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PLANT BREEDING

Genetic inheritance of ornamental components in pepper plants (*Capsicum annuum* L.)

Fátima de Souza Gomes[1], Gabriela Cristina Alves Custódio[1*], Samy Pimenta[1], Fabrícia Cardoso Oliveira[1], Allyson Gabriel Santos de Paula[1], Nadiany Souza Silva[1], Maria do Socorro Bezerra de Araújo[2] and Marlon Cristian Toledo Pereira[1]

[1]Universidade Estadual de Montes Claros, Campus Janaúba, Avenida Reinaldo Viana, 2630, Morada do Sol, 39448-524, Janaúba, Minas Gerais, Brazil. [2]Universidade do Estado de Mato Grosso, Cáceres, Mato Grosso, Brazil. *Author for correspondence. E-mail: gabrielac.agro@gmail.com

ABSTRACT. Limited information is available regarding the genetic inheritance of ornamental traits in peppers (*Capsicum* spp.), which is crucial for enhancing these plants for ornamental purposes in breeding programs. This study aimed to elucidate the genetic inheritance of ornamental traits in segregating populations of pepper plants (*C. annuum* L.) from distinct parents and to characterize them based on their flowering and fruiting cycles. The selected parents, UNI01 and UNI05, were sourced from the active germplasm bank of Universidade Estadual de Montes Claros, Janaúba, Minas Gerais State, Brazil. The experiment took place in a greenhouse, involving manual hybridization between UNI01 and UNI05 to obtain seeds of segregating populations, which included F1, RC1, RC2, F2, and F3 generations. Qualitative traits assessed included flower corolla color, immature fruit color, and shapes of longitudinal and transversal fruit sections. Quantitative traits encompassed mean flowering and fruiting days. We employed chi-square tests (χ^2) to evaluate segregation patterns. The descriptor "corolla color" exhibited codominance, with a white corolla and purple borders linked to heterozygous genotypes. Dominant inheritance controlled the color of immature fruits, primarily purple. Genetic inheritance for transversal and longitudinal fruit shapes remained unexplained in the tested segregations. Parental and segregating generations displayed similar flowering and fruiting cycles. These results provide valuable insights for future breeding programs aimed at using this species for ornamental purposes.

Keywords: codominance; complete dominance; hybridization; segregation.

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Introduction

Understanding the genetic inheritance of traits is essential for selecting effective breeding strategies that harness the genetic potential of crops (Navhale, Dalvi, Wakode, Bhave, & Burondkar, 2017; Rêgo, Rêgo, & Finger, 2015). Trait inheritance information aids decision-making in breeding programs (Cazassa et al., 2019) and streamlines the process, optimizing resources, and guides breeders to select optimal parents for initial generations (Zorzetto, Motta, Morais, Kiihl, & Silva, 2008).

Pepper plants (*Capsicum* spp.) serve various purposes in industries and local businesses, including food production, pharmaceutical and cosmetic applications, personal and collective defense weaponry, and recently, ornamental cultivation (Gomes et al., 2019). Ornamental pepper plants (*Capsicum annuum* L.) are chosen for their unique aesthetic attributes, such as variegated foliage, compact stature, and multi-colored fruits on the same plant (Rêgo & Rêgo, 2016). Their ease of cultivation, durability in pots, and resistance to pests and diseases make them ideal for ornamental purposes (Neitzke, Fischer, Vasconcelos, Barbieri, & Treptow, 2016).

Few breeding programs for ornamental peppers exist both in Brazil and globally. Consequently, there is a limited number of distinct cultivars available in the market. This situation contrasts with the substantial genetic variability present within the species, which remains largely untapped at the genetic breeding level. An initial step in establishing a successful breeding program, following the identification of parent plants with ornamental potential, involves conducting studies on the genetic inheritance of key contrasting traits present in these parents.

Pessoa, Rêgo, Santos, Carvalho, and Rêgo (2019) assessed the genetic inheritance in ornamental pepper plants and identified potential genetic improvements in traits such as plant height and leaf length. Similarly, Zixiang, Xiaowei, Jianguo, Zhujun, and Biao (2021) conducted a comparable study and revealed that the fruiting pattern is a recessive genetic trait controlled by a single gene.

Qualitative traits are typically governed by simple inheritance patterns and controlled by one or just a few genes, with minimal influence from the environment. These traits are often categorized into distinct classes. In the case of ornamental pepper plants, descriptors such as flower color, anther color, leaf characteristics, and fruit color tend to exhibit this straightforward pattern of inheritance. In contrast, quantitative traits are more complex in nature and are significantly influenced by environmental factors (Falconer, 1981).

The breeding program for *Capsicum* spp. at *Universidade Estadual de Montes Claros* (Unimontes) in Janaúba, Minas Gerais State, Brazil, identified two promising parents, UNI01 and UNI05, with the potential to be used as ornamental pepper varieties (Pimenta et al., 2020). This program was initiated based on the attributes of these parent plants, with a primary focus on developing new ornamental cultivars. Understanding the genetic inheritance of traits that contribute to a desirable ornamental ideotype is a crucial strategy for the successful execution of a breeding program. The selection of specific descriptors for the current study was guided by the contrasts observed between these parents (Pimenta et al., 2020).

In this context, our primary goal was to elucidate the genetic inheritance of traits related to ornamental characteristics in segregating populations of pepper plants (*C. annuum* L.) derived from these contrasting parents, while also characterizing them based on their flowering and fruiting cycles.

Material and methods

Experiment location

The experiment took place in a greenhouse, which was covered with a 50% shade screen. This greenhouse was located in the experimental area of *Universidade Estadual de Montes Claros* (UNIMONTES), Janaúba, Minas Gerais State, Brazil (latitude 15°48'09" S, longitude 43°18'32" W, at an altitude of 533 meters). The climate in this region is classified as AW, a tropical rainy savanna with a dry winter, according to the Köppen classification (Ometto, 1981).

Generation acquisition and experiment conduct

The study involved the analysis of seven generations: P_1 (parent UNI01), P_2 (parent UNI05), F_1, F_2, RC_1, RC_2, and F_3. The F_1 generation was obtained through biparental crossbreeding between the accessions UNI01 (P_1, *Capsicum annuum* var. *annuum* L.) and UNI05 (P_2, *C. annuum* var. *glabriusculum*), both sourced from the active germplasm bank of the pepper plant breeding program (*Capsicum* spp.) at Unimontes, Janaúba, Minas Gerais State, Brazil.

UNI01 displays flowers with a white corolla without any spots, along with blue anthers and white filaments. Its leaves have a medium width, strong roughness, and a moderately intense green color. The fruits are pungent and small, initially white-greenish before ripening and turning red (Pimenta et al., 2020).

UNI05 exhibits flowers with a purple corolla without any spots, along with purple anthers and filaments. Its leaves are narrow, dark green, and slightly rough. The fruits are pungent and short, initially dark purple before maturation and eventually turning red (Pimenta et al., 2020).

The F_1 generation was produced through manual hybridization between UNI01 and UNI05 (Cycle 01), followed by the generation of the F_2 generation through the self-pollination of F_1 individuals. Segregating populations (F_2, RC_1, RC_2, and F_3) were obtained by sowing the F_1 population alongside the parents and conducting targeted crosses. The F_2 generation resulted from the self-pollination of F_1 plants. Backcrosses were achieved as follows: RC_1 was produced by crossing UNI01 (female parent) with F_1 (male parent), and RC_2 was produced by crossing UNI05 (female parent) with F_1 (male parent). Additionally, seeds for F_1, P_1, and P_2 were renewed.

All crosses were manually performed using flower buds at the pre-anthesis stage. In the morning, the plants were emasculated, and pollen from another plant's anther was immediately transferred to the stigma of the recipient flower. Subsequently, the flowers were labeled and covered with aluminum foil to prevent contamination. Seeds for sowing the segregating population were collected from mature fruits.

The segregating population was evaluated through a greenhouse experiment. Seeds were sown in 128-cell plastic trays, with each cell containing a commercial substrate (Bioplant®) and a single seed. The number of seeds sown for each category was as follows: 10 seeds for parent P_1, 10 seeds for parent P_2, 15 seeds for the F_1 generation, 200 seeds for the F_2 generation, 200 seeds for the F_3 population, 60 seeds for RC_1, and 60 seeds for RC_2. The trays were kept in the greenhouse and received daily irrigation.

Seedlings with four to six definitive leaves were transplanted into 1-liter pots filled with a mixture of clayey soil, coarse sand, and bovine manure in a 1:1:1 ratio. These pots were arranged in rows and labeled for subsequent evaluations. Throughout the experiment, cultural practices were applied following conventional cultivation recommendations for the crop (Filgueira, 2012), with necessary adaptations for protected and potted cultivation.

Evaluations

Qualitative descriptors

The plants underwent morphological evaluation based on four qualitative descriptors: corolla color, the predominant shape of the transversal fruit section, the predominant shape of the longitudinal fruit section, and fruit color at the immature stage. These descriptors followed the recommendations of the National Service for Plant Variety Protection (Serviço Nacional de Proteção de Cultivares [SNPC], 2015), an agency affiliated with the Brazilian Ministry of Agriculture, Livestock and Supply - MAPA (Brasil, 2015).

For corolla color, pepper plants were categorized as having one of the following colors: white, white with a violet base, white with a violet margin, white-greenish, white greenish with a violet margin, light yellow, yellow, greenish-yellow, violet with a white base, or violet (Brasil, 2015).

For the predominant shape of the longitudinal fruit section, plants were classified as having one of the following shapes: flattened, rounded, heart-shaped, square, rectangular, trapezoidal, triangular, narrow-triangular, horn-shaped, oval, or elliptical (Brasil, 2015).

Regarding the predominant shape of the transversal fruit section, plants were classified as having one of the following shapes: elliptical, angular, or rounded (Brasil, 2015).

Fruit color before ripening was assessed based on the colors whitish-green, yellowish, green, or purple (Brasil, 2015). This evaluation considered immature fruits located at the second or third node of the plant.

These qualitative descriptors were evaluated through side-by-side comparisons, with distinctiveness determined by direct observation of genotypes in greenhouse tests. The evaluations were visual, and scores were assigned to each descriptor and genotype involved in the experiment, without using measurements.

Quantitative descriptors

Two quantitative descriptors were assessed: flowering and fruiting cycles, measured in days. The flowering cycle was determined by counting the days from sowing until 50% of the plants had at least one open flower. The fruiting cycle was measured by counting the days from sowing until the first fruit on each plant reached full maturation.

Statistical analyses

Qualitative descriptors

Parents and all generations resulting from the crosses were evaluated to determine genetic control, based on phenotypic segregations. For traits controlled by a single gene, segregation ratios of 3:1 and 1:2:1 were tested in the F_2 generation. In the F_3 generation, ratios of 5:3 and 3:2:3 were tested, while ratios of 1:1 and 1:0 were tested in the backcrosses (RC_1 and RC_2).

For traits controlled by two genes, segregation ratios tested included 9:7, 13:3, 15:1, 9:6:1, 12:3:1, and 9:3:4. For traits controlled by three genes, ratios of 27:37 and 63:1 were examined. Additionally, epistatic segregations, involving one or two genes, were tested.

Hypotheses concerning expected ratios were assessed using the chi-square test (χ^2) to analyze phenotypic segregation in parents and all generations resulting from the crosses, following Equation 1:

$$\chi^2 = \sum \frac{(Observed\ frequency - Expected\ frequency)^2}{Expected\ frequency} \quad (1)$$

The hypothesis of specific segregation (H0) for each locus was tested at a 1% significance level. These analyses were performed using the GENES software (Cruz, 2016).

Quantitative descriptors

Descriptive statistics, including frequency distribution, were employed to categorize values into proposed classes for each descriptor: the flowering cycle included early (<99 days), medium (100 to 114 days), and late (>114 days), while the fruiting cycle included early (<146 days), medium (147 to 158 days), and late (>158 days).

Results and discussion

The segregation ratio for flower corolla color was not significant, indicating agreement with the expected segregation pattern (Table 1). The evaluated generations conformed to the 1:2:1 ratio, suggesting that this trait is controlled by codominant inheritance and governed by a single gene with two alleles, resulting in three distinct phenotypes. Notably, one of these phenotypes displayed a combination of colors (white corolla with purple borders) (Figure 1).

Table 1. Ratios of qualitative descriptors for flower corolla color and immature fruit color in ornamental pepper plants (*Capsicum annuum* L.). *Universidade Estadual de Montes Claros* (Unimontes), Janaúba, Minas Gerais State, Brazil, 2023.

Corolla color						
Generation	Total	White	WPB	Purple	Hypothesis	*p-value*
P_1	10	10	0	0	1:0	-
P_2	10	0	0	10	0:1	-
F_1	15	0	15	0	0:1	-
F_2	180	39	92	49	1:2:1	0.5488^{ns}
F_3	171	50	48	73	3:2:3	0.0827^{ns}
RC_1	56	31	0	25	1:0:1	0.4226^{ns}
RC_2	58	0	23	35	0:1:1	0.1151^{ns}

Fruit color at the immature stage					
Generation	Total	Purple	WG	Hypothesis	*p-value*
P_1	10	0	10	0:1	-
P_2	10	10	0	1:0	-
F_1	15	15	0	1:0	-
F_2	178	138	40	3:1	0.4360^{ns}
F_3	171	121	50	5:3	0.256^{ns}
RC_1	57	26	31	1:1	0.5078^{ns}
RC_2	57	57	0	1:0	-

WPB: white with purple borders; WG: white greenish** and ^{ns} = significant at 1% level and not significant by the chi-square test.

Figure 1. Flower corolla color: a) white; b) violet; c) white with violet borders. *Universidade Estadual de Montes Claros* (Unimontes), Janaúba, Minas Gerais State, Brazil, 2023.

The contrast in corolla color between the parental lines UNI05 (*C. annuum* var. *glabriusculum*) and UNI01 (*C. annuum* var. *annuum*) resulted in the F_1 generation exhibiting flowers with an intermediate color, white with a violet margin. This intermediate phenotype alone is insufficient to determine the species of the F_1 genotypes, necessitating consideration of other descriptors. However, our results confirm that the type of interaction observed is codominance, as evidenced by observations in the F_2, RC_1, and RC_2 generations.

The purple corolla color is associated with the production of anthocyanin by the genotype. Chaim, Borovsky, Jong, and Paran (2003) mapped the A gene on chromosome 10, responsible for anthocyanin synthesis, in an F_2 population resulting from a cross between *C. annuum* L and *C. chinense* Jacq. Anthocyanin synthesis is partially controlled by the A gene, displaying partial dominance due to variations in pigment distribution in tissues. This variation includes both qualitative differences in the presence of purple color and quantitative differences in the intensity of purple color among genotypes.

The existence of distinct flower colors within this species can be harnessed for ornamental purposes. Combining these colors with other descriptors can lead to specific combinations, resulting in diverse products that cater to various consumer preferences. This descriptor is particularly important for species identification and phenotypic selection, as taxonomists often focus on flower characteristics (Carvalho & Bianchetti, 2008).

Similar to corolla color, the results for immature fruit color indicated a non-significant difference from the expected segregation pattern (Table 1). A segregation ratio of 3:1 (purple: white) was observed, suggesting that immature fruit color is governed by a gene with two alleles, and the allelic interaction is of the complete dominance type.

In *Capsicum* species, the presence or absence of green color in immature fruits is considered a qualitative trait (Brand et al., 2012), and in *C. chinense*, it has been molecularly linked to a single gene locus (Shu et al., 2023), detailed as an allelic series by Wang and Bosland (2006). It is worth noting that in *Capsicum* species, various fruit color stages are commonly observed during ripening (Song et al., 2022; Wu et al., 2022). However, this study focused solely on the coloration of immature fruits at the initial stage. A more comprehensive investigation considering the various possible colorations in segregating populations, as conducted by Votava, Balok, Coon, and Bosland (2000), would provide a better understanding of the genetic relationships governing distinct and expected phenotypic expressions during ripening.

Fruit color is a crucial trait for the appearance of peppers (*C. annuum* L.), as consumers primarily use it as a reference when selecting and purchasing peppers (Jang et al., 2020). Lightbourn et al. (2008) investigated two *C. annuum* L. genotypes with black and violet fruits and correlated fruit color with concentrations of carotenoid and anthocyanin pigments in plant tissues. They attributed the difference between violet and black colors in immature fruits to varying concentrations of chlorophylls and carotenoids.

In the case of fruit shape, genetic control could not be identified based on the tested hypotheses. The parents exhibited contrasting longitudinal fruit shapes, with P_1 showing a triangular shape and P_2 exhibiting an oval shape (Figure 2). However, the filial generation predominantly had a triangular shape (Figure 2).

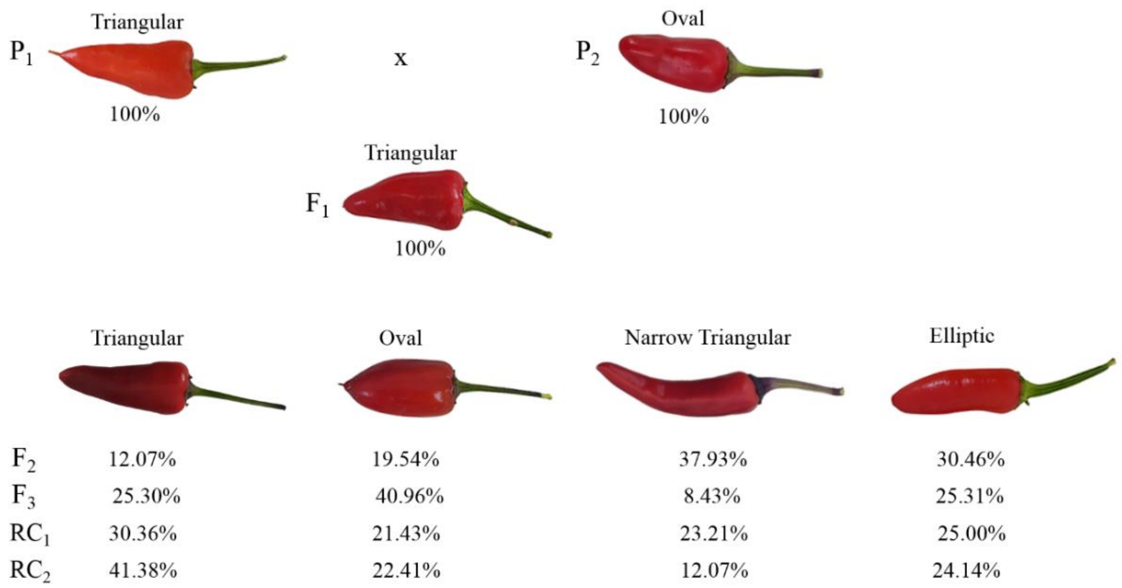

Figure 2. Frequency of longitudinal fruit section shapes observed in seven generations of pepper plants (*Capsicum annuum* L). *Universidade Estadual de Montes Claros* (Unimontes), Janaúba, Minas Gerais State, Brazil, 2023.

Although allelic interaction and dominance may play a role in the observed results for P_1, P_2, and F_1 generations, the F_2, F_3, RC_1, and RC_2 generations displayed significant variability and the emergence of an additional phenotype not observed in the parents and the F_1 generation: a narrow-triangular longitudinal fruit shape (Figure 2). These results highlight greater phenotypic variability in the F_2 populations, as this generation experienced increased segregation due to the self-pollination of the F_1 generation.

Concerning the shape of the transversal fruit section, the parents presented elliptical and rounded shapes (Figure 3). In contrast, the offspring generation predominantly expressed an elliptical shape, similar to parent P_1. The fruits of the segregating generations F_2, F_3, and RC_2 predominantly exhibited a rounded transverse shape (Figure 3).

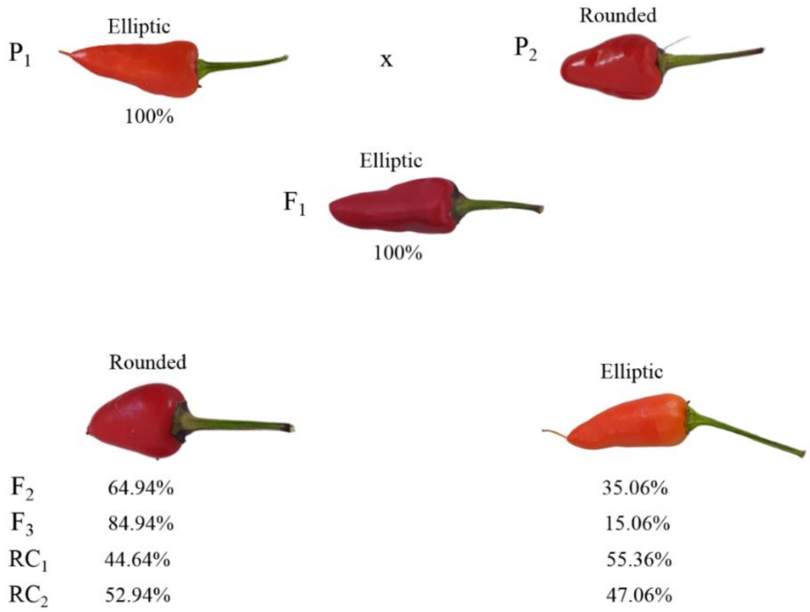

Figure 3. Frequency of observed transversal fruit section shapes in seven generations of pepper plants (*Capsicum annuum* L). *Universidade Estadual de Montes Claros* (Unimontes), Janaúba, Minas Gerais State, Brazil, 2023.

These variables related to fruit shape are influenced by multiple genes, indicating polygenic action. Other factors, such as the number of locules, can also impact pepper fruit shape. The number of locules has various effects on fruit shape and size in Solanaceae species (Munos et al., 2011). Ma, Qiao, Li, Yu, and Gong (2022) suggest that *CaBRX* plays a significant role in locule development in peppers and is associated with 17 other QTLs influencing fruit shape. Van der Knaap and Tanksley (2003) observed that previously identified fruit morphology loci in tomato, eggplant, and pepper may result from pleiotropic effects of the same orthologous loci in these species. According to Pimenta et al. (2020), the parents UNI01 and UNI05 have the same number of loci, which is two. Yet, despite this, the variation observed in the segregating generations (F_2, RC_1, and RC_2) confirms the influence of genetic multi-loci.

Species of the *Capsicum* genus are renowned for their extensive variation in fruit color and shape, offering a rich resource for ornamental purposes. The fruit shape in *Capsicum* species is under the control of multiple genes. Wang and Bosland (2006) have identified six genes that influence fruit shape in these species.

Mapping studies of quantitative trait loci (QTL) have played a crucial role in pinpointing various genetic loci responsible for controlling fruit shape in *Capsicum* spp. (Zygier et al., 2005; Barchi, Lefebvre, Sage-Palloix, Lanteri, & Palloix, 2009). Chaim et al. (2001) reported the identification of three QTLs associated with fruit shape in peppers, with one major QTL on chromosome 3 explaining over 60% of the phenotypic variation in fruit shape. Chunthawodtiporn, Hill, Stoffel, and Van Deynze (2018) suggested three candidate genes responsible for regulating fruit size and shape in bell peppers. In the case of *C. annuum*, *fs3.1* and *fs10.1* have been identified as controlling fruit shape, particularly the length-to-width ratio of the fruit (Han et al., 2016).

In the context of the frequency distribution analysis, the flowering cycle was categorized into three classes: early (<99 days), medium (100 to 114 days), and late (>114 days). Both parental plants and the F_1 generation displayed an early flowering cycle (Figure 4). Over 54% of individuals in the other generations also exhibited an early cycle, with only a small proportion of plants demonstrating a late flowering cycle (Figure 4).

The fruiting cycle was categorized into three groups: early (<146 days), medium (147 to 158 days), and late (>158 days). Both the parents and the F_1 generation exhibited an early fruiting cycle. Furthermore, more than 51% of individuals in the other generations also displayed an early fruiting cycle (Figure 5).

Growers have a preference for plants with early flowering cycles because it shortens the time it takes for the product to become commercially available (Silva, Rodrigues, Bento, & Pimenta, 2017). However, the classification used in this study can be a subject of debate and is inclined to complexity due to its association with a quantitative trait. According to Falconer (1987), such traits are significantly influenced by environmental factors, which can diminish the genetic contribution to the observed phenotypic expression.

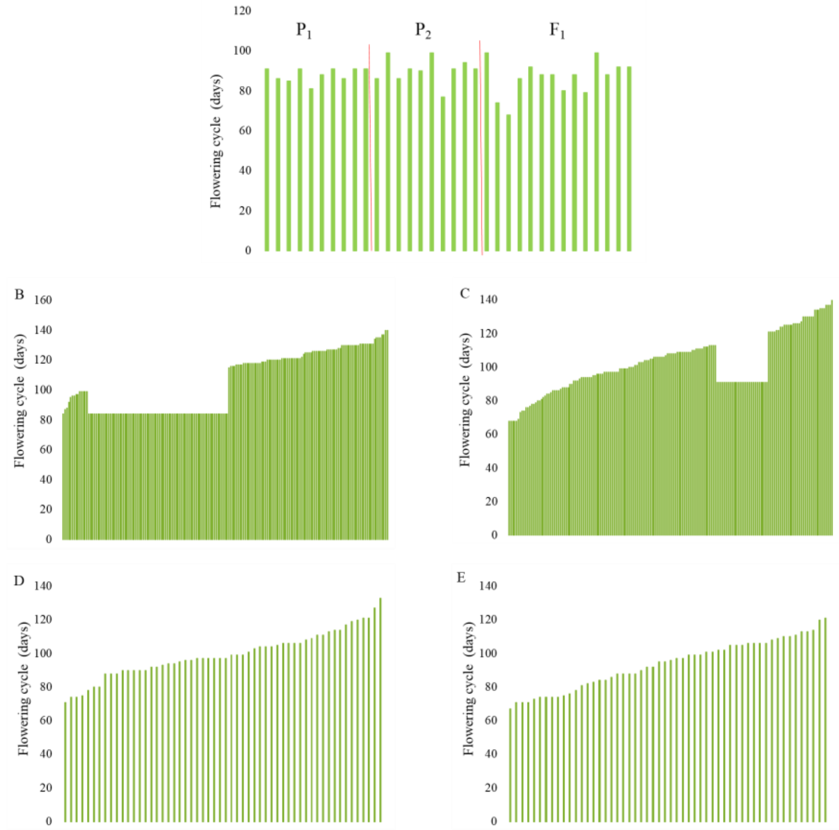

Figure 4. Mean flowering cycle (in days) for seven generations of *Capsicum annuum* L. A: accession UNI01 (P1); B: accession UNI05 (P_2); C: offspring generation (F_1); D: F_2 generation; E: F_3 generation; F: backcross 1 ($F_1 \times P_1$), and G: backcross 2 ($F_1 \times P_2$). *Universidade Estadual de Montes Claros* (Unimontes), Janaúba, Minas Gerias State, Brazil, 2023.

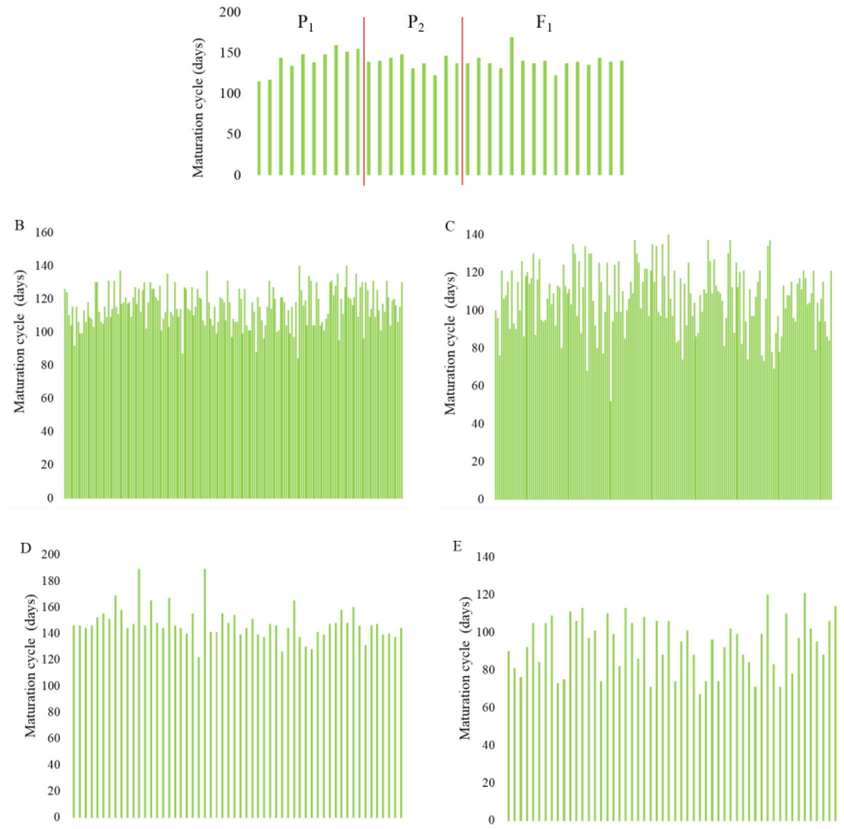

Figure 5. Fruiting cycle (in days) for seven generations of *Capsicum annuum* L. A: accession UNI01 (P1); B: accession UNI05 (P_2); C: offspring generation (F_1); D: F_2 generation; E: F_3 generation; F: backcross 1 ($F_1 \times P_1$), and G: backcross 2 ($F_1 \times P_2$). *Universidade Estadual de Montes Claros* (Unimontes), Janaúba, Minas Gerais State, Brazil, 2023.

The duration of the flowering cycle in pepper plants is directly linked to the timing of the fruiting cycle. In the context of ornamental pepper plants, the commercial stage is reached when the plants bear ripe fruits, as these are the primary attractors for consumers. Consequently, these cycles must be relatively short, as this reduces production costs related to irrigation, management, and inputs. Additionally, shorter cycles minimize the exposure of crops to potential risks such as pests and diseases.

The insights gained from studying the segregation patterns of the traits assessed in this research will prove invaluable for researchers involved in this breeding program when selecting the most suitable breeding strategy. These findings are expected to enhance the precision of the selection process, making it more effective. Furthermore, the characterization of flowering and fruiting cycles can aid in the planning of various activities within the breeding program, whether about management practices or the choice of breeding methods to be employed.

Conclusion

The key findings comprised that codominance is the genetic control mechanism for flower corolla color in ornamental pepper plants (*Capsicum annuum* L.) and dominant genetic inheritance plays a role in determining immature fruit color. However, genetic inheritance patterns for transversal and longitudinal fruit shapes cannot be elucidated based on the tested segregations. The parental and segregating generations under evaluation exhibit similar flowering and fruiting cycles. Both parents and the F_1 generation displayed a 100% incidence of early flowering and fruiting cycles, while the segregating generations had more than 50% of individuals with early cycles.

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