

Inheritance of seedling and plant traits in ornamental pepper (*Capsicum annuum*)

A.M.S. Pessoa, E.R. do Rêgo, C.A.P. dos Santos, M.G. de Carvalho and M.M. do Rêgo

Universidade Federal da Paraíba, Laboratório de Biotecnologia Vegetal, Areia, PB, Brasil

Corresponding author: A.M.S. Pessoa
E-mail: pbalegna@gmail.com

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ABSTRACT. Pepper has considerable genetic diversity and versatility. Knowledge of the genetic control of traits in peppers is of great importance for breeding programs given the large variety of types, sizes, colors and flavors. To this end, we examined the inheritance of seedling and plant traits in ornamental pepper (*Capsicum annuum*). The experiment was conducted in a greenhouse in Areia, Paraíba, Brazil. Seven ornamental pepper accessions (*C. annuum*) belonging to the Federal University of Paraíba's Germplasm Bank were investigated: UFPB001, UFPB004, UFPB77.3, UFPB099, UFPB134, UFPB137 and UFPB390. Morphoagronomic characterization was performed based on *Capsicum* descriptors, and 12 quantitative traits were evaluated in seedlings and plants. The data were subjected to variance analysis and subsequent diallel analysis performed according to Hayman's method. The t statistic was used to test the adequacy of the additive-dominance model. The traits seedling height, hypocotyl diameter, cotyledon leaf length, plant height, bifurcation height, leaf length and width and chlorophyll *a* and *b* are in agreement with the additive-dominant model. Correlations were positive and significant for seedling height (0.470) and hypocotyl diameter (0.885). Cotyledonary leaf length and width showed negative and significant values of -0.088 and -0.669, respectively. The correlations were positive for the following traits: plant height, stem diameter, first bifurcation height, canopy diameter, leaf length and chlorophyll *b*, with values ranging from 0.094 to 0.965. Leaf width and

chlorophyll *a* exhibited negative *r* correlation values. In the genetic parameters estimate, the positive *r* correlation for most of the traits indicates that the recessive alleles were generally responsible for the increase in these traits. Genetic gains for plant traits in ornamental peppers are possible using breeding programs. The parents UFPB001 and UFPB134 exhibited the highest concentration of favorable alleles for size traits and are indicated for selection for continued improvement programs.

Key words: Diallel; Hybridization; Plant breeding

INTRODUCTION

The pepper belongs to the Solanaceae family and the genus *Capsicum*. The species *C. annuum* originates from Central and South America. It has been introduced into numerous countries, and pepper is used for various purposes (Pickersgill, 1997; Collera-Zúniga et al., 2005; Li et al., 2007). In addition to its use in food (Bosland and Votava, 1999; Carvalho et al., 2006), pepper is included in the formulation of pharmaceutical and cosmetic products (Yamamoto and Nawata, 2005) and is also used ornamentally (Rêgo et al., 2016).

Ornamental use is based on the fact that it has several relevant traits that can be selected, including smaller plants, high leaf density, leaf color, flower and fruit color and various fruit shapes (Carvalho et al., 2006; Stommel and Bosland 2006; Rêgo et al., 2016). In addition to these aspects, pepper plants are easy to grow. As they are perennials, peppers are suitable for growing in pots (Neitzke et al., 2010). The demand for pepper plants is growing in Brazil, especially because their cultivation is of great social importance, as it involves a great deal of family farming labor (Nascimento et al., 2006; Finger et al., 2012). Although some ornamental pepper cultivars are currently on the market for production, such as Calypso, Pirâmide and Espaquetinho, there is a need for studies to develop new varieties to help take advantage of this market. This requires a study of inheritance of traits of interest from an ornamental point of view. Knowledge of the genetic control of a trait is of great importance for breeding programs helps develop appropriate procedures for use in selection and breeding programs (Cruz et al., 2012). Several genetic designs are available to this end, particularly diallel crossing (Cardoso et al., 2015).

Hayman's (1954a) method is based on knowledge of the environment and genetic nature expressed in terms of means, variances and covariances obtained from a diallel table. This method provides information on the inheritance mechanisms of the traits, the genetic values of their parents and selection limits (Viana et al., 1999). In Hayman's method, homozygous parents are crossed two by two to obtain F_1 plants, which give rise to the next generation (F_2) and so on (Baldissera et al., 2014). Within this context, our objective was to study the inheritance of ornamental pepper (*C. annuum*) seedling and plant traits.

MATERIAL AND METHODS

This study was conducted in a university greenhouse located in Areia, Paraíba, Brazil. Seven ornamental pepper accessions (*C. annuum*) belonging to CCA-UFPB's Germplasm Bank were tested: UFPB001, UFPB004, UFPB77.3, UFPB099, UFPB134, UFPB137 and UFPB390. These accessions exhibit diverse qualitative traits (Table 1).

Table 1. Description of six qualitative traits of the seven ornamental pepper accessions *Capsicum annuum* used in this study.

Accessions	Traits					
	BD	LC	CC	ASF	IFC	RFC
UFPB001	Intermediate	Clear green	White	Absent	Green	Yellow
UFPB004	Sparse	Green	White	Absent	Green	Red
UFPB77.3	Dense	Green	Purple	Present	Orange	Red
UFPB099	Sparse	Green	White	Absent	Orange	Orange
UFPB134	Intermediate	Green	White	Absent	Yellow	Orange
UFPB137	Dense	Green	White	Absent	Yellow	Orange
UFPB390	Intermediate	Clear green	White	Absent	Orange	Red

BD - branch density; LC - leaf color; CC - corolla color; ASF - anthocyanin spot in the fruit; IFC - intermediate fruit color; RFC - ripe fruit color.

The crossings were manually performed in floral buds at pre-anthesis. The plants were emasculated in the morning and immediately pollinated by introducing the pollen from the anther of another plant to the stigma of the receiving flower. Then, the flowers were labeled and covered with aluminum foil to prevent contamination (Nascimento et al., 2012a). When the fruit was ripe, it was collected, and the seeds were subsequently removed.

The seeds of the 42 hybrids and seven accessions were sown in 128-cell polystyrene trays filled with a commercial substrate (Plantmax[®]-Eucatex-Agro, Paulina, São Paulo, Brazil). When the plants produced six definitive leaves, they were transplanted to plastic pots containing 900 mL of the same substrate after 40 days.

Morphoagronomic characterization was performed based on *Capsicum* descriptors (IPGRI, 1995). Eleven quantitative seedling and plant traits were evaluated: seedling height (SH), cotyledon leaf length (CLL), cotyledon leaf width (CLW), plant height (PH), stem diameter (StD), first bifurcation height (FBH), canopy width (CW), leaf length (LL) and leaf width (LW). Two physiological traits, chlorophyll *a* (CLA), and chlorophyll *b* (CLB), were also evaluated.

A digital caliper (Lee Tools[®] Digital Caliper) was used to collect data on dimensions. Scales (Bel engineering[®]) were used to obtain weight data. Quantitative values were obtained by counting. The chlorophyll content in the leaf was measured using a digital chlorophyll meter (ClorofiLOG - Falker[®]).

The experimental design was fully randomized with 49 treatments and eight replications, comprising one plant per pot and consisting of 42 hybrids and seven parents. Detection of variation was achieved by applying an analysis of variance using the F test at 1% probability.

In order to use the method described by Hayman (1954a) and modified by Viana et al. (1999), it was necessary to test whether the seedling size and traits met the following assumptions: Mendelian inheritance and homozygous parents, absence of reciprocal effect, epistatic interactions and multiple alleles. Furthermore, the genes had to be randomly distributed across the parents. As a whole, possible flaws in the assumptions were determined by an adequacy test for the additive-dominant model as follows. The W_i and V_i values were used to test the data, to determine whether it fit the additive-dominant model as follows: a) the $W_i - V_i$ variation was evaluated by analysis of variance, testing for differences in values of this expression between the crossed matrix lines; b) Linear regression analysis of W_i in V_i , testing the significance of the angular coefficient of the straight line ($H_0: b = 1$ vs $H_a: b \neq 1$); c) W_i and V_i weighting by 45° rotation of the axes represented by these statistics, and the angular coefficient of the straight line was tested after rotation ($H_0: b = 0$ vs. $H_a: b \neq 0$) with the new values of W_i and V_i .

After verifying the adaptation of the data to the additive-dominant model, the analysis of variance interpretation and statistics obtained from the diallel table were used to estimate the genetic and environmental components: E, environmental variance effects; D, the additive effects of the genes; H_1 , H_2 and h^2 effects due to dominance; F, covariance effect between additive and non-additive effects; and D - H_1 , component that expresses the difference between additive and dominant gene effects.

The meaning of the different variation components was verified by the *t*-test by dividing the estimates according to their respective standard deviations. Genetic variation component estimates were divided by standard deviations and the significance determined by the *t* test, considering values greater than 1.96 with a significant probability of 5% (Singh and Chaudhary, 1979).

The following genetic parameters were also estimated: $\sqrt{H_1/D}$, mean degree of dominance; $H_2/4H_1$, distance between alleles; dominant/recessive relationship; number of dominant genes; restricted coefficient of determination; broad coefficient of determination; correlation between mean parent values (\hat{Y}_{ii}) and of the sum of covariance between the parent means and means of the *r*-th row (\hat{W}_r); variance between the means of the *r*-th row (\hat{V}_r); expected values of the coordinates \hat{W}_R , \hat{V}_R and \hat{W}_D , \hat{V}_R ; and predicted value for the parent with maximum concentration of dominant (\hat{Y}_R) and recessive (\hat{Y}_D) alleles. The significance of the components and parameters is explained by Hayman (1954b). All analyses were performed using the Genes computer program (Cruz, 2013).

RESULTS

A significant treatment effect (parents and hybrids) was observed at a 1% level of probability for all traits (Table 2). The coefficients of variation (CV) ranged from 7.736% for the canopy diameter to 44.497% for cotyledonary leaf length (Table 2).

Table 2. Analysis of variance and mean squares estimates of plant and seedling traits in ornamental pepper (*Capsicum annuum*).

Sources of variation	Mean squares				
	GL	SH	CLL	CLW	PH
Treatments	48	7.444**	2.878**	0.831**	80.748**
Residual	343	0.172	1.413	0.029	5.589
Total	391				
Overall mean	-	3.767	2.672	0.832	20.334
CV (%)	-	11.065	44.497	20.631	11.624
Source of variation	Mean squares				
	GL	StD	FFH	CW	LL
Treatments	48	0.029**	37.223**	58.805**	2.863**
Residual	343	0.004	1.534	4.409	0.621
Total	391				
Overall mean	-	0.632	8.535	27.144	6.115
CV (%)	-	10.480	14.511	7.736	12.886
Source of variation	Mean squares				
	GL	LW	CLA	CLB	
Treatments	48	0.539**	57.510**	30.298**	
Residual	343	0.082	13.829	7.241	
Total	391				
Overall mean	-	1.924	30.865	9.166	
CV (%)	-	14.920	12.058	29.359	

SH - seedling height; CLL - cotyledon leaf length; CLW - cotyledon leaf width; PH - plant height; StD - stem diameter; FFH - first bifurcation height; CW - canopy width; LL - leaf length; LW - leaf width; CLA - chlorophyll *a*; CLB - chlorophyll *b*. ** Significant at the 1% level of probability, according to the F test. CV - coefficient of variation.

The additive-dominant model adequacy test for the traits seedling height, cotyledonary leaf length, plant height, first bifurcation height, leaf length and width and chlorophyll *a* and *b* showed no significant values in the regression coefficients, indicating the adequacy of this model for these traits (Table 3). After logarithmic transformation of the data, the additive-dominant model proved adequate for cotyledonary leaf width, stem diameter and canopy width. The model was partially adequate, making the additive dominant model sufficient (Table 3).

Table 3. Adequacy test of the additive - dominant model for seedling and plant traits in ornamental pepper (*Capsicum annuum*).

Traits	MS Regression	MS deviation	Regression $W_i = a + b V_i$		T value and Significance ($H_0: \beta = 0$) after rotation	Fit to the model
			Intercept (a) Estimate (SD)	Coeff. Linear ($H_0: \beta = 1$) F estimate (SD)		
SH	0.176*	0.019	-0.087 (0.099)	0.864 (0.287) ^{ns}	-0.276 ^{ns}	Adequate
CLL	0.028 ^{ns}	0.014	0.007 (0.059)	0.267(0.190) ^{ns}	1.962 ^{ns}	Adequate
CLW	0.004 ^{ns}	0.002	0.001 (0.001)	- 0.141(0.109) ^{ns}	4.181**	Partially Adequate
PH	249.816**	2.568	4.279 (0.861)	0.963 (0.098) ^{ns}	0.127 ^{ns}	Adequate
StD	0.000 ^{ns}	0.001	0.002 (0.012)	0.003 (0.011) ^{ns}	47.241*	Partially Adequate
FBH	21.611**	0.094	2.584 (0.228)	1.099 (0.073) ^{ns}	-1.608 ^{ns}	Adequate
CW	31.690**	0.364	1.215 (0.623)	1.369 (0.147)*	-3.350 ^{ns}	Partially Adequate
LL	0.017*	0.001	0.085 (0.036)	0.682 (0.182) ^{ns}	1.008 ^{ns}	Adequate
LW	0.000 ^{ns}	0.000	0.026 (0.007)	0.398 (0.183) ^{ns}	1.848 ^{ns}	Adequate
CLA	19.133*	0.649	0.240 (0.729)	0.961 (0.177) ^{ns}	-0.229 ^{ns}	Adequate
CLB	10.734*	0.528	-0.437 (0.537)	1.031 (0.229) ^{ns}	-0.711 ^{ns}	Adequate

SH - seedling height; CLL - cotyledon leaf length; CLW - cotyledon leaf width; PH - plant height; StD - stem diameter; FBH - first bifurcation height; CW - canopy width; LL - leaf length; LW - leaf width; CLA - chlorophyll *a*; CLB - chlorophyll *b*.

^{ns} not significant; * and ** significant at the 5 and 1% level of probability, respectively, according to the t test with 5 degrees of freedom.

The correlations of $\hat{W}_i + \hat{V}_i$ and \hat{Y}_{ii} were positive for seedling height (0.470) and hypocotyl diameter (0.885). Cotyledonary leaf length and width showed negative values of -0.088 and -0.669, respectively (Table 4).

Table 4. Estimated parameters in diallel using Hayman's method (1954) for seedling traits in ornamental pepper (*Capsicum annuum*).

Accessions	SH		CLL		CLW	
	Mean	$\hat{W}_i + \hat{V}_i$	Mean	$\hat{W}_i + \hat{V}_i$	Mean	$\hat{W}_i + \hat{V}_i$
UFPB001	3.687	0.160	2.750	0.089	1.000	0.013
UFPB004	3.062	0.354	2.112	0.929	0.562	0.148
UFPB77.3	2.937	0.821	2.225	0.045	0.600	0.032
UFPB099	2.875	0.264	2.062	0.160	0.750	0.098
UFPB134	5.850	1.178	3.500	0.513	0.762	0.004
UFPB137	4.437	0.257	2.900	0.019	0.912	0.007
UFPB390	4.250	2.874	2.750	0.041	0.850	0.009
$r(\hat{Y}_{ii}, \hat{W}_i + \hat{V}_i)$	0.470		-0.088		-0.669	
(\hat{W}_R, \hat{V}_R)	(1.418, 1.742)		(1.002, 3.743)		(0.006, 0.000)	
(\hat{W}_D, \hat{V}_D)	(-0.088, 0.005)		(0.008, 0.000)		(-0.180, 1.290)	
Prediction equation	$\hat{Y}_i = 3.282 + 1.295(\hat{W}_i + \hat{V}_i)$		$\hat{Y}_i = 2.649 - 0.134(\hat{W}_i + \hat{V}_i)$		$\hat{Y}_i = 0.861 - 1.916(\hat{W}_i + \hat{V}_i)$	
\hat{Y}_R Limit	7.369		2.012		0.858	
\hat{Y}_D Limit	3.182		2.648		-1.265	

SH - seedling height; CLL - cotyledon leaf length; CLW - cotyledon leaf width.

The selection limits for seedling height were 3.182 in the most recessive accession and 7.369 in the dominant accession (Table 4). Among the accessions, UFPB134 exhibited the greatest concentration of recessive alleles (Table 4 and Figure 1a) by presenting $\hat{W}_i + \hat{V}_i$ equal to 1.178, which is the value closest to the estimate $(\hat{W}_R + \hat{V}_R)$.

The UFPB004 parent had the highest concentration of recessive alleles for cotyledonary leaf length and width, with $\hat{W}_i + \hat{V}_i$ values equal to 0.929 and 0.148, respectively. These results indicate the possibility of obtaining strains with greater cotyledonary leaf length and width. Selection limits regarding these traits were 2.012 for cotyledon leaf length and 0.858 for cotyledonary leaf width in the most recessive genotype (Table 4 and Figure 1b and 1c).

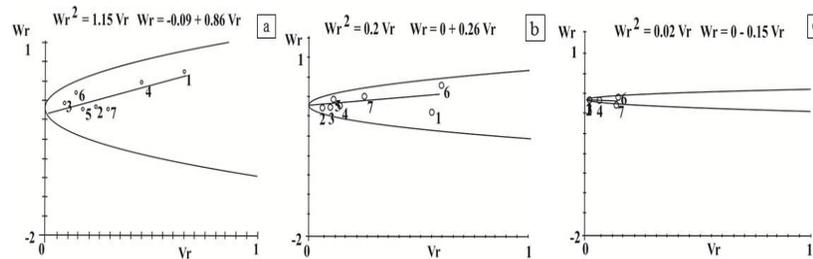


Figure 1 Straight line and parabola established by the relationships between covariance W_i , between means of parents and means within the i -th row, and the variance V_i between means within the row for the traits (a) seedling height, (b) cotyledon leaf length and (c) cotyledonary leaf width in ornamental pepper (*Capsicum annuum*). Parents: 1 = UFPB134, 2 = UFPB137, 3 = UFPB390, 4 = UFPB77.3, 5 = UFPB001, 6 = UFPB004 and 7 = UFPB099. Straight line established by $\hat{W}_i = \hat{a} + \hat{b}\hat{V}_i$, and parabola established by $\hat{W}_i^2 = \hat{p}\hat{V}_i$.

The r correlations ($\hat{W}_i + \hat{V}_i$ and \hat{Y}_{ii}) were positive for the following traits: plant height, stem diameter, first bifurcation height, canopy diameter, leaf length and chlorophyll b , with values ranging from 0.094 to 0.965 (Table 5). Leaf width and chlorophyll a exhibited negative r correlation values.

For the traits plant height, first bifurcation height and canopy width, recessive alleles had the highest concentrations, with positive values of 0.965, 0.888 and 0.655, respectively (Table 5). Among the parents, UFPB77.3 had the highest mean and concentration of recessive alleles, contributing to the increases in these traits with a $\hat{W}_i + \hat{V}_i$ value of 42.878 for plant height, 15.616 for first bifurcation height and 16.049 for canopy width (Table 5 and Figure 2a, 2c and 2d, respectively). In contrast, UFPB001 and UFPB004 parents exhibited the highest numbers of dominant alleles for the traits plant height and first bifurcation height, whereas UFPB001 and UFPB134 parents had the highest figures for canopy width (Table 5).

The r correlations ($\hat{W}_i + \hat{V}_i$ and \hat{Y}_{ii}) of 0.094 indicate that the recessive alleles were responsible for the increased stem diameter. The values of $(\hat{W}_D + \hat{V}_D)$ and $(\hat{W}_R + \hat{V}_R)$ were 0.003 and 415.583, respectively (Table 5). The parents with the greatest recessive homozygous stem diameter were UFPB004 (2241) and UFPB099 (2.242) (Table 5 and Figure 2b). The selection limit for this trait was 3.414 in the most recessive parent and 0.003 in the most dominant parent.

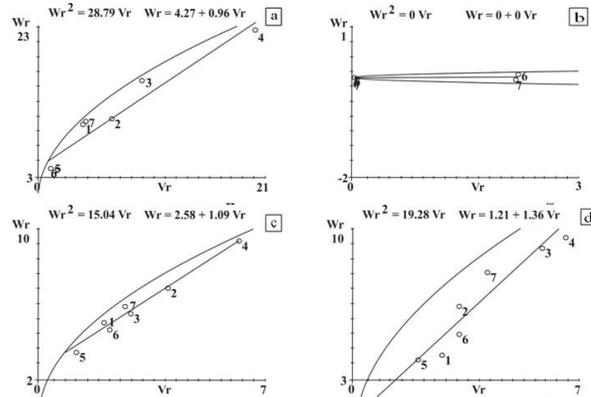


Figure 2. Straight line and parabola established by the relationships between covariance W_i , between means of progenitors and means within the i -th row, and variance V_i , between means within the row for the ornamental pepper plant traits (*Capsicum annuum*) (a) plant height, (b) stem diameter (c) first bifurcation height and (d) canopy width in pepper. Parents: 1 = UFPB134, 2 = UFPB137, 3 = UFPB390, 4 = UFPB77.3, 5 = PBU001, 6 = UFPB004 and 7 = UFPB099. Straight line established by $\hat{W}i = \hat{a} + \hat{b}\hat{V}i$, and parabola established by $\hat{W}i^2 = \hat{v}_p\hat{V}i$.

Table 5. Estimated parameters in diallel using Hayman's method (1954) for plant traits in ornamental pepper (*Capsicum annuum*).

Accessions	PH		StD		FFH		CW	
	Mean	$\hat{W}i + \hat{V}i$	Mean	$\hat{W}i + \hat{V}i$	Mean	$\hat{W}i + \hat{V}i$	Mean	$\hat{W}i + \hat{V}i$
UFPB001	16.875	6.002	0.651	0.004	5.500	4.673	24.062	6.323
UFPB004	19.000	5.897	0.589	2.241	5.662	6.164	23.425	7.896
UFPB77.3	32.250	42.878	0.637	0.005	15.875	15.616	35.125	16.049
UFPB099	18.437	10.952	0.724	2.242	5.812	7.430	24.000	12.124
UFPB134	17.562	10.704	0.517	0.002	8.187	6.449	24.375	6.836
UFPB137	22.687	14.994	0.736	0.005	10.687	10.052	30.500	9.362
UFPB390	23.312	24.609	0.655	0.006	11.437	7.376	27.375	15.433
$r(\hat{w}i, \hat{v}i)$	0.965		0.094		0.888		0.655	
$(\hat{w}R, \hat{v}R)$	(24.723, 21.228)		(1.535, 414.048)		(10.235, 6.963)		(12.730, 8.409)	
$(\hat{w}D, \hat{v}D)$	(5.175, 0.930)		(0.002, 0.001)		(3.457, 0.794)		(1.343, 0.093)	
Prediction equation	$\hat{Y}i = 14.957 + 0.391(\hat{w}i + \hat{v}i)$		$\hat{Y}i = 0.640 + 0.007(\hat{w}i + \hat{v}i)$		$\hat{Y}i = 1.211 + 0.947(\hat{w}i + \hat{v}i)$		$\hat{Y}i = 19.401 + 0.710(\hat{w}i + \hat{v}i)$	
$\hat{Y}R$ Limit	32.946		3.414		17.494		34.556	
$\hat{Y}D$ Limit	17.347		0.640		5.236		20.431	
Accessions	LL (cm)		LW (cm)		CLA		CLB	
	Mean	$\hat{W}i + \hat{V}i$	Mean	$\hat{W}i + \hat{V}i$	Mean	$\hat{W}i + \hat{V}i$	Mean	$\hat{W}i + \hat{V}i$
UFPB001	6.562	0.614	2.175	0.103	30.037	5.788	8.162	1.671
UFPB004	6.825	0.349	2.120	0.067	28.571	5.719	7.567	2.104
UFPB77.3	5.687	0.181	1.875	0.066	34.662	12.794	13.237	9.155
UFPB099	7.154	0.352	2.250	0.079	29.192	6.232	7.733	3.613
UFPB134	6.133	0.509	1.600	0.081	36.433	4.872	12.950	1.661
UFPB137	5.867	0.419	1.837	0.061	31.950	4.523	10.079	2.345
UFPB390	5.429	0.367	1.567	0.102	28.658	13.104	7.529	5.069
$r(\hat{y}i, \hat{w}i + \hat{v}i)$	0.180		-0.104		-0.039		0.383	
$(\hat{w}R, \hat{v}R)$	(0.481, 0.580)		(0.157, 0.329)		(9.898, 10.044)		(6.657, 6.879)	
$(\hat{w}D, \hat{v}D)$	(0.104, 0.027)		(0.031, 0.013)		(0.246, 0.006)		(-0.409, 0.026)	
Prediction equation	$\hat{Y}i = 5.795 + 1.109(\hat{w}i + \hat{v}i)$		$\hat{Y}i = 2.053 - 1.690(\hat{w}i + \hat{v}i)$		$\hat{Y}i = 31.611 - 0.033(\hat{w}i + \hat{v}i)$		$\hat{Y}i = 8.298 + 0.358(\hat{w}i + \hat{v}i)$	
$\hat{Y}R$ Limit	6.972		1.231		30.945		13.144	
$\hat{Y}D$ Limit	5.939		1.978		31.602		8.161	

PH - plant height; StD - stem diameter; FFH - first bifurcation height; CW – Canopy width; LL - leaf length; LW - leaf width; CLA - chlorophyll a; CLB - Chlorophyll b.

The r correlation value for leaf length ($\hat{w}_i + \hat{v}_i$ and \hat{y}_{ii}) was 0.180 (Table 5). The greatest values of ($\hat{w}_i + \hat{v}_i$) for recessive alleles were found in the UFPB001 parent (0.614), which was closest to the expected value ($\hat{w}_R + \hat{v}_R$) of 1.061 (Table 5 and Figure 3a). The parent UFPB77.3 (0.181) had the highest concentration of dominant alleles for this trait, with the recessive alleles contributing to the increase in this trait. The selection limit for leaf length was 6.972 in the most recessive accession and 5.939 in the most dominant (Table 5).

The predominance of dominant alleles was found for leaf width with an r correlation value ($\hat{w}_i + \hat{v}_i$ and \hat{y}_{ii}) of -0.104 (Table 5). The UFPB001 and UFPB390 parents had the highest $\hat{w}_i + \hat{v}_i$ values of 0.102 and 0.103, respectively (Table 5, Figure 3b). Considering the selection limit for this trait, the most dominant accession was 1.978 and the most recessive accessions were 1.231. The parents closest to the base of the regression line have a greater number of dominant genes, and these genes contribute to the increase in this trait (Figure 3b).

For the correlation r ($\hat{w}_i + \hat{v}_i$ and \hat{y}_{ii}) value, dominant alleles prevailed for chlorophyll a (-0.039), whereas recessive alleles contributed to the increase in chlorophyll b content (0.383). The parents UFPB390 and UFPB77.3 had the highest $\hat{w}_i + \hat{v}_i$ values for chlorophyll a (13.104 and 12.794) and for chlorophyll b (5.069 and 9.155) (Table 5, Figure 3c and 3d). The selection limit for chlorophyll a was 31.602 for the most dominant parents. For chlorophyll b , the selection limit for the most recessive parents was 13.144 (Table 5).

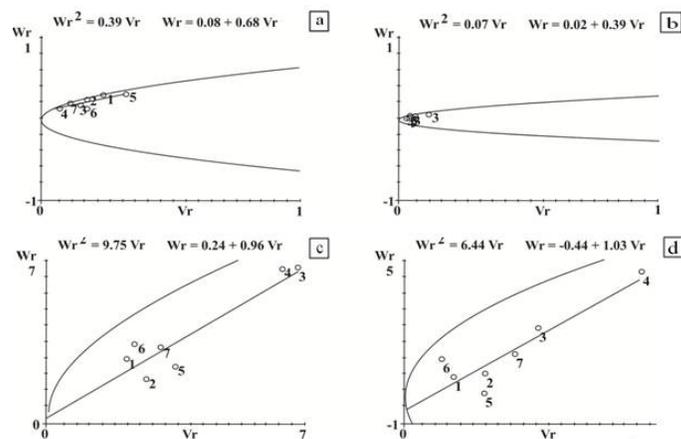


Figure 3. Straight line and parabola established by the relationship between covariance W_i , between means of progenitors and means within the i -th row, and variance V_i between means within the row for ornamental pepper plant traits (*Capsicum annuum*): (a) leaf length, (b) leaf width, (c) chlorophyll a and (d) chlorophyll b . Parents: **1** = UFPB134, **2** = UFPB137, **3** = UFPB390, **4** = UFPB77.3, **5** = UFPB001, **6** = UFPB004 and **7** = UFPB099. Straight line established by $\hat{w}_i = \hat{a} + \hat{b}\hat{v}_i$, and parabola established by $\hat{w}_i^2 = \hat{v}_p\hat{v}_i$.

Estimates of genetic variation components due to the additive gene effects (D) and due to dominance effects (H_1 and H_2) were significant ($P < 0.05$) for the seedling height trait, whereas cotyledonary leaf length and width exhibited no significance for these parameters (Table 6). The mean degree of dominance for seedling height, which is estimated by $\sqrt{H_1/D}$, was equal to 1.189. This trait also had a broad sense heritability of 0.937 and a strict sense of 0.239 (Table 6).

For the cotyledonary leaf length and width, mean degrees of dominance of 2.030 and 3.305 were observed, respectively (Table 6). Cotyledonary leaf width exhibited a high broad sense heritability (0.939) and low narrow sense heritability value (0.293), whereas the value for cotyledonary leaf length was low for both broad and narrow sense heritability (0.427) and (0.196), respectively.

Table 6. Estimates of genetic variation of parameters due to additive gene effects (D) due to dominance (H_1 , H_2 and h^2), the effect of the covariance between the additive and non-additive effects (F) and environmental effects (E) of the diallel for seedling traits in ornamental pepper (*Capsicum annuum*).

Estimation parameters \pm deviation	Traits		
	SH	CLL	CLW
E	0.021 \pm 0.035 ^{ns}	0.177 \pm 0.058*	0.004 \pm 0.019 ^{ns}
D	1.134 \pm 0.098*	0.092 \pm 0.164 ^{ns}	0.022 \pm 0.055 ^{ns}
H_1	1.605 \pm 0.237*	0.378 \pm 0.394 ^{ns}	0.236 \pm 0.132 ^{ns}
H_2	0.953 \pm 0.208*	0.285 \pm 0.348 ^{ns}	0.155 \pm 0.116 ^{ns}
h^2	0.033 \pm 0.140 ^{ns}	-0.073 \pm 0.235 ^{ns}	0.010 \pm 0.078 ^{ns}
F	-1.622 \pm 0.236*	0.065 \pm 0.393 ^{ns}	0.067 \pm 0.131 ^{ns}
D - H_1	-0.471 \pm 0.205 ^{ns}	-0.287 \pm 0.342 ^{ns}	-0.214 \pm 0.115 ^{ns}
Genetic information			
Mean degree of dominance (root of H_1/D)	1.189	2.030	3.305
Symmetry ($H_2/4H_1$)	0.148	0.188	0.164
Dominant/recessive ratio	4.014	1.421	2.780
Number of dominant genes	0.035	-0.257	0.067
Strict coefficient of determination	0.239	0.196	0.293
Broad coefficient of determination	0.937	0.427	0.939
Correlation ($\hat{Y}_{ij} - \hat{W} + \hat{V}_i$)	0.471	-0.089	-0.669

SH - seedling height; CLL - cotyledon leaf length; CLW - cotyledon leaf width. ^{ns} not significant and * significant (values higher than 1.96) at 5% probability.

The genetic variation components for plant traits due to additive genetic effects (D) and dominance (H_1 and H_2) were significant ($P < 0.01$) for canopy width, chlorophyll *a* and *b*, plant height and first bifurcation height ($P < 0.05$) (Table 7). The covariance effect between the additive and non-additive (F) effects were significant ($P < 0.01$) for the canopy diameter and chlorophyll *b*. The traits plant height, first bifurcation height and canopy width were also significant ($P < 0.05$) (Table 7).

The D - H_1 estimate exhibited significant positive values for plant height, first bifurcation height, canopy width, leaf length, leaf width and chlorophyll *a* (Table 7). The dominance effect expressed by the h^2 statistic was significant ($P < 0.05$) for plant height and first bifurcation height. For plant height, the broad sense heritability value was 0.775, and the narrow sense value was 0.727. For the first bifurcation height, heritability values in the broad and narrow sense were 0.735 and 0.629, respectively (Table 7).

Heritability values greater than 70% in the broad and strict sense were found for the traits canopy diameter (0.917 and 0.742), leaf length (0.775 and 0.727) and leaf width (0.856 and 0.805) (Table 7). The plant traits exhibited partial dominance, as the estimates for $\sqrt{H_1/D}$ ranged from 0.458 to 0.995 (Table 7).

High heritability in both the broad and narrow sense was noted for plant height, first bifurcation height, canopy width and leaf length and width (Table 7). For the stem diameter, negative heritability values were noted in both the broad and narrow senses. For the chlorophyll *a* and *b* traits, the heritability values were 0.735 and 0.721 for the broad sense and 0.629 and 0.519 for the strict sense, respectively (Table 7).

Table 7. Estimates of genetic variation of parameters due to additive genetic effects (D) due to dominance (H_1 , H_2 and h^2), the effect of the covariance between additive and non-additive effects (F) and environmental effects (E) of the diallel for eight plant traits in *Capsicum annuum*.

Estimation parameters \pm standard deviation	Traits			
	PH	StD	FBH	CW
E	0.698 \pm 0.396 ^{ns}	1.240 \pm 0.283*	0.192 \pm 0.088*	0.551 \pm 0.222*
D	28.095 \pm 1.122*	-1.234 \pm 0.800 ^{ns}	14.852 \pm 0.248*	18.733 \pm 0.627**
H_1	10.707 \pm 2.701*	-0.879 \pm 1.927 ^{ns}	3.120 \pm 0.597*	7.085 \pm 1.510**
H_2	7.079 \pm 2.379*	-0.312 \pm 1.698 ^{ns}	1.724 \pm 0.526*	4.663 \pm 1.331**
h^2	4.606 \pm 1.598*	-0.521 \pm 1.140 ^{ns}	0.859 \pm 0.353*	-0.163 \pm 0.894 ^{ns}
F	15.340 \pm 2.691*	-1.777 \pm 1.920 ^{ns}	7.608 \pm 0.595*	11.280 \pm 1.505**
D - H_1	17.388 \pm 2.344*	-0.354 \pm 1.673 ^{ns}	11.731 \pm 0.518*	11.647 \pm 1.311**
Genetic information				
Mean degree of dominance (Root of H_1/D)	0.617	0.844	0.458	0.615
Symmetry ($H_2/4H_1$)	0.165	0.089	0.138	0.164
Dominant/recessive ratio	2.586	0.079	3.534	2.918
Number of dominant genes	0.651	1.668	0.498	-0.035
Strict coefficient of determination	0.768	-0.011	0.874	0.742
Broad coefficient of determination	0.934	-0.079	0.961	0.917
Correlation ($\hat{Y}_{ii} \cdot \hat{W}_i + \hat{V}_i$)	0.965	0.094	0.888	0.655
Estimated parameters \pm standard deviation	Traits			
	LL	LW	CLA	CLB
E	0.078 \pm 0.011**	0.010 \pm 0.002**	1.729 \pm 0.197**	0.905 \pm 0.178**
D	0.322 \pm 0.031**	0.065 \pm 0.006**	8.025 \pm 0.559**	5.537 \pm 0.502**
H_1	0.084 \pm 0.074 ^{ns}	0.035 \pm 0.015*	4.676 \pm 1.345**	5.479 \pm 1.209**
H_2	0.066 \pm 0.065 ^{ns}	0.015 \pm 0.013 ^{ns}	2.784 \pm 1.185*	2.623 \pm 1.066*
h^2	0.021 \pm 0.044 ^{ns}	-0.005 \pm 0.009 ^{ns}	0.121 \pm 0.796 ^{ns}	0.339 \pm 0.716 ^{ns}
F	-0.162 \pm 0.074 ^{ns}	-0.030 \pm 0.015 ^{ns}	1.693 \pm 1.340 ^{ns}	5.019 \pm 1.205**
D - H_1	0.238 \pm 0.064**	0.029 \pm 0.013*	1.693 \pm 1.167*	0.057 \pm 1.050 ^{ns}
Genetic information				
Mean degree of dominance (Root of H_1/D)	0.509	0.738	0.763	0.995
Symmetry ($H_2/4H_1$)	0.197	0.105	0.149	0.119
Dominant/recessive ratio	0.338	0.517	1.321	2.674
Number of dominant genes	0.319	-0.329	0.043	0.129
Strict coefficient of determination	0.727	0.805	0.629	0.519
Broad coefficient of determination	0.775	0.856	0.735	0.721
Correlation ($\hat{Y}_{ii} \cdot \hat{W}_i + \hat{V}_i$)	0.240	-0.104	-0.039	0.383

PH - plant height; StD - stem diameter; FBH - first bifurcation height; CW - canopy width; LL - leaf length; LW - leaf width; CLA - chlorophyll *a*; CLB - chlorophyll *b*. ^{ns} non-significant and ** and * significant at 1% and 5% probability, respectively.

DISCUSSION

The significance observed in the treatments for the evaluated traits demonstrate genetic variability among genotypes. Promising genotypes can therefore be selected for use in breeding programs based on these traits (Ferrão et al., 2011; Medeiros et al., 2014).

The differences observed in the coefficient of variation (CV) between traits did not preclude variability between genotypes. Results similar to those obtained in this work were obtained by Rêgo et al. (2010) in a study of diversity among strains of ornamental pepper with variations in the CV value for traits and confirmation of diversity among genotypes. In their work with peppers, Silva et al. (2011) found that the CV values varied according to the trait under study, the accession and the species. In our study, the CV values identified for the analyzed traits did not affect experimental accuracy.

In the genetic parameters estimate, the positive r correlation (\hat{Y}_{ii} and $\hat{W}_i + \hat{V}_i$) for most of the traits indicates that the recessive alleles were generally responsible for the increase in these traits. Once these traits are determined, it is possible to obtain strains by selecting segregating populations. Andrade et al. (2015) reported positive and negative r correlations for traits evaluated in eggplant (*Solanum gilo*) and reported that many recessive and dominant alleles act to increase the traits. An allele providing an increase in the mean genotype of a particular trait may be dominant or recessive (Cardoso et al., 2015). When an allele is associated with an increase in a trait of interest, this allele can be used in breeding programs.

The accessions UFPB134, UFPB137 and UFPB390 are indicated for selection, as they have the highest recessive homozygous values, with mean values close to the selection limits for the seedling height trait. Dominant alleles are responsible for the increase in the cotyledonary leaf length and width traits, exhibiting negative r correlation values (\hat{Y}_{ii}) and ($\hat{W}_i + \hat{V}_i$). Among the accessions, UFPB001, UFPB134, UFPB137 and UFPB390 exhibited values greater than the selection limit, indicating that these parents are probably already at full homozygosity for the genes that control these traits.

Genotypic variation components provide greater contribution to the expression of seedling height due to the significance of the additive genetic parameters (D) and the dominance effects (H_1 and H_2). Given the estimates of these components, there are possibilities of additive and non-additive genetic effects in the control of this trait. Iftkharuddaula et al. (2008) reported that significant additive genetic parameters and dominance for traits indicate that additive effects are equally important in the inheritance of the characters.

For the cotyledonary leaf length trait, a greater influence of environmental components was noted, indicating that this trait is more affected by environmental parameters. Regarding cotyledon leaf width, genetic parameters could not be indicated, due to a lack of significance. Knowledge on the nature of genetic origin and environmental variations is essential for breeding activities, as improving certain agronomic traits depends on basic knowledge about the inheritance of traits, the genetic variability available for improvement and estimates of genetic parameters (Dias et al., 2011).

For seedling height and cotyledon leaf length, a value for mean degree of dominance greater than one indicates overdominance among alleles operating in the genetic control of these traits. In this type of interaction, the selection of superior individuals is not the best strategy for adoption in plant breeding programs, as the mean of generation F_1 differs from the mean of the parentals and generation F_2 (Ferreira, 2006; Santos et al., 2011). In this case, hybrid production is recommended (Gonçalves et al., 2011).

High broad sense heritability values for seedling height (0.937) and hypocotyl diameter (0.842) indicate that most of the phenotypic variation observed for these traits is genetic in nature and the possibility of genetic gains is increased. According to Ramalho et al. (2012), broad sense heritability considers all genetic variance. The higher the broad sense heritability value, the lower the influence of the environment on the expression of the trait (Fekadu et al., 2003) given that environmental influence hinders the efficient selection of genotypes.

Recessive alleles are mostly responsible for increases in plant height, stem diameter, first bifurcation height, canopy width, leaf length and chlorophyll b , as

demonstrated by the positive r correlation. The negative r values for leaf width and chlorophyll a indicate that dominant alleles act to increase these traits. For plant height and canopy diameter, the accession UFPB77.3 exhibited the maximum homozygosity expected for these traits with a value equal to the expected selection limit. This finding indicates that there is no possibility of increasing plant height in future generations.

Regarding stem diameter and first bifurcation time traits, recessive genes increase the expression of these traits, which indicates the possibility of obtaining superior strains in segregating populations derived from the diallel. For the traits leaf length (UFPB134, UFPB001, UFPB004 and UFPB099), leaf width (UFPB001, UFPB004 and UFPB099), chlorophyll a (UFPB134, UFPB137 and UFPB77.3) and chlorophyll b (UFPB77.3), parents having values greater than the selection limit shows that these parents are likely already in homozygosity, suggesting facility of improvement of these traits. The results of our study differ from those found by Fortunato et al. (2015), who observed negative r correlations for plant height, canopy diameter and leaf length in *C. annuum*. Their results indicate that dominant alleles are primarily responsible for the increase in these traits likely because other parents were used in obtaining the hybrids with the possibility of obtaining offspring with higher values for these traits.

The parents UFPB001, UFPB004 and UFPB134 are the most indicated for selection because they have the lowest first bifurcation height and canopy width ($\hat{W}_i + \hat{V}_i$) values. In terms of these traits, genotypes with a lower mean are sought because short plants are desirable for potted ornamental peppers. Rêgo and Rêgo (2016) reported a growing demand for new varieties of ornamental peppers that are small in size and have traits of ornamental interest.

Additive and non-additive effects controlled the traits plant height, first bifurcation height, canopy width and chlorophyll a and b due to the significance of the genetic parameters. These results are consistent with those found by Nascimento et al. (2011), who observed additive and non-additive effects when controlling these same traits in ornamental pepper. When evaluating general and specific combining ability in *C. baccatum* for plant height, canopy width and first bifurcation height, Rêgo et al. (2009) found that non-additive effects were more important in controlling these traits. When there is a predominance of additive and non-additive effects in the control of traits, it is recommended that strains are selected from segregating generations and that hybrids are obtained to explore heterosis from the diallel. Additive and non-additive genetic effects may vary between genotypes and species in the control of traits.

The mean degree of dominance indicates that the type of allelic interaction involved in the expression of plant height, first bifurcation height and canopy diameter is of the partial dominance type. In this type of interaction, the selection of superior individuals does not necessarily lead to the production of descendants similar to the selected individual; consequently this method does not represent a superior strategy to be adopted in a breeding program (Cruz, 2005). Hybrid production is indicated in such cases.

High broad and strict sense heritability values greater than 70% observed for plant height, first bifurcation height, canopy diameter, leaf length and leaf width suggest the possibility of obtaining genetic gains through selection based on these traits in segregating generations. High heritability for these ornamental pepper traits has also been found by other researchers (Neto et al., 2014; Santos et al., 2014; Fortunato et al., 2015; Pessoa et al.,

2015.) This magnitude of heritability values indicates that the traits are not greatly influenced environmental variation.

The significance of E and non-significance of genetic parameters for the stem diameter trait reveals that the environment has a strong influence on phenotypic expression, which is also reflected in the null heritability values. In a study of the inheritance and genetic parameters in *C. annuum*, Fortunato et al. (2015) also found no significant value for that trait, and genetic information was not interpreted because this trait is subject to environmental influence. Analysis and interpretation of genetic information are recommended, and the mean degree of dominance, distribution of alleles among parents, theoretical selection limit, relationship between favorable alleles and dominance, number of dominant genes, proportion between dominant and recessive genes and coefficient of genotypic determination are all significant (Hayman et al., 1954a).

Regarding leaf width and length traits, the significant values of D, which were confirmed by the significant positive value of D - H₁, indicate that additive genetic effects are involved in the control of these traits. In this case, selection of genotypes in early generations is recommended. This result can be compared by the high broad and strict sense heritability values of greater than 70% for these traits. Fekadu et al. (2003) report that the higher the broad sense heritability value, the lower the environmental influence on expression of the trait. Various authors consider that heritability values greater than 70% are high and transmit desirable alleles to future generations (Silva et al., 2004; Nascimento et al., 2012b; Neto et al., 2014; Pessoa et al., 2015).

Allelic interactions of the additive and non-additive type were found for the chlorophyll *a* and chlorophyll *b* traits. In this case, it is recommended that lines from advanced generations be selected and hybrids obtained to explore the heterosis indicated by the low strict sense heritability values.

The UFPB001 and UFPB134 parents are recommended for selection given that they exhibit the lowest mean values for plant height, first bifurcation height and canopy width; selection based on these traits is efficient because they have increased heritability values in both the broad and strict sense. For leaf length and width, the parents indicated for selection include UFPB77.3, UFPB134, UFPB137 and UFPB390, as they have small leaves.

CONCLUSIONS

Genetic gains in ornamental peppers are possible for the traits plant height, first bifurcation height, canopy width, leaf length and width. Hybrid production is recommended for seedling and plant traits as over dominance and partial dominance interactions are observed. UFPB001 and UFPB134 parents are indicated for use in crosses when the aim of the program is to obtain pepper plants of a reduced size for cultivation in pots.

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