

Inheritance of root distribution in common bean and selection strategy

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Crop Breeding and Applied Biotechnology
18: 373-381, 2018
Brazilian Society of Plant Breeding.
Printed in Brazil
<http://dx.doi.org/10.1590/1984-70332018v18n4a56>

Abstract: *The objective was to determine the predominant genetic inheritance in the trait root distribution in common bean and define the selection strategy. An experiment involving 40 genetic constitutions (segregating and fixed populations), was developed during the agricultural years 2014/15 and 2015/16. The experiment was arranged in a Federer's augmented block design with 3 replicates. The root distribution was evaluated by Bohm method. Estimates of mean contrasts between the F_4 progenies and their parents did not reveal any significant differences in any comparison. The generations F_5 and F_6 presented the same behavior. The distribution of the component of the additive genetic variance was similarly conducted for the segregating generations. Thus, since the predominant inheritance of the root distribution is additive, the selection of this trait is recommended to be performed at the end of the breeding program.*

Keywords: *Phaseolus vulgaris L., additivity, homozygous loci, contrasts, selection.*

INTRODUCTION

The development of a prominent root system is considered one of the major mechanisms of adaptation to abiotic stresses (Lynch 2007, Bishopp and Lynch 2015). Bean breeding programs developed worldwide report the relevance of roots in the search for drought tolerance (Urrea et al. 2009, Assefa et al. 2015) and efficient use of nutritional resources (Mendes et al. 2015, DoVale et al. 2013, Miguel et al. 2013). Water stress and soil infertility are the greatest yield limitations globally. The development of crops with root systems that can capture more water and nutrients would directly improve food security and economic development in poor nations and would also improve the sustainability of agriculture in rich nations by reducing reliance on intensive fertilization and irrigation. The latter consume large amounts of energy and natural resources and cause environmental pollution (Bishopp and Lynch 2015). However, since the phenotyping of this trait is expensive, research works on genetic inheritance are still scarce and incipient (Toaldo et al. 2013, De Melo et al. 2016).

Advances in research on the genetic control of root distribution are restricted to laboratory tests or highly controlled environmental conditions, such as the identification, cloning and characterization of QTL Dro1 (DEEPER ROOTING 1) in rice (Uga et al. 2013) and identification of Pup1 locus for tolerance to phosphorus deficiency in rice (Gamuyao et al. 2012). Particularly, the lack of knowledge

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Received: 11 July 2017
Accepted: 20 August 2018

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about the effects of the genotype and its interaction with the environment on phenotype makes it difficult to develop strategies to improve productivity and agricultural sustainability (Burridge et al. 2016, Topp et al. 2016). There is a lack of information to help breeders define how and when the selection for the trait should be effectively performed. For such, it is essential to carry out studies on the predominant inheritance of root distribution, under real cultivation conditions.

The main types of inheritance expected in a given trait depend on the average degree of dominance (Vencovsky et al. 2012). The following allelic interactions may occur: *i*) the performance of the progeny is similar to the average performance of the parents, given the additive variation and *ii*) the performance of the progeny is discrepant to the parents' average performance, given the non-additive variation (Fehr 1987). The selection of any trait is based on the quantification and interpretation of these components (Zemolin et al. 2016). The knowledge about the prevalence of a certain component of the genetic variance in the expression of root distribution is essential for the successful selection of genotypes adapted to low input agriculture (Burridge et al. 2016).

Therefore, the present study aimed to determine the predominant genetic inheritance of root distribution in common bean and define the selection strategy to improve this trait.

MATERIAL AND METHODS

Genetic constitutions assessed

Eight genotypes of common bean were evaluated as to the root distribution: six of them were accessions from the Bean Active Germplasm Bank (BAF 07, BAF 09, BAF 35, BAF 44, BAF 50 and BAF 63) from different parts of the state of Santa Catarina, and two are commercial cultivars (Perola and IPR Uirapuru). Four superior genotypes from the eight evaluated were chosen for the distribution of the root system, as follows: BAF 07, BAF 09 and IPR Uirapuru from the black commercial group, and BAF 50 from the Carioca commercial group (Figure 1).

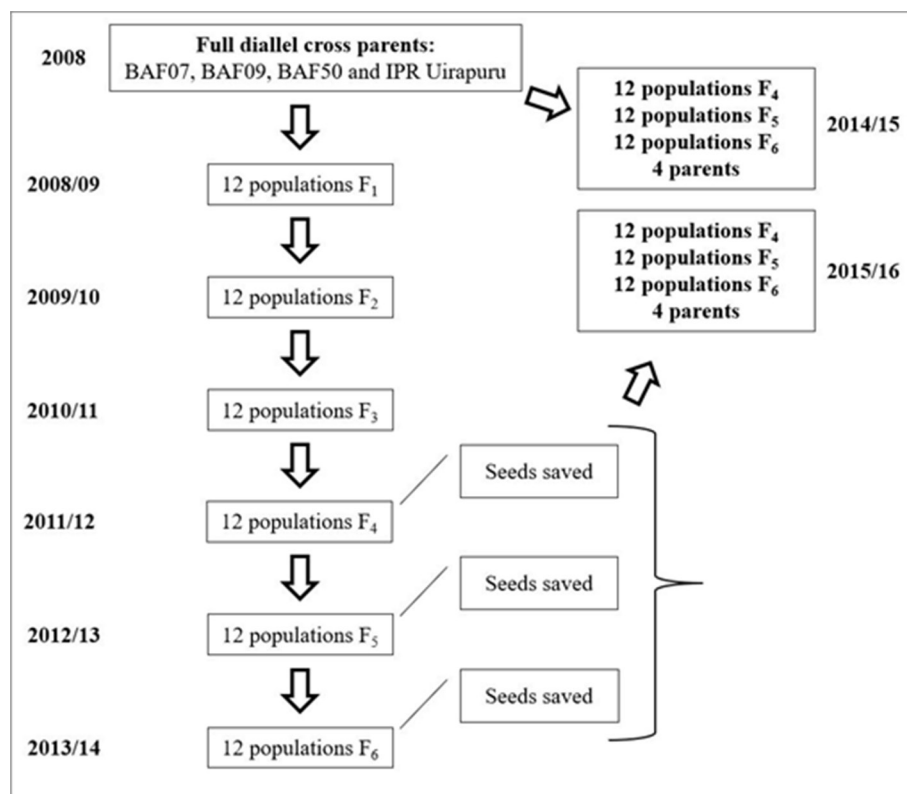


Figure 1. Scheme for obtaining the fixed and segregating populations evaluated in the present study.

The selected genotypes were crossed in a complete diallel scheme to obtain F_1 hybrids and their reciprocals. In the evaluation of the first segregating generation (F_2), the best plants were selected for the agronomic traits, forming a sample of the genotypic frequency of each population.

After successive generations of self-pollination, the segregating populations F_4 , F_5 and F_6 were obtained from the crosses and reciprocals: BAF07_BAF09, BAF07_BAF50, BAF07_Uira, BAF09_BAF07, BAF09_BAF50, BAF09_Uira, BAF50_BAF07, BAF50_BAF09, BAF50_Uira, Uira_BAF07, Uira_BAF09 e Uira_BAF50 which totaled 36 segregating populations. The 36 segregating populations and 4 parents (BAF07, BAF09, BAF50 and IPR Uirapuru) had their seeds saved and were conducted in two agricultural years (2014/15 and 2015/16), as shown in Figure 1.

Location and experimental design

The experiment was conducted in the experimental field of the Institute of Molecular Breeding and Genetics of the University of the State of Santa Catarina (UDESC) Brazil, State of Santa Catarina, Lages (lat 27° 48' S, long 50° 19' W, alt 930 m asl). According to Koppen, the site weather is classified as temperate cfb (moist mesothermal and mild summer). The soil at the study site is classified as Inceptisol Udepts Humudepts, with a moderate A horizon, clayey texture and undulating relief.

The experiment was arranged in Federer augmented block design with three replicates. In this design, four common treatments (parents) and 36 regular treatments (12 segregating populations in F_4 , F_5 and F_6 generations) were allocated. The plots were composed of four lines with four meters in length, spaced at 0.45 m. A seeding density of 12 seeds per linear meter was used in the internal and external lines, 2 seeds were used per linear meter (a spacing of 0.5 m between plants) to allow the visualization of the root system. In the external lines of the plot, two plants were evaluated to the trait.

Assessment of root distribution

Root distribution was quantified in full bloom by the method of the profile described by Böhm (1979), with some adaptations. The method is considered non-destructive and, therefore, important for evaluating segregating populations. Profiles perpendicular to the sowing line were opened on the outer lines of the experimental unit, 0.05 m from the plants. The roots were exposed with pointed stems. Next, a rectangle with 0.5 m of width, 0.3 m of height, subdivided into 60 squares (with 0.05 m x 0.05 m edges) was placed on the profile. The root distribution was evaluated by means of a digital image of the profile, at different depths (0 – 0.10 m; 0.10 – 0.20 m and 0.20 – 0.30 m), according to a binary system, and presence (1) or absence (0) was attributed in each square.

Statistical analysis and determination of the predominant inheritance

The analysis of variance was obtained using the SAS (Statistical Analysis System, version 9.2) and the GLIMMIX procedure. The Mixed Generalized Linear Model was used to meet the model assumptions. Since root distribution in this study is a variable that involves counting data, the main objective of the study is defining the scale on which an additive linear model occurs; in the present case, the definition of the binomial scale. The following mathematical model expressed root distribution behavior:

$$Y_{ijklm} = \mu + block_i + depth (population*generation*year)_{j(klm)} + e_{ijklm}$$

Where: Y_{ijklm} - values observed for root distribution in the i -th experimental unit in the j -th depth in the k -th population in the l -th generation for the m -th year; μ - effect of the overall average, $block_i$ - fixed effect of the i -th level of the block factor; $depth (population*generation*year)_{j(klm)}$ - fixed effect of the j -th level of the depth factor nested under the interaction of the k -th level of the population factor of the l -th level of the generation factor and m -th level of the year factor and e_{ijklm} - effect of the experimental error.

Differences between the segregating progenies (F_4 , F_5 and F_6) and the parents (P_1 , P_2 , P_3 and P_4) were determined from non-orthogonal mean contrasts to test the hypotheses for the genetic inheritance prevailing in the trait root distribution. In addition, the effect of the agricultural years on the trait was determined according to the same hypothesis test statistics.

RESULTS AND DISCUSSION

The trait root distribution revealed significant differences in the causes of controlled variation (Table 1). This trait is probably variable for the levels of the nested depth factor under the interactions of the levels of the year, population and generation factor. The assessment of the segregating populations in the same agricultural year, in repeated years, provides subsidies for breeders to define the predominant inheritance of a particular trait, besides preventing the effect of the segregating generation from being mistaken by the random effect of each agricultural year (De Melo et al. 2016).

The genetic control of any trait can be defined by the comparative evaluation of the segregating progenies and their parents (pure and contrasting), clearly distinguishing the genetic effects from the environmental effects. Thus, comparisons between the genetic value of the segregating populations and their respective parents were shown in Table 2. The transformed estimates of the average differences between the F_4 progenies and their respective parents showed no significant differences in any of the comparisons conducted. All segregating populations in the F_4 generation presented performance similar to that of the average of the parents, regardless of the agricultural year. Thus, the genetic variation can be attributed to genes with additive effects (Mukamuhirwa et al. 2015).

With only three generations of self-pollination, the proportion of loci in homozygosis increased significantly to the point of equating to the homozygous loci of the parents (BAF07, BAF09, BAF50 and Uirapuru). In the F_4 generation, for example, considering only one gene in a diploid species whose characteristic expresses complete dominance, 87.5% of the loci are expected to be homozygous (Fehr 1987). The results support this hypothesis. However, it is known that this trait is governed by numerous quantitative genes (Uga et al. 2013) and that under this condition, the number of self-pollinations to promote the expected proportion of loci in homozygosis is infinitely higher, unless the genetic inheritance is predominantly additive.

One of the most important characteristics of additivity is the fact that the average of the offspring of any individual or group of individuals is equal to that of this individual. In other words, the average of the offspring can be predicted by the average of the parents or by the phenotypic value of the self-pollinated individual (Chelaifa et al. 2013). When this type of interaction prevails, selection becomes easier, since when one individual or group of higher individuals is selected, a higher offspring is obtained as well. Since root distribution is a trait difficult to quantify, the allelic interaction of the additive type may facilitate the selection of better genetic constitutions.

Similarly to all species, the growth and development of the root system in common bean are discontinuous through the soil depths. The importance of the root system varies in each layer (Lynch 2011). Its importance is related to the superficial development of roots and the respective nutrient uptake through fertilization (Ramaekers et al. 2010). Besides, its importance is related to better absorption of water and nutrients in depth (Zadrznik et al. 2013). Therefore, it is fundamental to assess the genetic constitutions at each depth, 0 - 0.10 m (Figure 2) and 0.10 - 0.20 m (Figure 3).

The genetic behavior of the fixed (P_1 and P_2) and segregating (F_4 , F_5 and F_6) populations at the depth of 0 - 0.10 m, expressed in the original mean scale μ_0 , showed results similar to those previously discussed (Figure 2). In this figure, each graph presents the progenies compared to the parents over the agricultural years. No significant differences are

Table 1. Analysis of variance for the causes of fixed effect variation on the trait root distribution in common bean. Inference was carried out for two agricultural years

Causes of variation	df	F value	Pr > F
Block	2	0.75	0.4791
Depth (population*generation*year)	239	1.75	0.0120

Table 2. Estimates of non-orthogonal contrasts in transformed scale (μT) for the mean difference between F_4 segregating progenies and their respective parents for the trait root distribution. Genetic constitutions were assessed in two different agricultural years

Contrast	Estimate ^a	
	2014/15	2015/16
BAF07_BAF09 F_4 vs. (BAF07 and BAF09)	0.50	0.16
BAF07_BAF50 F_4 vs. (BAF07 and BAF50)	-0.76	0.25
BAF07_Uirapuru F_4 vs. (BAF07 and Uirapuru)	1.42	0.40
BAF09_BAF07 F_4 vs. (BAF09 and BAF07)	0.79	0.64
BAF09_BAF50 F_4 vs. (BAF09 and BAF50)	-2.29	-2.05
BAF09_Uirapuru F_4 vs. (BAF09 and Uirapuru)	1.02	0.71
BAF50_BAF07 F_4 vs. (BAF50 and BAF07)	-0.23	-1.13
BAF50_BAF09 F_4 vs. (BAF50 and BAF09)	-2.29	-0.12
BAF50_Uirapuru F_4 vs. (BAF50 and Uirapuru)	0.81	0.04
Uirapuru_BAF07 F_4 vs. (Uirapuru and BAF07)	0.14	-0.73
Uirapuru_BAF09 F_4 vs. (Uirapuru and BAF09)	0.93	-2.25
Uirapuru_BAF50 F_4 vs. (Uirapuru and BAF50)	-13.17	-2.30

^a $H_0: \mu_1 - \mu_2 = 0$. $H_A: \mu_1 - \mu_2 \neq 0$. Hypothesis H_0 tested by the *t* test at 0.05 probability.

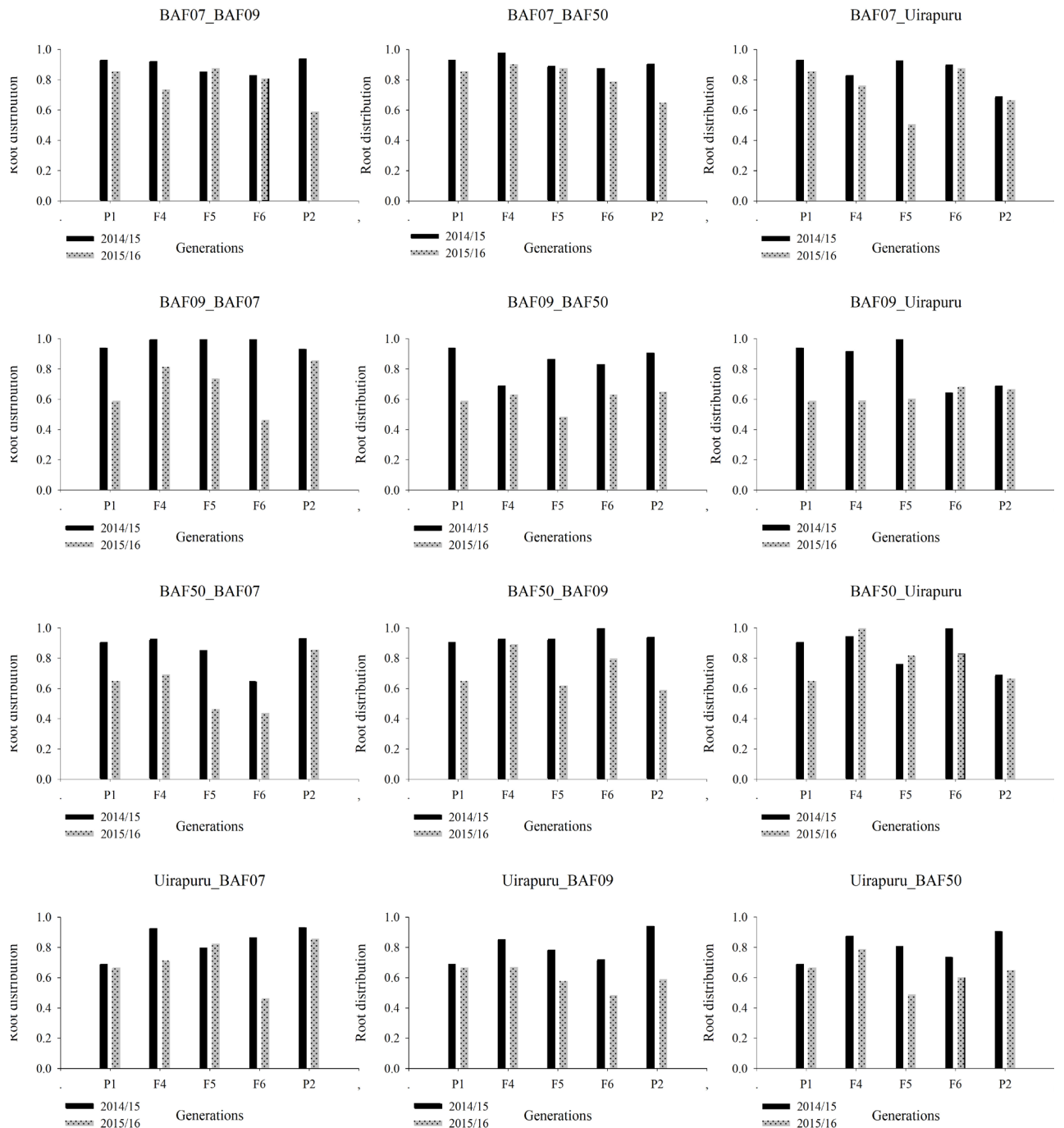


Figure 2. Root distribution (original mean scale μ_0) of twelve segregating genetic constitutions and their respective parents (P_1 and P_2) at the depth of 0 - 0.10 m. Estimates obtained for the agricultural years 2014/15 (black bar) and 2015/16 (gray bar) for each genetic constitution.

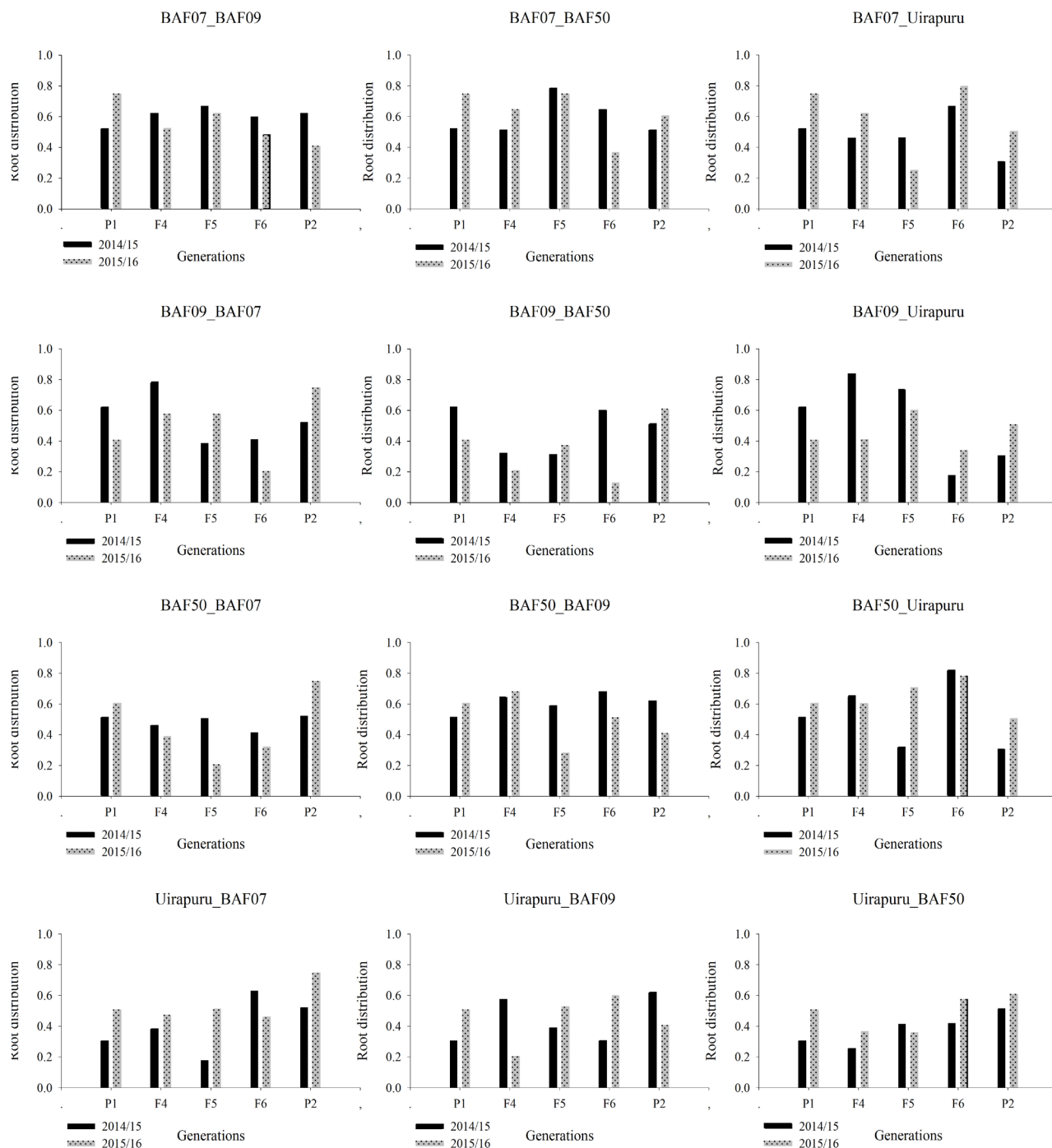


Figure 3. Root distribution (scale of original means μ_0) of twelve segregating genetic constitutions and their respective parents (P_1 and P_2) at the depth of 0.10 - 0.20 m. Estimates obtained for the agricultural years 2014/15 (black bar) and 2015/16 (gray bar) for each genetic constitution.

observed either between the average of the parents and the respective F_4 progeny in any of the agricultural years assessed. The performance of the segregating progenies (heterozygotes) was invariably revealed in the average of their parents and their superiority cannot be admitted.

In rare conditions, such as the comparison involving BAF50_BAF09 F_4 , BAF50_UIRA F_4 and UIRA_BAF50 F_4 , the mean root distribution seems to transcend the phenotype of the parents, in crude averages (Figure 2). However, the hypothesis test proves that the differences are not significant, at 5% probability of error. The progenies mentioned are the crosses with greater divergence, which bring together the black and carioca commercial groups in the same genetic constitution. The same behavior was observed for all genetic constitutions evaluated. Throughout the segregating generations, increased loci in homozygosis or decreased frequency of heterozygous genotypes naturally led to increased endogamy, which was rapidly achieved through self-pollination (Wright 1949).

Similar results were observed for the depth 0.10 - 0.20 m (Figure 3). No F_4 progeny revealed behavior different from that of their parents in any agricultural year, although phenotypic oscillations seem to be more usual, compared to the 0 - 0.10 m depth. However, phenotypically, the root distribution at this depth is considerably reduced, and the averages do not exceed 0.8 (μ 0). The less pronounced root distribution at the lower depths was already expected, due to the uneven growth and positive geotropism of the roots (Lynch 1995). In addition, another factor that reduces root distribution at lower depths is the fact that most breeding programs are performed under optimal conditions of cultivation or high input environments (fertilized and irrigated areas), which induces the selection of plants with denser root system in the basal or superior soil layer (Lynch 2007).

Now that the behavior of the F_4 segregating progenies in relation to the parents has been clarified, it must be verified whether the inferences can be valid for the other generations, so as to determine the prevailing genetic control of this trait (Table 3). The contrast of transformed means between the different generations did not reveal significant differences. The genotypic performance was similar, regardless of the number of generations. Throughout the segregating generations, increased loci in homozygosis or decreased frequency of heterozygous genotypes naturally led to increased endogamy, which was rapidly achieved through self-pollinations (three, four or five) and their respective genetic consequences for the heterozygous loci and restoration of the homozygous condition, as well as the segregating populations involved and their origins. Analogously, the F_5 and F_6 generations showed the same behavioral trend and no statistical differences. The distribution of the additive genetic variance component occurred similarly and evenly among the segregating generations, in all populations assessed.

The only significant differences observed among the populations of the respective study are due to their different commercial groups, such as BAF50_Uira F_6 (carioca) versus BAF09_BAF07 F_6 (black). The difference can be explained by the genetic divergence between the parents involved in these crosses, which results in increased hybrid vigor. The progeny BAF50_Uira F_6 has the parent BAF50 (carioca commercial group) in its genetic constitution and the parent IPR Uirapuru (black commercial group). On the other hand, BAF09_BAF07 F_6 came from parents of the black commercial group. Crosses involving highly divergent genetic constitutions (with contrasting alleles in the same locus) result in progenies with higher proportion of heterozygous loci - thus becoming the dominance variance component (Toaldo et al. 2013).

The study on the distribution of genetic variance over segregating generations that brings together the distinct generations in the same agricultural year (environment) is advantageous. The repetition of the same assay may be even more interesting to express the actual genetic behavior of the trait studied and determine the predominant mode

Table 3. Estimates of non-orthogonal contrasts in the transformed scale (μ T) for the mean difference between progenies at different segregation levels (F_4 , F_5 and F_6) for the trait root distribution. Estimates obtained for the agricultural year 2014/15

Genetic constitution	Estimates between segregating generations ^a	
	F_4 vs F_5	F_4 vs F_6
BAF07_BAF09	-0.69	0.75
BAF07_BAF50	-2.09	0.18
BAF07_Uirapuru	0.54	-1.22
BAF09_BAF07	14.03	-12.17
BAF09_BAF50	0.08	-1.16
BAF09_Uirapuru	-0.29	15.29
BAF50_BAF07	-0.50	13.88
BAF50_BAF09	-1.53	-0.57
BAF50_Uirapuru	1.21	-0.63
Uirapuru_BAF07	13.30	-14.75
Uirapuru_BAF09	1.65	12.60
Uirapuru_BAF50	-13.08	1.05

^a $H_0: \mu_1 - \mu_2 = 0$. $H_A: \mu_1 - \mu_2 \neq 0$. The null hypothesis H_0 tested by the t test at 0.05 probability.

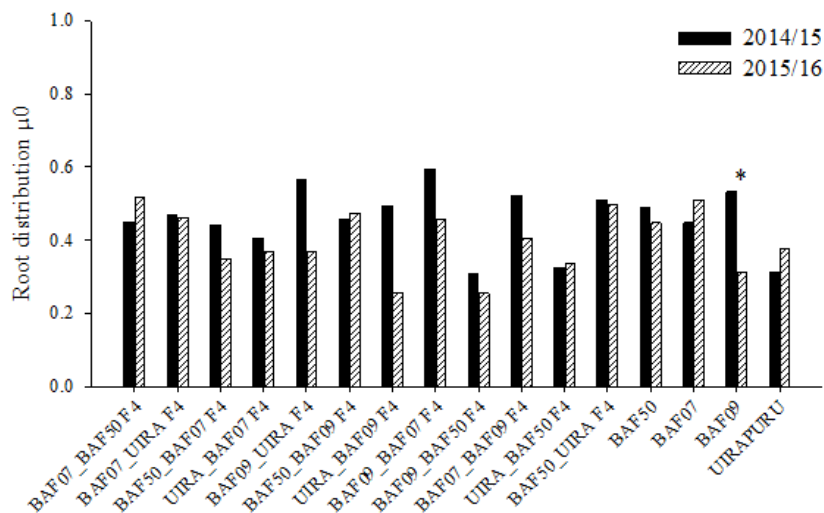


Figure 4. Original means (μ_0) of the trait root distribution for each F_4 segregating population and parents. Estimates of the mean difference between the agricultural years 2014/15 (black bar) and 2015/16 (dashed white bar). * Significant at 0.05 probability of type I error by the t test. $H_0: \mu_1 - \mu_2 = 0$. $H_A: \mu_1 - \mu_2 \neq 0$.

of inheritance (Valentini et al. 2011). Figure 4 shows the original means of the root distribution for each F_4 segregating population and the parents, in the different agricultural years, and the significant difference between the transformed means (if there is any) of the genetic constitutions in the different years. It was possible to verify that only the parent BAF09 presented a discrepant behavior between the evaluation years - 2014/15 and 2015/16. This fact indicates that the genetic breeding of this trait can be facilitated, since the environment was not able to mask the genetic behavior of the trait. The trait root distribution is insensitive to the intrinsic variations of the agricultural year. Therefore, the determination of the component of genetic variance and the selection of the trait can be facilitated. In other words, the trait studied reveals high expressiveness and can be selected by breeders, regardless of the agricultural year.

Comparisons between the means of the segregating progenies and of their respective parents did not reveal significant differences, regardless of the agricultural year and the genetic constitution itself. This reveals a strong characteristic of the additive-type inheritance, in which the performance of the segregating progenies resumes the average of their parents. In other words, the homozygous condition of the genes is restored due to the natural process of Throughout the segregating generations, increased loci in homozygosis or decreased frequency of heterozygous genotypes naturally led to increased endogamy, which was rapidly achieved through self-pollination and distribution of genetic variance (Fehr 1987). Previous studies conducted by Toaldo et al. (2013) and De Melo et al. (2016) found that the F_2 and F_3 hybrid populations showed hybrid vigor or heterosis, compared to their parents. However, due to the lack of economically feasible alternatives to obtain commercial hybrids in beans (Ramalho et al. 1993), the breeding program must advance the segregating generations to obtain a fixed population. These results corroborate the findings of De Melo et al. (2016), who assessed the same segregating populations separately, one in each crop year. The studies provide subsidies for the effective selection of the trait root distribution in common bean.

The present study revealed that, since the predominant mode of inheritance in the trait root distribution is additive, effective selection of the best genetic constitutions should be conducted at the end of the breeding program, rather than at early generations. Otherwise, genetic progress would be unsatisfactory. In addition, the conductance of segregating populations aiming to achieve faster results should be carried out by the SSD (*Single Seed Descent*) method. This method allows advancing more than one generation per year and performing selection only in advanced generations. This favors genetic progress, since selection can be conducted without the interference of non-additive effects.

ACKNOWLEDGEMENTS

To the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Coordenação de Aperfeiçoamento

de Pessoal de Nível Superior (CAPES) and Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina (FAPESC) for the scholarship granting and financial support provided to the present work.

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