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Combining Ability for Field Resistance to Disease, Fruit Yield and Yield Factors among Hot Pepper (*Capsicum annuum* L.) Genotypes in Uganda

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ABSTRACT

Productivity and quality of hot pepper in Uganda are low, mainly due to lack of superior cultivars. As a step towards cultivar improvement three exotic and three local hot pepper genotypes with varying genetic backgrounds were crossed in a half diallel to determine the combining ability of parents and crosses, and the gene effects of important disease, yield and related traits. The general (GCA) and specific (SCA) combining abilities were significant for most traits indicating the role of both additive and non-additive gene effects in the expression of most traits. Days to 50% flowering and fruit maturity, number of fruit per plant, number of seeds per fruit, primary branch numbers, plant width and height were predominantly controlled by non-additive gene action while fruit length, fruit width, secondary branch numbers, stem diameter, stem height were predominantly controlled by additive gene effects. Pedicel length seemed to be controlled by both additive and non-additive gene actions in equal proportions. Narrow sense heritability was low to moderate for most agro-morphological traits and for all disease incidences (16.1-46.1) and was moderate to high (43.4-98.5) for all agro-morphological traits and disease incidences. The exotic genotype PP9852-115, local genotypes CA-UGKI 09-4, CA-UGKI 09-6 and CA-UGCE 09-3 were good combiners for most traits. The Exotic genotype PP0537-7504 was a significant general combiner for reducing wilt disease incidence. Hybrids CA-UGCE 09-3xCA-UGKI 09-6, CA-UGKI 09-6xPP9852-115 and CA-UGCE 09-3xPP0337-7562 had the best SCA effects among all crosses for measured traits. For disease traits, hybrids CA-UGCE 09-3xPP9852-115 and CA-UGKI 09-6xPP9852-115 were the best for *Cercospora* leaf spot resistance while hybrid PP9852-115xPP0537-7504 was the best for virus resistance. The outstanding hybrids for various traits could be used to derive superior recombinant inbred lines for respective traits through transgressive segregation.

Keywords: disease resistance, additive and non-additive gene effects; half-diallel mating; heterosis

INTRODUCTION

Peppers (*Capsicum* spp.) are cultivated globally for their medicinal, nutritional and ornamental uses (Perucka and Materska 2001; Manjunatha and Srinivasan 2007; Bosland and Votava 2012). Five species namely, *Capsicum annuum* (Linnaeus), *Capsicum baccatum* (Linnaeus), *Capsicum chinense* (Jacquin), *Capsicum frutescens* (Linnaeus) and *Capsicum pubescens* (Ruiz & Pavon) have been domesticated and are widely cultivated (McMullan and Livsey 2007; Bosland and Votava 2012). In Uganda, the expansion of hot pepper production from subsistence to commercial scales occurred in the late 1990s specifically targeting the export market (Tusiime *et al.* 2010). However, production is still relatively low at 3700 t in 2010 compared to 142266 t, average for the 20 top producing countries (FAO 2012) and is characterized by poor quality partly due to lack of improved cultivars for disease resistance, fruit yield and associated traits.

Cultivar improvement for yield, fruit quality, biotic and abiotic stress resistance and other agronomic and market traits is essential. Cultivar improvement requires availability of genetic resources that could act as sources of genes conferring the desired traits that could be introgressed into the present cultivars (Lynch and Walsh 1998; Sitaresmi *et al.* 2010). Gene introgression could be achieved through combination of desired traits into target genotypes either using recombination breeding (open pollinated cultivars) or through exploitation of heterosis (hybrid varieties) under local conditions. Hybridization (cross-breeding) is essential to the generation of genetic diversity, heterosis and fixing genes in the progeny (Marame *et al.* 2009a; Zečević *et al.* 2011). This, however, involves a lengthy and costly process of identifying and combining superior inbred parents into superior hybrids and inbred lines (Rêgo *et al.* 2009).

Diallele crossing, which involves crossing parents in all possible combinations to generate hybrids (Griffing 1956), is useful in providing precise information about heritability, types of gene action involved in the expression of traits and in predicting the performance of progeny in latter segregating generations (Marame *et al.* 2008; Syukur *et al.* 2010). The study of parental general and specific combining ability could reveal the nature of gene action in the expression of traits and identify superior crosses from parental combinations. Therefore, the knowledge of combining ability of parents and crosses and the gene effects of various traits is necessary for the development of a hot pepper improvement programme in Uganda. Such studies provide a guideline for selecting elite parents or combiners which may later be hybridized either to exploit heterosis or to

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accumulate fixable genes through selection (Ahmed *et al.* 2003; Marame *et al.* 2008). Combining ability can be general (GCA) or specific (SCA), with GCA being a measure of additive gene action while SCA is due to non-additive (dominant or epistatic) gene action.

Studies on combining ability and genetic control of agro-morphological traits have been conducted in various *Capsicum* peppers elsewhere including sweet pepper (*Capsicum annuum*) (Marchesan *et al.* 2009; May *et al.* 2010) and chilli peppers (Reddy *et al.* 2008; Marame *et al.* 2009a; Sitaresmi *et al.* 2010; Syukur *et al.* 2010; Rodrigues *et al.* 2012). These studies reported both GCA and SCA for most traits, with GCA effects dominating in most traits. In addition, broad and narrow sense heritabilities were generally high for all traits (Marame *et al.* 2009a; Syukur *et al.* 2010). However, literature on gene action through combining ability for disease resistance in *Capsicum* species is scanty. Marchesan *et al.* (2009) reported significant GCA (additive) and SCA (non-additive) genetic effects involved in powdery mildew resistance in sweet pepper. In crops such as beans (Nkalubo *et al.* 2009), wheat (Bastam *et al.* 2010; Khorzoght *et al.* 2010), sweetpotato (Mwanga *et al.* 2002), potato (Osiru *et al.* 2001) and soybean (Kiryowa *et al.* 2009) both GCA and SCA were significant in the control of disease resistance although GCA variance components dominated. Broad and narrow sense heritabilities were found to be generally high (Mwanga *et al.* 2002; Bonos 2006; Kiryowa *et al.* 2009).

Approaches other than combining ability including quantitative trait loci (QTL) and Hayman diallel analysis have been used to study gene action determining the inheritance of resistance to *Capsicum* diseases such as powdery mildew (Blat *et al.* 2005a, 2005b, 2006), bacterial spot (Riva *et al.* 2004), bacterial wilt (Lafortune *et al.* 2005; Tran and Kim 2010) and viruses (Caranta *et al.* 1997a, 1997b). Non-additive gene action were reported to be more predominant for *Phytophthora* blight (Lefebvre *et al.* 1996; Yunianti *et al.* 2011), powdery mildew (Blat *et al.* 2005a, 2005b, 2006), bacterial spot (Riva *et al.* 2004) while additive gene effects were more predominant for powdery mildew (Marchesan *et al.* 2009), bacterial wilt (Lafortune *et al.* 2005; Tran and Kim 2010) and viruses (Caranta *et al* 1997a, 1997a). Moderately low to high broad sense heritabilities were also reported in chilli for powdery mildew (Blat *et al.* 2005a, 2006; Yunianti *et al.* 2011) and bacterial spot (Poulos *et al.* 1991; Scott *et al.* 2003; Riva *et al.* 2004). Since QTL and Hayman analyses do not give information on combining ability of parents which is needed to initiate a breeding program that is lacking in Uganda, combining ability studies were used in this research to identify the gene action governing inheritance of various traits among hot pepper genotypes and identify good parent combiners for improved disease resistance, yield and its components.

MATERIALS AND METHODS

Genotype mating design, procedures for hybridization and generation of F_1 hybrids

Six genotypes form diverse backgrounds with contrasting traits (**Table 1**) were crossed in a half diallel in a screen house at National Agricultural Research Laboratories Institute (NARL), Kawanda from August 2009-April 2010. Controlled hybridization was performed. Hand emasculation was done a day before the flowers opened. Pollen grains were collected from male parents between 7 am and 10 am using Eppendorf tubes and the pollination done immediately by rubbing pollen grains on to the stigma of the receptive flower. The pollinated flowers were then covered with a white cloth bag made from fine-net for 2 days. At full physiological maturity when fruits acquired their expected maturity colour (red or orange), the F_1 ripe fruits were picked and cured for 2-3 days. The crossing block during the dry season was heavily infested by mites and resulted into failure of two crosses (PP9852-115xPP0337-7562 and CA-UGKI 09-4xCA-UGCE 09-3) out of the expected 15 crosses (**Table 2**). Seed from mature fruits of 13 successful crosses were extracted and propagated to raise progeny of the F_1 hybrids (Geleta *et al.* 2004; Shankarappa *et al.* 2008).

Evaluation of parentals and hybrids

Seedlings were raised in the screen house at NARL from April-May 2010 in 5-litre plastic buckets using a field soil-sand-cow dung mixture (in the ratio 3:1:1) that had been steam-sterilized. Seedlings were sprayed with Ridomil (Syngenta Crop Protection AG, Basle, Switzerland) [(Metalaxyl-M 40 g/kg + Mancozeb 640 g/kg active ingredient (ai)], at the rate 60 g/15 l to control fungal infections and two pesticides: Tafgor (Rallis India Ltd, Mumbai, India) 40 EC (Dimethoate 40% EC ai, at the rate 30 ml/15 l) and Alfapor spray and dip (Alfasan International BV, Ja Woerden-Holland) (50 mg/ml alpha-cypermethrin EC, at the rate 15 ml/15 l) interchangeably twice a week for three weeks to protect against insect pests and mites, and to eliminate potential vectors that transmit viruses. Six-week old seedlings were transplanted into fine seedbeds at the National Crops Resources Research Institute (NaCRRI) located at 0°32'N and 32°7'E of the equator and stands at an elevation of 1150 m a.s.l. The soils are ferralitic (red sandy clay loams) and have a pH range of 4.9-5.0. The average annual rainfall is 1,270 mm and that of temperature is 22.2°C with mean minimum and maximum temperatures of 16°C and 28°C, respectively. The transplants were evaluated from May-October, 2010 in a 5 × 4 alpha lattice design with two replications, each of which contained 5 incomplete blocks with 4 plots totalling 20 experimental plots. The 19 entries (6 parents and 13 crosses) were randomly assigned to the experimental plots with a non-experimental hot pepper variety included to fill the vacant experimental plot. The experimental plots were made up of raised beds, 1 m × 3.6 m in size, with one row of plants at a spacing of 0.6 m × 0.45 m between and within rows, respectively. Two fertilizers; NPK (20:10:10) and urea (100 kgN/ha) were used in two splits and three splits respectively. NPK was applied at 200 kg/ha two weeks after transplanting and three weeks after the first application. Urea was applied at the rate of 30 kg/ha two weeks after transplanting and three weeks after the first application and 40 kg/ha after the second application. Transplants were protected for 5 weeks as described above to allow proper seedling establishment and then allowed for natural disease infection. Weeds were routinely removed from the trial to avoid competition for nutrients with plants.

Data collection and analyses

Data were recorded on 13 following agronomic traits: days to flowering, days to fruit maturity, plant height (cm), plant width (cm), fruit length (cm), fruit width (cm), pedicel length (cm), number of seeds per fruit, stem height at first bifurcation (cm), stem diameter (cm), primary branch numbers, secondary branch numbers, and number of fruits per plant. Plants were monitored for the occurrence of diseases under natural epiphytotics of four major diseases that occurred: bacterial spot, *Cercospora* leaf spot, viral and wilt diseases and their incidence calculated as the proportion of infected plants per plot expressed as a percentage (Galanihe *et al.* 2004).

General and specific combining abilities were analysed according to the Griffing (1956) fixed effect model I method II (with parents and one set of crosses excluding reciprocals) to estimate SCA and GCA effects for the hybrids and parents, respectively as:

$$Y_{ijk} = \mu + G_i + G_j + S_{ij} + E_{ijk:}$$

where: μ = general means effect; Yij is the mean (performance) of the cross between i^{th} female parent and j^{th} male parent over; G_i is the general combining ability (GCA) effect of the i^{th} female parent; G_j is the general combining ability (GCA) effect of the j^{th} male parent; S_{ij} is the specific combining ability (SCA) effect of the cross between i^{th} female genotype and j^{th} male genotype and E_{ij} is the experimental error effect. The GCA effects were estimated using the weighted parental means in order to adjust for missing crosses. Baker's ratio based on variances of both GCA and SCA was used to reveal the relative importance of GCA and SCA effects in the studied traits:

Table 1 Some attributes of six selected hot pepper genotypes for hybridisation recorded at Namulonge, Uganda, April-October 2010).

Genotype code	Name	Source	Fruit traits				
			Mature colour	**Length (cm)**	**Width (cm)**	**Position**	**Shape**
18	PP0337-7562	AVRDC, Taiwan	Red	14.0	2.0	Pendant	Elongate
25	PP0537-7504	AVRDC, Taiwan	Red	8.8	1.2	Intermediate	Elongate
28	PP9852-115	AVRDC-RCA, Tanzania	Red	14.7	1.9	Erect	Elongate
29	CA-UGKI 09-6[a]	Kisoro, Uganda	Orange	3.2	2.0	Erect	Triangular
31	CA-UGCE 09-3[b]	Wakiso, Uganda	Red	4.7	1.0	Erect	Elongate
35	CA-UGKI 09-4	Kisoro, Uganda	Orange	2.8	1.2	Pendant	Triangular

SED fruit length = 1.31; SED fruit width = 0.15

AVRDC-RCA = Asian Vegetable Research and Development Center, RCA = Regional Center for Africa.

[a] Local genotypes were designated names based on the place of origin with prefixes "CA" = *Capsicum annuum*, "UGCE" = Central, Uganda, "UGKI" = Kisoro, Uganda, year of collection and accession number.

[b] Local commercial variety

Table 2 Diallel of F_1 progeny and selfed hot pepper parents evaluated for 13 agronomic and 4 disease traits at Namulonge, Uganda from May-October 2010.

	Parental genotypes[d]	♀					
		18	**25**	**28**	**29**	**31**	**35**
	18	**18**					
	25	25x18	**25**[c]				
♂	28	M[a]	28x25	**28**			
	29	29x18	29x25	29x28	**29**		
	31	31x18	31x25[b]	31x28	31x29	**31**	
	35	35x18	35x25	35x28	35x29	M[a]	**35**

[a] Missing crosses

[b] This cross was susceptible to most diseases and gave no yield. It was scored for diseases and not quantitative traits.

[c] Bold figures are selfed parents

[d] For genotype accession codes and other details, please refer to **Table 1**

$$X = [2\sigma^2gca/(2\sigma^2gca+\sigma^2sca)]$$

where the ratio far below unity ($X<0.5$) implies predominance of non-additive gene action and predominance of additive gene action when it is far above ($X>0.5$) (Baker 1978).

The coefficient of genetic determination in the narrow sense (CGD-ns), which is the fixed parent equivalent of heritability in the narrow sense and the coefficient of genetic determination in the broad sense (CGD-bs), were estimated as follows (Falconer 1963; Adefris and Heiko 2005; P Gibson 2010, pers. comm.):

$$\text{CGD-ns: } [2\sigma^2gca/(2\sigma^2gca+\sigma^2sca+\sigma^2e)] * 100 \approx h^2$$

$$\text{CGD-bs: } [(2\sigma^2gca+\sigma^2sca)/(2\sigma^2gca+\sigma^2sca+\sigma^2e)]* 100 \approx H$$

where σ^2gca = Variance component of GCA, σ^2sca = Variance component of SCA, σ^2e = Error variance, h^2 = Narrow sense heritability, H = Broad sense heritability.

RESULTS

Specific and general combining abilities for measured trait

For all the traits studied, the mean square (MS) values of general combining ability (GCA) were significant except for wilt disease (**Table 3**). Similarly, the MS for specific combining ability (SCA) were significant for majority of the studied traits except fruit width, plant height, and stem height, stem diameter and wilt disease. The MS for GCA were always higher than those of SCA except for bacterial spot. To understand the relative importance of the general and specific combining abilities for studied parameters, estimates of components of GCA and SCA that approximate their variances were calculated according to Baker's ratio (Baker 1978). From this ratio, majority of the quantitative agronomic traits were far from unity except for secondary branch numbers (0.6), stem diameter (0.69), fruit length (0.85) and fruit width (0.91), stem diameter (0.8), virus incidence (%) (0.59) and wilt disease (%) (0.57) (**Table 3**).

Narrow sense heritability was low and inconsistent for most agro-morphological traits (21.3-35.4), moderate for fruit width, pedicel length, secondary branch numbers, stem diameter, stem height and high (83.3) for fruit length while broad sense heritability was high for all traits (69.8-98.5) and moderate (44.9-53.9) for plant width and stem height (**Table 3**). This inconsistency can be demonstrated for example, in traits such as days to flowering that had low h^2ns (24.4) compared to very high h^2bs (92.6) and secondary branch numbers had medium h^2ns (24.4) compared to very high h^2bs (92.6). Fruit width, stem diameter and stem height had consistently high narrow and broad sense heritabilities. This was the same trend for disease traits (**Table 3**). Inconsistency was shown in bacterial spot with very low h^2ns (16.1) but very high h^2bs (85.7).

General combining ability for measured traits

For all the studied traits, the parents exhibited significant and non-significant positive and negative GCA effects (**Table 4**). Parents PP9852-115, CA-UGCE 09-3 and PP0537-7504 significantly exhibited higher positive GCA effects for days to flowering respectively, with -3.28, -3.17 and -2.62. Only parent CA-UGKI 09-6 showed highly significant and positive GCA effect (6.36). With days to fruit maturity, significant negative GCA effects were shown by parents PP9852-115 (-5.45), and CA-UGCE 09-3 (-2.85) while significant positive effects were displayed by parents CA-UGKI 09-6 (5.41) and CA-UGKI 09-4 (5.96). All parents significantly showed high GCA effects for fruit length (**Table 4**). Negative effects were contributed by parents CA-UGKI 09-6 (-1.80), CA-UGCE 09-3 (-1.05), CA-UGKI 09-4 (-1.99) while parents PP0337-7562, PP0537-7504 and PP9852-115 contributed significantly positively with 1.91, 0.47 and 2.59 GCA effects, respectively. The high significant negative GCA effects for fruit width were displayed by parents PP9852-115 (-0.27) and CA-UGKI 09-4 (-0.32). The high significant positive GCA effects were contributed by only parent PP0337-7562 (0.79).

Parents CA-UGKI 09-6 (9.16) and CA-UGKI 09-4 (5.67) highly significantly showed positive GCA effects for number of fruit per plant whereas parents PP0337-7562 (-12.44) and PP9852-115 (-7.29) significantly showed high negative GCA effects. For number of seeds per fruit, significant high negative GCA effects were shown by parents CA-UGCE 09-3 (-13.57) and CA-UGKI 09-4 (-3.13) while three parents showed significant positive GCA effects with parents PP9852-115 and CA-UGKI 09-6 exhibiting the highest with 4.36 and 7.61 effects, respectively.

The most significant negative GCA effects for primary

Table 3 Mean squares, components of variance and heritability for combining ability for disease and quantitative traits in hot pepper evaluated at Namulonge, Uganda from May-October 2010.

Trait	**gca MS**	**sca MS**	**Error MS**	**σ^2 gca**	**σ^2 sca**	**Baker's Ratio**	**CGD-ns (h^2ns)[a]**	**CGD-bs (h^2bs)[b]**
Days to flowering	99.07***	87.40***	8.560	14.142	78.840	0.26	24.4	92.6
Days to fruit maturity	159.84***	92.69***	11.920	23.113	80.770	0.36	33.3	91.4
Fruit length (cm)	22.54***	1.41***	0.128	3.503	1.282	0.85	83.3	98.5
Fruit width (cm)	0.088*	0.024	0.026	0.010	0.002	0.91	41.1	44.9
Number of fruit per plant	467.4***	251.40***	26.490	68.892	224.910	0.38	35.4	93.2
Number of seeds per fruit	360.3***	314.70***	7.125	55.184	307.575	0.26	26.0	98.3
Primary branch numbers	4.40***	2.57***	0.325	0.636	2.245	0.36	33.1	91.5
Pedicel length	0.43**	0.15***	0.019	0.064	0.128	0.50	46.7	93.1
Plant height (cm)	44.28**	21.55	9.350	5.458	12.200	0.47	33.6	71.2
Plant width (cm)	56.03*	49.12**	13.555	6.637	35.565	0.27	21.3	78.3
Secondary branch numbers	26.96***	6.67*	1.336	4.004	5.334	0.60	54.6	90.9
Stem diameter	0.024**	0.01	0.004	0.003	0.003	0.69	48.4	69.8
Stem height	13.59*	4.18	3.397	1.592	0.782	0.80	43.2	53.9
Virus incidence (%)	1345.9***	399.70*	161.350	170.849	238.350	0.59	46.1	78.2
Cercospora leaf spot (%)	147.17**	78.28**	23.535	17.832	54.745	0.39	31.3	79.3
Wilt disease (%)	506.0	268.20	201.500	43.918	66.700	0.57	24.7	43.4
Bacterial spot (%)	549.3**	657.30***	111.950	63.079	545.350	0.18	16.1	85.7

gca = general combining ability, sca = specific combining ability, MS = mean square; *Significant at $P \leq 0.05$; ** highly significant at $P \leq 0.01$; *** highly significant at $P \leq 0.001$; the rest not significant.

[a]CGD-ns= Coefficient of genetic determination in the narrow sense which is analogous to heritability in the narrow sense (h^2ns)

[b]CGD-bs= Coefficient of genetic determination in the broad sense which is analogous to heritability in the broad sense (h^2bs)

Table 4 Estimates of general combining ability effects of parents for measured traits in a six half diallel cross of hot pepper grown at Namulonge, Uganda from May-October 2010.

TRAIT	**PARENT[a]**						**Mean**	**SE**
	18	**25**	**28**	**29**	**31**	**35**		
Days to flowering	1.44	-2.62*	-3.28**	6.36***	-3.17**	-0.32	-0.27	1.02
Days to fruit maturity	-3.50**	-0.74	-5.45***	5.41***	-2.85*	5.73***	-0.23	1.20
Fruit length (cm)	1.91***	0.47***	2.59***	-1.80***	-1.05***	-1.99***	0.02	0.12
Fruit width (cm)	0.79***	-0.07	-0.27***	-0.05	-0.09	-0.32***	-0.00	0.06
Number of fruit per plant	-12.44***	3.29	-7.29***	9.16***	0.12	5.67**	-0.25	0.74
Number of seeds per fruit	2.34*	-1.12	4.36***	7.61***	-13.57***	-3.13**	-0.59	0.93
Primary branch numbers	-0.87***	0.07	-1.23***	0.56**	0.53*	0.94***	-0.00	0.20
Pedicel length (cm)	0.47***	-0.01	-0.18**	-0.07	-0.11*	-0.10*	-0.00	0.05
Plant height (cm)	0.22	-1.01	-2.42*	2.00	-3.07**	3.46**	-0.14	1.07
Plant width (cm)	-2.74*	-0.30	-2.07	2.39	-1.94	3.93**	-0.12	1.28
Secondary branch numbers	-1.31**	0.29	-3.23***	1.32**	-0.02	2.73***	-0.04	0.40
Stem diameter (cm)	-0.07**	-0.03	-0.03	0.05*	-0.02	0.09***	-0.00	0.02
Stem height (cm)	-0.94	0.37	-2.56***	0.45	1.50*	1.36*	0.03	0.64
Virus incidence (%)	5.89	11.82**	-13.67**	7.33	-19.90***	7.30	-0.20	4.31
Cercospora leaf spot (%)	3.53*	1.95	2.93	-0.58	1.06	-8.81***	-0.02	1.65
Wilt disease (%)	12.08*	-12.70*	5.12	2.37	-4.28	-3.01	-0.07	4.83
Bacterial spot (%)	-2.79	3.21	-13.36**	-4.30	7.44	13.28**	0.58	3.59

*Significant at $P \leq 0.05$; ** highly significant at $P \leq 0.01$; *** highly significant at $P \leq 0.00$; the rest not significant; SE= standard error = (1/h)*(p-1)/ (p (p+2))*EMS; h = proportion of total number of parental combinations (crosses) present with inclusion of parents; p= number of parents; EMS= Error mean square.

[a]For parental accession codes and other details, please refer to **Table 1**

and secondary branch numbers were contributed by parents PP0337-7562 and PP9852-115 with their respective GCA effects of -0.87 and -1.23 for primary branch numbers and -1.31 and -3.23 for secondary branch numbers. Significant positive effects were demonstrated by parents CA-UGKI 09-6 (0.56), CA-UGCE 09-3 (0.53), and CA-UGKI 09-4 (0.94) for primary branch numbers while for secondary branch numbers, significant positive effects were demonstrated by parents CA-UGKI 09-6 (1.32) and CA-UGKI 09-4 (2.73)

For pedicel length, parent PP0337-7562 highly significantly expressed positive GCA effects with 0.47 while three parents PP9852-115, CA-UGCE 09-3 and CA-UGKI 09-4 significantly showed negative GCA effects of -0.18,-0.11 and -0.10, respectively. Parent CA-UGKI 09-4 exhibited high significant positive GCA effects for both plant height and width with GCA effects of 3.46 and 3.93, respectively while significant negative GCA effects were seen for plant height by parents PP9852-115 (-2.42) and CA-UGCE 09-3 (-3.07) and by parent PP0337-7562 (-2.74) for plant width. The highest significant positive GCA effects for stem diameter were shown by parents CA-UGKI 09-6 (0.05) and CA-UGKI 09-4 (0.09) while only parent PP0337-7562 expressed significant negative GCA effects (-0.07). Two parents CA-UGCE 09-3 and CA-UGKI 09-4 showed significant positive GCA effects for stem height with 1.50 and 1.36, respectively whereas, only parent PP9852-115 had significant negative GCA effects (-2.56).

Significant positive GCA effects were shown by parent PP0537-7504 (11.82) for virus incidence while they were parents PP9852-115 and CA-UGCE 09-3 that significantly exhibited negative GCA effects (-13.67) and (-19.90), respectively for this disease. With *Cercospora* leaf spot, only parent PP0337-7562 significantly portrayed significant positive GCA effects (3.53) while it was parent CA-UGKI 09-4 that significantly portrayed positive GCA effects (-8.81). For wilt disease significant GCA effects were shown by parent PP0337-7562 (12.08) positively and PP0537-7504 (-12.70) negatively. Similarly, only parent PP9852-115 exhibited significant negative GCA effects (-13.36) and parent CA-UGKI 09-4 positive GCA effects (13.28) for bacterial spot.

Specific combining ability for measured traits

Data on specific combining ability effects for quantitative traits were collected from only 12 crosses and disease traits from 13 crosses (**Table 5**). Significant negative SCA effects

Table 5 Estimates of specific combining ability effects of cross combinations for F_1 hot pepper generation grown at Namulonge, Uganda from May-October 2010.

Trait		**Days to flowering**	**Days to fruit maturity**	**Fruit length (cm)**	**Fruit width (cm)**	**Number of fruit per plant**	**Number of seeds per fruit**	**Primary branch numbers**	**Pedicel length (cm)**	**Plant height (cm)**
Crosses[a]	25x18	1.8	10.8**	0.5	-0.02	-6.8	-15.0***	0.9	-0.3	-2.4
	28x25	-2.7	-9.7**	-0.9*	-0.1	0.2	-5.2*	1.4**	-0.2	1.2
	29x18	-6.7*	3.8	-0.7*	-0.13	-2.1	29.2***	-0.3	-0.2	1.7
	29x25	-8.8**	-6.2	0.5	-0.07	5.5	30.1***	-2.4***	0.2	5.4
	29x28	-5.7*	-1.5	0.5	0.11	26.9***	-8.7**	2.5***	0.0	1.0
	31x18	-6.5*	-7.3*	0.2	-0.05	4.1	5.6*	-1.1	-0.2	-2.5
	31x28	6.9*	11.3**	-0.2	0.32*	-9.5	13.8***	-1.7**	-0.2	6.9*
	31x29	-2.1	-7.3*	0.6	0.09	17.6**	7.4**	2.1***	0.6***	4.6
	25x18	-3.7	-6.8*	-1.6***	0.18	-0.6	-11.9***	1.3*	-0.6***	-2.6
	28x25	6.9*	1.9	0.3	0.02	19.5***	7.6**	-0.4	0.5***	1.3
	29x18	0.7	0.5	-1.1**	-0.02	-12.7*	6.9**	0.7	0.3*	0.1
	29x25	-15.8***	-12.6***	0.5	0.0	11.5*	5.7*	0.6	0.0	3.0
	29x28	NT	NT	NT	NT	NT	NT	NT	NT	NT
	18x18	7.5**	-0.3	0.8*	0.01	2.7	-3.9	-0.4	0.6***	2.9
Selfed[a] parents	25x25	1.4	1.6	-0.2	0.08	-9.2	-8.7**	0.2	-0.1	-2.7
	28x28	0.4	-0.3	0.9**	-0.16	-2.4	-3.4	-1.5**	0.1	-4.5
	29x29	19.5***	11.9***	-0.6	0.0	-29.7***	-31.8***	-1.2*	-0.3*	-7.9**
	31x31	0.8	1.6	-0.3	-0.18	-6.0	-13.4***	0.3	-0.1	-4.5
	35x35	5.9*	8.5**	1.0**	-0.09	-8.8	-4.2	-1.1*	-0.1	-0.8
SE		2.59	3.06	0.32	0.14	4.56	2.37	0.51	0.12	2.71

Trait		**Plant width (cm)**	**Secondary branch numbers**	**Stem diameter (cm)**	**Stem height (cm)**	**Virus incidence (%)**	***Cercospora* leaf spot (%)**	**Wilt disease (%)**	**Bacterial spot (%)**
Crosses[a]	25x18	-1.9	1.3	0.05	-0.2	0.0	-1.8	2.7	-2.9
	28x25	0.7	2.4*	0.07	1.6	-29.4*	9.5*	-6.0	-14.9
	29x18	2.5	0.3	0.04	2.3	4.5	0.7	15.6	22.1*
	29x25	5.8	-0.6	-0.09	1.6	-12. 5	2.3	-21.1	-13.9
	29x28	1.2	3.6**	0.08	1.6	14.0	-8.7	-16.9	2.7
	31x18	-1.4	-1.3	-0.02	-0.1	19.2	-0.9	16.8	5.4
	31x28	8.7*	-3.3**	-0.02	-0.5	26.3*	-5.9	6.8	3.5
	31x29	10.2**	1.5	0.08	0.5	-8.2	3.2	-2.0	-18.1
	25x18	1.8	1.8	0.1	3.3	4.5	8.9	-23.9	-5.9
	28x25	4.3	-1.8	-0.1	0.4	-1.4	-0.5	6.3	-9.4
	29x18	-4.4	1.4	-0.1	1.0	24.1*	9.5*	-0.5	-14.9
	29x25	2.9	1 .8	0.0	-0.5	-3.9	13.0**	-14.3	19.8*
	29x28	NT	NT	NT	NT	25.8*	0.6	13.1	68.9***
	18x18	-0.5	-1.0	-0.08	-2.7	-14.1	-3.4	-5.6	-9.4
Selfed[a] parents	25x25	-4.4	-0.6	0.01	-1.6	-5.9	-0.3	-0.5	-21.4*
	28x28	-3.1	-2.0	-0.04	-1.8	-17.5	-2.2	8.3	11.8
	29x29	-11.2**	-3.3**	-0.07	-2.7	3.0	-5.2	19.3	-6.3
	31x31	-8.7*	1.6	-0.02	0.1	-31.5**	1.5	-17.4	-29.8**
	35x35	-2.2	-1.6	0.0	-2.1	3.1	-20.2***	19.3	12.7
SE		3.26	1.03	0.06	.63	11.26	4.3	12.58	9.38

*Significant at P ≤ 0.05; ** highly significant at P ≤ 0.01; *** highly significant at P ≤ 0.00; the rest not significant. SE= standard error = $(p^2+p+2)/ (p+1) (p+2)$*EMS; p= number of parents; EMS= Error mean square. [a]For the accession codes and other details of the genotypes used in the crosses and the selfed parents, please refer to **Table 1**

were shown by the crosses CA-UGKI 09-4xCA-UGKI 09-6 (-15.8), CA-UGKI 09-6xPP0337-7562 (-6.7), CA-UGKI 09-6xPP0537-7504 (-8.8), CA-UGCE 09-3xPP0337-7562 (-6.5) and significant positive SCA effects were shown by crosses CA-UGCE 09-3xPP9852-115 (6.1), CA-UGKI 09-4xPP9852-115 (6.7) for days to flowering. For days to fruit maturity, significant positive SCA effects were shown by crosses PP0537-7504xPP0337-7562 (10.8), CA-UGCE 09-3xPP9852-115 (11.3) while significant negative SCA effects were shown by crosses PP9852-115xPP0537-7504 (-9.7), CA-UGCE 09-3xPP0337-7562 (-7.3), CA-UGCE 09-3xCA-UGKI 09-6 (-7.3), CA-UGKI 09-4xCA-UGKI 09-6 (-12.6.), CA-UGKI 09-4xPP0337-7562 (-6.8).

Concerning fruit length, significant negative SCA effects were exhibited by crosses PP9852-115xPP0537-7504 (-0.9), CA-UGKI 09-6xPP0337-7562 (-0.7), CA-UGKI 09-4xPP0337-7562 (-1.6) and CA-UGKI 09-4xPP9852-115 (-1.1) while, no cross showed significant positive SCA effects (**Table 5**). Significant SCA effects for fruit width were only displayed by hybrid CA-UGCE 09-3xPP9852-115 (0.32), positively. The top performers for number of fruits per plant were hybrids CA-UGCE 09-3xCA-UGKI 09-6 (17.6), CA-UGKI 09-6xPP9852-115 (26.9), CA-UGKI 09-4xCA-UGKI 09-6 (11.5) and CA-UGKI 09-4xPP0537-7504 (19.5) with significant positive SCA effects, while hybrid CA-UGKI 09-4xPP9852-115 (-12.7) with significant negative SCA effects was the poorest performer. Other hybrids with high negative SCA effects were CA-UGCE 09-3xPP9852-115 (-9.8) and PP0537-7504xPP0337-7562 (-6.8). With number of seeds per fruit, crosses CA-UGKI 09-6xPP0337-7562, CA-UGKI 09-6xPP0537-7504, CA-UGCE 09-3xPP0337-7562, CA-UGCE 09-3xPP9852-115, CA-UGCE 09-3xCA-UGKI 09-6, CA-UGKI 09-4xPP0537-7504, CA-UGKI 09-4xPP9852-115 and CA-UGKI 09-4xCA-UGKI 09-6 were the best performers with significant positive SCA effects of 29.2, 30.1, 5.6, 13.8, 7.4, 7.6, 6.9, and 5.7, respectively, while crosses PP0537-7504xPP0337-7562, PP9852-115xPP0537-7504, CA-UGKI 09-6xPP9852-115 and CA-UGKI 09-4xPP0337-7562 performed poorly, with highly significant SCA effects of -15.0, -5.2, 8.6 and -11.9, respectively.

The significant positive SCA effects for primary branch numbers were found in crosses PP9852-115xPP0537-7504 (1.4), CA-UGKI 09-6xPP9852-115 (2.5), CA-UGCE 09-3xCA-UGKI 09-6 (2.1) and CA-UGKI 09-4xPP0337-7562 (1.3) while significant negative SCA effects were found in crosses CA-UGKI 09-6xPP0537-7504 (-2.4) and CA-UGCE 09-3xPP9852-115 (-1.7). For secondary branch numbers, significant positive SCA effects were seen in crosses CA-UGKI 09-6xPP9852-115 (3.6) and PP9852-115xPP0537-7504 (2.4) whereas significant negative SCA effects were found in cross CA-UGCE 09-3xPP9852-115 (-3.3). For pedicel length, crosses CA-UGCE 09-3xCA-UGKI 09-6, CA-UGKI 09-4xPP0537-7504 and CA-UGKI 09-4xPP9852-115 highly significantly exhibited positive SCA effects with 0.6, 0.5 and 0.3, respectively, while CA-UGKI 09-4xPP0337-7562 was the only hybrid with highly significant negative SCA (-0.6) effects. Only hybrid CA-UGCE 09-3xPP9852-115 exhibited high significant positive SCA effects for plant height (6.9) and none was significant negatively for this trait. However, crosses PP0537-7504xPP0337-7562 (-2.4), CA-UGCE 09-3xPP0337-7562 (-2.5) and CA-UGKI 09-4xPP0337-7562 (-2.6) had high negative SCA effects. For plant width, no significant negative SCA effects were observed among hybrids but significant positive effects were observed in crosses CA-UGCE 09-3xPP9852-115 (8.7) and CA-UGCE 09-3xCA-UGKI 09-6 (10.9). No significant positive and negative SCA effects were observed for both stem diameter and stem height (**Table 5**). But, hybrids CA-UGKI 09-6xPP0337-7562 (2.3) and CA-UGKI 09-4xPP0337-7562 (3.3) had high positive SCA effects for stem height.

Significant positive SCA effects were shown by hybrids CA-UGCE 09-3xPP9852-115 (26.3), CA-UGKI 09-4xPP9852-115 (24.1), CA-UGCE 09-3xPP0537-7504 (25.8), for virus incidence while one cross PP9852-115xPP0537-7504 significantly exhibited negative SCA effects (-29.4). For *Cercospora* leaf spot, significant positive SCA effects were realized in crosses PP9852-115xPP0537-7504 (9.5), CA-UGKI 09-4xPP9852-115 (9.5), CA-UGKI 09-4xCA-UGKI 09-6 (13.0) while no cross significantly registered negative SCA effects (**Table 5**). However, crosses CA-UGKI 09-6xPP9852-115 and CA-UGCE 09-3xPP9852-115 registered higher negative SCA of -8.7 and -5.9, respectively. With wilt disease, no significant SCA effects were seen among crosses. Nevertheless, crosses CA-UGKI 09-6xPP0337-7562 (15.6), CA-UGCE 09-3xPP0337-7562 (16.8), CA-UGCE 09-3xPP0537-7504 (13.1) had high positive GCA effects while crosses CA-UGKI 09-6xPP0537-7504 (-21.1), CA-UGKI 09-6xPP9852-115 (-16.9), CA-UGKI 09-4xPP0337-7562 (-23.9), CA-UGKI 09-4xCA-UGKI 09-6 (-14.3) had high negative GCA effects. Three crosses CA-UGKI 09-6xPP0337-7562 (22.1), CA-UGKI 09-4xCA-UGKI 09-6 (19.8) and CA-UGCE 09-3xPP0537-7504 (68.9), expressed significant positive SCA effects for bacterial spot while none of the hybrids expressed significant negative SCA effects. However, hybrids CA-UGKI 09-4xPP9852-115 (-14.9), PP9852-115xPP0537-7504 (-14.9), CA-UGKI 09-6xPP0537-7504 (-13.9), CA-UGCE 09-3xCA-UGKI 09-6 (-18.1) expressed the highest negative SCA effects for this disease.

DISCUSSION

Hybridization of genetically different parents normally results in hybrids with various heterotic effects from which selection for desirable traits among segregating populations in later generations are made (Marame *et al.* 2008; Marchesan *et al.* 2009; Sitaresmi *et al.* 2010; Zečević *et al.* 2011). Knowledge on combining ability of such desirable traits gives information on the gene effects on the expression of traits and identifies the best parents and crosses for the exploitation of heterosis and improvement of these traits (Hannan *et al.* 2007; Marchesan *et al.* 2009; Nagheri and Jelodar 2010; Payakhapaab *et al.* 2012). This study on the genetics of disease resistance, yield and associated traits through combining ability analysis in a half diallel was conducted to identify good parent combiners in hybridization for improved disease resistance, yield and its components in Uganda.

The significant differences observed among genotypes (parents and F_1s) for all evaluated traits except wilt disease indicates existence of genetic diversity (Marchesan *et al.* 2009) and heterosis (Zewdie and Bosland 2001; Patel *et al.* 2010). The significant GCA and SCA effects for most traits indicated the role of additive and non-additive gene action governing the expression of most traits. Additive and non-additive gene action has been reported for most agro-morphological and quality traits on chilli (Haynes *et al.* 2008; Rêgo *et al.* 2009; Marchesan *et al.* 2009; May *et al.* 2010; Yunianti *et al.* 2011; Rodrigues *et al.* 2012), sweet pepper (Marchesan *et al.* 2009) and other crops such as sweet potato, soybean and wheat (Mwanga *et al.* 2002; Kiryowa *et al.* 2009; Bastam *et al.* 2010).

The observation that the parents exhibited both significant and non-significant positive and negative GCA effects indicates that both desirable and non-desirable GCA effects were transferred by parents to the progeny. Parents with significant positive GCA and negative SCA effects increased and reduced favourable alleles for the expression of the traits in the studied genotypes, respectively (Zewdie and Bosland 2001; Marchesan *et al.* 2009). Consequently, parents such as CA-UGCE 09-3 and PP9852-115 with significant negative GCA effects are considered desirable and should be selected in a breeding program which targets traits that need reduced expression in the progeny including days to flowering and fruit maturity, pedicel length, and disease incidence. In contrast, parents with significant positive GCA effects are considered desirable for traits that require increased expression in the progeny such as fruit width, fruit length, number of fruits per plant, number of seeds per fruit, primary branch numbers, plant height, plant width, secondary branch numbers, stem diameter and stem height. This is shown for example, for the number of fruits per plant and plant height by local parents CA-UGKI 09-6 and CA-UGKI 09-4. Positive GCA effects for these traits result in increased fruit sizes and numbers that translate to increased yields per unit area. Taller plants with wider canopies are associated with increased branch numbers that bear many fruits resulting in increased yield per unit area.

In this study, none of the used parents exhibited good general combining ability for all studied traits as was reported by several authors on chilli (Prasath and Ponnuswami 2008; Marchesan *et al.* 2009; Payakhapaab *et al.* 2012) and tomato (Hannan *et al.* 2007). This indicates variability in the evaluated germplasm and difficulty in concurrently incorporating the evaluated traits in the progeny. Therefore, a pepper breeder should be mindful of the target traits when choosing parents in a breeding program. Parents with various GCA effects combined to produce crosses varying in SCA effects. For example, (i) good parents combining to give non-desirable SCA effects as demonstrated for days to fruit maturity where parents with negative GCA effects produced significant non-desirable positive SCA effects in the progeny (CA-UGCE 09-3xPP9852-115), (ii) a good and bad parent combining to give desirable SCA effects such as parents with negative and positive GCA effects producing a hybrid (CA-UGKI 09-6xPP0537-7504) with significant negative SCA effects for days to flowering, (iii) good parents producing desirable SCA effects such as parents having significant negative GCA effects producing a hybrid (CA-UGCE 09-3xPP0337-7562) with significant negative SCA effects for days to fruit maturity and (iv) bad parents combining to give desirable SCA effects such as parents with significant positive GCA effects producing a hybrid (CA-UGCE 09-3xPP9852-115) with significant negative SCA effects for days to flowering and CA-UGKI 09-4xCA-UGKI 09-6 for days to fruit maturity.

Similar observations have been previously reported and are attributed to non-additive complementary gene actions (Mwanga *et al.* 2002; Hannan *et al.* 2007; Marchesan *et al.*

2009) and/or additive complementary gene interactions from both parents in the desired direction (Rieseberg *et al.* 2003) for bad parents, good and bad parents giving desirable SCA effects and sizeable additive x additive gene action for good parents giving desirable SCA effects (Hannan *et al.* 2007). Majority of the significant negative SCA effects came from parents with contrasting significant GCA effects as well as those with significant positive GCA effects which is in conformity with earlier findings (Marchesan *et al.* 2009) and (Pace *et al.* 1998) which found parents with high and positive GCA effects produced hybrids with negative SCA effects and was attributed to gene complementation. These complementary gene interactions are the basis for heterosis from which superior transgressive segregates are selected from segregating hybrid populations to derive pure lines in later generations (Rieseberg *et al.* 2003; Marame *et al.* 2009b).

The significant negative and positive SCA effects observed among all crosses for all traits investigated indicates co-existence of dominant gene deviations that reduce and increase the expression of the traits (Marchesan *et al.* 2009). Since SCA measures the performance of a parent under consideration in a specific cross, it constitutes deviation from GCA of this parent. Therefore, the best cross is one with the highest SCA effects that has one of the parents with the highest GCA values (Marchesan *et al.* 2009). Accordingly, traits of cross combinations with desirable significant negative SCA effects are days to flowering and fruit maturity, pedicel length, and disease incidence whereas positive SCA effects in crosses are desirable for fruit length, fruit width, number of fruit per plant, number of seeds per fruit, primary and secondary branch numbers, plant height, plant width, stem height and stem diameter. Such crosses include CA-UGCE 09-3xCA-UGKI 09-6, CA-UGKI 09-6xPP9852-115 and CA-UGCE 09-3xPP0337-7562 which had the best SCA values for most traits and are considered the best for heterotic breeding to generate improved pure lines for desired traits through transgressive segregation in later generations (Bayoumi and El-Bramawy 2007; Chowdhary *et al.* 2007).

The GCA mean squares were greater than the SCA mean squares for all traits except bacterial spot as was reported for most traits by several authors (Marchesan *et al.* 2009; Rêgo *et al.* 2009; May *et al.* 2010). This would imply that additive gene action was more predominant in expression of most traits except bacterial spot. From Baker's ratio, days to 50% flowering and fruit maturity, number of fruit per plant, number of seeds per fruit, primary branch numbers, plant width and height were predominantly controlled by non-additive gene action and therefore, SCA effects contributed more to the genetic variation of these traits (May *et al.* 2010). Therefore, these traits can be effectively improved by exploiting breeding methods that take care of non-additive gene action such as hybridization (Marame *et al.* 2009b; Pérez-Grajales *et al.* 2009; May *et al.* 2010; Rodrigues *et al.* 2012). Selection of such traits should be done in later generations when the effects of non-additive gene action have been minimized and those of additive gene action effects have been fixed.

These results agree with those found by several researchers on chilli for various traits: plant width and plant height (Reddy *et al.* 2008; Rêgo *et al.* 2009; Rodrigues *et al.* 2012), number of fruits per plant and days to maturity (Marame *et al.* 2008; Marame *et al.* 2009b; Rodrigues *et al.* 2012), days to flowering (Reddy *et al.* 2008; Cvikić *et al.* 2010), number of primary branches and number of seeds per fruit (Reddy *et al.* 2008). Our findings however, do not agree with earlier reports for fruit length and diameter (Reddy *et al.* 2008; Syukur *et al.* 2010; Rodrigues *et al.* 2012), number of secondary branches (Reddy *et al.* 2008) and stem height (at first bifurcation height) (Rêgo *et al.* 2009) that were found to be controlled by additive gene action. Such contradictions could have been due to differences in the environmental conditions, genotypes used and/or models for analysis.

Five traits: fruit length, fruit width, secondary branch numbers, stem diameter, stem height were predominantly controlled by additive gene action due to GCA effects. Pedicel length seemed to be controlled by both additive and non-additive gene actions in equal proportions because of its intermediate Baker's ratio (X=0.5). Thus, the performance for these traits in the progeny can easily be predicted from the GCA of parents due to the additive effects that are fixable in the progeny (Haynes *et al.* 2008; May *et al.* 2010). These traits can also be improved by breeding methods that increase the frequency of favourable alleles to obtain superior combinations through repeated crossing and selection such as backcross, mass selection, recurrent selection in early generations (Nkalubo *et al.* 2009; Pérez-Grajales *et al.* 2009; Rêgo *et al.* 2009; Khorzoght *et al.* 2010; Syukur *et al.* 2010). These results agree with the findings of Prasath and Ponnuswami (2008), Marchesan *et al.* (2009), and Rodrigues *et al.* (2012) on average fruit length and width but differ with others on plant height (Prasath and Ponnuswami 2008; Rodrigues *et al.* 2012), days to flowering (Prasath and Ponnuswami 2008), number of fruits per plant (Prasath and Ponnuswami 2008), number of seeds per fruit (Prasath and Ponnuswami 2008; Schuelter *et al.* 2010) probably due to differences in genotypes, environments and methods used.

For disease traits, Baker's ratio indicated predominance of non-additive gene action in control of *Cercospora* leaf spot and bacterial spot incidences while, viral and wilt disease incidences were preponderantly controlled by additive gene action. Therefore, wilt and viral resistance can be selected in early generations due to fixable additive gene actions that increase favourable alleles for disease resistance while selection for bacterial and *Cercospora* leaf spot can be effected in later generations. There is no varied interpretation for non-significance of GCA and SCA effects for wilt incidence since it would imply no and/or very low additive and non-additive gene effects in the expression of its resistance. However, this resulted from the error being large enough to detect the differences among genotypes (parents and F_1s) (data not shown) probably due to the low levels and/or non-uniform distribution of the inocula common to natural field infections (Adipala *et al.* 2001; Agrios 2005).

These results are in agreement with earlier findings on bacterial spot (Poulos *et al.* 1991), viruses (Caranta *et al.* 1997a, 1997b) and bacterial wilt (Lafortune *et al.* 2005; Tran and Kim 2010). Caranta *et al.* (1997a) reported additive gene effects more predominant than digenic epistasis in the control of *Cucumber mosaic virus* resistance while Caranta *et al.* (1997b) reported additive gene effects controlling a large part of the resistance to PVY and potyvirus E compared to non-additive effect (epistasis). Tran and Kim (2010) reported predominance of additive effects governed bacterial wilt resistance although, dominance and duplicate epistasis (dominance × dominance interaction) seemed more predominant under very high virulence. Lafortune *et al.* (2005) also reported additive rather than a dominant gene action to control bacterial wilt inheritance under severe conditions. On a related crop (potato) in Uganda, Osiru *et al.* (2001) reported significant GCA and SCA effects indicating both additive and non-additive gene actions with additive gene effects six times more predominant than non-additive gene effects in the control of bacterial wilt resistance. However, Lefebvre *et al.* (1996) and Yunianti *et al.* (2011) reported non-additive gene action (dominance and epistasis) to influence phytophthora root rot, causing wilt disease more than additive gene effects. Also, our results on bacterial spot conflict with those of Riva *et al.* (2004) who reported predominance of non-additive gene effects in bacterial spot inheritance. Like the results of this study, several authors have indicated predominance of additive over non-additive gene effects in the expression of disease traits in various crops such as *Fusarium* head blight (scab) caused by *Fusarium graminearum* in wheat (Khorzoght *et al.* 2010), sweet potato virus disease in sweet potato (Mwanga *et al.* 2002), soybean rust disease in soybean (Kiryowa *et al.* 2009), powdery mildew on sweet pepper (Marchesan *et al.* 2009) and predominance of non-additive gene over additive gene action for the expression of powdery mildew in pepper (Blat *et al.* 2005a, 2005b, 2006).

The low narrow sense heritabilities for number of branches per plant, stem diameter, number of fruits per plant, days to maturity (33.1-48.4) and high broad sense heritabilities for plant height, number of fruits per plant, days to maturity, plant width and fruit length (71-92) observed are in the ranges reported in chilli pepper (Marame *et al.* 2008, 2009a, 2009b). Syukur *et al.* (2010) also reported high broad (97) and narrow sense (89.9) heritabilities for fruit length. The high broad sense heritabilities for branch numbers per plant (91.5 for primary and 90.9 for secondary branch numbers) and stem diameter were contrary (45.5 and 1.3, respectively) to those reported by Marame *et al.* (2009a). The narrow sense heritability for plant width (21.3) was lower than 51 reported by Marame *et al.* (2009a). Similarly, the narrow sense heritability for plant height (31.1) contradicts those reported, 74.4 (Marame *et al.* 2009a) and 63 (Marame *et al.* 2008, 2009b). The low narrow (41.1) and broad sense (44.9) heritabilities for fruit width disagree with those reported by Syukur *et al.* (2010), 82.7 and 93.9, respectively. All these contradictions were attributed to variations in the experimental material (genotypes), environmental effect and methods used (Bonos 2006; Falconer and Macky 2009; Khorzoght *et al.* 2010). With disease incidence, narrow sense heritability was low for wilt, bacterial spot and *Cercopsora* leaf spot incidence (16.1-31.3) and moderate for viral incidence (46.1%) while broad sense heritability was high for all disease incidences (78.2-85.7%) and moderate for wilt incidence (43.4%). Other authors reported moderately low narrow-sense heritabilities for resistance to bacterial spot (26-50.2%) (Poulos *et al.* 1991; Scott *et al.* 2003; Riva *et al.* 2004), *Phytophthora capsici* (55.9%) (Yunianti *et al.* 2011) and sweetpotato virus (31–41%) (Mwanga *et al.* 2002). High broad-sense heritabilities were also reported for bacterial spot (82.54%) (Riva *et al.* 2004), *Phytophthora capsici* (96%) and sweetpotato virus (73–98%) resistance (Mwanga *et al.* 2002).

The high broad sense heritability in most traits imply that the observed variance in the expression of traits was largely due to genotypic effects (additive, dominance and epistatic) with less influence from the environment except bacterial wilt disease, fruit width, stem height and diameter with moderately low broad sense heritablities of 43.4, 44.9, 53.9 and 69.8, respectively. These traits can therefore, be easily selected because of the close relationship of genotype and phenotype. Similarly, the low narrow sense heritability in most of the agro-morphological and disease traits further confirms the importance of non-additive gene action in the control of these traits as indicated in the combining ability studies. The high broad and narrow-sense heritabilities displayed by fruit length indicate high proportion of additive effects contribution to the genotypic variance. These results imply that apart from fruit width, wilt disease, stem height and diameter, the improvement of most most traits can be made using standard selection procedures based on the phenotypes of parents such as mass selection (Mwanga *et al.* 2002; Sharma *et al.* 2010). However, since most of these traits are controlled by non-additive genes, such selection procedures should take care of variance due to non-additive genes effects (Mwanga *et al.* 2002) such as selection in later generations when desirable genes have been fully fixed. The observed inconsistency in narrow and broad sense heritability in some traits such as days to flowering and number of seeds per fruit was also observed by Deb and Khaleque (2009) from studies on quantitative traits in chick pea and Ekvised *et al.* (2006) on peanut agronomic traits. Such inconsistency could be attributed to sampling error or environmental effects (Ekvised *et al.* 2006; Kiryowa *et al.* 2009; Deb and Khaleque 2009).

CONCLUSION

Differences in performance among hybrids and their parents allowed significance of GCA and SCA effects among various studied traits implying involvement of both additive and non-additive gene action in the expression of these traits. Such results clearly indicate that development of superior *Capsicum* hybrids and pure lines is possible in Uganda through use of a diverse germplam in a diallel cross. Non-additive gene effects were more predominant in the expression of days to flowering, days to fruit maturity, number of fruit per plant, number of fruit per plant, number of seeds per fruit, primary branch numbers, plant height *Cercospora* leaf spot and bacterial spot incidence selection for which should be deferred to later generations when desirable segregates become available in a hybridisation breeding program. Rapid genetic gain can be achieved for fruit length, fruit width, secondary branch numbers, stem diameter, stem height, virus and wilt disease incidences due to predominance of additive gene action in their control and can therefore be selected for in early generation through simple breeding methods such as back cross, pedigree breeding with recurrent selection and mass selections. Therefore, hybridisation (heterosis) breeding and pedigree breeding with simple selection methods can be used to concurrently improve most traits controlled by both additive and non-additive gene actions in a breeding program. The AVRDC genotype PP9852-115 and local genotypes CA-UGKI 09-4, CA-UGKI 09-6 and CA-UGCE 09-3 were the best combiners due to highly significant desirable GCA effects for most of the studied traits and have the potential to be used in the breeding program. However, for wilt disease, only the AVRDC parent PP0537-7504 emerged as a significant general combiner in reducing its incidence. Hybrids CA-UGCE 09-3xCA-UGKI 09-6, CA-UGKI 09-6xPP9852-115 and CA-UGCE 09-3xPP0337-7562 had the best SCA effects and were the best performers among all crosses for measured traits and can be used to derive desirable recombinant inbred lines from a segregating population through appreciable extensive progeny testing or tested for commercial use. Hybrids CA-UGCE 09-3xPP9852-115 and CA-UGKI 09-6xPP9852-115 were also better performers for *Cercospora* leaf spot resistance while hybrid PP9852-115xPP0537-7504 was the best for virus resistance and can be used to derive sources of resistance to these diseases. Multi-environment trials are, recommended to verify the observed gene action for the studied traits.

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REFERENCES

Adefris T, Heiko CB (2005) Heterosis and combining ability in a diallel cross of Ethiopian mustard inbred lines. *Crop Science* **45**, 2629-2635

Adipala E, Nampala PM, Biruma M, Warren H, Wilson H (2001) Field assessment of cowpea germplasm for disease and pest resistance in Uganda. *African Crop Science Conference Proceedings* **5**, 381-393

Agrios GN (2005) *Plant Pathology* (5th Edn), Elsevier Academic Press: Burlington, USA; California, USA; London, UK, 921 pp

Ahmed N, Hurra M, Wani SA, Khan SH (2003) Gene action and combining ability for fruit yield and its component characters in sweet pepper. *Capsicum and Eggplant Newsletter* **22**, 55-58

Baker RJ (1978) Issues in diallel analysis. *Crop Science* **18**, 533-536

Bastam SV, Ramezanpour SS, Soltanloo H, Kia S, Kalate M, Pahlevani MH (2010) Inheritance of resistance to *Septoria tritici* blotch (STB) in some Iranian genotypes of wheat (*Triticum aestivum* L.). *International Journal of*

Genetics and Molecular Biology **2 (3)**, 34-42

Bayoumi TY, El-Bramawy MAS (2007) Genetic analyses of some quantitative characters and *Fusarium* wilt disease resistance in sesame. *African Crop Science Conference Proceedings* **8**, 2198-2204

Blat SF, Costa CP, Vencovsky R, Sala FC (2005a) Inheritance of reaction to *Leveillula taurica* (Lev.) Arn. in *Capsicum baccatum. Crop Breeding and Applied Biotechnology* **5**, 467-472

Blat SF, Costa CP, Vencovsky R, Sala FC (2005b) Inheritance of reaction to *Leveillula taurica* (Lev.) Arn. in *Capsicum annuum* L. *Scientia Agricola* **62 (1)**, 40-44

Blat SF, Costa CP, Vencovsky R, Fernando CS (2006) Hot pepper (*Capsicum chinense*, Jacq.) inheritance of reaction to powdery mildew. *Scientia Agricola* **63 (5)**, 471-474

Bonos SA (2006) Heritability of dollar spot resistance in creeping bentgrass. *Phytopatholology* **96**, 808-812

Bosland PW, Votava EJ (2012) *Peppers: Vegetable and Spice Capsicums* (2nd Edn), Centre For Agriculture and Biosciences International, Oxfordshire, UK, 248 pp

Caranta C, Lefebvre V, Palloix A (1997b) Polygenic resistance of pepper to potyviruses consists of a combination of isolate-specific and broad-spectrum quantitative trait loci. *Molecular Plant-Microbe Interactions* **10 (7)**, 872-878

Caranta, C. Palloix A. Lefebvre V, Daubéze AM (1997a) QTLs for a component of partial resistance to cucumber mosaic virus in pepper: Restriction of virus installation in host-cells. *Theoretical and Applied Genetics* **94**, 431-438

Chowdhary AM, Sajad M Ashraf IM (2007) Analysis on combining ability of metric traits in bread wheat, *Triticum aestivum. Journal of Agricultural Research* **45 (1)**, 1-8

Cvikić D, Pavlović N, Brdar M, Girek Z (2010) The importance of earliness for creating new ms F1 pepper hybrids. *Genetika* **42 (3)**, 521-528

Deb AC, Khaleque MA (2009) Nature of gene action of some quantitative traits in chick (*Cicer arietinum* L.). *World Journal of Agricultural Science* **5 (3)**, 361-368

Ekvised S, Jogloy S, Akkasaeng C, Keerat-kasikorn M, Kesmala T, Buddhasimma T, Patanothai A (2006) Heritability and correlation of thrips resistance and agronomic traits in peanut. *Asian Journal of Plant Science* **5 (6)**, 923-931

Falconer DS (1963) Qualitatively different responses to selection in opposite directions. In: Hanson WD, Robinson HF (Eds) *Statistical Genetics and Plant Breeding*, Pub. 982, National Academy of Sciences-National Research Council, Washington, DC, pp 487-490

Falconer DS, Macky TFC (2009) *Introduction to Quantitative Genetics* (4th Edn), Dorling Kindersley Pvt. Ltd, India, 462 pp

FAO (2012) Statistical database. Available online: http:/www.faostat.fao.org

Galanihe LD, Priyantha MGDL, Yapa DR, Bandara HMS, Ranasinghe J (2004) Insect pest and disease incidences of exotic hybrids chilli pepper varieties grown in the low country dry zone of Sri Lanka. *Annals of Sri Lanka Department of Agriculture* **6**, 99-106

Geleta LF, Labuschagne MT, Viljoen CD (2004) Relationship between heterosis and genetic distance based on morphological traits. *Plant Breeding* **123**, 467-473

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing system. *Australian Journal of Biological Science* **9**, 463-493

Hannan MM, Ahmed MB, Roy UK, Razvy MA, Haydar A, Rahman MA, Islam MA, Islam R (2007) Heterosis, combining ability and genetics for brix%, days to first fruit ripening and yield in tomato (*Lycopersicon esculentum* Mill.). *Middle-East Journal of Scientific Research* **2 (3-4)**, 128-131

Haynes KG, Christ BJ, Vinyard BT (2008) Determining the importance of combining ability for late blight resistance in early generations of potato breeding when susceptible clones are discarded. *American Journal of Potato Research* **85**, 445-454

Khorzoght EG, Soltanloo H, Ramezanpour SS, Arabi MK (2010) Combining ability analysis and estimation of heterosis for resistance to head blight caused by *Fusarium graminearum* in spring wheat. *Austrarian Journal of Crop Science* **4 (8)**, 626-632

Kiryowa M, Tukamuhabwa P, Adipala E (2009) Genetic analysis of resistance to soybean rust disease. *African Crop Science Journal* **16 (3)**, 211-217

Lafortune D, Béramis M, Daubèze AM, Boissot N, Palloix A (2005) Partial resistance of pepper to bacterial wilt is oligogenic and stable under tropical conditions. *Plant Disease* **89**, 501-506

Lefebvre V, Palloix A (1996) Both epistatic and additive effects of QTLs are involved in polygenic induced resistance to disease: a case study, the interaction pepper-*Phytophthora capsici* Leonian. *Theoretical and Applied Genetics* **93**, 503-511

Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Genetics*, Sinauer Associates, Inc. Sunderland, MA

Manjunatha H, Srinivasan K (2007) Hypolipidemic and antioxidant effects of dietary curcumin and capsaicin in induced hypercholesterolemic rats. *Lipids* **42**, 1133-1142

Marame F, Desalegne L, Sing H, Chemeda F, Sigvald R (2008) Genetic components and heritability of yield and yield related traits in hot pepper. *Research Journal of Agriculture and Biological Sciences* **4 (6)**, 803-809

Marame F, Dessalegne L, Fininsa C, Sigvald R (2009a) Heterosis and heritability in crosses among Asian and Ethiopian parents of hot pepper genotypes. *Euphytica* **168**, 235-247

Marame F, Desalegne L, Fininsa C, Sigvald R (2009b) Genetic analysis for some plant and fruit traits, and its implication for a breeding program of hot pepper (*Capsicum annuum* var. *annuum* L.). *Hereditas* **146**, 13-40

Marchesan CB, Melo AMT, Paterniani MEAGZ (2009) Combining ability in sweet pepper for resistance to powdery mildew. *Horticultura Brasileira* **27 (2)**, 189-95

May AMP, Nájera GC, Suárez JMT, Elos MM, Cortés JOM, Gutiérrez AP, Moreno LL (2010) Combining ability and heterotic effects in sweet pepper populations (*Capsicum annuum* L.). *Revista Fitotecnia Mexicana* **33 (4)**, 353-360

McMullan M, Livsey J (2007) The *Capsicum* Genus. Available online: http://www.thechileman.org/guide_species.php

Mwanga ROM, Yencho GC, Moyer JW (2002) Diallel analysis of sweetpotatoes for resistance to sweetpotato virus disease. *Euphytica* **128**, 237-248

Nagheri N, Jelodar NB, (2010). Heterosis and combining ability analysis for yield and related-yield traits in hybrid rice. *International Journal of Biology* **2 (2)**, 222-231

Nkalubo ST, Melis R, Derera J, Laing MD, Opio F (2009) Genetic analysis of anthracnose resistance in common bean breeding source germplasm. *Euphytica* **167**, 303-312

Osiru MO, Rubaihayo PR, Opio AF (2001) Inheritance of resistance to tomato bacterial wilt and its implication for potato improvement in Uganda. *African Crop Science Journal* **9 (1)**, 9-16

Pace S, Piscioneri I, Settanni I (1998) Heterosis and combining ability in a half diallel cross of kenaf (*Hibiscus cannabinus* L.) in south Italy. *Industrial Crops and Products* **7**, 317-327

Patel MP, Patel AR, Patel JB, Patel JA (2010) Heterosis for green fruit yield and its components in chilli (*Capsicum annuum* var. *longicum* (D.G) Sendt) over environments. *Electronic Journal of Plant Breeding* **1 (6)**, 1443-1453

Payakhapaab S, Boonyakiat D, Nikornpun M (2012) Evaluation of heterosis and combining ability of yield components in chillies. *Journal of Agricultural Science* **4 (11)**, 154-161

Pérez-Grajales M, González-Hernández VA, Peña-Lomelí A, Sahagún-Castellanos J (2009) Combining ability and heterosis for fruit yield and quality in Manzano hot pepper (*Capsicum pubescens* R & P) landraces. *Revista Chapingo Serie Horticultura* **15 (1)**, 47-55

Perucka I, Materska M (2001) Phenylalanine ammonia-lyase and antioxidant activities of lipophilic fraction of fresh pepper fruits *Capsicum annuum* L. *Innovative Food Science and Emerging Techonolology* **2**, 189-192

Poulos JM, Reifschneider FJB, Coffman WR (1991) Heritability and gain from selection for quantitative resistance to *Xanthomonas campestris* pv. *vesicatoria* in *Capsicum annuum L. Euphytica* **56**, 161-167

Prasath D, Ponnuswami V (2008) Heterosis and combining ability for morphological, yield and quality characters in paprika type chilli hybrids. *Indian Journal of Horticulture* **65 (4)**, 441-445

Reddy MG, Kumar HDM, Salimath PM (2008) Combining ability analysis in chilli (*Capsicum annuum* L.). *Karnataka Journal of Agricultural Science* **21 (4)**, 494-497

Rêgo ER, Rêgo MM, Finger FL, Cruz CD, Casali VWD (2009) A diallel study of yield components and fruit quality in chilli pepper (*Capsicum baccatum*). *Euphytica* **168**, 275-287

Rieseberg LH, Widmer A, Arntz AM, Burke JM (2003) The genetic architecture necessary for transgressive segregation is common in both natural and domesticated populations. *Philosophical Transactions of the Royal Society London B: Biological Sciences* **358**, 1141-1147

Riva EM, Rodrigues R, Pereira MG, Sudré CP, Karasawa M (2004) Inheritance of bacterial spot disease in *Capsicum annuum* L. *Crop Breeding and Applied Biotechnology* **4**, 490-494

Rodrigues R, Gonçalves LSA, Bento CS, Sudré CP, Robaina RR, Amaral Júnior AT (2012) Combining ability and heterosis for agronomic traits in chili pepper. *Horticultura Brasileira* **30**, 226-233

Schuelter AR, Pereira GM, Júnior ATA, Casali VWD, Scapim CA, Barros WS, Finger FL (2010) Genetic control of agronomically important traits of pepper fruits analyzed by Hayman's partial diallel cross scheme. *Genetics and Molecular Research* **9 (1)**, 113-127

Scott JW, Francis DM, Miller SA, Somodi GC, Jones JB (2003) Tomato bacterial spot resistance derived from pi 114490; inheritance of resistance to race T2 and relationship across three pathogen races. *Journal of the American Society for Horticultural Science* **128 (5)**, 698-703

Shankarappa KS, Sriharsha KT, Aswathanarayana DS, Prameela HA, Kulkarni RS, Muniyappa V, Rao AM, Maruthi MN (2008) Development of tomato hybrids resistant to tomato leaf curl virus disease in South India. *Euphytica* **164 (2)**, 531-539

Sharma VK, Semwal CS, Uniyal SP (2010) Genetic variability and character association analysis in bell pepper (*Capsicum annuum L.*). *Journal of Horticulture and Forestry* **2 (3)**, 58-65

Sitaresmi T, Sujiprihati S, Syukur M (2010) Combining ability of several introduced and local chilli pepper (*Capsicum annuum* L.) genotypes and heterosis of the offsprings. *Jurnal Agronomi Indonesia* **38 (3)**, 212-217

Syukur M, Sujiprihati S, Yunianti R, Undang (2010) Diallel analysis using hayman method to study genetic parameters of yield components in pepper (*Capsicum annuum* L.). *Hayati Journal of Biosciences* **17 (4)**, 183-188

Tran NH, Kim BS (2010) Inheritance of resistance to bacterial wilt (*Ralstonia solanacearum*) in pepper (*Capsicum annuum* L.). *Horticulture, Environment and Biotechnology* **51 (5)**, 431-439

Tusiime G, Tukamuhabwa P, Nkalubo S, Awori E, Tumwekwase S (2010) Development of a hot pepper root rot and wilt disease management strategy through genetic resistance, chemical application and proper choice of rotational crops. Research Application Summary presented at the *Second RUFORUM Biennial Meeting*, 20-24 September 2010, Entebbe, Uganda

Yunianti R, Sastrosumarjo S, Sujiprihati S, Surahman M, Hidayat SH (2011) Diallel analysis of chili (*Capsicum annuum* L.) resistance to *Phytophthora capsici* Leonian. *Jurnal Agronomi Indonesia* **39 (3)**, 168-172

Zečević B, Đorđević R, Balkaya A, Damnjanović J, Đorđević M, Vujošević A (2011) Influence of parental germplasm for fruit characters in F_1, F_2 and F_3 generations of pepper (*Capsicum annuum* L.). *Genetika* **43 (2)**, 209-216

Zewdie Y, Bosland PW (2001) Combining ability and heterosis for capsaicinoids in *Capsicum pubescens. HortScience* **36 (7)**, 315-1317