Determining the inheritance of agronomic traits in chili pepper

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ABSTRACT

The *Capsicum* genus is widely studied in many countries but most of research focuses on *C. annuum*. Although its importance as potential genetic resource for breeding to disease resistance and fruit quality, studies on genetics and breeding in *C. baccatum* var. *pendulum* are still scarce and it still remains as an underexploited crop. This paper aimed to study the inheritance of agronomic characteristics, to estimate the genetic parameters for seven agronomic traits in *C. baccatum* var. *pendulum*, using generation mean analysis and to verify the existence of major genes and polygenes with additive and non-additive effects, using the method of maximum likelihood with the aid of Monogen software. The agronomic traits evaluated were: number of fruits per plant (NFP); average fruit mass per plant (AFM); fruit length (FRL); fruit diameter (FRD); fruit pulp thickness (FPT); soluble solids content (SSC) and fruit dry mass (FDM). There was a significant difference among generations (P1, P2, F1, F2, BC1 and BC2) for all traits evaluated. Narrow sense heritability estimates ranged from 45% for NFP to 75% for FRD. By estimating the average degree of dominance (ADD), we found that partial dominance is the gene action involved in the genetic control for FRL and FRD, while additive effect was observed for NFP, FPT and SSC, complete dominance for FDM and overdominance for AFM. The additive-dominant model was sufficient to explain the results obtained for all evaluated traits. Maximum likelihood method identified the existence of polygenes with additive and dominance effects in SSC, FPT and FDM. Major gene effect was identified for FRL and NFP characteristics. The results indicated the complexity of the inheritance of these traits with the presence of major gene involved.

Keywords: *Capsicum baccatum* var. *pendulum*, genetic control, heritability, major gene, additive-dominant model, segregating generation.

RESUMO

Determinação da herança de características agronômicas em pimenta

O gênero *Capsicum* é amplamente estudado em muitos países, porém a maioria das pesquisas se concentra em *C. annuum*. Apesar de sua importância como potencial recurso genético para a resistência a doenças e qualidade dos frutos, os estudos sobre a genética e o melhoramento de *C. baccatum* var. *pendulum* ainda são escassos, além de ser considerada uma espécie subexplorada. Este trabalho teve como objetivos: estudar a herança de sete características agronômicas; estimar os parâmetros genéticos para esses caracteres por meio da análise de médias de gerações e verificar a existência de gene de efeito maior e de possíveis poligenes de efeitos aditivos e não aditivos, utilizando-se o método da máxima verossimilhança com auxílio do programa Monogen. As características agronômicas avaliadas foram: número de frutos por planta (NFP); massa média de frutos por planta (MMF); comprimento do fruto (CPF); diâmetro do fruto (DFR); espessura de polpa do fruto (EPF); teor de sólidos solúveis totais (TSS) e massa seca de fruto (MSF). Houve diferença significativa entre as gerações (P$_1$, P$_2$, F$_1$, F$_2$, RC$_1$ e RC$_2$) para todas as características avaliadas. As estimativas da herdabilidade no sentido restrito variaram de 45% (NFP) a 75% (DFR). Constatou-se que a ação gênica de dominância parcial está envolvida no controle genético das características CPF e DFR, enquanto que a ação aditiva foi observada para NFP, EPF e TSS, dominância completa para MSF e sobredominância para MMF. O modelo aditivo-dominante foi suficiente para explicar os resultados obtidos para todas as características avaliadas. Já pelo método da máxima verossimilhança pode-se identificar a existência de poligenes com efeitos aditivos e de dominância nas características TSS, EPF e MSF. A ação de gene de efeito maior foi detectada para CPF e NFP. Os resultados apontam a complexidade da herança das características avaliadas, com presença de gene de efeito maior envolvido.

Palavras-chave: *Capsicum baccatum* var. *pendulum*, controle genético, herdabilidade, gene de efeito maior, modelo aditivo-dominante, geração segregante.

The *Capsicum baccatum* species is considered one of the main chili peppers from South America, with its origin center in Bolivia and southern Peru (Eshbaugh, 1970; D'Arcy & Eshbaugh, 1974). This species has botanical varieties classified as wild (*C. baccatum* var. *baccatum*, *C. baccatum* var. *praetermissum* and *C. baccatum* var. *umbilicatum*), and domesticated (*C. baccatum* var. *pendulum*) (Eshbaugh, 1970; Albrecht *et al.*, 2012).

The domestication of *C. baccatum* is relatively recent compared with many other cultivated species, occurring

approximately 4500 years ago in the highlands of Peru from wild types of Bolivia locally known as 'arivivi' (Pickersgill *et al.*, 1979; Albrecht *et al.*, 2012). The cultivation of *C. baccatum* lies mainly in lowlands and middle altitudes of Argentina, Bolivia, Peru, Ecuador, Paraguay, Colombia, Chile and largely in Brazil (Albrecht *et al.*, 2012).

In Brazil, the *C. baccatum* var. *pendulum* is widely produced by small farmers, and red chili pepper (or "deer horn" chili pepper) and cambuci (or friar's hat chili pepper) are the most cultivated chili peppers for fresh consumption and for making sauces, potted chili peppers and dehydrated flakes (Moreira *et al.*, 2006; Rêgo *et al.*, 2009; Rodrigues *et al.*, 2012). However, there is a lack of research on genetics and breeding, and consequently on the development of cultivars of this species. Only 15 cultivars were registered in the National Registry of Cultivars (*Registro Nacional de Cultivares* - RNC) of the Ministry of Agriculture, Livestock and Food Supply of Brazil (MAPA, 2013), with the majority belonging to private seed companies that lack of *Capsicum* breeding programs in the country (Rodrigues *et al.*, 2012).

Characteristics such as productivity, resistance and/or tolerance to biotic and abiotic stresses, plant architecture, earliness, ripe fruit persistence, as well as characteristics related to fruit quality are the targets of *Capsicum* breeding programs (Rêgo *et al.*, 2011; Rodrigues *et al.*, 2012). Obtaining adequate information on the nature and magnitude of the gene effects of these characteristics is of major importance for the identification of the most suitable method to be applied in the selection and prediction of responses of segregating generations for the development of cultivars of *C. baccatum* var. *pendulum*.

The potential of a base population and the selection efficiency for the development of cultivars can be investigated by means of the relative importance of additive, dominance and epistatic effects for each trait (Hallauer *et al.*, 2010; Gonçalves *et al.*, 2011). The existence of differences between the additive genetic values of individuals in a population is a necessary condition for intrapopulation improvement. However, the feasibility of a breeding program aimed at developing hybrids depends on the existence of dominance effects, which correspond to the interaction between allelic genes. If the goal of the breeding program is to develop superior inbred lines, the magnitude and sign of additive effects and additive x additive effects need to be evaluated. When the goal is to develop a hybrid, it is necessary to perform analysis of contributions of genetic effects of dominance, dominance x dominance, additive x dominance, selecting for heterosis in the desired direction, with greater heterosis expected when such effects are predominantly directional (Mather & Jinks, 1982; Marame *et al.*, 2009a).

Information about the genetic control of agronomic traits in *C. baccatum* var. *pendulum* is still scarce in the literature (Rêgo *et al.*, 2009; Gonçalves *et al.*, 2011; Rodrigues *et al.*, 2012) when compared with *C. annuum*. The knowledge of that information is important for the decision making about the breeding methods to be used or about the size of population to be conducted during the implementation of the improvement program. The aim of this paper was to study the inheritance of agronomic traits in *C. baccatum* var. *pendulum*.

MATERIAL AND METHODS

To estimate the nature and magnitude of the genetic variability available and gene effects for agronomic traits of *C. baccatum* var. *pendulum,* the segregating generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the crosses between parents UENF 1616 x UENF 1732 were evaluated. These parents were chosen based on preliminary results of the *C. baccatum* var. *pendulum* breeding program of the Plant Breeding Laboratory of the *Universidade Estadual do Norte Fluminense Darcy Ribeiro* (UENF), with the objective of obtaining resistant cultivars to *Pepper yellow mosaic virus* (PepYMV). The parent UENF 1616 comes from the genebank of collection held in Campos dos Goytacazes, Rio de Janeiro State, Brazil, and it is described as susceptible to PepYMV and has yellow fruits at the immature stage and orange at maturity. Its fruits are elongated with length around of 10 cm and diameter of 2.7 cm. The parent UENF 1732 was also collected in a local market in Campos dos Goytacazes, and it is characterized as resistant to PepYMV (Bento *et al.*, 2009), showing fruits of orange color in the immature stage and red at maturity, with campanulate shape, mean length of 4,4 cm and diameter of 4,5 cm.

The field experiment was carried out in *Unidade de Apoio à Pesquisa* located in the UENF, in Campos dos Goytacazes, from August 2010 to April 2011. The study adopted a randomized block experimental design with three replications and spacing of 1.10 m between rows and 0.60 m between plants. In each block, seven plants of each parent (P_1 and P_2), 12 plants of the F_1 generation, 83 plants of F_2 generation and 28 plants of each backcrossing (BC_1 and BC_2), totaling 495 plants, were cultivated. Regarding the F_2 generation, plants were arranged in blocks, but replications were not considered, since it was a segregating generation.

During the experiment, the cultural treatments usually recommended for the culture of chili pepper (Filgueira, 2012) such as weeding, staking, fertilization and irrigation by sprinkler system were performed. Seven harvests were performed and the following agronomic traits were evaluated: number of fruits per plant (NFP) (sum of the number of fruits obtained in the seven harvests); average fruit mass per plant (AFM) (average mass in grams, using the ratio of the total mass of fruits per plant and the number of fruits per plant); fruit dry mass (FDM) (average mass in grams of five dried fruits per plant, using forced circulation oven at 65°C and 72 h); fruit length (FRL) (measured in mm, considering ten ripe fruits per plant); fruit diameter (FRD) (measured in mm, considering ten ripe fruits per plant); fruits pulp thickness (FPT) (measured in mm, considering ten ripe fruits per plant) and total soluble solids content (SSC) (measured in ten ripe fruits per plant, using a digital refractometer).

Data were subjected to analysis of variance of the generations and, subsequently, the following estimates and parameters were calculated, according to Cruz *et al.* (2004).

Phenotypic variance (σ_f^2):

$$\sigma_f^2 = \sigma_{F_2}^2$$

Variance attributed to the environment in F_2 population (σ_{we}^2):

$$\sigma_{we}^2 = \left(\sigma_{P_1}^2 . \sigma_{P_2}^2 . \sigma_{F_1}^2\right)^{1/3}$$

Genotypic variance in the F_2 population (σ_g^2):

$$\sigma_g^2 = \sigma_{F_2}^2 - \sigma_{we}^2$$

Additive variance (σ_a^2):

$$\sigma_a^2 = 2\sigma_{F_2}^2 - \left(\sigma_{BC_1}^2 + \sigma_{BC_2}^2\right)$$

When $\sigma_a^2 > \sigma_g^2$, considered $\sigma_a^2 = \sigma_g^2$

Variance due to dominance deviations: $\sigma_d^2 = \sigma_g^2 - \sigma_a^2$

When σ_d^2 negative, considered $\sigma_d^2 = 0$

Broad sense heritability (h_a^2):

$$h_b^2 = \frac{\sigma_g^2}{\sigma_{F_2}^2}$$

Narrow sense heritability (h_η^2):

$$h_\eta^2 = \frac{\sigma_a^2}{\sigma_{F_2}^2}, \quad h_\eta^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_d^2 + \sigma_{we}^2}$$

Average degree of dominance (ADD) based on variances:

$$ADD = \sqrt{\frac{2\sigma_d^2}{\sigma_a^2}}$$

Minimum number of genes involved in determining a character (η):

$$\eta = \frac{R^2(1 + 0,5k^2)}{8\sigma_g^2}$$

where: $\sigma_{P_1}^2$ = variance of P_1 generation (UENF 1616); $\sigma_{P_2}^2$ = variance of P_2 generation (UENF 1732); = variance of F_1 generation (UENF 1616 x UENF 1732); $\sigma_{BC_1}^2$ = variance of generation of BC_1 (F_1 x UENF 1616); $\sigma_{BC_2}^2$ = variance of generation of BC_2 (F_1 x UENF 1732); R^2 = total amplitude in F_2; K = ADD; M = Mean

The analysis of parental and segregating generations' means was performed by complete and additive-dominant models. In the complete model (m, a, d, aa, ad, dd), the parameters were estimated by the method of ordinary least squares. In the additive-dominant model (m, a, d), the parameters were estimated by the weighted least squares method proposed by Mather & Jinks (1982). The adequacy of complete and additive-dominant model was evaluated using the coefficient of determination (R^2), which expresses the degree of similarities of the estimates between the estimated values and the observed ones. The analysis of variance and the analyses of the means of generations were performed by using the GENES software (Cruz, 2013).

In order to identify the existence of major genes and polygenes with additive effects and non-additive for all traits we used the maximum likelihood method by the statistical program Monogen v. 0.1 (Silva, 2003; Gonçalves *et al.*, 2007).

RESULTS AND DISCUSSION

There was a significant effect of generation by the F test for all traits, indicating the existence of variability among the generations evaluated. The coefficients of experimental variation ranged from 13.65% to 45.72%, values which are considered from medium to very high for chili pepper (Silva *et al.*, 2011); however, they are considered satisfactory since variance was highly significant for most of the traits (FRL, FRD, SSC and FDM) and significant for the others traits (NFP, AFM and FPT). The coefficients considered high and very high for the traits under study can be attributed to the great variability existing in the fruits, resulting from the extensive segregation observed in the F_2 generation.

From the phenotypic variances of generations, genetic parameters were estimated including the broad sense heritability (h_b^2), the narrow sense heritability (h_n^2), the average degree of dominance (ADD) and the minimum number of genes (σ) (Table 1). For NFP, the h_b^2 and h_n^2 were 45% with predominant additive gene effects, because the dominance variance was negative, being, in this case, considered equal to zero. The ADD indicated additive gene action and the number of genes controlling this trait was 16, featuring a polygenic inheritance. Rêgo

et al. (2009) and Rodrigues *et al.* (2012) evaluated diallel crosses in *C. baccatum* var. *pendulum* and found both additive and non-additive effects in genetic control for NFP, and dominance effects were predominant with different results from the ones obtained in the current study. Nevertheless, Medeiros *et al.* (2014) also evaluating the combining ability in diallel crosses of *C. baccatum* var. *pendulum*, found the predominance of additive effects, indicating the possibility of satisfactory gains with selection for this trait in segregating generations.

For AFM, it can be observed that the dominance variance (2.68) was greater than the additive variance (0.42), in accordance with the values obtained for narrow sense heritability (5%). In the broad sense, h_b^2 was 35% for this trait. Marame *et al.* (2009b) studied the heritability and heterosis in *C. annuum* var. *annuum* genotypes and observed low values of narrow sense heritability (14%) and high values in the broad sense heritability (72.6%) for yield per plant and they concluded that the components of dominance were important, while the additive components contributed very little to achieve high yields. Considering this, hybrids exploitation could be recommended for commercial purposes. Regarding ADD, there was prevalence of overdominance for this characteristic. This result is discordant to those observed by Juhász *et al.* (2009), who also estimated the gene effects involved in the inheritance of agronomic traits in *C. annuum* and found only additive effects for this trait. These authors determined that AFM was controlled by a large number of genes (15), and eventually strongly influenced by environmental conditions. Silva *et al.* (2013) estimated the genetic parameters for AFM in *C. annuum* and observed absence of dominance for this trait. These observations demonstrate the complexity of the AFM in *Capsicum* plants.

The FRL and FRD traits showed predominance of additive variance over the variance of dominance, with h_b^2 of 75% and 79%, respectively, while h_n^2 was 64% and 75%, respectively. For both traits, a partial dominance (0.59
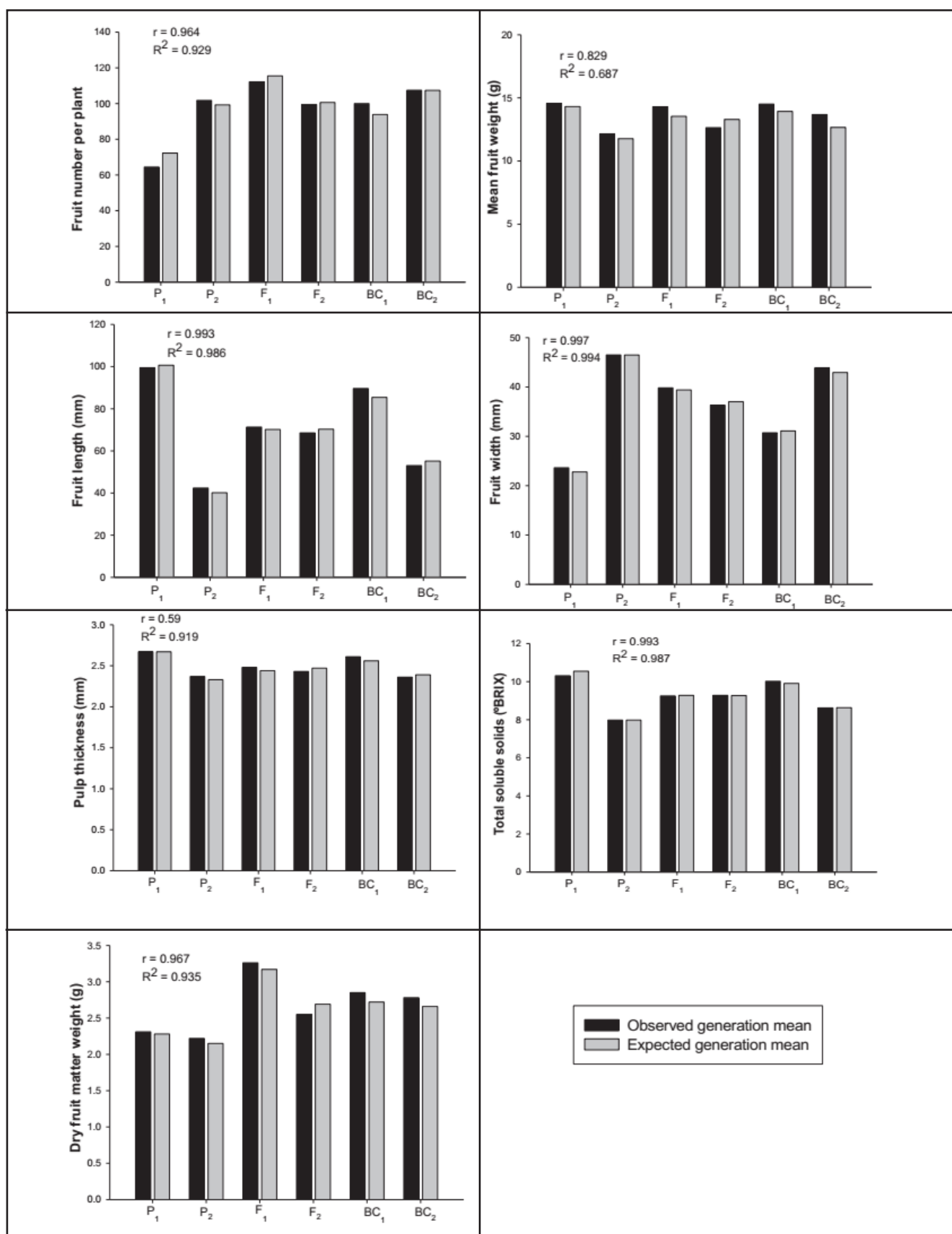
Figure 1. Average observed and expected for each of the generations in the additive-dominant model (m, a, d) for seven agronomic traits, from crosses between UENF 1616 x UENF 1732 *Capsicum baccatum* var. *pendulum* (médias observadas e esperadas para cada uma das gerações no modelo aditivo-dominante (m, a, d) para sete caracteres agronômicos, a partir do cruzamento entre UENF1616 x UENF 1732 de *Capsicum baccatum* var. *pendulum*). Campos dos Goytacazes, UENF, 2011.

Table 1. Estimates of genetic parameters obtained from variances of seven agronomic traits evaluated in plants of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations, from crosses between UENF 1616 x UENF 1732 *Capsicum baccatum* var. *pendulum* (estimativas dos parâmetros genéticos obtidos das variâncias de sete caracteres agronômicos avaliados em plantas das gerações P_1, P_2, F_1, F_2, RC_1 e RC_2, a partir do cruzamento entre UENF 1616 x UENF 1732 de *Capsicum baccatum* var. *pendulum)*. Campos dos Goytacazes, UENF, 2011.

Genetic parameters[2/]	Agronomic characteristics						
	NFP[1]	AFM	FRL	FRD	FPT	SSC	FDM
σ^2_f	2360.41	8.98	507.47	76.90	0.18	1.62	0.31
σ^2_{we}	1710.73	5.88	125.17	16.39	0.08	1.00	0.14
σ^2_g	649.68	3.10	382.30	60.51	0.10	0.62	0.17
σ^2_a	1072.18	0.42	324.86	57.71	0.10	0	0.11
σ^2_d	0	2.68	57.44	2.80	0	0.62	0.06
h^2_b	45.00	35.00	75.00	79.00	56.00	38.00	55.00
h^2_n	45.00	5.00	64.00	75.00	56.00	0	35.00
ADD	0	3.57	0.59	0.31	0	0	1.00
σ	16	-	5	5	7	-	11

[1]NFP= number of fruits per plant (número de frutos por planta), AFM= average fruit mass (g) {massa média do fruto (g)}, FRL= fruit length(mm) {comprimento médio do fruto (mm)}, FRD= fruit diameter (mm){diâmetro médio do fruto (mm)}, FPT= fruits pulp thickness (mm) {espessura da polpa (mm)}, SSC= total soluble solids content (teor de sólidos solúveis totais) and FDM= fruit dry mass (g) {massa seca de fruto (g)}. [2/]σ^2_f= phenotypic variance (variância fenotípica), σ^2_{we} = variance attributed to the environment (variância ambiental), σ^2_g = genotypic variance (variância genotípica), σ^2_a =additive variance (variância aditiva), σ^2_d = dominance variance (variância de dominância), h^2_b = broad sense heritability (herdabilidade no sentido amplo), h^2_n = narrow sense heritability (herdabilidade no sentido restrito), ADD= average degree of dominance (grau médio de dominância), and σ = minimum number of genes (número mínimo de genes).

Table 2. Coefficient of determination R^2 (%) for non-orthogonal decomposition of the sum of squares of adjusted parameters for seven agronomic traits in the complete model (m,a,d,aa,ad,dd), evaluated in plants of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations, from cross between UENF 1616 x UENF 1732 *Capsicum baccatum* var. *pendulum* {coeficiente de determinação (R^2 %) pela decomposição não-ortogonal da soma de quadrados de parâmetros ajustados para sete caracteres agronômicos, no modelo completo (m,a,d,aa,ad,dd), avaliados em plantas das gerações P_1, P_2, F_1, F_2, BC_1 e BC_2, a partir do cruzamento entre UENF1616 x UENF 1732 de *Capsicum baccatum* var. *pendulum*}. Campos dos Goytacazes, UENF, 2011.

Genetic parameters	Agronomic characteristics						
	NFP[1]	AFM	FRL	FRD	FPT	SSC	FDM
m/a,d,aa,ad,dd	40.08	35.41	15.93	18.17	90.86	85.42	31.62
a/m,d,aa,ad,dd	37.25	18.37	81.13	80.74	7.14	14.06	1.00
d/m,a,aa,ad,dd	9.69	15.32	0.37	0.39	0.27	0.12	32.37
Sub total	87.02	69.10	97.43	99.30	98.27	99.60	64.99
aa/m,a,d,ad,dd	2.93	22.18	0.58	0.29	0.78	0.03	24.62
ad/m,a,d,aa,dd	5.17	0.41	1.76	0.34	0.80	0.23	0.04
dd/m,a,d,aa,ad	4.89	8.32	0.23	0.07	0.15	0.14	10.34
Total epistasis	12.99	30.91	2.57	0.70	1.73	0.40	35.00

[1]NFP= number of fruits per plant (número de frutos por planta), AFM= average fruit mass (g) {massa média do fruto (g)}, FRL= fruit length (mm) {comprimento médio do fruto (mm)}, FRD= fruit diameter (mm) {diâmetro médio do fruto (mm)}, FPT= fruits pulp thickness (mm) {espessura da polpa (mm)}, SSC= total soluble solids content (teor de sólidos solúveis totais) and FDM= fruit dry mass (g) {massa seca de fruto (g)}.

and 0.31, respectively) was indicated and five genes were calculated for each of these traits. These results regarding the predominance of additive effects are also corroborated by those obtained for *C. baccatum* var. *pendulum* by Rêgo *et al*. (2009), Rodrigues *et al*. (2012) and Medeiros *et al*. (2014). Rêgo *et al*. (2011) studied the phenotypic diversity in fruits of *C. baccatum* var. *pendulum* and also observed high values for h^2_b, 99% and 98% for FRL and FRD, respectively. Sood & Kumar (2011) studied the genetic estimates of fruit traits in *C. annuum* and observed partial dominance for FRL and FRD (ADD = 0.62 and 0.84, respectively), results similar to those obtained in the current study.

For FPT trait, the additive variance was similar to the genotypic one, since the variance of dominance was negative, being, in this case, considered equal to zero. Moreira *et al*. (2013) studied the inheritance of traits of antixenosis resistance by *Solanum pennellii* to the tomato leafminer crossed with

Santa Clara, and they also identified dominance variance equal to zero for the number of eggs per leaf and for number of large mines. According to the authors, the negative values of dominance variance may be related to the low accuracy of the estimates of environmental variance. Thus, h^2_b and h^2_n were equal (56%) and ADD indicated additive gene action. The minimum number of genes was seven in the control of this trait. With respect to the SSC, the reverse was found, i.e., the dominance variance was similar to the genotypic one, with h^2_b of 38%. By presenting a negative additive variance (considered equal to zero) the ADD would not be a good parameter to estimate this variable, because by its

formula
$$ADD = \sqrt{\frac{2\sigma_d^2}{\sigma_a^2}},$$

its value would be 0.00, not consistent with the values observed in additive and dominance variances. The predominance of additive variance for FPT is in accordance with the study by Rêgo *et al.* (2009) and Rodrigues *et al.* (2012). For SSC, the predominance of dominance variance was different to that observed by Rodrigues *et al.* (2012), but it was consistent with that observed by Rêgo *et al.* (2009) and Medeiros *et al.* (2014).

Regarding the FDM, there was a genotypic, additive and dominance variance of 0.17, 0.11 and 0.06, respectively, and therefore, an h^2_b and h^2_n of 55% and 35%, respectively. This predominance of additive effects over the dominance ones is also consistent with the one found by Rêgo *et al.* (2009) and Rodrigues *et al.* (2012). A complete dominance gene action was observed in the control of this trait with a minimum number of genes equal to 11 (Table 1).

From the generation mean analysis, the complete model and the additive-dominant model were tested. In the additive-dominant model, the mean showed greater magnitude for all studied traits, by the non-orthogonal decomposition of the sum of squares of parameters, explaining respectively 94.01, 98.98, 85.07, 89.42, 99.51, 98.21 and 94.94% of the variability available

to NFP, AFM, FRL, FRD, FPT, SSC and FDM. Juhász *et al.* (2009) studied the detection of epistatic gene action in the genetic control of agronomic traits in pepper and found that the mean was also the main parameter in the inheritance of the traits studied in the additive-dominant model.

The additive-dominant model was sufficient to explain all the data in studies in which the correlation coefficients reached values of 0.96, 0.82, 0.99, 0.99, 0.95, 0.99 and 0.96 for NFP, AFM, FRL, FRD, FPT, SSC and FDM, respectively (Figure 1). Sood & Kumar (2011) also confirmed that the additive-dominant model is suitable for explaining the characteristics of fruit production in *C. annuum*.

For NFP and FDM traits, it was noted that plants of the F_1 generation had higher means than those of their parents (Figure 1) characterizing the presence of heterosis, although for NFP, there was the predominance of additive effect and, for FDM there was complete dominance. This probably occurred because the traits are complex due to the large number of genes that govern them (16 and 11, respectively), which had epistatic action of 12.99% for NFP and of 35% for FDM, resulting in a gene complementation for these traits. Another hypothesis could be the underestimation of the variance of dominance in relation to the additive one. According to Bernardo (2002), the method of least squares tends to reduce the dominance variance, underestimating these values. Juhász *et al.* (2009) identified epistatic action of 62.72% for NFP trait in *C. annuum*, corroborating the data obtained in this study.

Regarding the trait of fruit dry mass, the BCs obtained higher mean than the parents and the individuals of the F_2 generation. Regarding NFP, BC_2 produced more fruits than the parents. However, plants of the F_1 generation had fruits with lower average mass than the fruits produced by P_1 and BC_1, indicating that the F_1 generation plants produced more fruits, but they were lighter. Similar results were found by Rêgo *et al.* (2011) who identified a negative correlation for the NFP and

AFM traits in accessions of *C. baccatum* var. *pendulum*.

In the complete model, the gene effect attributed to epistatic effects was significant for AFM and FDM at the level of 1% probability by *t* test (data not shown). Both characteristics contributed respectively with 30.91 and 35.00% of the variability available for these traits (Table 2). Epistatic effects for AFM trait were also obtained by Juhász *et al.* (2009) in *C. annuum*. However, Gonçalves *et al.* (2011) studied the inheritance of traits related to fruit production in *C. baccatum* var. *pendulum* based on Hayman diallel analysis and they identified the absence of epistasis for FDM and AFM traits. Nevertheless, these authors evaluated only crossings of five parents, this number being considered insufficient for the accurate estimation of epistatic effects by Hayman analysis.

By means of the likelihood function was possible to detect the models of inheritance to determine the presence of major genes. For the SSC, FPT and FDM characteristics occur polygenic control with additive and dominance effects. However, for characteristic NFP there is action of a major gene and polygenes with only additive effect. Moreover, for FRL characteristic, the presence of a major gene with additive and dominance effects was observed, in agreement with the hypothesis of these characteristics have complex inheritance.

This study allows concluding that the inheritance of most agronomic traits in chili pepper (*C. baccatum* var. *pendulum*), was polygenic with additive and dominance effects and also that for the FRL and NFP traits major genes play an important role regarding genetic control. Epistatic gene effects were more important for number of fruits per plant, average fruit mass and dry mass of fruit.

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