

Morphological growth performance and genetic parameters on Korean pine in North-eastern China

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Abstract

Korean pine (*Pinus koraiensis*) is an economically valuable species owing to its excellent timber quality and nuts useful for various purposes. But few studies have been made on growth performance, and aspects combining the genetic gain and classification method on phenotypic similarity in the selection process of superior families. Thus, the present study aimed at analyzing the genetic variation and highlight suitable morphological traits for family selection; establishing trait correlations and families' ordination based on similarities in phenotypic characters, and selecting elite families and suitable parent trees. Full-sib families from 28 crosses established in randomized complete block design from Naozhi orchard in Northeast China were used, and 11 morphological traits were investigated. Significant differences were observed among families for all traits. The traits coefficients of variation ranged from 6.07 to 56.25 % and from 0.029 to 15.213 % in phenotype and genotypic variation, respectively. A moderate level of inherited genetic control was observed (broad sense heritability H^2 , varied from 0.155 to 0.438). Traits related to stem growth were highly positively correlated to each other whereas crown traits showed a weak correlation with stem traits (Pearson correlation r , ranged from -0.161 to 0.956). Based on multi-trait comprehensive analysis, we selected six elite families and six parents, which resulted in a genetic gain of 5.6 %, 16.9 %, and 36.4 % in tree height, diameter at breast height, and volume,

respectively. These results make a theoretical basis for selecting excellent families and establish orchards of Korean pine from improved seeds.

Keywords: *Combining ability; Full-sib families; Phenotypic variability; Pinus koraiensis*

Introduction

Pinus koraiensis Sieb. et Zucc (Korean pine), a coniferous tree species in the *Pinaceae* family, naturally occurs in the northeastern provinces of China, extends its distribution area to the Korean peninsula, the central region of Japan and southern part of Russian far-east (Zhang et al. 2015; Wang et al. 2018; Lee et al. 2021). Korean pine has great economic value owing to its good-quality lumber and nuts that are used for food, oil production, and medicine since ancient times (Yang et al. 2015). The Korean pine mixed-broadleaf forests play an important environmental role, including CO₂ sequestration, soil protection of forest plantations on slopes and streams regulation (Ren et al. 2018). Due to its economic importance and environmental role, Korean pine has been greatly recommended to restore degraded forest lands (Yao et al. 2014) and was widely planted in artificial forests (Zhang et al. 2014). To increase its wood quality as well as its nut yield, a large breeding program

has been initiated principally through seed orchard establishments (Han et al. 2013; Feng et al. 2010). Seed orchards are considered as the best way for producing improved seeds (Kjær & Foster 1996). All programs of tree breeding employ seed orchard at some point of the cycle of producing genetically superior seeds (Wright 2012). In order to limit the self-crossing events and crossing of undesirable individual trees, crossbreeding have been used to breed new varieties of forest trees (Pâques 1989). Crossing method was applied to produce genetically improved seed of Korean pine in the early 1960 (Wang 2000).

Efficient selection of elite materials of trees under breeding program passes through the evaluation of achieved genetic gain (Hill 2010). However, in order to maintain the viability and adaptability of elite trees to various environmental stresses, genetic diversity remains a key factor for the adaptability of plants to different environmental conditions (Thomas et al. 2017). The genetic analysis has been remained to be the main tool for estimating genetic parameters, predicting breeding values and genetic gain in progeny tests (Egbäck et al. 2017). Meyer and Kirkpatrick (2005) demonstrated that factor analysis using the principal components method may help to define important variables that explain the maximum of the variation observed among the individuals when apply a multiple-trait comprehensive evaluation and very valuable to fix the selection index on numerous characters. The general and specific combining ability (GCA and SCA) allow a good estimation of crossbreeding effects for choosing best parent trees and identify the most desirable combiner with high hybrid vigor of progenies of more wanted superior phenotypic characteristics than those of parental trees (Wu & Matheson 2004, Avin et al. 2016; Oghan et al. 2018).

Despite its enormous economic importance, few studies have been made on growth performance of Korean pine full-sib families. Particularly, aspects combining the genetic gain and classification method on genotypic similarity in selection process of superior families has not been considered previously. In the present study, 834 single trees from 28 *P. koraiensis* full-sib families at age 33 were used as experimental material. Eleven stem characteristics were investigated and analyzed. The objectives of this study were (1) to analyze the phenotypic variation and estimate the genetic variation parameters; (2) to determine typical traits and establish trait relationships and families' ordination based on both phenotypic and genotypic similarities; (3) to highlight suitable traits and determine growth indexes for family selection; (4) to evaluate the combining ability to select elite families and suitable parent trees for future Korean pine breeding operations.

Materials and Methods

Plant materials

Study materials were collected from the Naozhi Forestry farm located at the western hillside of Changbai Mountain in Linjiang city, Jilin province, Northeast of China (41°05'N, 126°06'E).

The mixed-climate broadleaf-conifer dominated by *P. koraiensis* are characteristic of this mountainous area and are found at the altitudinal range from 700 to 1000 m. The moderate temperate and continental monsoon climate is characteristic of this region with mean annual temperatures, rainfall, and frost-free period of 5°C, 800 mm, and 135 days, respectively. The soil from Linjiang region is classified as an Albi-boric Argosols according to the U.S. soil taxonomy (Zhu et al. 2010; Xu et al. 2018) and it is dominated by dark brown soil and has about 40 cm of thickness, with a textural proportion of sand (15.1%), silt (63.3%), and clay (21.6%), respectively.

Experiment design

Thirteen *P. koraiensis* male and female trees were randomly sampled from the natural Korean pine forest and control cross-pollination were made in the spring of 1985. Among the parent trees, 11 male and 12 female trees successfully produced progenies (Table 1). Seeds were collected in the autumn of 1986 and sown in 1987 and four-year-old seedlings from each family were planted. A randomized complete blocks design was applied with single tree plot. 10 progenies from each cross were randomly assigned in a block at spacing of 3.0 × 4.0 m in row. The plantation site was divided in five blocks.

Measurement of growth traits

A total of 834 full-sib families belonging to 28 crosses were measured. The following morphological traits were investigated on the living plants of each family in the 5 blocks in October 2017: tree height (Ht), basal diameter (BD), diameter at breast height (DBH), diameter at 3-m height (DIAM3), stem straightness degree (SSD), branches angle (BA), crown width (CB), crown height (CH) and branch number (BN). The volume (V) and the inter nodes distance between branch (DBN) were indirectly calculated. All traits related to diameter and heights were measured by the Vertex Laser (Haglof Sweden) and diameter tape. The SSD values were estimated following Zhao et al. (2014), who defined a scale of stem straightness ranging from 1 to 5 as follows: (1) when more than two bend points in the stem; (2) when more than two slightly bend points or one obviously bend point in the stem; (3) when two slightly bend points in the stem; (4) when one slightly bends point in the stem and (5) when the stem is straight completely. The CB was calculated by averaging the values of the north-south and east-west crown width (Liang et al. 2016) and the number of branches rounding a node was obtained by averaging the branches number on the first 5 nodes of branch level on each tree. The volume was estimated using the formula of Louppe (2015) with the form factor of 0.41 for coniferous trees as established in the equation (1).

$$V = DBH^2 \times Ht \times \pi \times fc / 40000, \quad (1)$$

With V, DBH, and Ht as defined above, $\pi=3.14$ and form factor, $fc=0.41$.

Table 1
Crossing design of parents of *P. koraiensis* at the Naozhi seed orchard on male and female trees

Male trees	Female trees											
	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13
M3	PK23	-	-	-	-	-	-	-	-	-	-	-
M4	PK24	-	-	-	-	-	-	-	-	-	-	-
M5	-	PK35	PK45	-	-	-	-	-	-	-	-	-
M7	-	PK37	PK47	-	-	-	-	-	-	-	-	-
M8	-	PK38	-	-	-	-	-	-	-	-	-	-
M9	PK29	-	PK49	PK59	-	PK79	PK89	-	-	-	-	-
M10	-	PK310	-	-	-	PK710	PK810	-	-	-	-	-
M11	PK211	-	-	-	-	-	PK811	-	-	-	-	-
M12	-	-	-	-	-	-	-	PK912	-	-	-	-
M13	-	PK313	-	-	PK613	PK713	-	PK913	-	-	PK1213	-
M14	-	-	-	-	PK614	-	-	PK914	PK1014	PK1114	-	PK1314

Note: PK was the family name following by female and male number for crossing having given offspring and (-) was the crossing having not given offspring. The table showed only the full-sib families present in the 5 blocks.

Statistical analyses

The analysis of variance (ANOVA) was performed to determine the significance of differences in growth traits among families. Family's growth mean performances were compared using the least squares means (LS means) comparison method. The linear model (Eq. 2) was used to determine the effects of families in different blocks for a given trait (Guo and Wang 2002). The statistical analysis was computed using Statistical Product and Service Solutions (IBM SPSS statistics 20) (George and Mallery 2019).

$$Y = X\beta + Z\gamma + \varepsilon \quad (2)$$

Where Y the vector of individual performances in phenotypic traits, β is the vector of fixed-effects (Overall mean and blocks), γ is the vector of random-effects parameters including general combining ability (GCA) and specific combining ability (SCA) for female and male parents, and ε is an unknown residual error vector. X and Z are the known design matrix for the fixed and random effects β and γ respectively. The analysis assumed all random effects to be normally distributed with mean equal to zero, and residuals in addition to have a normal distribution and are independent of each other ($E[\gamma]=0$, $\text{Var}[\gamma]=G$ and $\text{Var}[\varepsilon]=R$ and the covariance matrix of Y was $\text{Var}[Y]=ZGZ+R$).

The estimation of variance components for each trait were computed according to Becker (1984). The phenotypic and family genotypic coefficients of variation (CV_p and CV_g) (Eq.3 and 4) were calculated following Ewa et al. (2017).

$$CV_p = \frac{\sqrt{\sigma_p^2}}{\bar{X}} \times 100 \quad (3)$$

$$CV_g = \frac{\sqrt{\sigma_g^2}}{\bar{X}} \times 100 \quad (4)$$

Where \bar{X} was the trait's overall mean and σ_p^2 and σ_g^2 were the phenotypic and genotypic variance component of the trait.

Genetic control of family's growth performance was estimated in equation (5) by calculating the broad-sense heritability (H^2) based on family means by dividing the between family's variance component with the between plots residual variance and the variance component of random error (Courtney et al. 2008).

$$H^2 = \frac{\sigma_\gamma^2}{\sigma_\gamma^2 + \frac{\sigma_\varepsilon^2}{\beta}} \quad (5)$$

With σ_f^2 and σ_m^2 as variance component between family means, σ_ε^2 the variance component of random error, β represents the number of blocks.

Parental general combining ability (GCA) and specific combining ability values (SCA) were deduced from families/crosses performances following Liang et al. (2019) using the formulas (Eq 6 and 7).

$$GCA_i = \bar{X}_i - \bar{X} \quad (6)$$

$$SCA_{ij} = \bar{X}_{ij} - \bar{X} - GCA_i - GCA_j \quad (7)$$

The between traits phenotypic and genetic correlation coefficients and (r_p) and (r_g) were calculated as the fraction between traits phenotypic and genetic covariance by the square route of the multiplication product of phenotypic and genetic variances of traits (Kodad 2005). Correlation of family means (Equation 10) was calculated according to Isik (2009). Using correlation coefficients of family means, a heat map of family's similarity was made to determine different grouping of families/crosses based on traits similarity (Ramírez et al. 2014).

$$r_{P(xy)} = \frac{\sigma_{P(x,y)}^2}{\sqrt{\sigma_{P(x)}^2 \times \sigma_{P(y)}^2}} \quad (8)$$

$$r_{A(xy)} = \frac{\sigma_{A(x,y)}^2}{\sqrt{\sigma_{A(x)}^2 \times \sigma_{A(y)}^2}} \quad (9)$$

$$r_{P(xy)} = \frac{\sigma_{A(\bar{z}_x, \bar{z}_y)}^2}{\sqrt{\sigma_{z_x}^2 \times \sigma_{z_y}^2}} \quad (10)$$

Where $\sigma_{P(x,y)}^2$ and $r_{A(xy)}$ represent the phenotypic and genetic covariance between traits x and y; $\sigma_{P(x)}^2$ and $\sigma_{P(y)}^2$, $\sigma_{A(x)}^2$ and $\sigma_{A(y)}^2$ represented the phenotypic and genetic variance components of trait x and y, respectively. $\sigma_{A(\bar{z}_x, \bar{z}_y)}^2$ is the covariance between family means for traits X and Y and $\sigma_{z_x}^2$, $\sigma_{z_y}^2$ are family variances for traits X and Y.

We used with principal component method (PCA) for a factor analysis families' performances in StatistiXL software (<http://www.statistixl.com/default.aspx>) to identify variables (characters) that considerably explained the families' variation. These characteristic features from PCA and correlation analysis were finally chosen for the comprehensive evaluation to select elite families. A hierarchical clustering analysis was performed by nearest Neighbor method including all the morphological traits using the Bray and Curtis distance/similarity measure in the statistiXL software, to group all the family genotypes based on family's genetic and phenotypic resemblances. And based on family's genotypic values a heat map was carried out in order to determine typical traits of each phenotypic clustering within families (Ramírez et al. 2014). A comprehensive evaluation was executed to proceed with the multiple section index of the suitable traits (Zhao et al. 2016) in order to include traits that showed most of the variation among families in the selection process,

$$Q_i = \sqrt{\sum_{j=1}^n a_i}, \quad (11)$$

Where:

Q_i was the comprehensive evaluation value; $a_i = \bar{X}_{ij} / \bar{X}_{jmax}$;

\bar{X}_{ij} was the mean value of a given trait;

\bar{X}_{jmax} , was the maximum mean value of the trait.

The genetic gain was computed as given in equation 12 (Cobb et al. 2019).

$$\Delta G = H^2 W / \bar{X}, \quad (12)$$

Where W was the selection difference considering 30 % of high growth performance in family means, \bar{X} and H^2 were the overall mean value and heritability of family mean for a given trait, respectively.

Results

Family performances

The overall means regarding traits related to wood yield were 6.023 m, 12.324 cm and 0.032 m³ for Ht, DBH and V, respectively (Table 2). A large gap rounding three times units of measure was observed between the maximum and the minimum of average values in stem volume, while other traits were slightly spread to no more than one and half units of measures. The highest average in tree height (Ht = 7.05 m) was detected in family PK45, whereas family PK1213 displayed the lowest average (Ht = 5.50 m). Diameters were higher in families PK713 following by PK1014 and PK24 with 18.16 cm, 12.82 cm and 14.67 cm in BD, DIAM3 and DBH, respectively. Family PK313 presented the lowest diameters (BD = 13.19 cm, DBH = 10.68 cm, and DIAM3 = 8.62 cm). The minimum angle of opposite branches (152.63°) was observed in family PK79 while the maximum angle (173.03°) was observed in family PK35. Almost half of all full-sib families had higher stem straightness (5 degrees of SSD). The highest number of branches per node (5.27 branches) was observed in family PK1014 while family PK1213 had the lowest number of branches per node (4.12 branches). Family PK710 exhibited the highest distance between branches on nodes (DBN = 0.50 m) while the lowest distance (DBN = 0.38 m) was observed in family PK912. The highest crown dimensions (CB = 4.57 and CH = 5.08 m) were observed in family PK713 and PK710, respectively and the lowest crown dimension (CB = 3.23 and CH = 4.01 m) was observed in family PK810. Families with high and low gap between the maximum and minimum average values in BD and DBH showed also high and low gap in the maximum and minimum volume 0.048 and 0.021 m³, reflecting a strong correlation between tree diameters and volume. The ratio between maximum and minimum values in phenotypic performances varied between 1.08 in SSD to 2.021 in tree volume.

Variation parameters and genetic gain

The ranges, standard deviation and genetic variation parameters of different traits were shown in Table 3. The highest CV_p was obtained for tree volume (56 %) and highest CV_g were observed in trait related to crown; whereas moderate CV_p values (ranged from 12 to 27 %) were observed in diameters and traits related to stem and crown. The lowest CV_p and CV_g values (6 %) and (0.029 %) were obtained in stem straightness degree and distance between branch on node. The genotypic variance of family means was low in most traits except angle of opposite branches, which showed a variation approaching 25°. All the phenotypic traits showed a low to moderate genetic control in family performance with heritability at family mean ranged from 0.16 in DBN to 0.44 in CH. The heritability was relatively high in traits related to tree height (Ht, CH, SSD and CB).

The genetic gains of selected families ranged from 0.15 to 10.94 % for all traits. The highest gain was observed for volume followed by diameters with gain rounding 5 %. The lowest genetic gain was obtained in stem straightness degree reached only 0.15 %.

Correlation coefficients and Principal component analysis

The Pearson correlation coefficients between traits were given in Table 4. There were strong positive significant correlations between diameters (basal diameter, diameter at breast height, diameter at 3-m height) with each other and volume (r ranged from 0.895 to 0.956) and between tree height and crown height ($r = 0.824$). The same for individual phenotypic correlation (values below the diagonal), the relationship between traits based on the family averages (values above the diagonal) was stronger for diameters and the volume approaching the unit. Moderate correlation coefficients, ranged from 0.415 to 0.614, were observed between tree height with diameters and volume, also between crown width, crown height with diameters. Relatively weak correlations were gotten between branch number and distance between branch on node with other traits, ranged from 0.168 to 0.394. Two groups of strongly correlated traits were revealed in the heat map based on family's genetic correlation coefficients among which two typical traits related to tree height and stem diameter were detected (Fig. 1).

Three principal components with eigenvalue greater or equal to 1, were retained from the PCA analysis (Fig. 2 A). The cumulative variance contribution rate of the three retained components was 80.087 %. The three components explained 57.95 %, 12.9 % and 9.2 % of the total variation, respectively. Seven traits among which Ht, BD, DBH, DIAM3, V, CH, and CB displayed higher positive score coefficients (Eigenvectors) and loading values in the first component PC1, whereas BA had high positive score coefficients in second component PC2, and SSD displayed positive score coefficients and loadings in third component PC3 (Table 5). The PCA results revealed that the investigated Korean pine families were greatly varied in traits related to diameter followed by traits related to tree height and crown characteristics.

Table 2
Mean values on morphological traits of *P. koraiensis* full-sib grown at Naozhi seed Orchard

Families	Ht	BD	DBH	DIA3M	V
PK45	7.052 a	14.414 cdef	11.520 defg	9.710 fghi	0.032 bcdefg
PK710	6.655 ab	16.910 abcd	14.037 abc	12.292 abc	0.048 a
PK24	6.610 abc	17.188 abc	14.466 ab	12.775 ab	0.046 ab
PK1014	6.445 abcd	17.640 ab	14.484 ab	12.278 abc	0.045 ab
PK310	6.334 abcde	16.190 abcde	13.360 abcde	11.871 abcde	0.037 abcde
PK713	6.326 abcde	18.161 a	14.672 a	12.820 a	0.045 abc
PK49	6.260 bcdef	16.142 abcde	13.549 abcde	11.916 abcd	0.039 abcd
PK47	6.242 bcdef	15.914 abcdef	12.720 abcdefg	11.199 abcdefg	0.034 abcdefg
PK79	6.193 bcdef	17.439 ab	13.880 abcd	11.831 abcdef	0.040 abcd
PK914	6.147 bcdef	15.568 abcdef	12.570 abcdefg	10.789 abcdefgh	0.035 abcdefg
PK614	6.035 bcdef	16.212 abcde	13.083 abcdef	10.681 abcdefghi	0.036 abcdef
PK35	6.027 bcdef	14.217 def	11.480 efg	9.951 defghi	0.027 defg
PK313	5.964 bcdef	13.196 f	10.682 g	8.624 i	0.023 fg
PK29	5.953 bcdef	14.559 cdef	11.366 efg	9.929 defghi	0.026 defg
PK811	5.881 cdef	13.757 ef	11.538 defg	10.005 defghi	0.027 defg
PK613	5.849 cdef	13.814 ef	11.535 defg	9.084 ghi	0.030 defg
PK59	5.844 def	15.528 abcdef	12.377 abcdefg	10.721 abcdefghi	0.030 defg
PK37	5.832 def	13.710 ef	10.829 fg	9.097 ghi	0.025 efg
PK89	5.812 def	14.340 def	11.592 defg	9.865 defghi	0.028 defg
PK38	5.811 def	14.526 cdef	11.453 efg	9.754 efghi	0.026 defg
PK23	5.789 def	15.455 abcdef	12.699 abcdefg	10.634 abcdefghi	0.035 abcdefg
PK211	5.739 def	15.805 abcdef	12.739 abcdefg	10.565 abcdefghi	0.037 abcde
PK912	5.730 def	15.124 bcdef	12.168 abcdefg	10.420 abcdefghi	0.029 defg
PK1114	5.717 def	14.380 def	11.688 cdefg	10.410 abcdefghi	0.026 defg
PK1314	5.678 ef	15.857 abcdef	12.616 abcdefg	10.802 abcdefgh	0.031 cdefg
PK913	5.674 ef	13.215 f	10.651 g	9.113 ghi	0.021 g
PK810	5.586 ef	13.244 f	10.552 g	9.035 hi	0.023 fg
PK1213	5.509 f	13.456 ef	10.871 fg	9.358 ghi	0.023 fg

Continuation of table 2

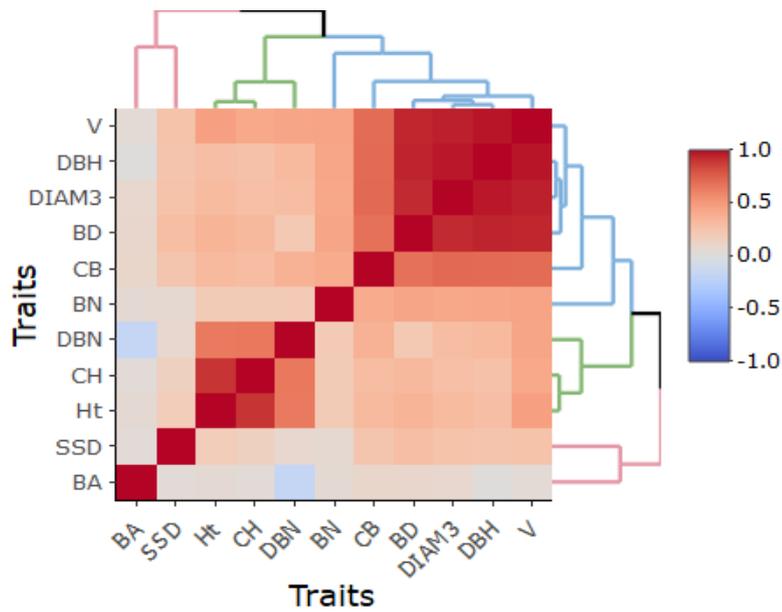
Families	BNN	BA	DBN	CB	CH	SSD
PK1314	5.288 a	165.400 abcd	0.410 cdefg	4.410 ab	4.077 fg	5.139 ab
PK1014	5.277 a	165.101 abcd	0.476 abc	3.903 abcdefg	4.831 abcd	4.188 ab
PK713	5.263 a	167.042 abcd	0.465 abcde	4.576 a	4.553 abcdefg	5.220 a
PK614	5.132 ab	159.803 abcd	0.415 cdefg	3.913 abcdefg	4.498 abcdefg	5.198 ab
PK35	5.108 ab	173.039 ab	0.424 cdefg	3.667 cdefg	4.451 abcdefg	5.046 b
PK310	5.067 abc	159.592 bcd	0.447 bcdef	4.109 abcde	4.757 abcde	5.191 ab
PK47	5.066 abc	164.617 abcd	0.420 cdefg	4.165 abcd	4.635 abcdefg	5.188 ab
PK912	5.027 abc	156.222 bcd	0.380 g	3.922 abcdef	4.146 efg	5.204 ab
PK710	5.026 abc	170.905 abc	0.508 ab	4.328 abc	5.083 a	4.208 ab
PK913	4.975 abc	163.344 abcd	0.408 defg	3.340 fg	4.209 defg	5.197 ab
PK24	4.921 abc	167.298 abcd	0.518 a	3.961 abcdef	4.989 abc	5.145 ab
PK45	4.919 abc	165.058 abcd	0.442 bcdefg	3.930 abcdef	5.018 ab	5.166 ab
PK59	4.900 abc	169.427 abcd	0.408 defg	3.674 cdefg	4.345 defg	5.200 ab
PK38	4.869 abc	162.078 abcd	0.402 efg	3.808 bcdefg	4.328 defg	5.188 ab
PK49	4.839 abc	154.593 d	0.465 abcde	4.180 abcd	4.634 abcdefg	5.191 ab
PK79	4.808 abc	152.636 d	0.455 abcdef	4.430 ab	4.687 abcdef	5.153 ab
PK914	4.785 abc	168.616 abcd	0.422 cdefg	3.900 abcdefg	4.524 abcdefg	5.197 ab
PK89	4.782 abc	172.640 abc	0.420 cdefg	3.993 abcdef	4.230 defg	4.149 ab
PK211	4.719 abcd	163.719 abcd	0.415 cdefg	3.696 cdefg	4.284 defg	4.187 ab
PK29	4.683 abcd	161.496 abcd	0.413 cdefg	3.714 cdefg	4.429 bcdefg	5.179 ab
PK811	4.659 abcd	168.132 abcd	0.433 cdefg	3.799 bcdefg	4.281 defg	5.188 ab
PK613	4.659 abcd	156.055 bcd	0.430 cdefg	3.441 efg	4.312 defg	5.188 ab
PK23	4.645 abcd	163.311 abcd	0.404 efg	3.891 bcdefg	4.203 defg	5.175 ab
PK37	4.599 bcd	169.396 abcd	0.406 defg	3.563 defg	4.366 cdefg	5.191 ab
PK1114	4.579 bcd	155.644 cd	0.448 bcdef	3.660 cdefg	4.123 efg	5.166 ab
PK810	4.566 bcd	163.824 abcd	0.450 bcdef	3.230 g	4.011 g	5.181 ab
PK313	4.425 cd	162.121 abcd	0.471 abcd	3.778 bcdefg	4.323 defg	5.119 ab
PK1213	4.122 d	180.172 a	0.398 fg	3.875 bcdefg	4.119 efg	4.148 ab

Note: The probability value was 0.5. The abbreviations BA, BD, BN, CB, CH, DBH, DBN, DIAM3, Ht, SSD and V meant: branches angle, basal diameter, number of branches per node, crown breadth, crown heights, diameter at breast height, distance between node, diameter at 3-m height, tree height, stem straightness degree and volume. Same for table below.

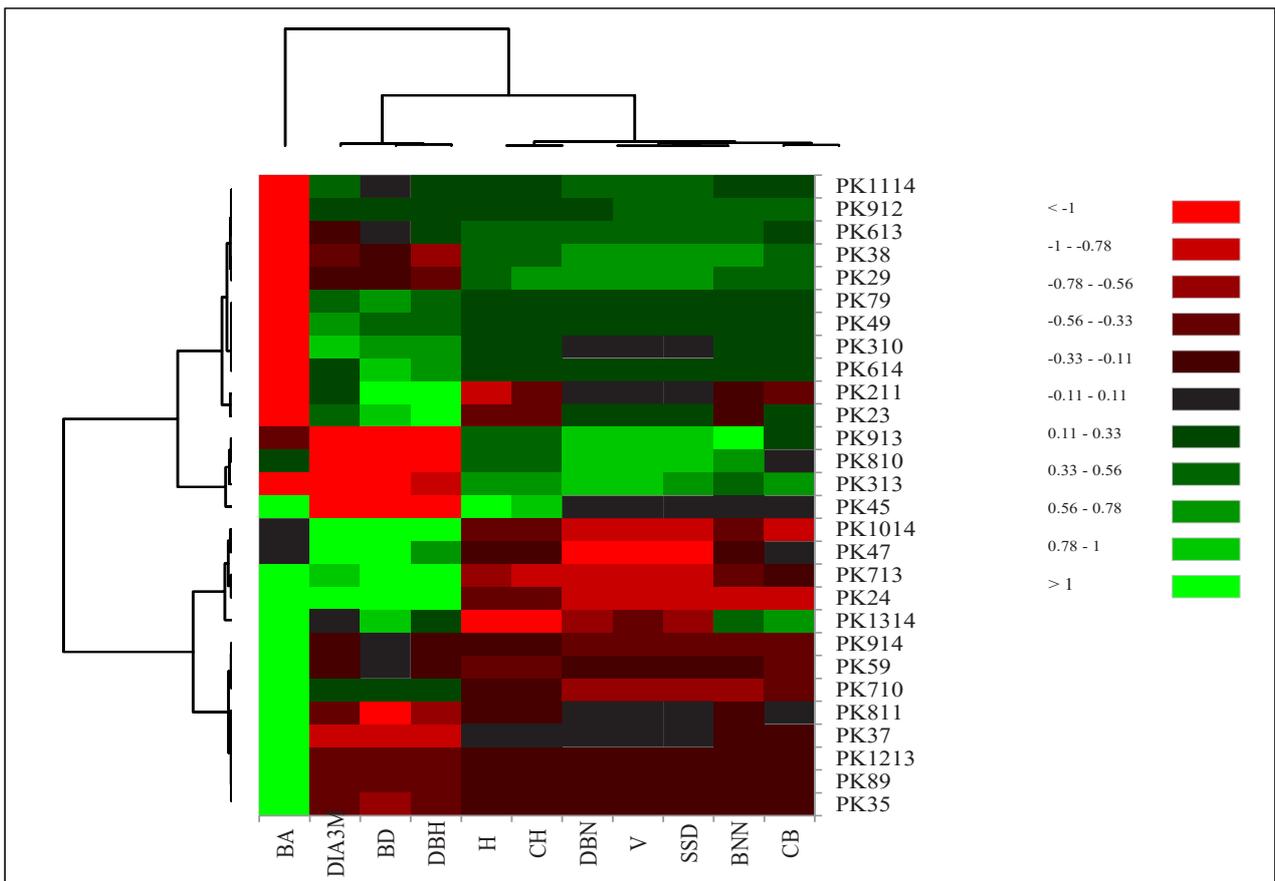
Table 3
Descriptive Statistics and variation parameters in different traits on 28 *P. koraiensis* families

Traits	Mean ± Std Err	Std Dev.	(%)	(%)
Ht (m)	6.024±0.03	0.856	14.219	2.94
BD (cm)	15.188±0.13	3.763	24.776	3.59
DBH (cm)	12.302±0.11	3.181	25.858	3.37
DIA3M(cm)	10.527±0.1	2.889	27.444	4.73
V(m ³)	0.032±0.001	0.018	56.25	10.94
BNN (-)	4.843±0.027	0.774	15.982	1.34
BA (°)	164.312±0.73	21.038	12.804	0.18
DBN (cm)	0.434±0.003	0.075	17.281	1.17
CB (cm)	3.884±0.028	0.814	20.958	2.99
CH (cm)	4.441±0.025	0.712	16.032	3.52
SSD (°)	2.174±0.005	0.132	6.072	0.15

Note: CV_p and CV_g ; σ_y^2 ; H^2 and ΔG (%) were phenotypic and genotypic coefficient of variation; variance of family means; broad-sense heritability and genetic gain.



(a)



(b)

Fig. 1

Heat map of 11 growth traits of 28 Korean pine full-sib families grown at the Naozhi orchard. (a) presents traits clustering based on trait genetic correlation coefficients and (b) presents family's clustering based on family's genotypic values.

Ht indicated three height , BD: basal diameter, DBH: Diameter at breast height, DIAM3: diameter at 3-m height, SSD: stem straightness degree, BA: branches angle, CB: crown width, CH: crown height and BN: branch number, DBN Inter distance between branches per node and V stem volume, respectively. The analysis was done in R software version 3.6.3 and StatistixL software (<http://www.statistixl.com/default.aspx>).

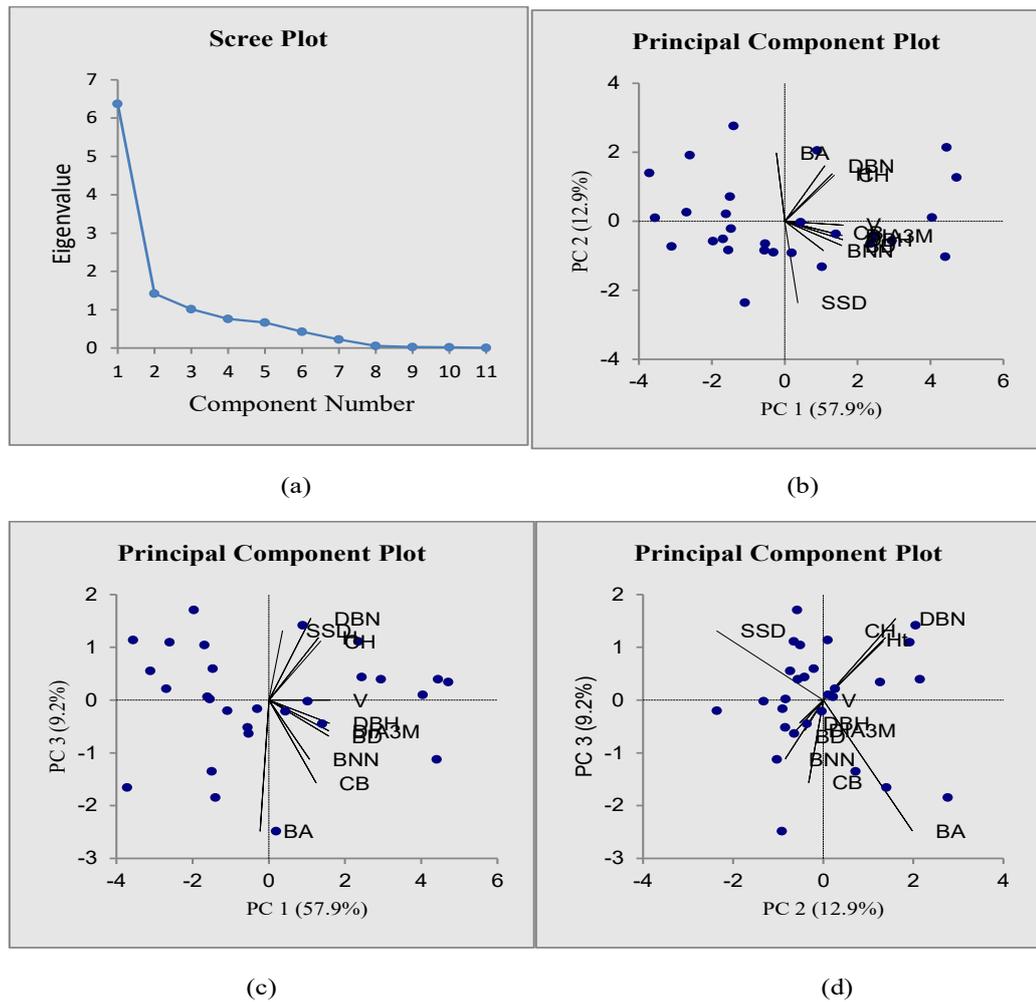


Fig. 2

Principal component analysis on 11 morphological traits on 28 *P. koraiensis* full-sib families growing at the Naozhi orchard. (a), presents the scree plot of components. (b, c, and d) represent the projections of the variables tree height (Ht), basal diameter (BD), diameter at breast height (DBH), diameter at 3-m height (DIAM3), volume (V), number of branches per node (BNN), branches angle (BA), distance between branches per node (DBN), crown breadth (CB), crown heights (CH), and stem straightness degree (SSD) in a Cartesian plane of extracted components 1×2, 1×3 and 2×3 respectively. The analysis was performed in StatistiXL software (<http://www.statistixl.com/default.aspx>).

Combining ability

Crossing effects were evaluated and based on the factor analysis and PCA method, three growth characteristics tree height (Ht), diameter at breast height (DBH) and straightness degree of stem (SSD) were chosen to select excellent parent trees based on wood yield and form of trees. Progenies from these parent trees would serve to build future generations of Korean pine orchards. Results of general and specific combining abilities (GCA and SCA) were presented in Tables 6 and 7. The GCA of female trees ranged from -0.005; -0.014, -0.004 to 0.022; 0.31 and 0.009 in Ht, DBH and SSD, respectively. The male parent trees displayed GCA values varied from -0.02, -1.012, -0.001 to 0.036, 0.312 and 0.015. The highest GCA (all the three traits together) was observed in females F10 and F9. The male trees with high GCA were M12 and M14. These high positive GCA

values revealed that these parents could promote the offspring's production through the assisted crossing and should be properly considered for the cross-parent selection.

Specific combining ability values of families ranged from -0.514, -1.771, -0.128 to 1.024, 2.291, 0.045 of tree height, diameter at breast height and stem straightness degree, respectively. In all the three traits together (Ht, DBH and SSD), the hybridized combination F3 × M14 and F10 × M14 showed the highest SCA among all the 28 cross combinations.

Families' classification and multiple trait comprehensive evaluation

Families were classified based on morphological traits using hierarchical clustering analysis based on the Nearest Neighbour method with Bray and Curtis similarity measure. Three

Table 4
Phenotypic correlation of different traits of *P. koraiensis* families

Traits	Ht	BD	DBH	DIA3M	V	BNN	BA	DBN	CB	CH	SSD
Ht	1	0.568**	0.592**	0.588**	0.695**	0.444*	-0.032	0.660**	0.475*	0.958**	0.057
BD	0.446**	1	0.982**	0.956**	0.938**	0.635**	-0.161	0.484**	0.744**	0.628**	0.246
DBH	0.453**	0.933**	1	0.972**	0.968**	0.599**	-0.160	0.564**	0.718**	0.656**	0.239
DIAM3	0.457**	0.908**	0.940**	1	0.924**	0.592**	-0.107	0.572**	0.731**	0.651**	0.225
V	0.579**	0.895**	0.956**	0.904**	1	0.544**	-0.101	0.637**	0.659**	0.753**	0.258
BNN	0.278**	0.361**	0.355**	0.385**	0.350**	1	-0.132	0.159	0.464*	0.422*	0.131
BA	0.036	-0.020	-0.015	0.002	0.001	0.080**	1	-0.061	-0.031	-0.007	-0.259
DBN	0.486**	0.299**	0.333**	0.324**	0.379**	0.210**	-0.013	1	0.312	0.679**	-0.070
CB	0.359**	0.614**	0.608**	0.613**	0.582**	0.316**	0.104**	0.283**	1	0.462*	0.074
CH	0.824**	0.415**	0.427**	0.415**	0.526**	0.265**	0.022	0.522**	0.329**	1	0.078
SSD	0.075**	0.056*	0.050	0.078**	0.066*	0.151**	-0.064*	0.026	0.034	0.085**	1

Note: Above the diagonal is the correlation coefficients based on family means and below the diagonal is the correlation coefficients based on individual trees. The ** was the significant correlation at 0.01 level (2-tailed) and * the significant correlation at the 0.05 level (2-tailed). The abbreviations BA, BD, BN, CB, CH, DBH, DBN, DIAM3, Ht, SSD and V displayed: branches angle, basal diameter, number of branches per node, crown breadth, crown heights, diameter at breast height, distance between node, diameter at 3-m height, tree height, stem straightness degree and volume.

Table 5
Component Score Coefficients and ANOVA on the Korean pine full-sib in the Naozhi orchard

Variables	Component Eigenvectors			Component loading values			Variation parameters		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	df	MS	F
Ht	0.31	0.329	0.282	0.782	0.392	0.284	27	3.856**	6.141
BD	0.373	-0.168	-0.162	0.942	-0.2	-0.163	27	61.30**	4.873
DBH	0.379	-0.126	-0.104	0.957	-0.151	-0.105	27	45.70**	5.118
DIAM3	0.375	-0.099	-0.138	0.945	-0.118	-0.14	27	41.39**	5.715
V	0.382	-0.027	0.001	0.963	-0.032	0.001	27	0.002**	5.934
BNN	0.254	-0.202	-0.267	0.641	-0.241	-0.269	27	2.16**	3.948
BA	-0.054	0.472	-0.591	-0.137	0.563	-0.596	27	1162.97**	2.779
DBN	0.262	0.384	0.368	0.661	0.458	0.372	27	0.03**	6.474
CB	0.294	-0.077	-0.373	0.743	-0.092	-0.376	27	2.98**	5.098
CH	0.324	0.319	0.266	0.817	0.381	0.268	27	2.53**	5.761
SSD	0.086	-0.564	0.313	0.216	-0.673	0.316	27	0.036**	2.13

Note: PC 1, PC 2 and PC 3 were the extracted tree first components at left and at right and df, MS, F were the degrees of freedom, mean square and the F, Fisher-Yates coefficients in ANOVA.

groups visibly emerged from the clustering analysis based on Bray and Curtis similarity distance (Fig. 3). Cluster 1 was composed by family PK1213; Cluster 2 included two families PK613, PK912 and PK1114, and the remaining families formed Cluster 3. Two genotypic groups were detected in family's genotypic values, from the heatmap clustering analysis showing also two typical groups of traits among which a group with unique trait of branches' angle and a large group with two subgroup composed by trait related to stem diameters and traits related to tree height, crown and tree straightness (Fig.1).

In order to simultaneously consider all the traits that greatly contributed to the variation in families growth, seven traits including Ht, BD, DBH, DIAM3, V, CB and CH were used to evaluate the families in a multiple-traits comprehensive analysis and family ranking based on Qi values, which ranged from 2.446 to 2.885 (Table 7). Applying a selection rate of 10%, six families including PK710, PK24, PK713, PK1014, PK79, and PK310, exhibited high Qi values and were selected as elite

families (Table 7). The average performances of these families were 6.42 m, 17.28 cm, 14.16 cm, 12.31 cm, 0.04 m³, 4.21 m and 4.82 m in Ht, BD, DBH, DIAM3, V, CB, and CH, respectively, which were higher by 6.61 %, 13.62 %, 14.91 %, 16.69 %, 34.49 %, 8.40 % and 8.37 % than the overall family means for Ht, BD, DBH, DIAM3, Ht, V, CB, and CH, respectively. The corresponded genetic gain, ΔG ranged from 0.18 to 10.94 % in branches angle and tree volume, respectively.

Discussion

The analysis of variance showed that all the growth traits differed significantly among Korean pine full-sib families ($p \leq 0.001$). This elucidates the perspective of this study for selection of excellent families and possible backward selection of elite parent trees for the continuing breeding program of Korean

Table 6

GCA values of *P. koraiensis* parent (F female and M male) in tree height (Ht), diameter at breast height (DBH) and stem straightness degree (SSD)

Females	Ht	DBH	SSD	Males	Ht	DBH	SSD
F2	0.020	-0.014	0.007	M3	0.030	0.023	0.015
F3	-0.005	0.031	0.001	M4	0.036	0.062	0.015
F4	-0.002	0.042	0.002	M5	0.027	0.040	0.011
F5	0.022	0.120	0.009	M7	0.027	0.029	0.011
F7	0.013	0.181	0.004	M8	0.028	0.069	0.012
F8	0.006	0.149	0.005	M9	0.021	-0.012	0.008
F6	-0.001	0.202	0.004	M10	-0.005	0.140	0.004
F9	0.005	0.298	0.002	M11	0.001	0.149	0.005
F10	0.001	0.310	0.000	M12	0.014	0.312	0.003
F11	0.000	0.269	-0.002	M13	-0.022	0.076	0.001
F12	-0.002	0.259	-0.003	M14	-0.008	0.187	-0.001
F13	0.002	0.294	-0.004				

Note: The unit of Ht and DBN was m and cm, respectively.

Table 7

SCA values and ranking of families by comprehensive analysis value, Qi.

Families	Combinations	Ht	DBH	SSD	Qi
PK710	F7×M10	0.632	1.713	0.034	2.885
PK24	F2×M4	0.554	2.291	-0.038	2.878
PK713	F7×M13	0.299	2.239	0.045	2.845
PK1014	F10×M14	0.422	2.160	0.014	2.830
PK79	F7×M9	0.171	1.592	-0.021	2.787
PK49	F4×M9	0.235	1.179	0.017	2.766
PK310	F3×M10	0.311	1.036	0.016	2.754
PK47	F4×M7	0.219	0.397	0.013	2.700
PK45	F4×M5	1.024	-0.808	-0.009	2.680
PK614	F6×M14	0.012	0.760	0.024	2.678
PK914	F9×M14	0.124	0.247	0.022	2.672
PK211	F2×M11	-0.284	0.416	0.013	2.649
PK23	F2×M3	-0.234	0.375	0.294E-3	2.639
PK1314	F13×M14	-0.345	0.293	-0.036	2.639
PK59	F5×M9	-0.179	0.053	0.026	2.610
PK89	F8×M9	-0.211	-0.732	-0.025	2.581
PK811	F8×M11	-0.142	-0.785	0.014	2.580
PK35	F3×M5	0.003	-0.843	-0.128	2.576
PK912	F9×M12	-0.296	-0.265	0.029	2.572
PK1114	F11×M14	-0.308	-0.669	-0.875E-2	2.569
PK29	F2×M9	-0.070	-0.958	0.005	2.566
PK613	F6×M13	-0.174	-0.788	0.014	2.563
PK38	F3×M8	-0.212	-0.871	0.014	2.554
PK313	F3×M13	-0.059	-1.642	-0.055	2.534
PK37	F3×M7	-0.191	-1.494	0.016	2.513
PK1213	F12×M13	-0.514	-1.452	-0.026	2.499
PK810	F8×M10	-0.437	-1.771	0.067E-2	2.477
PK913	F9×M13	-0.349	-1.672	0.022	2.467

Note: F, Female parent; M, male parent; SCA, specific combining ability. The unit of Ht and DBH was m and cm, respectively. Ht, DBH, SSD and Qi instead of tree height, diameter at breast height, stem straightness degree and Qi values.

pine. Although genetically closed individuals, full-sib progenies from same family (same parent trees) may display

extremely different phenotypic performances, which could be linked to different growth conditions from different microenvironment or different plots (Galloway 2005). Phenotypic variations within trees, groups or families resulting from the genetic and environment effects, are important concerns mostly for selection of elite materials in breeding program or more suitable materials in ecosystem restoration research (Medrano et al. 2018). Indeed, more the materials are significantly varied, more founded will be the effectiveness of the selection and a probable genetic gain will be achievable with the selected materials. The results in this study were in contrast with those reported on 18-year-old full-sib of Korean pine at site level (Liang et al. 2019), indicating similar growth performances in different blocks. The difference in growth can be attributed to different age of investigated trees that at the young age, families would not have remarkable difference in growth traits (Sun et al. 2016). At 18-year-old, trees would not display strong competitions considering the planting spacing in study by Liang et al. (2019), and therefore arduous for a clear differentiation unlike the big trees of 33-year-old that reached the maturity age in the present study (Looney et al. 2016).

Average values on performance of trees from different families or clones are most important for selection, primarily to minimize the environmental effects arising from individual trees when estimating genotype performance value for a given morphological traits and to establish straight order of genotypes based on their ranks (Mckeand et al. 2006; Peternelli et al 2018). In this study, 11 growth traits (7 related to stem and 4 to crown) were investigated on 28 full-sib families. The results showed an extremely significant difference among families in all the traits suggesting that basically all the traits were suitable for selecting elite families and that family ranking and genotype classification was founded.

Genetic parameters are evaluated to select excellent materials in forest improvement research for providing strategic direction in tree improvement programs (Callister and Collins 2008). Among these parameters, the coefficients of variation and the heritability are widely used in tree breeding

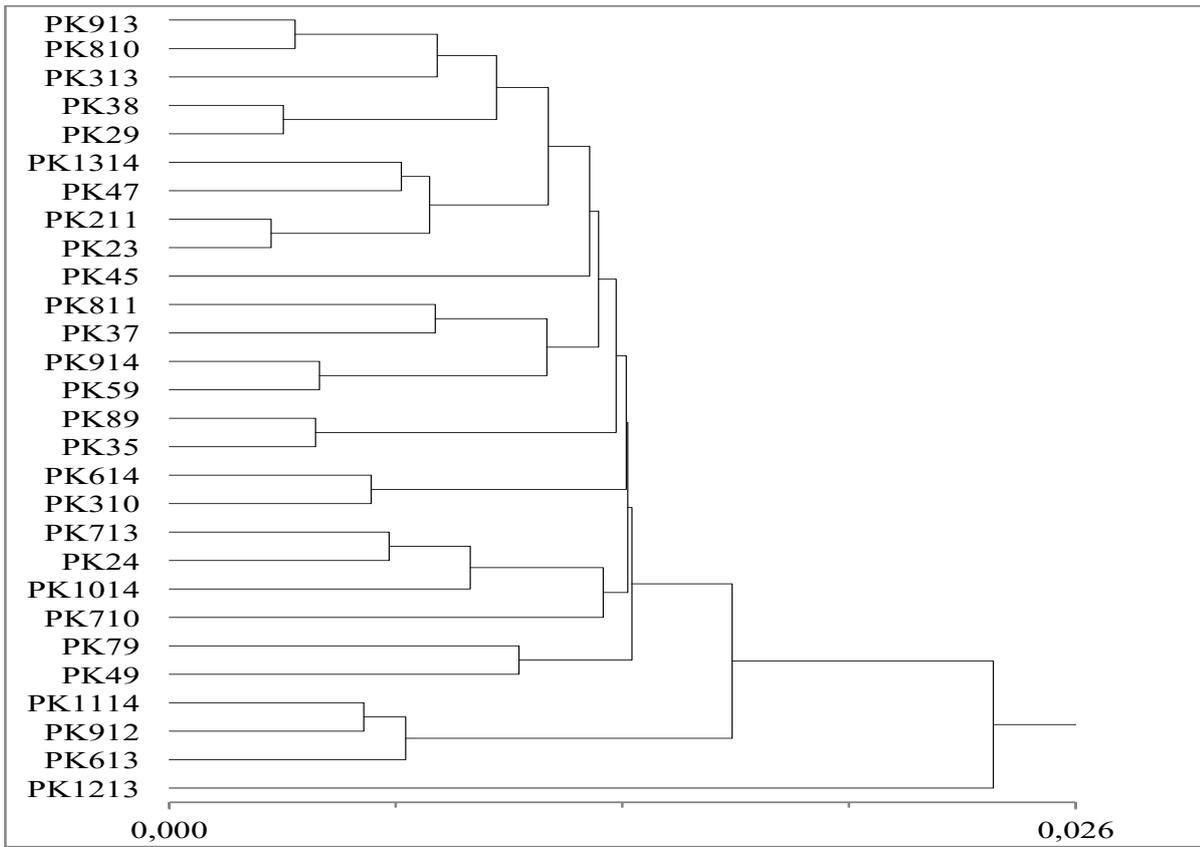


Fig. 3

Neighbour joining clustering dendrogram of 28 full-sib *P. koraiensis* families grown at the Naozhi seed orchard showing clusters pattern based on Bray and Curtis distance/similarity measure in StatistiXL software (<http://www.statistixl.com/default.aspx>) on the 11 morphological traits. The Cophenetic Correlation was $R, 0.645$ df 376, p -value 0.000

research to specify the extent of the phenotypic variation and the level of the genetic control in the studied materials (He et al. 2011). The phenotypic coefficient of variance gotten in this study was higher for volume (56.250 %), while the genotypic variation was low (0.146) for the volume since the materials are from the same species. The CV_p in volume was more than twice of the CV_p values for diameters (basal diameter, diameter at the breast height, diameter at 3 m height) with 24 %, 25 % and 27 %, respectively; indicating that volume was the most varied trait among families, that diameters and volume of these families would be use to improve these families through selective cross-breeding. The CV_p values observed in this study were greater than values reported by Fries (2012) for *P. pinaster* families and Wood et al. (2015) for *P. taeda*, with value varied from 5 to 20 % which revealed environment influences on full-sib families of these species and which contrasted the studies of Galal et al. (2017) and Balocchi et al. (1993) for mango trees and loblolly pine in the early development stage.

The family heritability as part of the total variance related to the additive genetic variance varies from 0 to 1 (Burdon 1992; Nanson 2004). In this study, all traits were rarely to moderately inherited at the genotypic level (family heritability ranged from 0.016 to 0.438. These indicated that the phenotypic

measurement does not completely reflect the underlying breeding value of trees thus selected families could be a little more influenced by environmental effects. The heritability values in this study were lower than those previously reported for tree height, diameter at the breast height and stem straightness degree of *P. mariana* families at 35 years old (Wang et al. 2018), but were close to studies of Ye and Jayawickrama (2012) and Yin et al. (2017) although realized at the young age of trees.

Determining the genetic gain is the hinge stage of diverse cycles of tree improvement program. Tree breeders, forest owners, and managers would need to know the achieved genetic gain at any stage of tree growth especially for improvement purposes (Kimberley et al. 2015). The genetic gain in the case of full-sib families is thus realized on the subsequent generation when the product of panmictic cross-breeding from the selected full-sib families exhibited high performance in the macro site at the same stage of development of their related parent (Nanson 2004). In this work, the genetic gains on the selected individual full-sib families were calculated following by Pereira (2008) using the difference between the mean value of the selected families and the overall mean value of all the families (Eq. 12). We found that high genetic gain was

realized for tree volume followed by diameters and traits related to crown size. These results indicated that the selected elite families would improve timber yield and some extent soil protection through better canopy cover. These results were also in agreement with previous researches on Loblolly pine (Li et al. 1999), *P. sylvestris* (Kroon et al. 2008) and *Tectona grandis* Linn. f. (Callister & Collins 2008), which reported high genetic gain in volume than other growth characters.

Several growth traits can appear as the characteristic traits of a tree species by marking significant difference between individuals or different population of clones or families (Fell et al. 2018). However, there are some relationships between characteristic traits (Weber et al. 2018). The correlation between different growth traits is an important parameter in a multiple-trait approach in the predicting breeding values on multiple traits and therefore guides the selection of trees in improvement programs (Rweyongeza 2016; Cappa et al. 2018). The narrow-sense genetic correlation is calculated on full-sib families to determine the association of breeding values between phenotypic traits (Hannrup et al. 2014). In this study, the genotypic correlation was calculated based on family's average breeding values. The genotypic correlation coefficients were somewhat similar to the phenotypic correlation, Fig. 2 a and b. High correlation coefficients were observed between phenotypic performances in volume and diameters (basal diameter, diameter at breast height and diameter at 3-m height) (0.895, 0.956 and 0.904) and between diameter at breast height and basal diameter (0.933) and more greatly correlated as well as in family's breeding values in different traits (Fig.1 b). The fact that stem volume was strongly correlated with the diameter would imply an effect of spacing on growth characteristics in the seed orchard. Spacing significantly influence the height and diameter growth in planting trees. The wider the spacing is, the larger the diameter will be (Lasserre et al. 2009), inversely to height growth which also involves the effects of competition for light (King 1994). In this study, the average value in tree height was lower compared to that reported by Liang et al. (2019) on young Korean pine full-sib families, but on a less reduced planting spacing of 2 m×3 m contrary to 3 m×4 m for the materials in the present study. Our finding suggested that selection for diameter or tree height, greatly improved stem volume or moderately crown traits. These results concurred with the observation by Liang et al. (2016) that *P. koraiensis* could be indirectly selected by using DBH to improve the tree height or volume. The moderate correlation of crown width and crown height with other traits agreed with that observed on loblolly pine (Isik et al. 2005), signifying that separate selection would be useful for specific purpose, i.e., either timber yield or environmental protection (ground cover).

PCA can reduce a large number of variables into a minor amount of common major components that abridge the large portion of the variation into a complex dataset (Ait-Sahalia & Xiu 2019) this makes the PCA to be an orientation tool to highlight the important variables for selecting multiple traits (Kaviriri et al. 2020). In this study, among eleven investigated traits, seven of them presented high eigenvalues ≥ 1 with three main components displayed 80.08 % of the total variation. These

traits explained most of the variation among the investigated full-sib families. Considering the CH,CW, Ht, BD, DBH, DIAM3 and V in the first component PC1 indicated that Korean pine primarily varied in characters related to the stem and crown. The cumulative contribution rate of the retained components was higher comparing to study of Wang et al. (2018) supporting that the crown growth as well as Ht, DBH and V, was valuable for characterizing Korean pine family variations, which was useful to select elite families. Three groups of typical traits were observed at the cluster analysis, both based on the family's phenotypic performances and based on the correlation coefficients.

Estimating the combining ability of parent trees can help to define the suitable parent trees to develop novel cultivars (Priya et al. 2018). Selection of appropriate parents can generate excellent offspring that, in reducing breeding time, can increase improvement effects (Ghosh & Das 2003). As defined by Sprague and Tatum (1942), in a progeny testing, the general combining ability (GCA) consists of the average performance of a genotype in a series of hybrid combinations. Thereby parents with high average combining ability in crosses are considered to have good GCA while if their potential to combine well is bounded to a particular cross. These parents are considered to have good specific combining ability (SCA) (Fasahat et al. 2016; Wu & Matheson 2004). Thus, the SCA effect mainly reflects differences in the gene frequencies between parents (Viana et al 2013). Considering wood yield and tree quality in this study, the GCA and SCA were calculated for tree height, diameter at breast height and stem straightness degree. The female (F9, F10, F13) and male (M11, M12, M14) parents showed high GCA with a difference of 25 % and 60 % on performance values with other parent trees. Thus, these trees should serve as parents in the following stage of the breeding program (Cervantes-Martinez et al. 2006). In addition, the average performance of progenies from these parents demonstrated relatively higher average growth in tree height, diameter at breast height and stem straightness degree than others cross. Our findings were consistent with Liang et al. (2019), reporting high GCA values for DBH and V on several parent trees of Korean pine. Hybridized combinations F2×M4, F10×M14, F7×M13, F7×M10, F7×M9, F4×M9 showed remarkable superior values in SCA which matched with Q_i values although obtained on a large scale of variables. The SCA effect gained by the above combinations was a clear indication of the presence of dominance gene action and such that these hybrids were highly appropriate for heterosis breeding to effectively exploit the dominant gene action and to improve wood yield and form of tree of these materials (Monicashree et al. 2017). However, the cluster analysis showed that the selected families belonged to the same group out of the three formed clusters, which was useful to clarify selection of Korean pine for its further breeding program (Peeters & Martinelli 1989; Naima et al. 2012; Rufai et al. 2013). These families displayed a strong phenotypic similarity; implying their good adaptation to the study site.

From the point of view of the selection index, several traits have been simultaneously highlighted as indexes for selection (Hamilton et al. 2005). Most cases on multi-character studies in

forest trees mainly focused on growth characteristics and characters of physical or chemical properties of wood (Köbölkuti et al. 2017; Yang et al. 2018). In general, characters used as a selection criterion for wood production include diameter at breast height, tree height, volume, and wood density (Fries 2012; Durán et al. 2017). In the present study, additionally to traits related to stem growth, the CB and CH were taken as the selection index based on correlation analysis. Traits related to crown as branch numbers, branches angle and crown width, were previously reported playing an important role in landscaping and afforestation projects (Pesola et al. 2017; Zhang et al. 2017). In this work, the angle of branches (varied from 152 to 181°) was higher than those reported by Liang et al. (2016). The average crown width ranged from 3 to 5 m was registered in families F12×M7 and F3×M4 and the number of branches per node was higher in family F7×M1. All these families with highest values in traits related to branches may be useful for plantations intended to protect the soil on the slopes. Compared to all trees, the selected families showed superior performances of 14.74 % in tree height, 19.00 % in diameter at breast height, 21.64 % in volume and 19.43 % in branch number.

Conclusions

This study detected significant differences in morphological traits among full-sib families of *P. koraiensis* which enabled selection of elite families. The estimated genetic parameters (heritability, phenotypic and genotypic coefficient of variance) were reasonably varied, indicating that there were significant genetic variations and that family selection would be effective. The most important traits (traits related to stem growth) were significantly correlated among each other, which indicated that those traits together promoted growth and wood production and that the indirect selection of wood production would be valuable. This study identified 7 characters as indices in the selection and evaluation of families, and 9 elite families and 6 pairs of parents were selected based on comprehension evaluation method. The crossing effects, with 30 % selection rate, resulted in 2.94 %, 3.37 and 10.94 % of genetic gain in tree height, diameter at breast height and volume, respectively. As a whole, these results provide valuable information to select excellent families and establish orchards of *P. koraiensis* from improved seeds. The families that were selected could be used for reforestation, and parent trees would be useful for establishing improved seed orchard.

Author Contributions

Data curation, David kombi kaviriri and Jiaqi Li; Formal analysis, Jiaqi Li, Zuoyi Fan and Muluaem Tigabu; Funding acquisition, Xiyang Zhao; Investigation, Zuoyi Fan, Jingyuan Wang and Liang Xu; Project administration, Xiyang Zhao and Huan-Zhen Liu; Software, Jingyuan Wang, Ling Yang and Yuhua Li; Writing – original draft, David kombi kaviriri and Muluaem Tigabu;

Writing – review & editing, Ling Yang, Yuhua Li, Huan-Zhen Liu and Xiyang Zhao.

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