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Combining Ability and Gene Action in Crosses among Asian and Ethiopian Genotypes of Hot Pepper (Capsicum annuum L. Var. Annuum)

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Abstract: Lack of availability/scarcity of genetic information has limited improvement work on hot pepper (*Capsicum annuum* L. var. *annuum*) in Ethiopia. However, information regarding the types and relative importance of gene actions can be generated using combining ability analysis and utilized in the selection of suitable genotypes for hybridization and for obtaining promising hybrids. This study aimed to generate useful information with respect to combining ability and gene action from p(p + 1)/2 half-diallel crossing pattern using twelve selected hot pepper genotypes of Ethiopian and Asian origins. Twelve parental lines and their 66 F_1s were tested in randomized complete block design with three replications at Melkasa Agricultural Research Center, Ethiopia, in 2004/2005 cropping season. Significant GCA and SCA effects were obtained for dry fruit yield per plant and related traits. The results showed the importance of both additive and non-additive gene actions with the predominance of the non-additive variances for dry fruit yield per plant and related traits, except for plant height and fruit length. An efficient breeding strategy for hot pepper could, therefore, be based on recurrent selection, inbred-derived hybrids or multiple crossing using genetically diverse hot pepper genotypes.

Keywords: Breeding Strategy; *Capsicum* spp.; Diallel Analysis; Fruit Yield; Genetic Diversity; Hybrids

1. Introduction

Hot pepper (*Capsicum annuum* L. var. *annuum*), 2n = 24, is a vegetable crop grown and consumed world-wide (Martelli and Quacqarelli, 1983). The first introduction of hot pepper to Ethiopia was by the Portuguese probably in the 17th century (Huffnagel, 1961). Nowadays, the crop is adapted to different agro-ecological zones and different local genotypes have evolved. Hot pepper fruits have a high nutritional value, particularly since they contain a considerable amount of vitamin C at green stage and are consumed as a fresh vegetable or, when dried or processed, as spice or condiment. The dried mature fruit of hot pepper is rich in Vitamin A (Poulos, 1993). The pungent types are preferred and have medicinal value; they stimulate saliva and the gastric juices that aid digestion.

In the past two decades, hot pepper genotypes of different origins have been introduced and local collections have also been made to address the problem pertaining to the narrow genetic base of the crop in Ethiopia. However, work on the genetic improvement of the crop is still at a low level and limited to selection of superior pure lines. Improved lines of hot pepper should be photosynthetically efficient with bigger canopy, earliness to mature, high fruit yield, less shrinkage of pericarp, good flavor, high pungency coupled with good aroma, a high number of seeds and larger fruit size.

The agronomic and environmental aspects for hot pepper improvement are well known, but there is a lack of genetic information on combining abilities for further improvement work. Thus, only a few superior genotypes have been produced and cultivated. Consequently, the dried fruit yield per hectare (ha) has remained very low (0.4 t/ha) with the quality of the marketable produce insufficient compared to a potential (2.5 t/ha dried fruit yield) of the crop in the country. Combining ability of inbred lines is the ultimate factor determining future usefulness of the lines for hybrids (Hallauer and Miranda, 1981). Sprague and Tatum (1942) were the first to partition total combining ability of the lines into general combining ability (GCA) and specific combining ability (SCA). They defined GCA as the average performance of a line in hybrid combinations and SCA as those instances in which certain hybrid combination is either better or poorer than would be expected on the average performance of the parent inbred lines included. General combining abilities are usually expressed as deviations from the overall mean (Kallo, 1988). This author described parent with zero GCA as having average GCA, and positive GCA as an indicator for a parent that produces above-average yield. He described negative GCA as an indicator for a parent that produces progeny with below average yield.

The concepts of GCA and SCA are useful for characterizing inbred lines in crosses and for enabling the interpretation of genetic variance and types of gene action operative in crosses of inbred lines (Hallauer and Miranda, 1981). Estimates of SCA describe those cases in which a certain hybrid combination does relatively better and is regarded as an estimate of non-additive gene action such as dominance and epistasis (Gowen, 1964). In the absence of epistasis, the additive variance (σ^2_A) equals the variance due to general combining ability (σ_g^2), and dominance variance (σ^2_D) equals the variance due to specific combining ability (σ_s^2) (Wricke and Weber, 1986). According to Jenkins (1940), a recurrent selection method that emphasizes GCA should be used if additive gene effect with partial dominance to complete dominance is important. However, recurrent selection method that emphasizes SCA would be appropriate if over-dominance is of primary importance (Hull, 1945). Comstock *et al.* (1949)

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designed the recurrent reciprocal selection to enhance gene action related to both GCA and SCA.

Information on combining ability among and within gene pools is required to make inferences regarding additive or non-additive gene effects (Franco *et al.*, 2001) and enable a search for potentially superior parents and hybrids (Singh *et al.*, 1992). As a rule, diallel analysis using less than ten parents will have low precision (Singh and Chaudhary, 1985). The GCA of each parent (g_i) should be examined when the objective is the development of superior genotypes, while the SCA effects (s_{ij}) provide information about hybrid performance (Cruz and Regazzi, 1994). Such knowledge is important in choosing appropriate breeding procedures (Pixley and Frey 1991; Gonzalez and Cubero, 1993; Singh 1993). Thus, studies on the understanding of genetics of combining ability are needed to identify the types of gene actions and suitable breeding strategy of hot pepper. Hence, the objective of the present study was to obtain genetic information with respect to combining ability and gene action for dry fruit yield per plant and related traits in crosses involving hot pepper genotypes.

2. Materials and Methods

2.1. Genetic Materials, Crossing Techniques, and Planting

Hot pepper genotypes (Table 1) used as parental lines were selected based on results of evaluation for adaptability and yield during 1990 to 2003. In December 2003, crosses were made among the twelve parents in all possible combinations in a half-diallel fashion {p(p+1)/2} to fit Griffing's (1956) Method 2 Model I analysis. Hand emasculation and single flower caging were employed to achieve the required mating. The seeds obtained from the crosses were harvested at the end of the cropping season during April to May 2004 to obtain F_1 crosses.

Seeds of all the twelve selfed parental lines and their 66 F_1 crosses were sown on a seedbed at the end of August 2004. Seedlings were transplanted to the field in October 2004 at Melkasa Agricultural Research Center (8° 24' N latitude; 39° 12' E longitude; 1550 m above sea level altitude; sandy loam soil with pH of 6.9 to 7.9; 763 mm average annual rainfall with annual mean maximum of 26-29 ^{0}C and minimum of 11-16 ^{0}C temperatures for the past five years). The intra-row spacing was 0.3 m and the inter-row spacing was 1 m. The treatments were arranged in a randomized complete block design and replicated three times. Plot size was 4.2 m x 4.0 m with four rows. Fifty-six plants were accommodated in each plot. All cultural practices were used as recommended by Lemma (1998).

Table 1. Description of Asian and Ethiopian hot pepper (*Capsicum annuum* L. var. *annuum*) genotypes involved in half-diallel crossing.

Serial code	Genotype	Region of origin as genotype	Field evaluation period
P1	PBC 972	Malaysia	1995 – 2003
P2	PBC 602	Taiwan	1995 – 2003
P3	PBC 223	Korea	1994 – 2003
P4	ICPN10#5	Taiwan	1990 – 2003
P5	ICPN10#6	Taiwan	1990 – 2003
P6	ICPN9#16	Malaysia	1990 – 2003
P7	PBC 731	Korea	1994 – 2003
P8	PBC 535	Indonesia	1994 – 2003
P9	PBC 580	Sri Lanka	1995 – 2003
P10	Marekofana	Ethiopia	Cultivated variety
P11	Bakolocal	Ethiopia	Cultivated variety
P12	Marekoshote	Ethiopia	Cultivated variety

2.2. Data Collection and Statistical Analysis

Thirteen traits (Table 2) were recorded on 24 plants from two middle rows in each plot by excluding border rows and the first and last plants in each row. The results were expressed as mean values.

Analysis of variance was performed based on mean values of 78 genotypes for each trait studied as suggested by Singh and Chaudhary (1985). Combining ability was analyzed following Griffing's (1956) Method 2 and Model I. The usual restrictions such as $\Sigma g_i = 0$ and $\Sigma s_{ij}+s_{ji} = 0$ (for each i) were imposed on combining ability elements.

The estimates of GCA and SCA effects were obtained using the following formula (Dabholkar, 1992; Sharma, 1998): $\mu = 2x_{..}/p\ (p+1)$; $g_i = 1/(p+2)/[x_{i.}+x_{ii}-2x_{..}/p]$; $s_{ij} = x_{ij} - (x_{i.}+x_{ii}+x_{.j}+x_{jj})/(p+2)+2x_{..}/(p+1)\ (p+2)$, where μ = population mean or overall mean, p = number of parents, $x_{..} = \sum(s_{ii} + s_{ij})$, $x_{..}$ being total of all [p(p+1)]/2 items of the diallel table, $x_{ij} = \mu + g_i + g_i + s_{ij}$, x_{ij} being the hybrid performance of a given trait, g_i = estimate of GCA effect of ith inbred line, g_j = estimate of GCA effect of jth inbred line, s_{ij} = SCA effects of ijth cross or hybrid involved ith and jth parents, s_{ii} = SCA effects of iith parent with itself, $x_{i.}$ = total of array involving ith parent, x_{ii} = parental value of the ith parent, $x_{.j}$ = total of array involving jth parent and x_{jj} = parental value of the jth parent.

2.3. Estimates of Variance Components and Tests of Significance

The variance components due to GCA ($\sigma^2 g$), SCA ($\sigma^2 s$) and environment ($\sigma^2 e$) were estimated as follows:

$\sigma^2 g_i = (p-1)\ \sigma^2 e/p(p+2) = (MSg - MSs)/(p+2)$,

$\sigma^2 s_{ij} = (p^2+p+2)\ \sigma^2 e/(p+1)\ (p+2) = (MSs - MSe)$,

$\sigma^2 e = MSe$; $\sigma^2\ (g_i - g_j) = 2\sigma^2 e/(p+2)$ and

$\sigma^2\ (s_{ij} - s_{ik}) = 2\sigma^2 e(p+1)/(p+2)$.

Significance of GCA and SCA estimates were tested using the standard error of difference (SE_d) and 't' test based on the following formulas:

$SE_d(g_i) = [(p-1)/p^2+2p)MSe]^{1/2}$

$SE_d(s_{ii}) = [\{p^2+(p+2)/(p+1)(p+2)\}MSe]^{1/2}$

$SE_d(g_i - g_j) = [2MSe/(p+2)]^{1/2}$

t_i (computed) = $g_i/SE_d(g_i)$ compared at df of (p-1)

t_{ij} (computed) = $s_{ij}/SE_d(s_{ij})$ compared at df of p(p-1)/2.

3. Results

3.1. Estimates of Variance Components

Analysis of variance based upon means over replication showed significant differences among the genotypes for all the studied traits (Table 2). The genotypic variance was then partitioned into components due to general (GCA) and specific (SCA) combining ability effects. The mean squares of both GCA and SCA effects were highly significant ($P < 0.001$) for all the traits.

3.2. Estimates of General Combining Ability Effects

The estimates of GCA effects of the parents depicted in Table 3 indicated significant and useful as well as significant and undesirable directions depending on the trait under consideration. The Asian genotype PBC 223 exhibited significant and positive GCA effects coupled with high *per se* performance for number of branches per plant, stem diameter, number of fruits per plant and dry fruit yield per plant. The Ethiopian genotype 'Marekofana' showed significant GCA effects in the desired direction for plant height, length of internode on primary branch, number of nodes on primary branch, days to maturity, single fruit weight, canopy diameter and dry fruit yield per plant. Another Ethiopian genotype 'Marekoshote' followed a similar trend in showing significant GCA effects in the wanted direction for plant height, length of internode on main stem, canopy diameter, fruit length and single fruit weight in addition to preferred GCA effects coupled with high mean values for dry fruit yield per plant and earliness. Similarly, the Asian genotypes ICPN9#16 and PBC 535 showed positive GCA effects for dry fruit yield per plant coupled with significant and important GCA effect for days to maturity.

Significant and positive GCA effects in PBC 535 and 'Marekoshote' for length of internode on primary branch, fruit length and canopy diameter are in an encouraging direction coupled with positive GCA effects of dry fruit yield per plant. Nevertheless, the GCA effects of PBC 972 among Asian and 'Bakolocal' among Ethiopian genotypes were significant in an undesirable direction for dry fruit yield per plant and days to maturity. Likewise, Asian genotypes ICPN10#5 and ICPN10#6 showed significant and unwanted GCA effects for dry fruit yield per plant and number of fruits per plant.

3.3. Estimates of Specific Combining Ability Effects

Significant and desirable SCA effects (s_{ij}) of F_1s were observed at very high levels within the crosses of Ethiopian and Asian (E x A) group in respect of dry fruit yield per plant (51.9% of 27 F_1s), number of fruits per plant (48.1% of 27 F_1s), single fruit weight (29.6% of 27 F_1s), canopy diameter (37.6% of 27 F_1s), days to maturity (48.1% of 27 F_1s) and length of internode on main stem (22.2% of 27 F_1s). This is in contrast to an absence of similar results either in the corresponding F_1 crosses within Ethiopian (E x E) group or in SCA effects (s_{ii}) within parental lines (self's) for the same traits (Table 4). Likewise, a considerable proportion of F_1 crosses within Asian (A x A) group achieved significant and desirable SCA effects (s_{ij}) for dry fruit yield per plant and majority of related traits but with relatively lower shares compared to the proportions that were observed in F_1 crosses of Ethiopian and Asian (E x A) group (Table 4).

Significant and highest desirable SCA effects coupled with high dry fruit yield per plant were recorded from PBC 223 x 'Marekoshote', ICPN10#5 x 'Marekofana' and PBC 580 x 'Marekoshote' crosses, all of which were generated from crosses between Ethiopian and Asian genotypes. Similarly, the majority of the significant and high level of desirable SCA effects as well as the top *per se* performances for all other traits were obtained from F_1 crosses of Ethiopian and Asian group. In general, high proportions of F_1 crosses of Ethiopian to Asian group were with significant and desirable SCA effects for dry fruit yield per plant, single fruit weight and number of fruits per plant. Similarly, some F_1 crosses of Ethiopian and Asian group performed outstandingly for most of the traits but F_1 crosses with negative SCA effects for all the traits were observed in all the groups (E x E, E x A and A x A).

Parents PBC 223 and 'Marekofana' exhibited significant and high level of GCA effect (g_i) in addition to resulting in F_1 crosses with significant and positive SCA effect for dry fruit yield per plant. However, ICPN10#5 x 'Bakolocal', ICPN9#16 x 'Bakolocal' and PBC 602 x PBC 731 crosses with significant and desirable SCA effects (s_{ij}) for number of fruits per plant evolved from parents with either negative and positive or positive and positive GCA effects. Similarly, most crosses that showed significant and top SCA effects for single fruit weight evolved from parents with either positive x negative, or positive x positive or negative x negative GCA effects. Moreover, the top five hybrids with the highest SCA effects for dry fruit yield per plant and number of fruits per plant (Table 4) were produced from crosses that involved parents with GCA of either negative x positive or positive and positive effects (Table 3). Significant and desirable SCA effects (s_{ii}) of parental lines were expressed by PBC 972 for number of branches per plant and number of nodes on main stem, PBC 602 for stem diameter, PBC 223 and ICPN10#6 for number of nodes on main stem, and 'Bakolocal' for length of internode on primary branch.

Table 2. Estimates of mean squares (MS) and variances of general (GCA) and specific (SCA) combining ability effects for 13 traits of 78 hot pepper genotypes at Melkasa in 2004/2005.

	Mean squares (degrees of freedom)			Variantes of genetic components			
Traits	Genotypes (77)	GCA effects (11)	SCA effects (66)	$\sigma_e^2 = V_e$	$\sigma_g^2 = (1/2)V_A$	$\sigma_s^2 = V_D$	σ_g^2 / σ_s^2 ratio
Number of branches per plant	3.737***	4.077***	0.774***	0.355	0.266	0.419	0.635
Plant height (cm)	259.857***	408.054***	33.047***	10.254	28.414	22.793	1.247
Stem diameter (cm)	0.045***	0.029***	0.013***	0.006	0.002	0.007	0.286
Number of nodes on main stem	11.765***	13.409***	2.340***	0.737	0.905	1.603	0.564
Length of internode on main stem (cm)	0.287***	0.207***	0.077***	0.021	0.013	0.056	0.232
Length of internode on primary branch (cm)	0.863***	0.354***	0.277***	0.051	0.021	0.226	0.092
Number of nodes on primary branch	15.220***	14.721***	3.465***	0.514	1.016	2.942	0.345
Number of fruits per plant	439.146***	457.239***	94.572***	6.168	32.219	88.404	0.364
Days from transplanting to maturity	99.115***	52.485***	29.797***	1.545	3.638	28.252	0.129
Fruit length (cm)	6.087***	9.456***	0.791***	0.170	0.663	0.621	1.067
Single fruit weight (g)	0.264***	0.282***	0.056***	0.013	0.019	0.043	0.442
Canopy diameter (cm)	148.199***	161.018***	30.797***	5.93	11.078	24.867	0.445
Dry fruit yield per plant (g)	1269.330***	431.595***	421.696***	47.197	27.457	374.5	0.073

*** = *Significant at* $P < 0.001$; V_A = *Additive variance;* V_D = *Dominante variance;* σ_g^2 = *Variance component due to GCA;* σ_s^2 = *Variance component due to SCA;* $\sigma_e^2 = V_e$ = *Environmental variante; figures in [arenthesis = Degrees of freedom.*

Table 3. Estimates of general combining ability (GCA) effects and standard errors (SE) along with the corresponding *per se* performance (indicated in parenthesis) for 13 traits of 12 parental lines of hot pepper genotypes at Melkasa in 2004/2005.

Serial code	GCA effects along with the corresponding *per se* performance for 13 traits [b]												
of parents [a]	B/P	PH	SD	NN/S	LI/S	LI/B	NN/B	F/P	DM	FL	FW	CD	FY/P
P1	0.04	10.21*	0.06*	0.48*	-0.13*	0.02 (3.48)	2.10*	-3.38*	0.89*	1.29*	-0.01	0.78	-5.07* (60.85)
	(6.44)	(62.07)	(1.30)	(15.17)	(1.34)		(18.17)	(40.95)	(90.00)	(12.32)	(1.49)	(47.93)	
P2	0.88*	-6.26*	0.00	-0.04	-0.06	-0.32	0.45*	3.49*	1.10*	-0.87*	-0.15*	-1.73*	-1.23 (46.36)
	(7.16)	(34.33)	(1.33)	(11.67)	(1.36)	(2.80)*	(14.50)	(51.83)	(87.00)	(9.15)	(0.90)	(42.00)	
P3	0.84*	-1.33	0.06*	0.22	-0.06	0.07 (2.71)	-0.10	15.80*	1.10*	-0.13	-0.20*	1.15	12.19* (87.08)
	(5.03)	(42.13)	(1.03)	(13.83)	(1.45)		(10.83)	79.00)	(91.67)	(9.29)	(1.10)	(45.90)	
P4	-0.21	-4.01*	-0.07*	-0.85*	-0.14*	-0.01	-1.17*	-5.65*	2.18*	0.01	0.04	-0.25	-7.75* (36.11)
	(3.83)	(32.00)	(0.90)	(9.67)	(1.19)	(3.57)	(7.83)	(23.63)	(91.67)	(9.52)	(1.52)	(48.27)	
P5	0.23	-4.81*	-0.01	-1.01*	0.06	-0.21*	-0.88*	-1.85*	-1.73*	0.06	-0.06	-1.02	-4.50* (54.52)
	(3.97)	(36.17)	(1.06)	(9.83)	(1.89)	(2.59)	(8.17)	(32.00)	(93.00)	(9.81)	(1.70)	(49.67)	
P6	-0.42*	-6.22*	-0.02	-0.81*	-0.06	-0.15*	-1.28*	-0.16	-2.14*	0.04	-0.01	-7.49*	1.78
	(3.56)	(33.00)	(1.05)	(8.67)	(1.83)	(2.39)	(9.00)	(34.67)	(88.33)	(10.37)	(1.36)	(30.00)	(47.06)
P7	-0.22	-1.28	0.06*	1.06*	0.07	-0.06	-0.49*	1.02	1.84*	-1.86*	-0.03	-2.15*	0.74
	(4.39)	(37.67)	(1.18)	(12.67)	(1.53)	(3.00)	(10.83)	(46.93)	(93.00)	(6.35)	(1.59)	(44.27)	(74.35)
P8	-0.44*	-3.56*	-0.06*	-0.51*	-0.12*	0.21* (3.53)	-1.00*	-2.78*	-1.11*	0.82*	0.10*	2.61*	0.76
	(4.40)	(31.63)	(0.99)	(10.50)	(1.48)		(10.83)	(35.93)	(88.67)	(11.45)	(1.80)	(49.30)	(64.94)
P9	0.08	6.25*	-0.02	-0.82*	0.15*	0.11	0.99*	1.23	-3.18*	-0.18	-0.07*	3.67*	-1.39 (68.23)
	(4.83)	(53.73)	(0.98)	(8.83)	(2.01)	(4.19)	(10.83)	(42.60)	(90.00)	(9.68)	(1.61)	(53.77)	
P10	-0.47*	2.99*	0.04	-0.25	0.24*	0.04	0.92*	-1.96*	-1.40*	-0.23*	0.24*	3.51*	6.63* (77.66)
	(3.00)	(56.67)	(1.25)	(8.50)	(2.30)	(3.59)	(14.67)	(34.13)	(83.33)	(9.16)	(2.29)	(55.27)	
P11	0.53*	2.86*	0.01	2.39*	-0.04	0.16* (4.95)	0.18	0.26	2.96*	0.19	-0.12*	-3.19*	-4.99* (40.60)
	(7.75)	(48.60)	(0.91)	(16.00)	(1.54)		(8.33)	(30.73)	(93.00)	(9.33)	(1.33)	(40.13)	
P12	-0.84*	5.11*	-0.04*	0.14	0.10*	0.13* (4.32)	0.27	-6.03*	-0.52	0.86*	0.26*	4.12*	2.82
	(4.28)	(58.00)	(1.10)	(10.00)	(1.82)		(11.17)	(37.33)	(83.33)	(11.06)	(2.01)	(59.07)	(75.63)
SE[gi]	0.15	0.82	0.02	0.22	0.04	0.06	0.18	0.64	0.32	0.11	0.03	0.62	1.76
SE[gi-gj]	0.23	1.21	0.03	0.33	0.06	0.09	0.27	0.94	0.47	0.16	0.05	0.92	2.60

* = *Significant at* $P < 0.05$; [a]*P1 = PBC 972; P2 = PBC 602; P3 = PBC 223; P4 = ICPN10#5; P5 = ICPN10#6; P6 = ICPN9#16; P7 = PBC 731; P8 = PBC 535; P9 = PBC 580; P10 = 'Marekofana; P11 = 'Bakolocal; P12 = 'Marekoshote;* [b]*B/P = Nnumber of branches per plant; PH = Plant height; SD = Stem diameter; NN/S = Number of nodes on main stem; LI/S = Length of internode on main stem; LI/B = Length of internode on primary branch; NN/B = Number of nodes on primary branch; F/P = Number of fruits per plant; DM = Days to maturity; FL= Fruit length; FW = Single fruit weight; CD = Canopy diameter; FY/P = Dry fruit yield per plant.*

Table 4. Significant desirable SCA effects of the top 5 progenies of 78 genotypes (12 parental selfs and 66 F_1s) along with *per se* performances and the proportion (%) of progenies with significant desirable SCA effects in each of the three groups and standard error of mean for 13 traits in crosses of Asian (A) and Ethiopian (E) genotypes of hot pepper grown at Melkasa in 2004/2005.

Trait[b]	Five top (selfs and F_1s)[a]		Proportion (%) of progenies with significant desirable SCA effects (%)				Standard error of mean	
	Significant and desirable SCA effects	*Per se* performance	Selfs (12)	E x E (3 F_1s)	E x A (27 F_1s)	A x A (36 F_1s)	s_{ii}	s_{ij}
B/P	P3XP10 (2.80), P11xP11 (2.02), P2XP7 (1.74), P5XP9 (1.63), P1xP1 (1.70)	P3XP10 (7.83), P11xP11 (7.75), P2xP2 (7.16),), P2XP7 (7.06), P3XP5 (6.67)	25.0	0.0	7.4	5.6	0.6	0.5
PH	P9XP12 (8.76), P4XP7 (8.38), P6XP11(7.95), P7XP8 (7.36), P5XP9 (7.22)	P1xP1 (62.07), P9XP12 (60.8), P1XP11 (60), P12xP12 (58), P1XP12 (57.33)	25.0	33.3	11.1	16.7	3.0	2.7
SD	P3XP10 (0.40), P2xP2 (0.22), P4XP10 (0.19), P6XP8 (0.14), P11xP12 (0.14)	P3XP10 (1.6), P2xP2 (1.33), P1xP1 (1.30), P5XP7 (1.28), P2XP7 (1.28)	8.3	33.3	7.4	5.6	0.1	0.1
NN/S	P1xP1 (4.17), P3xP3 (3.36), P11xP12 (3.27), P3XP4 (2.10), P5xP5 (1.82)	P11xP11 (16), P11xP12 (15.83), P3xP3 (13.83), P1xP1 (15.17), P1XP11 (14)	41.7	66.7	3.7	2.8	0.8	0.7
LI/S	P2XP4 (0.58), P3XP7 (0.58), P8XP11 (0.51), P3XP9 (0.47), P3XP9 (0.47)	P5XP10 (2.93), P3XP7 (2.33), P3XP9 (2.3), P10xP10 (2.3), P7XP11 (2.28)	0.0	0.0	22.2	16.7	0.1	0.1
LI/B	P11xP11 (1.30), P3XP7 (1.26), P5XP6 (1.25), P2XP4 (1.21), P7XP8 (0.91)	P11xP11 (4.95), P3XP7 (4.59), P7XP8 (4.38), P12xP12 (4.32), P2XP4 (4.21)	41.7	33.3	22.2	41.7	0.2	0.1
NN/B	P6XP11 (3.18), P5XP9 (3.12), P1XP3 (2.90), P7XP9 (2.74), P4XP11 (2.73)	P1xP1 (18.17), P1XP3 (17), P9XP12 (16), P1XP2 (15.67), P7XP9 (15.33)	16.7	0.0	29.6	27.8	0.7	0.6
F/P	P4XP11 (9.95), P6XP11 (9.93), P2XP7 (9.85), P3XP11 (8.87), P5XP7 (8.53)	P3XP12 (80.67) P3XP10 (79.67), P3xP3 (79), P3XP4 (75.73), P3XP11 (75.57)	0.0	0.0	48.1	25.0	2.3	2.1
DM	P8XP10 (-9.330), P5XP6 (-17.64), P2XP7 (-15.12), P8XP9 (-12.88), P3XP9 (-10.09)	P2XP7 (73), P6XP12 (73), P3XP9 (73), P5XP6 (63.67), P8XP9 (68)	0.0	0.0	29.6	25.0	1.2	1.1
FL	P9XP12 (1.69), P6XP8 (1.13), P1XP2 (1.07), P10XP12 (0.96), P4XP9 (0.96)	P1XP12 (13.86), P8XP12 (13.36), P9XP12 (13.3), P1XP5 (12.97), P6XP8 (12.94)	0.0	33.3	40.7	19.4	0.4	0.4
FW	P2XP11 (0.57), P5XP10 (0.41), P4XP12 (0.38), P7XP12 (0.34), P2XP6 (0.33)	P4XP12 (2.32), P8XP12 (2.31), P10xP10 (2.29), P8XP10 (2.28), P5XP10 (2.24)	0.0	0.0	29.6	16.7	0.1	0.1
CD	P9XP12 (9.12), P5XP6 (8.99), P4XP7 (8.58), P3XP7 (8.21), P3XP8 (7.66)	P9XP12 (67), P1XP10 (65.53), P9XP10 (63.38), P3XP8 (61.5), P1XP12 (61.4)	0.0	0.0	37.6	22.2	2.3	2.1
FY/P	P3XP12 (52.00), P5XP10 (33.82), P9XP12 (33.35), P5XP6 (31.84), P7XP12 (26.05)	P3XP12 (149.15), P2XP6 (123.2), P5XP10 (118.31), P9XP12 (117.12), P8XP10	0.0	0.0	51.9	13.9	6.4	5.9

[a] *P1 = PBC 972; P2 = PBC 602; P3 = PBC 223; P4 = ICPN10#5; P5 = ICPN10#6; P6 = ICPN9#16; P7 = PBC 731; P8 = PBC 535; P9 = PBC 580; P10 = 'Marekofana; P11 = 'Bakolocal; P12 = 'Marekoshote;* [b] *B/P = Nnumber of branches per plant; PH = Plant height; SD = Stem diameter; NN/S = Number of nodes on main stem; LI/S = Length of internode on main stem; LI/B = Length of internode on primary branch; NN/B = Number of nodes on primary branch; F/P = Number of fruits per plant; DM = Days to maturity; FL= Fruit length; FW = Single fruit weight; CD = Canopy diameter; FY/P = Dry fruit yield per plant.*

4. Discussion

Since the parental lines were deliberately selected for specific breeding objectives, combining ability and types of gene action for dry fruit yield per plant and related traits were studied using Griffing's (1956) combining ability analysis, Methods 2 in fixed effect. The highly significant mean squares for both GCA and SCA effects for all the traits suggested existence of large amounts of variability among the genotypes for both additive and non-additive gene actions that might be involved in the expression and inheritance of the traits studied. However, SCA variances (σ_s^2) were larger than the corresponding GCA variances (σ_g^2), i.e. σ_g^2/σ_s^2 ratio less than unity for all the traits except for plant height and fruit length, suggesting that non-additive gene action has been a more important source of variation for all the traits than the additive gene action.

As reported by Melchinger *et al.* (1987), the ratio of variances due to general combining ability to specific combining ability (σ_g^2/σ_s^2) is of central importance for predicting hybrid performance. However, more effective and superior hybrids can be identified and selected mainly on the basis of their SCA effects (Reif *et al.*, 2007). Thus, it could be predicted that the non-additive variance (SCA) might dominate the expression of the majority of the studied traits whereas the additive variance (GCA) might have played more significant roles for expression of both plant height and fruit length. Falconer (1989) defined GCA as the average performance of the progeny of an individual resulting from its mating with a number of other individuals in the population and recognized primarily as a measure of additive gene action. A positive GCA could be an indicator of a genotype that produces above-average progeny, whereas a genotype with a negative GCA could produce progeny that performs below average.

ICPN9#16, PBC 731, PBC 535 and 'Marekofana' parents, which exhibited desirable additive gene actions both for earliness and dry fruit yield per plant, suggested the possibility of simultaneous selection for earliness and high dry fruit yield per plant. Furthermore, the Asian parent PBC 223 and the Ethiopian parent 'Marekofana' showed significant GCA effects for dry fruit yield per plant and some of its related traits. Genotypes that showed good GCA for many desirable traits may be more useful for the simultaneous improvement of multiple traits. Good general combiners have multiple advantages in that they often have high probabilities of good SCAs, allow for the development of synthetic varieties, and are ideal choices as parents in a hybrid program (Welsh 1981). In addition, it is evident from the present study that the parents with good general combining ability possessed high mean values (Table 4). It is also important to note that there appeared to be good relationships between mean performance of parent *per se* and its GCA effect. For example, parents PBC 223, 'Marekofana' and 'Marekoshote' that were the top mean performers for dry fruit yield per plant and earliness also had high GCA effects for the same traits. This revealed that combining ability can be judged to some extent by *per se* performance in hot pepper especially for traits such as dry fruit yield per plant, number of fruits per plant and earliness. The results of the present study indicated that it is important to consider both GCA effects as well as *per se* performances in the improvement program to achieve the desired results. This is in agreement with the observations of Shrivastava and Seshu (1983) and others who reported similar relationships in different crops. Therefore, mean *per se* performance of parents may, to some extent, serve as predictors of GCA of parents in hot pepper. In a systematic breeding program, GCA of the parents is obviously important (Kalloo, 1988).

The hybrids with the highest SCA effects were observed resulting from any possible combination of parents having negative and positive GCA effects (Tables 3 and 4). Therefore, when the breeding interest is to develop synthetic varieties, good general combiners could be very useful. However, when the breeding interest is to develop superior specific hybrids, it may be more effective to search among all possible crosses between elite genotypes, including both good (positive) and poor (negative) general combiners. In view of the above results, due attention must be paid when selecting or rejecting parents in hot pepper breeding programs.

Crosses from Asian x Ethiopian group produced a higher proportion of hybrids with the highest SCA effects with respect to most of the studied traits, suggesting the importance of genetic diversity to obtain superior hybrids. High estimated values for variance of SCA for early and total fruit yield, fruit number per plant and fruit weight were also reported in crosses of homozygous varieties of *Capsicum annuum* (Khalf-Allah *et al.*, 1975). These authors indicated that the inheritances of these four traits are governed by a relatively high degree of non-additive gene action. High estimates of SCA were reported by Sharma and Saini (1977) for fruit yield and plant height in *Capsicum* pepper.

The recorded high SCA effects (s_{ii}) of parental selfs (PBC 972, PBC 602, PBC 223, ICPN10#5 and 'Bakolocal') were good indicators regarding their potential to improve dry fruit yield and related morphological traits in hybrid breeding programs. According to Cruz and Vencovsky (1989), the SCA of a parent with itself (s_{ii}) has great genetic significance and indicates the existence of unidirectional dominance. Negative s_{ii} values indicate that the deviations are predominantly positive and positive s_{ii} values indicate the *vice-versa* (Franco *et al.*, 2001). According to these investigators, the magnitude of s_{ii} is an indicator of varietal heterosis and their additive values express the mean values of such heterosis.

5. Conclusions

Inheritance of the majority of the studied traits appeared to be governed both by additive and non-additive genes. Crosses PBC 223 x 'Marekoshote', ICPN10#5 x 'Marekofana', PBC 580 x 'Marekoshote', ICPN10#6 x ICPN9#16 and PBC 731 x 'Marekoshote' exhibited maximum dry fruit yield per plant and, thus, can be promoted for commercial exploitation of hybrids for higher dry fruit yield in Ethiopia. There seems to be an opportunity to exploit some specific crosses such as ICPN10#6 x ICPN9#16 for earliness and enhanced dry fruit yield as it expressed significant and negative SCA effect coupled with minimum mean value for days to maturity and significant SCA effect for dry fruit yield per plant. However, there is a need to take great care in selecting or rejecting hot pepper parents in breeding programs based on general combining ability as superior specific hybrid could be obtained both from good (positive) and poor (negative) general combiners. An efficient breeding plan for the crop could be based on extensive recurrent selection, progeny tests and cross-breeding using genetically diverse hot pepper genotypes. This study, therefore, revealed a considerable amount of genetic information that can be utilized in hot pepper improvement programs.

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