

Diallel analysis and heterosis components in paprika peppers¹

Análise dialélico e componentes da heterose em pprica

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ABSTRACT - The aim of this study was to quantify and assess the components of heterosis in paprika hybrids related to yield, capsanten pigment content (estimated as ASTA degrees) and resistance to *Phytophthora capsici*, and to identify parental lines with high general combining ability (GCA) to be used in future breeding programmes and/or to obtain new hybrids. Fifteen hybrids were obtained through a complete diallel cross (reciprocal hybrids excluded) among six proprietary paprika breeding lines from HortiAgro Sementes S.A., four of which originally introduced from Peru (P_1 =PIM 032-03; P_2 =PIM 033-11; P_3 =PIM 034-19; P_4 =PIM 035-01) and two from the U.S.A. (P_5 =PIM 036-08; P_6 =PIM 037-18). Epistatic gene action was involved in the expression of heterosis for fresh and dry yields and carotenoid pigment contents, and heterosis was predominantly in the direction of higher yields. No significant heterosis effects were detected for resistance to *P. capsici*, and gene action was of incomplete dominance for the resistant phenotype. The parental lines P_1 and P_5 showed high GCA values for all characters, and may be used in breeding programmes to obtain new improved lines or for the production of higher yielding hybrids. The most promising hybrid was $P_3 \times P_5$, which outperformed the standard cultivar "Papri Queen" in fresh (68 t ha⁻¹) and dry (10 t ha⁻¹) fruit yields and ASTA degrees (157), in addition to being resistant to *P. capsici*. The parental line P_5 , as well as the hybrids in which it participated as a parent were assessed as resistant to *P. capsici*.

Key words: *Capsicum annum*. General combining ability. *Phytophthora capsici*. Hybrid vigor. Gene action. Epistasis.

RESUMO - O objetivo deste estudo foi quantificar e avaliar os componentes da heterose em hbridos de pprica para produtividade, teor de capsanteno (graus ASTA) e resistncia a *Phytophthora capsici*, e identificar as linhagens parentais elevada capacidade geral de combinao (CGC) para serem utilizados em futuros programas de melhoramento e/ou para obter novos hbridos. Para tanto, 15 hbridos foram obtidos por cruzamentos diallicos (excluindo os recprocos) entre seis linhagens from Hortiagro Sementes S.A. Elas so oriundas do Peru (P_1 =PIM 032-03; P_2 =PIM 033-11; P_3 =PIM 034-19; P_4 =PIM 035-01) e dos EUA (P_5 =PIM 036-08; P_6 =PIM 037-18). Os resultados indicam que a ao gnica episttica controla a heterose de produtividade de frutos frescos e secos, e o teor de capsantenos, sendo, em geral, a heterose no sentido de aumentar a produtividade. A resistncia a *P. capsici* no teve efeito hetertico significativo, sendo explicado por dominncia incompleta no sentido da Resistncia. As linhagens parentais P_1 e P_5 mostraram elevada CGC para os caracteres avaliados, e poderiam ser utilizadas em programas de melhoramento para obter novas linhagens melhoradas ou para a produo de hbridos com elevada produtividade.. O cruzamento $P_3 \times P_5$ superou  testemunha 'Papri Queen' em produtividade de frutos frescos (68 t ha⁻¹), secos (10 t ha⁻¹), graus ASTA (157) e resistncia a *P. capsici*. A linhagem P5 assim como nos hbridos onde participou como parental foram avaliados como resistentes.

Palavras-chaves: *Capsicum annum*. Capacidade geral de combinao. *Phytophthora capsici*. Vigor hbrido. Ao gentica. Epistasis.

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INTRODUCTION

The presence of heterosis in paprika set the possibility to create hybrid cultivars (REIFSCHNEIDER; RIBEIRO; CARVALHO, 2013; SOMOGYI, 2010; SOMOGYI *et al.*, 2011; SURYA KUMARI *et al.*, 2014). The knowledge of the F₁ hybrids behavior comparing to their parent cultivars let the breeder choose the best genetic combinations between the paprika lines for the considering trait.

The efficiency in the obtaining process of lines or cultivars that could be used for hybrid seeds production demands the knowledge of the genetic effects involved in the traits determination. One difficulty faced in the selection process is the non-information about the inheritance of the quantitative traits. The achievement of this information may enable highest genetic gains, increasing the breeding programs efficiency. Diallel crosses are important ways to obtain this information, providing useful parameters estimative in the selection of parents for hybridization (CRUZ; REGAZZI; CARNEIRO, 2012). The analyzing method proposed by Gardner and Eberhart (1966) preview a detailed study of the heterosis and its components, providing a fast way to evaluate the parent lines potential for hybrids achievement.

Amongst the available diallel analyzing methods, the one proposed by Jinks and Hayman (1953) bases in the environmental nature and statistics genetic knowledge (averages, variances and covariances) obtained from a diallel table, providing information about the studying trait genetic control, the genetic values and selection limits of the studying traits (CRUZ; REGAZZI; CARNEIRO, 2012; VENCOSKY; BARRIGA, 1992).

Somogyi (2010), tested experimental paprika hybrids in Hungry and related that for dry matter and ground color obtained by the powdering of dry fruits, the hybrids showed intermediary values related to the parents averages. However, the hybrids showed fruit production values five to six times higher than the obtained by the open population cultivars, defending the use of the hybrids for higher gains in yield for area unit.

The aim of this study was to evaluate the heterosis components in paprika hybrids for productivity, carotenoids pigments amount and resistance to *Phytophthora capsici*, and identify, between the used lines, parents with good general combining ability, that could be used in future breeding programs or to obtain new hybrids.

MATERIAL AND METHODS

Crosses

Six lines from Hortiagro Seeds S.A.'s *Capsicum annum* L. breeding program with paprika characteristics were used to obtain the experimental F₁ hybrids: four from Peru (P₁=PIM 032-03; P₂=PIM 033-11; P₃=PIM 034-19; P₄=PIM 035-01) and two from the USA (P₅=PIM 036-08; P₆=PIM 037-18). The lines were previously selected by the tasting test through two self-generations and characterized as non-pungent (no capsaicin).

The crosses were made manually in green houses with all the lines, through flower buds emasculations followed by controlled pollination, by the diallel scheme (without the reciprocal), obtaining 15 experimental hybrids.

Agronomic test

Fifteen hybrids from the previous step were tested, along the six parental lines (P₁=PIM 032-03; P₂=PIM 033-11; P₃=PIM 034-19; P₄=PIM 035-01; P₅=PIM 036-08; P₆=PIM 037-18) and the open population cultivar "Papri Queen" used as control, totalizing 22 treatments.

The experiment was carried out at the Vegetable Research Station of Hortiagro Sementes S.A., Ijaci-MG-Brasil (21°14'16" S, 45°08'00" W, altitude 920 m). Seeds were sown on October 23rd of 2011 in 128 cells Styrofoam trays and, 30 days after, they were transplanted to plastic covered beds. A random complete block design was used with four replications and 11 plants in each parcel, totalizing 968 plants. Was used the spacing of 0.75 m between lines and 0.35 m between plants in the line, resulting in a density of 38 thousand plants per hectare.

In the end of four consecutive harvestings (03/01/2012, 03/28/2012, 05/02/2012 and 05/31/2012) per experimental plots, done when the fruits achieved maturity and were completely red, was estimated the fresh fruits total production.

Samples of approximately 800 g of fresh fruits from each parcel were taken for the determination of dry weight. After measured their initial weight (fresh weight), the fruits were dried in laboratory oven with forced air circulation for five days at 50 °C until reach constant weight. The sample's weights were measured again and then estimated the percentages of dried matter that, multiplied by their fresh fruit yield, resulted in the dried fruit estimative.

The dried samples were stored in paper bags for 90 days at room temperature and later they were powdered in electric grinder (MARCONI MA 340).

The fruits capsantin content of each plot was determined by the ASTA 20.1 methodology (AMERICAN SPICE TRADE ASSOCIATION, 2004). The absorbances were measured, in spectrophotometer regulated to wave length of 460 nm, of each plot and the data were expressed in ASTA units.

Inoculation and resistance evaluation to *Phytophthora capsici*

The genotypes reactions to the pathogen *P. capsici* were determined in a side experiment, by inoculation with the pathogen. The plants were inoculated with solution containing a mix of the *P. capsici* isolates “Pc11” and “Pc31” when they achieved 10 cm high in a random complete block design with four replications and eight plants per plot. These isolates were obtained with the Sakata/Agroflora company, Bragança Paulista, SP, and were originally collected in the region of Bernardino de Campos, SP and Santa Cruz do Rio Pardo, SP, respectively. The isolates were kept, grown and cultivated following the methodology according to Urben (1980). After seven days, were deployed with Drigalsky handle. To release zoospores, the sporangia suspension was kept under incubation at room temperature for one hour. The suspension was then filtered into tissue and withdrawing a portion of filtrate for counting the zoospores amount in a Neubauer chamber. To stimulate zoospores encystment, the suspension was vortexed for one minute. After counting and established dilution at a concentration of 10^4 zoospores/5 ml the zoospores suspension was immediately used.

On January 15, 2012, at 45 days after seeds sown, the seedlings in the Styrofoam trays were inoculated with 5ml of the suspension in each cell, close to the plants stem. Daily evaluations were made after the inoculation, using a scale of scores (1 = no symptoms, 2 = wilting and necrosis and 3 = plant death). The plant mortality percentage was also registered. The evaluations started at the third day after inoculation until January 30, 2012, the 15th day after inoculation, date that was registered the scores and plants mortality percentage.

Statistics analyses

Dried and fresh fruit yield, ASTA degrees, scores and mortality rate data were analyzed according to the diallel model of Gardner and Eberhart (1966) assuming the fixed model:

$$y_{ij} = \mu + (v_i + v_j)/2 + \Theta(\bar{h} + h_i + h_j + s_{ij}) + e_{ij}, \text{ where } \Theta = 0 \text{ if } i=j, \text{ or } \Theta = 1 \text{ se } i \neq j$$

Wherein:

y_{ij} : average value of genotype ij.

μ : general average;

v_i e v_j : i-th or j-th variety effect, respectively;

\bar{h} : average heterosis

h_i e h_j : i-th and j-th variety heterosis effect, respectively;

s_{ij} : specific heterosi's effect

e_{ij} : average experimental error

The variety effects (v_i), average heterosis (\bar{h}) and varietal heterosis (h_i) from Gardner and Eberhart (1966) were analyzed in equal to the concepts of general and specific combining ability from Sprague and Tatum (1942):

$$g_i = 1/2v_i + \bar{h} + h_i$$

Wherein:

g_i = parental i's general combining ability

v_i = variety's effect

\bar{h} = average heterosis

h_i = varietal heterosis

The data were also graphically analyzed according to the diallel analyzing model proposed by Jinks and Hayman (1953), wherein the regression coefficient estimative “ β ” of W_r (parental line progeny's “r” covariance with the non-recurrent parental) in V_r (parental line's “r” variance) other than 1 indicates presence of epistasis; and, if not, its absence. Duncan test was used for averages comparison, with 5% probability.

RESULTS AND DISCUSSION

Fresh fruits yield

The treatments differed in fresh fruit total yield (Table 1). The average heterosis component, obtained by Gardner and Eberhart's analysis, was significant, indicating that hybrids averages were in general significantly higher than the parent's average, and that heterosis is predominantly unidirectional (in the way of higher yields) (Table 1). The varietal and specific heterosis components were not significant (Table 1), indicating that were not detected differences in the parents contribution to the heterosis and there were not differences in the parents allele frequency. The results indicate, therefore, that hybrids fresh fruit total yield may be estimated, in general, by the parent's average added the corresponding value of the average heterosis estimated for all hybrids.

The high positive value and significance of the GCA estimatives, according with the equivalence of Sprague

Table 1 - Analyses of variance according Gardner and Eberhart (1966) for fruits yield and color, and *Phytophthora capsici* resistance

Fonts of variation	GL	Mean Squares				
		Fresh fruit yield (t ha ⁻¹)	Dried fruit yield (t ha ⁻¹)	Color (ASTA degrees)	<i>P. capsici</i> resistance (score [†])	Mortality percentage caused by <i>P. capsici</i>
Treatments	20	276.48**	5.24*	1771.04**	0.4966**	1583.83**
Varieties	5	302.13*	4.47 ^{ns}	1419.24 ^{ns}	1.7231**	5382.87**
Heterosis	15	267.93*	5.49*	1888.31**	0.0877 ^{ns}	317.49 ^{ns}
Average Heterosis	1	918.11**	19.46*	235.04 ^{ns}	0.0032 ^{ns}	179.46 ^{ns}
Varietal Heterosis	5	219.40 ^{ns}	4.08 ^{ns}	1368.49 ^{ns}	0.1160 ^{ns}	551.36 ^{ns}
Specific Heterosis	9	222.66 ^{ns}	4.72 ^{ns}	2360.80**	0.0814 ^{ns}	202.89 ^{ns}
Error	60	120.06	2.87	748.12	0.1359	403.05
Coefficient of Variation (%)		21.82	20.93	24.58	18.05	33.39

*, ** (P<0.05) e (P<0.01) respectively; ns: no significant; † score:1 = no symptoms, 2 = wilting and necrosis and 3 = plant death

and Tatum (1942) concepts (Table 2), to a line's fresh fruit total yield are important indicators of their potentiality in generating good populations, because indicates high frequency of additive nature favorable alleles (CRUZ; REGAZZI; CARNEIRO, 2012). Thus, the parents P₁ and P₅, showing GCA of 11.3 and 16.1 t ha⁻¹, respectively (Table 2), have good potential in being utilized in breeding programs, looking for new lines selection and/or to obtaining more productive hybrids.

In the other hand, SCA estimates may have important genetic meaning, both their signal and their relative magnitude. The SCA (s_{ij}) average components estimates ranged from -9.63 to 11.2 t ha⁻¹ (amplitude of 20.8 t ha⁻¹) (Table 2), which is fairly representative of the average (μ=45.0 t ha⁻¹) and indicative that, beyond the additive genetic effects, the non-additives also may be important on traits expression of some hybrids. Indeed, however for the hybrid's majority, the s_{ij} estimates were close to the pattern-error (and, so, non significant), some cases the s_{ij} value were significantly positive (s₁₄ = 9.74; s₃₅ = 11.2) or negatives (s₁₅ = -9.63), which would indicates that, in these cases, the "per se" parental's average is not a good indicator for the hybrids average performance to fresh fruit total yield.

The highest SCA's positive estimates belong to the P₃xP₅ and P₁xP₄ hybrids with values of 11.2 e 9.74 t ha⁻¹, respectively (Table 2). These same hybrids showed, beyond a high SCA value, at least one parental with high GCA value, which is desirable. The SCA is related, in your major parts, to the non-additive allele frequency differences, presenting an important variation source to the fresh fruit total yield in these hybrids.

The significance of the heterosis effects (Table 1) highlights the importance of non-additives effects,

emphasizing the importance of the non-additive allele interactions in this trait control. Similarly, Shapturenko *et al.* (2014), Shrestha, Luitel and Kang (2011), Nascimento *et al.* (2010) and, Prasath and Ponnuswami (2008) also related significant heterosis for total fruit yield in *Capsicum annum*, suggesting that non-additive effects are more important.

In addition, the non-additive effects nature means to be epistatic, once the β regression coefficient between W_r and V_r, measured by Jinks and Hayman (1953) diallel analyses, was significantly other than 1 (Table 3).

Dried fruits yield

Differences were detected between the treatments for dried fruits total yield (Table 1). The non-significant varietal heterosis indicates that were not detected differences in the parents contribution to the heterosis. The non-significant specific heterosis indicates that there not to be, in general, differences in the allele frequencies between the parents (Table 1).

The average heterosis' component was significant and positive, indicative that the hybrids yield was higher than the parent's average (Table 1), whilst the varietal and specific heterosis' components were non-significant. The results indicate, however, that the hybrid's dried fruit total yield may, in general, be estimated as the parent's average plus the correspondent value estimated for the average heterosis (\bar{h}).

The parents P₁ and P₅, with GCA estimates of 1.67 and 1.98 t ha⁻¹, respectively, may be used in breeding programs, looking for selection of new lines and/or to obtain more productive hybrids, according to the equivalence of Sprague and Tatum's (1942) concepts mentioned before.

Table 2 - Estimates of average (μ), variety effect (v_i), average (\bar{h}) and varietal heterosis (h_i), general combination ability (g_i) and specific heterosis (s_{ij}) for fruits yield, color and *Phytophthora capsici* resistance

Mean components	Fresh fruit yield (t ha ⁻¹)	Dried fruit yield (t ha ⁻¹)	Color (ASTA degrees)	<i>P. capsici</i> resistance (score [†])	Mortality percentage caused by <i>P. capsici</i>
μ	45.0 (\pm 2.23)	7.33 (\pm 0.34)	113.9 (\pm 5.67)	2.03 (\pm 0.08)	57.4 (\pm 4.73)
V_i					
P ₁	2.01 (\pm 5.00)	0.40 (\pm 0.77)	-6.31 (\pm 12.69)	-2.80 (\pm 0.19)	-11.6 (\pm 10.6)
P ₂	6.54 (\pm 5.00)	1.25 (\pm 0.77)	11.2 (\pm 12.69)	0.11 (\pm 0.19)	3.87 (\pm 10.6)
P ₃	-5.84 (\pm 5.00)	-1.05 (\pm 0.77)	1.81 (\pm 12.69)	0.30 (\pm 0.19)	17.5 (\pm 10.6)
P ₄	-3.03 (\pm 5.00)	-0.56 (\pm 0.77)	-17.7 (\pm 12.69)	0.60 (\pm 0.19)	30.0 (\pm 10.6)
P ₅	1.80 (\pm 5.00)	-0.15 (\pm 0.77)	-10.4 (\pm 12.69)	-0.70 (\pm 0.19)	-36.6 (\pm 10.6)
P ₆	-1.48 (\pm 5.00)	0.12 (\pm 0.77)	21.4 (\pm 12.69)	-0.03 (\pm 0.19)	-3.27 (\pm 10.6)
\bar{h}	7.32 (\pm 2.64)	1.07 (\pm 0.40)	-3.71 (\pm 6.71)	0.02 (\pm 0.10)	3.74 (\pm 5.59)
h_i					
P ₁	3.06 (\pm 3.53)	0.40 (\pm 0.54)	7.22 (\pm 8.97)	0.05 (\pm 0.13)	-1.22 (\pm 7.48)
P ₂	-7.71 (\pm 3.53)	-1.17 (\pm 0.54)	-12.8 (\pm 8.97)	0.22 (\pm 0.13)	15.9 (\pm 7.48)
P ₃	-0.32 (\pm 3.53)	-0.01 (\pm 0.54)	-1.94 (\pm 8.97)	0.02 (\pm 0.13)	0.02 (\pm 7.48)
P ₄	-1.10 (\pm 3.53)	0.00 (\pm 0.54)	-6.29 (\pm 8.97)	-0.01 (\pm 0.13)	2.25 (\pm 7.48)
P ₅	7.97 (\pm 3.53)	0.99 (\pm 0.54)	22.7 (\pm 8.97)	-0.21 (\pm 0.13)	-13.7 (\pm 7.48)
P ₆	-1.90 (\pm 3.53)	-0.20 (\pm 0.54)	-8.92 (\pm 8.97)	-0.07 (\pm 0.13)	-3.26 (\pm 7.48)
	$g_i = 1/2v_i + \bar{h} + h_i$ (Sprague; Tatum, 1942)				
P ₁	11.3 (\pm 8.67)	1.67 (\pm 1.32)	0.35 (\pm 22.02)	-1.33 (\pm 0.33)	-3.28 (\pm 18.4)
P ₂	2.88 (\pm 8.67)	0.52 (\pm 1.32)	-10.8 (\pm 22.02)	0.29 (\pm 0.33)	21.6 (\pm 18.4)
P ₃	4.08 (\pm 8.67)	0.53 (\pm 1.32)	-4.74 (\pm 22.02)	0.18 (\pm 0.33)	12.5 (\pm 18.4)
P ₄	4.70 (\pm 8.67)	0.79 (\pm 1.32)	-18.8 (\pm 22.02)	0.30 (\pm 0.33)	21.0 (\pm 18.4)
P ₅	16.1 (\pm 8.67)	1.98 (\pm 1.32)	13.7 (\pm 22.02)	-0.54 (\pm 0.33)	-28.3 (\pm 18.4)
P ₆	4.68 (\pm 8.67)	0.93 (\pm 1.32)	-1.90 (\pm 22.02)	-0.06 (\pm 0.33)	-1.15 (\pm 18.4)
s_{ij}					
1x2	3.64 (\pm 4.24)	0.46 (\pm 0.65)	1.54 (\pm 10.77)	-0.06 (\pm 0.16)	-1.19 (\pm 8.98)
1x3	-5.78 (\pm 4.24)	-0.52 (\pm 0.65)	-34.5 (\pm 10.77)	0.16 (\pm 0.16)	3.72 (\pm 8.98)
1x4	9.74 (\pm 4.24)	1.40 (\pm 0.65)	6.03 (\pm 10.77)	-0.25 (\pm 0.16)	-8.93 (\pm 8.98)
1x5	-9.63 (\pm 4.24)	-1.47 (\pm 0.65)	-2.01 (\pm 10.77)	0.10 (\pm 0.16)	9.82 (\pm 8.98)
1x6	2.03 (\pm 4.24)	0.13 (\pm 0.65)	28.9 (\pm 10.77)	0.04 (\pm 0.16)	-3.43 (\pm 8.98)
2x3	-3.81 (\pm 4.24)	-0.45 (\pm 0.65)	-8.24 (\pm 10.77)	0.04 (\pm 0.16)	3.22 (\pm 8.98)
2x4	-5.74 (\pm 4.24)	-0.77 (\pm 0.65)	17.4 (\pm 10.77)	0.15 (\pm 0.16)	-0.50 (\pm 8.98)
2x5	5.88 (\pm 4.24)	0.99 (\pm 0.65)	-21.4 (\pm 10.77)	-0.13 (\pm 0.16)	-9.52 (\pm 8.98)
2x6	0.03 (\pm 4.24)	-0.23 (\pm 0.65)	10.7 (\pm 10.77)	0.00 (\pm 0.16)	7.98 (\pm 8.98)
3x4	1.06 (\pm 4.24)	0.17 (\pm 0.65)	12.6 (\pm 10.77)	0.13 (\pm 0.16)	8.57 (\pm 8.98)
3x5	11.2 (\pm 4.24)	1.42 (\pm 0.65)	30.2 (\pm 10.77)	-0.16 (\pm 0.16)	-4.62 (\pm 8.98)
3x6	-2.68 (\pm 4.24)	-0.62 (\pm 0.65)	-0.18 (\pm 10.77)	-0.17 (\pm 0.16)	-10.9 (\pm 8.98)
4x5	-6.58 (\pm 4.24)	-1.23 (\pm 0.65)	-1.70 (\pm 10.77)	0.01 (\pm 0.16)	-0.60 (\pm 8.98)
4x6	1.51 (\pm 4.24)	0.43 (\pm 0.65)	-34.4 (\pm 10.77)	-0.04 (\pm 0.16)	1.44 (\pm 8.98)
5x6	-0.90 (\pm 4.24)	0.29 (\pm 0.65)	-5.11 (\pm 10.77)	0.17 (\pm 0.16)	4.91 (\pm 8.98)

P₁=PIM 032-03; P₂=PIM 033-11; P₃=PIM 034-19; P₄=PIM 035-01; P₅=PIM 036-08; P₆=PIM 037-18; †score:1 = no symptoms, 2 = wilting and necrosis and 3 = plant death

Table 3 - Regression coefficients (β) for association of Wr and Vr from Jinks and Hayman (1953) diallel analyses for fruit yield and color and *Phytophthora capsici* resistance

Characteristic	β	H0: $\beta=0$	H0: $\beta=1$	Epistasis
Fresh fruit yield (t.ha ⁻¹)	0.064403	ns	**	sim
Dried fruit yield (t.ha ⁻¹)	0.123105	ns	**	sim
Color (ASTA degrees)	0.042529	ns	**	sim
<i>P. capsici</i> resistance (scores)	0.807188	**	ns	não
Mortality by <i>P. capsici</i> (%)	1.075527	**	ns	não

**,: *:($P<0.01$) and ($P<0.05$) respectively by t test. ns: no significant

The estimates of the SCA average's components (s_{ij}) ranged from -1.47 to 1.42 t ha⁻¹ (amplitude of 2.89 t ha⁻¹) (Table 2), which equates to about 40% of average ($\mu=7.33$ t.ha⁻¹) and indicative that, further the additive genetic effects, the non-additives may also be important on the trait's expression. Similarly to the exposed for fresh fruit total yield, also for dried fruit total yield the majority of the s_{ij} estimates didn't differ from zero. Just in the hybrids $P_1 \times P_4$ ($s_{14} = +1.40$) and $P_3 \times P_5$ ($s_{35} = +1.42$) the s_{ij} values were significantly higher than zero, whilst for $P_1 \times P_5$ ($s_{15} = -1.47$) and $P_4 \times P_5$ ($s_{45} = -1.23$) the s_{ij} values may be consider smaller than zero. Thus, only in these few cases the "per se" parent's average is not a good indicative of the hybrid's average performance for dried fruit total yield.

The hybrids $P_3 \times P_5$ and $P_1 \times P_4$ showed the highest positive estimates of SCA with values of 1.42 and 1.40 t ha⁻¹, respectively (Table 2). These hybrids also showed, besides the high value of SCA, at least one parent with high value of GCA, which is desirable.

The significance of the heterosis (Table 1), by the Gardner and Eberhart (1966) method, indicates the non-additive effects are responsible for the dry matter amount increase. Therefore, the use of hybrids may contribute to increase significantly the paprika cultivars yield. Prasath and Ponnuswami (2008) found heterosis over the best parent ranged from -40.35 to 126.32 percent, being non additive effects more important for this character.

The regression coefficient β between Wr and Vr, measured by Jinks and Hayman (1953) analysis, was significantly different of 1 (Table 3), pointing the non-additive effects are, at least in part, epistatic nature.

Parent 2 (PIM 033-11) showed the highest variety effect with 1.25 t ha⁻¹ (Table 2), becoming the most promising genitor for be used as "per se" variety, in the other hand it showed low GCA value (0.52 t ha⁻¹) (Table 2), what decreased its value as parental line for hybrids development. Nevertheless, parent 5 (PIM 036-08), with

the highest GCA ($g_5 = +1,98$) has good potential for be used as genitor line for hybrids production.

Fruits color

Capsaten is the main pigment in paprika (KEVRESAN *et al.*, 2009) for this reason ASTA method focus in quantify it. Parent lines PIM 033-11 (P_2) and PIM 037-18 (P_6) showed higher capsanten content (ASTA>125) than control line "Papri Queen" (ASTA=90.4) (Table 4). The observed heterosis for this trait can be mainly explained by specific heterosis (Table 1), indicating that heterosis is due to the difference in allele frequency amongst individual parents.

P_5 was the only parent line that showed high value of GCA (13.7 ASTA degrees) that however, cannot be considered as different from zero, due to the magnitude of the standard deviation of its estimate (Table 2).

The estimates of the SCA average components (s_{ij}) ranged from -34.5 to 30.2 ASTA degrees (64.7 ASTA degrees of amplitude) (Table 2), what equate to about 57% of the average ($\mu=113.9$ ASTA degrees) and indicates that, besides the additive gene effects, the non-additives are also important for the trait expression. Thus, just the parent's "per se" average is not a good indicative for the hybrid's performance on capsanten content.

The highest positive estimates for SCA (s_{ij}) belong to the hybrids $P_1 \times P_6$ and $P_3 \times P_5$ with values of 28.9 and 30.2 ASTA degrees, respectively (Table 2). The hybrid $P_3 \times P_5$ has the parent P_5 , which has the highest value of GCA, what makes it the hybrid with the best coloration amongst the hybrids tested (Table 4). On the other hand, in the hybrid $P_1 \times P_6$, the parents show low or negatives GCA values, presuming the non additive effects were more important for the superiority of this hybrid combination (Table 2), however, it was lower than the hybrid $P_3 \times P_5$.

The significance of just the heterosis indicates the non-additive effects are the most important on the expression of the trait. These findings are different from found by Surya Kurami *et al.* (2014), they could not

Table 4 - Averages of fruit yield and color, ASTA degrees and *Phytophthora capsici* resistance

Genotype	Fresh fruit yield (t ha ⁻¹)	Dried fruit yield (t ha ⁻¹)	ASTA degrees	<i>P. capsici</i> resistance (score [†])	Mortality percentage caused by <i>P. capsici</i>
P ₁ xP ₂	55.4 abc1	8.92 abcd	108.6 bcd	2.17 abcde	70.8 abcde
P ₁ xP ₃	47.2 bc	8.01 abcd	78.7 de	2.29 abcd	66.6 abcde
P ₁ xP ₄	63.3 ab	10.10 ab	105.1 bcde	2.00 bcdef	62.5 abcdef
P ₁ xP ₅	55.4 abc	8.58 abcd	129.7 abc	1.50 ef	31.9 efg
P ₁ xP ₆	55.6 abc	9.08 abcd	145.0 ab	1.92 bcdef	45.8 cdefg
P ₂ xP ₃	40.7 c	6.88 cd	93.7 cde	2.52 ab	91.0 ab
P ₂ xP ₄	39.4 c	6.81 cd	105.2 bcde	2.75 a	95.8 a
P ₂ xP ₅	62.4 ab	9.68 abc	99.0 cde	1.63 cdef	37.5 defg
P ₂ xP ₆	45.1 bc	7.44 abcd	115.5 abcd	2.24 abcd	82.1 abc
P ₃ xP ₄	47.4 bc	7.84 abcd	106.6 bcde	2.63 ab	95.8 a
P ₃ xP ₅	67.8 a	10.20 a	156.9 a	1.50 ef	33.3 efg
P ₃ xP ₆	43.6 c	7.09 bcd	110.7 bcd	1.96 bcdef	54.1 bcdefg
P ₄ xP ₅	51.8 abc	7.84 abcd	110.8 bcd	1.79 cdef	45.8 cdefg
P ₄ xP ₆	48.4 bc	8.34 abcd	62.4 e	2.21 abcde	75.0 abcd
P ₅ xP ₆	57.2 abc	9.38 abc	124.3 abcd	1.58 def	29.1 fg
P ₁ =(PIM-032-03)	46.9 bc	7.64 abcd	107.6 bcde	1.75 cdef	45.8 cdefg
P ₂ =(PIM-033-11)	51.4 abc	8.50 abcd	125.1 abcd	2.14 abcde	61.3 abcdef
P ₃ =(PIM-034-19)	39.0 c	6.31 d	115.7 abcd	2.33 abc	75.0 abcd
P ₄ =(PIM-035-01)	41.8 c	6.78 cd	96.1 cde	2.63 ab	87.5 ab
P ₅ =(PIM-036-08)	46.6 bc	7.10 abcd	103.4 bcde	1.33 f	20.8 g
P ₆ =(PIM-037-18)	43.1 c	7.34 abcd	135.3 abc	2.00 bcdef	54.1 bcdefg
Papri Queen	48.5 bc	7.57 abcd	90.4 cde	2.13 abcde	65.5 abcde

[†]Same letters at the columns indicate there not to be difference among genotypes by Duncan test ($P < 0,05$); [‡]score: 1 = no symptoms, 2 = wilting and necrosis and 3 = plant death

detect significance of any genetic effect for capsanten content.

The epistatic gene action contributes to the non-additive effects, once the β regression coefficient between W_r and V_r , measured by Jinks and Hayman (1953) diallel analyses, was significantly other than 1 (Table 3). This finding complement the findings of Prasath and Ponnuswami (2008), who reported importance of additive and non-additive effect for oleoresins content, which is a character related to capsanten content.

Resistance to *P. capsici*

According to Gardner and Eberhart (1966) analyses, heterosis was not detected to *P. capsici* resistance. The differences on the hybrids mortality rates may be explained basically to the differences on the variety's effect (v_i, v_j).

The GCA estimate values to the trait are of little magnitude. However, when positives, indicates a tendency

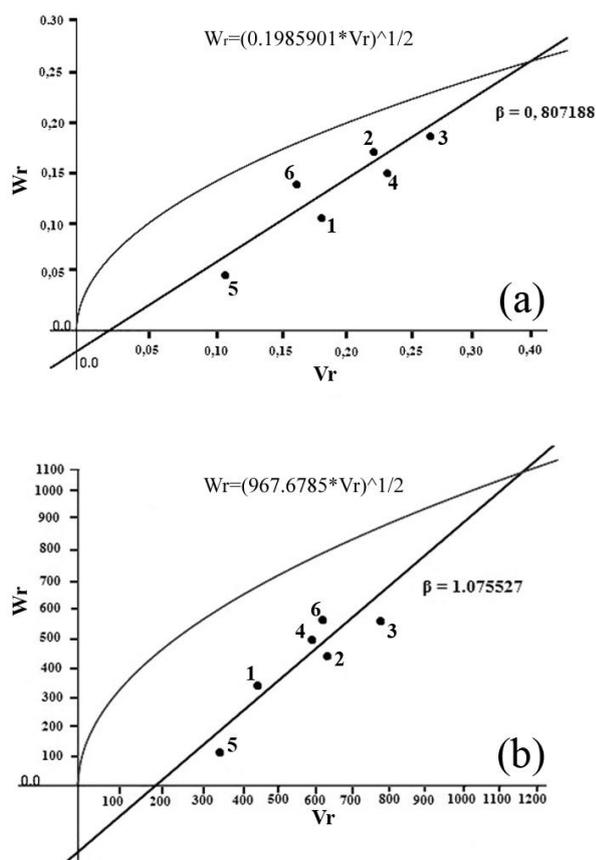
of the parents to originates plants with higher scores and higher mortality rates on the evaluation to *P. capsici* resistance. On the other hand, negative estimates indicates the parent contributes for a reduced mortality rate, what is desirable. The GCA estimate values for score ranged from -1.33 to 0.30 (1.63 amplitude) and for mortality rates the values ranged from -28.3% to 21.6% (49.9% amplitude) (Table 2). The parent P₅ stands out with the highest negative value of mortality rate (-28.3%), contributing favorably to the reduction of the trait expression (Table 2).

SCA estimates (s_{ij}) for scores ranged from -0.25 to 0.17 (0.42 amplitude), representing 20% of the average ($\mu=2.03$) (Table 2). For mortality rate, the SCA estimates ranged from -10.9% to 9.82% (20.7% amplitude), representing 36% of the average ($\mu=57.4\%$).

On Jinks and Hayman (1953) analyses, the regression coefficient between W_r and V_r , was estimated $\beta = 0.807$ for scores and $\beta = 1.075$ for mortality rate (Table 3), values that are not statistically different from

1 ($\alpha = 1\%$), but are statistically different from 0 ($\alpha = 1\%$), showing the additive-dominant model is adequate and there is no evidence of epistatic gene action. Line P_5 , showed the lowest scores and mortality rates (Table 4) and is located in the lower part of the regression lines (Figure 1), indicating to be the parent with more dominant alleles proportion.

Figure 1 - Regression between W_r and V_r and its limitant parabola for *Phytophthora capsici* scores (a) and mortality percent (b). (Parental lines: 1= PIM-032-03; 2= PIM-033-11; 3= PIM-034-19; 4= PIM-035-01; 5= PIM-036-08; 6= PIM-037-18.)



The graphical analyses (Figure 1) show the regression lines W_r in V_r intersect the y-axis in a negative value close to the source, which would indicate complete dominance gene action or mild over dominance of genes that control resistance. However, the most resistance parent (P_5) shows scores and plant mortality percentage slightly lower than the hybrids where it is a parent, indicating incomplete dominance, but with average dominance degree close

to 1. The alleles responsible to increase scores and mortality percentage are predominantly recessives, which concludes the correlations ($W_r + V_r$) and Y_r , $r = +0.895$ (scores) and $r = +0.848$ (mortality percentage). The most plausible hypothesis to the interpretation of the results is that *P. capsici* resistance found in P_5 is controlled by dominant allele(s), but with incomplete dominance.

CONCLUSIONS

1. In paprika, there is heterosis, in general, to increase fresh and dried fruit and capsanten content. The non-additive gene effects were at least in part epistatic;
2. Was not detected significant heterosis for *P. capsici* resistance, which is explained by incomplete dominance gene action;
3. The parent lines PIM 032-03 (P_1) and PIM 036-08 (P_5) showed high GCA, what makes them potential new lines or parents for being used in breeding programs for new hybrids;
4. The most promising hybrid for the traits evaluated was PIM 034-19 x PIM 036-08 (P_3 x P_5), outperforming the standard cultivar "Papri Queen" in fresh (68 t ha^{-1}) and dry (10 t ha^{-1}) fruit yields and ASTA degrees (157), in addition to being resistant to *Phytophthora capsici*;
5. The parental line PIM 036-08 (P_5), as the hybrids in which it was a parent were resistant to *P. capsici*.

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