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RESEARCH ARTICLE

Study of gene effects and genetics of transgressive segregation for yield and its components in basil (*Ocimum basilicum* L.)

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Abstract

Seven crosses of (*Ocimum basilicum* l.) involving thirteen were selected on the basis of generation mean analysis to study genetics of transgressive segregants for number and length of inflorescence, fresh and dry herb yield, and oil content. Generation mean analysis with three parameter model with $\chi 2$ test indicated that additive-dominance model was inadequate for all the traits in all the crosses except those for oil content used of six parameter model to estimate the gene effects. Three parameter models with $\chi 2$ test significantly indicated that non-allelic interaction was present. The generations mean analysis from both the sources was equally efficient in additive-dominance model. A comparison of generation mean analysis for observed and predicted frequencies of transgressive segregants indicated that the potential crosses for transgressive segregants were those that had additive and dominance gene effects. Prediction for transgressive segregants from F_2 was more accurate other then generations. Significant differences between predicted and observed transgressive segregants for most of the traits in F_2 population were observed in basil. The present study indicated that early generation selection is effective and should be practiced for future breeding program.

Introduction

The *Ocimum* genus belonging to the *Lamiaceae* family is characterized by a great variability of both morphology and chemo- types (Lawrence1988). The case of cross-pollination leads to a large number of subspecies, varieties, and forms (Guenther1949). Among all the species, *Ocimum basilicum* is economically more importance and is cultivated and utilized throughout the world. The Tulsi leaf, wheneaten, can control thirst, and so was invaluable to weary travelers (Lal *et al*., 2008, 2013 and Lal 2014).The aromatic leaves are used fresh or dried as a flavorings agent for foods, confectionery products and beverages. Traditionally, the plant has been used as medicine for its carminative, stimulant and antispasmodic properties. In Ayurveda, the traditional Indian medicine, basil is used as a remedy for many diseases. The essential oil, mainly used in food industries and perfumery, also possesses antimicrobial activity (Prasad *et al*., 1985), and some of its components, such as 1, 8-cineole, linalool and camphor are known to be biologically active (Morris *et al*., 1979). Camphor and 1, 8-cineole also seems to be involved as agents in allelopathic reactions (Rice, 1979). Based on chemical composition of basil, like methyl cinematic, methyl chavicol, eugenol and linalool rich have been identified (Pareek *et al.*, 1982 and Ramesh. *et. al*., 2012). Basil essential oil finds diverse uses in perfumery, pharmaceutical, cosmetics, food and flavor industries (Duglas, 1969).

The maximum diversity of species in this genus is met in the tropical rain forests of Africa with 59 species, the largest number of species in the genus so far reported from this region. Tropical Africa is followed by the subtropical regions of Africa (South Africa) with 19 species. Arabia and Brazil are hosts to 11 species each whereas India, Ethiopia and Madagascar are home to 9, 8 and 7 species respectively (Pushpangadan and Bradu, 1995). The genus *Ocimum* is widely distributed in the warmer regions of both hemispheres. About 160 species of Ocimum are

reported in Balyan and Pushpangadan, (1988). In India, it is grown in the states of Gujarat, Karnataka, Madhya Pradesh, Maharashtra, Rajasthan and Uttar Pradesh.

The additive type of gene action is operative when complete absence of allelic interactions both at inters and intra-allelic levels are envisaged. So is the case for all genes controlling non-additive type of gene action, which may result from interaction between alleles of the same gene or locus (dominance) and that between the alleles of different genes or loci (epistasis). Thus, non-additive type of gene action entails: (i) dominance action (ii) non-allelic interaction. Complementary epistasis involves two non-allelic genes complementing each other to produce a new phenotype, which is not ascribable to them individually. They mutually reinforce each other's effect. Such a variation is created by the interaction of two homozygote for the two genes, each acting additively, that is additive x additive (AA) interaction. Duplicate epistasis involves two non-allelic genes which tend to cancel or weaken the effect of each other when they occur in combination. They act in opposite directions hence dilute each other's effects. Such a variation arises from an interaction between a homozygote and a heterozygote or between two heterozygotes. Accordingly, they are termed as additive x dominance (AD) and dominance x dominance (DD) epistatic interactions, respectively. The estimates of genetic parameters can be used to predict the frequencies of transgressive segregants that would appear in a F_2 generation. In the present study, attempts were made to predict the frequencies of transgressive segregants for yield and its components using generation mean analysis (GMA) and to test the validity of predictions by isolating transgressive segregants detect for traits in F_2 population.

Material and Methods

The present study was conducted at the Research Farm, Department of Genetics and Plant Breeding (Formerly, Agricultural Botany), Ch. Charan Singh University, Meerut during 2007-08 and 2008-09. Experimental material of this study comprised thirteen accessions of Basil (*Ocimum basilicum*) obtained from National Bureau of Plant Genetic Recourses, New Delhi. The selection of parents was made on the basis of contrasting traits like number of inflorescence, length of inflorescence, fresh herb yield, dry herb yield and oil content. Thirteen accessions used in the study were, EC-388788, EC- 387893, EC-388896, EC-388887, EC-338785, EC-387837, IC-369247, IC-IC-344681, EC-333322, IC-326711, IC-386833, IC-370846 and IC-326735. The six basic generation of P_1, P_2, F_1, F_2, B_1 (F_1 x P_1) and B_2 (F_1x P_2) of seven crosses *viz*. (i) EC-388788/IC-333322, (ii) EC-387893/IC-326711, (iii) EC-388896/IC-369247, (iv) EC-388887/IC-386833, (v) EC-387837/EC-338785, (vi) IC-369247/IC-370846 and (vii) IC-IC-344681/IC-326735 were selected on the basis of generation mean analysis and were developed to determine gene effects and to predict the frequencies of transgressive segregants. Six basic generations were grown in a randomized block design with three replications The data on the following quantitative traits number and length of inflorescence, fresh and dry herb yield, and oil content were recorded on 5 randomly selected plants in each of P_1, P_2 and F_1 generations, 15 randomly selected plants each of B_1 and B_2 and 30 randomly selected plants of F_2 generation. The estimates of generation mean analysis following a three parameter model as suggested by Jinks and Jones (1958) with Joint Scaling test Cavalli, (1952) were carried out. A six parameter model suggested by Hayman (1958) was applied if the three parameter model was found to be inadequate. In order to identify transgressive segregants in F_2 population, a total of 30 plants in each F_2 population from each replication were taken randomly. The progeny showing equal or lower mean and or higher variance at 5 *per cent* level of probability were discarded and the rest were considered to be transgressive segregants. The frequencies of transgressive segregants were predicted on the basis of generation mean analysis and F_2 population. The estimates of (d) and (D) (where appropriate (d), (h), (i), (l) and (D) and (H) obtained from generation mean analysis) were used to predict the frequencies of transgressive segregants in F_2 population. The predicted and observed frequencies of transgressive segregants for different traits in F_2 population of seven crosses were compared and the validity of prediction was tested using χ^2 test (Jinks and Pooni, 1976- and 1980). The essential oil was extracted from the air dried herb by hydro-distillation using Clevenger's apparatus for 2.30 hrs. Chlorophyll content in the leaves of the parent and progeny was estimated to Arnon, (1949). 100 mg fresh leaf tissue sample was homogenized in 5 ml of acetone. The extract was centrifuged at 1000Xg for min and supernatant collected. Final volume was made up to 5ml and absorbance was read A_{645} nm and A_{663} nm or spectrophotometer. Following formula was used for quantification.

Mg total chlorophyll / gram tissue = $20.2(A_{645}) + 8.02(A_{663}) * V/1000 * W$.

Where –A= absorbption me at specific wave length.

V= final volume of chlorophyll extract in 80% acetone.

W= fresh weight of tissue extracted.

Result and Discussion

Analysis of variance: The analysis of variance for all the five traits recorded for 13 parents ($F_{1's}$, $F_{2's}$, $B_{1's}$ and $B_{2's}$ in the study are presented in Table 1. The mean squares due to treatment of all the five traits were highly significant thereby suggesting the presence of sufficient genetic variability in the materials under study.

Gene effects: The generation mean analysis was performed for the additive – dominance model on six generation for all the traits. The χ^2 **(**3d.f) values were found to be significant in all the five crosses for all the five traits except for oil content in EC-388788/IC-333322, IC-369247/IC-370846 and (vii) IC-344681/IC-326735 were showed absent of non-allelic interaction its mean that six parameter model were not used and rest of four traits, number and length of inflorescence, fresh and dry herb yield traits were used in six parameters model to estimates of gene effects, therefore the six parameter model of Hayman (1958) was applied in the presence study (Table 2). The additive components [d] was significant and very much pronounced for all the traits in all the crosses except to fresh herb yield for cross EC- 388788/IC- 333322, dry herb yield in cross EC- 388796/IC- 326711, length of inflorescence in cross EC- 387837 /EC- 358785. The dominance components [h] were found to be significant for all the traits in all crosses except length of inflorescence, fresh herb yield and dry herb yield in cross IC-344681/ IC – 326735. The additive x additive [i] components of epistasis were found to be significant for all the traits in all the crosses except to EC- 38887/IC- 386833 for dry herb yield, EC- 387837/EC- 358785 for length of inflorescence and IC- 344681/IC- 326735 for dry herb yield. The additive x dominance [j] components of epistasis were found to be significant all the crosses except to EC-369247/IC- 370846 for dry herb yield. The dominance x dominance [l] components of epistasis were found to be significant to all the traits in all the crosses except EC- 388788/IC-333322 for fresh herb yield, EC-38887/IC-386833 for length for inflorescence in crosses to EC-369247/IC- 370846 and IC-344681/IC – 326735 provide an indication that epistasis also played an important role in determining the inheritance of different traits. Generation mean analysis showed that dominance, additive x additive and dominance x dominance gene action play important role in the inheritance of oil content. Similar results were found by Dani and Kohil (1989). The negative additive, dominance x additive and dominance x dominance estimate shows the gene pairs responsible for oil content are in dispersive form (Mather and Jinks 1977). Having considered the relative importance of different gene effects for the above traits in the present study, a strategy could be developed for efficient breeding programs aimed at improvement that trait. As presented above, a trait has exhibited the preponderance of either additive gene effects or non-additive gene effects or both. Those traits showed that complimentary and duplicate types of gene interaction were present confirming the importance of dominance effects as suggested by Grewall, (1988). In conclusion, considerable non-additive genetic effects observed in this study suggests that selection in advanced generations may be more appropriate because effective selection in early generation of segregating material can be achieved only when additive gene effects are substantial and environment effects are small. All the crosses exhibited complimentary type of epitasis for the number of inflorescence except cross EC-388896/IC-369247 showed duplicate type of epistasis. For this trait dominance and dominance x dominance type of gene effect are predominant. The non fixable gene effects were higher than fixable gene effects indicating a greater role of non-additive gene effects for this trait, which suggested that this trait can be improved through recurrent selection. These results confirm the findings of Pathak *et al*. (2000); Kumar *et al*. (1994) and Noshin *et al*. (2003) who also reported the involvement of additive type of gene action for this trait. The non-additive type gene effect was found significant an all crosses. The crosses EC-387893/IC-326711, EC-388896/IC-369247 and EC-387837/EC-338785 showed duplicate type of interaction and the cross EC-388788/IC-333322 showed complimentary type of epistasis for the trait length of inflorescence. The non-additive gene effects were predominant for the trait of fresh herb yield. All types of gene effects were found significant in only three crosses, EC-387893/IC-326711, EC-388887/IC-386833 and EC-387837 /EC-338785. Additive type gene effects were found significant in crosses EC-387893/ IC-326711, EC-388887/IC-386833 EC-387837/EC-338785, IC-369247/IC-370846 and IC-344681/IC-326735. Dominance gene effect was observed in crosses namely, EC-388788/IC-333322, EC-387893/IC-326711, EC-388896/IC-369247, EC-388887/IC-386833 and EC-387837/EC-338785. All the three type of non-allelic gene interaction were significant in all the crosses except EC-388788/IC-333322. Duplicate type of interaction showed in cross EC-387893/IC-326711. EC-388896/IC-369247 and EC-388887/IC-386833 showed complimentary type of epistasis. All the types of gene effects were found in only one cross EC-388788/IC-333322, additive and dominance were found significant in crosses, EC-388788/IC-333322 and EC-387837/EC-338785. For dry herb yield, I-type was significant in crosses: EC-388788/IC-333322, EC-387893/IC-326711, EC-388896/IC-369247, EC-388887/IC-386833 and EC-387837/EC-338785. J type of interaction was significant in EC-388788/IC-333322, EC-388896/IC-369247, (iv) EC-388887/ IC-386833, (vii) IC-344681/ IC-326735 and (l) type of gene interaction were found in (I) EC-388788/ IC-333322, (ii) EC-387893/ IC-326711, (iii) EC-388896 / IC-369247, (vi) IC-369247/ IC-370846 and (vii) IC-344681/ IC-326735. In all the significant cases the magnitudes of (h), (i), (j) and (l) were higher than that of additive gene effects. Crosses (i) EC-388788 /IC-333322,

(ii) EC-387893 /IC-326711 and (vii) IC-344681/ IC-326735 showed complimentary type of epistasis while duplicate type of epistasis was showed in (ii) EC-387893/ IC-326711, (v) EC-387837/ EC-338785 (vi) IC-369247 /IC-370846. The crosses (iii) EC-388896 / IC-369247 showed complimentary and cross (v) EC-387837/ EC-338785 showed duplicate type of epistasis. This suggested that duplicate type of gene interaction was present confirming the importance of this observation as reported by Grewall, (1988). In crosses having considerable additive genetic affects with less environmental effects selections would be made in early generation of segregating materials.

Transgressive segregants: Transgressive segregants were also observed during the present study (**Table 2).** The frequencies of transgressive segregants were predicted as described by Yadav *et al*. (1998), on the basis of generation mean analysis and F_2 families. The estimates of d and D, D and H and d, h, i, j, and l were calculated from generation mean analysis and were used to find out the frequency of transgressive segregation in above populations (F_2 population). The significance of transgressive segregation was tested using $\chi 2$ test (**Table 2).** The results indicated significant transgressive segregants for only few traits. For instance significant transgressive segregants were observed for: fresh herb yield in cross IC-369247/IC-370846 (43.14), EC-388887/IC-386833(12.520), EC-388788/IC-333322 (11.824), IC-344681/IC-326735 (11.118), EC-387837/EC-338785 (8.157), EC-387893/IC-326711 (7.037), dry herb yield in cross EC-387893/IC-326711 (13.031), EC-388896/IC-369247 (13.976) EC-388887/IC-386833 (8.255) ,IC-369247/IC-370846 (10.299), EC-388896 / IC-369247 (4.942), IC-344681/IC-326735 (5.420), number of inflorescence in cross EC-388887/IC-386833 (4.791), EC-387837/EC-338785 (5.820), IC-369247/IC-370846 (17.63) and oil content in cross EC-388896/IC-369247 (4.942). Jinks and Pooni (1976,1980 and 1981) and Pooni and Jinks (1978,1979) used genetic parameter estimates from generation mean, F_2 and triple test cross analysis for predicting the frequencies of transgressive segregants in *Nicotiana rutica.* The results of the present investigation demonstrate that genetic studies can provide information that could help predict the frequencies of transgressive segregants for different traits in basil (*Ocimum basilicum*). The frequencies of transgressive segregants were predicted from generation mean analysis and F_2 family. However the limitation of generation mean analysis is the large amount of practical work required to produce the experimental generation. Therefore attempts were made to compare the prediction of generation mean analysis with those F_2 families. The results are in agreement with the results of some earlier workers i.e. (McGinnins and Shebeski, 1968; De Pauw and Shebeski, 1973; Sneep, 1981; Knott, 1994; Singh and Singh, 1997). Significant differences between predicted and observed transgressive segregants for most of the traits in F_2 population in basil in the present study has indicated that early generation selection is effective and should be practiced for future breeding programs. This approach will provide an opportunity for basil breeders to concentrate on a few potential crosses for getting transgressive segregants.

Table.1. Analysis of variance for five quantitative traits of 13 parents,P_1,P_2 F_1s,F_2s, B_1s, and B_2s of seven crosses in basil (*Ocimum basilicum* L.*)*.

Source of variation	**d. f.**	**NI**	**LI**	**FHY**	**DHY**	**OC**
Replication	2	0.75	0.50	18848.00	3966.00	.020
Treatment	40	391.30**	48.82*	390958.40**	103503.00**	2.63**
Error	80	0.94	0.36	9650.60	9887.36	0.04

Acronyms: NI =Number of inflorescence, LI = Length of inflorescences, FHY = Fresh herb yield, DHY = Dry herb yield, OC =Oil content.

Table.2 Estimates of genes obtained from three and six parameter model and observed and predicted frequencies transgressive segregants in F_2 population for five traits of seven crosses in basil *(Ocimum basilicum* L.*)*

Model	Traits					
	Parameter	Number of inflorescence	Length inflorescence (cm)	Fresh herb yield (g)	Dry herb yield (g)	Oil yield (%)
EC-388788 x IC-333322						

3-Parameter	m	91.37**±0.64	18.55**±0.64	2269.09**±0.64	1158.73**±0.60	3.45**±0.64
	[d]	19.83**±0.63	1.87**±0.63	68.09±0.63	-84.50**±1.18	0.10±0.63
	[h]	1.38±1.18	0.19±1.18	286.89**±1.18	-100.43**±1.18	0.07±1.18
χ2 (3 d.f)	Epistasis	25.71**	12.10**	38522**	26556.91**	1.20
χ2 ((1 d.f)	TS	0.115	0.260	11.824**	1.176	0.029
6-parameter	m	82.34**±0.56	14.25**±0.17	1580.00**±18.55	790.00**±5.77	……..
	[d]	24.53**±1.21	4.98**±0.47	21.66**±119.28	-277.00**±28.14	……..
	[h]	66.74**±3.20	19.22**±1.22	2435.83**±902.62	1531.45**±66.60	……..
	[i]	29.57**±3.10	7.48**±1.17	2070.00**±901.62	1059.33**±62.00	…….
	[j]	31.30**±1.20	4.31**±0.51	-1591**±443.94	-265.71**±31.40	…….
	[1]	38.40**±5.38	18.51**±0.21	18.51**±0.21	-2831±1800.00	1062.90**±127.06
Epistasis effects		C	C	…….	C	…….
EC-387893 × IC-326711						
3-Parameter	m	96.05**±0.964	20.78**±0.64	24.82.06**±0.64	1156.60**±0.64	2.75**±0.64
	[d]	10.29**±0.63	-1.87**±0.63	-111.00**±0.63	45.73**±0.63	0.43±0.63
	[h]	18.38**±1.18	1.14±1.18	-254.60**±1.18	4.07**±1.18	1.64±1.18
χ2 (3 d.f)	Epistasis	67.19**	22.45**	1648**	9733.26**	8.23**
χ2 (1 d.f)	TS	0.005	0.086	2.216	13.976**	4.942**
6-parameter	m	89.60**±0.83	17.17**±0.50	1655.00**±47.69	802.00**±27.15	4.59**±0.33
	[d]	21.50**±0.77	6.21**±0.35	320.00±658.33	-63.33±76.73	-1.02**±0.34
	[h]	49.96**±0.37	13.85**±2.48	1900.00**±655.54	1896.50**±189.10	6.07**±1.33
	[i]	44.60**±3.60	15.04**±2.46	675.00**±314.06	1412.20**±188.02	7.12**±1.33
	[j]					
	[1]	-98.33**±4.79	-13.70**±2.84	3288.00**±658.33	-2532.34**±328.23	9.31**±1.38
Epistasis effects		D	D	C	D	C
EC-388887 x IC-386833						
3-Parameter	m	90.49**±0.64	19.85*±0.64	2373.20**±0.64	997.24**±0.64	3.48**±0.64
	[d]	-2.81**±0.63	-3.43**±0.63	144.40**±0.63	-0.23±0.63	
	[h]	1.58±1.18	-3.01**±1.18	-357.40**±1.18	220.24**±1.18	0.51±1.18
χ2 (3 d.f)	Epistasis	30.71**	28.64**	73666.62**	24476.6**	1.33
χ2 (1 d.f)	TS	4.791**	0.568	12.52**	8.255**	0.278
6-parameter	m	93.86**±0.83	18.14**±0.50	2327.27**±14.05	1052.89**±37.78	……..
	[d]	14.43**±0.61	-7.81**±0.46	-632.00**26.55	-418.80**±32.77	……..
	[h]	31.38**±2.11	9.35*±2.43	-1285.00**±79.09	-197.12±183.36	……
	[i]	21.48**±1.78	10.30**±2.39	1445.00**±77.35	-309.00±164.00	…….
	[j]	11.04**±0.80	-1.48**±0.50	-976.31**±124.67	-472.64**±44.01	
	[1]	88.01**±3058	-24.43±30.02	1581.10**±124.67	-37.30±25.60	
Epistasis effects						

EC-387837 x EC-358785						
3-Parameter	m	88.80**±0.64	18.18**±0.64	1004.53**±0.64	1004.53**±0.64	4.90**±0.64
	[d]	6.40**±0.63	1.58**±0.63	8.33**±0.63	113.33**±0.63	-139±0.63
	[h]	-14.62**±1.18	-118±1.18	-357.40**±1.18	-19.09**±1.18	-1.73±0.63
χ2 (3 d.f)	Epistasis	44.83**	114.99**	73666.62**	61350.90**	9.66**
χ2 (1 d.f)	TS	0.015	5.820**	8.157**	1.231	0.107
6-parameter	m	90.26**±0.58	16.82**±0.19	1816.31**±230.02	860.88**±12.07	3.27**±0.13
	[d]	-25.66**±2.90	0.50±0.62	934.00**±81.25	196.00±11.16	0.48*±0.20
	[h]	24.27**±2.90	-3.53*±1.48	545.00**±115.57	-216.10**±60.30	-1.07**±0.10
	[i]	28.59**±2.83	-1.48±1.43	857.41**±111.29	-109.54**±53.19	-5.80**±0.07
	[j]	-14.55**±0.83	-4.01**±0.68	1098.00**±32.62	248.64**±27.29	-0.20±0.75
	[1]	50.40**±4.17	14.31**±2.69	1368.00**±167.30	471.40**±60.90	3.50*±0.17
Epistasis effects		D	D	C	D	D
IC-369247 x IC-370846						
3-Parameter	m	94.12**±0.64	23.20**±0.64	1140.41**±0.64	665.03**±0.64	3.56**±0.64
	[d]	5.14**±0.63	-3.50**±0.63	296.95**±0.63	121.66**±0.63	0.55±0.63
	[h]	-1.60±1.18	-1.60±1.18	705.64**±1.18	231.03**±1.18	0.12±1.18
χ2 (3 d.f)	Epistasis	139.95**	577.90**	554533.80**	10189.15**	0.49
χ2 (1 d.f)	TS	0.187	17.63**	43.14**	10.299**	0.074
6-parameter	m	101.10**±0.57	14.30**±0.14	2308.00**±22.04	900.00**±28.86	…….
	[d]	9.66**±0.55	-2.69**±0.43	-247.50**±55.43	45.33±69.19	
	[h]	55.15**±2.60	7.34**±129	36.33±152.40	1118.00**±186.68	…..
	[i]	44.30**±0.26	6.87**±1.11	-2583.00**±141.00	1117.33**±180.68	…….
	[j]	18.48**±0.58	-5.58**±0.45	444.16**±60.99	-60.66±75.63	……..
	[1]	74.70**±3.40	-2.62±2.18	593.33**±263.94	-1596.00**±315.00	
Epistasis effects		C	D		D	------
IC-344681 x IC-326735						
3-Parameter	m	91.03**±0.64	18.67**±0.64	1833.93**±0.64	815.57**±0.64	3.86**±0.64
	[d]	3.37**±0.63	-173**±0.63	179.53**±0.63	93.00**±0.63	-0.44±0.93
	[h]	-196±1.18	-196±1.18	160.27**±81.18	159.23**±1.18	-0.75±1.18
χ2 (3 d.f)	Epistasis	69.89**	56.61**	56991.24**	6964.56**	0.26
χ2 (1 d.f)	TS	0.056	0.063	11.118**	5.420**	0.290
6-parameter	m	97.03**±0.54	21.16**±0.38	2197.00**±53.50	105.00**±28.86	…..
	[d]	3.36**±0.69	-3.40**±0.80	-163.33**±67.16	-180.99**±48.69	……
	[h]	31.27**±2.62	-2.59±0.80	259.00±254.01	75.83±156.02	……
	[i]	31.27**±2.62	-6.98**±2.18	-880.00**±53.50	268.33±151.06	……
	[j]	19.16**±2.58	-2.80**±0.80	-577.00**±71.86	-1433.00**±52.53	…….
	[1]	18.01**±3.65	-6.50±3.54	-3.94.00**±356.41	-338.33**±239.53	……..
Epistasis effects		C	D	…..	…..	……..

*Significant at <0.05, **significant at P<0.01, C = Complementary epistasis, D = Duplicate epistasis, TS = Transgressive segregants

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