Genetic parameters and prediction of breeding values in *Castanopsis hystrix* A.DC. for growth and form traits

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Abstract

Castanopsis hystrix A.DC. is one of the most important and multipurpose tree species native to China. 157 open-pollinated families collected from 11 provenances in Guangdong, Guangxi, and Fujian province were used to estimate genetic parameters for height (H), diameter at breast height (DBH), ground diameter (GD), and crown width (CW) for each province and combined three provinces at ages from 3 to 9 years. The variance component was small and non-significant among provenances but was highly significant among families within provenances for H, DBH, GD, and CW. Heritability estimates were significant except for a few traits from Fujian's provenances. Heritability ranged from 0.20 to 0.57 for H, 0.19 to 0.38 for DBH, 0.21 to 0.55 for GD, and 0.09 to 0.39 for CW. Heritability estimates for H and DBH decreased with increased age for each province and combined three provinces. Significantly high genetic correlations were observed for ageage and trait-trait correlations, indicating that genetic performance at one trait was well correlated with another trait. In total, 22 families and 60 individuals were selected for backward and forward selection based on breeding values.

Keywords: Castanopsis hystrix; additive variance; individual heritability; genetic correlation; breeding values.

Introduction

Forest tree species typically have long rotations and long breeding cycles, indicating that tree improvement programs need to be well organized and structured at the start to maximize genetic gain for short and long-term

(White et al., 2007). Castanopsis hystrix A.DC. is one of the most important and multifunctional tree species native to China because of its good growth characteristics, desirable wood properties, and broad utilization range (HUANG et al., 2012). It is found naturally in southern China in Guangxi, Guangdong, Hainan, and Yunnan provinces between 21°N and 35°N and 109°E and 117°E. Castanopsis hystrix can be planted as pure stand or mixed with other species such as conifers and firs. Over the past three decades, C. hystrix resources in China have expanded as an important tree species of structural- and appearance-grade wood products with the combined plantation area in Guangdong and Guangxi has reached approximately 5000 ha (ZHU et al., 2005). A comprehensive provenance-progeny tests was initiated in the 1990s with the aim of further selective breeding (ZHU et al., 2005; HUANG et al., 2012).

Breeding of *C. hystrix* for commercially important traits is a relatively recent development for increasing the productivity of newly established plantations. The program is following the principle of two successful long-term tree breeding programs: radiata and loblolly pine. Genetic improvement of radiata pine [Pinus radiata D. Don] was initiated in the 1950s in Australia with the initial plus tree selection for open-pollinated (OP) family testing. The first two generations of radiata pine selective breeding focused on growth and form traits; the average rotation length for radiata pine plantations decreased from about 40-55 years to about 30-35 years (LI and Wu, 2005; Wu et al., 2007, 2008). The third generation of radiata pine breeding in Australia focused on genetic variation in wood quality traits (Matheson et al., 2008; Gapare et al., 2009). Genetic improvement of loblolly pine was also initiated in the 1950s, and the North Carolina State University Cooperative Tree Improvement Program (NCSU) with initial provenance and progeny trials and achieved genetic gains up to 30% using third-generation

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selectively bred loblolly pine when compared to unimproved genetic material (McKeand et al., 2001, 2003).

Genetic variance among individuals is typically partitioned into non additive and additive components. Non additive variance can be further divided into epistatic variance due to interactions of genes at two or more loci and dominance variance caused by intra-locus gene interactions (FALCONER and MACKAY, 1996). However, genetic parameter estimates based on OP seed orchards during forest tree breeding have largely focused on additive genetic models in the form of family or individual tree models. In *C. hystrix*, no reports are available on the use of OP progenies for describing the structure of the genetic variance. In addition, no estimates have been published of the breeding values of C. hystrix, although predictions of breeding values for other forest tree species are a standard prectices (XIE et al., 2007; ISIK et al., 2008; IWATA et al., 2011; HARDNER et al., 2012; DENIS and BOUVET, 2013). At this time, studies on the genetics of C. hystrix have focused on height (H), diameter at breast height (DBH), ground diameter (GD), and crown width (CW); these related traits are the most important for wood production at initial breeding effort (Greaves et al., 1997).

The objectives of this study were to (1) compare genetic variation at the additive levels in DBH, H, GD, and CW among the three provinces and combined three provinces; (2) estimate heritability for growth and form traits at different ages using the family model for each province and combined three provinces; (3) estimate additive genetic correlations between

the traits; and (4) estimate family and individual-tree breeding values based on combined three provinces to select elite trees for grafting into seed orchards.

Materials and Methods

Genetic material

Genetic materials were collected from three provinces as:

Guangdong provenance: Sixty-four OP families were collected from three provenances of Xinyi, Gaozhou, and Luhe in October and November 2001. Guangxi provenance: OP seeds from 51 plus trees were collected from five provenances of Pubei, Bobai, Rongxian, Pingxiang, and Donglan in October and November 2000.

Fujian provenance: OP seeds from 42 plus trees were collected from three provenances of Zhangzhou, Jinshan, and Huaan in October and November 2001. Details on seed source collection information for the 11 provenances at the three provinces are provided in *Table 1*.

Provenance-progeny trial and measurement

The 11 provenances from the three provinces were planted in 2002–2003 at Longyandong Forest Farm in Guanzhou City, Guangdong Province, China (23°10′–23°18′N, 113°21′–113°27′E). The site has an arenaceous shale lateritic red soil (pH 4.75–5.20) and receives an average annual rainfall of 1,760 mm (*Table 1*). Location of natural *Castanopsis hystrix* provenances in China is described in *Fig. 1*. 3–5 trees

Table 1. – Details of *Castanopsis hystrix* A.DC. provenance location.

Prov. Code	Prov.	No. of families	Spacing (m)	Location, Country	Longitude (E)	Latitude (N)	Altitude (m)	Temperature	Rainfall (mm/year)	Survival (%)
1	GD21	11	2 × 3	Xinyi, China	110'40 -111 40	22 16 -22 42	300	22.3	1700.0	
2	GD22	20	2×3	Gaozhou, China	110:36 -110 22	21 42 -22 18	404	22.9	1892.7	89.6
3	GD 23	33	2×3	Luhe, China	115 24 -115 19	23 06 -28 32	407	21.8	2100.0	
4	GX11	12	2×3	Pubei, China	109 14 -109 13	22 14 -22 41	230	21.4	1787.3	
5	GX12	14	2×3	Bobai, China	109'32 -111 17	22 16 -22 28	290	21.9	1743.2	
6	GX13	9	2×3	Rongxian, China	110 15 -110 53	22 28 -23 08	214	21.3	1660.2	82.1
7	GX15	4	2×3	Pingxiang, China	106'41 -106 59	21 51 -22 16	300	21.3	1376.5	
8	GX17	12	2×3	Donglan, China	107'05 -107 43	24 10 -24 30	394	20.1	1577.1	
9	FJ31	26	2×3	Jinshan, China	117 33 -117 34	24 57 -24 58	140	20.8	1631.5	
10	FJ32	4	2×3	Gaoche, China	117 16 -117 44	24 30 -25 12	200	20.6	1870.1	74.6
11	FJ33	12	2×3	Huaan, China	117'20 -117 44	24 27 -24 40	300	20.4	1870.1	

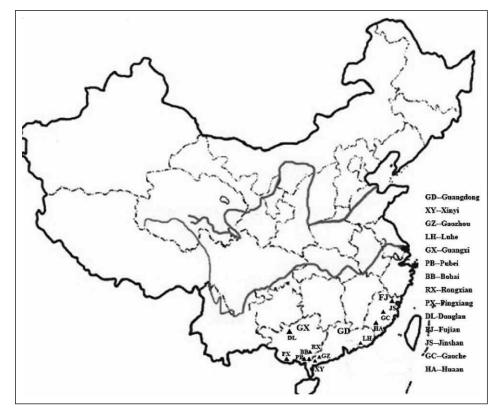


Figure 1. – Location of natural Castanopsis hystrix provenances in China: Xinyi, Gaozhou, Luhe, Pubei, Bobai, Rongxian, Pingxiang, Donglan, Jinshan, Gaoche, and Huaan.

for family plot Seedlings were planted using 2×3 m spacing, with five, six, and seven replications for populations from Guangdong, Guangxi and Fujian, respectively, using randomized complete block designs. H and DBH were measured during 2005–2010 for all families of the three provinces (e.g. age 3 to 9 based on populations and traits see detail from *Table 3*). DBH was measured at 1.3 m above the ground. GD of the three provinces was investigated and CW was the average of east-west and north-south directions in 2005, which were important for wood production.

Statistical analyses

Preliminary family mixed model analyses were performed using the statistical software ASReml (GILMOUR et al., 2009) to calculate different variance components. Provenance effects were not significant and were dropped in the final analyses. The data were analyzed using univariate and multivariate family mixed models. ASReml fits the general mixed model, and was used for combined and separate analyses for three provinces.

$$y = Xb + Zu + e, (1)$$

where y is an $n \times 1$ vector of observations in the trial. For combined province analysis, the b is a vector of fixed effects (including the trial mean, replication, province and year effect, respectively), **X** is an $n \times w$ design matrix that mapped the observations onto the fixed effects, **Z** is an $n \times m$ matrix that mapped the observations onto the genotype effects (including provenance, family within provenance), u is a p $\times 1$ vector of random effects (including familywithin-provenance, province by replication, and family-within-provenance by replication interaction), and e is an $n \times 1$ vector of unknown residuals. For each individual province analyses, the b is a vector of fixed effects (including trial mean, replication), and u is vector of random effects (including family across provenance, and family by replication).

Individual-tree narrow-sense heritability was estimated for each province and combined three provinces, as follows:

$$h^2 = \frac{4 \times \sigma_{Fam}^2}{\sigma_{Fam}^2 + \sigma_{Fam,Rep}^2 + \sigma_e^2}, \tag{2}$$

where σ^2_{Fam} is the family variance component within provenance, $\sigma^2_{Fam.Rep}$ is the interaction variance family by replication, and σ^2_e is the residual variance component.

To compare the levels of additive genetic variance in each trait independent of their means, we estimated the genetic coefficient of variation (CV_A) (CORNELIUS, 1994)

$$CV_{A} = \frac{\widehat{\sigma_{A}}}{x} \times 100\%, \tag{3}$$

where CV_A is the coefficient of additive genetic variation, σ_A is the square root of the additive genetic variance for a trait, and x is the trait phenotypic mean in the trial. The CV_A represents the genetic variance relative to the mean of the trait of interest: the higher the CV_A for a trait, the higher its relative variation.

Additive genetic correlation estimates between traits X and Y were obtained from the estimated additive covariance and variance components within provenance as

$$r_{A} = \frac{\text{cov}_{XY}}{\sqrt{\sigma_{X}^{2} \times \sigma_{Y}^{2}}},\tag{4}$$

where COV_{XY} is the additive genetic covariance component between trait X and trait Y, σ^2_X is the additive genetic variance for trait X within-provennace at each province, and σ^2_Y is additive genetic variance for trait Y within-provennaces at each province. The additive genetic correlation estimates for combined three provinces between two traits were computed similar to equation (4).

The efficiency of early selection relative to mature age per generation was calculated as

$$E = \frac{100 \times i_j h_j r_g}{i_m h_m},\tag{5}$$

where i_j and i_m are the selection intensity in the juvenile trait (dbh at age 5 and 6) and mature trait (dbh at age 8 and 9), respectively, assum-

ing that $i_j = i_m$, and h_j and h_m are the square root of heritability estimates for the juvenile age and the mature age, respectively; and r_g is the additive genetic correlation of juvenile and mature traits.

Results and Discussion

Provenance survival, growth, and form

Survival of Guangdong and Fujian provenances at age 8 years and Guangxi provenance at age 9 years were 89.6%, 74.6%, and 82.1%, respectively (*Table 1*). Generally, the best growth rate was observed in Guangxi provenances, but CW and GD were similar among the three provinces (*Table 2*). DBH at age 5 or 6 years at Guangdong and Guangxi provinces ranged from 3.88 cm to 8.21 cm and at age 8 or 9 years ranged from 11.19 to 13.02 cm. The differences between Guangdong and Guangxi was getting smaller from earlier age (5 or 6) to age 8 or 9 for DBH, but almost unchanged for HT.

Effect on variance and individual heritability

Variance components for all the traits at each province are shown in Table 3. The family variance (V_{Fam}) estimated for growth and form traits were significant at all ages for Guangdong and Guangxi populations, while only HT, CW and GD at age 3, and DBH at age 8 were significant for Fujian. The family by replication interaction was not significant for all traits except for DG4 of Guangxi province at age 4. The genetic coefficient of variation (CV) was between 2.9% to 7.9% and was similar for most traits at different ages. The additive and residual error variances for H, DBH and CW except for HT3 (4) increased with increased age, and we did not observe significant provenance variance components for combined three provinces.

Generally, heritabilities for most traits were low to moderate, and significant heritabilities were observed for all traits for each province

Table 2. – Means for growth and form traits of *Castanopsis hystrix* A.DC. by each province; means are followed by their standard deviations.

Prov.	DBH5 (6) (cm) ^a	DBH8 (9) (cm)	HT5(6) (m)	HT8(9) (m)	CW5(6) (m)	GD3(4) (cm)
Guangdong	3.88 ± 1.81	11.19 ± 3.25	4.64 ± 1.51	10.16 ± 3.52	2.16 ± 0.67	2.10 ± 0.70
Guangxi	8.21 ± 3.05	13.02 ± 3.12	7.32 ± 2.28	14.55 ± 4.51	3.87 ± 1.26	5.73 ± 1.78
Fujian	3.60 ± 1.73	9.35 ± 3.45	3.83 ± 1.42	7.08 ± 2.18	2.21 ± 0.77	2.19 ± 0.69

^a Measurement age are varied among different province population.

Table 3. – Variance components for family across provenance, family \times replication interaction, residual errors, heritability, and genetic coefficient of variation (CV) for different traits in each province.

Prov.	Trait	V_{Fam}	$V_{Fam \wedge Rep}$	V_{E}	Heritability	CV(%)
	НТ3	0.06***	0.01	0.37	0.55 ± 0.10	3.6
	HT5	0.24***	0.03	2.07	0.41 ± 0.09	3.3
	HT8	0.46***	NA	8.27	0.21 ± 0.06	7.9
	DBH3	0.02***	0.002	0.19	0.38 ± 0.09	5.0
Guangdong	DBH5	0.27***	0.001	3.09	0.32 ± 0.08	4.8
raungumg	DBH8	0.46***	NA	9.47	0.19 ± 0.05	2.9
	CW3	84.93***	13.35	776.21	0.39 ± 0.09	3.4
	CW5	136.67***	16.64	4320.61	0.12 ± 0.04	4.0
	GD3	0.07***	0.003	0.44	0.55 ± 0.12	3.4
	HT4	0.17***	0.04	1.57	0.38 ± 0.09	3.2
	HT6	0.25***	NA	4.76	0.20 ± 0.07	3.2
	HT9	1.07***	NA	17.4	0.23 ± 0.08	4.2
	DBH4	0.10**	0.01	1.67	0.22 ± 0.08	3.4
Guangxi	DBH6	0.42***	NA	8.39	0.19 ± 0.07	3.8
	DBH9	0.43***	NA	7.38	0.22 ± 0.08	2.9
	CW4	102.90*	164.86	4338.52	0.09 ± 0.05	3.5
	CW6	612.85***	NA	13267.9	0.18 ± 0.06	3.8
	GD4	0.16**	0.17**	2.74	0.21 ± 0.07	3.2
	HT3	0.03***	NA	0.3	0.36 ± 0.11	3.6
	HT8	0.034	NA	4.6	0.03 ± 0.09	5.2
	DBH3	0.007	0.01	0.16	0.16 ± 0.15	5.3
Fujian	DBH5	0.014	0.02	3.04	0.02 ± 0.07	4.9
	DBH8	0.60*	NΛ	10.68	0.21 ± 0.11	3.7
	CW3	88.40***	NA	829.17	0.39 ± 0.14	3.9
	GD3	0.06***	NA	0.44	0.48 ± 0.13	3.3

^{*,} P < 0.05; **, P < 0.01; ***, P < 0.001.

and combined three provinces except CW4 for Guangxi population and HT8, DBH3, and DBH5 for Fujian population (*Table 3*). Heritability estimates for HT and DBH decreased over time for Guandong population, from 0.55 to 0.21 for HT, and from 0.38 to 0.19 for DBH. Heritability estimates for Guangxi and Fujian population have no obvious age trend. Standard errors for heritabilities in Fujian were larger probably because of the small sample size. Heritability estimates for HT, DBH and CW decreased over time for combined three provinces, from 0.54 to 0.21 for HT, from 0.37 to 0.18 for DBH, and from 0.22 to 0.13 for CW, respectively (*Table 4*).

Among the three provinces, Fujian had the lowerest additive genetic variance for growth and form traits than the other two provinces.

There was only one reported heritabilities for DBH and HT (0.63 and 0.71 at age 3, respectively) for *C. hystrix*. (ZHU et al., 2005). The estimated heritability of HT and DBH at age 8 or 9 years in *C. hystrix* was similar to estimates in many other genetic studies such as radiata pine (JAYAWICKRAMA, 2001; WU and MATHESON, 2002; LI and WU, 2005; WU et al., 2007), loblolly pine (GWAZE et al., 2001; ERICSSON and FRIES, 2004; FRIES and ERICSSON, 2006, 2009; FRIES, 2012), and eucalyptus (LOPEZ et al., 2002; POTTS et al., 2004; FREEMAN et al., 2007).

Effect of province and combined three provinces on genetic correlation

The genetic correlations for age-age and traittrait were estimated for populations from

Table 4. – Variance components for province by replication, family-within-province, and family-within-province by replication interaction, residual errors, heritability and stand error for different traits combined three provinces analysis.

Trait	$V_{Province imes Rep}$	V_{Fam}	$ m V_{Fam imes Rep}$	$\mathbf{V}_{\mathtt{E}}$	Heritability
HT3(4)a	0.01	0.12***	NΛ	0.79***	0.54±0.07
HT5(6)	0.1	0.20***	0.22**	2.80***	0.24 ± 0.04
HT8(9)	0.27	0.59***	0.95***	9.54***	0.21 ± 0.04
DBH3(4)	0.01	0.09***	0.01	0.82***	0.37 ± 0.06
DBH5(6)	0.13*	0.28***	0.30***	4.69***	0.21±0.04
DBH8(9)	0.40*	0.39***	0.59***	7.62***	0.18 ± 0.04
CW3(4)	NA	0.06***	NA	0.20***	0.22 ± 0.04
CW5(6)	0.12*	0.03***	0.05***	0.73***	0.13±0.03
GD3(4)	NA	0.15***	0.03	1.26***	0.41±0.06

^a Measurement age are varied among different province population.

Table 5. – Genetic correlations of the same traits (height and diameter at breast height) at different ages for Guangdong, Guangxi province and combined three provinces.

Provenance	Trait	DBH3(4) ^a	DBH5(6)	Trait	HT3(4)	HT5(6)
C	DBH5	0.99 ± 0.03		HT5	0.96±0.02	_
Guangdong	DBH8	0.81±0.10	0.91±0.05	HT8	0.76±0.09	0.78±0.08
C	DBH6	0.95±0.05		нт6	0.99±0.02	
Guangxi	DBH9	0.56 ± 0.21	0.86 ± 0.09	HT9	0.85 ± 0.08	0.88 ± 0.07
Combined	DBH5(6)	0.99±0.06		HT5(6)	0.99±0.04	
provinces	DBH8(9)	0.68±0.11	0.99±0.09	HT8(9)	0.92±0.05	0.97±0.05

^a Measurement age are varied among different province population.

Table 6. – Genetic correlations among different traits for Guangdong, Guangxi provinces and combined three provinces.

		Height			Cro	own	Ground diameter	
Prov.	Trait	HT3(4) ^a	HT5(6)	HT8(9)	CW3(4)	CW5(6)	GD3(4)	
	DBH3	0.98±0.01	0.90±0.04	0.74±0.11	0.92±0.04	0.98±0.09	0.96±0.01	
	DBH5	0.97±0.02	0.97 ± 0.01	0.88 ± 0.05	0.97±0.03	0.97±0.04	0.97±0.02	
C	DBH8	0.84 ± 0.07	0.87 ± 0.06	0.99 ± 0.04	0.81±0.09	0.93 ± 0.08	0.81 ± 0.08	
Guangdong	CW3	0.94 ± 0.02	0.91±0.04	0.77 ± 0.09	-	-	0.97 ± 0.01	
	CW5	0.99±0.06	0.89 ± 0.06	0.93 ± 0.08	-	-	0.98±0.06	
	GD3	0.94±0.02	0.86 ± 0.04	0.82 ± 0.07	0.96±0.01	0.98 ± 0.06	-	
	DBH4	0.98±0.01	0.96±0.06	0.87±0.10	0.90±0.10	0.95±0.08	0.99±0.01	
	DBH6	0.92 ± 0.05	0.93 ± 0.04	0.99 ± 0.02	0.85 ± 0.15	0.97 ± 0.03	0.92±0.06	
Guangxi	DBH9	0.75 ± 0.13	0.82 ± 0.10	0.93 ± 0.05	0.81 ± 0.16	0.91 ± 0.07	0.81 ± 0.12	
Cidangxi	CW4	0.82 ± 0.11	0.73 ± 0.18	0.81 ± 0.16	-	-	0.91 ± 0.08	
	CW6	0.94 ± 0.06	0.97 ± 0.04	0.95 ± 0.04	-	-	0.99 ± 0.06	
	GD4	0.97±0.02	0.95±0.06	80.0 ± 0.0	0.91 ± 0.08		-	
	DBH3(4)	0.98 ± 0.01	0.99±0.39	0.94 ± 0.07	0.91 ± 0.03	0.99 ± 0.09	0.97 ± 0.01	
	DBH5(6)	0.99 ± 0.03	0.95 ± 0.01	0.99 ± 0.08	0.99 ± 0.05	0.95 ± 0.02	0.99 ± 0.04	
Combined armines	DBH8(9)	0.83 ± 0.06	0.96±0.06	0.89 ± 0.04	0.92±0.06	0.99 ± 0.07	0.85 ± 0.06	
Combined provinces	CW3(4)	0.83 ± 0.06	.99±0.05	0.97 ± 0.06	-	-	0.94 ± 0.02	
	CW5(6)	0.99 ± 0.04	0.91 ± 0.03	0.99 ± 0.08	-	-	0.99 ± 0.08	
	GD3(4)	0.96±0.01	0.99±0.04	0.98±0.05	0.94±0.02	0.99±0.08		

 $^{^{\}mbox{\tiny a}}$ Measurement age are varied among different province population.

Guangdong, Guangxi provinces and combined three provinces (Tables 5 and 6). Age-age correlations were all above 0.70 except correlation between DBH8 (9) and DBH3 (4) in Guangxi population and combined three provinces. In Guangdong population, the age-age genetic correlations for DBH and HT were significant and averaged 0.90 and 0.83, respectively (Table 5). In Guangxi population, the age-age genetic correlations for DBH and HT were significant and averaged 0.79 and 0.91, respectively. In combined three provinces, the age-age genetic correlations for DBH and HT were significant and averaged 0.89 and 0.96, respectively, indicating that HT genetic correlations were larger than DBH. The trait-trait genetic correlations for HT, DBH, CW, and GD were generally significant and high, ranged from 0.73 to 0.99 for both Guandong, Guangxi populations and combined three provinces. The standard errors for genetic correlations for all traits were less than 0.20 (*Table 6*).

Family and individual selections based on breeding values

The top six best provenances were FJ31, GX11, GX15, GD22, GD23 and GX13 according to the provenance best linear unbiased predictions (BLUP) effects based on combined three provinces, indicating that provenance selections were low in Fujian and high in Guangxi and Guangdong (Table 7). Some changes occurred in family ranking based on an analysis of each province and combined three provinces: 72.7% were the same families compared to the two analyses (data not shown for each province). Breeding values for families 64, 51, and 42 were predicted for DBH at age 8 and 9 years for combined three provinces. At a selection rate of 15%, families 9, 5, and 8 were selected for Guangdong, Guangxi and Fujian, respectively, and the genetic gains were 1.06 cm, 0.77 cm, and 0.74 cm, respectively. From these results, 22 families were used to establish first-generation clone orchards using only the highest-rank-

Table 7. – Growth performances and predicted breeding values of selected families and all provenances for combined three provinces at age 8 and 9 years.

D	Breeding value	Family	Growth p	erformance	Breeding value
Provenance	DBH8(9) ^a	Code	HT8(9)	DBH8(9)	DBH8(9)
FJ31	0.654	224	11.50	13.48	1.417
GX11	0.268	226	11.44	12.89	1.322
GX15	0.241	250	11.97	12.79	1.310
GD22	0.193	259	10.91	12.46	1.133
GD23	0.076	8	16.82	14.06	1.129
GX13	0.036	236	11.79	12.73	1.026
FJ33	-0.115	219	11.27	12.44	1.013
GX17	-0.199	314	8.29	11.79	0.999
GD21	-0.269	302	7.86	11.12	0.968
GX12	-0.346	225	11.27	12.30	0.902
FJ32	-0.539	49	16.52	13.75	0.804
		304	7.11	10.48	0.782
		214	11.64	12.39	0.760
		10	15.89	15.26	0.715
		332	7.81	10.41	0.706
		231	11.21	12.12	0.677
		305	7.92	10.52	0.645
		331	7.41	10.37	0.637
		41	18.73	17.80	0.597
		43	15.59	13.36	0.595
		324	7.29	10.41	0.590
		306	7.29	10.73	0.584
		Mean	11.25	12.44	

^a Measurement age are varied among different province population.

ing backward selections, and these families originated from the gene pools that were grafted.

Breeding values were predicted for DBH in 4,283 OP progeny within combined three provenances, which were achieved using a mixed linear model with pedigree information unbiased by selection; 60 individuals from the highest ranked 46 families from 11 provenances were selected for second seed orchard establishment (Table 8). Our study is the first to provide breeding values for C. hystrix. The breeding values of family and individual for growth and form traits are additive genetic values for studied traits; therefore, selection based on breeding values can enhance the average value of studied traits in the progeny and increase the frequency of progeny with improved characteristics.

Efficiency of early selection and implications for improvement of growth and form traits

Early selection is practiced in tree breeding because long-rotation time for each generation. For the Guangdong province, the heritability for DBH at ages 5 and 8 was significantly different (*Table 3*), and the genetic correlation was estimated 0.91 between age 5 and 8 years for DBH. Such high genetic correlation indicated that selection for DBH using age 5 data would be as effective as selection at age 8 years. For the Guangxi province and combined three provinces, the heritability for DBH at ages 6 and 9 years was nearly identical (Table 3 and Table 4), and the genetic correlation for DBH at two age years was 0.86 and 0.99. The early selection at age 6 years on DBH for Guangxi and combined three provinces appeared to yield

Table 8. – Growth performances and predicted breeding values of selected individuals for combined three provinces at age 8 and 9 years.

Tree	Provenance	Family	Growth p	erformance	BV	Tree	Provenance	Family	Growth p	erformance	BV
Code		Code	HT8(9)	DBH8(9)	DBH8(9)	Code		Code	HT8(9)	DBH8(9)	DBH8(9)
10536	GD23	233	11.5	22.4	1.127	10167	GD23	259	11	17.8	0.627
11494	GD23	259	18.6	21.8	0.948	10224	GD23	254	7	11.4	0.627
10215	GD22	220	12.5	21.3	0.945	11365	GD22	213	19.8	18.2	0.621
10163	GD23	244	12.5	20.7	0.890	14056	FJ31	312	10.3	16	0.615
14177	FJ31	301	11.9	19	0.888	11350	GD22	226	16.4	18.1	0.612
10251	GD21	205	10.5	19.8	0.809	11429	GD23	254	15.2	18.1	0.612
10533	GD22	222	9.5	18.9	0.809	10474	GD23	254	7.8	16.7	0.609
10534	GD22	213	10	18.9	0.809	13108	GX 15	43	19.4	18.5	0.603
10598	GD22	231	9.5	18.9	0.809	13109	GX12	26	19	18.5	0.603
10639	GD23	247	10.5	18.9	0.809	10531	GD23	264	9.5	16.6	0.600
10085	GD23	234	11.5	19.6	0.790	11871	GD22	216	17.7	19.2	0.598
14040	FJ31	322	12.6	17.9	0.788	11328	GD23	250	17.8	17.9	0.594
10557	GD23	252	9.5	18.6	0.781	11573	GD22	219	18	17.9	0.594
10498	GD22	226	9.5	18.2	0.745	10338	GD21	208	10	16.5	0.590
10550	GD22	224	9.5	18.1	0.736	13998	FJ32	327	8.2	15.7	0.588
11830	GD23	250	18	20.7	0.734	14171	FJ31	308	9.5	15.7	0.588
10615	GD23	256	10.5	17.7	0.700	12224	GX17	51	26.4	21.7	0.585
11947	GD21	207	18.7	20.3	0.698	11576	GD22	214	18	17.8	0.585
10136	GD21	201	10.5	18.5	0.690	10111	GD21	204	10.5	17.3	0.581
11907	GD23	250	19.1	20.2	0.689	10155	GD22	230	11.1	17.3	0.581
14169	FJ31	304	1.5	16.7	0.679	10530	GD22	218	11	16.4	0.581
13910	FJ31	304	8.2	17.5	0.674	10186	GD22	232	10	17.2	0.572
10505	GD22	212	8.5	17.4	0.672	10532	GD21	201	9.5	16.3	0.572
10483	GD23	234	8.6	17.3	0.663	10607	GD23	259	8.9	16.3	0.572
10523	GD22	219	7.9	17.3	0.663	14166	FJ31	323	9.6	15.5	0.569
14007	FJ31	314	11.5	16.4	0.651	11108	GD23	254	18.5	17	0.561
10193	GD23	235	11	18	0.645	13990	FJ33	335	8.6	15.4	0.560
14149	FJ31	320	12	16.3	0.642	11575	GD22	222	19.6	17.5	0.557
14180	FJ31	304	9.5	16.2	0.633	11855	GD22	229	19.1	18.7	0.552
14181	FJ33	338	9	16.2	0.633	11866	GD22	219	15.4	18.7	0.552

^a Measurement age are varied among different province population.

a similar genetic gain (E = 74.3% and 100%) as selection for DBH at age 9 years in *C. hystrix*.

Moderate to high heritability for HT, DBH, and CW (0.31, 0.24, and 0.22, respectively) as indicated by this study suggests that improvements in growth and form traits can be accomplished via phenotypic selection. The high significant positive genetic correlations for these growth and form traits suggest that selection for one trait would bring highly correlated genetic performance at another trait. The breeding values predicted in the study can be used to select families and individuals for immediate deployment using seed orchard or for further breeding purpose. In the future, fullsib progeny trials should be established to control pedigree while move breeding population into more advanced generation.

Conclusions

Our conclusions based on genetic parameters and selection of breeding values for growth and form traits in *C. hystrix* by analyzing each province population planted in China are summarized as:

- (1) Provenance effects were not significant for growth and form traits with each meta population delineated by province and family within provenaces has a significant variance component for each province population.
- (2) Significant heritabilities for most traits of HT, DBH, GD, and CW were observed for each province population and combined three provinces, Heritability estimates for H and DBH decreased with increasing age for Guangdong province population and combined three provinces.
- (3) Significant genetic correlations for age-age and trait-trait correlations were observed and the correlations were high for all traits at all ages, indicating that genetic performance will be highly correlated among traits and early selection was effective.
- (4) In total, 22 families from three provinces and 60 individuals for combined three provinces were selected based on breeding values to maximize breeding progress.

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