense heritability ($H^2 = 0.96$–0.97), but repeatability of WD was slightly higher than family broad-sense heritability ($R = 0.79$, $H^2 = 0.71$; Table 3).

Correlation analysis

The correlation of height and diameter was highly significant ($P < 0.01$; $0.46 < r < 0.99$) and positive for both clones and open- pollinated families (Table 4). For wood properties, there was a highly significant positive correlation between fiber length and fiber width in both clones and open- pollinated families ($0.16 < r < 0.26$). In open- pollinated families, stem form traits were significantly correlated with growth traits ($-0.14 < r < 0.63$). The correlation between growth traits and wood properties was insignificant in both clones and open-pollinated families. Most traits were not

Table 1 Results of ANOVA for growth and wood properties among 35 *P. koraiensis* clones and open- pollinated families

Source	Traits	Variance source	df	MS	F-statistic	Significance
Clones	H	Clone	34	45.148	29.761	0.000
	DBH	Clone	34	224.265	28.030	0.000
	V	Clone	34	0.030	21.872	0.000
	FL	Clone	34	298,850.202	7.271	0.000
	FW	Clone	34	64.522	4.683	0.000
	WD	Clone	34	0.013	4.869	0.000
Open-pollinated families	GD	Family	34	90.653	11.459	0.000
		Block	3	32.558	4.115	0.007
		Family×block	102	67.106	8.482	0000
	DBH	Family	34	70.139	9.419	0.000
		Block	3	97.524	13.097	0.000
		Family×block	102	61.824	8.303	0.000
	D_3	Family	34	61.359	8.689	0.000
		Block	3	192.790	27.301	0.000
		Family×block	102	58.603	8.299	0.000
	BA	Family	34	555.959	2.965	0.000
		Block	3	12,080.822	64.425	0.000
		Family×block	102	544.760	2.905	0.000
	CR	Family	34	6.534	6.880	0.000
		Block	3	12.816	13.496	0.000
		Family×block	102	4.734	4.985	0.000
	SS	Family	34	0.891	1.644	0.013
		Block	3	5.170	9.542	0.000
		Family×block	102	0.824	1.522	0.001
	1BH	Family	34	0.088	1.819	0.003
		Block	3	0.480	9.886	0.000
		Family×block	102	0.117	2.406	0.000
	6BH	Family	34	0.725	4.947	0.000
		Block	3	4.507	36.023	0.000
		Family×block	102	0.532	4.250	0.000
	FL	Family	34	956,195.742	35.767	0.000
	FW	Family	34	530.642	27.731	0.000
	WD	Family	34	0.015	3.392	0.000

Note: H, tree height (m); DBH, diameter at breast height (cm); V, volume (m^3); FL, fiber length (μm); FW, fiber width (μm); WD, wood density (g cm^{-3}); GD, ground diameter (cm); D_3, diameter at 3 m height (cm); BA, branch angle (°); CR, crown width (m); SS, stem straightness; 1BH, height at 1st branch whorl (m); 6BH, height at 6th branch whorl (m)

significantly correlated between clones and open-pollinated families. However, there were positive correlations among wood properties except for wood density ($0.11 < r < 0.22$).

General combining ability

The general combining ability of various traits of *P. koraiensis* open- pollinated families is shown in Table 5. The general combining ability of DBH of each family ranged from − 4.11 to 3.88, and it was higher for PK007, PK145, PK036 and PK429 than for the other families. This shows that using the parents of these families as hybrid parents, the genetic improvement of the progeny's DBH was greater. The general combining ability of CR (crown width) of each family ranged from − 1.03 to 1.00, being higher for PK150, PK025, PK429 and PK145 than for the other families. For SS (stem straightness) of each family, it varied from − 0.43 to 0.28; thus the clonal parents of PK424, PK066, PK064 and PK025 could be used as the hybridization parents, and the improvement of stem straightness in offspring will be stronger. The general combining ability of FL of each family ranged from − 512.99 to 284.27, and the clones PK036, PK004, PK014 and PK407 could be used as the hybridization parents.

Table 2 Estimates of variance components as percentage of the total variation

Traits	Clones	Residuals	Traits	Families (F)	Families×Block (FB)	Residuals
H	96.64	3.36	GD	5.18	51.85	42.97
DBH	96.43	3.57	DBH	2.04	52.98	44.99
V	95.43	3.33	D_3	8.72	53.67	45.61
FL	86.25	13.75	BA	0.18	23.25	76.56
FW	78.65	21.35	CR	4.48	37.28	58.25
WD	79.46	20.54	SS	0.51	7.31	92.18
–	–	–	1BH	1.64	18.03	80.33
–	–	–	6BH	1.55	33.68	64.77
			FL	52.96	–	47.04
			FW	46.39	–	53.61
			WD	20.00	–	80.00

Note: H, tree height (m); DBH, diameter at breast height (cm); V, volume (m^3); FL, fiber length (μm); FW, fiber width (μm); WD, wood density (g cm^{-3}); GD, ground diameter (cm); D_3, diameter at 3 m height (cm); BA, branch angle (°); CR, crown width (m); SS, stem straightness; 1BH, height at 1st branch whorl (m); 6BH, height at 6th branch whorl (m)

Table 3 Descriptive statistics of growth characteristics and wood properties of 35 *P. koraiensis* clones and families together with coefficient of variations (PCV), repeatability among clones (R), family broad-sense heritability (H^2) and narrow-sense heritability (h^2)

Source	Traits	Average	Range	SD	PCV	GCV	R / H^2	h^2
Clones	H	8.39	5.57 − 13.24	1.81	16.35	16.07	0.97	–
	DBH	17.78	10.67 − 24.77	4.09	17.19	16.88	0.96	–
	V	0.0957	0.0318 − 0.1895	0.05	37.17	36.31	0.95	–
	FL	2115.65	1855.47 − 2583.41	257.32	8.17	7.59	0.86	–
	FW	34.83	29.47 ~ 41.93	4.33	7.29	6.47	0.79	–
	WD	0.4994	0.4398 − 0.6213	0.06	7.36	6.56	0.79	–
Open-pollinated families	GD	20.05	15.38 − 24.60	4.31	9.69	4.94	0.91	0.21
	DBH	16.48	12.37 − 20.36	4.11	10.37	3.57	0.89	0.08
	D_3	14.90	11.18 − 18.63	4.02	10.73	2.27	0.88	0.03
	BA	148.32	130.83 − 157.08	16.98	3.25	0.46	0.66	0.01
	CR	4.21	3.18 − 5.21	1.30	12.39	6.50	0.85	0.18
	SS	4.35	3.92 − 4.67	0.78	4.43	1.21	0.39	0.02
	1BH	1.80	1.69 − 1.92	0.25	–	–	–	–
	6BH	4.11	3.79 − 4.36	0.46	3.90	1.45	0.80	0.06
	FL	1827.85	1314.86 − 2112.12	238.51	9.77	9.63	0.97	–
	FW	40.55	34.76 − 50.43	5.97	10.37	10.18	0.96	–
	WD	0.5149	0.4737 − 0.5716	0.07	4.31	3.63	0.71	–

H tree height (m); *DBH* diameter at breast height (cm); *V* volume (m^3), *FL* fiber length (μm); *FW* fiber width (μm); *WD* wood density (g cm^{-3}); *GD* ground diameter (cm); *D$_3$* diameter at 3 m height (cm), *BA* branch angle (°); *CR* crown width (m); *SS* stem straightness; 1BH, height at 1st branch whorl (m); *6BH* height at 6th branch whorl (m); *SD* standard deviation, *PCV* phenotypic coefficient of variation, *GCV* genotypic coefficient of variation; *R* repeatability; *H^2* broad-sense heritability, *h^2* narrow-sense heritability

Membership function comprehensive evaluation

The comprehensive evaluation index of the fuzzy mathematical membership function method was used to select superior clones and families with large DBH, high wood density and long fiber length (Table 6). According to the method, the standardized value of each trait is multiplied by the weight of each trait (0.4 for DBH and 0.3 for wood density and fiber length, according to Liu et al. 2017) in the evaluation system, and the membership function mean value of each trait for clones and families was obtained. The superior clones and families with average membership functions > 0.6 were selected. Consequently, eleven clones (PK124, PK051, PK042, PK003, PK415, PK036, PK162, PK303, PK004, PK025, PK423) and four families (PK003, PK066, PK124, PK401) were selected as superior breeding material for diameter growth and wood production in the establishment of Korean pine forests, as well as for the

Table 4 Correlation of phenotypic traits in 35 *P. koraiensis* clones and open- pollinated families

Source	Traits	Clones						Open-pollinated families									
		DBH	H	V	FL	FW	WD	GD	DBH	D₃	BA	CR	SS	1BH	6BH	FL	FW
Clones	H	0.46**															
	V	0.94**	0.63**														
	FL	0.05	-0.00	0.04													
	FW	-0.02	-0.06	-0.00	0.26**												
	WD	-0.13*	-0.04	-0.12*	0.10	0.09											
Open-pollinated families	GD	0.01	0.06	0.00	-0.04	0.09	-0.13*										
	DBH	-0.01	0.05	-0.01	-0.03	0.09	-0.15**	0.89**									
	D₃	-0.00	0.05	-0.00	-0.02	0.09	-0.13*	0.86**	0.99**								
	BA	0.04	0.01	0.04	-0.04	0.02	-0.03	0.05	0.03	0.01							
	CR	-0.01	-0.00	-0.03	0.02	0.09	-0.10	0.63**	0.58**	0.56**	0.06						
	SS	-0.06	-0.07*	-0.07	-0.06	-0.10	-0.01	-0.13**	-0.13**	-0.12**	0.02	-0.14**					
	1BH	0.02	-0.05	0.01	0.00	-0.01	-0.07	0.13**	0.02	0.01	0.01	0.07*	0.00				
	6BH	0.01	-0.06	0.00	0.05	-0.02	-0.06	0.24**	0.15**	0.13**	0.03	0.10**	0.08*	0.32**			
	FL	0.01	0.02	0.04	0.13*	0.07	0.07	0.04	0.01	0.02	0.03	0.04	-0.03	0.07	-0.01		
	FW	0.081*	0.13**	0.95**	0.22**	0.11*	0.06	-0.06	-0.09**	-0.09*	0.02	-0.06	0.06	-0.01	-0.05	0.16**	
	WD	-0.08*	-0.02	-0.08*	-0.00	-0.02	-0.02	-0.00	0.01	0.01	-0.05	-0.02	0.02	0.06	0.04	-0.04	0.02

Note: * significant at the 0. 05 level; ** significant at the 0. 01 level. H, tree height (m); DBH, diameter at breast height (cm); V, volume (m³); FL, fiber length (µm); FW, fiber width (µm); WD, wood density (g cm⁻³); GD, ground diameter (cm); D₃, diameter at 3 m height (cm); BA, branch angle (°); CR, crown width (m); SS, stem straightness; 1BH, height at 1st branch whorl (m); 6BH, height at 6th branch whorl (m)

Table 5 General combining ability of phenotypic traits in *P. koraiensis* clones

Clone	GD	DBH	D$_3$	BA	CR	SS	1BH	6BH	FL	FW	WD
PK003	−2.73	−3.00	−2.78	−5.61	−0.76	−0.06	0.02	−0.12	112.87	−3.50	0.01
PK004	1.26	1.45	1.58	−2.49	0.48	0.23	−0.09	0.17	230.02	5.54	−0.01
PK006	0.75	0.75	0.69	0.64	−0.14	0.23	0.08	0.08	114.96	0.56	0.00
PK007	4.55	3.88	3.73	5.64	0.37	−0.10	0.02	0.05	−16.81	−1.08	−0.01
PK014	−2.49	−2.56	−2.35	1.89	−0.41	−0.14	0.01	0.04	187.54	−3.50	0.00
PK020	1.95	0.00	−0.03	3.55	0.48	0.15	−0.02	0.06	37.21	9.88	0.00
PK023	1.35	0.64	0.47	−5.82	−0.15	0.07	−0.03	0.04	25.81	0.09	−0.01
PK024	−0.11	−0.08	−0.25	−2.69	0.21	0.23	0.10	0.25	−39.34	−3.36	−0.04
PK025	0.64	0.10	0.00	−3.11	0.90	0.28	−0.03	−0.15	138.02	−2.65	−0.02
PK036	3.04	2.14	1.87	−1.45	0.51	−0.02	−0.02	0.03	284.27	2.09	0.01
PK042	−0.35	−0.68	−0.70	3.35	0.26	−0.14	0.00	0.25	−157.86	5.76	0.06
PK049	0.85	1.31	1.43	−0.20	0.56	0.11	−0.11	−0.20	26.72	8.54	−0.03
PK051	−1.85	−1.30	−1.25	4.39	−0.59	0.03	0.03	−0.02	8.43	−1.49	0.04
PK064	−0.11	0.45	0.42	−7.90	0.35	0.28	−0.00	−0.01	147.66	−1.48	0.00
PK066	−2.00	−2.26	−2.03	4.18	−0.85	0.32	0.03	0.23	−14.04	4.50	−0.01
PK071	−3.10	−2.53	−2.63	−17.49	−1.03	0.19	−0.02	−0.24	−269.06	−5.13	−0.01
PK107	0.32	0.15	0.16	3.35	−0.34	−0.31	0.06	0.19	−65.10	−4.09	−0.01
PK118	0.07	0.81	0.41	−0.40	−0.05	−0.31	−0.05	−0.13	75.74	−0.35	−0.02
PK124	−0.05	0.83	0.81	−1.65	−0.19	−0.27	−0.03	−0.11	144.84	5.33	0.02
PK145	2.76	2.27	2.13	3.85	0.66	−0.18	0.04	0.05	−81.83	−2.54	0.00
PK150	1.70	1.79	1.80	0.43	1.00	−0.18	−0.09	0.14	−110.09	−0.84	−0.02
PK162	0.90	0.97	0.83	8.76	0.28	−0.14	0.01	0.11	119.95	5.92	0.04
PK169	−2.95	−1.94	−1.66	5.43	−0.61	−0.02	−0.08	0.16	168.75	−5.05	0.03
PK189	1.31	1.46	1.64	−2.90	0.06	0.03	−0.10	−0.11	−512.99	−2.51	0.01
PK303	0.19	−1.39	−1.19	−0.61	0.07	−0.02	0.08	−0.01	45.51	−5.79	0.01
PK305	−1.16	−0.68	−0.65	−2.28	−0.08	0.03	0.08	0.23	−348.21	−0.23	0.05
PK311	−4.67	−4.11	−3.72	3.76	−0.69	0.15	−0.06	−0.32	−128.27	1.16	0.01
PK314	0.18	0.52	0.38	−3.11	0.28	−0.02	0.08	−0.09	−377.47	−1.95	0.02
PK401	−2.69	−2.03	−1.83	−2.49	−0.87	−0.06	−0.08	−0.24	160.45	−0.64	−0.00
PK405	0.12	1.12	1.10	1.26	−0.26	−0.02	−0.04	0.18	−119.44	−2.59	0.02
PK407	0.33	0.19	0.18	−0.61	−0.23	0.03	0.12	0.03	186.96	−2.76	0.02
PK415	−0.24	−0.36	−0.08	1.89	−0.07	−0.23	−0.05	−0.30	140.05	3.53	0.03
PK423	−0.44	0.04	−0.08	0.22	0.26	0.07	−0.03	−0.01	−83.48	6.91	0.01
PK424	0.38	−0.00	0.16	6.68	−0.07	0.32	−0.00	−0.13	37.75	−3.29	−0.01
PK429	2.43	1.97	1.58	1.68	0.76	−0.43	0.06	0.16	−69.59	−4.84	0.00

Note: H, tree height (m); DBH, diameter at breast height (cm); V, volume (m^3); FL, fiber length (μm); FW, fiber width (μm); WD, wood density (g cm^{-3}); GD, ground diameter (cm); D$_3$, diameter at 3 m height (cm); BA, branch angle (°); CR, crown width (m); SS, stem straightness; 1BH, height at 1st branch whorl (m); 6BH, height at 6th branch whorl (m)

establishment and upgrading of seed orchards as sources of regeneration material.

Discussion

Genetic variation is the driving factor of tree breeding (Mwase et al. 2008). In this study, analysis of variance showed highly significant variations among clones ($P < 0.01$) and open- pollinated families ($P < 0.01$) in growth and wood properties. This indicates that there was a great variation in

the clones and families that can be used for further selection of superior breeding material.

The phenotypic and genotypic coefficients of variation (PCV and GCV, respectively) reflect the degree of variation of each trait, and a high value indicates the suitability for selection of superior clones and families (Metougui et al. 2017). In the present study, the PCVs of clones ranged from 7.3 to 37.2%, and the GCVs from 6.5 to 36.3%; volume had the largest PCV and GCV. These results are similar to those of Xu et al. (2012) for Olga Bay larch (*Larix olgensis* A. Henry), where the improvement potential was high

Table 6 Average membership function and comprehensive evaluation of different clones and open- pollinated families

Clone	Mean value of membership function	Clone	Mean value of membership function	Family	Mean value of membership function	Family	Mean value of membership function
PK124	0.821	PK107	0.481	PK003	0.763	PK042	0.382
PK051	0.745	PK023	0.463	PK066	0.663	PK405	0.371
PK042	0.741	PK429	0.460	PK124	0.648	PK169	0.344
PK03	0.706	PK311	0.443	PK401	0.612	PK023	0.326
PK415	0.704	PK424	0.439	PK415	0.532	PK407	0.326
PK036	0.6601	PK006	0.433	PK423	0.530	PK314	0.325
PK162	0.658	PK145	0.416	PK311	0.517	PK06	0.309
PK303	0.642	PK049	0.398	PK118	0.514	PK162	0.301
PK004	0.611	PK066	0.398	PK424	0.493	PK007	0.300
PK025	0.611	PK314	0.387	PK004	0.491	PK051	0.300
PK423	0.610	PK014	0.382	PK305	0.459	PK145	0.290
PK064	0.586	PK118	0.368	PK024	0.459	PK036	0.282
PK407	0.585	PK150	0.357	PK014	0.444	PK189	0.270
PK169	0.566	PK007	0.352	PK020	0.410	PK429	0.256
PK401	0.554	PK071	0.312	PK064	0.407	PK049	0.244
PK305	0.510	PK024	0.299	PK071	0.404	PK150	0.195
PK020	0.498	PK189	0.293	PK303	0.402	PK025	0.185
PK405	0.493			PK107	0.388		

when volume was used as an index. The PCV of family traits ranged from 3.2 to 12.4%, the GCVs from 0.5 to 10.2%; among them, crown width had the largest PCV, which is similar to the results of Chen (2016) for *Eucalyptus grandis* W. Hill. This indicates that there is great potential for improvement using crown width as an index to evaluate and select. The ratio of genetic and phenotypic coefficients of variation of growth and wood traits among clones was more than 90%. The same results were obtained for families for wood traits, which are higher than those reported by Ji et al. (2007) for Chinese red pine (*Pinus massoniana* Lamb.). Overall, these results show that the growth and wood property traits were more genetically controlled.

This study shows that the repeatability of clones was higher than 75.0%, higher than the results of Jiang et al. (2019) for 38-year-old *P. koraiensis*. The broad-sense heritability of open- pollinated families was > 50% except for stem straightness, which is similar to a previous study on 24-year-old *P. koraiensis* (Wang et al. 2019d). These results show that all traits of different clones and families could be stably inherited, as repeatability is an index to measure trait stability. The higher the repeatability, the less the trait is affected by the external environment (Wu and Mao 2012). Heritability is also an index that informs about the ability of a parent to pass on a trait to their offspring. Higher heritability means that the trait is more stable to be passed on (Maniee et al. 1998). In this study, for growth traits, the repeatability of clones were higher than the family broad-sense as well

as narrow-sense heritability. For wood traits, particularly for fiber length and width, repeatability of clones was slightly lower than the family broad-sense heritability. Therefore, the selection of clonal material is a valuable alternative for the establishment or upgrading of seed orchards. The broad-sense heritability of families for wood properties was higher than that for growth characteristics, indicating that wood characters are strongly genetically controlled. The narrow-sense heritability of families for growth traits is lower than 0.3, implying that non-additive effects dominate variations in growth traits.

The correlation between traits is important in the process of tree improvement, and can provide reference for comprehensive evaluation of multiple traits. In this study, the correlation coefficient between DBH and volume was greater than 0.9, indicating that they were not inherited independently. Our result is consistent with Liang et al. (2018b) on 32- year- old *P. koraiensis* clones. In open-pollinated families, most of the growth traits were highly positive correlated and stem straightness was negatively correlated with the ground diameter, diameter at breast height, the diameter at the 3-m height, and the crown width. The greater the stem straightness, the smaller all these were, which may be caused by the high stand density and the longitudinal growth of the trees. Correlations between growth traits and wood properties were not significant in both clones and open- pollinated families, indicating that these are not synchronized, which are similar

to results by Zhou et al. (1991) and Liang et al. (2016). Some results indicate that the growth rate may not significantly affect wood properties (Zhou et al. 1991). The correlation of growth traits between clones and open- pollinated families was insignificant, and the heritability of DBH was lower than repeatability. The phenotypic variation was mainly influenced by heredity and environment. In this study, growth traits of families were more influenced by environment; studies have shown that phenotypic traits are more easily affected by environmental factors (Liu et al. 2021). Wood physical properties, except for density, showed positive correlations between clones and open- pollinated families, which is similar to Wang (2020) for *L. olgensis*. The heritability of wood traits was higher than repeatability, indicating that wood properties may be strongly genetically controlled. Thus, superior breeding material can be selected by the combined analysis of clones and families for subsequent research.

General combining ability (GCA) refers to the relative ability of parents to pass elite traits on to their offspring (Zhou et al. 2004; Moterle et al. 2012). Superior parents can be selected through progeny testing, which is widely used in crop breeding. In this study, 35 open- pollinated families were analyzed for GCA, and the parents were evaluated and selected with a 10% selection rate. When considering wood production as the main breeding objective, DBH used as an evaluation index, the general combining ability of PK7, PK36, PK145 and PK429 families was higher. For landscaping, crown width and stem straightness are used as evaluation indexes; PK25 performed well. When high-quality wood is considered as a breeding objective, fiber length can be used as evaluation index; families such as PK4, PK14, PK36 and PK407 had higher GCA, indicating that the genetic improvement of fiber length was stronger in offspring. The selected superior materials can provide references for subsequent research.

Because the traits with high general combining ability (GCA) were different among families, it is difficult to combine the traits to screen. Therefore, the membership function comprehensive evaluation method was used to evaluate and select clones and open- pollinated families separately. With DBH, fiber length, and wood density as evaluation indexes, superior clones and families were selected. The superior clones were PK124, PK051, PK042, PK003, PK415, PK036, PK162, PK303, PK004, PK025, and PK423. The superior families were PK003, PK066, PK124 and PK401. PK124 and PK003. These clones and families selected in this study can be used in the establishment of plantations to produce furniture and high-quality wood, and provide superior materials for genetic improvement of *P. koraiensis*. However, since the repeatability estimates from the clonal trees were higher than h^2 estimates, selection of the best clones would be an effective alternative.

Recently, with further advancement of forest genetics, the establishment of high-quality seed orchards has great significance. In this study, the clones and families of PK124 and PK003 performed well. The superior families provide the basis for the reconstruction and upgrading of the seed orchard. Based on breeding objectives, superior clones can be propagated asexually to obtain higher ecological and economic value, and provide materials for the popularization and establishment of high-quality *P. koraiensis* plantations. These results also provide reference for backward and forward selection for *P. koraiensis* propagation.

Conclusions

The results demonstrate that the genetic impact on growth traits of grafted plants is higher than seedlings of open-pollinated families as shown by their higher repeatability. Correlation in growth traits between clones and open- pollinated families were insignificant but significant in wood traits. Considering diameter at breast height, wood density, and fiber length as indexes, a comprehensive evaluation of clones and families was carried out by the membership function method to select superior families. Consequently, two families, PK003 and PK124, performed well in both clones and open- pollinated families. Thus, these selected clones and families can provide the foundation for establishing or upgrading *P. koraiensis* seed orchards to provide material for the establishment of high-quality *P. koraiensis* plantations in the future.

References

Chen GC (2016) Selection for *Eucalyptus grandis* superior provenances and families in three districts. Master's Thesis, Northeast Forestry University; Harbin, China. (**in Chinese**)

Ding BY, Zhang SS, Zhang SY (1981) Research on the growth law of seasonal period of *Pinus koraiensis* plantations. J Northeast For Inst 4:19–32. https://doi.org/10.13759/j.cnki.dlxb.1981.04.003(inChinese)

Guerra FP, Richards JH, Fiehn O, Famula R, Stanton BJ, Shuren R, Sykes R, Davis MF, Neale DB (2016) Analysis of the genetic variation in growth, ecophysiology, and chemical and metabolomic composition of wood of *Populus trichocarpa* provenances. Tree Genet Genomes 12(1):6. https://doi.org/10.1007/s11295-015-0965-8

Ji KS, Fan ML, Xu LA (2007) Variation analysis and fine family selection on half-sib progenies from clonal seed orchard of *Pinus massoniana*. Front for China 2(3):340–346. https://doi.org/10.1007/s11461-007-0055-7

Jiang LP, Wang JY, Zhang P, Liang DY, Zhang QH, Wang BY, Pei XN, Zhao XY (2019) Variation and selection of growth and seed setting traits of 170 Korean pine clones. For Res 32(1):58–64. https://doi.org/10.13275/j.cnki.lykxyj.2019.01.008 (**in Chinese**)

Kaviriri DK, Li YX, Zhang DW, Li HT, Fan ZY, Wang JH, Wang LF, Wang Q, Wang DQ, Chiang VL, Zhao XY (2021) Clonal variations in cone, seed, and nut traits in a *Pinus koraiensis* seed orchard in Northeast China. J Forestry Res 32(1):171–179. https://doi.org/10.1007/s11676-019-01094-6

Li X, Liu XT, Wei JT, Li Y, Tigabu M, Zhao XY (2020) Genetic improvement of *Pinus koraiensis* in China: current situation and future prospects. Forests 11(2):148. https://doi.org/10.3390/f11020148

Li X, Zhao MH, Xu YJ, Li Y, Tigabu M, Zhao XY (2021) Genetic diversity and population differentiation of *Pinus koraiensis* in China. Horticulturae 7(5):104. https://doi.org/10.3390/horticulturae7050104

Liang DY (2021) Study on genetic variation of parents and progenies in *Pinus koraiensis* seed orchards. Doctoral Thesis, Northeast Forestry University; Harbin, China. (**in Chinese**)

Liang DY, Ding CJ, Zhao GH, Leng WW, Zhang M, Zhao XY (2018a) Variation and selection analysis of *Pinus koraiensis* clones in northeast China. J Forestry Res 29(3):611–622. https://doi.org/10.1007/s11676-017-0471-y

Liang DY, Jin YZ, Zhao GH, Dong YH, Leng WW, Chen CL, Wang H, Zhao XY (2016) Variance analyses of growth and wood characteristics of 50 *Pinus koraiensis* clones. J Beijing For Univ 38(6):51–59. https://doi.org/10.13332/j.1000-1522.20150465 (**(in Chinese)**)

Liang DY, Wang BY, Song SL, Wang JY, Wang LF, Wang Q, Ren XB, Zhao XY (2019) Analysis of genetic effects on a complete diallel cross test of *Pinus koraiensis*. Euphytica 215(5):92. https://doi.org/10.1007/s10681-019-2414-5

Liang DY, Zhang XX, Wang C, Wang XW, Li KL, Liu GF, Zhao XY, Qu GZ (2018b) Evaluation of *Betula platyphylla* families based on growth and wood property Traits. Forest Sci 64(6):663–670. https://doi.org/10.1093/forsci/fxy027

Liu CY, Liu GF, Fang GG, Jiang CM, Jiang J (2017) Comparison of tetraploid *Betula platyphylla* wood fiber traits and selection of superior seed trees. J Beijing For Univ 39(2):9–15. https://doi.org/10.13332/j.1000-1522.20160091 (**(in Chinese)**)

Liu XT, Li JJ, Li YX, Zhao N, Hu BC, Gao HY, Li ZM, Ge LL, Ding WY, Zhao XY (2020) Variation analysis and elite family selection of *Pinus koraiensis* half-sib families. Mol Plant Breed 18(13):4473–4482. https://doi.org/10.13271/j.mpb.018.004473 (**(in Chinese)**)

Liu XT, Wei JT, Wu PL, Wu L, Xu QS, Fang YL, Yang B, Zhao XY (2021) Phenotypic variation and diversity of natural *Pinus koraiensis* populations in Jilin Province of northern China. J Beijing For Univ 43(4):25–34. https://doi.org/10.12171/j.1000-1522.20200250 (**(in Chinese)**)

Ma JL, Zhuang LW, Chen D, Li JW (1992) Geographic distribution of *Pinus koraienis* in the world. J Northeast For Univ 5:40–48. https://doi.org/10.13759/j.cnki.dlxb.1992.05.007 (**(in Chinese)**)

Maniee M, Kabrizi D, Mohammadi R (1998) Genetic variability of some morpho-physiological traits in durum wheat (*Triticum turgidum* var. durum). Afr J Biotechnol 9(30):4687–4691. https://doi.org/10.1186/1475-2859-9-60

Metougui ML, Mokhtari M, Maughan PJ, Jellen EN, Benlhabib O (2017) Morphological variability, heritability, and correlation studies within an argan tree population (*Argania spinosa* (L.) Skeels) preserved in situ. Int J Agric For 7(2):42–51. https://doi.org/10.5923/j.ijaf.20170702.02

Mo C, Zhang HX, Zhang L, Hou D, Zhang HG (2017) Variations in nutrition compositions and morphology characteristics in different hybrid combination of Korean pine (*Pinus koraiensis*). Bull Bot Res 37(5):700–708. https://doi.org/10.7525/j.issn.1673-5102.2017.05.009 (**(in Chinese)**)

Moterle LM, Braccini ADE, Scapim CA, Pinto RJB, Goncalves LSA, Rodrigues R, Junior ATDA (2012) Combining ability of popcorn lines for seed quality and agronomic traits. Euphytica 185(3):337–347. https://doi.org/10.1007/s10681-011-0458-2

Mwase WF, Savill PS, Hemery G (2008) Genetic parameter estimates for growth and form traits in common ash (*Fraxinus excelsior* L.) in a breeding seedling orchard at Little Wittenham in England. New For 36(3):225–238. https://doi.org/10.1007/s11056-008-9095-6

Sun WS (2006) Study on management techniques of Korean pine seed orchard for high genetic quality and ample production of seeds. Doctoral Thesis, Beijing Forestry University, Beijing. (**in Chinese**)

Wang BY (2020) Evaluation selection of clones and half-sib families in the *Larix olgensis* seed orchard of Wang Qing Forestry Bureau. Master's Thesis, Northeast Forestry University,; Harbin. (**in Chinese**)

Wang BY, Zhao XY, Wang HW, Jiang GY, Shen G, Wang LK, Li YL, Lin J, Wang ZL (2019) Variance analysis of growth characteristics of 30 *Pinus koraiensis* half-sib families. J Northeast For Univ 47(4):8–11. https://doi.org/10.13759/j.cnki.dlxb.2019a.04.002 (**(in Chinese)**)

Wang FJ, Xia XY, Zhang N, Fu Q, Guo QQ (2019) Kinetic model, fatty acid composition and antioxidant activity of Korean pine seed oil extracted by decompression assisted ultrasonic. J Central South Univ For Technol 39(11):110–117. https://doi.org/10.14067/j.cnki.1673-923x.2019b.11.016 (**(in Chinese)**)

Wang H, Shi SL, Zhang XY, Zhang L (2016) Determination of general combining ability and estimation of genetic parameters for yield and quality in alfalfa. Acta Prataculturae Sin 25(3):126–134. https://doi.org/10.11686/cyxb2015170 (**(in Chinese)**)

Wang PH, Chen Z, Yu GR, Wang QF, Jia YL, Han SJ (2019) Regulation effects of temperate broadleaved Korean pine forest on temperature and humidity in Changbai Mountains, China. Chin J Appl Ecol 30(5):1521–1528. https://doi.org/10.13287/j.1001-9332.2019c05.023 (**(in Chinese)**)

Wang WH, Chen YT, Dang QS, Hou D, Li ZX, Zhang HG, Qang JN, Zhao CH (2019a) Analysis of characters and nutritional components of *Pinus koraiensis* seeds on clones and superior trees. For Eng 35(2): 11–20+26. https://doi.org/10.16270/j.cnki.slgc.2019d.02.002 (**in Chinese**)

Wu Y, Mao CL (2012) Simple introduction to heritability, repeatability and genetic gain in percent in tree breeding. Trop Agric Sci

Technol 35(1):47–50. https://doi.org/10.16005/j.cnki.tast.2012. 01.017 ((**in Chinese**))

Xu JR (2006) Tree quantitative genetics. Higher Education, Beijing, p 38–51. (**in Chinese**)

Xu YL, Zhang HG, Yao Y, Zhang L, Liu L, Wang YH (2012) Genetic variation in dominant and inferior tree populations and family selection of *Larix olgensis* Henry. Bull Bot Res 32(3):284–289. https://doi.org/10.7525/j.issn.1673-5102.2012.03.007 ((**in Chinese**))

Yin SP, Xiao ZH, Zhao GH, Zhao X, Sun XY, Zhang Y, Wang FW, Li SC, Zhao XY, Qu GZ (2017) Variation analyses of growth and wood properties of *Larix olgensis* clones in China. J For Res 28(4):687–697. https://doi.org/10.1007/s11676-016-0359-2

Zhang H, Zhang YHY, Zhang DW, Dong LH, Liu KJ, Wang Y, Yang CP, Chiang VL, Tigabu M, Zhao XY (2020) Progeny performance and selection of superior trees within families in *Larix olgensis*. Euphytica 216(4):60. https://doi.org/10.1007/s10681-020-02596-9

Zhang H, Zhou XY, Gu W, Wang LD, Li W, Gao YK, Wu LG, Guo XW, Tigabu M, Xia DA, Chiang VL, Yang CP, Zhao XY (2021) Genetic stability of *Larix olgensis* provenances planted in different sites in northeast China. For Ecol Manage 485(7):118988. https://doi.org/10.1016/j.foreco.2021.118988

Zhang M, Liang SH, Yang M, Wang MY (2017) Physicochemical properties and fatty acid compositions of pine nut oils with different varieties. J Henan Univ Technol 38(6):26–31. https://doi.org/10.16433/j.cnki.issn1673-2383.2017.06.005 ((**in Chinese**))

Zhang QH, Wang HW, Jiang GY, Shen G, Wang LK, Li YL, Wang L, Wang LX, Li YJ, L R, Zhao XY (2019) Variation analysis and selection of *Pinus koraiensis* half-sib families. Bull Bot Res 9(4):557−567. https://doi.org/10.7525/j.issn.1673-5102.2019.04.010 (**in Chinese**)

Zhang SK, Zhan W, Zhang H, Song SL, Qu XB, Wang JY, Tigabu M, Li X, Zhang QH, Zhao MH, Liu HZ, Zhao XY (2022) Genetic Improvement in *Juglans mandshurica* and its uses in China: Current Status and Future Prospects. Phyton B 91(3):489–505. https://doi.org/10.32604/PHYTON.2022.018321

Zhang Z, Zhang HG, Zhou Y, Liu L, Yu HY, Wang X, Feng WJ (2015) Variation of seed characters in Korean pine (*Pinus koraiensis*) multi-clonal populations. J Beijing For Univ 37(2):67–78. https://doi.org/10.13332/j.cnki.jbfu.2015.02.020 ((**in Chinese**))

Zhao GH, Leng WW, Zhang T, Xu LS, Jin X, Feng L, Li HB, Zhao XY (2018) Variance analysis of growth traits of 51 *Pinus koraiensis* seedling families. Bull Bot Res 38(4):590–596. https://doi.org/10.7525/j.issn.1673-5102.2018.04.014(inChinese)

Zhao XY (2010) Study on hybridization and evaluation of multiple characters of hybrid clones in Chinese white poplar. Doctoral Thesis, Beijing Forestry University, Beijing, China. (**in Chinese**)

Zhao XY, Li Y, Zhao L, Wu PL, Zhang ZY (2013) Analysis and evaluation of growth and adaptive performance of white poplar hybrid clones in different sites. J Beijing For Univ 35(6):7–14. https://doi.org/10.13332/j.1000-1522.2013.06.010 ((**in Chinese**))

Zhao XY, Li Y, Zheng M, Bian XY, Liu MR, Sun YS, Jiang J, Wang FW, Li SC, Cui YH, Liu GF (2015) Comparative analysis of growth and photosynthetic characteristics of (*Populus simonii* × *P. nigra*) × (*P. nigra* × *P. simonii*) hybrid clones of different ploidides. PLoS ONE 10(4):e0019259. https://doi.org/10.1371/journal.pone.0119259

Zhou XY, Gao HY, Li ZM, Zhao YK, Ge LL, Hou WQ, Ding WY, Zhao XY (2020) Evaluating parents of *Pinus koraiensis* seed orchards with growth and fruiting. Bulletin of Botanical Research 40(3):376–385. https://doi.org/10.7525/j.issn.1673-5102.2020.03.008(inChinese)

Zhou ZC, Jin GQ, Qin GF, Zhang JM, Luo XH (2004) Analysis on combining ability and heterosis of main economic traits of *Pinus massoniana* for pulp production. Sci Silvae Sin 4:52–57. https://doi.org/10.11707/j.1001-7488.20040409(inChinese)

Zhou ZC, Wang MC, Lv Q (1991) The growth and wood properties of clones in a seed orchard of Masson pine. J Zhejiang For Sci Technol 5:23–26 ((**in Chinese**))