

Genetic control of plant size-related traits and fruit in ornamental pepper (*Capsicum annuum* L.)

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Abstract

Peppers present a very diversified market and have a high economic and nutritional value. The study of genetic control of quantitative traits helps to conduct an efficient breeding program. This study aimed to estimate the genetic parameters and gene effects involved in the inheritance of morpho-agronomic traits in ornamental pepper (*Capsicum annuum* L.). The experiment was carried out in a greenhouse, at the Plant Biotechnology Laboratory, at the Federal University of Paraíba. Two accessions of ornamental pepper (*C. annuum* L.) belonging to the vegetable germplasm bank of the Federal University of Paraíba were used as parents: UFPB 347 and UFPB 356. The experimental design was completely randomized, with five plants of each parent being evaluated, 20 plants of generation F_1 , 90 plants of generation F_2 and 40 plants of BC_1 and BC_2 . Twelve quantitative characters referring to the plant size-related traits and fruit traits were evaluated. The obtained data were subjected to generation analysis, and the effects of the models were subjected to the t test at a level of 5% and 1% of significance. High broad-sense heritability was found for fruit weight, fruit length and pericarp thickness. The narrow-sense heritability was low for all evaluated traits. The additive-dominance model (m, a, d) was adequate to explain the genetic parameters of all evaluated characteristics, except dry matter content.

Keywords: *Capsicum annuum*, generation analysis, inheritance

Introduction

Ornamental peppers for landscaping in indoor and/or outdoor environments are a new market trend among Brazilian consumers (Silva et al., 2015). This ever-growing worldwide interest has encouraged genetic studies to assist in the decision-making of breeders in ornamental pepper breeding programs (Ari et al., 2016).

Several studies have sought to clarify the genetic control of size-related and fruit traits in pepper plants, as demonstrated in the thorough review conducted by Do Rêgo and Do Rêgo (2018). However, many studies contrast with regard to the main effects that determine these traits, requiring further investigations with different germplasm sources, including some recent research (Gomes et al., 2020; Sahid et al., 2020; Pessoa et al., 2021).

Plant architecture, fruit position and number, and the shape and color of leaves and fruits are some features that favor the use of *Capsicum* as ornamental

plants (Neitzke et al., 2016). From this perspective, small and compact plants with colorful and erect fruits are the most suitable for ornamental purposes (Neitzke et al., 2016; Rêgo et al., 2009; 2012a). In addition, fruits with different colors in the same plant, contrasting with the foliage, constitute an important factor in marketing ornamental pepper plants (Neitzke et al., 2016).

Genetic variability among *Capsicum* species for the shape and color of fruits, leaves, and flowers is a basic condition for the genetic improvement of this genus (Ferrão et al., 2011). The selection of fast-growing, aging-resistant genotypes with a longer postproduction shelf life is one of the purposes of any breeding program in order to obtain pepper cultivars for ornamental purposes (Rêgo et al., 2015; Do Rêgo & Do Rêgo, 2018).

Knowledge about the inheritance of evaluated traits is essential to choose the most suitable breeding method and maximize the use of the genetic potential

(Manu et al., 2014; Navhale et al., 2017; Rêgo et al., 2015; Do Rêgo & Do Rêgo, 2018; Gomes et al., 2020; Sahid et al., 2020; Pessoa et al., 2021). The study of the genetic control of quantitative traits assists in the conduction of an effective breeding program and can guide the size of the population to be conducted during its implementation (Bento et al., 2016; Rêgo et al., 2012a). Adequate information about the nature and magnitude of genetic effects is also important to predict the responses of segregating generations in the development of new cultivars (Nascimento et al., 2014; Santos et al., 2014; Ferreira et al., 2015; Bento et al., 2016; Silva et al., 2017; Do Rêgo and Do Rêgo, 2018; Gomes et al., 2020; Sahid et al., 2020; Pessoa et al., 2021). This information can be investigated through generation analysis, allowing the simultaneous evaluation of several generations or populations, including parents, hybrids, and segregating generations (Marame et al., 2009).

From this perspective, the present study aimed to estimate the genetic parameters and genetic effects involved in the inheritance of plant size and fruit traits in ornamental pepper plants (*Capsicum annuum* L.), adding new data to previously conducted studies and subsidizing the decision-making of breeders to select

plants with adequate plant and fruit sizes for ornamental purposes.

Materials and Methods

The experiment was developed in a plant nursery of the Laboratory of Plant Biotechnology at the Center of Agricultural Sciences (CCA) of the Federal University of Paraíba (UFPB), Areia - PB.

Two ornamental pepper accessions (*Capsicum annuum* L.) belonging to the vegetable germplasm bank of the Federal University of Paraíba (BGH-UFPB) were used as parents: UFPB 347 and UFPB 356. These accessions were selected based on a previous study (Fortunato et al., 2019). Although the parents had the same leaf and ripe fruit colors, they contrasted for qualitative traits such as stem color, flower color, and immature fruit color, thus allowing some differentiation (Table 1). The parents also contrasted for quantitative size-related and fruit traits, which are the object of the present genetic study (Table 2, Figure 1). Parents 347 and 356 were crossed to obtain the F_1 generation, which, by self-fertilization, originated the F_2 generation. The backcross generations BC_1 and BC_2 were obtained by crossing the F_1 with parents P_1 and P_2 , respectively.

Table 1. Qualitative traits of pepper parents (*Capsicum annuum*) used to obtain the F_1 , F_2 , BC_1 , and BC_2 generations.

Traits	Parents	
	UFPB 349	UFPB 356
Stem color	Green and purple	Purple
Leaf color	Variegate	Variegate
Flower color	Purple	Purple and white
Fruit Anthocyanin	Present	Present
Fruit color in intermediary stage	Green/ deep purple	Green/ deep purple / orange
Mature fruit color	Red	Red

Table 2. Amplitude for plant size related traits and fruit traits to parents (347 and 356) of ornamental pepper (*Capsicum annuum*).

Parents	PH	FBH	CW	SW	FW
347	33.52 - 40.48	18.89 - 23.91	21.58 - 26.42	0.51 - 0.63	0.55 - 0.59
356	32.08 - 33.72	16.88 - 20.52	32.35 - 33.45	0.69 - 0.91	0.49 - 0.75
Parents	FL	LFW	SFW	PL	PT
347	0.96 - 1.06	0.90 - 1.00	0.61 - 0.75	1.58 - 1.68	0.09 - 0.11
356	0.72 - 0.86	0.54 - 0.68	0.29 - 0.43	1.11 - 1.79	0.05 - 0.11
Parents	PLL	SYF	DMC		
347	0.72 - 0.82	38.13 - 50.67	13.09 - 17.65		
356	0.51 - 0.85	19.71 - 24.95	7.29 - 27.21		

PH – Plant height, FBH – first bifurcation height, CW – canopy width, SW – stem width, fruit weight -, FL – fruit length, LFW – larger fruit width, SFW – smaller fruit width, PL – Pedicel length, PT – Pericarp thickness, PLL – placenta length, SYF – seed yield per fruit, and DMC – dry matter content.

The crosses were performed in a plant nursery, and the flower buds were emasculated before anthesis. After emasculation, the flowers were pollinated by pollen transport from one plant to the stigma of the recipient flower. Subsequently, the flowers were labeled and covered with aluminum foil to avoid contamination (Rêgo et al., 2012b). The ripe fruits were harvested approximately

one to two months after pollination, followed by seed removal.

The sowing of the parents (P_1 and P_2), their progeny (F_1), the segregating generation (F_2), and the backcrosses (BC_1 and BC_2) was performed in 128-cell polystyrene trays filled with the commercial substrate Plantmax®, containing two seeds per cell. When the

seedlings had from four to six true leaves, approximately 50 days after sowing, they were transplanted to 900-mL plastic bags, where they were grown while kept in a plant nursery.

The morpho-agronomic characterization was performed based on the list of descriptors suggested by *Biodiversity International*, and 12 quantitative traits related to plant, inflorescence, and fruit were evaluated. The plant traits evaluated were plant height, canopy width, and stem width. Fruit descriptors were evaluated when the plant reached 50% of ripe fruits. These descriptors were fruit weight, fruit length, largest fruit width, smallest fruit width, pedicel length, pericarp thickness, placenta length, seed yield per fruit, and dry matter content.

The evaluation comprised five plants of each parent (P_1 and P_2), 20 plants of the F_1 generation, 90 of the F_2 generation, and 40 plants of the RC_1 and RC_2 generations.

The data obtained were subjected to generation analysis by calculating the means, phenotypic variances (σ_f^2), environmental variances (σ_m^2), genetic variances (σ_g^2), additive variances (σ_a^2), and variances due to dominance effects (σ_d^2). In addition, broad-sense heritability (h_a^2) and narrow-sense heritability (h_r^2) were also calculated.

The complete model included the estimation of the midparent (m), the additive (d), dominant (h), and epistatic: additive x additive (i), additive x dominant (j), and dominant x dominant (l), gene effects. The additive-dominance model included the estimation of additive effects (d), dominant effects (h), and midparent (m) gene effects.

All effects of both models were subjected to the t-test at 5% and 1% significance. All analyses were performed with the statistical software Genes (Cruz, 2006).

Results and Discussion

Mean of the generations

The mean value of the F_1 generation was below the mean of its parents for plant height, pedicel length, pericarp thickness, seed yield per fruit, and dry matter content (Figure 1), indicating an allelic interaction of negative overdominance. The production of hybrids for ornamental purposes is indicated for the traits of plant height.

The mean values of fruit weight, fruit length, and placenta length in the F_1 generation were higher than the mean values of its parents (Figure 1), characterizing an overdominant allelic interaction and indicating the occurrence of positive heterosis or hybrid vigor.

The superiority of the hybrid (F_1) may be due to an accumulation of favorable alleles (Marame et al., 2009),

and hybrids are recommended for overdominant traits (Barroso et al., 2015; Pessoa et al., 2021). The obtainment of hybrids with favorable traits is advantageous for breeding programs as they can be readily registered and protected, reducing the time to obtain a new cultivar as it is not necessary to conduct segregating populations.

The mean values of canopy width, stem width, largest fruit width, and smallest fruit width in the F_1 generation were within the range of the parental means (Figure 1), characterizing and additive allelic interaction. When studying the inheritance of plant and fruit traits in ornamental peppers (*Capsicum annuum*), Santos et al. (2014) described an additive allelic interaction for most evaluated traits, similar to the present study for stem width and fruit length. Selection in early generations is indicated to improve these traits (Marame et al., 2009; Do Rêgo & Do Rêgo, 2018; Pessoa et al., 2021). Thus, when the allelic interaction is additive, even in an early generation, the breeder is certain that the descendants will have superior mean values by selecting superior parents.

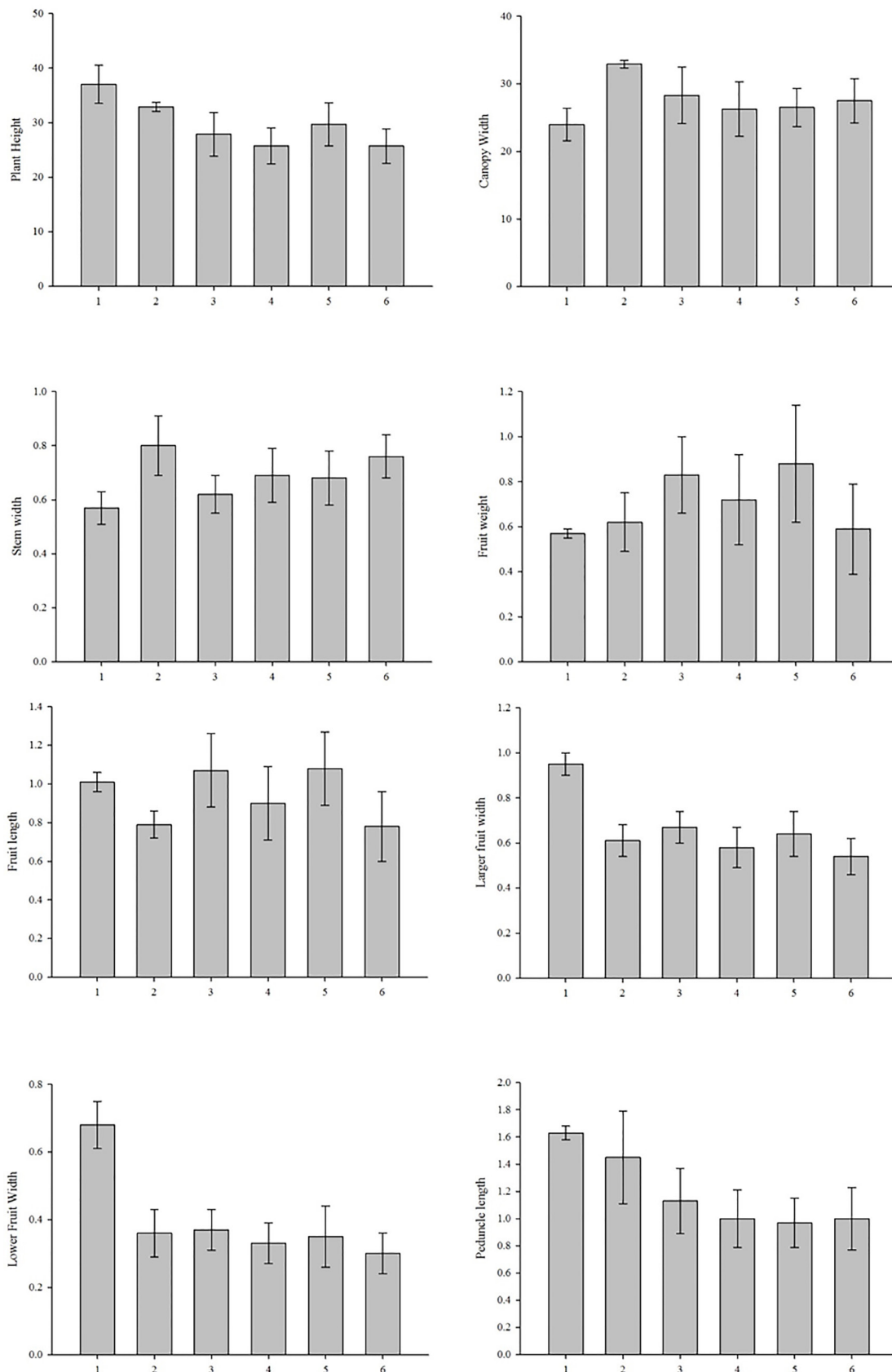
The mean of the F_2 generation was below the average of the F_1 generation for most traits (Figure 1), which is expected when there are allelic interactions of overdominance and dominance. However, the traits stem width and dry matter content showed higher means in the F_2 generation than in the hybrids.

Transgressive individuals in the F_2 generation were found for most traits, except for canopy width, stem width, and dry matter content (Figure 1). According to Wesp et al. (2008), transgressive segregation is the formation of individuals in segregating populations that are outside the range of the parents for the studied trait. The fruit length had transgressive individuals in the F_2 generation for maximum and minimum values (Figure 1). Transgressive individuals only for maximum values were found for fruit weight and placenta length (Figure 1). The remaining traits showed transgressive individuals only for minimum values (Figure 1). According to Marame et al. (2009), transgressions in segregating populations may occur due to a wider genetic distance between parents. In this study, the contrast was observed between parents for all quantitative traits (Figure 1). According to Fortunato et al. (2019), the parents used in this study showed differences in the size-related and fruit traits.

Transgressive individuals for minimum values of plant height are desired to the breeding of ornamental peppers since small plants are one of the main objectives of any breeding program with potted ornamental peppers (Rêgo et al., 2009; 2011; Santos et al., 2014; Do Rêgo & Do Rêgo, 2018). According to Barroso et

al. (2012), only the pepper cultivars with small size and proportion can be marketed as ornamental plants since plant height and canopy width should be proportional to the pot size in order to maintain the harmony between

plant architecture and its container. On the other hand, larger plants should not be discarded as they can be used for landscaping in outdoor environments (Bărcanu et al., 2017; Do Rêgo & Do Rêgo, 2018).



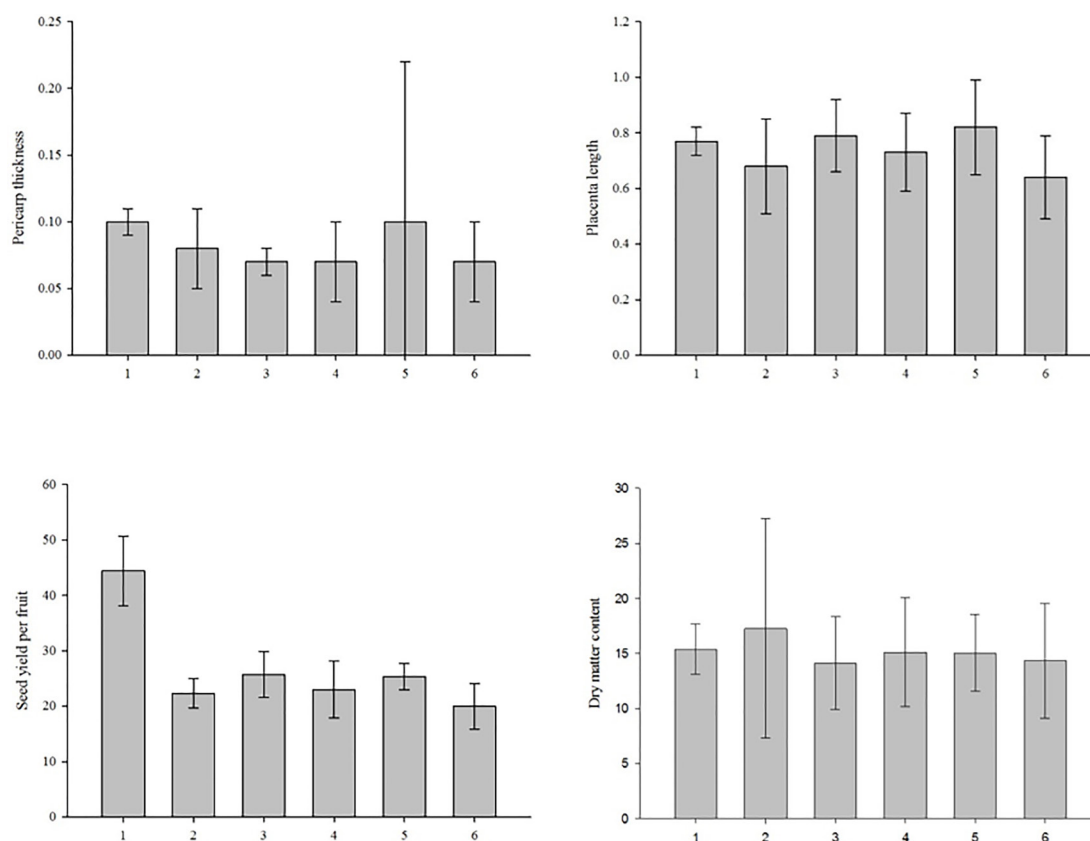


Figure 1. Mean and standard deviation for plant size-related and fruit quantitative traits of ornamental pepper (*Capsicum annum* L.). 1 - P_1 (UFPB 347); 2 - P_2 (UFPB 356); 3 - F_1 ; 4 - F_2 ; 5 - RC_1 ; 6 - RC_2 .

Fruit weight had transgressive individuals only for maximum values, and selection based on this trait is not recommended since heavier fruits could lead to plant lodging. On the other hand, fruit length had transgressive individuals for maximum and minimum values, and the selection of individuals with minimum values is recommended since smaller fruits are ideal for ornamental purposes because they are more proportional to plant size (Silva et al., 2015). Santos *et al.* (2014) highlighted the importance of selecting plants with adequate plant and fruit sizes for pot cultivation meant to decorate indoor environments.

Transgressive individuals for minimum values were observed for the largest and smallest fruit width, which is interesting for breeding ornamental peppers since smaller fruits maintain the balance with plant architecture. Pedicel length was another feature that also had transgressive individuals for minimum values. However, fruits with shorter pedicels are not interesting for breeding ornamental peppers as they do not favor fruit visualization within the foliage. Therefore, the selection of these individuals is not recommended. According to Melo et al. (2014), fruits with longer pedicels stand out in the foliage and are interesting for potted plants and flower arrangements (Melo et al., 2014; Pessoa et al., 2021) as

well as outdoor environments (Do Rêgo & Do Rêgo, 2018).

Pericarp thickness had transgressive individuals only for minimum values, and selection based on this trait is not recommended. Fruits with thicker pericarps are best suited for selection in pepper breeding programs, since they are more resistant to damage caused by postproduction handling and shipping (Rêgo et al., 2009).

Placenta length had transgressive individuals only for maximum values. Individuals with longer placentas are more desirable as this structure concentrates the largest amounts of capsaicinoids, a substance responsible for the characteristic pungency of fruits and rich in antioxidant agents (Rêgo et al., 2012c).

The seed yield per fruit is an important variable to determine the variability between accessions (Bento et al., 2007). This trait had transgressive individuals in the F_2 only for minimum values, which is not desirable in breeding programs since plants whose fruits have more seeds should be selected to facilitate the propagation of the species and supply germplasm banks.

Furthermore, the mean of backcrosses families (BC_1 and BC_2) was skewed toward the respective recurrent parents for stem length, canopy width, stem width, fruit length, pericarp thickness, placenta length, and dry matter content (Figure 1).

Estimates of genetic parameters

The negative variance estimates obtained in this study were considered null estimates (Table 3). Bento et al. (2016) observed negative variance due to dominance for the number of fruits per plant in *C. baccatum* by considering it zero and establishing that all variation observed was additive. The variables plant height, fruit weight, pericarp thickness, and placenta length showed negative estimates for some variances. In contrast, all variance estimates for pedicel length and dry matter content were null, except for phenotypical variance (Table 3), probably due to data variation within the generations (Table 3).

The broad-sense heritability values ranged from zero to 64.71. High broad-sense heritability values indicate that most of the variation observed is due to genetic variation, with little influence of the environment (Pessoa et al., 2015; Silva Neto et al., 2014). On the other hand, narrow-sense heritability values ranged from zero to 53.53 (Table 5). This parameter quantifies the relative importance of the additive proportion of the genetic variance, allowing genetic gain for these traits by

selection in early generations (Yang et al., 2017).

The traits stem length, canopy width, stem width, fruit length, and seed yield per fruit showed higher additive variance values, whereas plant height, fruit weight, pericarp thickness, largest and smallest fruit width, and placenta length showed higher variance due to dominance estimates (Table 5). Selection is indicated in early generations for the traits in which additive effects predominated (Rêgo et al., 2021; Fortunato et al., 2015; do Rêgo & do Rêgo, 2018). Similar result was observed by Bento et al. (2016) for total soluble solids in *Capsicum annum*. The predominance of dominant genetic effects complicates the breeder's work (Bnejdi et al. 2009) since it is not possible to be sure whether the superior phenotype observed corresponds to the desired genotype (Bento et al., 2013). Therefore, the production of hybrids or selection in advanced generations is indicated for these traits (Barroso et al., 2015; do Rêgo & do Rêgo 2018; Pessoa et al., 2021). In this case, the SSD (single seed descent) method is recommended as it allows a rapid advancement of generations for late selection (Bento et al., 2013).

Table 3. Genetic parameters of quantitative traits in ornamental pepper (*Capsicum annum* L.).

Traits	σ_p^2	σ_e^2	σ_g^2	σ_a^2	σ_d^2	h_b^2	h_n^2	ADD
PH	10.8359	9.5463	1.2897	0	2.3350	11.9019	0	0
CW	16.0458	7.8513	8.1945	18.1826	0	51.0695	51.0695	0
SW	0.00998	0.0070	0.0029	0.00286	0.00007	29.3854	28.6395	0.2282
FW	0.0409	0.0152	0.0257	0	0.0430	62.8804	0	0
FL	0.0366	0.0147	0.0219	0.0172	0.0047	59.8919	46.9367	0.7430
LFW	0.0085	0.0042	0.0042	0.0005	0.0037	49.9598	6.1581	3.7717
SFW	0.0040	0.0047	0	0	0.0033	0	0	0
PL	0.0432	0.0586	0	0	0	0	0	0
PT	0.0009	0.0003	0.0006	0	0.0139	64.7173	0	0
PLL	0.0190	0.0165	0.0024	0	0.0162	12.8215	0	0
SYF	26.7742	21.183	5.5909	4.6151	0.9758	20.8818	17.2371	0.6503
DMC	22.5875	448.91	0	0	0	0	0	0

PH-Plant height, CW-canopy width, SW-stem width, FW-fruit weight, FL-fruit length, LFW-larger fruit width, SFW-smaller fruit width, PL-Pedicel length, PT-Pericarp thickness, PLL-placenta length, SYF-seed yield per fruit, and DMC-dry matter content.

σ_p^2 -Phenotypic variance, σ_e^2 -environmental variance, σ_g^2 -genotypic variance, σ_a^2 -additive variance, σ_d^2 -Variance due to dominance, h_b^2 -broad-sense heritability, h_n^2 -narrow-sense heritability, ADD-average dominance degree.

Gene effects

The additive-dominance model (m, a, d) showed correlation coefficient values (r) that ranged from 0.68 to 0.93 for all evaluated traits, except for dry matter content (DMC) (r = 0.53) (Table 4), suggesting the suitability of this model to explain the genetic parameters of all traits but DMC. The presence of epistasis complicates selection (Bnejdi et al., 2009; 2010). In the present study, the absence of this phenomenon, for the majority of evaluated traits, facilitates selection based on all variables analyzed.

For the additive-dominance model, the midparent gene effect (m) was significant at 1% probability for all evaluated traits (Table 4). The additive

(a) and dominance (d) genetic effects were significant at 1% and 5% probability for plant height, canopy width, stem width, fruit length, largest fruit width, smallest fruit width, and placenta length (Table 4), indicating that both additive and dominance gene effects are involved in the expression of these traits.

Additive gene effects were more important than dominance effects for canopy width, stem width, fruit length, largest fruit width, smallest fruit width, pericarp thickness, placenta length, and seed yield per fruit. Predominance of additive gene effects was showed to fruit width and fruit length (Nascimento et al., 2014; Santos et al., 2014; Silva et al., 2017), plus to pericarp thickness

(Santos et al., 2014) besides placenta length and seed yield per fruit (Nascimento et al., 2014). According to Rêgo et al. (2009), these traits are easily fixed in early generations and can be improved by the pedigree method. These same authors suggested using recurrent or mass selection to release new cultivars for traits with predominant additive effects.

The dominance effects were predominant for plant height, fruit weight, and pedicel length, and then these traits cannot be improved by simple selection

methods. Heterosis breeding can be explored for these traits. According to Buthia et al. (2015) the fruit yield are governed by non-additive effects. Pessoa et al. (2021) also reported predominance of dominance effects determining the fruit weight and pedicel length.

The dry matter content showed significant midparent (m), dominance (h) and dominance x dominance (l) gene effects, but only m gene effect showed significance (Table 4).

Table 4. Gene effects of complete model and additive-dominance model for plant size-related traits and fruit traits of ornamental pepper (*Capsicum annuum*).

Gene effects	Traits							
	PH		CW		SW		FW	
	Estimate	R ²	Estimate	R ²	Estimate	R ²	Estimate	R ²
m	29.75**	68.51	25.56**	61.36	0.59**	69.43	0.55**	33.70
d	8.40**	19.35	-4.45**	30.28	-0.11**	13.56	-0.03ns	1.71
h	0.26ns	0.60	0.10ns	0.0001	0.40*	4.64	0.43ns	2.94
i	2.63**	6.06	2.89ns	0.83	0.10ns	2.37	0.05ns	0.26
j	1.48ns	3.41	6.92**	7.30	0.07ns	0.85	0.64**	60.59
l	0.89ns	2.05	2.64ns	0.22	-0.37**	9.15	-0.15ns	0.80
Additive-dominance model								
m	33.40**	97.56	29.02**	98.05	0.74**	96.93	0.53**	90.41
d	-2.43**	0.53	-3.62**	1.63	-0.11**	2.54	0.04ns	0.40
h	-8.62**	1.89	-3.49**	0.31	-0.09**	0.52	0.33**	9.18
r	0.68		0.83		0.89		0.72	
Gene effects	FL		LFW		SFW		PL	
	Estimate	R ²	Estimate	R ²	Estimate	R ²	Estimate	R ²
	m	0.76**	46.71	0.73**	54.88	0.55**	49.74	1.61**
d	0.11**	31.96	0.17**	30.28	0.16**	20.53	0.09ns	0.81
h	0.21ns	0.55					-1.94**	13.40
i	0.14ns	1.52	-0.53**	4.21	-0.69**	10.46	-0.07ns	0.18
j	0.38**	19.04					-0.23ns	0.99
l	0.09ns	0.21	0.05ns	0.31	-0.02ns	0.136	1.45**	16.13
Additive-dominance model								
m	0.87**	96.16	0.67**	94.12	0.38**	92.71	1.38**	92.12
d	0.16**	3.42	0.15**	5.30	0.10**	6.39	0.19**	1.85
h	0.12**	0.42	-0.09**	0.58	-0.06**	0.89	-0.64**	6.03
r	0.87		0.93		0.82		0.72	
Gene effects	PT		PLL		SYF		DMC	
	Estimate	R ²	Estimate	R ²	Estimate	R ²	Estimate	R ²
	m	0.03ns	7.60	0.71**	87.12	34.85**	50.05	27.67**
d	0.01ns	23.81	0.04ns	1.83	11.03**	25.54	-11.32ns	10.46
h	0.13ns	15.37	-0.002ns	0.0001	-38.15**	8.51	-37.22ns	11.54
i	0.05ns	23.59	0.02ns	0.08	-1.48ns	0.11	-1.03ns	0.71
j	0.04ns	13.68	0.26*	10.61	-11.38**	4.51	23.47ns	11.08
l	-0.09ns	15.94	0.08ns	0.36	29.03**	11.28	23.65ns	10.49
Additive-dominance model								
m	0.08**	97.88	0.66**	96.05	25.30**	94.18	15.48**	99.75
d	0.01*	1.50	0.12**	2.96	5.71**	5.43	0.04ns	0.0009
h	-0.01ns	0.62	0.12**	0.99	-2.76ns	0.39	-1.27ns	0.25
r	0.7839		0.7825		0.8697		0.5319	

PH-Plant height, CW-canopy width, SW-stem width, FW-fruit weight -, FL-fruit length, LFW-larger fruit width, SFW-smaller fruit width, PL-Pedicel length, PT-Pericarp thickness, PLL-placenta length, SYF-seed yield per fruit, and DMC-dry matter content.

m - midparent, d - additive, h - dominance, i - additive x additive, j - additive x dominance e l - dominance x dominance, r - correlation coefficient. R²-coefficient of determination.

*, ** Significant by t test at 5% and 1% of probability, ns - not significant.

Conclusions

Additive genetic effects were more important than dominance effects for canopy width, stem width,

fruit length, largest fruit width, smallest fruit width, pericarp thickness, pedicel length, and seed yield per fruit, and selection is indicated in early generations. On the other

hand, plant height, fruit weight and placenta length showed higher variance estimates due to dominance and, therefore, selection in late generations is indicated for these traits.

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