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# Genetic analysis of crossing effects for growth traits of *Pinus massoniana* and selection of cross combinations

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**Abstract** Two groups of filial generations derived from two different *Pinus massoniana* complete-diallel crosses were analyzed. Results show that the general combining ability (GCA), specific combining ability (SCA) and reciprocal effects were significant for some growth traits, including height, DBH and volume index. The heredity of these growth traits was controlled by additive and non-additive genes, of which the additive genes played a dominant role. The epistatic effect was greater for group I (cross in 1992) than group II (cross in 1993). The SCA of *P. massoniana* growth traits was significantly greater than GCA, which may be related to different geographical provenance for parents and the indirect selection by GCA. Inbreeding depression was commonly observed for *P. massoniana* growth traits. The extent of inbreeding depression was  $-17.8\%$ – $-18.4\%$ ,  $-23.3\%$ – $-27.7\%$  and  $-44.3\%$ – $-50.6\%$  for height, DBH and volume index, respectively. It was observed that parents with small GCA values exhibited a greater extent of inbreeding depression. Large differences in hybrid vigor of different crosses were observed and the difference between original cross and reciprocal cross was not significant. Based on the volume index, 10 fine crosses were selected for two groups respectively, and the average increment of volume index was 59.41% and 41.76%, respectively, in comparison with the average of the testing groups, and was 100.58% and 74.61% in comparison with the local commercial variety.

**Keywords** *Pinus massoniana*, complete-diallel cross, combining ability, heterosis, selfing effects

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## 1 Introduction

Crossbreeding is an important approach for plant genetic improvement, including parent selection, progeny test and identification for new varieties (Li and Wang, 2001). Parent selection is the precondition of crossbreeding (Zhang, 1994). Progeny test can estimate breeding value of parent clones and be used as a basis for the rouging of the original seed orchard for backward selection and offer breeding materials for selecting superior individuals in the process of advanced-generation genetic improvement for forward selection (Wang, 2001). In addition, main traits of species can be learned and effective plans for genetic improvement can be made by combining ability breeding (Qi, 1996). Different genetic cross designs for crossbreeding are used to select high-yield, superior and highly resistant new variety according to different cultivation objectives. Diallel cross design is an effective method of estimating parameters, which can stably estimate GCA and SCA simultaneously (Kearsey, 1965; Pederson, 1972). It was widely used in genetics and breeding in trees and crops (Huber et al., 1991; King et al., 1997; Li et al., 2002; Li et al., 2006). Diallel cross design and combining ability were used in many important coniferous species, such as loblolly pine (*Pinus taeda*) (Sluder, 1993), slash pine (*P. elliottii*) (Sluder, 1996), radiata pine (*P. radiata*) (Wilcox, 1982) and Chinese fir (*Cunninghamia lanceolata*) (Pei zhong et al., 1981; Wang and Chen, 1988; Ye et al., 1991; Zhi et al., 1994; Li et al., 2000).

Masson pine (*Pinus massoniana*) is a main native tree species for afforestation in southern China which has great economic value and ecological benefit. Its pollen is a natural nutritional health food and a cosmetic of high quality. Its turpentine is of rosin and its wood is an important material for pulp making. The species has a wide range of natural distribution, rich variations of geographical provenance and strong adaptability and thus, has great prospects for genetic improvement. This species was one of important species in the National Science-Tech Key Project of China and was developed for provenance test, seed

orchard establishment and crossbreeding since the “Sixth Five-Year Plan” period. The study of crossbreeding by two-parent controlled pollination in Masson pine started relatively late. At present, only Zhou et al. (2004) studied the combining ability and heterosis for main economic traits of Masson pine. The aims of our study were to reveal the genetic control model, estimate cross parents and combination and study selfing depression and intraspecific heterosis in order to offer a theoretical basis for advanced-generation breeding and intraspecific heterosis by analyzing two groups of filial generations derived from two different *Pinus massoniana* complete-diallel crosses.

## 2 Materials and methods

### 2.1 Materials

One thousand superior clones of Masson pine from eleven provinces were selected to establish a breeding garden in the Laoshan Forest Farm of the Chun'an County in the Zhejiang Province, which were grafted from 1986 to 1988 and most of which flowered and fruited in 1992. Hybrid seed production was carried out according to a 6×6 complete-diallel cross in 1992 and 1993, and parent clones from Guangdong (No.1003), Jiangxi (No.6610, 6627), Zhejiang (No.5163, 5907) and Anhui (No.3412) followed the same regime. The progeny test forest was established in the subsequent three years. The afforestation experiment adopted a completely randomized block design with five replicates each consisting of 8 plots. The test forest was located at 29°37'N and 119°03'E, and its elevation ranged from 250 to 300 m. The average annual temperature is 17°C and annual accumulated temperature ≥ 10°C is 5410°C. The average annual rainfall for this area is 1430 mm and annual solar duration was 1951 h. The progeny of local natural superior seed stands was selected as the control. Some parameters, including tree height and diameter at breast height (DBH), were measured in the first trial stand of eleven years old and the second trial stand of ten years old.

### 2.2 Statistical analysis

The statistical analysis was based on individual trees to calculate volume according to the model:

$$V = 0.000062341803 \times \text{DBH}^{1.8551497} \times H^{0.95682492}$$

Analyses of variance between the different cross combinations were carried out using the GLM procedure. If the effect of cross combination was significant, according to Griffing's diallel data I, the mean value was used in the variance analysis of combining ability. GCA, SCA and REC were estimated using a fixed model and genetic variance component was estimated using a random model (Griffing, 1956; Ma, 1982; Wang, 1989; Zhu, 1997; Xu, 2006). Models of variance analysis of combining ability for traits are shown in Table 1. The extent of inbreeding depression ( $D_i$ ) was estimated according to Kheradnam's (1975) method:  $D_i = (F_{Si} - \overline{OP}) / \overline{OP} \times 100\%$ , where  $D_i$  denotes the extent of inbreeding depression,  $F_{Si}$  is the mean value of any parents inbred with  $F_1$  and  $\overline{OP}$  is the mean value of open pollinated progeny of corresponding parents with some self-fertilized families. Heterosis of cross combination was evaluated using Bahman's method (1975):  $H = (F_i - \overline{OP}) / \overline{OP} \times 100\%$ , where  $H$  is the extent of heterosis,  $F_i$  is the mean value of each cross combination,  $\overline{OP}$  is the mean value of open pollinated progeny of dominant parents in some  $F_i$  combinations.

## 3 Results

### 3.1 Genetic variation of growth traits

Variance analysis (Table 2) shows that significant difference existed among father parents at  $p \leq 0.05$  level in the traits of DBH and height in material II and combinations and significant difference existed among combinations, father parents or mother parents at  $p \leq 0.01$  level in other traits. This suggested that there were various populations for breeding in the next generation, which made it possible

**Table 1** Model of variance analysis of combining ability

source of variation	df	SS	MS	expected mean square	
				model I	model II
GCA	$P-1$	$S_g$	$M_g$	$\sigma_e^2 + 2P(1/(P-1)) \sum g_i^2$	$\sigma_e^2 + (2(P-1)/P)\sigma_s^2 + 2P \cdot \sigma_g^2$
SCA	$P(P-1)/2$	$S_s$	$M_s$	$\sigma_e^2 + (2/P(P-1)) \sum \sum S_{ij}^2$	$\sigma_e^2 + (2(P^2 - P + 1)/P^2)\sigma_s^2$
REC	$P(P-1)/2$	$S_r$	$M_r$	$\sigma_e^2 + 2(2/P(P-1)) \sum \sum r_{ij}^2$	$\sigma_e^2 + 2\sigma_r^2$
error	$(P^2-1)(B-1)$	$S_e$	$M_e$	$\sigma_e^2$	$\sigma_e^2$

$P$ : number of parents;  $B$ : number of blocks;  $g_i^2$  (or  $\sigma_g^2$ ),  $S_{ij}^2$  (or  $\sigma_s^2$ ) and  $r_{ij}^2$  (or  $\sigma_r^2$ ) are variance components in the general combining ability (GCA), the specific combining ability (SCA) and reciprocal effect (REC), respectively. The same below.

**Table 2** Variance analysis for major growth traits

source of variation	test material I				test material II			
	df	height	DBH	volume	df	height	DBH	volume
block	4	0.481583**	2.226602**	0.000109**	4	34.333694**	104.428556**	0.002500**
combination	35	3.568514**	17.621458**	0.000484**	35	3.268356**	12.453046**	0.000338**
female parent (P <sub>1</sub> )	5	9.058400**	39.625736**	0.001229**	5	5.235289**	27.157122**	0.000823**
male parent (P <sub>2</sub> )	5	1.543333**	12.974376**	0.000381**	5	3.378089**	7.476856*	0.000227*
error	130	0.120808	0.617678	0.000013	130	0.439095	2.815691	0.000083

\* and \*\* indicate significant difference at  $\alpha = 0.05$  or  $\alpha = 0.01$  level, respectively.

for selecting superior combinations during the cross process between different provenances of Masson pine.

### 3.2 GCA, SCA and REC of growth traits and their relative importance

Analysis of combining ability on main traits and disclosure of the mode of gene action can help make effective breeding plans. Variance analysis of the combining ability (Table 3) shows that the significant difference at  $p \leq 0.01$  level existed among the GCA, SCA and REC of height, DBH and volume in the two groups, and the significant difference at  $p \leq 0.05$  level existed between the REC of height in group II.

According to the theory of full-sib genetic variance, variance of GCA, SCA and REC were controlled by additive genes, dominant genes and epistatic genes (Mullin et al., 1992). Therefore, genetic control can be explained by the value of variance component. The result (Table 4) shows that the variance component of GCA for main traits is lower than that of SCA.  $\sigma_g^2/\sigma_s^2$  of height, DBH and volume in the two groups was 2.80%–13.62%, 5.54%–12.10% and 8.99%–29.23% respectively, which suggested that the dominant genes play a major role in the two groups, especially in group II and the effect of additive genes is relatively less important. The proportion of variance component of REC for main traits was different, which was caused by different materials. In group I, variance component for height, DBH and volume was 48.94%, 54.11% and 61.81%, respectively, which suggested that epistatic genes play a dominant role. In contrast, in group II, variance component for height, DBH and volume was 12.25%, 31.08% and 32.39%, respectively, which suggested epistatic genes play an important role.

### 3.3 Selfing depression, heterosis and selection for cross combination

The effect of self-cross of six parents (Table 5) shows that depression commonly existed in growth traits for progeny of self-cross parents and the extent of selfing depression was decided by test material and crossing parents. In group I, the  $D_i$  for height, DBH and volume of parents was  $-8.0\%$  (1003)  $-28.7\%$  (6610),  $-12.5\%$  (1003)– $-40.5\%$  (6610) and  $-16.8\%$  (1003)  $-71.6\%$  (6610), respectively, and the mean value was  $-17.8\%$ ,  $-27.7\%$  and  $-50.6\%$ , respectively. In group II, the  $D_i$  for height, DBH and volume of parents was  $-4.6\%$  (6627)– $-45.3\%$  (6610),  $-6.8\%$  (1003)  $-50.8\%$  (6610) and  $-14.5\%$  (1003)– $-84.5\%$  (6610), respectively, and the mean value was  $-18.4\%$ ,  $-23.3\%$  and  $-44.3\%$ , respectively. In two groups, the extent of selfing depression for parents 6610 was the highest and for parents 1003 was the lowest.

Correlation analysis shows that there were significant correlations between  $D_i$  and GCA for height, DBH and volume. This suggested that if the GCA of the parents is minor, there is an increasing tendency for the extent of selfing depression of parents.

Different advantageous effects existed between different research materials and open-pollinated progeny. The heterosis of various cross combinations for the major growth traits of full-sib progeny test forest of Masson pine of ten and eleven years old show that heterosis was significant among different cross combinations (Table 6). In group I, the variation range for height, DBH and volume of cross combinations was  $-19.15\%$ – $-18.57\%$ ,  $-24.14\%$ – $-35.36\%$  and  $-50.44\%$ – $-82.48\%$ . There was strong heterosis in 11 cross combinations including 6627×6610, 1003×3412, 6627×3412, 6627×1003,

**Table 3** Variance analysis of combining ability for major growth traits

source of variation	test material I				test material II			
	df	height	DBH	volume	df	height	DBH	volume
GCA	5	0.974784**	5.046563**	0.000139**	5	1.552088**	4.979586**	0.000170**
SCA	15	0.852110**	3.856509**	0.000092**	15	0.878438**	3.094957**	0.000072**
REC	15	0.960923**	5.355487**	0.000174**	15	0.278785*	2.135003**	0.000058**
error	140	0.098134	0.490385	0.000014	140	0.143428	0.770575	0.000023

**Table 4** Variance components of combining ability for major growth traits

variance components of combining ability		test material I			test material II		
		height	DBH	volume	height	DBH	volume
absolute value	$\sigma_g^2$	0.012250	0.108220	0.0000409	0.058113	0.163301	0.00000832
	$\sigma_s^2$	0.437792	1.954523	0.00004552	0.426780	1.349641	0.00002846
	$\sigma_r^2$	0.431394	2.432551	0.00008030	0.067678	0.682214	0.00001762
proportion/%	$\sigma_g^2$	1.39	2.41	3.15	10.52	7.44	15.29
	$\sigma_s^2$	49.67	43.48	35.04	77.24	61.48	52.32
	$\sigma_r^2$	48.94	54.11	61.81	12.25	31.08	32.39
	$\sigma_g^2/\sigma_s^2$	2.80	5.54	8.99	13.62	12.10	29.23

5163×3412, 6627×5907, 1003×6610, 5163×6627, 3412×1003, 1003×5907 and 5163×1003, in which heterosis for volume was above 20%. However, hybrid weakness for volume existed in these cross combinations including 5907×6627, 3412×6627, 6610×1003 and 1003×6627. In group II, the variation range for height, DBH and volume of cross combinations was -14.02%–-11.27%, -18.40%–-26.07% and -36.43%–-46.63%. There was strong heterosis in six cross combinations including 6627×5163, 1003×3412, 6627×6610, 6627×1003, 6610×5163 and 1003×5907, in which heterosis for volume was above 15%. However, hybrid weakness for volume existed in these cross combinations including 3412×6627, 5907×1003, 5163×6610 and 3412×5163. Comparison shows that there was great difference between the same materials in two groups and even opposite result. In general, there was the same tendency in two groups.

Of the three traits of height, DBH and volume, volume is closely related to economic value. Based on the analysis of heterosis in different cross combinations, volume increment was selected as the index of superior cross combinations. Ten superior combinations were selected including 1003×3412, 6627×6610, 6627×1003, 1003×6610, 3412×1003, 1003×5907, 5163×1003, 5163×3412, 6627×3412 and 5163×6627. Realized genetic gains for the volume of superior cross combinations was 38.17%–101.98% when the mean value was taken as

control. Realized genetic gains for the volume of superior cross combinations was 73.86%–154.16% when CK was taken as the control. In the same way, ten superior combinations were selected including 6627×5163, 1003×3412, 6627×1003, 1003×5907, 6627×6610, 5163×1003, 1003×6627, 3412×1003, 6610×5163 and 1003×6610. Realized genetic gains for volume of superior cross combinations was 20.80%–67.92% when mean value was taken as the control. Realized genetic gains for the volume of superior cross combinations was 48.80%–106.84% when CK was taken as the control. There were seven same superior combinations (Table 7).

#### 4 Conclusions and discussion

The combining ability test of parents is an important issue in crossbreeding. Estimation of GCA, SCA and REC can reveal the model of genetic control and help to make efficient breeding strategies. The value and relative importance of the combining ability is related to the test materials. This study found that the GCA, SCA and REC were significant for main growth traits of Masson pine, which shows that the heredity of these growth traits was controlled by additive and non-additive genes, of which the additive genes played a dominant role. Although relative importance was different between two combining abilities,

**Table 5** Selfing depression ( $D_i$ ), general combining ability ( $g_i$ ) of six parents and correlation coefficients

cross parent	test material I						test material II					
	height		DBH		volume		height		DBH		volume	
	$D_i$ %	$g_i$	$D_i$ %	$g_i$	$D_i$ %	$g_i$	$D_i$ %	$g_i$	$D_i$ %	$g_i$	$D_i$ %	$g_i$
1003	-8.0	0.394	-12.5	0.934	-16.8	0.00523	-6.0	0.396	-6.8	0.772	-14.5	0.00540
3412	-19.9	-0.026	-28.8	-0.220	-57.3	-0.00069	-26.3	-0.354	-29.2	-0.579	-63.0	-0.00358
5163	-14.4	0.089	-17.6	0.599	-29.1	0.00218	-6.6	0.087	-8.6	0.302	-21.7	0.00060
5907	-21.7	-0.357	-30.1	-0.682	-63.5	-0.00405	-21.8	-0.030	-31.0	-0.524	-55.1	-0.00279
6610	-28.7	-0.284	-40.5	-0.597	-71.6	-0.00296	-45.3	-0.469	-50.8	-0.609	-84.5	-0.00302
6627	-13.8	0.184	-36.6	-0.033	-65.0	0.00028	-4.6	0.370	-13.4	0.638	-26.7	0.00339
average	-17.8	—	-27.7	—	-50.6	—	-18.4	—	-23.3	—	-44.3	—
correlation coefficients	0.916*		0.859*		0.897*		0.922**		0.874*		0.874*	

**Table 6** Heterosis of various cross combinations for major growth traits (unit: %)

parent		test material I						test material II					
P <sub>1</sub>	P <sub>2</sub>	heterosis of original cross			heterosis of reciprocal cross			heterosis of original cross			heterosis of reciprocal cross		
		height	DBH	volume	height	DBH	volume	height	DBH	volume	height	DBH	volume
1003	3412	12.15	27.26	62.27	12.31	10.03	23.48	0.71	9.94	33.77	11.27	7.76	7.62
	5163	-10.06	-14.47	-36.53	3.34	14.19	20.81	1.60	3.10	-11.64	2.77	-4.39	8.72
	5907	8.13	10.85	21.57	-3.97	-13.62	-28.46	2.94	16.13	17.45	0.58	-18.40	-32.37
	6610	6.56	16.11	27.26	-13.32	-18.41	-43.69	2.30	1.29	-1.88	-8.11	-11.14	-19.62
	6627	-4.90	-20.19	-41.76	8.47	17.22	33.66	-6.19	4.04	7.82	7.05	8.40	25.18
3412	5163	1.90	-1.81	-6.26	9.92	14.61	32.29	-8.76	-8.73	-22.67	3.06	-0.71	-5.59
	5907	-2.99	-4.60	-15.08	-2.72	-10.31	-29.31	-5.96	-1.99	-18.89	-2.43	-6.58	-11.45
	6610	0.00	-8.01	-19.69	-8.84	-17.38	-37.74	-3.37	-2.94	-7.34	4.47	10.98	8.17
	6627	-13.29	-24.14	-49.58	11.80	20.72	41.19	-14.02	-15.96	-36.43	-3.11	-5.56	-18.66
5163	5907	4.69	3.20	2.77	-10.74	-2.09	-10.52	-0.28	-2.96	0.68	4.90	0.46	-6.00
	6610	1.94	-2.51	-5.78	4.84	2.57	2.70	-8.26	-13.06	-29.70	-4.59	8.09	18.68
	6627	6.73	12.92	25.36	7.36	5.60	15.49	-4.81	-3.79	-12.17	10.46	26.07	46.63
5907	6610	-9.34	-14.93	-36.35	2.61	1.77	-5.34	-5.45	0.08	-10.08	7.05	8.02	10.51
	6627	-19.15	-22.29	-50.44	10.85	16.22	29.13	7.13	-1.79	3.65	9.27	0.79	0.72
6610	6627	-5.82	-7.43	-20.89	18.57	35.36	82.48	-0.29	-4.02	-4.82	3.02	16.75	26.22

**Table 7** Superior cross combinations and realized genetic gains of volume

cross combinations	test material I			cross combinations	test material II		
	volume mean/cm	> test mean/%	> CK/%		volume mean /cm	> test mean/%	> CK/%
1003×3412	0.043176	101.98	154.16	6627×5163	0.039250	67.92	106.84
6627×6610	0.039520	84.88	132.63	1003×3412	0.038496	64.70	102.87
6627×1003	0.035563	66.37	109.34	6627×1003	0.036024	54.12	89.84
1003×6610	0.033860	58.40	99.32	1003×5907	0.033799	44.60	78.11
3412×1003	0.032856	53.71	93.41	6627×6610	0.033787	44.55	78.05
1003×5907	0.032347	51.32	90.41	5163×1003	0.031289	33.86	64.89
5163×1003	0.032143	50.37	89.21	1003×6627	0.031030	32.75	63.52
5163×3412	0.031169	45.81	83.48	3412×1003	0.030971	32.50	63.21
6627×3412	0.030578	43.05	80.00	6610×5163	0.028458	21.75	49.97
5163×6627	0.029536	38.17	73.86	1003×6610	0.028236	20.80	48.80
mean	0.034075	59.41	100.58	mean	0.033134	41.76	74.61

it was important to determine and select combining ability when its effect was significant, no matter whether the value of variance components was high or low. The effect of epistatic genes was caused by the environmental factors and was decided by test materials, which was greater for groups I than for group II. This indicated that interaction between genes and environment existed in the test forest. The result of relative importance for GCA and SCA of Masson pine is different from that of maize (*Zea mays*) and Chinese fir (Qi, 1996; Li et al., 2000; Zhou et al., 2004), which was caused by two reasons. Firstly, the six test parents were early blossoming clones, which led growth traits of crossing parents to be selected indirectly although their GCAs were not measured. Secondly, the crossing parents used in this study came from different provenance zones, which made it possible to produce superior cross

combinations with strong SCA according to crossbreeding theories. Most of the 36 cross combinations represents hybridizations that happened in different provenances. Therefore, genetic improvement is not only realized by utilizing the effect of combining ability, but also by creating cross combination for high SCA.

Masson pine is a self-fertility species and the self-crossing rate can reach about 30% (Jin et al., 2000). Depression existed in height, DBH and volume of self-crossing progeny of Masson pine parents, and the extent was decided by test materials and parent clones. In the two groups, selfing depression in height, DBH and volume of parents was -17.8% -- 18.4%, -23.3% -- 27.7% and -44.3% -- 50.6%, respectively. Meanwhile, there was a significant correlation between  $D_i$  and GCA for growth traits, which suggested if the GCA of parents is minor,

there is an increasing tendency to the extent of selfing depression of parents.

Crossing combination with strong heterosis was created on the basis of selected cross parents. Wang and Chen (1988) found parents having high combining ability could increase the changes of gained heterosis during the research period for the growth traits of Chinese fir. This study found great variation existed in different crossing combinations of Masson pine, such as the combinations of 6627×6610 and 1003×3412. However, obvious hybrid weakness existed in 3412×6627. Moreover, we found that the extent of selfing depression for parents with high GCA was lower. Selfing without depression or low selfing depression was related to two parents with high GCA, which was also found in Chinese fir (Chen et al., 1982). When selecting superior combinations based on the analysis of heterosis of different cross combinations, we should take volume index as a major index for SCA and GCA because of the significant effect of REC. Asexual reproduction can be for superior cross combinations to make full use of heterosis. In addition, because of existence of selfing depression and REC of growth traits, we should select parents according to the effect of SCA and consider the effects of self-cross and back-cross in the establishment of hybrid seed orchard, especially for bi-clonal hybrid seed orchard.

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