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High genetic gains in wood volume and fecundity can be both achieved by direct selection in half-sib families of *Pinus yunnanensis* Franch

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Abstract

Key message This study demonstrates the potential of *Pinus yunnanensis* Franch. for multi-trait selection in breeding programs, highlighting positive co-variation of growth traits with fecundity, trunk straightness, and crown health in 16-year-old progenies. Integrated trait selection could enhance wood productivity and seed yield, supporting both commercial and ecological goals in reforestation efforts.

Context The genetic improvement of *P. yunnanensis*, a species widely used for reforestation in Southwest China, is essential due to its economic importance and adaptability to harsh environments. Despite its extensive use, studies on mature trees are limited, particularly in multi-trait selection involving fecundity and trunk quality.

Aims This study aimed to characterize phenotypic variation among and within provenances of *P. yunnanensis*, explore relationships among key traits, and evaluate the feasibility of joint selection for growth, fecundity, and trunk straightness.

Methods We evaluated nine phenotypic traits in 3467 plus-tree progenies from six provenances in a common garden setting. Using structural equation modeling and "random forest" analysis, we identified key predictors of cone production and trunk straightness and assessed trait interrelationships.

Results Significant phenotypic variations were observed among and within provenances of *P. yunnanensis*, with intra-provenance variation accounting for most of the total variation. Notably, 16.2% of trees exhibited twisted trunks, leading to a 14.9% decrease in wood volume compared to trees with straight trunks. The top 20% of individuals contributed 87.8% of total cone production, indicating substantial variation in fecundity. Growth, crown size, and crown health positively correlated with fecundity and trunk straightness, with tree height and diameter being the most important predictors. Both pairwise and multivariate analyses revealed significant and positive relationships among growth, fecundity, and crown health, suggesting high potential for multi-trait selection.

Conclusion This study supports the feasibility of combined selection to optimize wood productivity, cone production, and crown health in breeding programs. These findings provide a valuable foundation for refining *P. yunnanensis*

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breeding strategies that meet the dual demands of economic utility and environmental adaptation in a changing climate.

Keywords Cone production, Crown health, Multi-trait selection, Phenotypic integration, Trunk straightness

1 Introduction

Forest degradation is a growing global concern, leading to biodiversity loss, soil erosion, and increased carbon emissions. Reforestation and afforestation efforts, including species-specific breeding programs, are crucial strategies to counter these environmental challenges (IUCN and WRI 2014). However, reforestation with native species often requires substantial genetic improvement to ensure that trees can both thrive in degraded environments and meet commercial standards. For reforestation efforts, genetic variation within and among populations is essential, as it enables breeders to identify high-quality provenances and families that can maximize genetic gains through targeted selection (Singh and Thapliyal 2012; Diao et al. 2016).

Pinus yunnanensis Franch. is naturally distributed in a variety of geographical areas ranging from 23° to 30° N and 96° to 108° E at elevations from 700 to 3000 m a.s.l. in Southwest China. The existing forest area covers over 6 million hectares, and the forest stock volume was 28.7 million m^3 (Yang et al. 2019). Features like high-quality wood, deep-rooting, drought resistance, and tolerance of poor, rocky soils make *P. yunnanensis* a desirable forest species extensively used in reforestation and restoration efforts. In addition, as one of the most important commercial and industrial raw materials, *P. yunnanensis* can be used for high-value solid wood products such as furniture. Unfortunately, after prolonged anthropogenic disturbance including agriculture development, overharvesting for timber, and natural disasters, the *P. yunnanensis* resource has been damaged and the remaining, lower-quality forests (e.g., with twisted stems) mainly regenerate naturally. To restore these forests effectively, selective breeding and genetic improvement are essential.

Pine breeding programs worldwide have used common garden plantations to assess phenotypic variability within and between provenances and families. For species like *P. radiata* D. Don and *P. pinaster* Aiton, breeding programs are well-established and have focused on multi-trait selection, including growth, wood quality, and adaptability traits (Cameron et al. 2012; Climent et al. 2024). These programs have advanced to include long-term assessments of traits like fecundity and trunk straightness that are critical for both reproductive success and wood quality. In comparison, the breeding program for *P. yunnanensis* is still in its early stages. Initial breeding efforts have primarily focused on assessing genetic diversity within and among natural populations (Xu et al. 2016) and selecting provenances with superior growth traits (Liu et al. 2022). However, a large environmental variability across the natural range of this species complicates the establishment of standardized tests, thus hindering consistent assessment of genetic variation (Kang et al. 2003). Additionally, due to the long reproductive cycle of *P. yunnanensis*, traits such as trunk straightness and fecundity (e.g., cone production) cannot be evaluated in the early years. As a result, most research has focused on short-term growth assessments of young families or seedlings (Liu et al. 2022). Such studies overlook reproductive capacity (fecundity) and trunk straightness, which are critical for producing high-quality breeding material that meets the demands of both developing high-quality seed orchards and commercial use. This situation highlights an urgent need to evaluate the feasibility of a multi-trait selection approach for *P. yunnanensis* that includes fecundity and trunk straightness, along with traditional growth traits, to better address the breeding requirements of *P. yunnanensis*.

Understanding fecundity variation is essential for managing seed orchards, predicting plant fitness, and influencing population dynamics (Singh and Thapliyal 2012; Ayari et al. 2014; Davi et al. 2016). Selecting individuals with high reproductive output could significantly enhance seed production, as inter-individual seed production variability within a single year can vary by up to two orders of magnitude (Krouchi et al. 2004). This variation can result from several endogenous factors, including tree size, crown structure, and branching architecture (Davi et al. 2016; Harja et al. 2012). Moreover, stem straightness is a crucial characteristic in forestry due to its significant impact on wood quality and processing efficiency. Crooked stems often produce inferior timber, including compression wood and irregular grain patterns (MacDonald et al. 2009; Cameron et al. 2012). Therefore, improving stem straightness is a primary goal in tree breeding. Visual scoring systems are commonly used to assess straightness, enabling breeders to integrate these evaluations into multi-trait selection indices for greater efficiency and economic value (Río et al. 2004; Cameron et al. 2012; Kim et al. 2020). However, understanding how endogenous traits correlated to fecundity and trunk straightness remains challenging, particularly for *P. yunnanensis*, and limits the ability to develop robust,

multi-trait breeding strategies. In forest tree breeding, simultaneous improvement of multiple traits, such as growth, wood properties, and fecundity, often relies on correlations among traits (Murren 2012; Climent et al. 2024). Recent studies indicate that certain growth traits, such as crown height, are useful predictors of seed and cone production in forest stands (Ayari et al. 2012). Cone production, in particular, has been shown to increase with tree diameter, height, and crown volume (Goubitz et al. 2004). However, trade-offs often arise in resource allocation between growth and reproductive investment, as reproduction demands resources that could otherwise be used for vegetative growth (Knops et al. 2007; Lundgren and Marais 2020). Likewise, stem straightness, under strong genetic control, can modulate tree growth (Río et al. 2004). For example, in younger stands, stem straightness is correlated to the height-to-diameter ratio and overall tree height (Mahmood et al. 2003; Cameron et al. 2012), underscoring the importance of understanding these relationships in multi-trait selection (Hai et al. 2015; Yin et al. 2017).

As forest management objectives have evolved to include a broader array of ecosystem services (Garzón 2021), breeding programs now emphasize the selection of trees with broad adaptability to both biotic and abiotic stressors, rather than focusing solely on productivity. This shift acknowledges the need for resilience in forest ecosystems as well as the economic demands placed on reforested stands (Santini et al. 2019; Climent et al. 2024). Given that trade-offs among phenotypic traits can profoundly affect the conservation of forest genetic resources, it is essential to determine if economically important traits can be separated from detrimental effects (Climent et al. 2024). Beyond simple pairwise correlations, a complex multivariate approach known as phenotypic integration is gaining prominence in recent biological research (Santini et al. 2019; Garzón 2021). Research on phenotypic integration has primarily aimed to verify strong correlations among traits within a single functional unit (module), which refers to a set of traits that are biologically related and function together to influence a particular aspect of the organism's phenotype (Murren 2012). For instance, growth and fecundity could be viewed as two distinct modules; thus, investigating their phenotypic integration would involve examining correlations within each module as well as the independence between them. Structural equation modeling (SEM) provides a valuable statistical approach for testing complex relationships among multiple traits, making it particularly suitable for forest tree breeding (Garzón, 2021). While SEM has been largely applied to ecological studies, its potential remains largely untapped in tree breeding programs, where it could provide valuable insights for multi-trait selection, especially for relatively understudied species like *P. yunnanensis*.

In this study, we evaluated nine phenotypic traits in a common garden trial of 3467 plus-tree progenies, aged 16 years (half a rotation period), from six provenances of *P. yunnanensis* in Southwest China. Our analysis focused on characterizing phenotypic variation among and within provenances, with an emphasis on key traits such as cone production, trunk straightness, and crown health, as well as their relationships with traditional growth traits like tree height, diameter at breast height, and wood volume. Specifically, the objectives were to (1) characterize the variation of each trait within and among provenances; (2) assess inter-trait relationships, exploring patterns of co-variation and potential trade-offs; and (3) evaluate the feasibility of multi-trait selection strategies that aim for simultaneous improvements in growth, trunk straightness, and fecundity, contributing valuable insights for advancing *P. yunnanensis* breeding efforts.

2 Materials and methods

2.1 *Pinus yunnanensis* common garden

The studied *P. yunnanensis* common garden is located in Lufeng County, central Yunnan Province (102° 12′ E, 25° 13′ N), at an altitude of 1860 m in the transition area from the subtropical humid climate in eastern Yunnan to the sub-humid climate in southwest Yunnan. The climate is characterized by dry and warm winters and humid and hot summers with 15.5 °C mean annual temperature and 900–1000 mm mean annual precipitation. The dry season extends from November to April, accounting for 6–17% of the annual precipitation. The common garden was installed in 2006, by multiplying 179 plus trees from six provenance regions, including Anning County (AN), Qujing City (QJ), Yongren County (YR), Yulong County (YL), Tengchong County (TC), and Ninglang County (NL), with 30 families per provenance, except for one provenance with 29 families (Table 1). The minimum distance between any two provenances was over 30 km, and they were located in variable geographical sites and separated by a typical topographic feature such as a mountain ridge, forest, city, or river. Plus trees were selected using a comparison method, in which candidate trees were evaluated against neighboring trees of similar age and growing conditions to ensure they exhibited superior phenotypic traits. Selected trees were spaced at least 100 m apart to minimize the likelihood of close genetic relationships. The common garden has an area of about 3 ha, with a random block design, and a planting scheme of 2 m × 3 m. To minimize environmental variation across the study site, a horizontal banding method was used for land preparation prior to planting. In each block, six

Table 1 Geographic locations of plus tree selection sites and the number of families and individuals in the test

Provenance	Site	Longitude (°E)	Latitude (°N)	Altitude (m a.s.l.)	Plus tree number	Plus-tree progeny number
AN	Anning	102.26	24.73	1920	29	576
QJ	Qujing	103.4	26.4	2320	30	586
YR	Yongren	101.6	26.34	2055	30	568
YL	Yunlong	99.25	25.94	2392	30	571
TC	Tengchong	98.32	25.37	2125	30	582
NL	Ninglang	100.37	27.29	2870	30	585

provenances were randomly arranged, and families were randomly arranged within the provenance. Five plants of each family were arranged in rows, and the block was repeated 4 times. A total of 3467 plus-tree progenies of 179 plus trees (families) from six provenances were used for the test.

2.2 Measurement of phenotypic traits

Nine phenotypic traits were measured on living plants of each family in October 2022 at the age of 16 years. The traits measured included quantitative traits (plant height, diameter at breast height, crown diameter, height under the branch, wood volume, and cone production) and qualitative traits (trunk straightness and crown health). Tree height (*H*, m) was directly measured by the Vertex Laser instrument (DZH-30, Haerbin, China), and diameter at breast height (*D*, cm) was measured with a circumference ruler. The crown diameter and height under the branch (TH, m) were measured with a tower ruler. Long crown diameter (LCD, m) and short crown diameter (SCD, m) were referred to as the maximum and minimum tree crown diameter, respectively. The wood volume (V, m^3) was estimated using the formula ($V = 0.000058290117 D^{1.9796344} H^{0.90715154}$) proposed by forestry industry standard for *P. yunnanensis* (Agriculture and Forestry Ministry of China 1977). The cone of *P. yunnanensis* can be retained in the canopy for many years, so we recorded the number of open and closed cones as cone production (CP) in the canopy, including serotinous and non-serotinous cones for evaluating fecundity. We used a grading system to describe the two qualitative traits by purely visual assessment. The trunk straightness (ST) was described by the stem sinuosity classification: 1—for a very twisted stem with > 2 serious bends (serious bends occur when the main stem is bent to the right or left with more than 20° along its axis); 2—for twisted stem with 2 serious bends; 3—for slightly twisted stem with 1 serious bend and/or > 2 small bends (small bends occur when the main stem is bent to the right or left with less than 10° along its axis); 4—for almost straight stem with 1–2 small bends; and 5—for a perfectly straight stem (Hai et al. 2015; Yin et al. 2017). Crown health (CH) was assessed through visual observation and used as an indirect indicator of a tree's potential resilience or adaptability to disturbance (Hartini and Ompusunggu 2019; Kim et al. 2020). The grade was scored 1—for very unhealthy crown with > 50% crown damaged; 2—for unhealthy crown with 30–50% crown damaged; 3—for less healthy crown with 10–30% crown damaged; 4—for moderate healthy crown with less than 10% crown damaged; and 5—for healthy crown with a perfectly crown.

2.3 Data analyses

All statistical analyses were conducted in the R environment (version 3.6.3). A Nested variance analysis was performed to assess the significance of differences and to partition the variation in phenotypic traits among and within provenances. The linear model used was:

$$Y_{ijlk} = \mu + B_i + P_j + F_{l(j)} + \varepsilon_{ijlk}$$

where Y_{ijlk} is the kth observation value of the lth family in the jth provenance within the ith block. In this model, μ represents the overall mean, B_i is the fixed effect of the ith block, P_j is the main effect of the jth provenance, $F_{l(j)}$ is the random effect of the lth family nested within the jth provenance, and ε_{ijlk} denotes the experimental error.

Due to the data distribution characteristics, square-root transformations were applied to qualitative and count traits (e.g., CP, ST, and CH) before analysis. Multiple comparisons among provenances were conducted using a non-parametric test (Wilcoxon signed-rank test) to determine significant differences. The phenotypic differentiation coefficient was calculated as the ratio of among-provenance variance to total variance, indicating the extent of phenotypic variation attributed to provenance differences (Gandour et al. 2007). Spearman rank correlation was performed to assess the relationships among phenotypic

traits. To explore the dimensional structure of the data and identify dominant patterns, principal component analysis (PCA) was conducted on a standardized matrix containing data on all nine phenotypic traits.

Based on the PCA results, a structural equation model (SEM) was developed to examine the direct and indirect pathways among traits, using growth (*H*, *D*, *V*), crown size (LCD, SCD, TH), fecundity (CP), trunk straightness (ST), and crown health (CH) as variables. SEM analyses were conducted using the "Lavaan" package in R (Rosseel 2012). An a priori model was created to illustrate hypothesized interactions among these traits. We tested our proposed causal pathways by comparing the model with observations, allowing us to validate or refine our hypotheses and evaluate the fit between our model and the data. Model fit was assessed using the goodness of fit index (GFI), chi-square test, and standardized residual root mean square (SRMR). The model was considered acceptable if chi-square tests were not significant, GFI > 0.95, and SRMR < 0.08 (Grace et al. 2016). From the SEM results, we obtained standardized direct, indirect, and total effects, along with associated *P*-values, to explain the relative influences of each trait.

To further investigate the importance of specific traits in predicting fecundity (CP) and trunk straightness (ST), random forest (RF) analysis was performed using the "randomForest" package. For fecundity (CP), RF regression was conducted with growth traits (*H*, *D*, *V*), crown size (LCD, SCD, TH), trunk straightness (ST), and crown health (CH) as predictors. For the trunk straightness (ST), RF classification analysis was conducted with growth traits (*H*, *D*, *V*), crown size (LCD, SCD, TH), crown health (CH), and fecundity (CP) as predictors. Predictor importance was measured by the percentage increases in mean squared error (MSE) and mean decrease in accuracy; higher values indicated greater importance (Breiman et al. 2001). Each RF model used 1000 decision trees to ensure stable importance measures, and predictor significance was further validated using the "rfPermute" package. Multiple regression models with variance decomposition analysis were also used to complement the RF results, employing the "lm" and "calc.relimp" functions in the "relaimpo" package.

2.4 Superior families and individual selection method

To identify superior families and individuals in the common garden, we used the membership function method and principal component analysis. First, based on the values of the nine phenotypic traits, we applied the membership function method from fuzzy mathematics to calculate the membership function value for each trait. The membership function value $U(X_{ij})$ was calculated as:

$$U(X_{ij}) = (X_{ij} - X_{i\min})/(X_{i\max} - X_{i\min})$$

where $U(X_{ij})$ is the membership function value of the *i*th trait of the *j*th individual, X_{ij} is the observed value of the *i*th trait for the *j*th individual, $X_{i\min}$ is the minimum value of the *i*th trait, and $X_{i\max}$ is the maximum observed value for the *i*th trait (Su et al. 2016). All families and individuals were then ranked based on the average membership function values of traits, and superior families and individuals were selected with a selection rate of 10%.

Principal component analysis (PCA) was also used for selection. We extracted principal components with a cumulative contribution rate above 90% and then calculated the comprehensive weight of each principal component by dividing its variance contribution rate by the total accumulative contribution rate. Families and individuals were then ranked based on the comprehensive trait score, and the top 10% were selected as superior.

3 Results

3.1 Variations in phenotypic traits among and within provenances

The nine phenotypic traits varied significantly among and within provenances (Table 2). However, as illustrated in Fig. 1, the absolute differences in trait values among provenances were generally small, resulting in a high degree of homogeneity across provenances. Despite this general homogeneity, some trends were observable. The values of growth traits, including plant height (*H*), diameter at breast height (*D*), wood volume (*V*), and crown diameters (LCD and SCD), as well as for cone production (CP), were the largest in the Yongren provenance. Traits associated with stem shape, such as stem height under the branches (TH) and trunk straightness (ST), showed slightly higher averages in Anning and Yongren than in other provenances. Conversely, Ninglang presented the lowest mean values for most of the traits. Crown health (CH) was higher in Yongren and relatively lower in Qujing, yet the differences remained minor. Overall, the Yongren provenance displayed somewhat superior phenotypic traits and Ninglang showed relatively lower values.

3.2 Phenotypic variance characteristics among and within provenances

According to the results of nested analysis of variance, the proportion of different variance components to the total variation was analyzed (Fig. 2). On average, the variance among provenances accounted for 6.3% of the total variation, while the variance among families within provenances accounted for 27.6%. The remaining 66.0% was attributed to individual and error variance, which reflects the phenotypic variation at the individual tree level and measurement error. Growth traits including plant height

Table 2 Nested variance analysis of phenotypic traits among and within *P. yunnanensis* provenances

Traits	Mean square (Df)				*F* value		
	Block	Provenance	Family	Residuals	Block	Provenance	Family
H	0.97 (3)	497.15 (5)	38.69 (173)	3.73 (3286)	0.26	133.37***	10.38***
D	5.04 (3)	910.04 (5)	90.61 (173)	9.78 (3286)	0.52	93.03***	9.26***
V	0.001 (3)	0.234 (5)	0.022 (173)	0.002 (3286)	0.26	110.02***	10.39***
LCD	0.23 (3)	87.98 (5)	6.63 (173)	0.69 (3286)	0.34	128.28***	9.67***
SCD	0.09 (3)	84.27 (5)	6.73 (173)	0.70 (3286)	0.13	120.52***	9.63***
TH	0.19 (3)	2.18 (5)	0.34 (173)	0.07 (3286)	2.55	29.62***	4.59***
ST	0.06 (3)	1.06 (5)	0.19 (173)	0.06 (3286)	1.12	18.32***	3.27***
CP	0.44 (3)	60.84 (5)	7.15 (173)	2.03 (3286)	0.22	29.95***	3.52***
CH	0.03 (3)	0.26 (5)	0.07 (173)	0.02 (3286)	1.96	14.33***	3.69***

*** $P < 0.001$; *H*, plant height; *D*, diameter at breast height; *V*, wood volume; *LCD*, long crown diameter; *SCD*, short crown diameter; *TH*, height under the branch; *ST*, trunk straightness; *CH*, crown health; *CP*, cone production

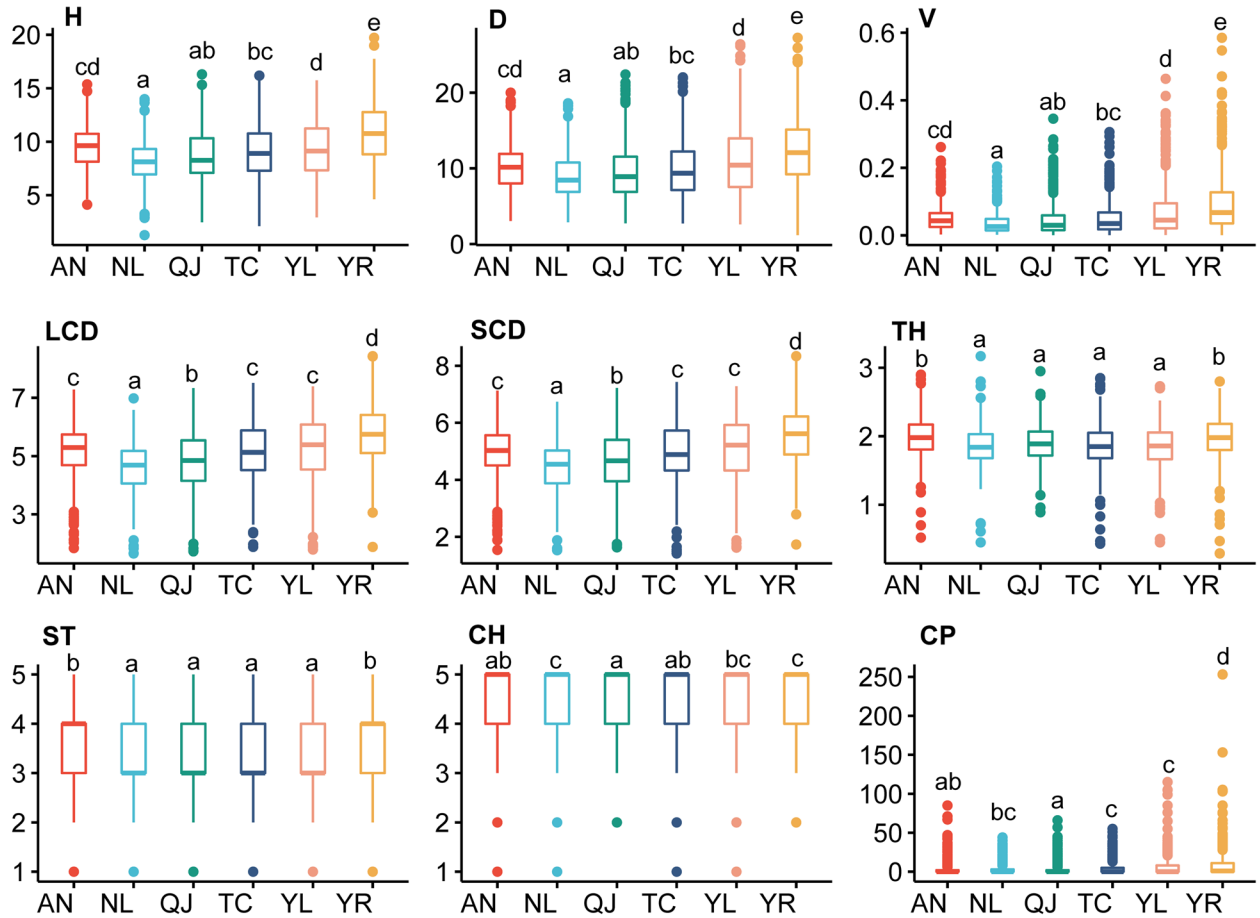

Fig. 1 Phenotypic traits of six *P. yunnanensis* provenances. Different letters within each graph indicate significant differences at $P < 0.05$ based on the Wilcoxon signed-rank test. *H*, plant height (m); *D*, diameter at breast height (cm); *V*, wood volume ($m.^3$); LCD, long crown diameter (m); SCD, short crown diameter (m); TH, height under the branch (m); ST, trunk straightness; CH, crown health (scale 1–5); CP, cone production (number of cones). Provenances are AN (Anning), QJ (Qujing), YR (Yongren), YL (Yulong), TC (Tengchong), and NL (Ninglang)

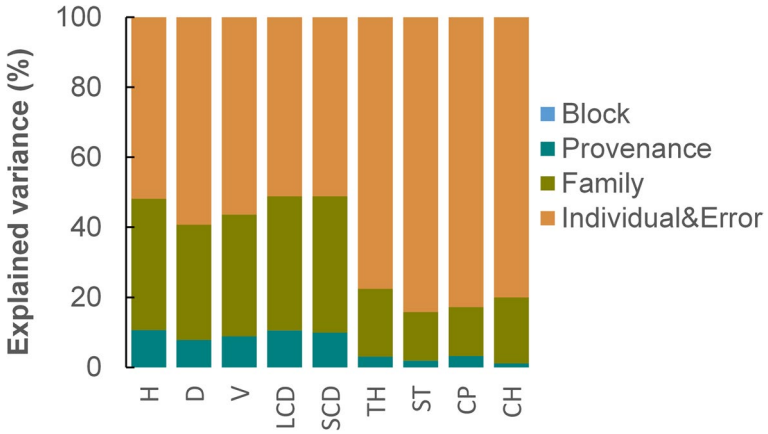

Fig. 2 The variance components of the phenotypic traits of *P. yunnanensis*. *H*, plant height; *D*, diameter at breast height; *V*, wood volume; LCD, long crown diameter; SCD, short crown diameter; TH, height under the branch; ST, trunk straightness; CH, crown health; CP, cone production

(*H*), diameter at breast height (*D*), and wood volume (*V*) had higher variance components at the provenance and family levels compared to traits related to stem shape (TH and ST), cone production (CP), and crown health (CH). Overall, the phenotypic differentiation coefficients for each trait were less than 50%, and the average value of the phenotypic differentiation coefficient of nine traits was 17.0%, indicating that a large diversity of phenotypic traits was within provenances rather than among them, and the family component contributed substantially to the variation, particularly in growth traits.

3.3 Distribution characteristics of the trunk straightness and cone production in the common garden

In the common garden, 16.2% of trees displayed twisted trunks (grades 1 and 2), while only 14.7% exhibited excellent trunk straightness (graded 5) (Fig. 3A). Trees with straighter trunks contributed a higher proportion of wood volume; although only 14.7% of the trees achieved grade 5 straightness, these trees accounted for 20.7% of the total wood volume. This suggests a positive association between trunk straightness and wood volume. Cone production was highly uneven among individuals, with the top 20% of trees contributing 87.8% of the total cone production (Fig. 3B). Trunk straightness was correlated with other traits, which differed among trunk straightness grades (Fig. 4). In general, trees with higher trunk straightness grades had large mean values for growth traits. However, cone production tended to be lower in trees with straighter trunks.

3.4 Correlation analysis between phenotypic traits

Positive correlations were detected among traits associated with growth, including plant height (*H*), diameter at breast height (*D*), wood volume (*V*), and crown diameter (LCD and SCD) (Fig. 5A). These growth traits were also correlated with stem shape traits (TH and ST) and crown health (CH). Principal component analysis (PCA) confirmed two main clusters of traits (Fig. 5B). The first component (Dim1), explaining 54.5% of the total variation,

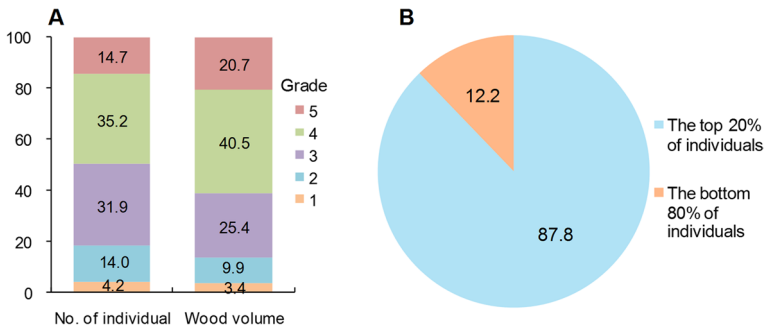

Fig. 3 Distribution characteristics of trunk straightness and cone production in *P. yunnanensis* individuals in the common garden. **A** Distribution percentage (%) of individual counts and cumulative wood volume across different trunk straightness grades. **B** Distribution percentage (%) of total cone production contributed by the top 20% of individuals compared to the bottom 80%

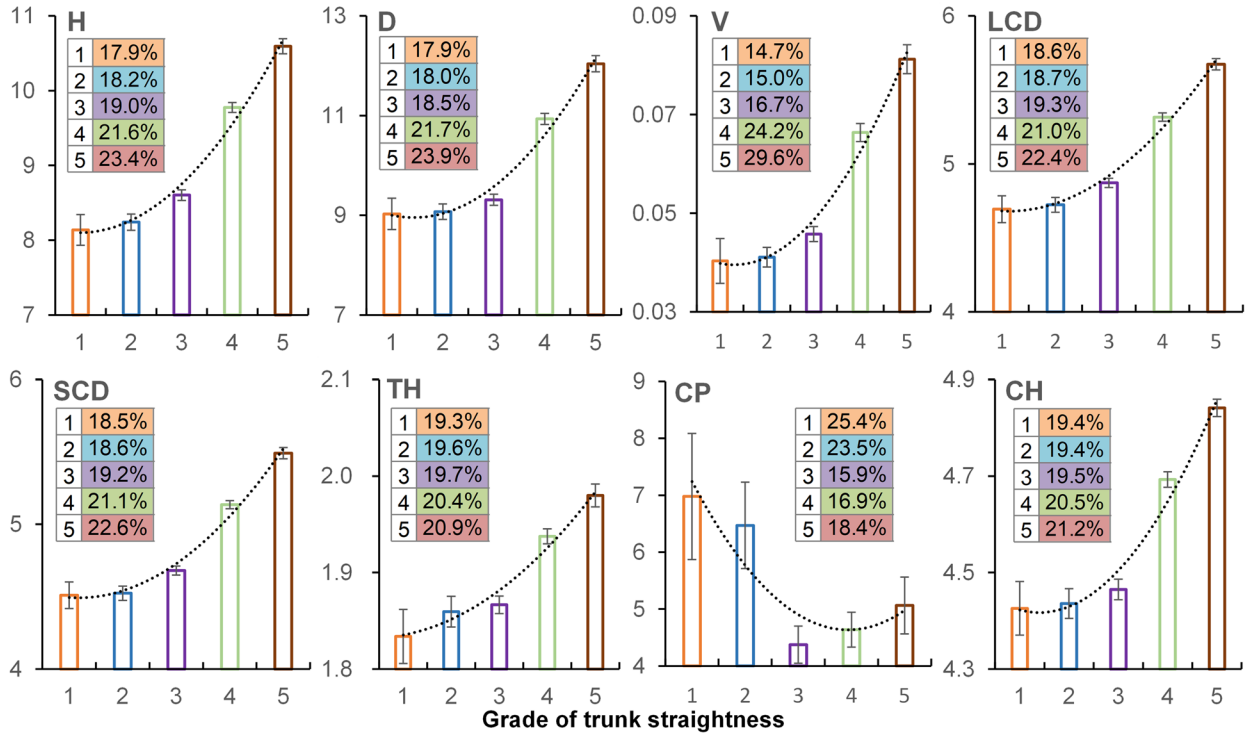

Fig. 4 Mean values and distribution percentage (%) of phenotypic traits according to the 5 straightness classes. *H*, plant height (m); *D*, diameter at breast height (cm); *V*, wood volume (m.^{3}); LCD, long crown diameter (m); SCD, short crown diameter (m); TH, height under the branch; ST, straightness of the trunk (m); CH, crown health (scale 1–5); CP, cone production (number of cones)

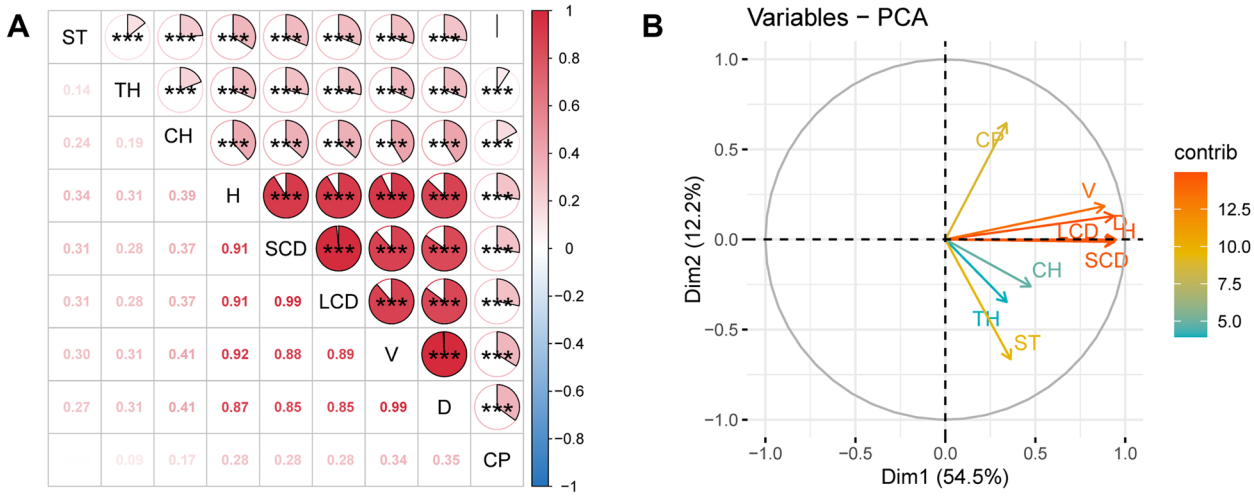

Fig. 5 Correlation analysis between phenotypic traits of *P. yunnanensis*. **A** Spearman correlation coefficients (*r* values) among nine phenotypic traits. *** $p < 0.001$. **B** Principal component analysis of phenotypic traits. *H*, plant height; *D*, diameter at breast height; *V*, wood volume; LCD, long crown diameter; SCD, short crown diameter; TH, height under the branch; ST, Trunk Straightness; CH, crown health; CP, cone production

was mainly linked to growth traits. The second component (Dim 2), explaining 12.2% of the variation, was primarily associated with straightness (ST) and cone production (CP). These clusters confirmed the grouping of growth traits, trunk straightness, and cone production as distinct categories.

Based on the PCA results, we used SEM analysis to explore the relationships among growth, crown size,

fecundity, trunk straightness, and crown health (Fig. 6). The SEM results showed that crown health was directly and positively correlated with growth, crown size, trunk straightness, and fecundity, the path coefficients of which were 0.366, 0.388, 0.211, and 0.127, respectively. Crown health was associated with both trunk straightness and fecundity, with growth and crown size potentially mediating this relationship. Furthermore, growth and crown size displayed direct associations with trunk straightness (path coefficients of 0.256 and 0.300, respectively) and fecundity (0.322 and 0.241, respectively), with indirect associations mediated through interactions between growth and crown size. A weak negative correlation was observed between trunk straightness and fecundity.

3.5 Important phenotypic traits for predicting cone production and trunk straightness

To examine the importance of phenotypic traits in relation to cone production (CP) and trunk straightness (ST), we identified the significant predictors for CP and ST by random forest (RF) analysis (Fig. 7A). Growth traits including plant height (*H*), diameter at breast height (*D*), and wood volume (*V*) were the most important predictors for both CP and ST. Other relevant variables were crown diameter (LCD and SCD) for predicting CP, and SCD and CP being important for predicting ST. These observations differed somewhat from the results of multivariate regression analysis (Fig. 7B), which showed that CP was most strongly associated with *D* (effect size = 0.25). For ST, the strongest association was with *H* (effect size = 0.34). These results suggest that *D* and *H* had the greatest relative importance in association with CP and ST, respectively.

3.6 Superior families and individual selection of *P. yunnanensis*

Based on the selection criteria using the membership function method (SMF) and principal component analysis (PCA), we identified 18 superior families, with 16 families overlapping between the two methods (Fig. 8A). The actual gain for each trait in these families ranged from approximately 5% to 143%, with wood volume and cone production showing the higher gain (Fig. 8B). The mean actual gain of the overlapping families selected by both methods (PCA*SFM) was higher than when selected by either method individually.

For superior individuals, 347 individuals were selected by each method, with 290 individuals overlapping between the two methods, representing an 8.36% selection rate (Fig. 9B). These superior individuals spanned 101 families for SMA and 90 families for PCA, with 87 families overlapping (Fig. 9A). The Yonren provenance contained the highest number of superior individuals and families, and Ninglang the lowest (Fig. 9D). The actual gain of traits in these individuals ranged from approximately 7% to 244%, with the higher gains in wood volume and cone production but the lowest in crown health (Fig. 9C).

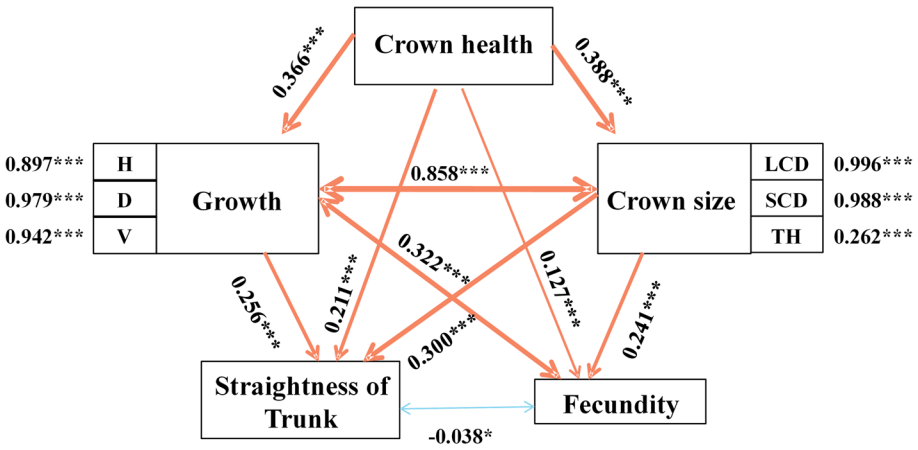

Fig. 6 Structural equation model (SEM) illustrating the relative relationships among crown health (CH), growth, crown size, straightness of trunk (ST), and fecundity (CP). The test parameters were comparative fit index (CFI) = 0.966, standardized root mean square residual (SRMR) = 0.045, root mean square error of approximation (RMSEA) = 0.078. Standardized regression weights are shown for each path, with arrow widths indicating the strength of the relationships (red = positive; green = negative). *$P < 0.05$ and ***$P < 0.001$. *H*, plant height; *D*, diameter at breast height; *V*, wood volume; LCD, long crown diameter; SCD, short crown diameter; TH, height under the branch

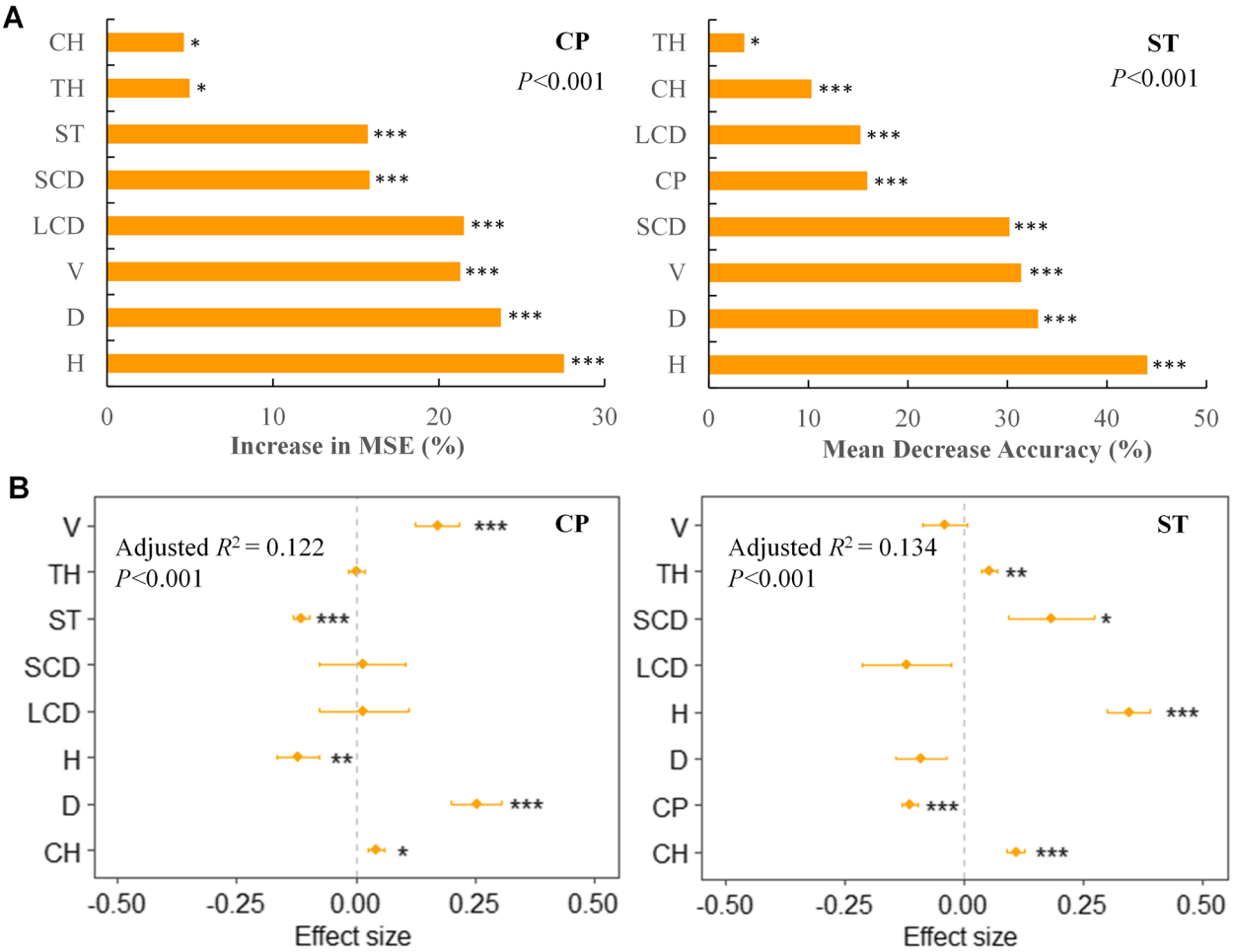

Fig. 7 Important phenotypic traits for predicting cone production (CP) and trunk straightness (ST). **A** Importance of phenotypic traits to CP and ST based on random forest analysis with 1000 decision. Predictor importance is estimated by the percentage increases in mean squared error (MSE) and mean decrease in accuracy. **B** Effect size (mean ± SE) of phenotypic traits on CP and ST based on multiple regression models. *$P < 0.05$ and ***$P < 0.001$. *H*, plant height; *D*, diameter at breast height; *V*, wood volume; LCD, long crown diameter; SCD, short crown diameter; TH, height under the branch, CH, crown health

4 Discussion

We found that intra-provenance phenotypic diversity was the primary source of variation in *P. yunnanensis*. Tree height and diameter were the most important predictors of the straightness of trunk and cone production, respectively. Furthermore, both pairwise correlations and multivariate correlations by SEM yielded significant and positive relationships among growth, fecundity, and crown traits, suggesting a phenotypic integration, and the potential for combined selection of these traits.

4.1 Phenotypic variation characteristics

In natural environments, populations often exhibit significant phenotypic variations due to genetic-environmental interaction (Leal-Sáenz et al. 2020). Our study demonstrated that the nine assessed phenotypic traits in *P. yunnanensis* varied significantly both within and among provenances (Table 2; Fig. 1), which was consistent with earlier reports on other conifer plants (Ji et al. 2011; Singh and Thapliyal 2012; Leal-Sáenz et al. 2020). Specifically, the contribution of intra-provenance variation accounted for a majority of the total variation (Fig. 2). This pattern is shared with other outcrossing conifers, where high pollen-mediated gene flow results in substantial variation within the provenance (Rubio-Moraga et al. 2012), as observed in *P. albicaulis* Engelm. (Garcia et al. 2009) and *P. tabuliformis* Carr. (Ji et al. 2011). *P. yunnanensis* has high outcrossing rates and a general intolerance of selfing. This cross-pollinated plant with winged seeds and air sacs in pollen can be dispersed at long distances, resulting in high levels of gene flow between populations and weakening genetic differentiation between populations. However, unlike highly

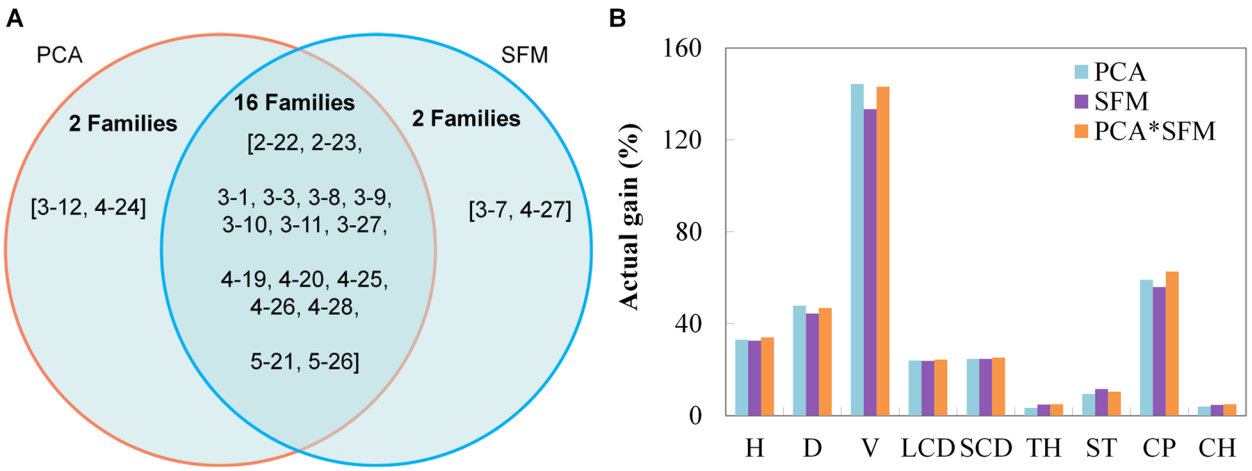

Fig. 8 Superior families of *P. yunnanensis* selected from the common garden trial. **A** Venn diagram showing the number of superior families selected by the membership function method (SFM), principal component analysis (PCA), and families identified by both methods (PCA*SFM); **B** the actual gain (%) of each trait among the superior families selected by SFM, PCA, and the families selected by both methods (PCA*SFM). *H*, plant height; *D*, diameter at breast height; *V*, wood volume; LCD, long crown diameter; SCD, short crown diameter; TH, height under the branch; ST, trunk straightness; CP, cone production; CH, crown health

domesticated pines such as *P. radiata*, which display relatively greater inter-provenance variation due to selective breeding within specific environmental zones (Wu et al. 2007; Raymond and Henson 2009), the relatively minor inter-provenance differences observed in *P. yunnanensis* suggest maintained genetic homogeneity across provenances (Wang et al. 2013). This is consistent with findings for *P. tabulaeformis*, another Chinese pine, which also shows a similar pattern of low inter-provenance variability due to its extensive distribution and adaptation to diverse environments (Ji et al. 2011). Given the observed pattern of substantial intra-provenance variability and moderate inter-provenance differentiation, a focus on capturing intra-provenance diversity could maximize resilience and adaptability, enabling breeders to select superior families and individuals while preserving a broad genetic foundation.

4.2 Correlation between phenotypic traits

Both pairwise correlations (Fig. 5) and multivariate correlations by SEM (Fig. 6) revealed significant and positive relationships among growth and fecundity traits in *P. yunnanensis*, indicating that selecting for one of these traits could simultaneously enhance others, potentially facilitating multi-trait selection. This positive association can be interpreted as an adaptive phenotypic integration, where traits such as tree height (H) and diameter at breast height (D) indirectly support fecundity by facilitating structural and physiological factors conducive to reproduction (Davi et al. 2016; Climent et al. 2024). This pattern aligns with previous studies indicating that under controlled, resource-rich environments (such as common garden trials), trees can allocate resources efficiently to both growth and reproduction, resulting in phenotypic integration across these traits (Garzón, 2021). Furthermore, fecundity traits, such as cone production, appear to be heavily dependent on internal factors, including crown trait (Harja et al. 2012; Yazici and Bilir 2023) and branching architecture (Seki 2008; Leslie et al. 2014). Our findings, consistent with these studies, support the mechanical constraints hypothesis, which suggests that smaller or less structurally developed trees are limited in their capacity to produce cones due to branch fragility. In contrast, larger trees with robust branches can support higher fecundity levels (Seki 2008). Additionally, SEM showed that crown size was significantly correlated to cone production, suggesting that larger crown dimensions enhance light capture and resource allocation, further promoting fecundity (Guo et al. 2010). These findings are consistent with previous studies (Ayari et al. 2012; Yazici and Bilir 2023) that identified crown traits as reliable predictors of reproductive success in conifers. Our study also yielded positive correlations between trunk straightness (ST) and both growth (*H*, *D*, *V*) and crown traits (LCD, SCD, TH). This suggests that straightness may be linked with overall vigor, as larger, more structurally sound trees often exhibit superior form (Garzón, 2021). The strong correlation between trunk straightness and height further supports findings from Cameron et al. (2012) and Yin et al. (2017), where increases in height and diameter contribute to a higher likelihood of trees being classified in superior straightness classes. However, in other productive species like *Eucaliptus*, both height and radial growth have shown a

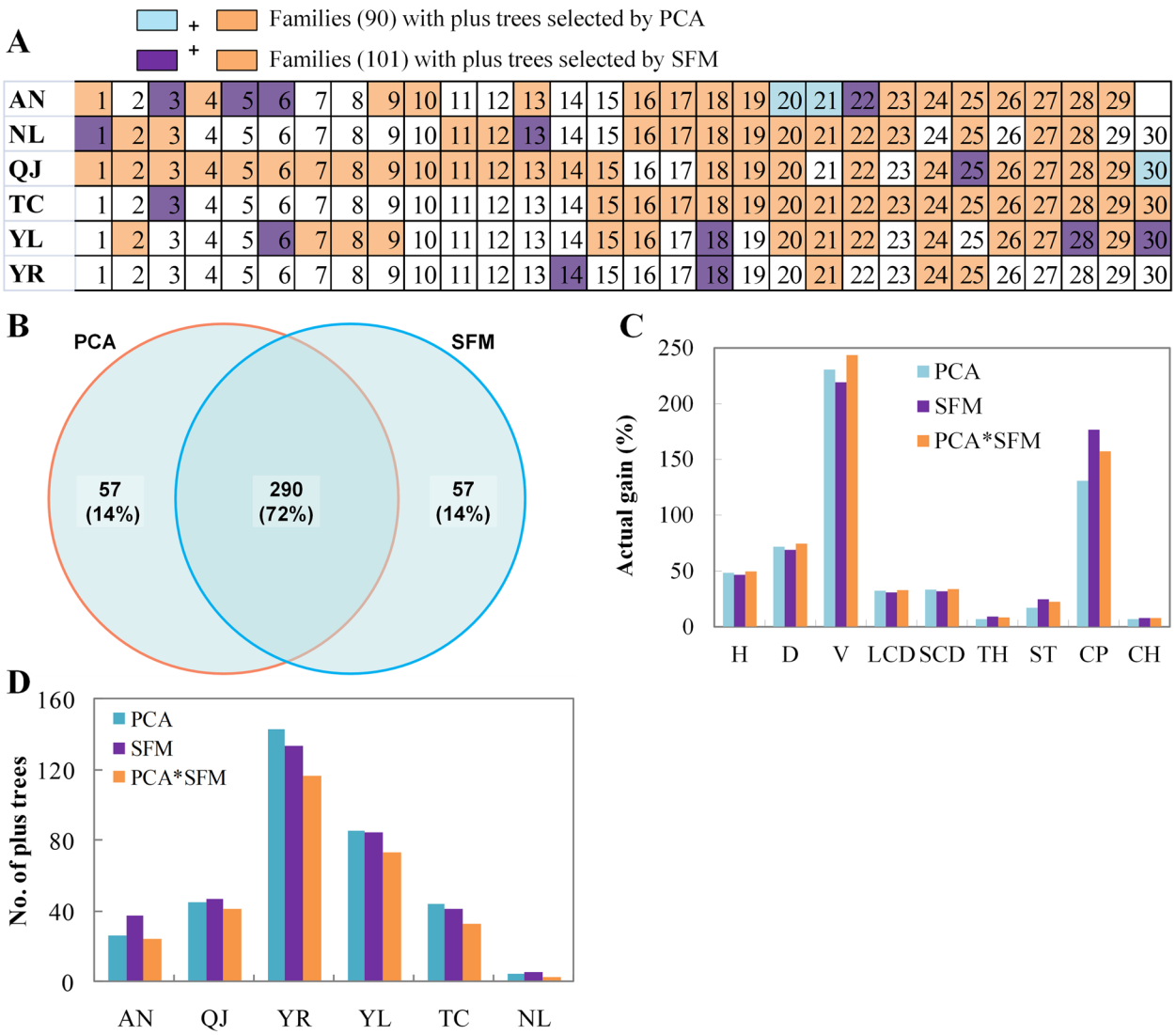

Fig. 9 Superior individuals of *P. yunnanensis* selected from the common garden trial. **A** Families with superior individuals selected by the membership function method (SFM) and principal component analysis (PCA). **B** Venn diagram showing the number of superior individuals identified by SFM, PCA, and those selected by both methods (PCA*SFM). **C** The actual gain (%) of each trait among superior individuals identified by SFM, PCA, and those selected by both methods (PCA*SFM). **D** Distribution of selected superior individuals across different provenances. *H*, plant height; *D*, diameter at breast height; *V*, wood volume; LCD, long crown diameter; SCD, short crown diameter; TH, height under the branch. ST, trunk straightness; CP, cone production; CH, crown health. Provenances are AN (Anning), QJ (Qujing), YR (Yongren), YL (Yulong), TC (Tengchong), and NL (Ninglang)

negative relationship with stem straightness (Mora et al. 2019), indicating a trade-off between growth and stem quality. These varying results could be attributed to differences in the definition of straightness or the research materials used. Differences in wood anatomy, environmental adaptation, and genetic control over growth and form likely contribute to these contrasting patterns (Wu et al. 2007). The observed relationship in *P. yunnanensis* suggests that, at least within this species, growth and stem quality traits may be co-selected without compromising wood form, highlighting its suitability for multi-trait selection in breeding programs. Our random forest (RF) analysis of main predictors for cone production (CP) and trunk straightness (ST) further supports the central roles of growth traits in driving these outcomes (Fig. 7). SEM and RF both indicated that *H* and *D* were the most critical traits for predicting fecundity and trunk straightness, respectively. These findings align with previous studies that suggest tree size explains substantial variation in reproductive output, with larger trees

supporting more cones and exhibiting better stem form (Davi et al. 2016; Río et al. 2004).

Empirical evidence suggests that intraspecific variation in resistance to specific pests and pathogens may negatively correlate with growth in several tree species (Zas et al. 2005). However, there are counterexamples where no relationship or even a positive relationship between growth and resistance to certain parasites has been observed in other pine species (Villari et al. 2014). The positive relationships between crown health and traits such as trunk straightness further indicate a potential integration between resilience and quality traits in our study (Fig. 6). This aligns with findings that suggest pest or pathogen damage, which affects tree health, can alter stem morphology, often leading to deformities due to induced lateral branch dominance (Río et al. 2004). Therefore, healthier trees with less susceptibility to biotic stressors tend to maintain superior straightness, supporting Ayari et al. (2014), who observed that pest pressures could indirectly reduce fecundity by compromising tree structure. This suggests that resilience traits, like crown health, can be indirectly beneficial for preserving wood quality traits, making them important considerations in selection indices for *P. yunnanensis*.

4.3 Evaluation of the feasibility of multi-trait selection strategy for *P. yunnanensis*

In forest breeding, phenotypic integration is crucial for developing superior varieties that meet economic, ecological, and adaptive requirements. Understanding the complex interrelationships among these traits is essential for optimizing tree selection processes (Climent et al. 2024). Previous studies often focused on traits closely related to growth, such as plant height, diameter at breast height, and crown diameter (Ayari et al. 2014; Davi et al. 2016; Yazici and Bilir 2023), as these are directly linked to productivity. Positive correlations are frequently observed among these traits, which guides the selection of trees based on multiple growth characteristics in tree improvement research. However, because plant organisms are complex and integrated systems, trade-offs may occur due to the concomitance of multiple traits (Mora et al. 2019), potentially leading to the loss of key trait gains (Mauro and Ghalambor 2020). For example, rapid growth has been associated with reduced wood density and lower disease resistance in species such as *P. taeda*, highlighting a constraint in achieving balanced improvement across growth, wood quality, and resilience (Isik et al., 2008). In our study, we observed no significant trade-off between growth and fecundity, with growth traits positively correlated with trunk straightness and crown health. This pattern suggests the potential in *P. yunnanensis* for multi-trait selection targeting rapid growth, improved stem form, and enhanced resilience. This aligns with multi-trait selection programs in species like *P. radiata*, where breeding indices aim to balance growth, wood density, and adaptability to environmental stressors (Climent et al. 2024). The feasibility of multi-trait selection in *P. yunnanensis* is further supported by the observed gains in key traits, particularly wood volume and fecundity (Figs. 8 and 9). These gains suggest that within *P. yunnanensis*' genetic pool, favorable combinations of growth, fecundity, and stem quality traits exist, which could reduce the need for extensive selective breeding cycles. This has practical implications for afforestation and seed orchard programs, where the simultaneous improvement of wood productivity and seed yield is critical (Ayari et al., 2014; Davi et al. 2016).

4.4 Limitations

In this study, the fecundity trait was characterized by the cumulative cones for many years based on the number of open and closed cones in the canopy. It is likely that including year-to-year variation in cone production that may be relevant to annual variation in other traits would contribute to rigorously detect the phenotypic variations in fecundity traits (Kroon et al. 2009), and whether such a within-year variation pattern and relationship among endogenous traits of *P. yunnanensis* presented here changes with age needs further investigations. The sustainability of plantation forestry is significantly challenged by climate-change-induced abiotic stress, pests, and diseases. Further research is essential to integrate additional traits such as wood properties and tree defense mechanisms (Villari et al. 2014). By considering these traits alongside those studied here, the selection process can be better guided by integrated phenotypes rather than single traits. Moreover, the impact of environmental factors on key trade-offs needs more attention when deploying forest reproductive materials. Harsh environments could exacerbate negative trade-offs, adversely affecting the resilience of forest tree populations (Climent et al. 2024). Although both pairwise and multivariate correlations in this study indicated positive relationships among growth, fecundity, and crown health, suggesting phenotypic integration, it is crucial to investigate whether these relationships change across different environments to select superior materials with varying adaptability.

5 Conclusion

This study highlighted the substantial phenotypic diversity within provenances of *P. yunnanensis*, suggesting that selecting superior families and individuals within provenances could be an effective strategy to enhance growth, fecundity, and trunk straightness while maintaining

genetic diversity. The observed positive relationships among growth, fecundity, and trunk straightness traits, without apparent trade-offs, highlight the strong potential for integrated multi-trait selection in this species. This integration supports the combined selection of high growth rates, good stem form, and reproductive capacity, which are essential for both wood productivity and seed orchard establishment. Additionally, the positive correlations between crown health and both growth and trunk quality suggest that *P. yunnanensis* has the potential to withstand abiotic and biotic stresses, making it a promising candidate for resilience-focused breeding. In the context of climate change, these results highlight the viability of selecting resilient genotypes that can adapt to fluctuating conditions while meeting economic demands. The identified phenotypic relationships provide a strategic foundation for optimizing *P. yunnanensis* breeding programs, enabling the enhancement of multiple traits in a single selection cycle, potentially accelerating breeding timelines and improving resilience in reforested stands. Future studies should explore these trait relationships in diverse environmental conditions to better understand their adaptability and resilience in a changing climate.

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Authors' contributions
Conceptualization: CG and KC; methodology: CG and KC; formal analysis and investigation: CG, ZL, and JL; writing—original draft preparation: CG; writing—review and editing: KC, CG, and ZL; funding acquisition: KC. The authors read and approved the final manuscript.

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Data availability
The data supporting the results are available in a public repository at: https://doi.org/10.5281/zenodo.1413033.

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors gave their informed consent to this publication and its content.

Competing interests
The authors declare that they have no competing interests.

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