DIALLEL ANALYSES AND ESTIMATION OF GENETIC PARAMETERS OF HOT PEPPER (*Capsicum chinense* Jacq.)

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ABSTRACT: The degree of heterosis in the genus *Capsicum* spp. is considered high; however, most of the studies refer to the species *Capsicum annuum* L. In spite of the potential use of F_1 hybrids in pungent peppers of the species *Capsicum chinense*, few studies are available which assess the magnitude of heterosis in this species . This study was carried out to assess heterosis and its components in F1 hybrids from a diallel cross between hot pepper lines (*Capsicum chinense*) and to obtain data on the allelic interaction between the parents involved in the crosses. Trials were made in Rio Branco-Acre, Brazil, from March through October 1997. A randomized complete block design with fifteen treatments and three replications was used. The treatments were five *C. chinense* accessions (from the Vegetable Germplasm Bank of the Universidade Federal de Viçosa – BGH/UFV) and 10 F1 hybrids derived from single crosses between them (reciprocals excluded). Diallel analyses were performed for total yield, fruit length/diameter ratio, fruit dry matter per plant, *Xanthomonas campestris* pv. *vesicatoria* incidence, capsaicin yield per plant and number of seeds per fruit. Non-additive genetic effects were larger than additive effects for all the traits assessed. Epistasis was detected for fruit dry matter per plant, capsaicin yield per plant and number of seeds per fruit. In these cases, epistasis seemed to be largely responsible for heterosis expression. Dominant gene action, ranging from incomplete dominance to probable overdominance, was responsible for heterosis in those traits where no epistatic genetic action was detected.
Key words: *Xanthomonas campestris* pv. *vesicatoria*, hot pepper, gene action, capsaicin

ANÁLISE DIALÉLICA E ESTIMAÇÃO DE PARÂMETROS GENÉTICOS EM PIMENTAS PUNGENTES (*Capsicum chinense* Jacq.)

RESUMO: Embora o grau de heterose no gênero *Capsicum* seja considerável, a maioria dos estudos refere-se à espécie *Capsicum annuum* L., sendo pouco frequentes os estudos na espécie *Capsicum chinense*. Objetivou-se com esse trabalho, avaliar a heterose e seus componentes em híbridos F_1 provenientes de um cruzamento dialélico de pimentas pungentes, da espécie *C. chinense*, bem como obter informações sobre o modo de interação alélica entre os genitores envolvidos no referido cruzamento. O trabalho foi conduzido em RioBranco-Acre, de março a outubro de 1997. O delineamento utilizado foi o de blocos completos casualizados com três repetições. Utilizaram-se 15 tratamentos, sendo 5 introduções de *Capsicum chinense* Jacq. (provenientes do Banco de Germoplasma de Hortaliças da Universidade Federal de Viçosa- BGH/UFV) e 10 híbridos F_1 resultantes do cruzamento entre esses genitores (sem distinção dos recíprocos). Os caracteres estudados foram produção total, relação comprimento/diâmetro de fruto, matéria seca de frutos por planta, incidência de *Xanthomonas campestris* pv. *vesicatoria*, rendimento de capsaicina por planta e número de sementes por fruto. Constatou-se a importância e predominância de efeitos gênicos não aditivos para todos os caracteres avaliados. O efeito de epistasia foi importante para matéria seca de frutos por planta, rendimento de capsaicina por planta e número de sementes por fruto. Nestes casos, a epistasia parece ser, em grande parte, responsável pela expressão da heterose. Para as demais características, onde não se detectou ação gênica epistática, a heterose se explica pela ação gênica dominância, nos seus mais variados graus, de dominância incompleta à provável sobredominância.
Palavras-chave: *Xanthomonas campestris* pv. *vesicatoria,* pimenta, ação gênica, capsaicina

INTRODUCTION

Significant levels of heterosis in F_1 hybrids are often the main reasons for the extensive use of hybrid cultivars of vegetable crops. Commercial exploitation of heterosis in hot peppers (*Capsicum chinense*), however, is virtually non-existent in Brazil, even through high levels of heterosis have been found in this species (Vallejo-Cabrera, 1986). Almost all the genetic studies on the *Capsicum* genus have been carried out on the *C. annuum* species, in spite of the high genetic variability of *C. chinense* for a large number of traits of agronomic interest (Ribeiro, 1987).

Information is rare on allelic interaction and heterosis in *C. chinense*. Diallel analyses could be deployed to study the combinig ability among hot pepper *C. chinense* lines. Diallel crosses can also help in parental selection, supplying data on parental genotypic values and, mainly, on their ability to combine in hybrids that produce promising segregant populations. Diallel

analysis also allows understanding genetic control of the trait, which helps the breeder to advance and select the segregant populations (Vencovsky & Barriga, 1992; Ramalho et al., 1993; Cruz & Regazzi, 1994).

The method proposed by Jinks and Hayman (Jinks & Hayman, 1953; Miranda et al., 1982) for diallel analysis allows a quick and general estimate of the genetic relationship among the parents involved in a diallel cross. Alternatively, the method of analysis proposed by Gardner & Eberhart (1966) provides a detailed study of heterosis and its components. Either diallel analyses in *Capsicum chinense* would provide a quick way of assessing the potential use of heterosis in this species.

The objectives of this work were to assess heterosis and its components in *Capsicum chinense* and to obtain data on the allelic interaction among the parents involved in crosses within this species.

MATERIAL AND METHODS

Five *C. chinense* lines (BGH-81; BGH – 4196; BGH-4285; BGH-1810; BGH-433), from the Vegetable Germplasm Bank (BGH) of the Federal University of Viçosa – MG (UFV) were used as parents of the ten possible experimental F_1 hybrid combinations (reciprocals excluded). The parents were identified as follows throughout this paper: BGH-81 =1, BGH-4196 = 2, BGH-4285 = 3, BGH-1810 = 4, BGH-433 = 5.

Seedlings of all treatments (5 lines + 10 F_1 hybrids) were produced in 128-cell extruded polystyrene trays and transplanted into a plastic house when the plants had four to six true leaves. Liming was carried out about 90 days earlier using 3.3 t ha^{-1} of dolomite lime (PRNT = 90%). The soil (Orthic Acrisol) was fertilized just before transplanting with 500 grams of a 4-14-8 formulation and 2 L of organic fertilizer (poultry manure) per linear meter of row. Cover fertilizer was applied four times starting 25 days after transplanting with 15 grams of urea per linear meter of row during the crop cycle. Standard crop management procedures used for the crop were deployed. Sprinkler irrigation was applied twice a day in the early phase, followed by furrow irrigation applied daily in the later phase.

The experiments were carried out in Rio Branco AC, Brazil, from March through October 1997 (latitude 9°58' S and longitude 67°48' W). A randomized complete block design with 15 treatments and three replications was used. Each experimental unit was a single three meter row plot with six plants, spaced at 1.40 m × 0.5 m. Sixteen harvests, scheduled every seven days, were carried out during a period of 3½ months. The following traits were assessed: total fruit yield; fruit length/diameter ratio; fruit dry matter per plant; *Xanthomonas campestris* pv. *vesicatoria* incidence (XVC); capsaicin yield per plant and number of seeds per fruit. Fruit characteristics were assessed from the sixth to the tenth harvests using a 20 fruit sample per plot. Capsaicin content analyses were carried out by the Weaver & Awde (1986) method at CTAA/Embrapa, Rio de Janeiro, RJ, Brazil. Five independent evaluations of the *Xanthomonas campestris* pv. *vesicatoria* incidence were carried out by different research staff using a scale of scores ranging from 1 to 5 for each plot. Score 1 corresponded to pathogen absence, and score 5 to the highest level of disease incidence.

Data was submitted to an analyses of variance and the means were compared by cluster analysis, according to Scott & Knott (1974). Heterosis relative to midparent was estimated for every hybrid and trait studied, and was statistically tested for significance by the t test. Diallel analyses were performed according to the procedures by Gardner & Eberhart (1966), and by Jinks & Hayman (1953).

RESULTS AND DISCUSSION

Mean squares indicated differences among treatments (α=0.05) for all the assessed traits. Differences were similarly detected for the parent and heterosis effects (Table 1). These results indicate the presence of considerable genetic variation among the genetic materials used.

In the model of diallel analysis proposed by Jinks & Hayman (1953), a "β" regression coefficient estimate different from 1 indicates the presence of epistasis; otherwise, its absence. There was no epistasis for total fruit yield, fruit length/diameter ratio or *Xanthomonas campestris* pv. *vesicatoria* incidence (Table 2). Graphic representations of Wr on Vr (Jinks & Hayman, 1953) for these traits are presented in Figures 1 to 3, with the limiting parabola and the straight line equations. Epistasis was detected for fruit dry matter per plant, capsaicin yield per plant and number of seeds per fruit, therefore further analysis by Jinks & Hayman's method did not apply to these cases, and was not performed. Table 3 shows the correlation coefficient between (Wr +Vr) and the mean (Yr) of the r parents, for the traits fully assessed by the analysis of Jinks & Hayman (1953).

Total fruit yield - The Scott & Knott test distinguished three groups among the parents and hybrids. Parent 3 and the 3× 5 hybrid, which formed an isolated group and were outstanding (Table 4) when compared to the other genotypes, showed the two greatest total yield means, 591.1 g per plant and 705.5 g per plant, respectively. Parents 1 and 4 and the 1× 5, 2× 5, 3× 4 and 4× 5 hybrids formed the group with the lowest means for this trait, 76.8, 96.7, 80.3, 133.6, 75.8, and 80.4 g per plant, respectively. The other groups, that were formed by parents 2 and 5 and the remaining hybrids, showed intermediate values (Table 4). Heterosis was negative for more than half of the hybrids, and ranged from –78% (3 × 4 hybrid) to +197% (hybrid 1× 4) (Table 4). However, heterosis should be jointly analyzed with its corresponding "per se" parent mean and hybrid mean,

because the hybrid displaying the greatest percent heterosis was not always the highest yielding one. Low performance parents can generate hybrids with high degree of heterosis, as was the case of hybrid 1× 4. Therefore, commercial heterosis can be better assessed by comparison with the superior parent, or when possible, by comparison with the yield of a check cultivar. This is the case of hybrid 3× 5, which although not highly heterotic, was the best performer.

The mean heterosis component ($\hat{b}_1$) obtained obtained from the Gardner-Eberhart analysis was not significant, indicating that the mean of the hybrids was not significantly different from the mean of the parents (Table 5). The varietal heterosis component was not significant either, indicating that there were no significant differences among hybrid arrays of the different parental lines. The significance of the specific heterosis component, however, indicated that there are specific hybrid combinations with a high degree of heterosis (Table 4). In spite of the negative heterosis obtained for some hybrids (Table 4), the use of F1 hybrids in *C. chinense* may in some cases result in significant yield increases, as was the case in hybrid 3 × 5.

The importance of the non-additive genetic effects (dominance and/or epistasis) for yield expression was demonstrated by the high contribution of the specific heterosis component to the treatment sum squares. Therefore, in spite of the significance of the parental effects (Table 1), the *per se* parental performance is not a good indicator of the hybrid total yield.

The amplitude of the specific heterosis estimates (specific combining ability) was 499.81 g per plant (Table 5), with the maximum value (positive) and the minimum (negative) of +327.46 grams/plant and –172.35 grams/plant, obtained by hybrids 3 × 5 and 3 × 4, respectively. This wide range was expected based on the significance of the specific heterosis effects (Table 1).

Analysis of total fruit yield using the Jinks & Hayman method indicated a Wr-Vr regression coefficient of $\beta = 0.845$ (Table 2), which differed from zero ($\alpha = 0.01$), but did not differ from one. Thus, the additive-dominance model was adequate to explain the genetic variability of this trait, and there was no evidence of epistatic gene action. The value of the correlation between (Wr + Vr) and $\overline{Y}r$ (r =0.802) (Table 3), positive and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields.

The rank of the parents according to a decreasing number of dominant genes for the trait was 4, 2, 1, 3 and 5, with small differences among the first three lines and between the last two lines, but with a large

Table 1 - Analyses of variance in for total fruit yield, fruit length/diameter ratio, fruit dry matter per plant, incidence of *Xanthomonas campestris* pv. *vesicatoria* - XCV, capsaicin yield per plant and number of seeds per fruit, in a diallel cross of *Capsicum chinese*. Rio Branco-AC, 1997.

Source of Variation	D.F.	MEAN SQUARES					
		Total fruit yield	Length/diameter ratio	Fruit dry matter per plant	XCV incidence	Capsaicin yield per plant	Number of seeds per fruit
Block	2	48926.62 *	0.1217 ns	910.353 *	0.0009 ns	90671.556 ns	5.104 ns
Treatment	14	107810.41 **	4.2364 **	2391.097 **	3.1916 **	182867.969 **	1971.538 **
Parents	4	189870.69 **	13.4840 **	3286.132 **	8.0432 **	289541.125 **	1787.501 **
Heterosis	10	74986.30 **	0.5373 **	2033.083 **	1.2510 **	140198.703 **	2045.154 **
Mean Heterosis	1	999.71 ns	1.3627 **	4.759 ns	5.0884 **	411842.750 **	2449.225 **
Varietal Heterosis	4	12772.14 ns	0.0696 ns	352.874 ns	0.3509 ns	107680.344 *	711.116 **
Specific Heterosis	5	139554.95 **	0.7464 **	3782.915 **	1.2036 **	111884.578 *	3031.570 **
Error	28	12635.00	0.0581	220.429	0.3942	30019.664	55.796
Means		246.81	2.1308	38.128	2.8355	306.118	31.213
C.V. (%)		45.54	11.3120	38.939	22.1422	56.600	23.931

**; * Significant at 1% and 5% by the F test, respectively.

Table 2 - Regression coefficient (β) values and respective t tests for total fruit yield, fruit length/diameter ratio, fruit dry weight per plant, *Xanthomonas campestris* pv. *vesicatoria* - XCV incidence, capsaicin yield per plant and seed number per fruit evaluated by the Jinks & Hayman (1953) diallel analysis. Rio Branco - AC, 1997.

Characters	β	$H_0 : \beta = 0$	$H_0 : \beta = 1$	Presence of Epistasis
Total fruit yield	0.8451024	**	ns	No
Fruit length/diameter ratio	0.9256034	**	ns	No
Fruit dry weight per plant	0.7403736	**	*	Yes
XCV incidence	0.8626796	*	ns	No
Capsaicin yield per plant	0.1277522	*	**	Yes
Seed number per fruit	0.6920375	**	*	Yes

**; * Significant at 1% and 5% by the t test, respectively. ns non-significant.

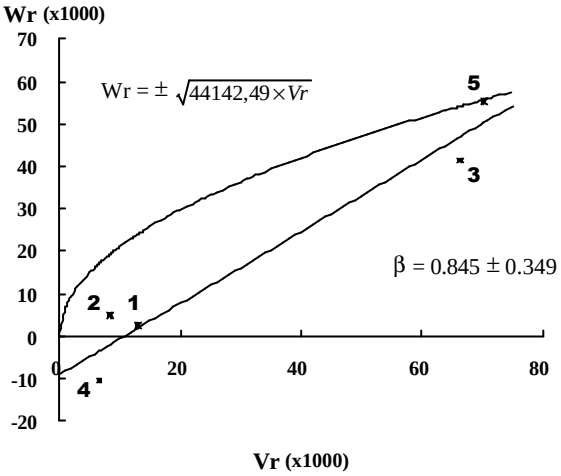

Figure 1 - Regression of Wr on Vr and limiting parabola for total fruit yield. Parents: 1= BGH-81; 2= BGH-4196; 3= BGH-4285; 4= BGH-1810; 5= BGH-433.

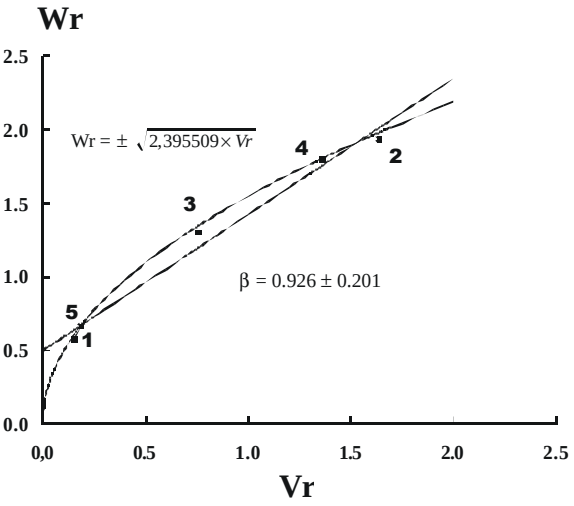

Figure 2 - Regression of Wr on Vr and limiting parabola for fruit length/ diameter ratio. Parents: 1= BGH-81; 2= BGH-4196; 3= BGH-4285; 4= BGH-1810; 5= BGH-433.

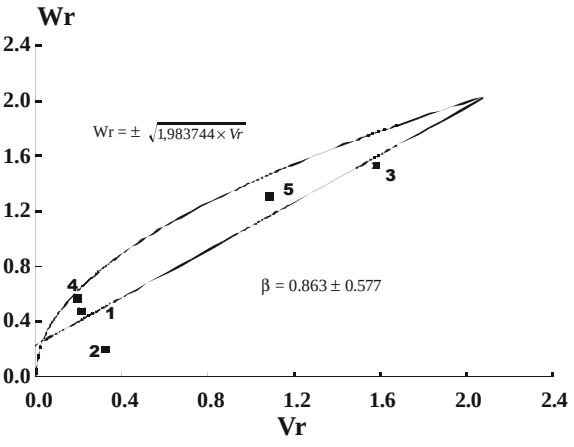

Figure 3 - Regression of Wr on Vr and limiting parabola for *Xanthomonas campestris* pv. *vesicatoria* incidence. Parents: 1= BGH-81; 2= BGH-4196; 3= BGH-4285; 4= BGH-1810; 5= BGH-433.

Table 3 - Regression coefficient (β) values, correlation coefficient between (Wr+Vr) and the r^{th} parent mean ($\overline{Y}r$) for total fruit yield, fruit length/diameter ratio, *Xanthomonas campestris* pv. *vesicatoria* - (XCV) incidence evaluated by the Jinks & Hayman (1953) diallel analysis. Rio Branco - AC, 1997.

Characters	β ± std. error	Correlation (r) (Wr + Vr) vs $\overline{Y}r$
Total fruit yield	0.8451024 ± 0.349	0.8017055*
Fruit length/diameter ratio	0.9256034 ± 0.201	0.9946718**
XCV incidence	0.8626796 ± 0.577	- 0.7850968*

**; * Significant at 1% and 5% by the t test, respectively. ns non-significant.

difference between the two groups. Indeed, parent 3, which is the highest yielding among those used in this study (Table 4), is located in the upper part of the straight line (Figure 1), indicating high number of recessive alleles. Parents 1, 4 and 2, which were the lower yielding, were located in the lower part of the straight line, showing that these parents have a greater proportion of dominant alleles. The straight line intercepted the ordinate axis (Wr) below the origin (Figure 1), indicating the presence of overdominance. This explains the considerable amount of heterosis previously detected for the trait.

Length/diameter ratio - The fruit length/diameter ratio allows inference on the fruit classification and shape. Round fruits have a ratio close to 1.0, whereas long fruits the have a ratio greater than 1.0. Parents 1and 5 were assigned to the same group (Table 4) and had round fruit, with ratio values of 0.93 and 0.84, respectively. Parent 2 showed the highest ratio (4.34) and was the most elongated parent among those used in this study. Among the hybrids, only two (1 × 3 and 1 × 5) were similar to the round shape parents, with ratio values of 1.01 and 0.92, respectively. Hybrid 2 × 4, with a ratio value of 4.28, was the only one that did not differ from the most elongated parent. The remaining hybrids showed intermediate ratio values which ranged from 1.38 to 3.19 (Table 4).

Most hybrids showed negative heterosis. The two exceptions were hybrids 1 × 5 and 2 × 4 which showed low positive values of heterosis, +4% and +9%, respectively (the former value was not significant). Similar results for this trait were obtained in studies with sweet pepper (*Capsicum annum)* (Miranda, 1987; Tavares, 1993).

Heterosis effects for fruit length/diameter ratio were significant, and largely due to the mean ($\overline{h}$) and specific heterosis (S_{ij}) components. The significant mean heterosis indicated that the hybrid means differed from the parent means (Table 5). Its negative value resulted from the fact that the hybrid mean fruit length/diameter ratios were usually lower than the parent means (Table

5). The varietal heterosis component was not significant (Table 1), indicating that there were only minor differences (if any) among the hybrid means from the different parents.

Considering the significance and contribution of the specific heterosis sum of squares for the treatment sum of the squares (Table 1), the importance of the non-additive genetic effects (dominance and epistasis) for the expression of this trait cannot be disregarded. Therefore, the parental performance does not efficiently predict the hybrid fruit length/diameter ratio.

The amplitude of the specific heterosis estimates was 1.05 with the maximum (+0.62) and minimum (-0.43) values shown by hybrids 2 × 4 and 2 × 5, respectively (Table 5). This amplitude reflects the specific heterosis effect.

Jinks & Hayman's analysis showed no evidence of epistatic gene action for fruit length/diameter ratio, as the Wr on Vr regression showed $\beta = 0.926$ (Table 2), which was not different from 1 ($\alpha = 0.01$), but was different from zero. The additive-dominance model was therefore adequate to explain genetic variability for this trait.

The high positive correlation (r = 0.995) between (Wr+Vr) and Yr (Table 3) indicates that dominant alleles are responsible for round shaped fruit phenotypes. The graphic analysis (Figure 2) showed that parents 1 and 5, which present length/diameter ratio close to one (Table 4), are located closer to the lower extremity of the straight line, indicating that these parents contain a high proportion of loci with dominant alleles. In contrast, parents 2 and 4 showed the highest length/diameter ratios and are located at the upper portion of the straight line; these parents, therefore, contain a high proportion of recessive alleles (Figure 2). Parent 3 presented an intermediate ratio value (Table 4) when compared to the other parents, suggesting that it contains a higher proportion of dominant alleles than parents 1 and 5, but lower than in parents 2 and 4. Therefore, it lied in an intermediate position in the straight line (Figure 2).

The straight line intercepted the vertical axis (Wr) above the origin (Figure 2), indicating incomplete dominance of the genes controlling fruit length/diameter ratio.

Fruit dry matter per plant - Hybrid 3 × 5, by large the highest yielding treatment, yielded 113.8g of fruit dry matter per plant. Parents 3 and 5 showed the second best results with values of 65.59 g per plant and 68.38 g per plant, respectively, and formed a distinct group from the other treatments. The remaining treatments formed two intermediary groups, with fruit dry matter ranging from 10.23 g per plant for parent 1 to 51.09 g per plant for hybrid 1 × 2 (Table 4). Over half the hybrids showed negative heterosis when compared to the respective parent mean or higher scoring parent (Table 4). Hybrids 1 × 4 (+234%) and 3 × 5 (+70%) were the most heterotic.

Fruit dry matter is very important for industry, since a large proportion of the pepper produced in the world is used in the form of powder. Best materials for processing purposes should show the highest percentage of fruit dry matter. However, from the

Table 4 - Means of total fruit yield, fruit length/diameter ratio, fruit dry weight per plant and respective hybrid heterosis. Rio Branco - AC, 1997.

Treatment	Total fruit yield		Fruit length/diameter ratio		Fruit dry weight per plant	
	Means[1]	Heterosis	Means[1]	Heterosis	Means[1]	Heterosis
	g per plant	------- % -------		------- % -------	g per plant	------- % -------
1	76.8 A	---	0.936 A	---	10.23 A	---
2	193.1 B	---	4.347 F	---	33.94 B	---
3	591.1 C	---	2.251 D	---	65.59 C	---
4	96.7 A	---	3.503 E	---	14.78 A	---
5	309.6 B	---	0.847 A	---	68.38 C	---
1 x 2	334.7 B	199.7* (+148)	1.702 C	-0.94** (-35)	51.09 B	29.00* (+131)
1 x 3	234.3 B	-99.6ns (-30)	1.018 A	-0.57** (-36)	34.34 B	-3.57ns (-9)
1 x 4	257.4 B	170.6* (+197)	1.640 C	-0.58** (-26)	41.81 B	29.30** (+234)
1 x 5	80.3 A	-112.9ns (-58)	0.924 A	0.03ns (+4)	13.74 A	-25.56* (-65)
2 x 3	336.0 B	-56.1ns (-14)	3.199 E	-0.10ns (-3)	43.82 B	-5.94ns (-12)
2 x 4	196.6 B	51.7ns (+36)	4.284 F	0.36* (+9)	33.10 B	8.74ns (+36)
2 x 5	133.6 A	-117.7ns (-47)	1.823 C	-0.77** (-30)	21.41 A	-29.75** (-58)
3 x 4	75.8 A	-268.1** (-78)	2.453 D	-0.42* (-15)	11.25 A	-28.93* (-72)
3 x 5	705.5 C	255.1** (+57)	1.381 B	-0.17ns (-11)	113.89 D	46.90** (+70)
4 x 5	80.4 A	-122.7ns (-60)	1.654 C	-0.52** (-24)	14.52 A	-27.1* (-65)

[1]Means followed by the same letter in each column did not differ at 5% by the Scott & Knott test (1974).
**; * Significant at 1% and 5% by the t test, respectively.
ns non-significant.
Parents: 1 = BGH - 81; 2 = BGH - 4196; 3 = BGH - 4285; 4 = BGH - 1810; 5 = BGH - 433.

agronomic point of view, the most important factor is the fruit dry matter produced per area, that is, per plant. A genotype showing a high percentage of fruit dry matter but low dry matter yield per area would not be desirable. This situation may result in unsatisfactory economic returns when compared to the other materials with a lower percentage of fruit dry matter, but with a high production per area. Since it is often difficult to obtain materials that carry both characteristics at high levels, a good compromise would be to select towards intermediate fruit dry matter percentage and high yield. In this sense, hybrid 3 × 5 showed the best combination between fruit dry matter content and dry matter yield per plant (Table 4).

The analysis of Gardner & Eberhart showed that high heterosis for fruit dry matter per plant was mainly due to the significance of the specific heterosis component (Table 5). However, the overall mean of the hybrids did not differ from the mean of the parents, as the mean heterosis component did not differ from zero (Table 5). The specific heterosis sum of squares contributed to the treatment sum of squares (Table 1), showing the importance of the non-additive genetic effects (dominance or epistasis) for this trait expression. Therefore, parental performance is not a good indicator of the hybrid performances for this trait.

The amplitude of the specific heterosis values was 81.68 g per plant (Table 5), with the maximum positive and minimum negative value of +54.76 g per plant and –26.92 g per plant for hybrids 3 × 5 and 3 × 4, respectively. This amplitude shows that specific heterosis must be taken into account when general inferences are made on the parents of these hybrids. Epistatic gene action appears to contribute to this trait heterosis as detected by the diallel analysis of Jinks & Hayman (Table 2).

Incidence of *Xanthomonas campestris* pv. *vesicatoria* (XCV) - Table 6 shows a clear distinction between the treatments into three groups according to incidence of *Xanthomonas campestris* pv. *vesicatoria*. Parents 3 and 5 and hybrid 3 × 5 formed one such group. A second group was formed by parent 2, and a third by parents 1, 4, and all the remaining hybrids. Treatments with incidence values close to one were least affected by the pathogen. Among all crosses, only the F1 hybrid between parents 3 and 5 showed a low

Table 5 - Estimates of the mean (μ - parent mean), varietal effect (Vi), heterosis effect (h_i), mean ($\bar{h}$) and specific (Sij) heterosis for total fruit yield, fruit length/diameter ratio, fruit dry weight per plant, *Xanthomonas campestris* pv. *vesicatoria* - XCV incidence, capsaicin yield per plant and seed number per fruit. Rio Branco - AC, 1997.

Mean component	Total fruit yield	Fruit length/ diameter ratio	Fruit dry weight per plant	XCV incidence	Capsaicin yield per plant	Seeds number per fruit
μ	246.812	2.131	38.128	2.835	306.118	31.213
V_i						
Parents 1	-176.64**	-1.44**	-28.36**	0.64ns	-148.31ns	-5.46ns
Parents 2	-60.35ns	1.97**	-4.64ns	-0.09ns	34.54ns	12.97**
Parents 3	337.63**	-0.12ns	27.00**	-1.36**	68.59ns	-8.13*
Parents 4	-156.78*	1.13**	-23.80**	2.04**	-91.72ns	12.30**
Parents 5	56.14ns	-1.53**	29.80**	-1.23**	136.90ns	-11.68**
$\bar{h}$	-10.00ns	-0.37**	-0.69ns	0.71**	202.94**	-15.65**
h_i						
Parents 1	65.95ns	-0.20*	10.64ns	-0.18ns	151.78*	15.78**
Parents 2	39.17ns	0.01ns	1.60ns	0.19ns	22.01ns	3.26ns
Parents 3	-42.89ns	0.07ns	3.74ns	0.33ns	180.98*	-12.90**
Parents 4	-42.82ns	0.10ns	-5.07ns	-0.31ns	-139.98*	4.29ns
Parents 5	-19.41ns	0.01ns	-10.91ns	-0.03ns	88.77ns	-10.43**
S_{ij}						
1 x 2	104.60*	-0.38**	17.45**	-0.62*	-13.41ns	17.43**
1 x 3	-112.70*	-0.08ns	-17.26**	0.08ns	-28.23ns	-18.80**
1 x 4	157.51**	-0.12ns	24.42**	0.01ns	146.7*	20.28**
1 x 5	-149.41**	0.58**	-24.61**	0.53*	-105.08ns	-18.91**
2 x 3	-42.41ns	0.19ns	-10.59ns	0.60*	22.47ns	-14.64**
2 x 4	65.35ns	0.62**	12.89*	-0.27ns	117.01ns	12.30**
2 x 5	-127.54**	-0.43**	-19.76**	0.29ns	-126.06ns	-15.09**
3 x 4	-172.35**	-0.23*	-26.92**	0.20ns	-244.56**	-16.57**
3 x 5	327.46**	0.12ns	54.76**	-0.88**	250.32**	50.02**
4 x 5	-50.51ns	-0.27*	-10.40ns	0.05ns	-19.17ns	-16.02**

**; * Significant at 1% and 5% by the t test, respectively. ns non-significant.
Parents: 1 = BGH - 81; 2 = BGH - 4196; 3 = BGH - 4285; 4 = BGH - 1810; 5 = BGH - 433.

trait mean. All other hybrids involving parents 3 or 5 showed means close to or higher than the highest scoring parent.

All hybrids showed positive heterosis, that is, showed greater susceptibility to the pathogen but in a few cases (such as with hybrid 3 × 5) the magnitudes of the heterotic effects were non-significant. Parents 3 and 5 and their derived hybrid 3 × 5 showed resistance to the *X. campestris* bacteria. Since all other hybrids involving either parent (3 or 5) were susceptible, the resistance must controlled by recessive allele(s).

The analysis by Gardner & Eberhart indicated highly heterosis effects, especially the mean and specific heterosis components (Table 1). The significant mean heterosis value (different from zero) for this trait indicated that the mean of the hybrids differed from the mean of the parents.

The observed contribution of the sum of the squares of the mean and specific heterosis components to the treatment sum of the squares (Table 1) depicted the importance of the non-additive genetic effects (dominance and/or epistasis) in the *Xanthomonas campestris* pv. *vesicatoria* incidence. The performance of the parents *per se* should not be used as an indicator of the behavior of the hybrids for this trait.

The estimated specific heterosis for *X. campestris* pv. *vesicatoria* incidence was variable, with an amplitude of 1.48, a minimum value of –0.88 for hybrid 3× 5 and a maximum value of +0.60 for hybrid 2 × 3 (Table 5). This amplitude, which reflects the significant specific heterosis effects (Table 1), showed that this source of variation must be taken into account when breeding towards resistant hybrids. To obtain high level of resistance it is necessary to cross two resistant parents as was the case for hybrid 3 × 5. According to the Jinks & Hayman analysis, the regression of Wr on Vr resulted in β = 0.863 (Table 2), which differed from zero (a = 0.05), but did not differ from one. Therefore, there was no evidence of epistatic gene action and the additive-dominance model alone could adequately explain the results. This trait was assessed using a ascending score scale, from the lowest to the highest disease incidence. The negative close to –1 value of the correlation (r = -0.785; Table 3) between (Wr + Vr) and Yr indicated that the dominant alleles expressed increases in the scores and, therefore, less resistance to the bacteria. The analysis therefore confirms the conclusion that XCV resistance is controlled by recessive allele(s). Parents 3 and 5, which showed resistance to *X. campestris* pv. *vesicatoria* (Table 6), grouped together in the upper part of the regression line (Figure 3) indicating that recessive alleles are largely responsible for resistance expression. Parents 1, 2 and 4 grouped in the lower part of the regression line, indicating the presence of dominant alleles and, indeed, these parents were susceptible to the disease (Table 6).

The fact that the straight line intercepted the vertical axis (Wr) above the origin (Figure 3) would indicate the presence of incompletely dominant gene action. However, as the intercept is very close to the origin, and also taking into account the errors involved in the β estimate, it can be assumed that the loci controlling the trait showed near-complete or complete dominance.

Table 6 - Means of *Xanthomonas campestris* pv. *vesicatoria* - (XCV) incidence, capsaicin yield per plant, seed number per fruit and respective hybrid heterosis. Rio Branco - AC, 1997.

Treatment	XCV incidence		Capsaicin yield per planto		Seed number per fruit	
	Means[1]	Heterosis	Means[1]	Heterosis	Means[1]	Heterosis
		------- % -------	mg per plant	------- % -------	seed per fruit	------- % -------
1	3.00 C	---	22.51 A	---	36.18 B	---
2	2.27 B	---	205.37 A	---	54.62 C	---
3	1.00 A	---	239.41 A	---	33.52 B	---
4	4.40 C	---	79.10 A	---	53.95 C	---
5	1.13 A	---	307.73 A	---	29.97 B	---
1 x 2	2.73 C	0.09ns (+4)	173.69 A	59.75ns (+52)	66.22 D	20.82**(+46)
1 x 3	2.93 C	0.93* (+46)	334.87 A	203.91ns (+156)	3.28 A	-31.57**(-90)
1 x 4	3.93 C	0.23ns (+6)	108.71 A	57.90ns (+114)	69.77 D	24.70**(+55)
1 x 5	3.10 C	1.03* (+50)	199.96 A	34.84ns (+21)	3.87 A	-29.20**(-88)
2 x 3	3.47 C	1.83** (+112)	650.80 B	428.41** (+193)	4.13 A	-39.94**(-91)
2 x 4	3.67 C	0.33ns (+10)	344.21 A	201.97ns (+142)	58.48 C	4.19ns(+8)
2 x 5	2.87 C	1.17* (+69)	444.21 A	187.66ns (+73)	4.38 A	-37.91**(-90)
3 x 4	3.63 C	0.93* (+34)	158.63 A	-0.62ns (-0.4)	2.90 A	-40.83**(-93)
3 x 5	1.20 A	0.13ns (+13)	996.58 C	723.01** (+264)	42.78 B	11.03*(+35)
4 x 5	3.20 C	0.43ns (+16)	325.97 A	132.55ns (+68)	4.15 A	-37.81**(-90)

[1]Means followed by the same letter in each column did not differ significantly at the 5% by the Scott & Knott test (1974).
**; * Significant at 1% and 5% by the t test, respectively. ns non-significant.
Parents: 1 = BGH - 81; 2 = BGH - 4196; 3 = BGH - 4285; 4 = BGH - 1810; 5 = BGH - 433.

The fact that the points corresponding to parents 1, 2 and 4 are concentrated close to the lower point of intersection between the straight line and the parabola and the points corresponding to parents 3 and 5 are close to the upper point of the intersection (Figure 3) suggest that resistance is controlled by one or by few genetic loci.

The distributions of points corresponding to the parents in the graphs for bacteria incidence (Figure 3) and total fruit yield (Figure 1) are similar. Under the conditions of this experiment, it is possible that the total yield was strongly influenced by resistance to *X. campestris* which lead to a strong correlation between the two traits.

For pepper breeding purposes, the selection of parents resistant to *X. campestris* pv. *vesicatoria* is essential to develop cultivars for regions where the disease causes economic losses, as is probably the case of a great part of Northern Brazil. The disease is difficult or impossible to control or prevent by chemical and/or crop management methods.

Capsaicin yield per plant - Except for hybrid 3× 5 (which had the highest mean, 996.58 mg per plant) and hybrid 2× 3 (with the second highest mean, 650.80 mg per plant) all the other treatments formed a single group with the means ranging from 22.51 mg per plant to 444.21 mg per plant (Table 6).

Hybrid 3× 4 showed negative heterosis while all others showed positive heterosis. However, only hybrids 2× 3 and 3× 5 presented significant heterosis by the t test (Table 6). Heterosis for capsaicin yield per plant was due to the mean, varietal and specific heterosis components, which were all significant (Table 1). The significance of the mean heterosis indicated that the hybrid means differed from the parent means (Table 1). The high sum of the squares of the heterosis components, which contributed significantly to the treatment sum of the squares, depicted the importance of the non-additive (dominance or epistasis) genetic effects for expression of this trait (Table 1). Therefore, the performance of the parents "per se" is not a good indicator of the capsaicin yield per plant hybrid performance.

Specific heterosis component estimates ranged from +250.32 mg to –244.56 mg of capsaicin per plant, for hybrids 3× 5 and 3× 4, respectively, resulting in an amplitude of variation of 494.88 mg of capsaicin per plant (Table 5). A range of variation of this magnitude indicates that this source of variation is important and must be taken into account. This conclusion is corroborated by the fact that parent 3 is present in the hybrids that showed the highest and lowest capsaicin yields per plant values (Table 5). Epistasis seemed to contribute to heterosis for this trait, as detected by the diallel analysis of Jinks & Hayman (Table 2).

Number of seeds per fruit - The treatments were assigned by the Scott-Knott test into four groups based on the number of seeds per fruit. The hybrids 1× 2 and 1× 4 stood out with 66.22 and 69.77 seeds per fruit, respectively, and were significantly different from the other treatments. Hybrids 1× 3, 1× 5, 2× 3, 2× 5, 3× 4 and 4× 5 formed a group with the lowest means among the treatments, with values that ranged from 2.90 to 4.38 seeds per fruit. The other treatments were divided in two different groups with means ranging from 29.97 to 58.48 seeds per fruit (Table 6).

Heterosis for number of seeds per fruit was positive for hybrids 1× 2, 1× 4, 2× 4 and 3× 5, with values ranging from +8% to +55%. The other hybrids showed negative heterosis with much higher values that ranged from –88% to –93% (Table 6).

The subgroup formed by parents 1, 2 and 4 showed high seed number values (>20), both in the parents "per se" and in their intra-subgroup hybrids. Heterosis in this sub-group was always positive. Similarly, the subgroup formed by parents 3 and 5 and hybrid 3× 5, also showed high values (>20) of seeds per fruit, and the heterosis of hybrid 3×5 was also positive. In hybrids derived from parents belonging to the two different subgroups, that is, hybrids 1 × 3, 1 × 5, 2 × 3, 2 × 5, 3 × 4 and 4 × 5, the mean number of seeds per fruit was always very small (<5) and heterosis was always negative (Table 6). The results suggest the existence of sub-fertility in the inter-subgroup hybrids, which may have resulted from a probable reproductive isolation of accessions (parents) 1, 2 and 4 from accessions 3 and 5, or further, that the subgroups may represent different subspecies within the *C. chinense* species: one made up of parents 1, 2 and 4, and the other by parents 3 and 5.

The marked expression of heterosis for number of seeds per fruit was demonstrated by the significance of the heterosis effect, and all of its components: mean, varietal and specific heterosis. The significant and negative mean heterosis component indicated that the mean of the hybrids differed from the mean of the parents and that, on average, the hybrids produced fewer seeds per fruit than their parents (Table 5). This fact was already expected, considering the already commented sub-fertility aspects observed when parents belonging to probably different groups were crossed.

The sum of the squares of all heterosis components contributed significantly to the treatment sum of the squares, demonstrating the importance of the non-additive genetic effects (dominance or epistasis) for the expression of the number of seeds per fruit. Thus, in spite of significant parent effects, their "per se" performance should not be used to predict the hybrid behavior for this trait (Table 1). The observed amplitude of 68.93 seeds per fruit in the specific heterosis estimates resulted from the maximum value of +50.02 seeds per fruit obtained for hybrid 3× 5 and from the minimum value of –18.91 seeds per fruit for hybrid 1× 5 (Table 5). Such wide amplitude

indicated that this source of variation is important for the trait expression. A fact that corroborated this conclusion was the existence of different hybrids with one common parent producing either high and low numbers of seeds. Epistasis certainly played a role in determining heterosis, as can be seen by the corresponding test in the Jinks & Hayman analysis (Table 2).

CONCLUSIONS

The Gardner & Eberhart diallel analysis showed that the non-additive genetic effects predominated in the control of all the assessed traits. The Jinks & Hayman analyses detected the presence of significant epistasis for fruit dry matter per plant, capsaicin yield per plant and number of seeds per fruit. In these cases, epistasis seems to be in large part responsible for the expression of heterosis. For the other traits, where no epistatic genetic action was detected, heterosis was explained by dominant gene action, which varied from incomplete dominance to probable overdominance. There was evidence of incomplete dominance for the trait fruit length/diameter ratio. There was complete dominance or near-complete dominance for *Xanthomonas campestris* pv. *vesicatoria* incidence. Overdominance was detected for total fruit yield.

The hybrid 3 × 5 (BGH-4285 × BGH-433) was the best performing for most of the assessed traits, suggesting that its commercial use is viable in the short term. In the medium and/or long term, this hybrid and its parents are an excellent alternative in breeding programs of this species, or in other species of *Capsicum*, mainly when the program aims *Xanthomonas campestris* pv. *vesicatoria* resistance.

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