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Implications of gene action on the selection of cooking time in common bean

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Abstract: The cooking time of common beans is crucial for consumer acceptance, although its genetic basis is not yet fully understood. Thus, the objective of this study was to estimate the components of genotypic variation to verify the predominance of gene action and its implications for improving the cooking time trait in common beans. The genotypes used were obtained from a cross between the parents BAF50 x BAF07, with 16 progenies sampled in each of the $F_{2:3}$, $F_{3:4}$, $F_{8:9}$, and $F_{9:10}$ generations, resulting in 66 genotypes tested, considering the progenies along with the parents. These were evaluated in the field in a randomized block design with three replicates. The cooking time of the beans was measured 30 days after harvest using the Mattson cooker, with a temperature of 100°C, and the response variable was obtained in minutes until cooking was complete. The components of phenotypic variation were estimated according to the mixed model, with genotypic variation divided into additive and dominant components. The dominance genetic variance component was higher than the additive component. The estimates of dominance genetic variance were greater than expected for the cooking time trait in the segregating generations. The estimates of additive genetic variance and selection gains in advanced generations of self-fertilization were better when compared to the early generations. Despite this, the genotypic effects demonstrated the possibility of selecting for reduced cooking time in the early generations. However, genotype elimination is more effective at higher levels of homozygosity due to the reduction in dominance genetic variance and the increase in additive genetic variance.

Keywords: *Phaseolus vulgaris* L, Cockerham, Additive variance, Dominance variance, Plant breeding.
Abbreviation: SNP_single nucleotide polymorphisms; R^2_coefficient of determination; $\hat{\sigma}_g^2$_genotypic variance; σ_A^2_additive variance; σ_D^2_dominance variance; $\hat{h}^2$_heritability; $\hat{h}_r^2$_ narrow-sense heritability; χ^2_chi-square.

Introduction

The common bean (*Phaseolus vulgaris* L., 2n=2x=22) is a staple crop widely cultivated and consumed in Brazil, valued for its high protein, carbohydrate, fiber, and mineral content (Los et al., 2018). Over the years, plant breeding has played a crucial role for both consumers and farmers. The primary goals of breeding programs have been the development of cultivars with superior agronomic traits and the production of higher quality grains (Almeida et al., 2018).

When considering the characteristics related to grain quality, cooking time holds significant importance for consumers. A long cooking time discourages frequent use in the diet, as it requires more time and energy for preparation, which directly impacts consumer perception of the food. This factor plays a crucial role in the acceptance of a cultivar in the market (Carbonel et al., 2003). As a result, numerous studies have investigated the occurrence and extent of genetic variation in the cooking time trait among bean genotypes (Cichy et al., 2019; Katuuramu et al., 2020; Pereira et al., 2017; Wiesinger et al., 2016).

The genotypic differences observed for the cooking time trait derive from physical and chemical factors intrinsic to the genotypes, which shape the seed structure and affect the different phases of the cooking process (Bassett et al., 2021). Despite the relevance of the genotype in the phenotypic expression of this trait, in practice, in the breeding of this crop, selection is carried out for the grain yield trait. Thus, cooking quality is measured only in the final phase of the breeding programs in the genotypes selected for grain yield.

Since the progress of genetic breeding is influenced by the magnitude and nature of genetic variation in the population being selected (Allard, 1971), understanding the components of genetic variation for the cooking time trait is essential for devising appropriate strategies to manage segregating populations. In this context, the existing studies in the literature do not reach a consensus regarding the nature of genotypic variation. In other words, it remains unclear whether the predominant gene action is due to additive effects or dominance allelic interactions (Elia et al., 1997; Hernandez et al., 2003; Ribeiro et al., 2006).

The Impact of gene action on the Improvement of cooking time In common bean Is primarily Influenced by the nature of the genotypic variation. If the predominant variation is additive, the genetic values of individuals tend to stabilize in the progeny as generations of self-fertilization progress (Falconer and Mackay, 1996). This occurs through the redistribution of heterozygous alleles into homozygous forms at various loci (Mather and Jinks, 1982). On the other hand, if dominance plays a significant role in influencing the phenotypic value, it introduces a complicating factor in identifying genotypes with reduced cooking time in segregating populations. This is primarily due to unpredictable shifts in genotypic values, as dominant gene action stems from deviations caused by dominance at heterozygous loci, which reduce by half with each successive generation of self-fertilization in segregating common bean populations. Therefore, when breeding for the cooking time trait, the magnitude of the additive variance component becomes crucial in determining the appropriate selection method.

Recent molecular studies have contributed to the understanding of the genetic basis of cooking time in common bean. An initial genome-wide association study with 206 accessions from the Andean Diversity Panel identified significant single nucleotide polymorphisms associated with cooking time on chromosomes Pv02, Pv03, and Pv06 (Cichy et al., 2015). The subsequent expansion of the analysis to 430 additional accessions revealed new SNPs on chromosomes Pv03, Pv04, Pv06, Pv07, Pv08, and Pv11 (Bassett et al., 2020), reinforcing the polygenic nature of this trait. These findings suggest that multiple genomic regions contribute to the variability in cooking time, which may have implications for breeding strategies aimed at this trait, making further molecular and phenotypic research essential.

Therefore, this work aimed to estimate the components of genotypic variation, with the purpose of verifying the predominance of gene action and its effects on the improvement of cooking time in bean progeny.

Results

Variance components and heritability

Advances in genetics and classical plant breeding methods are briefly based on the assumption that the phenotype is the result of the joint action of the genotype and environment, in addition to the interaction of genotypes by environments. These causes of variation are expressed in terms of their variances associated with the effects of these random factors on quantitative traits (Mather and Jinks, 1982). Accordingly, it is known that the most important aspect of a quantitative trait revolves around its variation, assuming that it is not possible to distinguish each of the genes that segregation presents in the form of continuous variation. Therefore, verifying the presence and magnitude of the variance components is essential for the analytical study of the properties of a population.

Thus, the variance components provide knowledge of the genetic structure of a given population, also allowing the achievement of estimates of genetic parameters. These parameters relate the genotype with the phenotype of the individuals, mainly by supporting the choice of the best selective strategies to be applied in breeding. In this sense, Table 1 presents the magnitudes of the estimates of the components of phenotypic variance, genotypic variance between progeny, variance between generations and environmental variance, together with the heritability coefficient for the cooking time in the respective bean progeny.

The genotypic variance component (56.04) had its null hypothesis (H_0: $\hat{\sigma}_g^2 = 0$) rejected by the Z test ($p < 0.05$). This event reveals the occurrence of variance in this cause of random variation of the mixed model, considering the different progeny (H_1: $\hat{\sigma}_g^2 \neq 0$), thus evidencing the feasible selection of plants for the cooking time trait. Additionally, an environmental variance (203.90) was found to be greater than the genotypic variance, which together composes the phenotypic variance (259.94), an indication of a broad sense heritability coefficient of approximately twenty percent.

Genetic parameters across generations

The knowledge of the magnitude of the components of genotypic variance can guide breeding work, as well as provide information on the predominant gene action in different generations obtained from these estimates. Based on these components, it is possible to obtain important information to support plant selection for the cooking time trait in common beans. Considering the generations of self-fertilization with different levels of homozygosity, the additive (σ_A^2) and dominant (σ_D^2) variance parameters were estimated based on the hierarchical genetic model. The model considered all generations of the study ($F_{2:3}$, $F_{3:4}$, $F_{8:9}$, $F_{9:10}$), and obtained the following estimates of the genetic parameters: σ_g^2 = f (27.48 k_A + 101.27 k_D). The estimate of the coefficient of determination (R^2) was high (0.98), which reveals that a significant part of the genotypic variance was represented. Using this adjusted model, it is observed that the estimate of the dominance genetic variance component was approximately 3.7 times higher than the additive component, considering the coefficient equal to 1 for the additive (k_A) and dominance (k_D) variance.

Table 2 presents the estimates of additive and dominance variance among progeny, together with the narrow-sense heritability coefficient inherent to self-fertilization generations. In the $F_{2:3}$ generation, an estimate of 27.50 was observed for the additive component of genotypic variance; the magnitude of this estimate reflected a narrow-sense heritability of 0.10. This value corresponds to approximately 50% of the total genotypic variance among progeny. The observed magnitude for this estimate in the $F_{3:4}$ generation was 41.25, which resulted in a narrow-sense heritability of 0.15 (Table 2). As the self-fertilization generations progressed to $F_{8:9}$ and $F_{9:10}$, the additive variance presented narrow sense heritabilities close to 0.20 in the progeny, since, in practice, all loci are in homozygosity as a result of inbreeding advance.

The additive component of genetic variation (σ_A^2) presented no distinction between the estimated and expected values, according to the Cockerham genetic model (1963), which is in agreement with the Chi- square test with significance level of 5%. On the other hand, the magnitude of the estimate inherent to the dominance component observed in the $F_{2:3}$ generation was approximately 25.33. This is higher than the variation expected for the coefficient $1/4\ \hat{\sigma}_D^2$, which represents an expected

Table 1. Estimates of phenotypic variance, variance between generations of self-fertilization, genetic and environmental variance, along with the estimate of broad-sense heritability (%) for cooking time in common bean progeny.

Parameter	Estimate
Phenotypic variance ($\hat{\sigma}_F^2$)	254.83
Genotypic variance ($\hat{\sigma}_g^2$)	55.96[1/]
Environmental variance ($\hat{\sigma}_e^2$)	198.87
Heritability ($\hat{h}^2$)	0.22

[1/]Significant at 5% probability by the Z test, with $H_0: \hat{\sigma}_g^2 = 0$.

Table 2. Estimates of additive genetic variance ($\hat{\sigma}_A^2$), dominance genetic variance ($\hat{\sigma}_D^2$) and narrow-sense heritability ($\hat{h}_r^2$), for the cooking time trait in progeny obtained from the self-fertilization generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$.

Generation	Additive variance (σ_A^2)		Dominance variance (σ_D^2)		$\hat{h}_r^2$(%)
	Estimated	Expected	Estimated	Expected	
$F_{2:3}$	27.50	28.02	25.33	7.00	0.10
$F_{3:4}$	41.25	42.03	19.03	5.25	0.15
$F_{8:9}$	54.45	55.60	0.43	0.21	0.20
$F_{9:10}$	54.72	55.82	0.39	0.11	0.21
χ^2	0.22 [1/]		85.09 [2/]		

[1/]Not significant; and [2/]Significant by the Chi-square test at 5% probability.

value of 7.00 (Table 2). This value in the $F_{3:4}$ generation was 19.03 for the estimate of the dominance variance component, whose expected value was 5.25. Furthermore, in the self-fertilization generations $F_{8:9}$ and $F_{9:10}$, the estimate of this component was close to what was expected. The distortions observed between the expected and observed values in the $F_{2:3}$ and $F_{3:4}$ generations resulted in a high Chi-square value (85.09), where the alternative hypothesis for the test is accepted, thus reflecting a discrepancy between the estimated and expected values.

The estimates of narrow-sense heritability, along with the magnitude of the additive and dominance variance components in the early and advanced self-fertilization generations, align closely with the redistribution of the genotypic variance component. Initially, these results suggest that the dominance component accounted for a larger portion of the genotypic variance than would be expected based on the Cockerham genetic model. Therefore, negative effects are observed when considering the performance of plant selection in the early self-fertilization generations, with the goal of developing genotypes with shorter cooking times.

Selection efficiency and expected genetic gains

The comparison of the efficiency of the breeding strategies in the present study can be carried out based on the expected progress with selection. Considering the different generations at the beginning of the assessment of the progeny ($F_{2:3}$, $F_{3:4}$, $F_{8:9}$, $F_{9:10}$), it is observed, in Table 3, that this expected genetic progress was -2.81 minutes in the $F_{2:3}$ generation. While waiting for a generation of self-fertilization to derive the progeny and start the phenotypic evaluation aiming at plant selection, the expected genetic gain was -4.22 minutes with selection in $F_{3:4}$, which means an additional gain close to 50% of the gain observed in the $F_{2:3}$ generation. On the other hand, the expected gains in the $F_{8:9}$ and $F_{9:10}$ generations were close to -5.60 minutes (12.5%), which demonstrates greater efficiency in plant selection in advanced generations of self-fertilization, aimed at reducing cooking time in common bean.

The estimates of genotypic values presented in Fig. 2 consider the random effects of 64 progeny, from the self-fertilization generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$, for the trait cooking time in common bean. These values reveal a dispersion of the random effects for both generations under study. BLUP (Best Linear Unbiased Prediction) is a technique used to estimate the genotypic values of individuals based on mixed models that consider both fixed and random effects. In the two smallest genotypic effects in each generation, it is observed for the $F_{2:3}$ generation, that the progeny F2:3-11 and F2:3-14 present the smallest effects, with negative genotypic values, indicating potential for reducing cooking time. In the $F_{3:4}$ generation, the progeny F3:4-1 and F3:4-5 presented the smallest effects. It suggests that these lines can contribute to the reduction of cooking time, which is desirable for the objective of the breeding.

In the generations with the highest level of inbreeding, where homozygosity increased, the F8:9-8 and F8:9-6 progeny exhibited the lowest genotypic effects in the $F_{8:9}$ generation, with values similar to those found in previous generations, which is consistent with the expression of alleles favorable to the reduction of cooking time in common bean throughout the generations. In the $F_{9:10}$ generation, the F9:10-4 and F9:10-7 progeny exhibited the lowest genotypic effects, which only reinforces the importance of these lines in the selection for reduced cooking time. Furthermore, these results expand the inference space, provide an accurate assessment of genetic effects and allow the selection of the best progeny.

Discussion

Phenotypic variation and heritability for cooking time

The decomposition of the phenotypic variation observed in the results is a crucial step in a breeding program. Understanding the magnitude of genetic variance present in a specific trait is essential to determine the heritable proportion of this variation, which refers to the part of the total variance attributed to the genotypic effects of the individuals, also known as

Table 3. Expected genetic progress with selection (G_s) in minutes (min) and percentage (%), for cooking time in common bean progeny in generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$.

Generation	Cooking Time (min)	G_s (min)	G_s (%)
$F_{2:3}$	46.36	-2.81	6.06
$F_{3:4}$	46.47	-4.22	9.08
$F_{8:9}$	44.25	-5.57	12.58
$F_{9:10}$	44.86	-5.60	12.48

heritability (Falconer and Mackay, 1996). Based on these estimates, several studies have assessed the occurrence and magnitude of genetic variation for cooking time in bean crops.

A study demonstrated marked phenotypic variation among 14 genotypes evaluated in 15 environments for cooking time, with a considerable fraction of the phenotypic variation attributed to the genotypes (Cichy et al., 2019). Another study for this trait described and studied the genetic variability of a collection of 295 bean genotypes, originating from germplasms from the Americas, Europe and Africa (Sadohara et al., 2022). These authors indicated the occurrence of variation among the genotypes evaluated, with values for cooking time ranging from 17 to 120 minutes.

As observed, the vast majority of the studies reveal wide genetic variability for the cooking time trait. These heritability values in the studies mentioned above for this trait are generally high (above 0.5), which indicates presumable plant breeding success. When these values are compared with the estimates obtained in the populations considered in this study, no agreement is observed in their magnitudes. In regard to this distinction, it is important to point out mainly the genetic constitution of these genotypes, since in the mentioned studies, the authors basically used sets of accessions and lines with high homozygosity and absence of segregating individuals.

Some studies available in the literature that used segregating populations also reported lower heritability values (Baldoni and Dos Santos, 2005; Carvalho et al., 2017). Therefore, the genetics accumulated knowledge leads us to a major aspect of this condition, mainly related to the genotypic constitution of the populations, so that the genetic parameters estimated in a given population allow inferences to be made only for these individuals (Mather and Jinks, 1982). These lower values of heritability coefficients in segregating populations reflect a hindrance related to the need to replace a large number of alleles in the different loci, aiming to determine cooking time reduction. This is mainly due to the low contribution of each of these alleles in the genotypic variance, added to the marked environmental effect.

Moreover, recent molecular studies have significantly contributed to the understanding of the genetic basis of cooking time in common bean. One of these studies, conducted by Cichy et al. (2015), identified significant single nucleotide polymorphisms (SNPs) associated with cooking time on chromosomes Pv02, Pv03, and Pv06. These findings indicate that certain genetic loci play a fundamental role in determining cooking time, and these SNPs can serve as useful molecular markers for the genetic selection of cultivars with shorter cooking times.

Additionally, a subsequent study by Bassett et al. (2020) expanded the analysis to include 430 additional bean accessions, which resulted in the identification of new SNPs on chromosomes Pv03, Pv04, Pv06, Pv07, Pv08, and Pv11. The inclusion of a larger number of genotypes allowed for the detection of greater genetic diversity related to cooking time, further reinforcing the polygenic nature of this trait, i.e., the fact that multiple loci on different chromosomes are involved in the variation of cooking time. This genetic complexity is an important factor to consider in breeding programs, as demonstrated in the present work, which also identified a significant phenotypic variation in cooking time among genotypes, being an evident aspect of polygenic traits. The evidence of multiple genomic regions contributing to the variability in cooking time suggests that the control of this trait is more complex than initially thought. This information has direct implications for breeding strategies, as it indicates the need for an approach with different selection strategies.

Composition of genotypic variation for cooking time in common bean progeny

The knowledge of narrow-sense heritability considers only the heritable component of genotypic variation in sexually reproducing plants. This component is composed exclusively of the additive variance present in the genotypic variation over the phenotypic variation. This fraction of the variation originating from genetic values is fixed in the genotypic values of the progeny as generations of self-fertilization progress in autogamous species, and it is fundamental during plant selection (Wricke and Weber, 1986).

The genotypic variation in the segregating generations resulting from the crossing of two lineages follows a model over the course of the self-fertilization generations. Thus, the distribution of genetic variance between progeny from the crossing of two lineages in the additive and dominant components results from the redistribution of the heterozygous and homozygous allelic forms, with the advancement of inbreeding. It must be considered that this decomposition was performed for the F_2 generation of the crossing of two lineages. The expected components of genetic variance in F_2 are $\hat{\sigma}_A^2 + \hat{\sigma}_D^2$, resulting from the fact that half of the divergent loci for the two parental lines are in the homozygous form, and half of the loci are in the heterozygous form, reaching up to $2\hat{\sigma}_A^2$ when the loci are in homozygosity, due inbreeding advance in the F∞ generation (Cockerham, 1963). Based on this understanding, the key factors that distinguish classical breeding methods in autogamous plants are the way in which these generations are driven towards homozygosity and how they capitalize on the variation arising from genetic values.

Therefore, when the ratio between genotypic variation and phenotypic variation is sufficiently high, with the predominance of the additive component, breeding methods that involve the evaluation of progeny in early segregating generations are preferable. This approach allows for the selection and elimination of undesirable genotypes for cooking time, resulting from the fixation of genotypic values in the progeny. However, when the dominance component has a significant influence on genotypic variance in segregating generations, the evaluation and selection of progeny should be prioritized in advanced

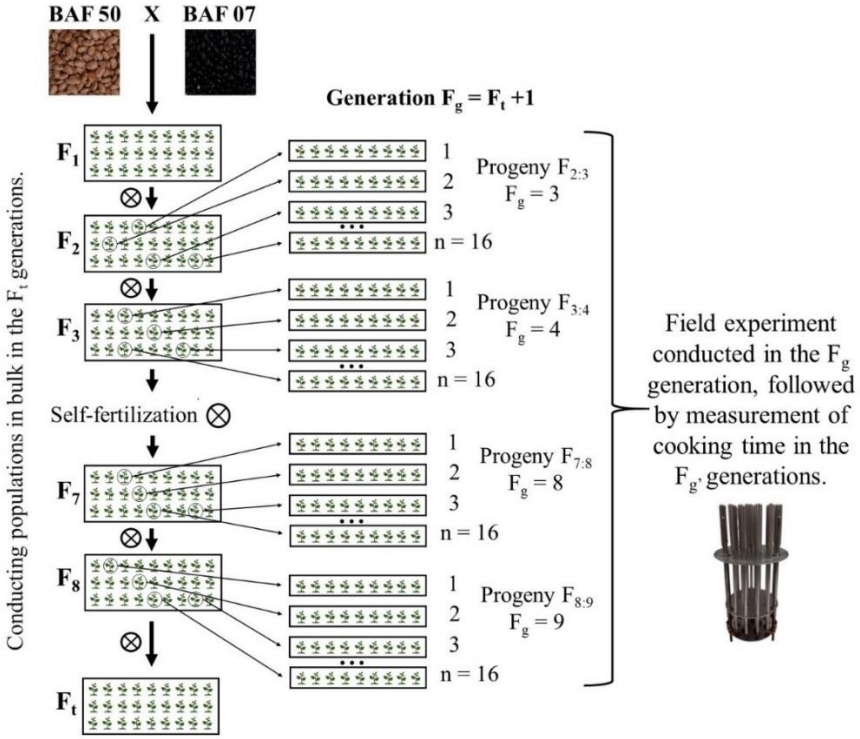

Fig. 1 Diagram of the breeding method applied over the years for the different F_t generations, along with the acquisition of $F_g = F_t + 1$ progeny, resulting from the BAF50 (P1) x BAF07 (P2) cross, representing the hierarchical genetic design for conducting the progeny test and estimating the components of genetic variance.

generations, with higher levels of homozygosity. This is mainly due to the lack of fixation of genotypic values in the progeny in segregating generations, caused by dominance arising from heterozygosity at different loci. Thus, the fixation of genotypic values will only occur after the reduction of heterozygous allelic combinations, in favor of an increase in homozygous loci, which leads to a decrease in dominance variation and an increase in additive variance (Mather and Jinks, 1982).

Thus, critical information can be obtained to support the plant selection process for the cooking time trait, based on estimates of additive and dominant variance in different generations of self-fertilization. The relevance of this information is mainly evidenced by the scarcity in the literature of studies related to quantitative genetics for the cooking time trait. One of the pioneering studies was conducted with 16 genotypes, using the North Carolina II design (Elia et al., 1997). The authors found that the additive variance presented a magnitude of 76.5% of the total genotypic variance and dominance variance of 23.5% in the first environment, while for the second, the additive genetic variance was 96.9% and the dominance variance was 3.1%. Finally, in the third environment, the additive variance was 87.1% and the dominance fraction was 13% of the total genetic variance.

Contrary to the results obtained in this study, these authors found the prevalence of additive gene action in the genetic control of cooking time. These estimates must be compared with caution, mainly due to the differences in the genetic designs used. The genetic components estimated in the diallel genetic design performed by the authors (Elia et al., 1997) must be considered only for the population of the genotypes used in the study, since bean plants reproduce by autogamy. Thus, the components of genotypic variance estimated by diallels in autogamous plants present low practical application in these crops (Wricke and Weber, 1986), mainly because the estimates of variance components cannot be used in the selection theory in these species. The main aspect to be considered for selection must be the genotypic variation within each cross performed, and not between the crosses.

Another study considering the genetics of this trait evaluated 104 genotypes originating from a cross between contrasting lines for cooking time, advanced to the F_6, F_7 and F_8 generations, which indicated the dominance (Hernandez et al., 2003). Dominance was also verified by considering the genetic model of means in these populations (Ribeiro et al., 2006). In the latter, the authors verified dominant gene action towards the increase of cooking time. In addition, they also reported a maternal effect for this trait in the bean crop, which reveals that the expression occurs one generation later, compared to the mother plant.

Therefore, the relevant occurrence of dominance variance is observed in segregating populations, according to the results obtained in this work, along with the studies available in the literature for the cooking time trait in bean crops. The proven magnitude of this component leads to a series of problems in the selection of plants in segregating generations. This fact derives from the fact that the development of bean cultivars is carried out in its entirety aiming at obtaining lineages. In other words, the segregating genotypes present advance in generations of self-fertilization, until practically all loci are considered homozygous, although this is never theoretically achieved due to low intercrossing rate. Thus, in bean cultivars with homozygous allelic forms, the genetic variance originates only from the additive gene action, while no available methods allow the obtaining of commercial hybrids in this crop.

Based on the occurrence of the observed dominance gene action, genotypic values considered equal in early segregating generations can be attributed to genetically distinct individuals. This is explained by the high level of heterozygosity in the

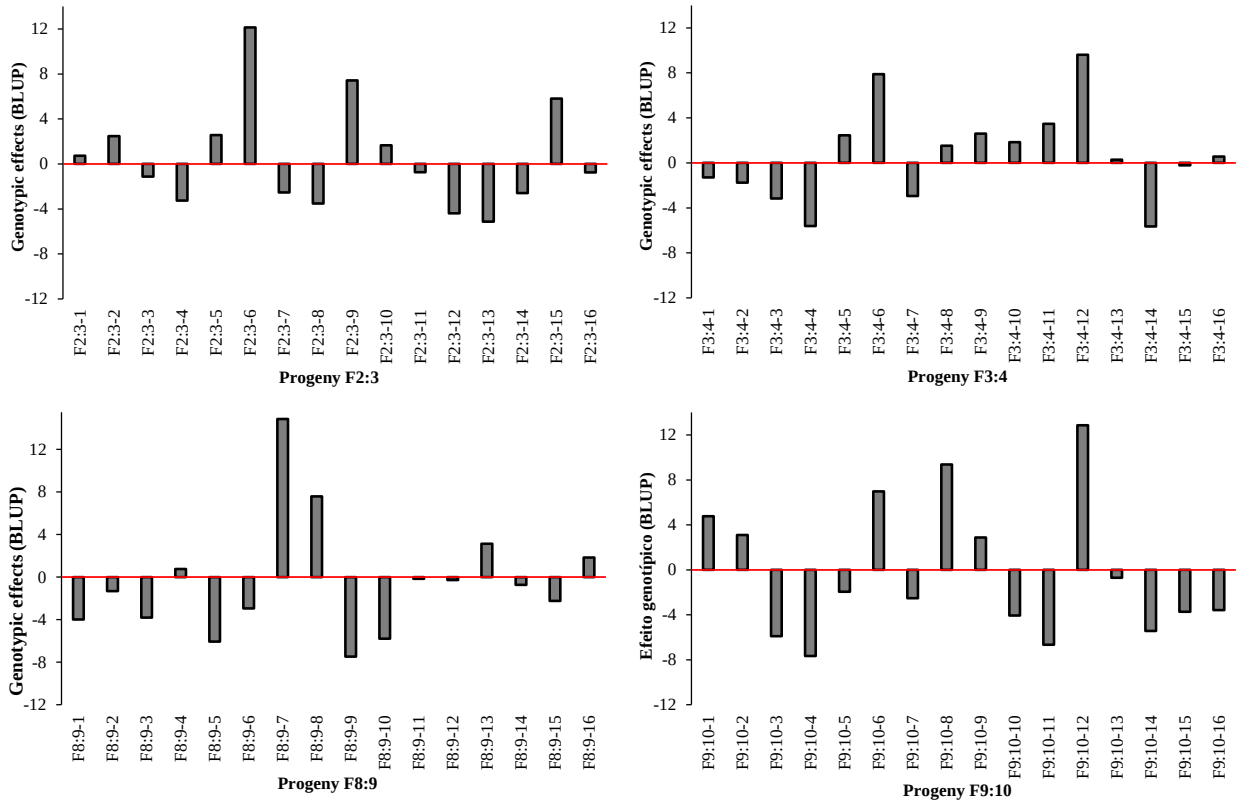

Fig. 2. Genotypic effects (BLUP) of common bean progeny in different generations of self-fertilization ($F_{2:3}$, $F_{3:4}$, $F_{8:9}$, and $F_{9:10}$) for the cooking time trait in minutes.

progeny that can overshadow the expected gains from selection in the segregating generations ($F_{2:3}$ and $F_{3:4}$). Thus, changes in the phenotypic values of the selected progeny can be observed in subsequent generations, basically due to the sum of the different gametic values of the individuals, redistributed by the recombination process in meiosis (Vencovsky and Barriga, 1992). This process is performed successively with each self-fertilization, which leads to the hypothesis that it is not possible to perform selection in segregating generations, aiming at the development of bean genotypes with reduced cooking time.

Selection for cooking time

An initial factor for any comparison regarding plant selection is related to whether the population was subdivided into progeny or whether the information is inherent to the behavior of the progeny in individual plants. This is a relevant aspect, since the method used to manage segregating populations directly reflects the expectation of possible results through the breeding of autogamous plants. Considering the feasibility of selection in early generations, it would allow for a potential increase in the percentage of genotypes with shorter cooking times. Additionally, it would be possible to discard genotypes with longer cooking times in these generations, based on the genotypic values of the progeny (Bos and Caligari, 1995). Thus, defining the best genetic breeding strategies aimed at increasing selection efficiency may result in more significant gains through selection.

Therefore, the main difference between the methods applied to the management of segregating populations in autogamous plants is precisely based on the time when the evaluation of the progeny and, consequently, the artificial selection of plants begins. The genealogical and population ("*bulk*") methods were first developed over 100 years ago (Allard, 1971). The genealogical method is based on the behavior of the progeny from the initial generations, in which selection is carried out along with inbreeding increase. On the other hand, the "*bulk*" method is characterized by the increase in self-fertilization generations, and selection is performed after inbreeding increase. Based on these two main aspects, the breeder needs to define whether to wait for a certain number of self-fertilizations to perform the selection, aiming at an increase in homozygosity and additive variance or to start by subdividing the progeny derived from individual plants into segregating generations with higher levels of heterozygosity.

Considering the subdivision of the population into progeny derived from individual plants, selection can be performed based on the average behavior of these progeny, and can also be conducted within the progeny, depending on the level of inbreeding (Ramalho and Vencovsky, 1978). These issues are fundamental for the purpose of carrying out effective selection and need to be defined based on the variation to be explored by the breeder. In this sense, the comparison between the method that conducts "bulk" segregating populations, and the other methods (genealogical, sample within progeny and descendant of a single seed) requires the consideration of the magnitude and composition of the genotypic variance, besides which method will allow separating the desirable plants from the undesirable ones. Furthermore, it is necessary to define whether the selection will be performed between and within the progeny, or only between the progeny.

Considering the selection process only among progeny, in addition to the composition of the observed genetic variance, the sample methods within populations and genealogical methods present no advantage compared to the "*bulk*" and single-seed descent methods for cooking time. This is explained by the fact that the additive variance remains unchanged among

progeny as self-fertilization increases in these methods (genealogical and sample within progeny), and that only the dominance variance is reduced due to heterozygosity reduction (Wricke and Weber, 1986). Besides, the "*bulk*" and single-seed descent methods exhibit successive increases in additive genetic variance, as inbreeding advances. However, one factor to be considered in the single-seed descent method is whether only one seed will represent the genetic variation of the F_2 genotypes, which may lead to the loss of alleles favorable to cooking time reduction.

In the "*bulk*" method used in this study, the composition of the genotypic variance between progeny depends on the last generation in which the population was randomly managed (F_t), where the subdivision of the population into progeny derived from individual plants will definitely occur. A relevant aspect concerns the number of progeny evaluated in the self-fertilization generations, since sampling problems may have occurred due to the use of only 16 progeny in each generation. However, it is worth highlighting that this trait is difficult to phenotype (Carvalho et al., 2017). Thus, this number of progeny is used considering a feasible number for carrying out the experiment and measurement of the cooking, according to the available resources.

Therefore, considering these aspects, selection in early generations and within progeny would not be justified, according to the magnitude of the dominance component observed. In addition, the cooking test using the Mattson cooker is difficult to perform in early generations (F_2 and F_3), for demanding a considerable amount of time and work. This would simplify the evaluation of progeny in advanced generations. Thus, it is expected that a method that values the advancement of homozygosity will enable more significant genetic gains, since the subdivision of the population into progeny derived from individual plants presents greater additive variance in advanced generations of self-fertilization. These advances in inbreeding with self-fertilization make it possible for the genotypic value of the progeny (additive effect and dominance deviations of genes) to resemble the genetic values (additive effect of genes) (Snape and Riggs, 1975).

Thus, according to the findings of this study, the successful breeding for the cooking time trait depends on the amount of genotypic variance available and how much of this variation will be fixed in the genotypic value of the progeny, in order to effectively contribute to reduce cooking time. Management methods that value the advancement of inbreeding have proven to be convenient for the improvement of the cooking time trait in common bean, based on the components of genetic variance. It is recommended to wait for the increase in the magnitude of additive genetic variation and reduction of dominance genetic variance, with the advances in the number of self-fertilizations. Next, plant selection is carried out, since the occurrence of genetic dominance is a negative factor in obtaining progeny with reduced cooking time. Therefore, this process can obtain better progress with the selection of plants in generations with higher levels of homozygosity, for requiring the advancement of segregating populations with a considerable number of plants, to minimize sampling problems.

Additionally, however, selection in early generations can be justified, even considering the magnitude of the dominance component observed and the respective selection progress for the cooking time trait, since it is verified that dominance for this trait can favor the increase of cooking time (Melo et al., 2024). Thus, the selection of genotypes with reduced cooking time is feasible, but the elimination of genotypes is not an appropriate practice in these segregating generations. Therefore, regardless of the method of managing segregating populations in common bean, any estimate regarding the merit of genotypes, which allows the early selection or elimination of genotypes with low potential, is clearly advantageous (Allard, 1971), because all breeding programs have limitations in their capacity to manage populations, and the early selection or the elimination of these inferior genotypes enhances the probability of finding segregants with shorter cooking time.

Considering these various aspects discussed, the breeder must develop a rigorous attitude in the selection and dispel the idea that among the plants he eliminates there may be one that leads to the idealized superior genotype. If this natural tendency is not kept under control, the breeding program will soon be overloaded with genotypes that were not eliminated, and the efficiency of the plant breeder may be impaired or even nullified. Therefore, based on the results, the study demonstrated that breeding aimed at reducing cooking time in common bean can be substantially more complicated than expected by most breeders of this species.

Material and Methods

Plant materials and genotypic constitutions

The genetic constitutions used originated from the directed cross between the parents BAF50 x BAF07, both lines obtained from the Active Bean Germplasm Bank (BAF) of the State University of Santa Catarina. BAF50 has a carioca-type grain, type III growth habit and was collected in the municipality of Lebon Régis/SC. On the other hand, BAF07 has a black-type grain, presents type III growth habit and originates from the municipality of Lages/SC. Since the parents differ in grain color, with BAF50 presenting carioca-type grains and BAF07 black-type grains, a broad segregation for this trait was observed in the segregating populations. This diversity is associated with variations in the chemical and structural composition of the seed coat, which directly influences cooking time. Artificial hybridization was performed, with prior emasculation of the flower bud in 2008 (Rocha et al., 2014). In addition, the crosses were performed again in 2015 and 2016 in a greenhouse, aiming to obtain seeds in initial generations of self-fertilization (segregants). The crossing between the parents resulted in different segregating populations in the F_2, F_3, F_4, F_5, F_6, F_7 and F_8 generations, advanced by the "bulk" conduction method under field conditions, without the application of artificial selection in the different generations, so as to advance the levels of homozygosity with generations of self-fertilization in the populations (Fig. 1).

From these populations, a sample of seeds from the F_2, F_3, F_7 and F_8 populations (F_7 and F_8 were the last generations conducted in *bulk*) were obtained using a soil divider sampler and sown in a greenhouse in 2022. After physiological maturation, the seeds were collected from individual plants so that the progeny could be evaluated experimentally in the following generation, totaling 16 progenies sampled in each of these generations (Fig. 1). This number of progeny was

considered due to the difficulty for evaluating this trait using the Mattson cooker method (Carvalho et al., 2017). Thus, a total of 66 genotypes were used in this work, including 64 progeny of self-fertilization in initial (segregating) and advanced generations originating from the cross between the parents BAF50 x BAF07: *i)* 16 progeny in the $F_{2:3}$ generation ; *ii)* 16 progeny in the $F_{3:4}$ generation; *iii)* 16 progeny in the $F_{7:8}$ generation; and *iv)* 16 progeny in the $F_{8:9}$ generation; *v)* along with the parents BAF50 and BAF07.

Conduction of field experiment

The field experiment was developed in the experimental area of the Institute for Breeding and Molecular Genetics (IMEGEM), located at the Center for Agroveterinary Sciences (CAV), of the State University of Santa Catarina (UDESC) in Lages, Santa Catarina, Brazil, in the 2022/23 agricultural harvest. The geographic coordinates of the experimental area are 27 º 47'S latitude, 50 º 18'W longitude, at an altitude of 950 meters, with its climate classified according to Köppen as a temperate Cfb climate (C = Warm temperate, f = Fully humid, b = Warm summer), humid mesothermal with a mild summer. The soil is classified as an Inceptisol Udepts Humudepts, with a moderate A horizon, clayey texture, and undulating relief. It was used a randomized block design with three replications, considering samples of progeny from different generations of self-fertilization, and all experimental factors (*block + progeny)* were considered random (sampled factors). Therefore, 16 progenies sampled in each of the generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$ (totaling 64) was conducted along with the parents (totaling 66), which resulted in 198 experimental units, composed of a 2-meter line, with 8 seeds per linear meter.

During the cycle, the cultural practices were carried out according to the technical recommendations for bean crops, while sowing and topdressing fertilization were conducted according to soil analysis interpretation, following the provisions of the Soil Chemistry and Fertility Commission, aiming at a grain yield of 4000 kg ha^{-1} (CQFS-RS/SC, 2016). Topdressing nitrogen fertilization was carried out in stages, in the vegetative phases of the first (V_3) and third (V_4) trifoliate leaves, when they were completely open. At physiological maturity, the plants in the plots were harvested and subsequently manually threshed, and the grains were dried in an oven to approximately 13% moisture content. Then, the grains were stored in paper bags for a period of one month at room temperature, until the time of the cooking test. These seeds correspond to the generations $F_{2:4}$, $F_{3:5}$, $F_{8:10}$ and $F_{9:11}$. However, to estimate the genetic parameters, the integument generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$ were considered, since the maternal effect had been reported for this trait in the literature, along with the absence of xenia. Thus, the cooking time has its phenotypic expression one generation later than the plant generation, that is, the seeds harvested from plants of a certain self-fertilization generation represent the mother plant own generation for this trait, since the integument presents significant effect, deriving from the development of the ovary wall, determined prior to fertilization (Hernandez et al., 2003; Ribeiro et al., 2006).

Cooking time assessment

The cooking time of the plots was determined 30 days after harvest using the Mattson cooker (Mattson, 1946), modified by Proctor and Watts (1987). The cooker consists of 25 vertical rods, each with a 2 mm diameter tip and a standard weight of 90 g, which remain supported on the bean grains during cooking in boiling distilled water. The cooking time in minutes was determined when 13 units of rods pierced the grains. Each sample of the plots, composed of 16 g of grains, was immersed in 100 mL of distilled water in a 1:6.25 ratio, respectively, and kept at 25°C for a hydration period of 12 h. After the hydration period, 25 bean grains were placed under the Mattson cooker support, with the rods supported under the grains. Then, the cooker was placed in a stainless steel pan with 3 L of boiling distilled water at a constant temperature of 100°C, at which point the cooking time was started and continued until the 13th bean grain in the sample was pierced, thus characterizing the cooking of 52% of the grains (T50).

Statistical analysis

The statistical analysis for the cooking time variable was carried out by estimating the genotypic variance and residual components (variances associated with the random effects of the statistical model), considering the mixed model, denoted in matrix form by: $Y = Xb + Zu + \theta$, where: Y is the vector of observations; X is the incidence matrix for fixed effects (*mean*); b is the vector of fixed effects; Z is the incidence matrix of random effects (*block + progeny*); u is the vector of random effects; θ composes the random vector inherent to the experimental error. The estimates of the random components were based on the restricted maximum likelihood method (REML), since its properties are considered superior than those of the least squares and maximum likelihood estimates. This is explained by the fact that its estimators are obtained by maximizing the likelihood function, with the negative variance components restricted to mean zero, which is divided into two independent parts, referring to the fixed and random effects, while the likelihood function is inherent to the sum of each part (Searle et al., 1992).

Subsequently, the genotypic variance of the progeny (σ_g^2) was decomposed into additive (σ_A^2) and dominant (σ_D^2) components for the integument generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$, according to the proposal by Cockerham (1963) , where: $\sigma_g^2 = k_A \sigma_A^2 + k_D \sigma_D^2$ ..., with $k_A = (1 + I_t)$ and $k_D = ((1+I_t)(1-I_t)^{-1})(1-I_g)^2$; k_A is the coefficient of the additive variance; k_D is the coefficient of dominance variance; I_t is the inbreeding coefficient in the reference generation (last generation of "bulk" conduction); I_g is the inbreeding coefficient in the generation g of the offspring (generation of the opening of the " *bulk "*/beginning of progeny evaluation). The hierarchical genetic model used in the study is characterized by the fact that the progeny of one generation are not represented in subsequent generations, due to the different times of the subdivision of the progeny (opening of the bulk/beginning of progeny evaluation). Thus, the model used to obtain the estimates of the components of genetic variance considered all generations of self-fertilization assessed in the study ($F_{2:3}$, $F_{3:4}$, $F_{8:9}$, $F_{9:10}$). This decomposition of genetic variance was performed using the least squares method, and the estimates were obtained according to the following estimator: $\hat{\beta} = (X'X)^{-1} X'Y$, where $\hat{\beta}$ is the vector inherent to the estimates of the components of

genetic variance; X is the matrix of genetic components; Y is the matrix of genetic variance observed in the progeny (Vencovsky and Barriga, 1992).

The heritability coefficients were obtained as follows: $\hat{h}^2 = \hat{\sigma}_g^2 \ (\hat{\sigma}_g^2 + \hat{\sigma}_e^2)^{-1}$ and $\hat{h}_r^2 = \hat{\sigma}_A^2 \ (\hat{\sigma}_g^2 + \hat{\sigma}_e^2)^{-1}$, where $\hat{h}^2$ is the broad sense coefficient of heritability; $\hat{h}_r^2$ is the narrow sense coefficient of heritability; $\hat{\sigma}_g^2$ is the component of genetic variance, $\hat{\sigma}_e^2$ is the environmental variance between plots, while $\hat{\sigma}_A^2$ is the additive component of genetic variance. For these estimates to fulfill their purpose, they must be considered based on the units in which plant selection will be carried out. Therefore, in this study, heritability estimates were obtained based on phenotypic variation at the plot level, that is, the sum of genetic variation and environmental variation among the bean progeny was evaluated for the cooking time trait.

The expected progress with the selection was estimated based on its general expression: $G_s = -i \ \hat{\sigma}_A^2 / \ \hat{\sigma}_F^2$, where G_s corresponds to the expected gain with the selection; -i refers to the standardized negative selection differential (i = -1.65), which is related to the percentage of selected individuals with shorter cooking time, considering the selection of the 8 best progeny for the generations $F_{2:3}$, $F_{3:4}$, $F_{8:9}$ and $F_{9:10}$, corresponding to 12.5% of the progeny; and $\hat{\sigma}_F^2$ is the phenotypic deviation inherent to the phenotypic variation. The analyses were performed with the aid of SAS software (SAS OnDemand for Academics), using the Mixed Linear Models (MIXED) procedure to estimate the variance components and random (genotypic) effects based on the best linear unbiased prediction (BLUP). The Interactive Matrix Language (IML) procedure was used to obtain the least squares estimates.

Conclusion

The estimate of the parameter inherent to the dominance component of genetic variance presents a higher magnitude than the additive component in the adjusted model, which results in estimates of dominance variances higher than expected for the cooking time trait in bean progeny. Thus, the dominant gene action was predominant in the segregating generations in this study. With the increased inbreeding coefficient in advanced generations of self-fertilization, the estimates of additive genetic variance increased as expected, resulting in higher coefficients of restricted heritability and progress with selection, compared to the estimates in early generations. This evidences that the selection of plants aiming at reducing cooking time in common bean can be carried out in early segregating generations, considering progeny derived from individual plants. However, the elimination of genotypes with high cooking time presents greater success with the advancement of homozygosity, due to the reduction of heterozygosity and, consequently, of the dominance genetic variance.

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Authors contribution

Luan Tiago dos Santos Carbonari: Conceived and designed the study, collected the data, performed statistical analysis, and wrote the manuscript. Paulo Henrique Cerutti: Monitored environmental conditions and organized experimental data. Rita Carolina de Melo: Critically analyzed the data and wrote and revised the manuscript. Carlos Zacarias Joaquim Júnior: Reviewed the literature and interpreted the results. Altamir Frederico Guidolin: Revised the manuscript and critically reviewed. Jefferson Luís Meirelles Coimbra: Revised the manuscript, suggested improvements in data analysis, and critically reviewed.

Conflict of interests

The authors have not declared any conflict of interests.

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