



Integrating parental breeding value, genetic gain, and gamete contribution for elite family selection in *Platycladus orientalis*

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Abstract *Platycladus orientalis* (L.) Franco seed orchards play an important role in sustainable forestry in China but balancing genetic gain and genetic diversity remains a significant challenge. Two key factors influence the success of seed orchards: parental breeding value and gamete contribution, as they determine both the genetic gain and diversity of the seed crops produced. This study aimed to optimize breeding strategies by analyzing parental breeding value, gamete contribution, and genetic gain across two growth periods (89 families in 2008 and 52 families in 2021). We evaluated height, diameter at breast height, and stem volume of progeny in a primary seed orchard,

uncovering significant genetic variation among families. Interestingly, no correlation was found between growth traits and gamete contribution, indicating their independence. Using comprehensive scoring and PCA-biplot analysis, we consistently identified several elite families with superior growth performance in both years. We propose an optimal breeding strategy that combines 30% selective harvesting and 50% selective thinning to effectively balance genetic gain and genetic diversity, addressing a critical goal in tree improvement programs. The selected families and optimized strategy provide a scalable framework not only for *P. orientalis* but also for other conifer species globally, enhancing both productivity and genetic diversity in afforestation efforts.

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Introduction

Seed orchards serve as a critical bridge between tree breeding activities and silvicultural practices. The genetic efficiency of seed orchards, determined by how well seed crops reflect parental genetic superiority, directly impacts

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the levels of captured genetic gain and diversity—essential metrics for reforestation success (Funda and El-Kassaby 2012). Progeny testing plays an integral role in determining the rank and breeding value of selected individuals. Additionally, assessing the parental breeding value and gametic contribution of seed orchards enables prediction of the genetic worth of their crops. This process optimizes breeding strategies and enhances the quality of forest tree plantations (White 1987; White and Hodge 1988; Stoehr et al. 2004; Funda and El-Kassaby 2012; Vidal et al. 2017).

In reforestation programs, striking a balance between genetic gain and genetic diversity is essential for maintaining ecological adaptability and ensuring long-term sustainability. Traditional forest improvement strategies often emphasize genetic gain, which can result in genetic bottlenecks and reduced resilience. To address this challenge, it is crucial to adopt practices that preserve genetic diversity while maximizing genetic gain, ensuring the success of seed orchard programs (Park et al. 2017). Significant disparities in gametic contributions among seed orchard parents have been documented which leads to imbalanced genetic compositions and unpredictable levels of genetic gain and diversity (Sønstebo et al. 2018; Jiao et al. 2021). Therefore, understanding the relationship between parental genetic parameters and gametic contributions is critical for developing effective seed orchard management strategies that optimize both productivity and genetic diversity.

Platycladus orientalis (L.) Franco (Cupressaceae), an endemic and ecologically significant conifer in China, is widely used in afforestation programs and for timber production. Native to northern China, it has been introduced to over 50 countries (Huang et al. 2018). Over the past four decades, significant progress has been made in the genetic improvement of *P. orientalis* through provenance trials and the establishment of seed orchards (Huang et al. 2018). Since the 1990s, progeny trials using open-pollinated (half-sib) families from the breeding program's parental population have been conducted to evaluate growth traits and genetic variation. As genetic improvement advances to subsequent generations, a critical gap remains: the interplay between seed orchard gametic contributions and parental breeding values is not fully understood. This knowledge gap hinders

the optimization of seed orchard management strategies, which are essential for balancing genetic gain and diversity.

This study examines the parental population of a *P. orientalis* seed orchard, focusing on breeding value and gamete contribution over a two-year period. The objectives were to: (1) estimate genetic parameters for growth traits of each parent, (2) evaluate parental gametic contributions, (3) analyze the correlation between parental growth traits and their gametic contributions, and (4) identify elite families that consistently excelled across the study period. By developing optimized breeding strategies, this research will provide valuable insights and practical guidance for advancing the genetic improvement of *P. orientalis* and other conifer seed orchards. Ultimately, it will contribute to enhancing the sustainability and productivity of global reforestation efforts.

Materials and methods

2.1 Seed orchard and data collection

The seed orchard is located in Jiaxian County, Henan Province, China (33°48'00" N–34°11'50" N, 113°01'45" E–113°24'50" E) (Jin et al. 2016). Established in the 1980s, the orchard consists of 166 clones randomly planted at a spacing of 2 m × 2 m × 6 m (Huang et al. 2018; Jiao et al. 2021). In 1989, open-pollinated seeds were collected from clonal mother trees in their native environments to establish a progeny trial. The trial followed a completely randomized design, with single-tree plots spaced at 2 m × 2 m (Jin et al. 2016). Growth traits were evaluated in 2008 (at age 19) and in 2021 (at age 32), with 89 and 52 families included in the assessments, respectively. These family sets represent two distinct generations or developmental stages, providing comparative insight into genetic performance over time.

In 1989, a progeny trial was established using seeds collected from 89 plus trees representing nine provenances across regions located south and north of the Yellow River, including LuoYang, LinXian, HuaJia, HuiXian, JiXian, JiYuan, MiYang, LongMeng and YiYang. Concurrently, scions from the same plus trees were grafted to establish a clonal seed orchard for long-term conservation and genetic improvement. However, by the 2021 assessment, families from LongMeng and YiYang were found to be partially missing due to inadequate management and other factors, resulting in only 52 families from the remaining seven provenances being available for evaluation. During the surveys in 2008 and 2021, the control families representing the original provenances were also assessed, enabling comparative analyses of genetic performance over time and among provenances.

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As part of the seed orchard upgrading process, both growth traits and reproductive output were considered for improvement. In this study, the female strobili production of all ramets from surviving clones in the orchard was evaluated during the summers of 2017, 2018, and 2020, following Woods (2005) (Method F1: visual assessment of female cone yield for each ramet of all parents). Similarly, the male strobili production of all ramets was assessed during the springs of 2017, 2019, and 2021 (Method M3: visual assessment of male strobili reproduction for each ramet of all clones) (Woods 2005). The proportion of female seed-cone and male strobili production contributed by each parent to the total reproductive output was calculated to represent their respective female and male gametic contributions (Griffin 1984).

Growth traits, including tree height (HT), measured using a measuring pole, with an accuracy of 0.1 m, diameter at breast height (DBH), measured with a diameter gauge, with an accuracy of 0.1 cm, and stem volume (VOL), were assessed in 2008 and 2021. The VOL of each tree in m³ was calculated using the following equation (Meng 2006):

$$\text{VOL} = 0.000091972184 * \text{DBH}^{1.863977} \text{HT}^{0.83156779} \quad (1)$$

2.2 Estimation of genetic parameters

2.2.1 Breeding values

The breeding value of each family, as measured by the performance of its offspring, represents its genetic quality. Breeding value is defined as the additive genetic variance component of an individual's genotypic value, which indicates the genetic advantage it can transmit to future generations.

In this study, breeding values were estimated to assess the genetic potential of each family's contribution to the genetic improvement of the orchard's crop. The breeding values were calculated following Chen (2006), who employed a linear mixed model to partition the additive genetic effects. The basic linear model is:

$$Y_{ijk} = \mu + F_i + R_j + FR_{ij} + e_{ijk} \quad (2)$$

where Y_{ijk} is the observed value of the k -th individual in the i -th family and j -th replication; μ is the population mean of the experimental group; F_i is the family effect; R_j is the replication effect; FR_{ij} is the interaction effect between family and replication; e_{ijk} is the residual term, i.e., the within-plot effect.

Due to the unequal coefficients within various sources and the absence of certain subunits, the variance analysis was conducted using the GLM method. The significance

levels and mean square components between varieties and families were determined using the random model. The heritability of the family was estimated as:

$$H^2 = \frac{\delta_f^2}{\delta_f^2 + \frac{\delta_{fb}^2}{b} + \frac{\delta_e^2}{nb}} = \frac{V_f - V_{fb}}{V_e} \quad (3)$$

where H^2 represents the family heritability; δ_f^2 is the genetic variance of the family; δ_{fb}^2 is the genetic variance due to the interaction between the family and the plot; δ_e^2 is the variance within the plot; b is the degree of freedom of the plot; n is the number of plants per plot; V_f is the variance between families; V_{fb} is the variance due to the interaction between the family and the plot; V_e is the variance of error.

This method aligns with the methodology outlined in the document breeding values of parental trees, genetic worth of seed orchard seed lots, and yields of improved stocks in British Columbia, which underscores the importance of additive genetic components in determining genetic worth (Xie and Yanchuk 2003). The breeding values were estimated as follows:

$$AC_i = H_i(Y_i - M)/M \quad (4)$$

where AC represents the relative breeding value of each superior tree family; H_i is the genetic correlation in each family; Y_i is the average value of observed traits in each family; M is the average across all families.

2.2.2 Genetic gain

Genetic gain is a key indicator of genetic progress in tree breeding, as it reflects the potential improvement in target traits across generations. The genetic gain for growth traits among the studied families in the seed orchard was estimated following Chen (2006):

The genetic gain (Eq. 5) was calculated following conventional plant breeding methodology, where the degree of improvement is assessed relative to a control population. The control value (X_c) in Eq. 5 represents the mean phenotypic performance of progenies derived from local individuals collected near the elite tree source regions. These control families were sampled from seven geographic provenances involving LuoYang, LinXian, HuaJia, HuiXian, JiXian, JiYuan, MiYang, LongMeng and YiYang, and were included in the progeny test as a reference group. These families were chosen as controls because they reflect the characteristics of the local, unimproved population. In contrast, X_i denotes the phenotypic performance of progeny families derived from elite trees selected within the same provenance regions.

$$G_f = (X_i - X_c) / X_c \quad (5)$$

where G_f represents the relative genetic gain of each family; X_i is the average value of the observed trait in each family; X_c is the performance value of local family (control).

2.2.3 Genetic worth

Genetic worth (Eq. 6) integrates concepts from Griffin (1984) and Nielsen and Hansen (2012), combining breeding value with reproductive contribution. This assumes: (1) gamete contributions accurately reflect reproductive success, (2) no pollen contamination from outside sources, and (3) equal viability of male and female gametes. The parameters M_i and F_i represent proportional contributions to maintain genetic diversity while AC_i ensures genetic quality.

Following Griffin (1984), the genetic worth (GW) of the orchard's clones was estimated by combining their estimated gamete contributions and breeding values across the study's years (Stoehr et al. 2004; Nielsen and Hansen 2012). Analyzing the genetic worth across different years enables the assessment of temporal variation in genetic contributions and breeding efficiency.

The genetic worth (GW) of each clone was calculated using:

$$GW = AC_i (M_i + F_i) / 2 \quad (6)$$

where AC_i represents the relative breeding values of each elite family; M_i is the male proportional gamete contributions of clone i ; F_i is the female proportional gamete contributions of clone i .

2.3 Data analysis

Statistical summaries of three growth traits including tree height (HT), diameter at breast height (DBH), and stem volume (VOL) across the study years were calculated using the psych package in R (R version 4.0.3; R Foundation for Statistical Computing, Vienna, Austria) (Revelle 2025). All statistical analyses, including the nested-analysis of variance (ANOVA) and Pearson's product-moment correlation, were performed using SPSS Version 24.0 (SPSS Inc., Chicago, IL, USA). The analysis was carried out across provenances and families nested within provenances to assess the genetic variation in growth traits.

Pearson's product-moment correlations were used to assess the association between growth traits and their related genetic parameters. These included breeding values, genetic gain, and the contribution of female and male gametes of clones, evaluated across multiple years of study. To identify the main patterns of variation and relationships between

growth trait genetic parameters and gamete contributions for reproductive traits, a PCA-biplot was computed using the Facto Mine package in R (R version 4.0.3; R Foundation for Statistical Computing, Vienna, Austria) (Lê et al. 2008). The PCA-biplot (Gower et al 2011) represents variables with calibrated axes and observations as points, enabling the projection of observations onto variable axes to approximate the original values. The years 2008 and 2021 were chosen to represent early and later stages of offspring growth in the seed orchard trials. The combination of ANOVA, Pearson's correlation analysis, and PCA-biplot provided a comprehensive framework for understanding the relationships among genetic parameters, gamete contributions and their combined influence on growth and reproductive traits.

2.4 Comprehensive evaluation

A comprehensive evaluation requires the conversion of measured values of multiple traits into new independent indicators (Han et al. 2017), which are used to replace multiple existing traits and generate comprehensive scores to collectively evaluate families. First, we implemented dimensionality reduction (Swisher et al. 2004). Before conducting factor analysis, the raw data of eight primary growth traits were standardized (zero mean and unit variance) to eliminate the effects of differing units and scales among traits. Factor extraction was based on the Kaiser criterion (eigenvalue > 1), and the number of common factors retained was determined by the cumulative contribution rate exceeding 85%. Five common factors met these conditions, with cumulative contribution rate of 98.2% (in 2021, The variance contribution rate of Dim.1 was 0.5114, that of Dim.2 0.3647, that of Dim.3 0.0620, that of Dim.4 0.0326, and that of Dim.5 0.0116.) and 98.9% (in 2008, the variance contribution rate of Dim.1 was 0.5073, Dim.2 0.4040, Dim.3 0.0448, Dim.4 0.0201 and that of Dim.5 0.0128). The comprehensive score (D_n) for each sample was obtained from the following equation:

$$D_n = \sum_{j=1}^m F_{jn} * E_j \quad (7)$$

where E_j is the contribution rate of the j th common factor, F_{jn} is the score of the j th common factor of the n th sample, m is the number of common factors.

In the improvement of seed orchards, it is important to determine the optimal selection strategy to improve genetic quality. In this study, two selection strategies, selective harvesting and thinning, were simulated. To explore the effects of different selection intensities, we chose 30% and 50% as representative thresholds for harvesting and thinning, respectively. A 30% selection intensity is commonly adopted in tree breeding and orchard management practices as a

moderate level that balances selection gains with genetic diversity retention. In contrast, 50% represents a more intensive strategy often applied when the objective is to rapidly eliminate inferior genotypes or restructure the stand for greater gain. We also combined selective harvesting with inferior thinning, 50% inferior thinning was carried out first, and 30% of the parents were selected according to their traits. Based on the comprehensive evaluation scores of families, families were screened to suit for different selection strategies, and the overall genetic gains under the corresponding genetic strategy for the seed orchard were calculated. The optimal selection strategy for *P. orientalis* seed orchard was determined based on the method. The overall genetic gain was estimated as follows:

$$\Delta G = (X - \bar{X}) / \bar{X} \quad (8)$$

where ΔG represents the relative genetic gain of the seed orchard after selection; X is the average value of an observed trait in unselected orchard; $\bar{X}$ is the average value of an observed trait the seed orchard after selection.

Results

3.1 Variation of growth traits in progeny tests across years

We measured three growth traits (tree height [HT], diameter at breast height [DBH], and stem volume [VOL]) of *P. orientalis* families in 2008 and 2021. The statistical analyses for each over multiple years are presented in Tables S1 and S2. The nested-ANOVA results for each across provenances and families nested within provenances are shown in Table 1 and Table S3.

The analysis revealed significant differences among provenances and families nested within provenances for all traits in 2008 and 2021 ($P < 0.001$).

In 2008, average tree height was 4.5 m, ranging from 1.5 m (Family 118) to 7.9 m (Family 141). By 2021, the average tree height had increased to 6.7 m, with a range of 1.8 m (Family 143/144) to 10.0 m (Family 177). Similarly, DBH varied between 3.0 cm (Family 138) and 16.2 cm (Family 155) in 2008, with an average of 8.4 cm at age 19. In 2021, DBH ranged from 2.0 cm (Family 62) to 25.0 cm (Family 153/161). The highest stem volume was observed in Family 155 (0.077 m³) in 2008 and in Family 161 (0.23 m³) in 2021. At the same time, the lowest stem volume recorded was in Family 138 (0.0004 m³) in 2008 and Family 58 (0.0004 m³) in 2021. The average stem volume increased from 0.0192 m³ in 2008 to 0.0615 m³ in 2021.

3.2 Estimation of genetic parameters for growth traits from progeny tests

Breeding values (AC) and genetic gain (G) were calculated for height, DBH, and stem volume for each family in 2008 (19-years-old) and 2021 (32-years-old) (Tables S4, S5). The breeding values for three traits varied widely among families and between years (Figs. 1 and 2). For height, the AC in 2008 ranged from 0.822 (Family 65) to −0.677 (Family 198), with an average of 0.045. By 2021, the average breeding value had decreased to −0.012, ranging from 0.617 (Family 108) to −0.810 (Family 134).

Similarly, DBH breeding values ranged from −0.698 (Family 198) to 1.220 (Family 147) in 2008, with an average of −0.018. In 2021, they ranged from −0.991 (Family 134) to 1.190 (Family 63), with an average of 0.012. Stem volume breeding values exhibited the largest variation, ranging from

Table 1 ANOVA of *P. orientalis* height (HT), diameter at breast height (DBH) and stem volume (VOL) across provenance and families in 2021

Traits	Units	SOV	Df	SS	MS	F v	Pr (>F)
HT	m	Region	1	0.5	0.489	0.399	0.528
		Provenance	6	78.9	13.158	10.732	1.10e-11 ***
		Family/Provenance	45	173.7	3.859	3.147	3.34e-11 ***
		Residuals	1360	1667.4	1.226	—	—
DBH	cm	Region	1	87	87.01	7.469	0.00636 **
		Provenance	6	724	120.65	10.356	3.03e-11 ***
		Family/Provenance	45	1448	32.17	2.762	7.45e-09 ***
		Residuals	1360	15,845	11.65	—	—
VOL	m ³	Region	1	0.006	0.00599	5.486	0.0193 *
		Provenance	6	0.0732	0.0122	11.184	3.26e-12 ***
		Family/Provenance	45	0.1259	0.0028	2.564	1.06e-07 ***
		Residuals	1360	1.484	0.00109	—	—

SOV: source of provenance; Df: degree of freedom; Sum Sq: sum of square; Sq: Square; Signif. codes: *** 0.001; ** 0.01; * 0.05

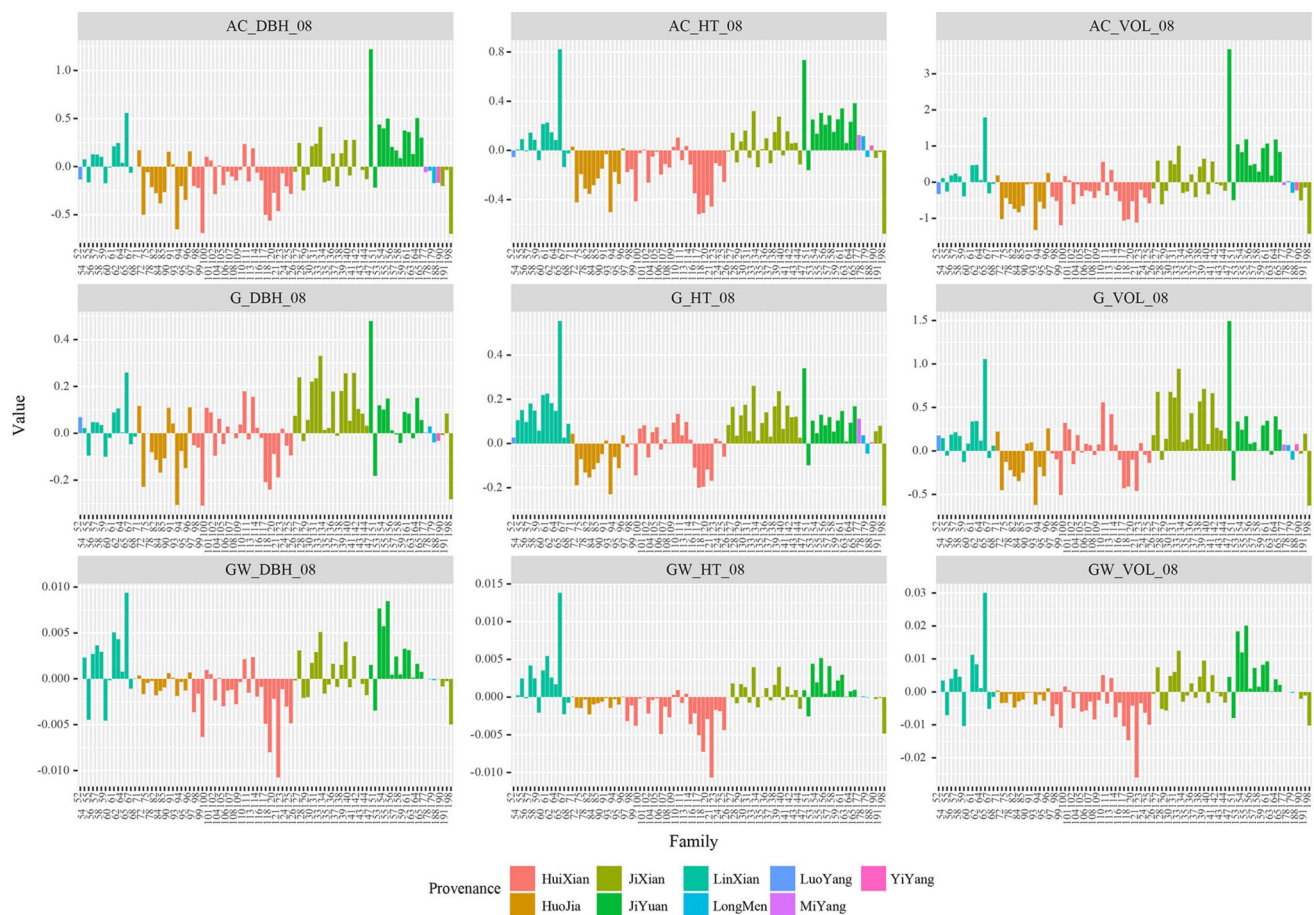


Fig. 1 Genetic parameters of height, DBH, and stem volume of each family in the *P. orientalis* seed orchard in 2008. AC-HT: the breeding value of tree height; G-HT: the genetic gain of height; GW-HT: the genetic worth of height; AC-DBH: the breeding value of DBH;

G-DBH: the genetic gain of DBH; GW-DBH: the genetic worth of DBH; AC-VOL: the breeding value of stem volume; G-VOL: the genetic gain of stem volume; GW-VOL: the genetic worth of stem volume

–1.426 (Family 198) to 3.678 (Family 147) in 2008, with an average of –0.031. In 2021, the average increased to 0.037, ranging from –1.662 (Family 134) to 2.922 (Family 63). Some families maintained a high degree of consistency in breeding values across traits and years. For example, Family 147 had the highest breeding values for all three traits in 2008 and continued to perform well in 2021. In contrast, Family 198 consistently ranked among the lowest across all traits and years.

The genetic gain (G) of height, DBH, and stem volume also varied widely among families. For height, it ranged from –0.281 (Family 198) to 0.554 (Family 65) in 2008, and from –0.387 (Family 134) to 0.319 (Family 126) in 2021. The mean genetic gains for height were 0.046 and 0.045 in 2008 and 2021, respectively. For DBH, genetic gain ranged from –0.309 (Family 99) to 0.479 (Family 147) in 2008, and from –0.461 (Family 134) to 0.807 (Family 63) in 2021, with means of 0.020 and 0.056, respectively. For stem volume, the genetic gain ranged from –0.629 (Family 198)

to 1.493 (Family 147) in 2008, and from –0.809 (Family 134) to 2.356 (Family 63) in 2021, with means of 0.110 and 0.129, respectively.

The genetic contribution of each clone was calculated by combining estimates of their gamete contribution in the seed orchards (Figs. 3 and 4). In the 2008 progeny test involving 89 plus-tree families, Clone 188 had the lowest gametic contribution. Its male gametic contributions in 2017, 2019, and 2021 were 0.000148, 0.000140, and 0.000123, respectively, with a mean of 0.000137. The female gametic contributions of Clone 188 in 2017, 2018, and 2020 were 0.000341, 0.000329, and 0.000118, yielding a mean of 0.000263. In contrast, Clones 114 and 68 showed the highest levels of gametic contribution. For Clone 114, male contributions were 0.03127 (2017), 0.02946 (2019), and 0.02886 (2021), with an average of 0.02987; for Clone 68, the values were 0.03290, 0.03274, and 0.03311, averaging 0.03292. In terms of female gametic contribution, Clone 68 contributed 0.02941 (2017), 0.03265 (2018), and 0.03370



Fig. 2 Genetic parameters of height, DBH, and stem volume of each family in *P. orientalis* seed orchard in 2021. AC-HT: the breeding value of height; G-HT: the genetic gain of height; GW-HT: the genetic worth of height; AC-DBH: the breeding value of DBH; G-

DBH: the genetic gain of DBH; GW-DBH: the genetic worth of DBH; AC-VOL: the breeding value of stem volume; G-VOL: the genetic gain of stem volume; GW-VOL: the genetic worth of stem volume

(2020), with a mean of 0.03192, while clone 114 contributed 0.03100, 0.03223, and 0.03524 in the same years, averaging 0.03283. The total clonal contributions of Clones 68 and 114 were 0.06484 and 0.06269, respectively.

In the 2021 progeny subset of 52 families, Clone 68 remained the most dominant contributor. Its male gametic contributions in 2017, 2019, and 2021 were 0.05050, 0.05027, and 0.05091, resulting in a mean of 0.05056. Female contributions in 2017, 2018, and 2020 were 0.04469, 0.05025, and 0.05089, with an average of 0.04861. In contrast, Clone 117 had the lowest total gametic contribution in this cohort. Its male contributions were 0.01558 (2017), 0.01608 (2019), and 0.01552 (2021), averaging 0.01573. Female contributions from Clone 117 in 2017, 2018, and 2020 were 0.01380, 0.01506, and 0.01375, respectively, yielding a mean of 0.01420.

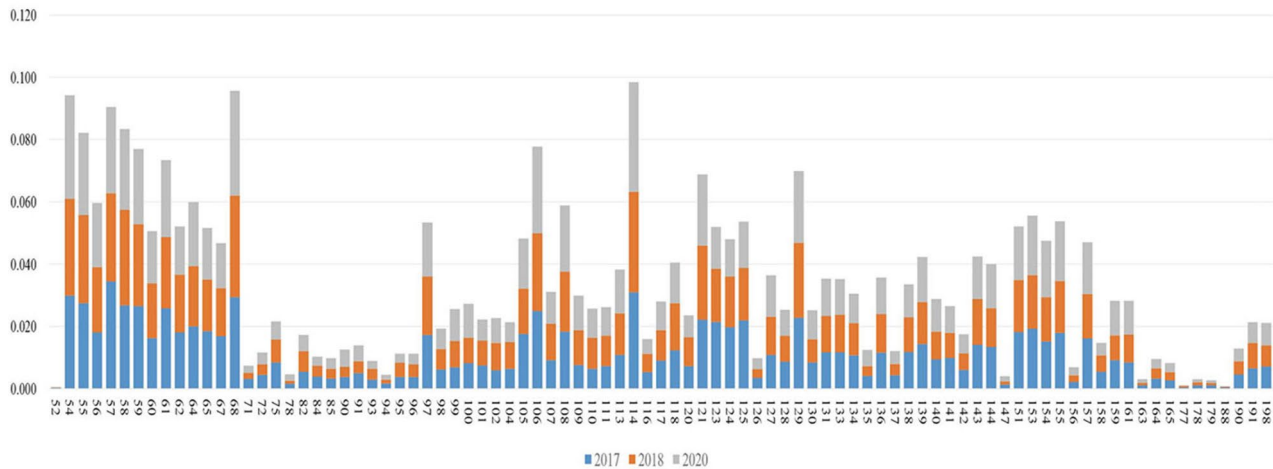
The genetic worth of each elite tree was estimated by combining its breeding value and gametic contribution in the context of the seed orchard. In 2008, the genetic worth

of height, DBH, and stem volume ranged from -0.011 to 0.014 , -0.011 to 0.008 , and -0.026 to 0.030 , respectively. By 2021, the ranges had expanded to -0.013 to 0.018 , -0.015 to 0.034 , and -0.027 to 0.083 , respectively. Notably, Family 134 and Family 198 consistently ranked among the lowest in all genetic parameters, while Family 147 and Family 63 were consistently among the highest performers. These results highlight significant genetic variations among families, providing valuable insights for selective breeding and seed orchard improvement.

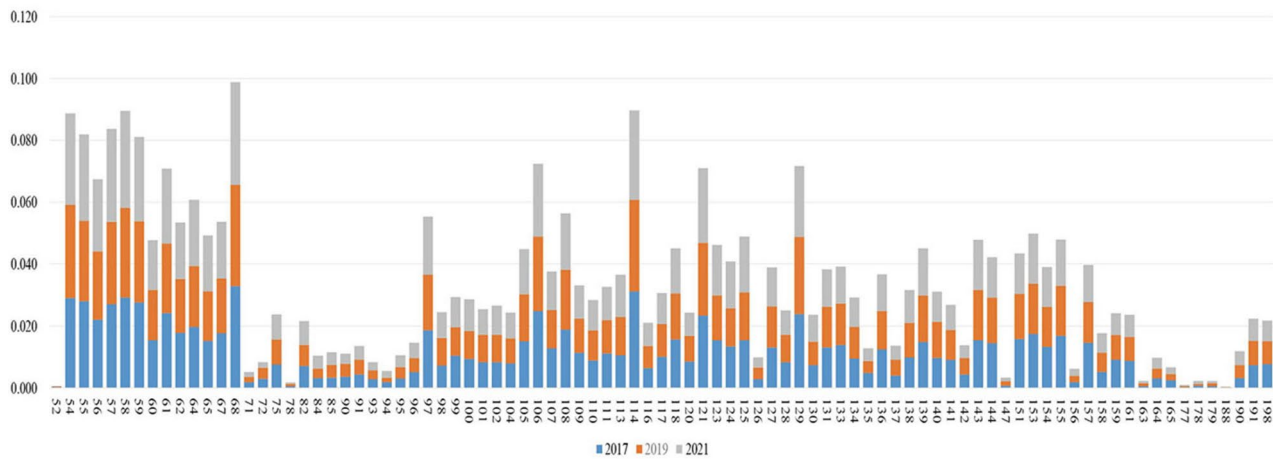
3.3 Correlation between the two study years in growth performance

Pearson correlation coefficients revealed significant positive correlations among the breeding value, genetic gain, and genetic worth for the three traits. However, the gamete contributions from male and female strobili production showed no correlation for the three growth traits in either 2008 or 2021 (Table 2 and Table S6).

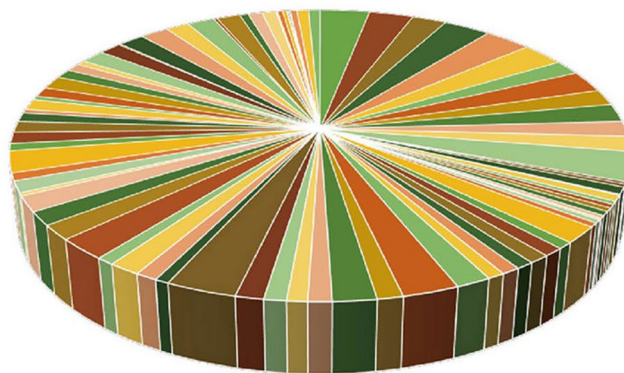
Female Gamete Contribution



Male Gamete Contribution



Clone Contribution



52 54 55 56 57 58 59 60 61 62 64 65 67 68 71 72 75 78
 82 84 85 90 91 93 94 95 96 97 98 99 100 101 102 104 105 106
 107 108 109 110 111 113 114 116 117 118 120 121 123 124 125 126 127 128
 129 130 131 133 134 135 136 137 138 139 140 141 142 143 144 147 151 153
 154 155 156 157 158 159 161 163 164 165 177 178 179 188 190 191 198

Fig. 3 Gamete contribution of clones incorporated in the measurement in 2008 in the *P. orientalis* seed orchard in 2008. Proportion of female seed-cone and male strobili production contributed by each parent to the total reproductive output was calculated to represent their respective female (upper panel) and male (middle panel) gametic contributions, and the average of female and male gametic contribution is visualized in the lower panel

In addition, there was a significant positive correlation between the male and female gamete contributions across years. Specifically, as the male gamete contribution increased, the female gamete contribution from the same family also increased. These findings are further illustrated in the PCA-biplot (Figs. 5, 6), which was performed for the three genetic parameters and gamete contributions.

In 2008, PC1 and PC2 explained 91.1% of the total variation in the genetic parameters and gamete contributions of the progeny test. In 2021, they explained 87.6% of the total variation, with 51.1% and 36.5% representing PC1 and PC2, respectively. The PCA-biplot further showed the contributions of each variable and their interactions. In both 2008 and 2021, the results consistently showed no significant correlation between the genetic parameters and gamete contributions, as these variables were located in distinct orthogonal dimensions in the PCA-biplot.

3.4 Comprehensive selection

The PCA-biplot revealed the differences among families and enabled the clear identification of seven families with excellent genetic parameters and gamete contributions across years (Figs. 5 and 6). All excellent families were also identified by the comprehensive score method (Tables S7, S8). In 2008, 18 families were universally recognized by both methods as excellent. In 2021, 12 families were selected by both methods. Across the study years, seven families were consistently identified as excellent by both methods. In addition, 12 excellent families were selected only by the comprehensive score method in 2008 and 2021. Further, 10 families were solely identified as excellent in 2008, while in 2021, only Family 66 and Family 86 were selected.

3.5 Genetic gain determined with different strategies and different selection intensities

Based on the results of the composite score, elite families for various improvement objectives were screened using different selection intensities under selective harvesting and genetic thinning strategies. The genetic gains achieved by these strategies were compared to determine the optimal genetic improvement strategy for the seed orchard (Tables

S9, S10). The final selection of elite families is shown in Table S11.

Under a harvest selection strategy with a selection intensity of 30%, 27 families were identified as elite at age 19 in 2008, with genetic gains in height, DBH, and stem volume of 7.6, 9.3, and 21.6%, respectively. The average values for HT, DBH, and VOL of these families were 4.9 m, 9.2 cm, and 0.02 m³, respectively. At age 32 in 2021, 16 families were identified as elite under the same strategy, with mean values of 6.7 m, 13.3 cm, and 0.06 m³ for HT, DBH, and VOL, and genetic gains of 0.15%, −0.07%, and −0.15%, respectively. At a selection intensity of 50%, 45 and 26 families were identified as elite in 2008 and 2021, respectively. The genetic gains in HT, DBH, and VOL were 5.2, 6.6, and 15.0% at age 19, and 0.86, 1.01, and 2.41% at age 32, respectively.

Using a thinning strategy, 62 and 44 families were identified as elite at the selection intensities of 30% and 50% at age 19, respectively. At the same time, the genetic gains in height, DBH, and stem volume were 3.4, 4.3, and 9.3% at the selection rate of 30% and 5.4, 6.9 and 15.8% at the selection rate of 50%. At age 32 in 2021, 36 and 26 families were selected as elite families under thinning strategies with selection intensities of 30% and 50%, respectively. The genetic gains were 0.4, 1.2, and 2.5% under the 30% selection ratio, and 0.9, 1.0, and 2.4% under the 50% selection ratio.

A combination strategy of 30% selective harvesting and 50% thinning resulted in higher genetic gains compared to individual strategies. Under this improvement strategy, genetic gains in height, DBH, and stem volume in 2008 were 21.7, 35.4, and 87.6%, respectively. In 2021, the genetic gains were 17.8, 28.9, and 68.2%, respectively. These findings demonstrate that the combination strategy is highly effective for maximizing genetic improvement as compared to any individual strategy.

Discussion

4.1 Phenotypic and genetic variation of different growth traits

Understanding genetic variation within populations, families, or clones is critical for effectively utilizing genetic resources in breeding programs (Safavi et al. 2010). In this study, ANOVA revealed significant variation among families in growth traits, providing a strong foundation for selecting superior genetic material for *P. orientalis* improvement. These findings align with other studies, such as those on *Betula platyphylla* (Zhao et al. 2016) and common ash (*Fraxinus excelsior* L.) (Mwase et al. 2008),

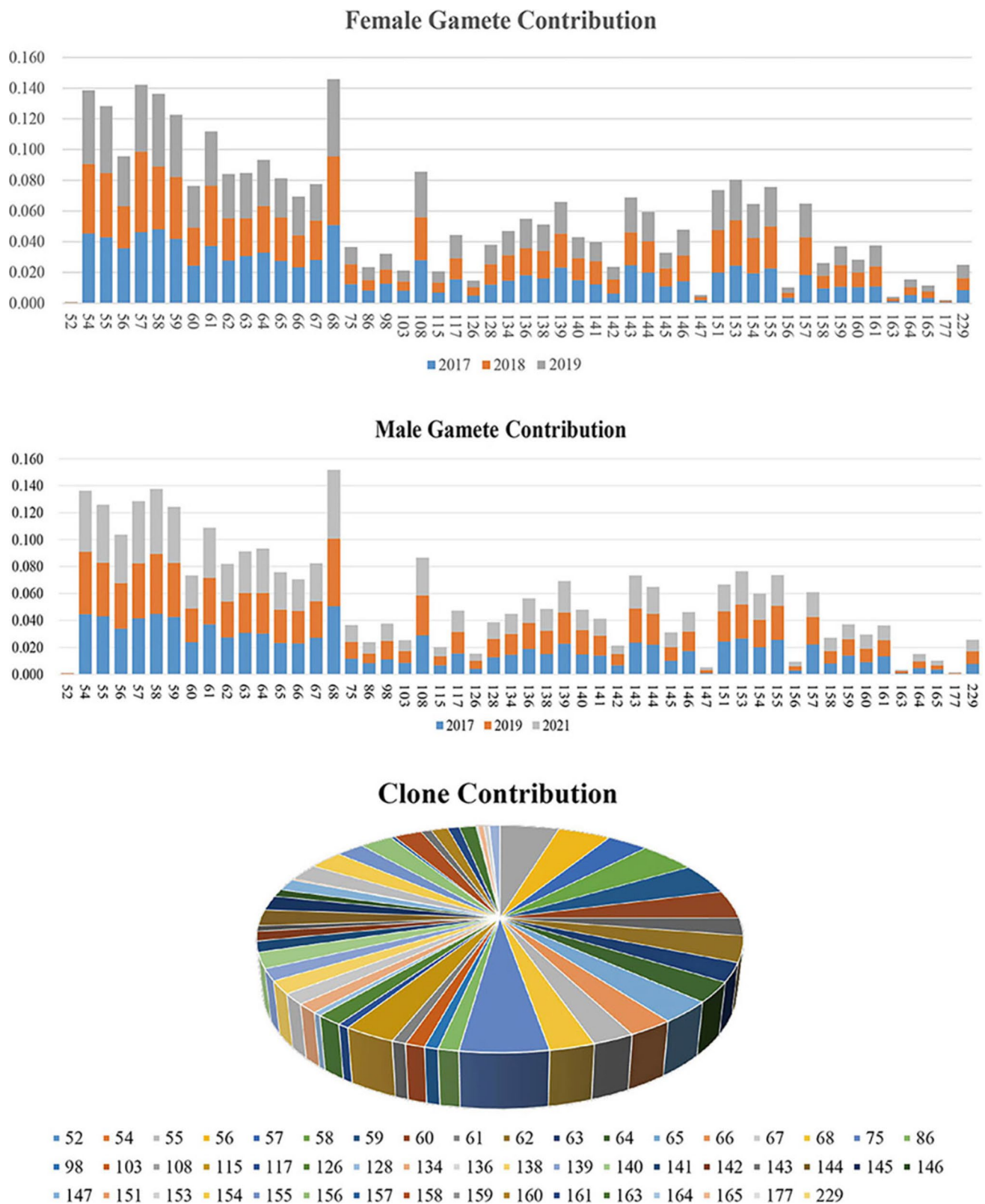


Fig. 4 Gamete contribution of clones incorporated in the measurement in 2021 in the *P. orientalis* seed orchard. Proportion of female seed-cone and male strobili production contributed by each parent to the total reproductive output was calculated to represent

their respective female (upper panel) and male (middle panel) gametic contributions, and the average of female and male gametic contribution is visualized in the lower panel

Table 2 Pearson's correlation coefficient among genetic parameters and gamete contributions of *P. orientalis* in 2021

	AC-HT	G-HT	GW-HT	AC-DBH	G-DBH	GW-DBH	AC-VOL	G-VOL	GW-VOL	Clone contribution	M-2017	M-2019	M-2021	F-2017	F-2018	F-2020
AC-HT	1															
G-HT	0.839**	1														
GW-HT	0.861**	0.660**	1													
AC-DBH	0.637**	0.582**	0.527**	1												
G-DBH	0.539**	0.676**	0.410**	0.936**	1											
GW-DBH	0.535**	0.491**	0.628**	0.806**	0.782**	1										
AC-VOL	0.703**	0.605**	0.601**	0.951**	0.867**	0.754**	1									
G-VOL	0.324*	0.059	.318*	.377**	0.162	0.238	0.394**	1								
GW-VOL	0.602**	0.505**	0.715**	0.747**	0.694**	0.912**	0.817**	0.277*	1							
Clonal contribution	-0.028	.351*	-0.068	-0.008	0.197	-0.029	-0.041	-0.157	-0.037	1						
M2017	-0.017	0.360**	-0.053	0.006	0.21	-0.008	-0.025	-0.146	-0.016	0.997**	1					
M2019	-0.05	0.332*	-0.092	-0.023	0.187	-0.036	-0.057	-0.149	-0.046	0.995**	0.995**	1				
M2021	-0.054	0.348*	-0.101	-0.009	0.208	-0.031	-0.048	-0.142	-0.048	0.992**	0.991**	0.993**	1			
F2017	-0.024	0.346*	-0.048	-0.011	0.189	-0.028	-0.046	-0.182	-0.039	0.988**	0.978**	0.972**	0.972**	1		
F2018	-0.025	0.356**	-0.067	-0.001	0.203	-0.028	-0.035	-0.15	-0.038	0.997**	0.994**	0.991**	0.989**	0.982**	1	
F2020	0	0.345*	-0.045	-0.01	0.175	-0.04	-0.034	-0.167	-0.035	0.986**	0.979**	0.973**	0.961**	0.975**	0.982**	1

AC-HT: the breeding value of tree height; G-HT: the genetic gain of tree height; GW-HT: the genetic worth of tree height; AC-DBH: the breeding value of DBH; G-DBH: the genetic gain of DBH; GW-DBH: the genetic worth of DBH; AC-VOL: the breeding value of stem volume; G-VOL: the genetic gain of stem volume; GW-VOL: the genetic worth of stem volume; M2017: male gamete contribution in 2017; M2019: male gamete contribution in 2019; M2021: male gamete contribution in 2021; F2017: female gamete contribution in 2017; F2018: the female gamete contribution in 2018; F2020: female gamete contribution in 2020



Fig. 5 PCA-biplot of genetic parameters and gamete contributions for clones incorporated in measurement in 2008. AC-HT: the breeding value of height; G-HT: the genetic gain of height; GW-HT: the genetic worth of height; AC-DBH: the breeding value of DBH; G-DBH: the genetic gain of DBH; GW-DBH: the genetic worth of DBH; AC-VOL: the breeding value of stem volume; G-VOL: the genetic gain of stem volume; GW-VOL: the genetic worth of stem volume. Contributions of genetic parameters and gamete contributions in the first two and four PCA dimensions are visualized in the upper left and right panel; PCA-biplot is visualized in the lower panel

which demonstrate the feasibility of estimating and selecting superior families.

Height, diameter, and stem volume are critical traits for tree breeders, especially for species with ecological and timber values (Huang et al. 2023). However, breeding strategies and selection criteria must be tailored to each species based on their adaptive and ecological significance. Studies have shown that *P. orientalis* has substantial economic importance, and understanding its phenotypic variation provides valuable insights for enhancing growth traits in China's breeding programs (Deng et al. 2021). In this study, the breeding material was sourced from a *P. orientalis* seed orchard, with growth trait variations assessed at ages 19 and 32, spanning a 13-year interval, to identify superior breeding material. Our results indicate that families with consistently superior performance over multiple years are highly adapted to local environments, offering valuable material for reforestation programs. The observed variations underscore the importance of sustained evaluation across different growth stages to ensure reliable selection outcomes. This consistent performance of superior families underscores the value of selecting individuals with enhanced growth potential in future breeding efforts.

Recent studies have further emphasized the importance of phenotypic plasticity and environmental adaptation in tree breeding (Li et al. 2024), which supports our findings that superior families of *P. orientalis* have adapted well to the ecological conditions in Jia County (the seed orchard location). Additionally, advancements in genomic tools and molecular markers (e.g., genome-wide association studies and genomic selection) are increasingly being utilized to accelerate the identification of superior genetic material in forestry breeding programs (Hasan et al. 2021; Ide 2021; Kumar et al. 2024). This is an important direction for future research, as it could complement traditional phenotypic selection and improve the efficiency of breeding programs.

4.2 Independence between growth genetic parameters and gamete contribution

In breeding programs, the correlated response between different traits significantly influences breeding strategies,

as the relationship between growth traits is complex and multifaceted (Zhao et al. 2019). Previous studies have highlighted significant correlations between growth traits in species such as *Pinus taeda* L. (Xian et al. 2003) and *Pinus massoniana* Lamb. (Zeng et al. 2013). In this study, there were significant positive correlations between all genetic parameters for each growth trait in the two years, suggesting that the correlation between genetic parameters of growth characteristics tends to remain consistent over time. Additionally, the correlation coefficients in the early year were higher than in the later year, which implying that early evaluation and selection of elite families could be feasible. This finding aligns with previous studies on *Pinus radiata* D. Don (Kumar and Lee 2003) and *Larix kaempferi* (Lamb.) Carrière (Zhao et al. 2019). However, despite less correlation in the later growth years, it is suggested that the selection and evaluation of elite families in these years remains highly reliable due to the consistency of the correlation between the two growth years.

Highly significant positive correlations ($p \leq 0.01$) were found between female and male gamete contributions of families across years (Table 2 and Table S6). Similar findings were reported in *P. orientalis* (Jiao et al. 2021) and other conifers such as *Pinus* species (Schmidtling 1983; Bilir et al. 2004). These results highlight the importance of the correlation between female and male gamete contributions when estimating the total parental gamete contribution, as demonstrated by Kang and El-Kassaby (2002). As carried out in the present study, the total gamete contributions of the families were estimated using both female and male gamete contributions and their correlation coefficients.

The correlation coefficients quantify the degree of correlation between different traits, which aids in the simultaneous screening of multiple traits (Xia et al. 2016). In this study, there were no significant correlations between the three growth traits and reproductive traits, suggesting that the selection of seed production-related traits and growth traits should be considered in a more integrated manner. Previous studies on *P. orientalis* seed orchards primarily focused on either growth traits or reproductive traits and had limitations (Mao et al. 2010; Jiao et al. 2021). In contrast, this study is the first to estimate the correlation between genetic parameters and gamete contributions, and we propose the combination of reproductive and growth traits to evaluate and select elite families. This is a novel approach for the genetic improvement of *P. orientalis*, providing new avenues for advancing breeding strategies.

4.3 Comprehensive assessment

Breeding objectives determine the strategic approaches used in forest genetics (Isik 2014). Comprehensive evaluation and selection are essential for stabilizing desired traits in tree

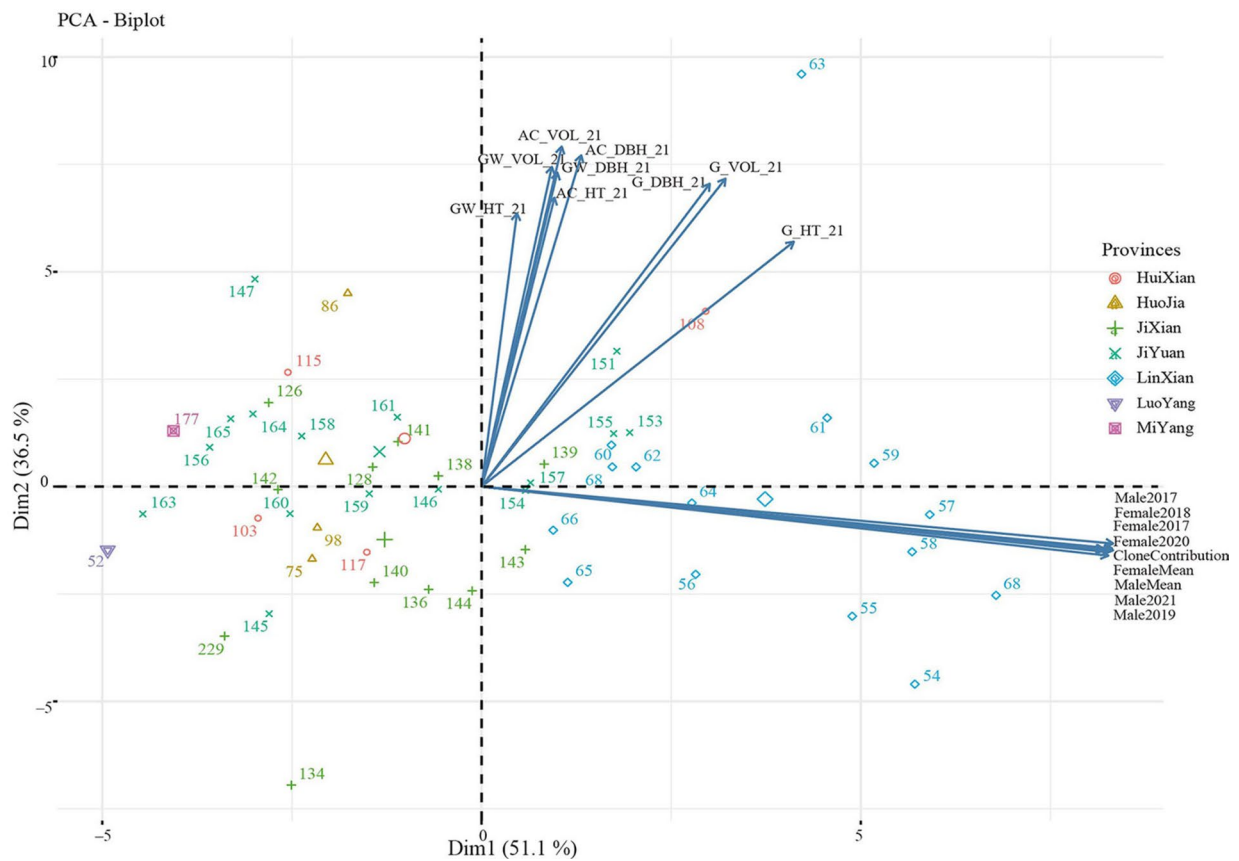
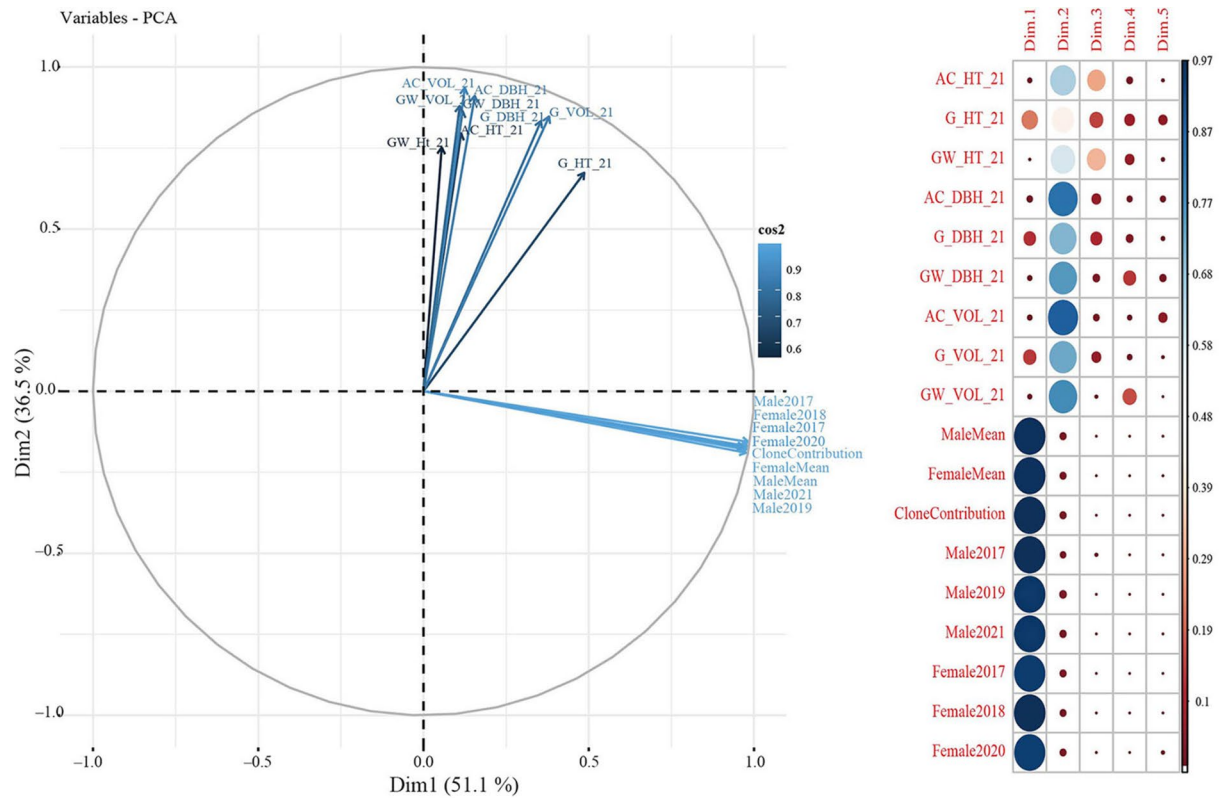


Fig. 6 PCA-biplot of genetic parameters and gamete contributions for clones incorporated in measurement in 2021. AC-HT: the breeding value of height; G-HT: the genetic gain of height; GW-HT: the genetic worth of height; AC-DBH: the breeding value of DBH; G-DBH: the genetic gain of DBH; GW-DBH: the genetic worth of DBH; AC-VOL: the breeding value of stem volume; G-VOL: the genetic gain of stem volume; GW-VOL: the genetic worth of stem volume. Contributions of genetic parameters and gamete contributions in the first two and four PCA dimensions are visualized in the upper left and right panel; PCA-biplot is visualized in the lower panel

breeding programs (Gwazel and Bridgwaterz 2002). This approach ensures that selected traits are consistent over time, which is crucial for long-term breeding success (Isik 2014; Kim et al. 2024). In this study, the PCA-biplot and composite scoring methods provided consistent results, with seven families consistently identified as elite across study years. The PCA-biplot, through visualizing the interactions among traits, offers a valuable tool to traditional scoring methods, enabling the identification of families with complex trait profiles.

Platycladus orientalis is a species of significant ecological and timber value, with traits such as height and diameter playing a critical role in evaluating growth. These traits provide reliable and robust assessments when analyzed collectively (Gwazel and Bridgwaterz 2002). Consistent performance of growth traits over multiple years is essential for the success of genetic breeding programs (Hasan et al. 2021). In addition to growth traits, reproductive output is equally important in seed orchard management. Traits influencing reproductive success are vital for ensuring sustained genetic improvement (Jiang et al. 2019). However, several studies have focused narrowly on either growth or reproductive traits, often leading to the selection of individuals with overly homogenous characteristics. This narrow focus has introduced limitations in the seed orchard selection process, reducing genetic diversity and adaptability. To address these challenges, our study adopted an integrated approach by combining genetic parameters for both growth and reproductive traits with gamete contributions. Principal Component Analysis (PCA) biplots and the composite score method were used to comprehensively evaluate families. This approach overcomes the limitations of prior studies that emphasized single traits, enabling the identification of families with diverse and desirable characteristics. By doing so, it supports the development of more resilient and productive seed orchards for *P. orientalis* improvement.

In this study, distinct growth patterns were observed across families (Jansson et al. 2003; Zhao et al. 2019), particularly among families with contrasting genetic parameters and gamete contributions. Although family rankings varied across growth years, seven families were consistently identified as elite under different selection

methods throughout the study period. This highlights the importance of selecting appropriate methods for elite family selection. The PCA-biplot results corroborated the elite families identified through the composite scoring method, further validating the reliability of these selection techniques. In addition, 12 families were selected as superior families in both 2008 and 2021 based on the composite score method. These families demonstrated fast growth over multiple years, a finding consistent with earlier studies (Jansson et al. 2003).

4.4 Genetic gain and seed orchard management and advancement

Genetic gain is a critical metric for selecting elite families and is one of the most direct indicators of evaluating the effectiveness of seed orchards in tree improvement (Zhao et al. 2019). Most breeding programs aim to maximize genetic gain, which may be achieved by setting appropriate breeding strategies such as adjusting selection ratios and intensities (Sotelo Montes et al. 2008). Relatively high genetic gain can be achieved when selection relies on high heritability, broad genetic variation, and low selection intensity (Hong et al. 2014). Moreover, the genetic gain of seed orchards is strongly influenced by breeding strategies and selection intensity, as they directly affect the selection of elite families (Leksono et al. 2006; Lee et al. 2021).

Our results demonstrate that higher selection intensities yield greater genetic gains. This is consistent with the findings with other conifer species (Chen 2006; Zhao et al. 2019). The combination of 30% selective harvesting and 50% thinning achieved the highest genetic gains across all traits in both study years, making it a promising strategy for seed orchard crop management. Our results are consistent with Lee et al. (2021) who also emphasized the importance of selecting the optimal combination of breeding strategies to maximize genetic gain. We suggest that, for future genetic improvement of conifer seed orchards, breeding strategies should be tailored to specific improvement objectives and the genetic characteristics of the target population. Additionally, simulation of different improvement strategies can further support the development and optimization of seed orchard management, ensuring sustainable and efficient genetic improvement. These simulations can help fine-tune harvesting selection methods and increase the long-term success of breeding programs. Simulation models can also predict genetic gain under different scenarios, guiding decision-making in seed orchard improvement.

Conclusion

In the process of optimizing seed crop genetic gain and genetic diversity within seed orchards, developing optimal strategies and selection ratios is crucial for identifying superior families. In this study, significant differences in phenotypic and genetic variation parameters were observed among families across various growth traits. Notably, no significant correlation was found between growth traits and reproductive traits, highlighting the need to integrate both aspects for a comprehensive evaluation of each family. To achieve this, we employed two methods, including comprehensive scoring and PCA-biplot analysis, to evaluate families holistically. Across study years, seven families were consistently identified as elite under different selection methods. Importantly, all elite families identified via PCA-biplot were also present among those selected through comprehensive scoring. Additionally, 12 families were consistently rated as outstanding by the scoring method over both growth periods. These elite families exhibited rapid and stable growth across traits during the study years. Under selective harvesting and selective thinning strategies, elite families were selected using selection ratios of 30 and 50%, respectively, with corresponding genetic gains calculated for each scenario. Collectively, this work establishes an integrated framework for balancing genetic gain and diversity in conifer breeding programs. The proposed strategy (30% selective harvesting and 50% selective thinning) and identified elite families provide actionable solutions for *P. orientalis* improvement, with methodological implications extending to other conifers in sustainable forestry.

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Author contributions J.F.M. and S.Q.J. conceived and designed the study. M.Y.L., Y.T.B., Z.C.L., S.Q.J., H.J.Z., S.P.C., and X.L.Y. prepared the materials, conducted the experiments, analyzed the data, and compiled the results. S.Q.J. drafted the manuscript, while M.Y.L., Y.A.E., S.P.C., and J.F.M. contributed to data interpretation and the finalization of the manuscript draft. All authors reviewed and approved the final version of the manuscript.

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Data availability Data of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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