Effects of Genetic Improvement on Needle, Cone, and Seed Traits of Chinese Fir (Postprint)

Authors: Zhang Xuefeng, Yang Shuangyun, Cai Hong, soybean, Daiquan Ye, Bian Liming, Bian Liming

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Abstract

To reveal the impacts of genetic improvement on leaf and cone traits of major afforestation timber species and to elucidate trait variation trends, this study investigated needle and cone trait indicators of 218 clones in Chinese fir (Cunninghamia lanceolata), using elite trees from the fourth-cycle breeding program (improved population) and phenotypically superior trees and ancient trees from five locations across four provinces (unimproved population) as research subjects. Analysis of variance and multiple comparison methods were employed to examine phenotypic differences in Chinese fir and different Chinese fir types resulting from genetic improvement; correlation analysis was conducted to explore the effects of genetic improvement on partial phenotypic traits of needles and cones in Chinese fir; and principal component analysis and cluster analysis were utilized for classification. The results showed that: (1) Needle length, needle width, and seed extraction rate of the unimproved population were 13.28%, 10.81%, and 33.90% lower, respectively, than those of the improved population, while other traits were greater in the unimproved population than in the improved population, with differences ranging from 10.90% to 27.03%. The coefficients of variation for cone length, cone width, and seed extraction rate in the unimproved population were 9.14%, 12.73%, and 15.38% higher, respectively, than those in the improved population. (2) For the four traits of cone length, cone width, bract scale length, and bract scale width, only cone length and cone width (0.931), and bract scale length and bract scale width (0.622) showed extremely significant positive correlations in the unimproved population, whereas after genetic improvement, all pairwise combinations among these four traits exhibited significant or extremely significant positive correlations. (3) The cone length and cone width traits of Sichuan Ya' an (SCYA) were 48.83% and 53.26% greater than those of the improved population, and the 100-seed weight of Anhui Huangshan (AHHS) was 16.92% greater than that of the improved population. (4) Genetic improvement led to a decrease in the proportion of Chinese fir with loose-type cones and an increase in the proportions of Chinese fir with tight-type and reflexed-type cones. This study concludes that genetic improvement in Chinese fir results in reduced cone size, alters the proportions of different needle and cone types, and simultaneously changes the correlations between needle traits and cone traits, which will provide a basis for germplasm resource evaluation and future multi-objective breeding of Chinese fir.

Full Text

Effects of Genetic Improvement on Needle and Cone Traits of *Cunninghamia lanceolata*

Xuefeng Zhang[12], Shuangyun Yang[12], Hong Cai[12], Dou Huang[12], Daiquan Ye[3], Liming Bian[12]*

[1]Key Laboratory of Forest Genetics & Biotechnology of the Ministry of Education, Nanjing Forestry University, Nanjing 210037, China
[2]Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, China
[3]Yangkou State Forest Farm, Shunchang 353211, Fujian, China

Abstract

To reveal the impacts of genetic improvement on leaf and seed traits of major afforestation timber species and to clarify trait variation trends, this study investigated needle and seed traits across 218 clones of Chinese fir. The materials comprised selected trees from the fourth breeding cycle (improved population) and phenotypically superior trees and ancient trees from five locations across four provinces (unimproved population). Using variance analysis and multiple comparison methods, we examined phenotypic differences resulting from genetic improvement in Chinese fir and among different fir types. Correlation analysis explored how genetic improvement affected phenotypic relationships between needle and cone traits, while principal component analysis and cluster analysis were employed for classification. The results showed: (1) The unimproved population exhibited 13.28%, 10.81%, and 33.90% smaller values than the improved population for needle length, needle width, and seed extraction rate, respectively. Other traits were larger in the unimproved population, with differences ranging from 10.90% to 27.03%. The coefficients of variation for cone length, cone width, and seed extraction rate in the unimproved population were 9.14%, 12.73%, and 15.38% higher than those in the improved population. (2) For the four traits of cone length, cone width, bract scale length, and bract scale width, only two pairs showed extremely significant positive correlations in the unimproved population: cone length with cone width ($r = 0.931$) and bract scale length with bract scale width ($r = 0.622$). After genetic improvement, all pairwise correlations among these four traits became significant or extremely significant. (3) Cone length and width in Sichuan Ya' an (SCYA) were 48.83% and 53.26% larger than in the improved population, while hundred-grain weight in Anhui Huangshan (AHHS) was 16.92% greater. (4) Genetic improvement reduced the proportion of Chinese fir with loose-stretched cones while increasing the proportions of tightly-packed and inverted cone types.

This study demonstrates that genetic improvement in Chinese fir leads to reduced cone size, altered proportions of different needle and cone types, and modified correlations between needle and seed traits. These findings provide a basis for germplasm resource evaluation and future multi-target breeding programs.

Keywords: *Cunninghamia lanceolata*, genetic improvement, breeding population, needle, cone

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Introduction

Genetic improvement of target traits inevitably produces responses in other traits, essentially reflecting genetic correlations where a single locus influences multiple trait expressions. In crops, plant height represents a key factor affecting plant architecture and directly or indirectly influences yield and other agronomic traits. In maize, multiple major-effect single nucleotide polymorphism (SNP) loci associated with plant height have been identified, with candidate genes primarily involved in hormone synthesis and signal transduction, carbohydrate metabolism, and cell division regulation. Some of these genes simultaneously regulate plant height, ear height, and ear position coefficient, showing significant correlations with yield traits (Ma Yajie, 2022). In wheat, 25 dwarfing genes have been characterized, revealing 331 QTLs, 270 GWAS-linked loci, and 83 plant height-related genes, forming 66 QTL clusters controlling plant height. Some clusters simultaneously control both plant height and grain length, while others affect only plant height without influencing grain-related traits (Zhang Hongjie, 2021). Rice plant height genes such as *qPH-IAA30* also regulate panicle length, spikelet number per panicle, yield, and thousand-grain weight (Tang Jialong, 2021).

Growth traits represent primary breeding objectives in forest trees, especially timber species. For major afforestation timber species, growth traits are typically the first targets for improvement. However, sustained genetic improvement for growth has revealed direct or indirect effects on other traits. On one hand, negative genetic correlations exist between growth and wood quality traits—as genetic gains in growth traits continuously increase, wood density and other quality traits tend to decline (Huang Shouxian, 2004). On the other hand, sustained growth improvement also leads to reduced reproductive capacity such as flowering and seed production (Wu et al., 2021).

Chinese fir (*Cunninghamia lanceolata*) constitutes one of the most important afforestation timber species in southern China. According to the ninth national forest inventory, Chinese fir plantations cover 9.9 million hectares, accounting for approximately 20% of China' s total plantation area, with a standing volume of 755 million m^3, representing about 25% of the nation' s total plantation volume. Chinese fir exhibits diverse natural types with abundant variation, and certain correlations exist among traits. For instance, gray-type trees show approximately 5% faster height increment than yellow-type trees, but their mean individual volume is about 10% lower (Ye Peizhong and Chen Yuewu, 1964). Since systematic genetic improvement began in the 1950s, growth traits have remained the primary breeding objective. Multiple generations of selection have yielded significant genetic gains, with volume gains averaging 25–40% (Fang Lejin et al., 1998; Chen Xiaochou, 2001; Zou Bin et al., 2003; Zheng Renhua et al., 2014; Zheng Renhua et al., 2014; Wu Hanbin et al., 2019). However, whether sustained genetic improvement for growth traits has caused significant changes in needle and seed traits, and whether trait correlations have been altered, remain unreported.

To clarify the effects of genetic improvement on Chinese fir needle and seed traits, this study measured nine needle and cone traits across 116 clones from the fourth-cycle breeding population (improved population) and 106 clones from phenotypically superior and ancient trees from five locations across four provinces (unimproved population). Using variance analysis, multiple comparison, correlation analysis, principal component analysis, and cluster analysis, we investigated how genetic improvement affects trait variation and correlations in needle and cone traits, as well as differences among Chinese fir types before and after improvement. These results provide a foundation for high-generation multi-target breeding and theoretical support for indirect selection of Chinese fir phenotypes.

Materials and Methods

1.1 Study Site Description The improved population (fourth-cycle breeding population, designated 4TH) was located at Daoping Management Station (Forest compartment: 14-8-2) of Yangkou State Forest Farm in Fujian Province (117°53 E, 26°49 N). The site experiences a subtropical monsoon climate with a mean annual temperature of 21.6 °C (ranging from -0.6 °C to 39.0 °C), average annual precipitation of 1,737 mm, and relative humidity of 73% at an elevation of 175–240 m. The previous vegetation consisted of mixed coniferous-broadleaved forests including Chinese fir, masson pine, and *Schima superba*. The site quality class was II, with mountainous red soil (pH 3.9–4.6), southwest aspect, and 25°-30° slope. The plantation was established in 2016 with manual strip preparation (1.2 m strip width), 3 m × 3 m spacing, and planting holes measuring 60 cm × 40 cm × 40 cm.

The unimproved population (phenotypically superior tree population) was collected and preserved at Datieng Management Station (Forest compartments: 11-7-4 and 11-6-5) of Yangkou State Forest Farm. The collection site for superior and ancient trees previously supported mixed coniferous-broadleaved forests of Chinese fir, *Betula luminifera*, and *Schima superba* with site quality class II and mountainous red soil (pH 4.0–4.6), northwest aspect, and 20°–28° slope. Climate conditions, planting configuration, and hole specifications were identical to the improved population, with establishment in 2018.

1.2 Experimental Materials The improved population comprised elite selections from third-generation progeny test forests, hybrid progeny test forests, and second-generation progeny test forests. Grafted clones were randomly arranged with at least eight ramets per elite tree in continuous rows. The unimproved population consisted of untested individuals, including superior trees and ancient trees from secondary forests originating from five locations across four provinces: Anhui Huangshan (AHHS), Hunan Jiahe (HNJH), Jiangxi Ganzhou (JXGZ), Sichuan Dechang (SCDC), and Sichuan Ya’ an (SCYA) (material sources detailed in Table 1). Scions were collected and grafted in 2018 using the same clone configuration. The study utilized grafted clones that flowered and fruited in 2021, comprising 112 improved clones and 106 unimproved clones.

1.3 Trait Measurement Methods For each clone, three moderately vigorous ramets were randomly selected. In November 2021, the presence of powdery mildew coverage on new needles was recorded as A1 (present) or A0 (absent). Needles were collected from the middle canopy on the sunny, disease-free side of each tree, and needle density was recorded (needles per 10 cm) following Ye Peizhong and Chen Yuewu (1964). Ten random needles were selected to measure needle length and width. Cones were collected from upper, middle, and lower canopy positions, with three cones per layer measured for fresh weight. Three bract scales were sampled from the upper, middle, and lower thirds of each cone to measure bract scale length and width. Cones were oven-dried, all seeds extracted, and total seed weight and hundred-grain weight measured. Based on bract scale opening degree, cones were classified into three types: tightly-packed (B1), loose-stretched (B2), and inverted (B3) (Ye Peizhong and Chen Yuewu, 1964). Length measurements used vernier calipers (precision: 0.001 cm) and weight measurements used electronic balances (precision: 0.01 g).

1.4 Statistical Analysis Methods The seed extraction rate was calculated as (Guan Kanglin et al., 1997):

$$\text{Seed extraction rate} = \frac{\text{Total seed weight}}{\text{Cone fresh weight}} \times 100\%$$

The coefficient of variation (CV) was calculated as:

$$CV = \frac{\sigma}{\mu} \times 100\%$$

where σ is the standard deviation and μ is the population mean.

R software was used for t-tests between improved and unimproved populations and one-way ANOVA for different fir types. Pearson correlation coefficients estimated phenotypic trait relationships. Duncan' s multiple range test was used for comparisons. Principal component analysis identified major traits, and cluster analysis employed Euclidean distance with sum of squares method.

Results

2.1 Comparison of Trait Characteristics Between Populations Statistical characteristics of traits in both populations are presented in Table 2 . All traits differed significantly between populations ($P < 0.05$), with differences exceeding 10%. The unimproved population showed 13.28%, 10.81%, and 33.90% smaller values than the improved population for needle length, needle width, and seed extraction rate, respectively. Other traits were larger in the unimproved population, with differences ranging from 10.90% to 27.03%. The largest difference occurred in needle density (27.03%), followed by cone length (22.24%), with the smallest difference in bract scale length (10.90%). The remaining three traits differed by approximately 15%.

Needle density exhibits a significant negative correlation with mean annual growth increment (Cheng Jianhong, 2017). Since Chinese fir improvement programs, particularly early-generation selections, prioritized fast-growing superior materials, this likely explains the sharp decrease in needle density from 81.3 (needles/10 cm) in the unimproved population to 64.0 (needles/10 cm) in the improved population.

Both populations showed moderate to weak phenotypic variation. The unimproved population' s coefficient of variation ranged from 10.49% to 48.70%, with seed extraction rate showing the highest variation, followed by cone width (22.58%), and needle width the lowest. The improved population' s CV ranged from 9.85% to 33.32%, with seed extraction rate highest, followed by hundred-grain weight (24.92%), and cone width lowest. CVs changed to varying degrees after improvement. The unimproved population showed lower CVs than the improved population for needle length, needle width, needle density, bract scale width, and hundred-grain weight, while bract scale length CV was higher. However, changes in these six traits were within approximately 5%. The unimproved population exhibited higher CVs for cone length, cone width, and seed extraction rate, with changes of 9.14%, 12.73%, and 15.38%, respectively, suggesting that genetic improvement may reduce population diversity. Regarding trait category diversity, the ranking before improvement was needle traits < seed traits < cone traits, which shifted to cone traits < needle traits < seed traits after improvement, indicating reduced cone variation following genetic improvement. Overall, trait CVs ranked as: needle width < bract scale length < bract scale width < cone width < cone length < needle length < needle density < hundred-grain weight < seed extraction rate, ranging from 13.94% to 44.13%, representing moderate variation.

2.2 Changes in Trait Correlation Coefficients at the Population Level

Genetic improvement altered trait correlation coefficients (Figure 1 [Figure 1: see original paper]). Eight trait pairs shifted from non-significant correlations before improvement to moderate positive correlations after improvement: needle length with needle width, cone length with bract scale length, cone width with bract scale length, cone length with bract scale width, cone width with bract scale width, hundred-grain weight with seed extraction rate, bract scale length with seed extraction rate, and needle density with seed extraction rate.

For cone length, cone width, bract scale length, and bract scale width, only two trait pairs showed extremely significant positive correlations in the unimproved population: cone length with cone width (r = 0.931) and bract scale length with bract scale width (r = 0.622). After genetic improvement, all pairwise correlations among these four traits became significant or extremely significant, indicating that genetic enhancement strengthened relationships between cone size and bract scale dimensions.

Two trait pairs shifted from significant negative correlations to non-significant weak correlations: needle length with cone length and needle length with cone width. After improvement, needle traits showed non-significant weak correlations with cone traits, demonstrating that genetic improvement reduced associations between these trait categories. The correlation coefficient between bract scale width and hundred-grain weight decreased from 0.211 to 0.166 (a reduction of 0.045), shifting from a significant positive correlation before improvement to a weak correlation after improvement. Other trait pairs maintained non-significant weak correlations in both populations without significant changes.

Significant differences in phenotypic traits were observed among the six provenances (Table 3). The fourth-cycle breeding population (4TH) showed maximum values for needle width and seed extraction rate, but minimum values for needle density, cone length, bract scale length, bract scale width, and hundred-grain weight. Its needle length ranked second only to SCDC, while cone width was greater than HNJH and SCDC.

Compared with 4TH: (1) Except for SCDC needle length (10.95% greater than 4TH) and AHHS and HNJH seed extraction rates (more than 50% smaller than 4TH), the other five provenances showed needle length, needle width, and seed extraction rates approximately 10-20% smaller than 4TH. (2) For cone length, SCDC was only 3.50% greater than 4TH, while AHHS, HNJH, and JXGZ were approximately 15% greater. SCYA showed the largest difference at 64.93% greater than 4TH. (3) For cone width, HNJH and SCDC were smaller than 4TH, while AHHS, JXGZ, and SCYA were larger, though the first four provenances differed from 4TH by less than 10%. SCYA exhibited the maximum cone width, 63.89% greater than 4TH. (4) Differences in bract scale dimensions between the five provenances and 4TH ranged from 1% to 20%, with AHHS (9.75%), HNJH (1.09%) for bract scale length and SCDC (6.21%) for bract scale width differing by less than 10%, while other provenances differed by approximately 15%. (5) Hundred-grain weight in AHHS and JXGZ exceeded 4TH by 26.67%

and 21.67%, respectively, while the other three provenances differed from 4TH by approximately 5%.

2.4.1 Needle Types Overall, 114 clones (52.29%) exhibited A1-type needles (with powdery mildew), yielding an approximately 1:1 ratio between types. However, distribution differed dramatically between populations. The improved population contained only 28 A1-type clones (25.00%), while the unimproved population had 86 A1-type clones (81.13%). Except for cone width and hundred-grain weight, all other phenotypic traits differed significantly between needle types. A0-type needles (without powdery mildew) showed greater needle length, needle width, and seed extraction rate, but smaller values for remaining traits. Specifically, A0-type seed extraction rate was 28.24% higher than A1-type, while differences in other traits were within 10%.

2.4.2 Cone Types The three cone types occurred at similar overall frequencies: 70 tightly-packed (32.11%), 71 loose-stretched (32.56%), and 77 inverted (35.32%). However, proportions differed between populations. In the unimproved population, tightly-packed, loose-stretched, and inverted types accounted for 21.69%, 51.89%, and 26.42%, respectively. In the improved population, tightly-packed and inverted types increased by 20.26% and 11.97%, respectively, while loose-stretched types decreased by 32.24%.

Multiple phenotypic traits differed significantly among cone types. Tightly-packed types showed maximum needle width but minimum bract scale width, with other traits intermediate. Loose-stretched types exhibited maximum needle density, cone length, cone width, bract scale length, bract scale width, and hundred-grain weight, but minimum needle length, needle width, and seed extraction rate. Inverted types showed maximum needle length and seed extraction rate, but minimum needle density, cone length, cone width, and bract scale length. Although significant differences existed among cone types for various traits, most phenotypic differences relative to overall means were within 5%, except for seed extraction rate in inverted and loose-stretched types, which deviated by +10% and -10%, respectively.

2.5 Principal Component Contributions To reduce trait dimensionality and concentrate variation information, principal component analysis was performed on nine phenotypic traits. The first four principal components had eigenvalues > 1, individual contribution rates $> 10\%$, and a cumulative contribution rate of 75.19%, effectively capturing variation across all traits. The first principal component (contribution rate: 34.76%) primarily comprised needle density, cone length, cone width, bract scale length, and bract scale width. The second component (15.09%) mainly contained bract scale length and width. The third component (14.38%) was dominated by cone width. The fourth component (11.52%) primarily reflected hundred-grain weight. These four principal components adequately represented all original variation and were used for subsequent cluster analysis.

2.6 Trait Clustering Based on the principal component results, cluster analysis using the first four components classified 218 clones into three groups containing 83, 59, and 76 clones, respectively (Figure 2 [Figure 2: see original paper]). All three groups showed significant phenotypic differences. Group I exhibited maximum needle size, minimum cone size, and highest seed extraction rate. Group III showed the opposite pattern to Group I, while Group II ranked second for all traits.

Composition analysis revealed that Group I primarily comprised improved population clones with larger needles, smaller cones, and low hundred-grain weight and seed extraction rate. Group III mainly consisted of unimproved population clones with smaller needles, larger cones, and low seed extraction rate. Group II included improved population clones with larger cones and high hundred-grain weight and seed extraction rate, plus unimproved population clones with smaller cones and low seed extraction rate. Although genetic improvement reduced cone size, the improved population still exhibited internal differentiation during clustering rather than forming a single category, likely because Chinese fir has not undergone intensive artificial selection for cone traits. Notably, Group III contained 11 improved clones that exceeded 4TH means for all traits except needle length, with hundred-grain weight and seed extraction rate 20.58% and 19.73% higher than 4TH means, respectively. These clones warrant greater attention in future breeding.

Discussion

3.1 Cone Size In gymnosperms, cone traits significantly influence seed yield and quality (Codesido et al., 2014; Chen Suying et al., 2014). This study found that genetic improvement significantly reduced Chinese fir cone size, likely resulting from multi-generational improvement targeting tree height and diameter at breast height (DBH). Tree height negatively correlates with cone weight, which in turn shows extremely significant positive correlations with cone length and width (Chang Enfu et al., 2017; Jiang Luping et al., 2019). In Japanese black pine (*Pinus thunbergii*), seed size tends to decrease with increasing DBH (Wang Guangmei et al., 2009). From an energy allocation perspective, when trees prioritize vegetative growth, reproductive growth becomes suppressed (Zhang Gui et al., 2014). The superior growth performance of improved populations represents the main reason for reduced cone size. Although genetic improvement increased seed extraction rate, hundred-grain weight decreased, possibly because improved populations produce higher proportions of empty seeds, reducing seed quality—a finding confirmed by previous studies (Sun Hongyou et al., 2003; Han Lu et al., 2021). For forest trees, especially timber species, breeding objectives typically focus on rapid growth and superior wood quality. Intensive multi-generational selection for growth reduces diversity in advanced breeding populations (Feng Yuanheng et al., 2018). Therefore, to facilitate breeding population management and ensure stable inheritance of new variation created through hybridization, seed traits should be incorporated into high-generation breeding objectives.

3.2 Trait Correlations Trait correlations represent the phenotypic manifestation of gene pleiotropy. Chinese fir height and DBH show correlation coefficients as high as 0.9 (Fu Shunhua et al., 2007; Zhao Linfeng and Gao Jianliang, 2021), indicating extremely significant positive correlations. Quantitative trait locus (QTL) results demonstrate that markers closely associated with height and DBH also show extremely significant interaction effects (He Zhenxiang et al., 2000). Intensive genetic improvement has achieved high genetic gains in Chinese fir growth traits (Zheng Yongping et al., 2007; Yu Rongzhuo, 2008), but changes in phenotypic trait correlations remain unreported. This study found that in the improved population, highly correlated traits concentrated within the same trait categories, with most pairwise correlations among needle traits or cone traits reaching significant positive levels, while correlations between needle and cone traits were mostly non-significant. In the unimproved population, highly correlated traits showed no clear patterns. As one of China' s most advanced tree breeding programs, Chinese fir' s recurrent breeding strategy in high generations has utilized superior individuals or families across multiple generations to construct breeding populations (Yu Rongzhuo, 2008), increasing the inbreeding coefficient and consequently elevating trait correlations. The enhanced correlations among seed traits after genetic improvement suggest the presence of minor-effect genes simultaneously controlling both growth and seed traits.

3.3 Chinese Fir Needles Most coniferous species maintain stable genetic characteristics for needles and cones that do not change with tree age. Age effects on needles primarily manifest physiologically and biochemically—for example, needle nitrogen and phosphorus contents increase with age, but needle size and number are not significantly affected (Pang Zhenghong et al., 1994; Wang Zexin et al., 2022). Cone traits are minimally influenced by site conditions and age, with genetic variation representing the primary source. Poor pollination and pest damage constitute important anthropogenic factors affecting cone traits, but within the same stand with identical management practices, cone trait differences depend mainly on genetic variation (Wang Zhaomin et al., 1998; Lin Yihui et al., 2000; Cheng Lin et al., 2021). Therefore, classification of coniferous species can be based on partial phenotypic characteristics of needles and cones, such as powdery mildew coverage, cone morphology, and bract scale morphology. Chinese fir is classified into green, yellow, and gray types based on fresh needle powdery mildew coverage and color (Ye Peizhong and Chen Yuewu, 1964). According to cone and bract scale morphology, nine types have been identified, including long-scale tightly-packed and wide-scale inverted types (Ye Peizhong and Chen Yuewu, 1964). Based on bract scale orientation before cone maturity—outwardly reflexed, tightly appressed to the cone axis, or loosely erect —three types are commonly recognized: tightly-packed, loose-stretched, and inverted (Peng Zhenhua and Xing Zizhuo, 1987). Loose-stretched Chinese fir exhibits low proportions of empty seeds and high seed quality (Lin Ping et al., 1990). However, genetic improvement reduced the proportion of loose-stretched types because their vigorous growth period is short and decline occurs rapidly, leading to their elimination during thinning or mature stand selection. Tightly-packed Chinese fir maintains a long vigorous growth period with slow decline and superior volume performance, attracting attention during artificial selection (Ye Peizhong and Chen Yuewu, 1964). This explains why tightly-packed types increased and loose-stretched types decreased after artificial improvement.

3.4 Geographic Provenance Geographic variation in tree cones primarily relates to altitude and latitude, with species-specific relationships. In spruce (*Picea asperata*), natural population cone size negatively correlates with altitude ($r < -0.4$) (Luo Jianxun et al., 2003). Masson pine (*Pinus massoniana*) cone size shows extremely strong negative correlations with altitude and latitude ($r < -0.9$) (Chen Yuewu and Rong Wenchen, 1990). Blue pine (*P. wallichiana*) cone volume negatively correlates with altitude ($r < -0.4$), while cone volume, seed length, seed width, and seed thickness show moderate negative correlations with latitude ($r < -0.4$) (Rawat et al., 2011). Stone pine (*P. pinea*) differs, showing positive correlations between cone diameter and seed weight with altitude ($r > 0.8$), weak correlations between cone size and longitude, and negative correlations with latitude ($r < -0.6$) (Balekoglu et al., 2020). Temperature changes associated with altitude and latitude variations constitute the primary cause of cone size variation (Wang Chongyun et al., 2012).

Long-term genetic improvement has reduced Chinese fir cone size while increasing needle size and density, and strengthened correlations between cone dimensions and bract scale dimensions. Improvement has also altered the composition of different needle and cone types, decreasing the proportion of new needles with powdery mildew coverage (gray type) and increasing the proportions of tightly-packed and inverted cone types. This study has limitations, including incomplete coverage of the entire Chinese fir distribution in the unimproved population. Future research should expand material sources and sample sizes to analyze relationships between growth trait genetic gains and needle/seed traits, investigate variation patterns in cone types, and employ GWAS to elucidate molecular mechanisms governing growth and reproduction, thereby providing foundations for developing high-generation breeding strategies.

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