COMPREHENSIVE SELECTION AND VARIATION ANALYSIS OF GROWTH TRAITS AND WOOD COLOR OF *CASTANOPSIS HYSTRIX* HALF-SIB FAMILIES

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Abstract

Castanopsis hystrix is an economically valuable tropical/subtropical timber species naturally distributed in various Asian regions. Studies on genetic variations affecting *C. hystrix* growth and wood color traits can increase the wood value. Trees in a 17-year-old forest of 32 *C. hystrix* half-sib families were analyzed to determine genetic variations in growth traits. Genetic variations affecting wood color ($L*$ (lightness), chromaticity coordinate $a*$, and chromaticity coordinate $b*$ were evaluated in tree cores. Annual growth rates of diameter at breast height, tree height, and stem volume were 1.27 cm, 1.08 m, and 0.02 m^3, respectively, indicating high growth. The $L*$, $a*$, and $b*$ values of *C. hystrix* heartwood were 47.55 ± 5.02, 15.50 ± 1.86, and 19.26 ± 2.35, respectively. Block was the decisive factor affecting variations in L^* of heartwood and family main affected heartwood $a*$ differentiation. Block × family interactions significantly affected stem volume, heartwood $a*$, and heartwood $b*$ but to a lesser extent than the individual effects of family and environment. The family heritability of diameter at breast height, tree height, volume, heartwood $a*$, and heartwood $b*$ were 0.53, 0.56, 0.76, 0.85, 0.68, respectively. The individual heritability of corresponding characters were 0.10、0.14、0.11、0.11、and 0.04. The wood color of heartwood and sapwood had no genetic correlation with growth characters, which indicated that the wood color of heartwood and sapwood was independent of growth traits. Six half-sib families with excellent growth and heartwood color were selected by using a multi-trait comprehensive evaluation method. The mean genetic gain of diameter at breast height, tree height, volume, heartwood $a*$, and heartwood $b*$ were 12.093%, 7.166%, 39.054%, 10.265% and 7.235%. These results provide a theoretical basis for the evaluation and selection of families with superior growth and wood color traits for genetic improvement and directed breeding of *C. hystrix*.

Key words: *Castanopsis hystrix*, Growth trait, Wood color, Genetic variation, Comprehensive selection.

Introduction

Wood color is a basic attribute of decorative solid wood materials. The wood colors perceived by the human eye result from the absorption and reflection of light (in the wavelength range of 400–700 nm) by the surfaces of wood materials (Janin *et al*., 2001; Prades *et al*., 2017). Changes in wood color determine the visual aesthetic appeal and decorative effects of wood materials, which in turn affect the quality of wood materials and value of wood products (Valverde & Moya, 2014; Cui *et al*., 2016). To evaluate the color and degree of aesthetic appeal of wood materials, wood color characteristics are often quantified using the CIELAB system. This quantification approach is widely used in quantitative studies on chromaticity indices of wood materials obtained from timber species and provides a theoretical basis for wood product selection and comprehensive evaluation of surface quality of decorative wood materials (Liu *et al*., 1995a; Bradbury *et al*., 2010).

The chromaticity indices of wood differ considerably among tree species (Liu *et al*., 1995b; Nishino *et al*., 1998; Jones *et al*., 2014; Sousa *et al*., 2019) and can be used as a practical tool for identifying woody plants. Wood colors can also differ among individuals of the same species (Mosedale *et al*., 1996). Particularly, decorative solid wood materials with reddish hues are popular among consumers, whereas certain wood colors with poor color stability, poor homogeneity, and a high degree of difficulty in processing and utilization are less popular (Miyamoto *et al*., 2016). The color of wood products is an important factor in the international hardwood market (Torres *et al*., 2010). Therefore, studies of genetic variations in wood color and screening of

germplasm with superior wood colors for popularization and application can enhance the cultivation value of timber production forests.

Whether wood color traits are controlled by environmental factors or genetic factors or are jointly influenced by both types of factors remains controversial. Some studies reported that differences in wood color are mainly caused by environmental factors (Rink, 1987; Janin *et al*., 1990), whereas others demonstrated that wood color variations are highly influenced by genetic factors (Mosedale *et al*., 1996; Miyamoto *et al*., 2016; Damayanti *et al*., 2019). However, previous studies have also suggested that wood color is jointly determined by genetic and environmental factors (Kijidani *et al*., 2012; Damayanti *et al*., 2019). Therefore, analysis of the dominant factors influencing wood color variations and estimation of genetic parameters for the corresponding traits are important to facilitate genetic improvement of timber species, particularly valuable species.

The main goals of genetic improvement of high-value timber species are rapid growth, high yield, and aesthetic wood colors. Therefore, analysis of the genetic correlations between growth and color traits will be beneficial for planning breeding strategies for the selection of superior forest tree breeds. Hannrup *et al*., (2004) found that the diameter at breast height (DBH), tree height, and stem volume of 19-year-old *Picea abies* were positively correlated with wood color, and wood color could be improved by selecting clones with high growth. In contrast, growth traits are weakly correlated with wood color in the valuable tree species *Tectona grandis* (Moya *et al*., 2013) and *Paulownia* (Cui *et al*., 2016). Therefore, the selection of rapid-growing genetic materials may not contribute to genetic improvement in wood color of these species. To

shorten breeding cycles and enhance forest tree improvement efficiency, a multi-trait comprehensive evaluation approach should be adopted for the selection of genetic materials with appropriate trade-offs.

Castanopsis hystrix is an evergreen broadleaf tree species belonging to the family Fagaceae. Its natural distribution region runs along east Nepal and northeast India and spans the Indochinese Peninsula (Cambodia, Laos, Thailand, and Vietnam) to southwest and south China (Li *et al*., 2007; Ripu *et al*., 2008; Suresh *et al*., 2014). *Castanopsis hystrix* wood materials mainly consist of heartwood and are widely used in China and India for producing luxury ornaments and wooden furniture because of their reddish hues, aesthetically pleasing grain patterns, and superior quality (Sharma *et al*., 2011; Xu *et al*., 2013). In South China, *C. hystrix* is widely cultivated, as it has been listed as a valuable tree species with a high priority for development; man-made forests of *C. hystrix* currently cover an area of more than 5,000 ha (Shen *et al*., 2014). The accurate enhancement of wood yield and quality of *C. hystrix* is heavily dependent on the selection of high-quality breeds. Previous selective breeding efforts were mainly concentrated on selecting growth traits such as DBH, tree height, and stem volume (Fang, 2021) to obtain rapid-growing and high-yielding breeds for wood production. However, few studies have investigated the wood quality, which is a crucial factor in the cultivation of valuable timber species, particularly because large variations exist in the wood color of *C. hystrix* wood materials, ranging from red to reddish brown. Wood materials with reddish hues generally have a higher value and are in greater demand in the wood market because of their popularity among consumers.

Based on the hypothesis that the wood market might demand more high-value red *C. hystrix* heaetwood, the native wood producer are in urgent needs of high-quality special germplasm resources. Considering the future wood production and seeding supply, the genetic variations in growth patterns and wood color traits of *C. hystrix* were analyzed using a 17-year-old experimental forest of *C. hystrix* families as the study site to provide a basis for genetic improvement of *C. hystrix* and other valuable tree species and assurance of germplasm resources for large-scale development of man-made forests. The present study aimed to (a) analyze the genetic variation in growth patterns of *C. hystrix* trees and wood color traits of *C. hystrix* heartwood and sapwood, (b) estimate the genetic parameters for growth and wood color traits, (c) determine the relationships between growth and wood color traits, and (d) accurately select superior families through comprehensive evaluation.

Materials and Methods

Study area: The study area is located in Compartment 13 at the Fubo Experimental Site of the Experimental Center of Tropical Forestry, Chinese Academy of Forestry in Pingxiang City of Guangxi Zhuang, Autonomous Region of China (106°53′37″E, 22°02′25″N). It is situated on a low-relief terrain at an elevation of 304 m and has a south Asian tropical monsoon climate characterized by warm and humid weather, higher rainfall during hotter months, a mean annual temperature of 19.9–21.5°C, and mean annual precipitation of 1,200–1,550 mm, providing conditions suitable for the growth of man-made *C. hystrix* forests. The soil of the study area mainly consists of granite-derived red earth with a depth of > 1 m.

Experimental forest of *C. hystrix* families: In early December 2000, seeds of 32 open-pollinated half-sib families of *C. hystrix* were collected from Guangxi Zhuang Autonomous Region. (Table 1) shows the geographical and climate information of the provenances of the seeds. The minimum distance requirement of 100 m was strictly adhered between two parent trees during seed collection. In March 2002, an experimental forest of *C. hystrix* half-sib families was developed using 2-year-old seedlings cultured from the collected seeds. Planting holes with dimensions of 50 × 50 × 40 cm were established, and seedlings were planted with a spacing of 2 × 3 m. The experimental forest was spread across the mid and lower slopes, and a randomized block experimental design was adopted. A total of three blocks was established, with each block consisting of zones of all half-sib families (each zone consisted of eight individual plants from a single half-sib family). Two blocks were on the mid slope and one block was on the lower slope. Weed removal was performed by hole-smoothing and fertilizer was not applied during the first 3 years after forestation; regular management measures, such as pest control, weeding, tending and thinning, were performed as required from the 4th year onwards.

Determination of traits: In April 2019, the DBH and tree height (H) of each tree were measured using a DBH measuring tape and ultrasonic altimeter (Vertex III, Haglöf IV, Sweden). The stem volume (S_V) was measured using the equation $S_V = H \times \pi \times DBH^2 \times f/4$, where S_V is the stem volume of a single plant, H is the tree height, DBH is the diameter at breast height, and f is the form factor with a value of 0.421 (Pang *et al*., 2016). Cores (5 mm diameter) were extracted at breast height using an increment borer, with core extraction performed in three trees and repeated three times for each half-sib family. Wood color was systematically evaluated using the CIELAB system (Liu *et al*., 1995b; Nishino *et al*., 1998) as follows: (1) the boundary between heartwood and sapwood was determined based on wood color changes; (2) wood color was measured starting from the pith, and lightness (L^*), chromaticity coordinate a^*, and chromaticity coordinate b^* were measured at each annual ring until the outermost ring was reached; (3) the mean values of the measurements were used as the chromaticity indices of heartwood and sapwood. The total color difference between heartwood and sapwood (ΔE^*) was calculated using the following equation:

$$\Delta L^* = L_h^* - L_s^*; \Delta a^* = a_h^* - a_s^*; \Delta b^* = b_h^* - b_s^*; \Delta E^* = \sqrt{(\Delta L^*)^2 + (\Delta a^*)^2 + (\Delta b^*)^2} \text{ (Moya \& Marín, 2011)}$$

where, L_h^*, a_h^*, and b_h^* are the L^*, a^*, and b^* are values of heartwood, L_s^*, a_s^*, and b_s^* are the L^*, a^*, and b^* are values of sapwood, ΔL, Δa, and Δb are the differences in L^*, a^*, and b^* between heartwood and sapwood, and ΔE^* is the total color difference between heartwood and sapwood.

Data analysis

Estimation of genetic parameters: The experimental data were statistically analyzed using Microsoft Excel 2010 (Redmond, WA, USA), and the variance components and genetic parameters of the growth traits and wood colors of the various half-sib families were estimated using Genstat 18.0 (VSNI, England) with the following model: $Y_{ij} = \overline{X} + B_i + F_j + B_i \times F_j + E_{ij}$, where Y_{ij} is the mean value for the zone of the jth half-sib family of the ith block, $\overline{X}$ is the mean value of the population, B_i is the effect size of the ith block, F_j is the effect size of the jth half-sib family, $B_i \times F_j$ is the block × family interaction effect, and E_{ij} is random error.

Genetic coefficient of variation, CV_g: $CV_g = \sqrt{\sigma_F^2/\overline{X}} \times 100\%$

Family heritability, h_F^2: $h_F^2 = \sigma_F^2/(\frac{\sigma_E^2}{n \times b} + \frac{\sigma_{F \times B}^2}{b} + \sigma_F^2)$

Individual heritability, h_S^2: $h_S^2 = 2 \times \sigma_F^2/(\sigma_E^2 + \sigma_{F \times B}^2 + \sigma_F^2)$

Genetic gain, ΔG: $\Delta G = si \times \delta_p \times h^2/\overline{X}$

Genetic correlation coefficient, r_g: $r_g = Cov_{g(j,m)}/\sqrt{\sigma_{gj}^2 \times \sigma_{gm}^2}$

where σ_F^2, $\sigma_{F \times B}^2$, and σ_E^2 are the variance components for the family, family × block interaction, and environment, respectively; n, and b are the numbers of half-sib families and blocks, respectively; $\overline{X}$ is the mean trait value; si is the selection intensity; δ_p is the standard deviation; σ_{gj}^2 and σ_{gm}^2 are the genetic variance components for trait j and trait m of the family; and $Cov_{g(j,m)}$ is the genetic covariance component between trait j and trait m of the half-sib family.

Comprehensive evaluation index for half-sib family selection: The comprehensive evaluation index of each half-sib family was calculated using the formula $Q_i = \sqrt{\sum_{j=1}^{n} X_{ij}/X_{max}}$ (Wang, 2018), where Q_i is the comprehensive evaluation index of half-sib family i, X_{ij} is the observed value for trait j of half-sib family i, X_{jmax} is the maximum phenotypic value of trait j, and n is the number of observed traits.

Results

Genetic variations in growth traits: (Table 2) shows the results of analysis of variance of the growth traits *C. hystrix* trees aged 17 years old. The block and family were the main sources of variations in DBH, tree height, and stem volume. Particularly, the contributions of block to the differentiation of various growth traits exceeded 94%, whereas family contributions were < 3.1%. This indicates that the site (slope position) is the key determinant of wood yield in man-made *C. hystrix* forests. The family × block interaction effect was only significant in DBH among the three growth traits; however, the block and family effects on DBH were still greater than the interaction effect.

As shown in Table 3, the mean annual DBH, tree height, and stem volume growth rates of the studied *C. hystrix* families were 1.27 cm, 1.08 m, and 0.02 m³, respectively. Differences in DBH, tree height, and stem volume among the 32 studied families were significant ($p<0.05$). Specifically, half-sib families No. 1, 11, and 12 showed superior growth, with the mean annual growth rates of DBH, tree height, and stem volume exceeding 1.45 cm, 1.15 m, and 0.025 m³, respectively, which were 14.17%, 6.48%, and 25% higher than the population mean values (Table 3). Half-sib family No. 5 showed the poorest growth, as the values for DBH, tree height, and stem volume growth were 81.74%, 92.51%, and 58.06%, respectively, of the corresponding population mean values.

Genetic variations in wood color traits: (Table 4) shows the results of analysis of variance of the wood color traits of 17-year-old *C. hystrix* trees. The heartwood L^* value varied significantly only among blocks, and the block variance component contributed to 64.881% of total variance. This indicates that the site environment determined L^* variations in heartwood. The family and family × block interaction effects on the heartwood a^* value were highly significant and significant, respectively, contributing to 58.284% and 41.407%, respectively. Therefore, family and family × block interactions were considered as the main sources of heartwood a^* variations. Block, family, and family × block interactions caused changes in heartwood b^* variations, contributing to 64.153%, 19.181%, and 16.666%, respectively. Sapwood a^* and b^* varied significantly among families and blocks, but the effect of family × block interactions was not significant. The differentiation of sapwood L^* was only significant among families.

The results of descriptive statistical analysis of the L^*, a^*, and b^* values of *C. hystrix* heartwood and sapwood are shown in Table 5. Heartwood L^*, a^*, and b^* values were 47.55 ± 5.02, 15.50 ± 1.86, and 19.26 ± 2.35, respectively. Changes in these values compared with those in sapwood (ΔL^*, Δa^*, Δb^*) were −6.24, 3.60, and 2.28, respectively, indicating that heartwood was darker, redder, and yellower than sapwood, and the total color difference, ΔE^*, was 7.56. Half-sib family No. 2 showed the highest heartwood a^* value (12.77% higher than the population mean), suggesting that heartwood in this family appeared redder than that of other families. Half-sib family No. 10 exhibited the lowest heartwood a^* value, which was 90.77% of the population mean. The highest and lowest heartwood b^* values were observed for half-sib family No. 7 (9.40% higher than the population mean) and half-sib family No. 32 (89.62% of the population mean), respectively. The lowest sapwood L^*, a^*, and b^* values were measured in half-sib families No. 27, 11, and 12 and the highest values were measured in half-sib families 20, 2, and 9, accounting for 51.02–55.55, 11–13.08, and 16.11–18.79 and values of 4.53, 2.08, and 2.68, respectively. Variations in heartwood and sapwood L^*, a^*, and b^* values among the studied families were significant ($p<0.05$) (Table 5).

Table 1. Geographical and climate information of the provenances of the studied *Castanopsis hystrix* half-sib families.

Family No.	Provenance	Latitude/ (N)	Longitude (E)	Elevation (m)	Mean annual temperature (°C)	Mean annual rainfall/ mm
1–4	Bobai	22°16′–22°28′	109°32′–111°17′	290	21.9	1756.0
5–10	Donglan	24°10′–24°30′	107°05′–107°43′	294	20.1	1546.0
11–13	Pingxiang	21°51′–22°08′	106°41′–106°59′	300	21.3	1376.5
14–23	Pubei	22°14′–22°41′	109°13′–109°14′	230	21.5	1757.4
24–32	Rongxian	22°28′–23°08′	110°15′–110°53′	214	21.3	1660.0

Table 2. Results of ANOVA of growth traits in *Castanopsis hystrix*.

Trait	Source	f	Mean square	F	p_r	Contribution (%)
DBH	Family	31	26.561	1.91	0.0045[**]	2.799
	Block	2	901.995	64.96	<0.0001[**]	95.193
	Family × block	62	19.087	1.37	0.0535	2.001
	Random error	287	22.570			
Tree height	Family	31	16.944	2.28	0.0004[**]	3.01
	Block	2	534.071	71.90	<0.0001[**]	94.99
	Family × block	62	11.207	1.51	0.0184[*]	1.99
	Random error	287	12.942			
Stem volume	Family	31	0.033	1.58	0.0340[*]	2.019
	Block	2	1.596	75.61	<0.0010[**]	96.614
	Family × block	62	0.023	1.07	0.3510	1.367
	Random error	287	0.021			

[*]: Significant at the 0.05 level; [**]: Significant at the 0.01 level

Table 3. Results of descriptive statistical analysis of DBH, tree height, and stem volume of *Castanopsis hystrix* families.

Family No.	DBH (cm)	Tree height (m)	Stem volume (m³)
1	24.76 ± 2.95cd	19.92 ± 1.98bc	0.42 ± 0.13bc
2	22.72 ± 6.42abcd	17.94 ± 4.71abc	0.37 ± 0.26abc
3	20.44 ± 5.41abcd	18.56 ± 3.98abc	0.30 ± 0.21abc
4	19.94 ± 3.37abc	18.66 ± 1.96abc	0.26 ± 0.11abc
5	17.68 ± 2.20a	16.91 ± 1.39abc	0.18 ± 0.05a
6	24.31 ± 4.59bcd	18.88 ± 2.81abc	0.40 ± 0.20abc
7	21.21 ± 3.58abcd	17.59 ± 2.44abc	0.27 ± 0.11abc
8	21.78 ± 5.20abcd	19.48 ± 3.31bc	0.34 ± 0.20abc
9	22.23 ± 1.51abcd	18.43 ± 2.44abc	0.31 ± 0.07abc
10	21.22 ± 3.41abcd	17.79 ± 2.94abc	0.28 ± 0.14abc
11	25.30 ± 3.32d	19.93 ± 3.12bc	0.44 ± 0.20c
12	25.07 ± 2.91cd	19.59 ± 3.38bc	0.42 ± 0.16bc
13	23.76 ± 3.62bcd	19.12 ± 2.48abc	0.37 ± 0.14abc
14	23.46 ± 1.26bcd	18.99 ± 1.68abc	0.35 ± 0.06abc
15	20.38 ± 7.85abcd	15.98 ± 4.08ab	0.28 ± 0.25abc
16	20.72 ± 5.50abcd	18.68 ± 5.59abc	0.32 ± 0.22abc
17	22.71 ± 4.40abcd	18.57 ± 3.52abc	0.35 ± 0.18abc
18	21.60 ± 3.81abcd	17.59 ± 2.35abc	0.29 ± 0.13abc
19	22.21 ± 2.44abcd	19.36 ± 1.92bc	0.32 ± 0.09abc
20	20.09 ± 4.81abcd	18.53 ± 1.62abc	0.26 ± 0.10abc
21	20.37 ± 7.28abcd	17.88 ± 5.80abc	0.32 ± 0.24abc
22	19.42 ± 3.61ab	16.99 ± 4.40abc	0.23 ± 0.11ab
23	20.58 ± 3.89abcd	16.12 ± 3.82ab	0.25 ± 0.14abc
24	20.91 ± 3.40abcd	18.51 ± 2.92abc	0.28 ± 0.13abc
25	20.88 ± 6.60abcd	17.74 ± 5.54abc	0.31 ± 0.26abc
26	23.10 ± 51.7bcd	17.94 ± 3.71abc	0.35 ± 0.20abc
27	22.40 ± 2.50abcd	20.38 ± 1.85bc	0.34 ± 0.09abc
28	22.28 ± 4.58abcd	18.72 ± 3.78abc	0.33 ± 0.15abc
29	21.23 ± 2.59abcd	18.24 ± 2.36abc	0.28 ± 0.09abc
30	17.71 ± 5.97a	15.30 ± 4.47a	0.20 ± 0.15a
31	22.11 ± 6.31abcd	19.46 ± 4.21bc	0.37 ± 0.27abc
32	19.48 ± 3.56ab	17.32 ± 3.18abc	0.23 ± 0.11ab
Mean	21.63 ± 4.63	18.28 ± 3.43	0.31 ± 0.17

Note: Lowercase letters in the same column denote significant differences in growth among the studied families ($p<0.05$)

Table 4. Results of ANOVA of wood color traits of *Castanopsis hystrix*.

Trait	Source	f	Mean square	F	p_r	Contribution (%)
Heartwood L^*	Family	31	19.945	0.82	0.745	14.613
	Block	2	88.555	3.62	0.029*	64.881
	Family × block	62	27.989	1.14	0.245	20.506
	Random error	287	25.190			
Heartwood a^*	Family	31	6.040	2.16	0.001**	58.284
	Block	2	0.032	0.01	0.989	0.309
	Family × block	62	4.291	1.54	0.015*	41.407
	Random error	287	28.260			
Heartwood b^*	Family	31	8.031	1.80	0.009**	19.181
	Block	2	26.861	6.02	0.003**	64.153
	Family × block	62	6.978	1.56	0.011*	16.666
	Random error	287	5.545			
Sapwood L^*	Family	31	11.011	2.04	0.002**	47.345
	Block	2	4.786	0.89	0.414	20.579
	Family × block	62	7.460	1.38	0.051	32.076
	Random error	287	6.464			
Sapwood a^*	Family	31	2.056	2.26	<0.0001**	29.401
	Block	2	3.947	4.35	0.014*	56.442
	Family × block	62	0.990	1.09	0.325	14.157
	Random error	287	1.071			
Sapwood b^*	Family	31	3.653	1.64	0.024*	8.967
	Block	2	34.298	15.42	<0.0001**	84.308
	Family × block	62	2.728	1.23	0.15	6.725
	Random error	287	2.711			

*: Significant at the 0.05 level; **: Significant at the 0.01 level

Table 5. Results of descriptive statistical analysis of heartwood and sapwood L^*, a^*, and b^* values of *Castanopsis hystrix* families.

Family No.	Heartwood L^*	Heartwood a^*	Heartwood b^*	Sapwood L^*	Sapwood a^*	Sapwood b^*
1	46.63 ± 3.14	15.03 ± 2.04abcde	18.81 ± 1.75abc	52.67 ± 1.55abcd	11.85 ± 0.97abcde	16.55 ± 1.07ab
2	48.49 ± 3.27	17.48 ± 2.00f	20.87 ± 1.88c	53.14 ± 4.21abcde	13.08 ± 1.36f	18.23 ± 1.16bc
3	47.38 ± 4.63	15.51 ± 0.80ababcdef	19.44 ± 2.34abc	54.80 ± 1.05cde	12.41 ± 5.44cdef	17.70 ± 1.12abc
4	47.26 ± 5.12	15.05 ± 1.85abcde	18.88 ±3.19abc	53.90 ± 1.99bcde	12.17 ± 0.75bcdef	17.61 ± 2.02abc
5	49.14 ± 4.73	14.28 ± 1.26ab	18.44 ± 1.47abc	54.72 ± 1.23cde	11.48 ± 0.84abc	16.67 ± 1.10ab
6	47.96 ± 8.31	14.87 ± 2.36abcd	17.82 ± 2.01ab	55.00 ± 4.26cde	11.67 ± 1.43abcd	16.77 ± 1.78ab
7	50.15 ± 7.39	15.25 ± 1.02abcde	21.07 ± 2.67c	54.42 ± 1.18cde	12.20 ± 0.62bcdef	17.29 ± 1.53abc
8	47.83 ± 6.00	14.91 ± 1.13abcd	18.71 ± 5.20abc	54.03 ± 1.06bcde	11.71 ± 0.53abcd	16.42 ± 0.95ab
9	46.98 ± 4.33	15.10 ± 0.84abcde	20.51 ± 2.92c	54.19 ± 0.95cde	12.88 ± 0.84ef	18.79 ± 1.31c
10	50.07 ± 2.93	14.07 ± 1.95a	19.04 ± 2.77abc	52.18 ± 1.65abc	11.60 ± 0.88abc	16.42 ± 1.20ab
11	49.23 ± 4.33	15.54 ± 1.12abcdef	18.98 ± 0.91abc	54.07 ± 1.78bcde	11.45 ± 1.10abc	16.12 ± 1.27a
12	45.25 ± 4.73	14.79 ± 1.29abcd	18.56 ± 0.96abc	54.27 ± 2.07cde	11.38 ± 0.95abc	16.11 ± 1.77a
13	46.23 ± 4.37	14.75 ± 2.63abc	17.80 ± 2.87ab	53.38 ± 1.06abcde	12.27 ± 1.23bcdef	17.30 ± 1.88abc
14	48.57 ± 2.89	16.10 ± 1.23abcdef	20.35 ± 2.51bc	54.82 ± 2.51cde	11.91 ± 0.68abcde	17.78 ± 2.56abc
15	45.50 ± 5.42	15.49 ± 1.40abcdef	18.90 ± 2.58abc	52.55 ± 2.69abcd	11.98 ± 1.07abcdef	16.57 ± 1.56ab
16	46.82 ± 4.03	15.51 ± 1.62abcdef	19.73 ± 1.77abc	51.32 ± 2.92ab	12.17 ± 0.86bcdef	16.81 ± 10.4ab
17	47.90 ± 4.03	15.35 ± 1.64abcde	19.44 ± 1.77abc	54.74 ± 2.55cde	11.64 ± 0.47abcd	16.77 ± 1.51ab
18	46.60 ± 5.77	16.14 ± 1.63abcdef	19.68 ± 2.03abc	53.70 ± 2.49abcde	11.73 ± 1.33abcd	16.60 ± 0.87ab
19	47.99 ± 3.29	15.31 ± 1.29abcde	19.19 ± 0.87abc	53.42 ± 0.65abcde	11.32 ± 0.47abc	16.33 ± 0.46a
20	45.54 ± 4.55	15.48 ± 1.20abcdef	18.96 ± 1.94abc	55.55 ± 3.12e	11.00 ± 1.12a	16.64 ± 1.14ab
21	47.26 ± 5.09	16.30 ± 2.38bcdef	20.29 ± 2.85bc	53.12 ± 2.06abcde	12.36 ± 0.94cdef	17.39 ±1.85abc
22	46.15 ± 6.26	17.05 ± 1.76ef	20.26 ± 2.40bc	52.94 ± 2.84abcde	11.68 ± 0.71abcd	16.58 ± 1.83ab
23	47.17 ± 5.87	16.86 ± 2.81def	19.90 ± 2.75abc	54.54 ± 3.96cde	12.03 ± 1.06abcdef	17.88 ± 2.25abc
24	47.16 ± 5.23	16.60 ± 2.20cdef	19.89 ± 3.24abc	53.55 ± 1.50abcde	11.46 ± 0.98abc	16.96 ± 2.92ab
25	49.93 ± 5.12	14.27 ± 1.98ab	18.74 ± 2.59abc	54.72 ± 2.16cde	11.84 ± 1.20abcde	16.90 ± 1.24ab
26	48.30 ± 5.22	15.39 ± 1.47abcde	18.65 ± 2.26abc	53.09 ± 0.96abcde	11.85 ± 0.63abcde	16.54 ± 1.96ab
27	44.04 ± 4.08	15.14 ± 1.68abcde	18.46 ± 2.47abc	51.02 ± 1.81a	12.75 ± 1.58def	17.74 ± 2.34abc
28	49.58 ± 7.30	15.60 ± 2.14abcdef	18.50 ± 2.09abc	53.94 ± 4.95cde	11.15 ± 1.35ab	16.60 ± 1.67ab
29	47.18 ± 3.10	16.44 ± 2.05cdef	19.82 ± 2.54abc	54.25 ± 2.66cde	12.22 ± 1.11bcdef	17.04 ± 1.02abc
30	49.49 ± 5.42	14.99 ± 1.47abcde	18.43 ± 2.72abc	54.06 ± 2.05bcde	11.99 ± 0.67abcdef	16.98 ± 1.94ab
31	46.73 ± 3.07	16.42 ± 2.03cdef	20.83 ± 2.44c	55.41 ± 2.24de	11.56 ± 0.64abc	16.98 ± 1.05ab
32	47.09 ± 4.21	14.95 ± 2.03abcd	17.26 ± 1.29a	52.65 ± 2.03abcd	12.09 ± 0.84abcdef	16.27 ± 1.32a
Mean	47.55 ± 5.02	15.50 ± 1.86	19.26 ± 2.35	53.79 ± 2.54	11.90 ± 1.04	16.98 ± 1.65

Note: Lowercase letters in the same column denote significant differences in wood color among the studied families (*p*<0.05)

Table 6. Genetic parameters for growth and wood color traits of *Castanopsis hystrix*.

Trait	σ_F^2	$\sigma_{F\times B}^2$	σ_E^2	CV_g	h_F^2	h_S^2
DBH	0.83	1.73	13.89	3.60	0.53	0.10
Tree height	0.64	1.26	7.43	4.01	0.56	0.14
Stem volume	0.0012	0.0005	0.0211	10.13	0.76	0.11
Heartwood L^*	NSF	NSF	NSF	NSF	NSF	NSF
Heartwood a^*	0.19	0.50	2.79	1.67	0.85	0.11
Heartwood b^*	0.12	0.84	4.46	2.11	0.68	0.04
Sapwood L^*	0.39	0.69	5.40	2.32	0.86	0.12
Sapwood a^*	0.12	0.03	0.91	0.95	0.92	0.22
Sapwood b^*	0.10	0.17	2.22	1.49	0.80	0.08

Notes: σ_F^2, $\sigma_{F\times B}^2$, and σ_E^2 are the variance components for family, family × block interaction, and environment, respectively, CV_g is the genetic coefficient of variation and h_F^2 and h_S^2 are family and individual heritability, respectively. NSF means no significant in analysis of variance, so heritability was not calculated

Table 7. Trait-trait genetic correlations in the lower diagonal part andand phenotypic correlations in the upper diagonal part.

Trait	DBH	Tree height	Stem volume	Heartwood L^*	Heartwood a^*	Heartwood b^*	Sapwood L^*	Sapwood a^*	Sapwood b^*
DBH	1	0.778*	0.956**	-0.174	0.018	-0.046	-0.095	-0.043	0.016
Tree height	0.719	1	0.827*	-0.238	-0.069	-0.142	-0.156	-0.067	-0.059
Stem volume	0.947**	0.789*	1	-0.190	0.021	-0.035	-0.103	-0.003	0.048
Heartwood L^*	-0.121	-0.188	-0.132	1	-0.269	0.173	0.293	-0.191	0.048
Heartwood a^*	0.034	-0.068	0.038	-0.286	1	0.670	0.060	0.268	0.325
Heartwood b^*	-0.077	-0.182	-0.080	0.206	0.686	1	0.196	0.139	0.482
Sapwood L^*	-0.108	-0.172	-0.085	0.291	0.034	-0.077	1	-0.194	0.297
Sapwood a^*	-0.044	-0.045	-0.006	-0.202	0.291	0.075	-0.161	1	0.598
Sapwood b^*	-0.027	-0.102	-0.008	0.097	0.348	0.449	0.351	0.547	1

Note: $r(0.05) = 0.7545$, $r(0.01) = 0.8745$; *: Significant at the 0.05 level; **: Significant at the 0.01 level

Estimation of genetic parameters for growth traits and wood color: (Table 6) shows the estimated genetic parameters for growth and wood color traits. The genetic parameters for heartwood L^* could not be estimated because the differences among the various families were not significant. Family variance components of DBH, tree height, heartwood a^*, heartwood b^*, sapwood L^*, sapwood a^*, and sapwood b^* were 0.10–0.83, indicating that growth traits (DBH and tree height) and wood color (heartwood a^*, heartwood b^*, sapwood L^*, sapwood a^*, and sapwood b^*) were genetically controlled. The family variance component of stem volume was only 0.0012; however, the variance components for family × block interactions and environment were also relatively small, indicating that stem volume is also a genetically controlled trait. Genetic coefficients of variation in growth traits (3.60%–10.13%) were larger than those in wood color traits (0.95%–2.32%), indicating that the genetic stability of growth traits was inferior to that of wood color. Except for the slightly lower family inheritability of heartwood b^* (0.68) compared with that of stem volume (0.76), the family heritability values of the wood color traits heartwood a^* and sapwood L^*, a^*, and b^* (0.80–0.92) were higher than those of DBH, tree height, and stem volume (0.53–0.76). This indicates that wood color traits were strongly genetically controlled, indicating that the appearance quality of wood obtained from man-made forests can be enhanced by selecting superior families. In addition, the family heritability values of the eight traits mentioned above (0.53–0.92) were higher than the individual heritability values within families (0.04–0.22), indicating that greater genetic gain can be achieved by selecting families with superior qualities.

Correlation analysis of growth traits and wood color: (Table 7) shows that the genetic and phenotypic correlations among growth and wood color traits were not significant ($r_{0.05} = 0.7545$, $r_{0.01} = 0.8745$). Therefore, growth and wood color traits were weakly genetically correlated and relatively independent of each other. These results suggest that targeted selection of germplasm that grow rapidly and provide high yields, possess superior wood color, or excel in both growth and wood color traits to achieve different breeding objectives can be applied in directed breeding of high-value *C. hystrix* in man-made forests.

Comprehensive evaluation of C. hystrix half-sib families: Heartwood is mainly used to produce *C. hystrix* wood materials. Based on the insignificant differences in heartwood L^* among the studied families, the DBH, tree height, stem volume, heartwood a^*, and heartwood b^* in different families were comprehensively evaluated (Table 8). By setting a selection proportion of 20%, six half-sib families with superior growth traits (rapid growth and high yield) were selected (No. 11, 1, 12, 6, 13, and 31); the mean genetic gains in DBH, tree height, stem volume of these families were 13.017%, 7.314%, and 43.268%, respectively (Table 9). Based on heartwood color traits, six half-sib families with superior wood color were selected (No. 2, 22, 31, 23, 21, and 24); the mean genetic gains in heartwood a^* and heartwood b^* were 13.988% and 7.689%, respectively (Table 7). Based on the growth and heartwood color traits, six half-sib families with both superior wood color and growth were selected (No. 11, 1, 12, 2, 31, and 14); the mean genetic gains in growth and wood color traits were 12.093%, 7.166%, 39.054%, 10.265%, and 7.235% (Table 9).

Table 8. Comprehensive evaluation indicator values and ranking of *Castanopsis hystrix* families.

Family No.	Q_i for growth traits	Rank	Family No.	Q_i for heartwood color	Rank	Family No.	Q_i for growth and heartwood color traits	Rank
11	1.726	1	2	1.411	1	11	2.184	1
1	1.706	2	22	1.392	2	1	2.159	2
12	1.705	3	31	1.389	3	12	2.153	3
6	1.672	4	23	1.382	4	2	2.147	4
13	1.649	5	21	1.377	5	31	2.144	5
31	1.634	6	24	1.376	6	14	2.131	6
27	1.630	7	14	1.374	7	6	2.120	7
14	1.629	8	29	1.372	8	13	2.099	8
2	1.618	9	7	1.368	9	17	2.099	9
17	1.614	10	18	1.363	10	27	2.098	10
8	1.609	11	9	1.355	11	26	2.087	11
26	1.609	12	16	1.35	12	19	2.084	12
19	1.598	13	3	1.345	13	8	2.081	13
28	1.597	14	17	1.342	14	9	2.080	14
9	1.577	15	11	1.338	15	28	2.078	15
16	1.569	16	19	1.337	16	21	2.075	16
21	1.552	17	20	1.336	17	16	2.070	17
3	1.549	18	15	1.335	18	24	2.065	18
25	1.549	19	28	1.331	19	29	2.062	19
18	1.541	20	26	1.329	20	18	2.058	20
24	1.540	21	4	1.326	21	3	2.052	21
29	1.540	22	1	1.324	22	7	2.046	22
10	1.532	23	27	1.32	23	25	2.026	23
7	1.522	24	8	1.319	24	23	2.020	24
4	1.515	25	30	1.316	25	20	2.020	25
20	1.515	26	12	1.314	26	22	2.015	26
15	1.492	27	10	1.307	27	10	2.014	27
23	1.474	28	25	1.306	28	4	2.013	28
32	1.464	29	6	1.302	29	15	2.002	29
22	1.457	30	5	1.301	30	32	1.954	30
5	1.392	31	13	1.299	31	30	1.907	31
30	1.380	32	32	1.294	32	5	1.905	32

Table 9. Estimation of genetic gains of selected *Castanopsis hystrix* half-sib families.

Families with superior growth traits		Families with superior wood color traits		Families with both superior growth and wood color traits	
Trait	Genetic gain	Trait	Genetic gain	Trait	Genetic gain
DBH	13.017	Heartwood a^*	13.988	DBH	12.093
Tree height	7.314	Heartwood b^*	7.689	Tree height	7.166
Stem volume	43.268			Stem volume	39.054
				Heartwood a^*	10.265
				Heartwood b^*	7.235

Discussion

Genetic variations affecting growth traits: In the present study, the differences in the DBH, tree height, and stem volume of *C. hystrix* were significant or highly significant among blocks, indicating that environmental factors are key factors influencing these traits, which is consistent with the results of genetic testing conducted on 26 full-sib Masson pine (*Pinus massonina* Lamb.) families aged 8 years at three different sites (Yuan *et al*., 2021). As the soil parent material, soil type, and slope face were similar among the three blocks in our study site, we found that slope position was the environmental factor affecting the differentiation of *C. hystrix* growth traits. In a study by Lu

et al., (1999) on the effects of slope position within the same slope face on *C. hystrix* growth, *C. hystrix* on the lower slope showed superior growth, and the DBH, tree height, and stem volume were 67.60%, 48.32%, and 328.10% higher compared to values for plants on the mid slope. These results confirm that the slope position is a key environmental factor that determines the growth rate and yield of man-made *C. hystrix* forests. Family also served as the main source of growth trait variations in *C. hystrix*, considering higher family heritability values for DBH, tree height and stem volume. These results indicate that the growth traits of *C. hystrix* were subjected to moderate to strong genetic control, which is consistent with the results of Zhu *et al*., (2014).

Genetic variations affecting wood color: Both environmental and genetic factors can lead to wood color variations in *C. hystrix*. Our results revealed the presence of significant differences in heartwood L^* and b^* values and sapwood a^* and b^* values among blocks, demonstrating that environmental factors are the key factors influencing these traits. This is consistent with the results of genetic testing performed on the wood color of black walnut (*Juglans nigra* L.) and sessile oak (*Quercus petraea* Liebl) in progeny test forests (Rink, 1987; Janin *et al*., 1990). In the present study, we also found that family was the main source of variations in heartwood a^* and b^*, and sapwood L^*, a^*, and b^*. Family heritability values were within the range of 0.68–0.92 (heritability values may have been higher, as they were estimated based on single-point testing), indicating relatively strong heritability. Therefore, wood color traits are key factors that may be stably inherited. Duan *et al*., (2015) utilized 21 simple sequence repeat markers to construct a genetic map for red-heart Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.).

In addition, we observed that family × block interactions significantly affected heartwood a^* and b^*, indicating that wood color was controlled by both genetics and the environment. Montes *et al*., (2008) performed a provenance/ progeny test on the wood color of *Calycophyllum spruceanum* and found that wood color was jointly controlled by genetic and environmental factors, with these factors showing significant interaction effects. The heritability of L^* in the infertile planting zone was low, revealing a lower level of genetic control, whereas the heritability values of a^* and b^* in planting zones with good environmental conditions were higher, indicating moderate genetic control (Montes *et al*., 2008). Therefore, in addition to germplasm/family adaptability, growth, and wood color selection, the interactions between genetics and the environment should be considered when selecting superior *C. hystrix* breeds for man-made timber forests to achieve site-germplasm matching.

These results also revealed significant differentiation in heartwood color among the 32 studied families, with a total color difference (ΔE^*) between the best- and worst-performing families as high as 7.97, which can be easily perceived by the human eye (Cui *et al*., 2004). Similar differentiation patterns in heartwood color among families have also been reported in studies on the valuable tree species *Santalum austrocaledonicum* (Page *et al*., 2010) and *T. grandis* (Moya & Marín, 2011). Studies have proposed various theories to explain the mechanisms of wood color variations. Yazaki *et al*., (2015) suggested that specific color changes were caused by changes in the components and contents of wood extracts. It is generally considered that two pathways exist for extract synthesis and transport: (1) precursors synthesized in the leaves or vascular cambium are transferred to the heartwood area and used to synthesize extracts (Frey-Wyssling & Bosshard, 1959) and (2) extracts are synthesized *in situ* by sapwood cells, which are converted to heartwood cells (Neales, 1959). Wood color is also associated with extract degradation and related chemical reactions. Charrier *et al*., (1995) and Zahri *et al*., (2007) separately subjected the wood of European oak (*Quercus robur*) to kiln drying and UV light irradiation and found that changes in wood color were related to the degradation and conversion of ellagitannins and total phenols. Therefore, the components and conversion of extracts such as phenols (Chen *et al*., 1993; Burtin *et al*., 1998) may be related to the formation and variations of the wood color of *C. hystrix*.

Correlations between growth traits and wood color and comprehensive selection of superior half-sib families: It was found that the growth traits of *C. hystrix* were weakly correlated with heartwood and sapwood color, which is consistent with the results of previous studies on the genetic correlations of growth traits and wood color in *C. spruceanum* (Montes *et al*., 2008) and *T. grandis* (Moya *et al*., 2013). Thus, wood color may be inherited independently of growth traits. This enables the selection of superior germplasm with both good growth and good color traits. Thus, families with excellent wood color traits can be selected from existing rapid-growing and high-yielding germplasm based on current demands and future trends of wood markets, which will contribute to directed breeding of valuable tree species in man-made forests. In the present study, six families with both superior heartwood color and growth traits were selected using a selection proportion of 20%. Notably, darkening and reddening of heartwood color occurs in valuable tree species as the trees age (Mosedale *et al*., 1996; Liu *et al*., 2005). Therefore, wood color variations caused by age should also be considered in germplasm/family selection. In the present study, we evaluated the wood color variations of 17-year-old *C. hystrix* germplasm/families. Our results only reflect the early wood color variations in *C. hystrix*; thus, further studies are required to obtain more reliable results to set forth guidelines for efficient selective breeding and utilization of superior *C. hystrix* breeds.

Conclusion

The growth traits and wood color of *C. hystrix* are controlled by both genetic and environmental factors. Therefore, targets for selective breeding of superior breeds and site selection should be optimized for directed breeding in man-made timber forests. Family heritability values for DBH, tree height, stem volume, heartwood a^* and heartwood b^* were moderately or strongly genetically controlled. Using a multi-trait comprehensive evaluation method, six families with superior growth traits (rapid growth and high yield), superior wood color (reddish heartwood color), and both superior growth and wood color traits were selected to provide high-quality germplasm for directed breeding in man-made forests of high-value tree species. Considering that growth traits and wood color are inherited independently of each other, rapid-growing and high-yielding parent plants may be matched with parent plants with a superior heartwood color, and intraspecific hybridization may be performed to develop new germplasm carrying the superior traits of both parents.

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