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Analysis on combing ability and estimation of genetic parameters for chlorophyll content in maize

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Chlorophyll closely related to photosynthetic capacity and developmental stage in crops. In order to reveal the genetic characters of chlorophyll content in leaf above ear, ear leaf and leaf under ear (three-ear-leaves) of maize, ten inbred lines from five different heterotic groups were selected to make crosses by a completely diallel cross design. The combining ability analysis and genetic parameters estimations of chlorophyll content of three-ear-leaves were carried out. The results showed that highly differences existed among ninety F_1 crosses including reciprocal crosses, the general combining ability (GCA) effects and special combining ability (SCA) effects were different and $p < 0.01$. The inbred lines No.10 (Xu178), 1(Ye478) and 7(Dan340) were observed with positive GCA effects while other inbred lines showed negative GCA effects. The crosses 4x9 (Chang7-2x8085Tai) and 6x9 (Zi330x8085Tai) with significantly positive SCA effects were found. The cross 4x6 (Chang7-2xZi330) appeared maximum negative SCA effect for three-ear-leaves investigated in this study. The GCA effect of inbred lines was not corresponding to the SCA effect. The correlation coefficients between three-ear-leaves were all more than 0.7 which were highly positive correlations. Chlorophyll content showed reciprocal crosses differences ($p < 0.05$). Broad sense heritability and narrow sense heritability were about 55 and 33.5% respectively. The additive effect was greater importance than non-additive effect.

Key words: Maize, chlorophyll content, reciprocal effect, heritability.

INTRODUCTION

Combining ability of inbred lines, is widely and extensively used to evaluate the genetic nature of quantitatively inherited traits in maize. During the process of analysis for combining ability, the two main genetic parameters general combining ability (GCA) and special combining ability (SCA) which had been defined (Sprague and Tatum, 1942). The variance of GCA is usually considered to be an indicator of the extent of

additive type of gene action, whereas SCA is taken as the measure of non-additive type of gene actions. In previous studies, the results of several researches showed that the yield and some yield components were due to variance of GCA and SCA (Sedhom, 1994; Al-Naggar et al., 2002; Alamnie et al., 2006; El-Badawy, 2013; Hefny, 2010). The photosynthesis plays an important role for the yield formation in maize. It is well

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Table 1. Origin and chlorophyll content of three-ear-leaves for ten maize inbred lines as parents (Unit, SPAD).

No.	Lines	Heterotic group	Origin	Chlorophyll content		
				Leaf above ear	Ear leaf	Leaf under ear
1	Ye478	Reid	8112x5003	60.13	59.48	55.98
2	Zheng58	Reid	Mutant from Ye478	54.75	51.53	54.78
3	K12	Tangsipingtou	Huangzaosix>Weichun	62.40	53.18	47.15
4	Chang7-2	Tangsipingtou	Changdan7xS901	42.73	44.48	45.80
5	Mo17	Lancast	Line187-2x103	54.83	49.10	49.60
6	Zi330	Lancast	Oh43xKeli67	45.75	46.20	48.85
7	Dan340	Lüdahonggu	White cob Lü9 xWild close relationship awn maize	50.15	56.58	55.68
8	E28	Lüdahonggu	A619Ht xlü9 kuan	46.85	44.48	48.25
9	8085Tai	Tropical group	Line selected from tropic germplasm	39.88	40.18	38.85
10	Xu178	Tropical group	American hybrid 78599	60.48	56.80	55.80

Three-ear-leaves refer to leaf above ear, ear leaf and leaf under ear.

know that the chlorophyll content as the most important crop biophysical characteristic can be related to photosynthetic capacity and developmental stage. Chlorophyll accounted for more than 98% of gross primary production variation in maize (Gitelson et al., 2008). So, the chlorophyll was suggested as the community property most directly relevant to the prediction of productivity (Dawson et al., 2003). In addition, chlorophyll content usually was used as one of important secondary traits to reflect soil nitrogen and improved selection efficiency for maize inbred lines and hybrids with high nitrogen use efficiency (Ajala et al., 2007; Medici et al., 2004; Betrán et al., 2003).

Presently, little information of the combining ability and the genetic parameters about chlorophyll content of leaf above ear, ear leaf and leaf under ear (three-ear-leaves) is available. The objectives of this study were to evaluate the combining ability, reciprocal effect and genetic parameters for chlorophyll content of three-ear-leaves.

MATERIALS AND METHODS

Experimental materials

Ten inbred lines had been selected on the basis of chlorophyll content and genetic diversities from different heterotic groups in maize. The origins and the chlorophyll contents of these inbred lines as the parents are listed in Table 1. The crosses were made intermating parents by completely diallel cross design for developing the ninety F_1 with reciprocal crosses (Griffing, 1957).

Field experiment design

The field trial was conducted in Zhengzhou, 34:44° N Lat., 113:42° E Long. Ninety F_1 crosses including reciprocal crosses were planted in a complete block design with two replications. Each genotype was accommodated in a single row of 4 m length per plot with a row spacing of 0.66 m and the distance of 0.20 m between two adjacent plants, and the population density was approximately 75,000 plants

ha^{-1} . Three grains were sown per hole and the plants were thinned at the 5-leaf stage. All field managements were same to those of local maize production practices.

Determination for chlorophyll content

Five representative plants were selected randomly in each replication. Chlorophyll meter SPAD-502, Minolta Osaka Co. Ltd. Japan, had been used to measure the chlorophyll content of three-ear-leaves. The determination for chlorophyll concentration of each leaf was represented by the averages of three times in choosing randomly different zones near the middle of each leaf in each plot at the pollinating stage.

Estimation of variance components

The Formula (1) statistical model was used for data analysis:

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + r_{ij} + b_k + (bv)_{ijk} + e_{ijk}. \quad (1)$$

Where, μ was the overall mean, g_i was the effect of GCA for i th parent, g_j was the effect of GCA for j th parent, s_{ij} the effect of SCA for the i th and j th parent, r_{ij} the reciprocal effect the i th and j th parent, b_k was the effect of block, $(bv)_{ijk}$ was the effect of genotype from the cross of the i th and j th in k block, and e_{ijk} was the error term.

The broad sense heritability (h_B^2) and narrow sense heritability (h_N^2) are estimated following by formula (2) and (3) respectively,

$$h_B^2 = V_G / V_P \times 100 \quad (2)$$

$$h_N^2 = V_A / V_P \times 100 \quad (3)$$

Where, V_P was the phenotype variance, V_G was the genotype variance and V_A was additive variance.

Table 2. Analysis of variance for crosses from ten inbred lines.

Leaves	Resources of Variance	DF	SS	MS	F value	F _{0.05}	F _{0.01}
Leaf above ear	Repeats	1	2.94	2.94	0.30	3.95	6.93
	Crosses	89	2743.80	30.83	3.18**	1.42	1.64
Ear leaf	Repeats	1	0.21	0.21	0.03	3.95	6.93
	Crosses	89	2660.15	29.89	3.86**	1.42	1.64
Leaf under ear	Repeats	1	0.56	0.56	0.06	3.95	6.93
	Crosses	89	3202.33	35.98	3.75**	1.42	1.64

*, ** represent significance at the 0.05 and 0.01, respectively; DF, degree of freedom; SS, sum square; MS, mean square.

DPS 14.10 (Data Processing System) software was used to analyze data collected from each trial (Tang, 2013), and Excel 2007 were applied for correlation and other analyses.

RESULTS AND DISCUSSION

Variance analysis

Analysis of variance for three-ear-leaves revealed significant differences among the ninety F_1 crosses including reciprocal crosses ($p < 0.01$) (Table 2). Obviously, the highly significance was exist among the crosses due to the diverse nature of the selecting inbred lines. But the variance between replications was no statistical difference for three-ear-leaves, which indicated uniform fertility in the field trial.

Analysis of variance components for combining ability

The highly statistical differences ($p < 0.01$) were observed for GCA and SCA, but the mean squares (MS) of GCA for leaf above ear, ear leaf and leaf under ear were 71.30, 61.63, 78.30 respectively higher than those of SCA. For the reciprocal effects, the variance of the ear leaf appeared highly difference ($p < 0.01$), the statistical differences ($p < 0.05$) were detected in the variance for the chlorophyll contents of leaf under ear and leaf above ear (Table 3).

Analysis for GCA of ten inbred lines

The effects of GCA for chlorophyll content of three-ear leaves from ten inbred lines were presented in Table 4. The estimates of GCA showed that among the inbred lines No.10 (Xu178), 1 (Ye478) and 7 (Dan340) have exhibited positive GCA effects for three-ear-leaves, positive GCA effect of chlorophyll content for leaf above ear was No. 3(K12) inbred line which was only 0.14, while

the GCA effects of other inbred lines were negative values. Especially, the No. 10 and 1 two inbred lines have highest positive GCA effects than any other lines, while the negative GCA effects of chlorophyll content in all three-ear-leaves were observed in lines No.9 (8085 Tai) and No.4 (Chang7-2). The average performance of crosses from No.10 was the highest among ten inbred lines, the chlorophyll contents in leaf above ear, ear leaf and leaf under ear were 60.82, 60.95 and 60.71 respectively, and average performance of crosses from No.1 inbred line were the second, the chlorophyll contents in leaf above ear, ear leaf and leaf under ear were 59.87, 59.20 and 58.88. While the mean performance of crosses from No.9 was the lowest, the chlorophyll contents were 54.36 in leaf above ear, 54.99 in ear leaf and 54.59 in leaf under ear, respectively (Figure 1).

Analysis for SCA and reciprocal effects

The SCA effects of chlorophyll content of all three-ear-leaves were showed in Table 5. Among 45 crosses, positive SCA effect of leaf above ear was detected in 21 crosses which occupied 46.67% overall crosses, 23 crosses and 25 crosses were positive SCA effects for ear leaf and leaf under ear respectively. Especially, two better crosses 4×9 (Chang7-2×8085Tai) and 6×9(Zi330×8085Tai) with positive SCA effects for chlorophyll content of three-ear-leaves. The crosses 4×6 (Chang7-2×Zi330), 4×10 (Chang7-2×Xu178), 5×9 (Mo17×8085Tai), 1×7 (Ye478×Zi330) and 8×9 (E28×8085Tai) were ranked five top crosses with negative SCA of chlorophyll content of leaf above ear, the SCA effects of crosses 4×6 and 4×10 reached highly differences. The crosses which exhibited negative SCA effects for both ear leaf and leaf under ear were 4×6, 3×9 (K12×8085Tai) and 2×5 (Zheng58×Mo17), while the SCA effect of cross 3×5 (K12×Mo17) reached only for the leaf under ear. Among all the crosses, 4×6 cross expressed maximum negative

Table 3. Variance analysis for GCA, SCA and reciprocal effect of three-ear-leaves.

Resources of variance	Leaf	DF	SS	MS	F-value	F _{0.05}	F _{0.01}
GCA	Leaf above ear	9	641.68	71.30	14.72**		
	Ear leaf	9	554.68	61.63	15.93**	1.99	2.61
	Leaf under ear	9	704.73	78.30	16.31**		
SCA	Leaf above ear	35	490.87	14.02	2.90**		
	Ear leaf	35	438.77	12.54	3.24**	1.56	1.86
	Leaf under ear	35	569.66	16.28	3.39**		
Reciprocal effect	Leaf above ear	45	331.36	7.36	1.52*		
	Ear leaf	45	336.63	7.48	1.93**	1.51	1.79
	Leaf under ear	45	326.78	7.26	1.51*		

GCA, general combining ability; SCA, special combining ability.

Table 4. Comparison of GCA effect for chlorophyll content of three-ear-leaves.

Leaf above ear				Ear leaf				Leaf under ear			
Inbred lines	Mean	Significance		Inbred lines	Mean	Significance		Inbred lines	Mean	Significance	
		5%	1%			5%	1%			5%	1%
10	3.64	a	A	10	4.00	a	A	10	4.55	a	A
1	2.57	ab	AB	1	2.03	b	AB	1	2.49	ab	A
7	1.21	bc	ABC	7	1.39	bc	BC	7	1.72	bc	AB
3	0.14	cd	BCD	2	-0.03	cd	BCD	6	-0.43	cd	BC
2	-0.04	cd	BCD	3	-0.50	cd	BCDE	8	-0.48	d	BC
5	-0.05	cd	BCD	5	-0.67	d	CDE	4	-0.68	d	BC
8	-0.77	cd	CDE	6	-0.77	de	CDE	2	-1.47	d	C
6	-1.16	d	CDE	8	-1.04	de	CDE	5	-1.61	d	C
4	-1.91	de	DE	4	-1.70	de	DE	3	-1.75	d	C
9	-3.63	e	E	9	-2.71	e	E	9	-2.34	d	C

Figures with same lowercase letters at 0.05 level and capital letters at 0.01 level do not differ significantly, respectively.

SCA effects for all three-ear-leaves.

For reciprocal effects, highly differences were existed in chlorophyll content of three-ear-leaves. So, further analysis was gone for the effects of each reciprocal cross which were showed in Table 5. The ratios of the crosses with positive and negative effects for the leave above ear were 53.33 and 46.67%, respectively among all reciprocal crosses. The reciprocal effect of 23 crosses was positive and that of 22 crosses was negative for ear leaf. For the reciprocal effect of leaf under ear, positive reciprocal effects were detected for 29 crosses, only 16 crosses showed negative reciprocal effects. The crosses of 5×9(Mo17×8085Tai), 2×10 (Zheng58×Xu178), 1×8 (Ye478×E28), 3×10 (K12×Xu178), 2×8 (Zheng58×E28) and 9×10 (8085Tai×Xu178) have shown positive reciprocal effects, while the reciprocal effects of cross 2×4 (Zheng58×Chang7-2) was -3.56 which appeared negative effect for the ear leaf. The crosses 5×9 (Mo17×8085Tai)

and 2×10 (Zheng58×Xu178) appeared the higher positive reciprocal effects and the cross 2×9(Zheng58×8085Tai) showed the lower negative reciprocal effects for both ear leaf and leaf under ear, the cross 4×5 (Chang7-2×Mo17) demonstrated negative reciprocal effect for all three-ear-leaves among all reciprocal crosses. For leaf above ear, the positive reciprocal effect reached significance only for cross 2×7 (Zheng58×Dan340). The difference of average chlorophyll concentration between crosses and reciprocal crosses for each of the ten inbred lines showed in Figure 2. The maximum difference appeared in the inbred line No.10 for both the ear leaf and leaf under ear and in the No.1 inbred line for the leaf above ear, while the inbred lines No.2 (Zheng58) presented minimum difference for all three-ear-leaves.

The absolute values of difference for inbred lines No.10 in ear leaf and leaf under ear were 1.80 and 4.71 respectively, and that of No.1 in leaf above ear was

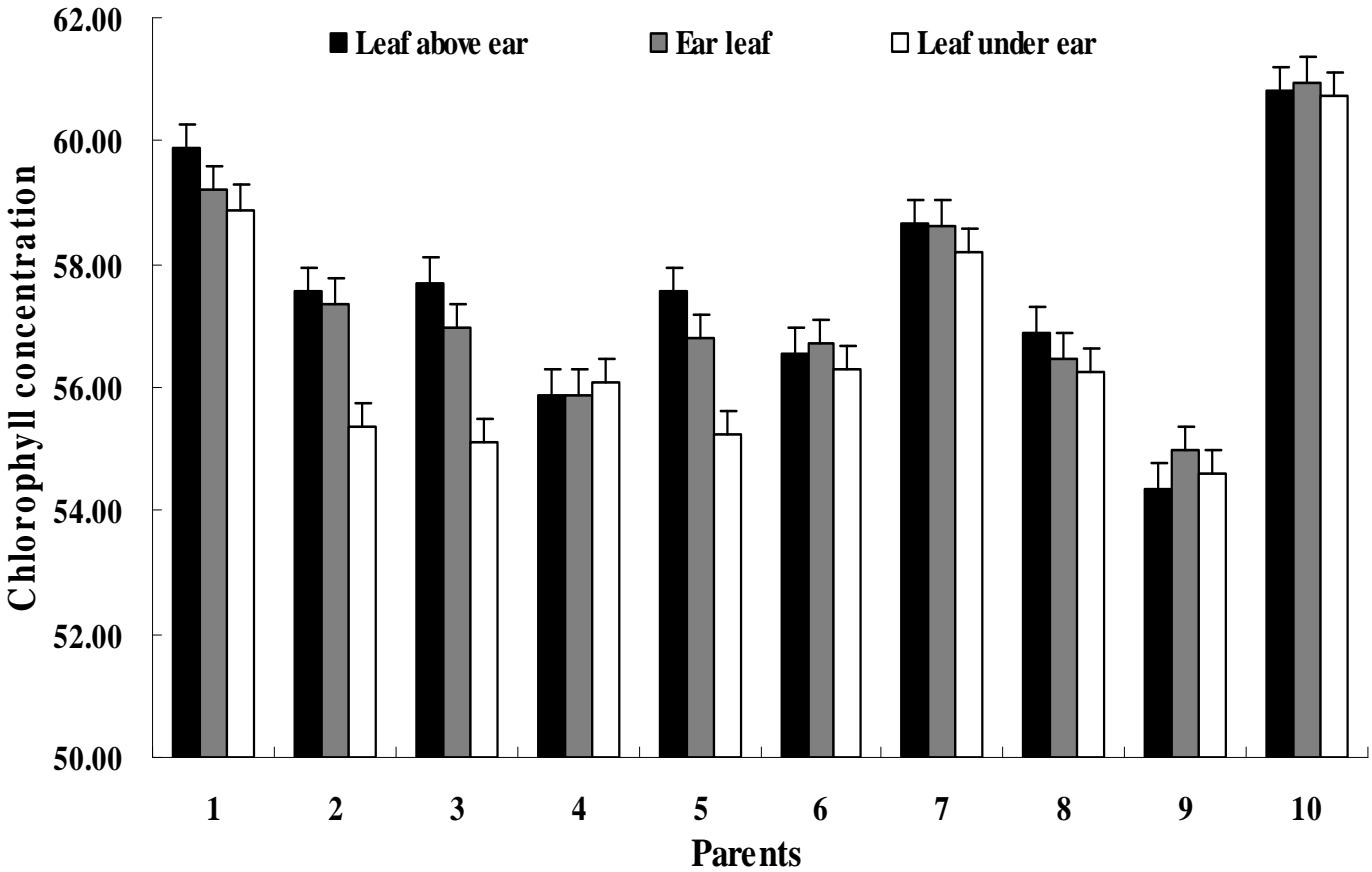


Figure 1. Average chlorophyll contents of crosses from different inbred lines in three-ear-leaves.

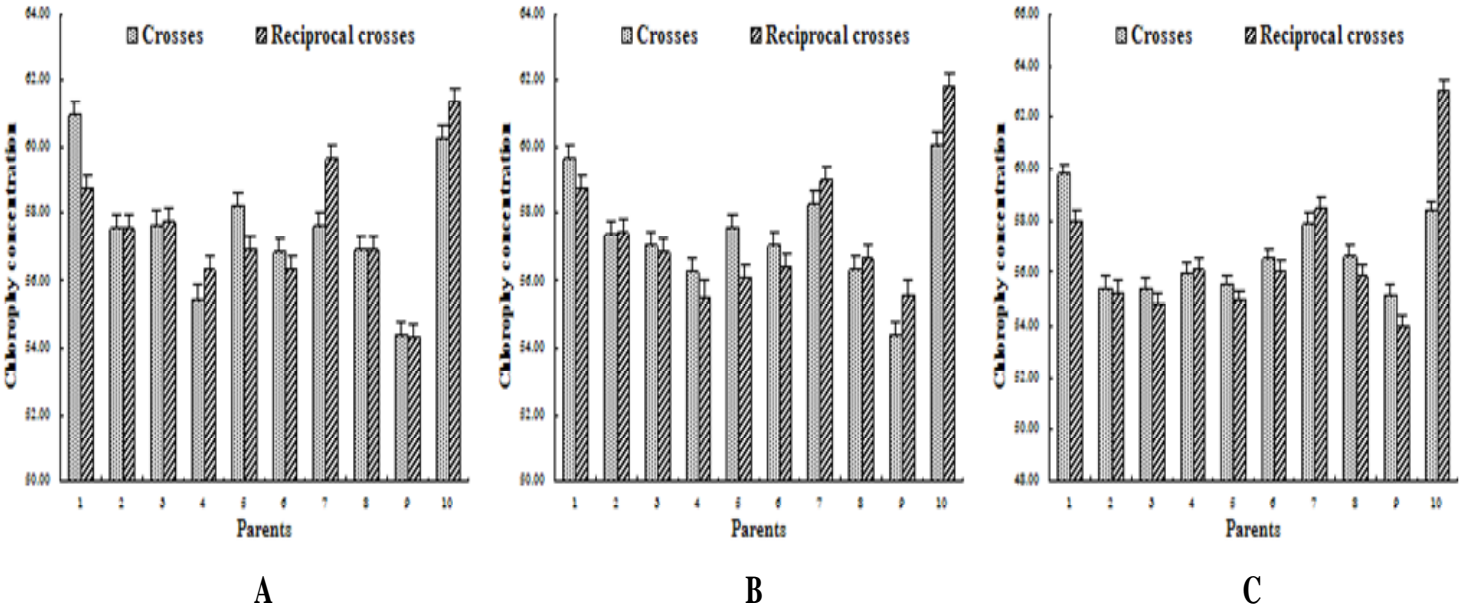


Figure 2. Comparison for chlorophyll content of three-ear-leaves between crosses and reciprocal crosses. (A) leaf above ear, (B) ear leaf, (C) leaf under ear.

Table 5. SCA and reciprocal effects of chlorophyll concentration in three-ear-leaves.

Leaf	Parents	1	2	3	4	5	6	7	8	9	10
Leaf above ear	1	-	0.8	0.99	1.48	0.93	2.34	-1.18	2.79	2.1	-0.23
	2	-0.31	-	-0.17	-0.84	0.14	-2.52	3.02*	0.46	-2.18	2.91
	3	1.04	-1.4	-	0.57	0.18	-2.16	1.6	1.18	-0.85	-0.18
	4	-0.47	2.73	-0.98	-	-4.98**	-0.54	1.47	-0.35	-0.21	1.84
	5	0.51	0.64	-0.57	-2.16	-	-1.29	1.25	0.4	1.31	0.57
	6	-0.34	0.19	1.43	-6.23**	2.07	-	-0.26	-3.06*	1.94	-0.37
	7	-3.03	-1.4	1.4	3.68	1.74	-0.8	-	-0.47	-1.99	-0.74
	8	2.31	0.76	0.45	2.78	-0.83	-0.64	-2.63	-	0.81	-0.06
	9	-2.35	-1.08	-2.73	4.88*	-3.66	4.44*	3.51	-2.93	-	1.24
	10	2.65	-0.13	1.38	-4.23*	2.27	-0.1	-2.47	0.73	-0.09	-
Ear leaf	1	-	2.5	-1.61	1.61	-0.48	-0.76	-0.34	3.16*	1.03	-0.74
	2	0.87	-	-0.46	-3.56*	1.12	-0.81	2.06	2.98*	-2.81*	3.63*
	3	1.14	-0.86	-	-2.24	-1.76	0.52	1.73	-1.59	-0.98	3.08*
	4	-0.66	4.87**	-0.41	-	-3.13*	-1.43	0.4	0.84	1.31	0.78
	5	1.01	-3.84*	-0.09	-2.55	-	-2.16	-1.1	1.65	3.89*	0.45
	6	1.18	-0.1	1.61	-6.38**	1.57	-	0.03	-2.66	2.11	-1.25
	7	-1.31	-1.48	0.66	0.42	1.07	-0.27	-	-1.82	2.16	-0.76
	8	1.06	-1.09	0.75	2.15	2.35	-1.99	0.05	-	1.36	-0.03
	9	-2.79	1.33	-4.55**	4.67**	-2.65	3.43*	1.87	-1.04	-	2.93*
	10	-0.5	0.29	1.76	-2.11	3.12	0.97	-1	-2.25	-0.27	-
Leaf under ear	1	-	1.1	0.39	-0.49	0.69	1.8	1.38	2.61	-0.13	0.98
	2	0.07	-	-0.14	0.86	0.19	-0.88	2.64	0.26	-4.87**	3.76*
	3	1.41	0.18	-	-0.14	-1.18	1.06	-0.11	1.61	-0.1	1.68
	4	-2.01	0.92	2.22	-	-4.29**	-0.81	1.12	0.37	-0.63	3.74*
	5	3.5	-5.03**	-3.89*	0.06	-	-2.13	-1.62	0.16	0.41	0.8
	6	2.89	-0.7	3.75	-6.40**	0.11	-	1.12	-3.44*	1.84	1.57
	7	-3.28	1.86	1.52	2.45	1.57	-3.37	-	-0.69	0.22	2.51
	8	-0.3	2.43	-1.44	2.25	2.63	-1.64	-0.28	-	2.21	2.22
	9	-0.89	-2.07	-4.05*	3.87*	-1.71	4.15*	1.13	-1.95	-	3.95*
	10	-1.41	2.33	0.31	-3.36	2.74	1.2	-1.62	-1.71	1.5	-

Values in the lower left diagonal are for SCA effects while those in the upper right diagonal are for reciprocal effect in each entry.

2.23, but for the inbred lines No.2, the absolute values of difference were only 0.01, 0.08 and 0.16 in leaf above ear, ear leaf and leaf under ear respectively.

Estimation of genetic parameters for chlorophyll content

The estimations of broad sense heritability for chlorophyll content of leaf above ear, ear leaf and leaf under ear were 54.81, 57.50 and 58.43% respectively, which showed variation from genetic factor was more important than variation from environment among phenotype variation, while the estimated narrow sense heritability were similar about 33.5% for chlorophyll content of three-ear leaves. The ratio of V_A / V_G for leaf above ear, ear leaf

and leaf under ear was 0.61, 0.59 and 0.57, which indicated that the additive effect was greater importance than non-additive effect for the traits investigated (Table 6).

DISCUSSION

In this study, ten inbred lines were selected as parents that represented five different heterotic groups (Table 1) and included the parents of main commercial hybrids, for example, inbred lines No.2 (Zheng58) and No.4 (Chang7-2) were the parents of hybrid Zhengdan958, the most popularized variety in China presently. At the same time, the ten inbred lines were developed from different main maize planting areas in China, No. 1, 2, 4 and 9 were

Table 6. Genetic parameters for chlorophyll content of three-ear-leaves.

Genetic parameter	Leaf above ear	Ear leaf	Leaf under ear
V_P	21.44	18.21	23.09
V_G	11.75	10.47	13.49
V_A	7.16	6.14	7.75
V_D	4.59	4.33	5.74
h_B^2	54.81%	57.50%	58.43%
h_N^2	33.40%	33.70%	33.58%

Table 7. Analysis of correlations between chlorophyll content of three-ear leaves.

Traits	Leaf above ear	Ear leaf	Leaf under ear
Leaf above ear	1		
Ear leaf	0.81**	1	
Leaf under ear	0.73**	0.77**	1

developed from Huanghuai maize planting area, No.6 (Zi330), 7, 8 (E28) and 10 from north east and the No.3 from north west of China. Therefore, these ten elite inbred lines employed in this study represented the breeding materials in use in maize breeding programs in China. In this study, the broad sense heritability was about 55% which showed the genetic factors was main reason for variation of chlorophyll content of three-ear-leaves, and narrow sense heritability was about 33%, additive effect was more important than non-additive effects in genetic variation which was useful information for maize breeders, this founding was similar to the results of days to 50% maturity and number of rows per ear studied previously by El-Badawy (2013). But Kanagarasu et al. (2010) studied 72 hybrids from 24 lines and 3 testers, the findings showed that variance due to SCA was greater than GCA variance for the traits grain yield per plant, cob diameter, cob length, plant height, ear height, leaf length, 100 grain weight, grain rows per cob, days to 50% tasseling and days to 50% silking which indicated the predominance of non-additive type of gene action in the governance of above mentioned traits, the similar findings had been reported (Borghi et al., 2012). For the GCA of chlorophyll content of three-ear leaves in ten elite inbred lines, the inbred lines No.10 and No.1 exhibited the higher GCA effects for the leaf above ear, ear leaf and leaf under ear, but the SCA effect of cross 1x10 (Ye478xXu178) was negative value for ear leaf and leaf under the ear, and positive value (2.65) for leaf above ear. While No.9 and 4 inbred lines showed the lower GCA effect, but the SCA effect of cross 9x4 (8085TaixChang7-2) for leaf above ear, ear leaf and leaf under ear were 4.88, 4.67 and 3.87, respectively. So, the correspondence between SCA and GCA effects in the inbred lines was not existed all the time for chlorophyll concentration of three-ear leaves. For the leaf above ear, but the average SCA

effects of 6 crosses from No.10, 1, 7 and 3 with positive GCA effect as parents was 0.97, four of 6 crosses show the positive SCA effect, but the SCA effects of 3 crosses from No.10, 1 and 7 inbred lines as parents showed the negative effect for both ear leaf and leaf under ear. Therefore, it verified the view above, namely, the inbred lines with high GCA effect must not be high for SCA effect. So breeders paid more attention to the GCA, meanwhile, SCA was also important for chlorophyll content in maize breeding practice.

For the same crosses, the SCA effect of chlorophyll content showed similar effects for leaf above ear, ear leaf and leaf under ear in this study. For instance, the cross 6x4 (Zi330xChang7-2), its SCA effect of leaf above ear was -6.23, the lowest among all crosses, and this cross also showed the lowest SCA effect for both ear leaf and leaf under ear. By further analysis, the correlations demonstrated highly positive between the chlorophyll content of three-ear leaves, the correlation coefficients were 0.81 between leaf above ear and ear leaf, 0.73 for leaf above ear and leaf under ear, and 0.77 for ear leaf and leaf under ear (Table 7).

The studies of differences between reciprocal F_1 crosses for important characters can help breeders to make decisions at many steps in a breeding program (Hansen and Baggett, 1977). The reciprocal crosses differences about some agronomic characters except for chlorophyll concentration have been reported by several studies in maize (Melchinger et al., 1985; Revilla et al., 1999). Ordás et al. (2008) has reported reciprocal effects for agronomic traits as emergence, early vigor, and silking date in the sugaryxsugary enhancer hybrids in sweet corn. In this study, reciprocal crosses difference were investigated for the chlorophyll content of the three-ears leaves, the highly reciprocal effects were detected for chlorophyll content of ear leaf. The reasons of reciprocal

crosses differences may be due to chlorophyll existing chloroplast in cytoplasm which showed cytoplasmic inheritance characters.

Conflict of Interest

The authors have not declared any conflict of interest.

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