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Analysis of genetic effects on a complete diallel cross test of *Pinus koraiensis*

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Abstract Thirty-four full-sib *Pinus koraiensis* families were used to evaluate and identify elite *P. koraiensis* material. Tree height (*H*) and diameter at breast height (dbh) were assessed. The results from variance analyses showed that familial variance sources for different traits in different growth years were extremely significantly different. The average phenotypic variation coefficients of *H*, dhb and volume (*V*) among families in different growth years ranged from 7.57 to 15.70, from 10.37 to 12.89 and from 24.44 to 28.13%, respectively. The family heritabilities of all traits ranged from 0.910 to 0.990, which are high values. A significant and positive correlation was observed among all traits, with values ranging from 0.43 to 0.99. According to the analyses of general and special combining ability, female parents F4 and F2 and male parents M7 and M13 had high levels of general combining ability for all three traits evaluated. Families PK05 (F9 × M14) and PK06 (F2 × M14) showed the highest and the lowest specific combining ability values in all traits evaluated. Using the comprehensive multiple-traits method to evaluate the families by traits in the 18th growth year at the rate of $< 10\%$, we selected families PK40, PK05 and PK22 as elite families; the genetic gains for these families in *H*, dbh and *V* were 14.43, 11.29 and 24.72%, respectively. This study provides materials and basic theoretical knowledge that can be used to improve seed orchards and develop special hybrid seed orchards.

Keywords *Pinus koraiensis* · Full-sib family · Variation · Heritability · Genetic gain

Introduction

Pinus koraiensis is one of the most important native and economically valuable tree species in northeastern China, as well as in the far eastern region of Russia and on the Korean peninsula (Barnes et al. 1992). This tree species is fond of light although it grows normally under poor light conditions (Yang 2013). For centuries, *P. koraiensis* has been extensively used as a major source of timber and for natural remedies and edible pine nuts because of the excellent properties of

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its wood and the nutritional value of the pine nuts (Imbs et al. 1998; Nergiz and Donmez 2004). The economic importance of *P. koraiensis* has resulted in it being the focus of many studies, with various researchers analyzing its growth traits (Han et al. 2015; Wang et al. 2002), leaf traits (Liu et al. 2015b), flowering characteristics (Wang et al. 2007), wood properties (Liang et al. 2016), photosynthetic index (Sun et al. 2016), sap flow (Moon et al. 2016), nutritional components of the seed (Azad et al. 2009) and net primary productivity (Fang et al. 2016).

P. koraiensis has proven to be difficult to propagate by cuttage, tissue culture and other asexual propagation methods (Zhao et al. 2018), resulting in seed orchards being the principal method used to improve *P. koraiensis*. Several seed orchards were established in northeastern China in the 1960s, and a large number of seeds have been produced at each seed orchard since the beginning of the 21st century (Xia et al. 2016). Although several variance analysis studies have been conducted on the selection of *P. koraiensis* families (Zhang et al. 2003; Zhao et al. 2018), the primary focus of these studies was half-sib families; the effects of the male parent were seldom investigated and analyzed. In this study, 34 *P. koraiensis* full-sib families were used as study material, and the traits tree height and diameter at breast height in different growth years were investigated and evaluated. This primary aim of this study was to provide materials and basic theoretical knowledge that can be used to improve *P. koraiensis* seed orchards and establish second-generation seed orchards.

Materials and methods

Experimental sites

The experiments were performed at the Naozhi Forestry Seed Orchard (41°05′N, 126°06′E) located in the western hillsides of Changbai Mountain, Linjiang City, Jilin Province, northeastern China. The temperate monsoon climate of the region features an average frost-free season and a mean annual precipitation, mean annual temperature and mean elevation of 128 days, 744 mm, 8.2 °C and 510 m a.s.l., respectively.

Materials and experimental design

The experimental material consisted of 34 *P. koraiensis* full-sib families (Table 1), all of which were selected from the local provenance. Control pollination was conducted in the spring of 1998. Seeds were collected in the autumn of 1999 and sown in 2000. The experimental design consisted of three blocks planted in 2004 with 4-year-old seedlings of each family using a completely randomized block design in row plots. Each row contained 12 trees, inter-tree distance was 2 m, and inter-row spacing was 3 m.

Method

Tree height (H) and diameter at breast height (DBH) of all living and unbroken trees were measured in the autumn of 2009 (10th growth year), 2011 (12th growth year), 2013 (14th growth year), 2015 (16th growth year) and 2017 (18th growth year). The volume (V) of a single tree was calculated using the method of Zhang et al. (2016) as follows:

$$V = (H + 3)_{g1.3} f \tag{1}$$

where f is the experimental form factor of 0.33 and $g1.3$ is a cross sectional area of stem at 1.3 m height.

Statistical analysis

Statistical analysis was carried out using SPSS version 19.0 software (IBM Corp., Armonk, NY, USA). The significance of fixed effects was tested by analysis of variance (ANOVA) F tests. Variation among families in the same year was analyzed by ANOVA according to Hansen and Roulund (1997) using Eq. (2):

$$y_{ij} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ij} \tag{2}$$

where y_{ij} is the performance of an individual of family i within block j, μ is the overall mean, α_i is the family effect (i = 1,…, 34), β_j is the block effect (i = 1,…, 3), $\alpha\beta_{ij}$ is the random effect of family i within block j and ε_{ij} is the random error.

Genotypic (σ_{γ}^{2}) and phenotypic (σ_{p}^{2}) variances were calculated by ANOVA using the mean square and the following formulas (Metougul et al. 2017):

Table 1 Name and parents of the 34 *Pinus koraiensis* families used in the study

Female parent	Male parent						
	M7	M9	M10	M11	M12	M13	M14
F2	PK14	PK29	PK40	PK19	–	PK34	PK06
F3	PK22	–	PK33	PK09	PK17	PK07	–
F4	PK25	PK37	–	PK49	–	–	–
F6	PK23	–	PK50	–	–	PK24	PK20
F7	–	PK02	PK31	PK16	–	PK30	PK42
F8	–	PK21	PK12	PK26	PK08	PK39	PK46
F9	–	–	PK44	PK15	PK47	PK01	PK05

$$\sigma_{\gamma}^{2} = \frac{A - B}{r}, \tag{3}$$

$$\sigma_{p}^{2} = \sigma_{\gamma}^{2} + \sigma_{\varepsilon}^{2}, \tag{4}$$

where A is the mean square between families ($A = \sigma_{\varepsilon}^{2} + r\sigma_{\gamma}^{2}$) and B is the mean square within families ($B = \sigma_{\varepsilon}^{2}$); r is the number of replications.

The general combining ability (GCA) and specific combining ability (SCA) were calculated using the following formulas according to Chen and Shen (2005):

$$\mathrm{GCA}_{i} = \bar{X}_{i.} - \bar{X}. \tag{5}$$

$$\mathrm{SCA}_{ij} = X_{ij} - \bar{X}.. - \mathrm{GCA}_{i} - \mathrm{GCA}_{j} \tag{6}$$

The phenotypic coefficient of variation (PCV, %) was estimated using the following formula (Jonah et al. 2011):

$$\mathrm{PCV} = \frac{\sqrt{{}^{2}_{p}}}{\bar{X}} \times 100 \tag{7}$$

where $\bar{X}$ is the mean value of a growth characteristic among all families.

The estimation of heritability (h^2) of a character for the families was calculated using Eq. (8) (Hansen and Roulund 1997):

$$h^{2} = \frac{\sigma_{A}^{2}}{\sigma_{A}^{2} + \sigma_{b}^{2} + \sigma_{e}^{2}} \tag{8}$$

where σ_{A}^{2} is the additive genetic variance component between families, σ_{b}^{2} is the block variance and σ_{e}^{2} is the error variance component.

The phenotypic correlation coefficient (r_A) was calculated using Eq. (9) (Fernando et al. 2016):

$$r_{A}(xy) = \frac{\sigma_{a(xy)}}{\sqrt{\sigma_{a(x)}^{2} \cdot \sigma_{a(y)}^{2}}} \tag{9}$$

where $\sigma_{a(xy)}^{2}$ denotes the phenotypic covariance between traits of x and y, and $\sigma_{a(xy)}^{2}$ and $\sigma_{a(y)}^{2}$ denote the phenotypic variance of trait x and y, respectively.

The comprehensive evaluation was conducted with the method of Q_i value evaluation where Q_i was calculated using Eq. (10) (Liu et al. 2015a, b):

$$Q_{i} = \sqrt{\sum_{j=1}^{n} a_{i}} \tag{10}$$

where $a_i = X_{ij}/X_{j\max}$, Q_i is the comprehensive valuation value of family i, X_{ij} is the mean of a character, $X_{j\max}$ is maximum value of a character, and n is the number of the evaluation index.

The estimated genetic gain was calculated using Eq. (11) (Silva et al. 2008):

$$\Delta G = (h^{2}W/\bar{X}) \times 100\% \tag{11}$$

where ΔG is the genetic gain of a trait for the families, h^2 is the heritability of the trait, W is the difference in the average values of the traits between the selected families and all families (i.e. the selection difference) and $\bar{X}$ is the mean value of the growth characteristic among all families.

Results

Analysis of variance

The ANOVA results are shown in Table 2. These results reveal that there were extremely significant

Table 2 Analysis of variance of the traits height, diameter at breast height and volume of *Pinus koraiensis* in different growth years

Age (growth year)	Traits	Variance source	*df*	SS	MS	*F*-statistic	Significance
10th	*H*	Family	33	206.07	6.24	101.33	0.000
		Block	2	2.14	1.07	17.54	0.000
		Family × block	66	4.49	0.07	1.10	0.296
	DBH	Family	33	40.37	1.22	45.18	0.000
		Block	2	1.40	0.70	25.85	0.000
		Family × block	66	3.25	0.05	1.82	0.001
	V	Family	33	8.72 × E−05	2.64 × E−06	23.67	0.000
		Block	2	2.62 × E−06	1.31 × E−06	11.74	0.000
		Family × block	66	9.57 × E−06	1.40 × E−07	1.30	0.086
12th	*H*	Family	33	264.17	8.01	80.50	0.000
		Block	2	0.17	0.08	0.85	0.429
		Family × block	66	8.65	0.13	1.32	0.075
	DBH	Family	33	52.34	1.59	39.95	0.000
		Block	2	0.78	0.39	9.82	0.000
		Family × block	66	5.02	0.08	1.92	0.000
	V	Family	33	2.37 × E−04	7.18 × E−06	18.42	0.000
		Block	2	1.84 × E−06	9.20 × E−07	2.35	0.098
		Family × block	66	3.33 × E−05	5.10 × E−07	1.30	0.088
14th	*H*	Family	33	309.43	9.38	57.36	0.000
		Block	2	0.81	0.41	2.48	0.086
		Family × block	66	24.18	0.37	2.24	0.000
	DBH	Family	33	61.44	1.86	32.47	0.000
		Block	2	0.12	0.06	1.05	0.350
		Family × block	66	7.92	0.12	2.09	0.000
	V	Family	33	4.90 × E−04	1.48 × E−05	12.66	0.000
		Block	2	1.04 × E−06	5.20 × E−07	0.44	0.642
		Family × block	66	1.01 × E−04	1.53 × E−06	1.31	0.079
16th	*H*	Family	33	395.95	12.00	62.38	0.000
		Block	2	0.10	0.05	0.27	0.766
		Family × block	66	21.22	0.32	1.67	0.004
	DBH	Family	33	77.54	2.35	31.70	0.000
		Block	2	0.45	0.22	3.03	0.051
		Family × block	66	13.56	0.21	2.77	0.000
	V	Family	33	1.05 × E−03	3.20 × E−05	11.32	0.000
		Block	2	8.85 × E−05	4.42 × E−06	1.57	0.211
		Family × block	66	2.63 × E−04	3.98 × E−06	1.41	0.036
18th	*H*	Family	33	425.76	12.90	56.10	0.000
		Block	2	0.27	0.14	0.59	0.553
		Family × block	66	75.14	1.14	4.95	0.000
	DBH	Family	33	83.74	2.54	33.42	0.000
		Block	2	0.09	0.04	0.59	0.554
		Family × block	66	9.24	0.14	1.84	0.001
	V	Family	33	1.47 × E−03	4.47 × E−05	11.08	0.000
		Block	2	4.50 × E−06	2.25 × E−06	0.56	0.573
		Family × block	66	3.40 × E−04	5.15 × E−06	1.28	0.101

Significance values > 0.05 showed no significant difference, $0.05 >$ Significance values > 0.01 showed significant difference and significance values < 0.01 showed extremely significant difference among variance source, respectively

df, Degree of freedom; SS, sum of squares; MS, mean squares

[a] *H*, Height of tree (m); DBH, diameter at breast height (cm); *V*, volume of tree (m^3)

Table 3 Genetic and variation parameters of the traits height, diameter at breast height and volume in different years

Age (growth year)	Traits	Average	Standard deviation	Minimum	Maximum	PCV	h^2
10th	*H*	5.31	0.83	3.47	6.90	15.70	0.990
	DBH	2.87	0.37	1.84	3.57	12.89	0.978
	V	0.0018	0.0005	0.0006	0.0029	27.78	0.958
12th	*H*	6.63	0.94	4.53	8.43	7.57	0.988
	DBH	3.51	0.42	2.34	4.28	11.97	0.975
	V	0.0032	0.0009	0.0012	0.0049	28.13	0.946
14th	*H*	7.84	1.02	5.57	9.84	13.01	0.983
	DBH	4.09	0.45	2.82	4.90	11.00	0.969
	V	0.0048	0.0013	0.0019	0.0072	27.08	0.921
16th	*H*	9.18	1.15	6.88	11.59	12.52	0.984
	DBH	4.78	0.51	3.28	5.65	10.67	0.968
	V	0.0074	0.0019	0.0031	0.0106	25.68	0.912
18th	*H*	9.92	1.20	7.33	12.30	12.10	0.982
	DBH	5.11	0.53	3.60	6.03	10.37	0.970
	V	0.0090	0.0022	0.0037	0.0129	24.44	0.910

Units for traits are as given in Table 1

PCV, Phenotypic coefficient of variation (%) h^2, estimation of heritability

differences among families in different growth years. There was also a significant difference among blocks in different traits at the 10th growth year, but with the exception of DBH at the 12th growth year, there are no significant differences among blocks for any traits. There were no significant differences for most family × block effects.

Genetic and variation parameters

The genetic and variation parameters of *H*, DBH and *V* among the different families are shown in Table 3. The average *H*, DBH and *V* ranged from 5.31 to 9.92 m, from 2.87 to 5.11 cm and from 0.0018 to 0.0090 m^3 (from 10th to 18th year), respectively. The PCVs of *H*, DBH and *V* ranged from 7.57 to 15.70%, 10.37 to 12.89% and 24.44 to 27.78%, respectively, and the values showed decreased trends with increasing age. The heritability values of all the traits in different growth years were > 0.91.

Correlation analysis

Correlations among *H*, DBH and *V* in different growth years are shown in Table 4. In the same growth year, the correlation coefficients between *H* and DBH ranged from 0.46 (16th growth year) to 0.51 (12th growth year), those between *H* and *V* ranged from 0.65 (10th growth year) to 0.73 (18th growth year) and those between DBH and *V* ranged from 0.85 (10th growth year) to 0.93 (18th growth year), respectively. In all, there were extremely significant positive correlations among all growth traits (0.43–0.94) in the same or different growth year.

General combining ability

The results of the analysis of GCA of the different parents are shown in Table 5. Female parents F4 and F2 had a high level of GCA for all three traits evaluated, while female parent F9 had the lowest level of GCA for all three traits evaluated. Interestingly, female parent F3 had a negative GCA value for *H* ($-$ 0.069) but the highest value for DBH (0.229) and a relatively higher value for *V* ($7.241 \times$ E$-$04). For the male parents, M7 and M13 had a higher level of GCA in all three traits evaluated, while male parent M12 had the lowest level of GCA in all three traits. Also, interestingly, male parent M11 had the highest GCA value for *H*, but negative GCA values for DBH ($-$ 0.107) and *V* ($-$ $5.882 \times$ E$-$06).

Table 4 Correlation coefficients for the traits height, diameter at breast height and volume in different years

Age (growth year)	Traits	10th growth year			12th growth year			14th growth year			16th growth year			18th growth year	
		H	DBH	*V*	*H*	DBH	*V*	*H*	DBH	*V*	*H*	DBH	*V*	*H*	DBH
10th	DBH	0.48**													
	V	0.65**	0.85**												
12th	H		0.50**	0.71**											
	DBH	0.50**		0.94**	0.51**										
	V	0.71**	0.93**		0.72**	0.87**									
14th	H		0.50**	0.71**		0.52**	0.73**								
	DBH	0.48**		0.94**	0.50**		0.93**	0.50**							
	V	0.70**	0.93**		0.71**	0.94**		0.72**	0.86**						
16th	H		0.50**	0.72**		0.51**	0.73**		0.50**	0.71**					
	DBH	0.45**		0.91**	0.47**		0.91**	0.47**		0.91**	0.47**				
	V	0.68**	0.93**		0.69**	0.93**		0.70**	0.93**		0.71**	0.91**			
18th	H		0.52**	0.73**		0.53**	0.74**		0.51**	0.72**		0.48**	0.71**		
	DBH	0.43**		0.92**	0.45**		0.91**	0.45**		0.92**	0.45**		0.92**	0.46**	
	V	0.67**	0.94**		0.68**	0.94**		0.69**	0.94**		0.69**	0.92**		0.73**	0.93**

**Correlation is significant at the 0.01 level (2-tailed), *Correlation is significant at the 0.05 level (2-tailed)

Table 5 Analysis of the height, diameter at breast height and volume general combining ability of different parents

Traits	Female parent	GCA	Male parent	GCA
H	F 4	0.920	M 11	0.697
	F 2	0.570	M 13	0.463
	F 8	0.342	M 7	0.006
	F 3	− 0.069	M 9	− 0.039
	F 6	− 0.339	M 10	− 0.190
	F 7	− 0.427	M 14	− 0.507
	F 9	− 0.879	M 12	− 1.050
DBH	F 3	0.229	M 7	0.233
	F 2	0.186	M 13	0.135
	F 4	0.106	M 14	0.057
	F 8	0.095	M 10	0.021
	F 6	− 0.095	M 9	− 0.040
	F 7	− 0.147	M 11	− 0.107
	F 9	− 0.407	M 12	− 0.450
V	F 2	8.941 × E−04	M 7	6.941 × E−04
	F 4	8.441 × E−04	M 13	6.608 × E−04
	F 3	7.241 × E−04	M 14	1.041 × E−04
	F 8	4.108 × E−04	M 11	− 5.882 × E−06
	F 7	− 4.759 × E−04	M 9	− 5.588 × E−05
	F 6	− 7.559 × E−04	M 10	− 1.725 × E−04
	F 9	− 1.716 × E−03	M 12	− 1.989 × E−03

GCA, General combining ability

Specific combining ability

The results of the SCA of the different parents are shown in Table 6. For *H*, family PK05 (F9 × M14) had the highest SCA value (2.999), followed by PK40 (F2 × M10, 1.783) and PK34 (F2 × M13, 1.350). PK25 (F4 × M7), PK33 (F3 × M10), PK01 (F9 × M13) and PK06 (F2 × M14)) had lower SCA values − 1.002, − 1.178, − 1.381 and − 2.592, respectively. For DBH, PK05 also had the highest SCA value (0.963), followed by PK37 (F4 × M9, 0.696) and PK31 (F7 × M10, 0.519). PK33 (F3 × M10), PK49 (F4 × M11), PK34 (F2 × M13) and PK02 (F7 × M9) had lower SCA values, o—− 0.587, − 0.596, − 0.628 and − 1.320, respectively. For *V*, PK05 had the highest SCA value (5.06E−03), followed by PK37 (2.66E−03) and PK22 (F3 × M7, 2.53E−03). PK14 (F2 × M7), PK06 (F2 × M14), PK33 (F3 × M10) and PK02 (F7 × M9) had lower SCA values, —− 2.34E−03, − 2.35E−03, − 2.71E−03 and − 4.32E−03, respectively.

Multitrait comprehensive evaluation and genetic gain

Using the of multiple-traits comprehensive method, we evaluated all families for *H*, DBH and *V* in the 18th growth year, at the selected rate of 10%, and selected families PK40, PK05 and PK22 as elite families (Table 7). PK40, PK05 and PK22 had an average *H* of 11.46 m, an average DBH of 5.82 cm and an average *V* of 0.277 m^3; these values were higher than the total average by 15.46, 12.34 and 24.96%, respectively, and the genetic gain was 14.43, 11.29 and 24.72%, respectively.

Discussion

Analysis of variance

Understanding genetic variation within populations, families or clones is very important in terms of gaining

Table 6 Analysis of the height, diameter at breast height and volume specific combining ability of different parents

Family	Combination	SCA		
		H	DBH	*V*
PK01	F9 × M13	− 1.381	0.055	− 1.00E−03
PK02	F7 × M9	− 0.151	− 1.320	− 4.32E−03
PK05	F9 × M14	2.999	0.963	5.06E−03
PK06	F2 × M14	− 2.592	− 0.210	− 2.35E−03
PK07	F3 × M13	0.409	0.289	1.46E−03
PK08	F8 × M12	0.332	0.179	5.23E−04
PK09	F3 × M11	− 0.905	− 0.419	− 2.07E−03
PK12	F8 × M10	0.212	− 0.143	− 2.94E−04
PK14	F2 × M7	− 0.982	− 0.486	− 2.34E−03
PK15	F9 × M11	− 0.365	− 0.203	− 1.03E−03
PK16	F7 × M11	− 0.557	0.397	5.26E−04
PK17	F3 × M12	0.932	0.424	1.61E−03
PK19	F2 × M11	0.177	0.474	2.06E−03
PK20	F6 × M14	− 0.221	− 0.149	− 9.04E−04
PK21	F8 × M9	− 0.459	0.048	− 4.11E−04
PK22	F3 × M7	0.816	0.461	2.53E−03
PK23	F6 × M7	0.087	− 0.215	− 5.94E−04
PK24	F6 × M13	− 0.271	− 0.167	− 6.61E−04
PK25	F4 × M7	− 1.002	− 0.186	− 1.29E−03
PK26	F8 × M11	0.965	0.285	1.84E−03
PK29	F2 × M9	− 0.907	0.336	4.06E−04
PK30	F7 × M13	0.667	0.225	8.59E−04
PK31	F7 × M10	− 0.640	0.519	7.93E−04
PK33	F3 × M10	− 1.178	− 0.587	− 2.71E−03
PK34	F2 × M13	1.350	− 0.628	− 1.31E−03
PK37	F4 × M9	0.113	0.696	2.66E−03
PK39	F8 × M13	0.028	0.364	1.57E−03
PK40	F2 × M10	1.783	0.215	2.32E−03
PK42	F7 × M14	0.257	0.113	1.62E−03
PK44	F9 × M10	− 0.008	0.049	− 6.75E−05
PK46	F8 × M14	− 0.452	− 0.349	− 1.77E−03
PK47	F9 × M12	− 0.658	− 0.520	− 1.55E−03
PK49	F4 × M11	0.227	− 0.596	− 1.99E−03
PK50	F6 × M10	0.633	0.086	8.73E−04

F, Female parent; M, male parent; SCA, specific combining ability

a better understanding of the structure of experimental materials (Safavi et al. 2010). In this context, ANOVA is one of the most important methods used to estimate the extent of variability in breeding research (Zhao et al. 2015). In this study, we found significant differences among families in all three of the investigated traits in different growth years, which indicates that it is possible and feasible to identify excellent families (Liang et al. 2018). The source of variation in the blocks effect showed no significance after the 14th growth year in different traits, suggesting that the edaphic conditions of different blocks were similar and that the variation was mainly caused by genotype.

Genetic variance parameters

The coefficients of variation and heritability are the most important genetic and variation parameters in tree genetics and breeding (He et al. 2011). PCV, which denotes the discrete degree of groups, is an important index of plant selection within breeding programs (Ren et al. 2010). In the present study, PCVs of the different traits investigated ranged from 7.57 to 28.13%, indicating a wide range of phenotypic performance in different growth years. The PCVs of *H* (range 7.57–15.70%) were similar to those of DBH (range 10.37–12.89%); however, they were lower than the PCVs of *V* (range 24.44–28.13%) in different growth years, which indicates that evaluating and selecting families using *V* at young ages is a reasonable strategy. To the contrary, from the 10th growth year to the 18th growth year, the PCVs of *H*, DBH and *V* showed a downward trend, similar to the trends observed in previous studies on *P. koraiensis* (Zhang et al. 2016) and Masson Pine (Zhang et al. 2013) but different from the trend observed by Zhao et al. (2013) in poplar. It is possible that different tree species, environments and ages have different growth trends and patterns, leading to different variation trends in different growth years (Xia et al. 2016). The heritability can reflect the ability of a trait to be passed on to offspring (Jiang et al. 2018). Traits are more stable when the heritability is higher and, in addition, the environmental effect will be smaller (Seyed 2011). In this study, the heritabilities of all traits ranged from 0.910 to 0.990, which indicates high heritability, in agreement with the results from other studies on *P. koraiensis* (Wang et al. 2007) and *Larix olgensis* (Yin et al. 2016). High PCV and heritability values indicate that the traits would be less influenced by environmental effects. The results were beneficial for the selection and evaluation of elite families (Maniee et al. 1998).

Table 7 Multi-character comprehensive evaluation of *P. koraiensis* families

Family	Q_i	Family	Q_i	Family	Q_i
PK40	1.71	PK17	1.58	PK08	1.52
PK05	1.70	PK49	1.58	PK20	1.50
PK22	1.69	PK21	1.58	PK44	1.49
PK37	1.68	PK50	1.58	PK42	1.49
PK26	1.68	PK25	1.57	PK06	1.48
PK19	1.68	PK16	1.56	PK15	1.47
PK07	1.67	PK24	1.55	PK33	1.47
PK39	1.66	PK23	1.54	PK01	1.46
PK34	1.65	PK31	1.54	PK02	1.38
PK30	1.64	PK14	1.54	PK47	1.31
PK29	1.59	PK09	1.53		
PK12	1.59	PK46	1.52		

See section Statistical analysis for explanation of Q_i

Correlation analysis

Phenotypic correlation reflects the relationship among different traits, and the age–age correlation of growth traits is an important parameter for early selection (Goncalves et al. 2005). In this study, an extremely significant, positive correlation ($P < 0.01$) was found among *H*, DBH and *V* in different growth years, similar to the correlation observed in previous studies on *Pinus radiata* (Matheson et al. 1994) and poplar (Zhao et al. 2013). This correlation indicates that a strong correlation also existed between *H*, DBH and *V* with relatively little influence from environmental factors. In addition, the phenotypic correlation coefficients among *H*, DBH or *V* in different growth years ranged from 0.43 to 0.93; these are similar to but higher than the phenotypic correlation coefficients reported for *Castanopsis fissa* (Zhong et al. 2015), Masson pine (Zeng et al. 2013) and larch (Sun et al. 2016). Our results may suggest that the slow growth rate of *P. koraiensis* and the higher age–age correlation coefficient could provide an effect indicative of anticipated mature growth, which would provide a benefit in terms of early selection of slow-growing tree species and could also shorten the breeding cycle (Jesus and Adams 1992; Kumar and Lee 2002; Greaves et al. 1997; Hannrup and Ekberg 1998; Osorio et al. 2003).

Combining ability analysis

For trees, especially coniferous tree species, it is difficult for breeders to improve even a single trait by crossing due to long life cycles. Information on GCA and SCA is critically important when the aim is to estimate crossbreeding effects in tree breeding (Owusu et al. 2017). The selection of appropriate parents can generate elite families which can enhance breeding effects and shorten the breeding period (Sluder 1996). GCA is determined by the additive gene action of the parental genotype that is passed to the offspring (Qi 2010). In this study, female parents F4 and F2 showed higher GCA values in traits *H*, DBH and *V*, which indicated that with these two clones as female parents, the offspring will grow well in terms of these traits. The male parents M7 and M13 showed higher GCA values in different growth traits, which indicates that these two clones should be considered as male parents in the next step of the breeding program (Youngkoo and Scott 2011). The SCA effect primarily reflects differences in the gene frequencies between the parents (Viana et al. 2013). It is the deviation of the expected result based on the average performance of the hybrid combination and its parents, and it is affected by external environmental conditions. In our study, although SCA could not be stably inherited between the parents and offspring, the results can serve as a guide to the utilization of heterosis and the breeding of hybrids in breeding programs (Rumpunen and Kviklys 2013). In this study, PK05 (F 9 × M14) had the highest SCA values of all the investigated traits, which indicates that strong heterosis appeared with a cross of these two parents. We therefore suggest that F9 and M14 could provide excellent materials for establishing a special hybrid seed orchard (Chen and Shen 2005)

Multitrait comprehensive evaluation and genetic gain

There are many different methods for selecting elite materials depending on different breeding targets (Zhao et al. 2016). *P. koraiensis* is one of the most important commercial tree species throughout Asia. Growth traits are the most important characteristic for evaluating *Pinus* families. Comprehensive evaluation methods have been developed to select for multiple characteristics in order to cultivate plant types with a strong integrated ability (Yin et al. 2017). However, in a study of *Populus deltoids*, Guan et al. (2005) found that too many characteristics lead to low genetic gains in individual characteristics and to unclear selection targets. In the present study, we investigated three traits, namely height, diameter at breast height and volume, to evaluate in each family. At the selected rate of 10%, families PK40, PK05 and PK22 were selected as elite families, whose genetic gains of *H*, DBH and *V* were 14.43, 11.29 and 24.72%, respectively. These values are lower than those reported in other studies on *P. koraiensis* (Wang et al. 2007). One explanation for this difference may be the experimental materials thermselves, which were obtained by controlled pollination, and all the parents were superior plant materials that were selected by natural distribution (Harry and Leopoldo 2011). The elite families that were selected could be used in applied studies to improve variety, and the elite parents could be used to establish an improved seed orchard (Wang et al. 2000).

Conclusion

Due to long breeding and rotation cycles, the selection of superior families in *P. koraiensis* is very important for efforts designed to enhance genetic gain and improve breeding efficiency. In this study, 34 *P. koraiensis* full-sib families were used as breeding material, and the *H*, DBH and *V* of different single trees were investigated. Three elite families and four elite parents were selected based on analysis of the combining ability and comprehensive evaluation according to three growth traits. The elite parents could be used to establish improved seed orchards and special hybrid seed orchards. The elite families could be used in applied studies to improve variety. This study provides the materials and basic theoretical knowledge that can be used to improve seed orchards and develop special hybrid seed orchards.

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