

Genetic parameters in intra-gene and inter-gene pool crosses of common bean (*Phaseolus vulgaris* L.) for root distribution¹

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ABSTRACT

The knowledge about the genetic behavior of roots can be the solution to the main climatic problems and the key for increased production of agricultural crops. In inheritance studies, breeders usually conduct crosses between contrasting individuals to obtain a significant fraction of the genetic variance. To determine genetic parameters in beans from crosses within and between Middle American and Andean gene groups, 64 populations (breeders, F₁ and F₂) were evaluated under field conditions for the trait root distribution. Crosses between Middle American and Andean gene groups revealed significant estimates for genetic parameters (genetic variance, heritability, and average degree of dominance) compared to intra-pool crosses. However, only 4% of all hybrid combinations evaluated (F₁ and F₂) showed significant effects when compared to fixed populations (parents). Coupled with the insignificant number of progenies different from the parents, the differences detected revealed inferior performance, compared to the parents. The joining of alleles with identical provenance may be the main cause of the observed effects. The breeding strategy for root distribution should consider more divergent parents.

Keywords: Middle American and Andean; stress environments; heterosis; heritability; average degree of dominance; genetic models.

INTRODUCTION

The breeding of agricultural crops has always focused on the generation of superior genetic constitutions, considering traits of the aerial parts.⁽¹⁾ However, by examining current climate predictions and the limited water and nutritional resources, the development of genotypes taking into account the root system can be a promising strategy to ensure grain yield in favorable and stress environments.⁽²⁻⁴⁾ However, the genetic study on this trait is still a challenge because of the “hidden” characteristic and complexity of this trait.^(5,6)

Studies related to root distribution in beans (*Phaseolus vulgaris* L.) are scarce, especially under field conditions and involving segregating populations.^(7,8) There are important tools to quantify the variability and extent to which the traits are inherited, which can help in the conductance of studies on breeding programs. Therefore, it is possible to use the estimation of genetic parameters that generate valuable knowledge for research works. These parameters are studied from heterozygous populations, derived from directed hybridization. They provide knowledge about the inheritance mechanisms and help establishing the conductance and selection of plants.^(9,10)

In many cultures, it was established that cross-breeding between genotypes from distinct gene pools increases the estimates of genetic parameters (genetic variance, heritability and average degree of dominance) compared to crosses conducted within each pool.⁽¹¹⁾ Beans originated from the Americas and were domesticated, which resulted in two major gene pools: the Andean and Middle American. Geographic isolation, combined with different biotic and abiotic stresses associated with different climatic conditions and human intervention, led these groups to develop genetic differences in many traits. Thus, it is believed that the cross between these groups can provide greater genetic variability and favor the development of promising cultivars within breeding programs⁽¹²⁾, including for root distribution.

Based on the generation of segregating populations together with the parents (fixed populations), it is possible to estimate several genetic parameters of interest, which provide information on the genetic behavior of the first generations⁽¹³⁾. The estimation of genetic parameters plays an important predictive role for the goals of breeding programs as to the selection of the most promising genotypes⁽¹⁴⁾. The present study aimed to determine genetic

parameters for root distribution in hybrid and segregant bean populations within and between the gene groups.

MATERIAL AND METHODS

Genetic constitutions

A complete diallel with reciprocals was carried out, involving six genotypes of common bean. The parents used included three genotypes of the Middle American gene group and three genotypes of the Andean gene group. These genotypes are described in Table 1. Hybridizations between the parents were carried out in June 2016 in a greenhouse with controlled temperature and humidity, to obtain the F_1 hybrids. The cycle differences between the genotypes demanded stepped sowing, which provided flowering on different days. Hybridization was performed with floral button emasculation.⁽¹⁵⁾

During hybridization, one progeny produced less seeds than the amount required for the composition of the experiment, which resulted in 29 hybrid populations. In general, the combinations with CBS14 mother parent it was the major problem to obtain seeds. In the 2016/17 crop year, F_1 hybrid seeds were sown in the field to obtain F_2 seeds. After 29 hybrid populations (F_1 seeds) and 29 segregant populations (F_2 seeds) were obtained, the experiment was implanted under field conditions, in October 2017/18.

Location and experimental design

The 64 populations (29 F_1 hybrids, 29 F_2 populations and six parents) were evaluated in an experiment conducted in Lages, Santa Catarina, Brazil (27°48'S and 50°19'W). The experimental area was located at 950 m of altitude, with a characteristic cfb (C = Warm temperate, f = Fully humid, b = Warm summer), humid mesothermic climate and mild summer, according to Köppen classification system. The soil is classified as Inceptisol Udepts Humudepts, with a moderate A horizon, clayey texture and undulating relief.

The experimental design was a 8x8 simple partially balanced lattice, with two replicates. This design was chosen due to the extensive number of populations evaluated and the refining of the experimental technique that it promotes. The plots were composed of three 2m rows with spacing of 0.50m. The plots were separated by a space of 1.00m so as to allow the execution of the root distribution assessment. The rows of each experimental unit were sown with a spacing of 0.50m between the seeds, totaling five seeds per row. This sowing density was used to allow the evaluation

of the root system of a single plant.

During the characterization of the genotypes for choosing the parents, among all the evaluated characteristics related to the root (dry matter, total length, number of intersections, root distribution), the root distribution trait was considered the most discriminating through statistical analyses performed in previous studies. In addition, this character is related to all other root measurements. Root distribution involves understanding how much the genotype can take advantage of the resources in the soil (water and nutrients). The more distributed the root in the evaluated plane (horizontal and depth), the greater the capacity of the plants to acquire the resources present in the soil.

For root distribution, the plants were evaluated in full bloom according to stage R₆ of the CIAT scale. A sample of two plants was randomly chosen for root distribution assessment. Root distribution involves the understanding how much the genotype can use soil resources (water and nutrients). The more distributed the root in the evaluated plane (horizontal and depth), the greater capacity the plants will have to capitalize resources. A profile perpendicular to the sowing row on the outer side was opened in each plant, 0.05m apart, and the roots were exposed with sharp tool, in compliance with the Bohm method⁽¹⁶⁾, which is suitable for the evaluation of adult plants and segregant populations. In addition to the profile opening, some adaptations were performed in the method for the quantitative evaluation of the root system, including the placement of a 0.50m wide x 0.30m high rectangular wooden frame, subdivided into 0.05m squares (totaling 60 squares). After the placement of the rectangular wooden frame, a profile photo was taken for further evaluation. The root distribution in the binary system, called presence (1) and absence (0) of roots in each grid was determined by digital photography. The entire grid

frame was photographed and each of the 60 squares was evaluated for presence or absence of roots (1 or 0, respectively), indicating the percentage of total roots per plant in the template space: $(\sum 1/60) \cdot 100$.

Statistical Analysis

The assumptions of normality of errors and homogeneity of variances were satisfied after the transformation of the data into square root.⁽¹⁷⁾ The data were analyzed according to the following model: y_{ijk} = overall mean + population_{*i*} + replicate_{*j*} + replicate(block)_{*ij*} + error_{*ijk*}. So that: *i* = 1, 2, ..., 62; *j* = 1, 2; *k* = 1, 2, ..., 8. Following the general variation analysis, estimates of the genetic parameters of phenotypic variance (σ_F^2), genetic variance (σ_G^2), environmental variance (σ_E^2), broad sense heritability (h_a^2) and average degree of dominance (GMD) were obtained:

$$\sigma_{F_2}^2 = \sigma_G^2 + \sigma_E^2; \sigma_G^2 = \sigma_{F_2}^2 - \sigma_E^2; \sigma_E^2 = \frac{\sigma_{P_1}^2 + \sigma_{P_2}^2 + \sigma_{F_1}^2}{3};$$
$$h_a^2 = \frac{\sigma_G^2}{\sigma_{F_2}^2}; GMD = \frac{2 * \bar{F}_1 - (\bar{P}_1 + \bar{P}_2)}{\bar{P}_1 - \bar{P}_2} \quad (1)$$

Where: $\sigma_{F_2}^2$ - phenotypic variance of the F₂ generation, σ_G^2 - genetic variance, σ_E^2 - environmental variance, $\sigma_{P_1}^2$ - maternal parent variance (P₁), $\sigma_{P_2}^2$ - paternal parent variance (P₂), $\sigma_{F_1}^2$ - hybrid variance (F₁) and h_a^2 - broad sense heritability. The genetic parameters were determined only for three populations, so as to represent the crosses within and between the gene groups: *i*) BAF53 x CBS14 (Andean versus Andean), *ii*) BAF07 x IPR Uirapuru (Middle American versus Middle American) and *iii*) BAF07 x BAF53 (Middle American versus Andean). The estimates of the genetic parameters were obtained using the Genes software system (GENES, version 2009.7.0).

Table 1: Traits of the Middle American (BAF07, BAF35, IPR Uirapuru) and Andean (BAF53, CBS14 and BRS Embaixador) parents selected to compose the complete diallel with reciprocals

Genotype	Gene Group	Group	Type ^a	Origin
BAF07	Middle American	Black	III	Genotype CAV/UDESC
BAF35	Middle American	Carioca	III	Genotype CAV/UDESC
IPR Uirapuru	Middle American	Black	II	Cultivar
BAF53	Andean	Color (beige)	I	Genotype CAV/UDESC
CBS14	Andean	Color (white)	I	Genotype Curitiba/UFSC
BRS Embaixador	Andean	Color (red)	I	Cultivar

^a I: Determinate growth, erect plant habit; II: Undetermined with short guides, erect plant habit; III: Indeterminate with long guides, semi-erect to prostrate plant habit.

In addition to these parameters, heterosis estimates were obtained from comparisons by contrast of means; the means of progeny F_1 is compared to the means of the parents. We also compared the mean of F_2 progenies with the mean of the parents. Genetic models based on the least squares method were suggested for the behavior of some populations studied. For such, the following model parameters were used: mean (m), homozygous deviation in relation to the mean (d) and heterozygous deviation in relation to the mean (h).

RESULTS

Genetic parameters: genetic variance, heritability and average degree of dominance

The analysis of variance for the trait root distribution showed significant effects for all controlled sources of variation (Table 2). The use of lattice design improved local control. In general, it can be verified by the significance of the effects of *replicate* and *replicate(blocks)*, which evidences the quality of the experimental performance. In addition, this design allowed for the improved control of the causes of variation, as demonstrated by the low coefficient of variation and the high coefficient of determination.

The population effect was significant and indicated a different behavior of root distribution for the genetic constitutions evaluated (Table 2). The evaluated populations can be used for the selection of superior genotypes for root distribution. When genetic differences occur, the study on genetic parameters can be effective to assist in the use of the most suitable methods for the selection and conduction of segregant populations.⁽¹⁰⁾

For purposes of comparison, estimates of genetic parameters were obtained for the following crosses: *i*) BAF53 x CBS14, *ii*) BAF07 x IPR Uirapuru and *iii*) BAF07 x BAF53 (Table 3). In the selection of these three progenies, priority was given to the hybridization obtained from crosses within

each gene pool and between gene pools. The phenotypic component (σ_F^2) ranged up to 260% between the progenies studied. This variation can be attributed to both genetic and environmental causes. The progeny BAF53 x CBS14 (Andean versus Andean) showed only 17% of the phenotypic component, compared to the progeny BAF07 x BAF53 (Middle American versus Andean), which obtained 39%.

Regarding the genetic component, the directed hybridization between the BAF53 and CBS14 parents revealed the lowest value ($\sigma_G^2=0.0035$) among the hybrid combinations. This result suggests that the parents involved in the cross presented high genetic similarity for the trait root distribution. In this case, both parents belong to the Andean gene pool. The percentage variation between the progenies BAF07 x Uirapuru and BAF53 x CBS14 was 69% but did not exceed the value obtained between the progenies BAF07 x BAF53 and BAF53 x CBS14, which was 72%. This indicates that the contribution of the genotypes from different gene pools should be explored, as observed in progeny BAF07 x BAF53 ($\sigma_G^2 = 0.0126$). The values of the environmental component were similar between the progenies, which was already expected, considering that the genetic constitutions were conducted in the same culture environment.

Consequently, the broad heritability coefficient expression was higher when genotypes from different gene pools were involved (Middle American x Andean) ($h_a^2 = 74.10\%$). The results obtained for the heritability coefficients followed proportionally the values of genetic and environmental variance. It is also understood that crosses between gene pools may help in the selection of improved progenies for root distribution.

Finally, the estimation of the average degree of dominance allows us to infer which crosses are more likely to present heterosis. The average degree of dominance measures the relative position of the heterozygote in relation to the mean of the homozygotes. This parameter was higher in progenies from crosses between gene groups,

Table 2: Analysis of variance and their respective degrees of freedom corresponding to the root distribution, considering six parents, 29 F_1 hybrid populations and 29 F_2 segregating common bean populations from crosses between genotypes from different gene groups

Sources of variation ^a	Degrees of Freedom	Mean square	Pr > F
Replicates	1	0.0449	0.0002
Populations	63	0.0056	0.0022
Replicates (blocks)	14	0.0057	0.0362
Residue	47	0.0025	
Total	125		

^a General mean on a scale of 0 to 1 = 0.63; Coefficient of variation = 6.62%; $R^2 = 0.79$

such as BAF07 x BAF53 (GMD = 20.51). Oppositely, crosses between progenies of the same gene group, such as BAF07 x Uirapuru, showed lower average degree of dominance – the lowest of all (GMD = -0.34). It is worth mentioning that the average degree of dominance exposed in this study was obtained based on the means of the parents and F_1 , which explains the variation observed in the values of this parameter among these progenies. In general, however, the high GMD value is related to the genetic divergence of the parents involved in the cross. When the loci are similar - distance between loci in small homozygosis - high GMD values are unlikely to occur. Regarding the progeny BAF53 x CBS14, no significant GMD (0.82) was detected either, which reveals similarity between the parents.

Thus, it is assumed that divergence between the parents is observed in the progenies with high GMD values. In these cases, non-additive interactions prevail. Our study detected GMD close to zero, which correspond to additive interactions. In addition, they indicate that the parents involved in the cross are probably very similar as for root distribution, or even that non-allelic additive interactions may be involved in the manifestation of this trait.

Presence or absence of heterosis?

Although the estimation of the average degree of dominance indicates the hybrids that lead to greater heterosis, a comparison of the means between the offspring and the parents can provide stronger evidence. Thus, in order to corroborate the genetic parameters, the means were contrasted and the comparison was conducted between F_1 hybrids and the mean of the parents to identify the magnitude of the heterosis effect (Table 4). The comparisons allow us to identify whether the heterosis expression is actually more likely when parents from different gene groups are hybridized, besides its direction.

Only 7% of the 29 F_1 hybrid populations obtained

presented significant effects when compared to the performance of the parents. The combinations of the hybrids BAF07 x BAF53 and BAF07 x CBS14 showed heterosis effects. These progenies, however, showed inferior performance (less percentage of root distribution), compared to the parents, which resulted in negative heterosis values. The hybrid BAF07 x BAF53 (0.5033), for example, presented on average 32% less root-filled squares, compared to the parents. On the other hand, as for the progeny BAF07 x CBS14 (0.2050), the hybrid resulted in 15% less root-filled squares, compared to the mean of their parents. It is possible to observe that the root distribution of the offspring was not better than that of their parents (Table 4).

Similar results are reported (Table 5) for the segregating F_2 progenies in relation to the mean of the parents. Only two progenies showed significant differences in relation to their parents (Uirapuru x BAF53 and BAF07 x BAF53). In the case of the Uirapuru x BAF53 progeny, lower performance is observed for the offspring, compared to the parents, and less than 17% of the squares were filled. On the other hand, the progeny BAF07 x BAF53 showed positive behavior in relation to the parents and a 17% increase in filled squares. Progenies and parents showed similar behavior for root distribution. However, there is evidence of heterosis and use of the genetic variation available for the hybrids between the Andean and Middle American gene groups.

Genetic Models

Particularly, a genetic model based on parameters related to the populations under study can be developed by using the least squares method. Thus, hypotheses about genotypes related to the mean of the parents can be formulated [m], which depends on the general conditions of the observations, the additive component [d] and the dominance component [h]. The expected relationships can be used to test the suitability of the model.

Table 3: Estimates of genetic parameters for root distribution, considering genetic combinations from crosses within and between Andean and Middle American gene groups

Parameters ^a	BAF53 x CBS14	BAF07 x IPR Uirapuru	BAF07 x BAF53
σ_F^2	0.0073	0.0190	0.0171
σ_G^2	0.0035	0.0113	0.0126
σ_E^2	0.0038	0.0077	0.0044
h_a^2 (%)	47.50	59.60	74.10
GMD	0.82	-0.34	20.51

^a σ_F^2 : phenotypic variance; σ_G^2 : genetic variance; σ_E^2 : environmental variance; h_a^2 : broad sense heritability; GMD: average degree of dominance (based on means).

For BAF07 x BAF53, for example, a heterosis model was proposed (Table 6). The model $y = 0.6142 + 0.0150d + 0.2937h$ revealed significance for the parameters tested ($p = 0.0001$). In addition, the deviation showed no significance ($p = 0.4551$), which is favorable for the adequacy of the proposed model.

The tested model demonstrates that the phenomenon of heterosis is explained by a deviation of the heterozygous loci equal to 0.2937. Meanwhile, the homozygous loci deviation was only 0.0150. This may explain the low occurrence of heterosis in the populations tested, since the greater the deviations of the loci in homozygosis, the greater the effects of heterosis, which has not been overly

demonstrated. Although the deviation of the heterozygotes (0.2937) is higher than that of the homozygotes (0.0150), the excess of [h] over [d] may be merely due to the fact that more d 's of the various genes are canceled, compared to their h 's.

However, if the heterosis genetic model does not (fully) explain the behavior of the root distribution between Andean and Middle American populations, in contrast, inbreeding may be the most adequate response. For such, a model of inbreeding was proposed, based on the BAF07 x IPR Uirapuru population (combination within the Middle American gene group) (Table 7). The inbreeding model $y = 0.6573 + 0.0192d + 0.0135h$ makes it clear that the

Table 4: Effect of heterosis for root distribution of direct (above diagonal) and reciprocal (below diagonal) progenies in relation to the mean of the parents. Estimates obtained for 28 F1 populations from crosses between and within Middle American (1-BAF07, 2-BAF35 and 3-IPR Uirapuru) and Andean (4-BAF53, 5-CBS14 and 6-BRS Embaixador) groups. Positive values indicate superiority of the progenies in relation to the parents.

$\begin{smallmatrix} \sigma \\ \varphi \end{smallmatrix}$	1	2	3	4	5	6
1	-	-	-0.0206	0.5033*	0.2050*	0.0387
2	-	-	-0.0494	0.0672	-0.1824	0.1580
3	-0.1266	0.0477	-	-0.1374	0.0459	0.1172
4	-0.0402	0.0460	0.1736	-	0.1080	0.0094
5	0.0293	-0.0269	-0.1630	0.1080	-	0.1868
6	0.1572	0.0172	0.1732	0.1928	0.0756	-

*Significant at 5% error probability by the t test. $H_0: \mu_1 - \mu_2 = 0$. $H_A: \mu_1 - \mu_2 \neq 0$

Table 5: Effect of heterosis of direct (above diagonal) and reciprocal (below diagonal) progenies in relation to the mean of the parents. Estimates obtained for 28 F2 populations from crosses between and within Middle American (1-BAF07, 2-BAF35 and 3-IPR Uirapuru) and Andean (4-BAF53, 5-CBS14 and 6-BRS Embaixador) groups. Positive values indicate superiority of the progenies in relation to the parents

$\begin{smallmatrix} \sigma \\ \varphi \end{smallmatrix}$	1	2	3	4	5	6
1	-	-	0.0440	-0.2062*	-0.2521	-0.1757
2	-	-	-0.1108	0.0120	-0.1060	0.0735
3	0.1030	0.0217	-	0.2106*	0.1654	0.1128
4	-0.0846	-0.1508	0.0885	-	0.0380	-0.0527
5	-0.0113	-0.0952	0.0660	0.1343	-	0.0688
6	0.0346	-0.0993	-0.0174	-0.0154	-0.0113	-

*Significant at 5% error probability by the t test. $H_0: \mu_1 - \mu_2 = 0$. $H_A: \mu_1 - \mu_2 \neq 0$.

Table 6: Test of the heterosis model $y = 0.6142 + 0.0150d + 0.2937h$ for the populations P_1 , P_2 , F_1 and F_2 of the BAF07 x BAF53 crossing, considering the parameters m -mean, d - deviation of homozigotes and h - deviation of heterozygotes

Sources of variation	DF	SS	MS	F	P > F
Model	1	0.1028	0.1028	41.15	0.0001
Desviation	2	0.0040	0.0020	0.80	0.4551
Experimental residue	47	0.1175	0.0025		

contribution of the loci in homozygosis is similar to the contribution of the loci in heterozygosis. Therefore, their effects are nullified. Then, no contrasting effects between progenies and parents are observed. The effects of inbreeding can be expected, given the common ancestry of the parents, especially when within the same gene group.

DISCUSSION

The analysis of genetic parameters of a quantitative trait is strong when many genotypes are considered. In addition, the experimental precision with incomplete block designs and the comparison between the treatments performed in this study can explain numerous hypotheses involving genetic parameters.

Genetic variation is fundamental for the selection of superior individuals.^(1,18) In the case of root distribution, possible variants were found among the 64 evaluated populations (Table 2). In terms of breeding, other studies have also found significant differences in root distribution between bean accessions, cultivars and mutant populations⁽¹⁹⁾; differences between bean strains with different growth habits were also detected⁽²⁰⁾. In the presence of genetic differences, the study on genetic parameters can be effective, since they help in the choice of the appropriate selection method⁽⁹⁾.

Five genetic parameters were estimated for the trait under study (phenotypic variance, genetic variance, environmental variance, broad sense heritability and average degree of dominance). All the parameters presented high values when the progeny BAF07 x BAF53 was involved (Table 3), compared to the others, mainly for the parameters of genetic variance (0.0126), heritability (74.10) and average degree of dominance (20.51). Heritability is an important tool in breeding programs because it allows estimating how much the phenotypic variation of the trait resulted from genetic effects, as well as the expected genetic gains and the genetic values of individuals from a certain population⁽¹⁰⁾. In other words, additivity is the predominant inheritance of the trait root distribution⁽⁸⁾.

Regarding the average degree of dominance, the results indicated that the progeny BAF07 x BAF53 presents non-additive allelic interactions. The average degree of dominance can be defined as the relative position of the heterozygote in relation to the mean of the homozygotes, about the type of interaction between the alleles (absence of dominance)⁽⁹⁾. Together, these results indicate that the hybridization between genotypes from different gene pools may increase the use of available genetic variability, which has already been observed in other species, including maize⁽¹¹⁾.

In contrast, estimates of the progenies of the same gene group showed high genetic similarity (Table 3). The likely common ancestry for the two gene groups is reported worldwide, and the Andean group originated from few individuals belonging to the Middle American group^(21,22). In Brazil, the lack of studies on the origin of the genotypes and information about commercial cultivars makes it difficult to determine which types of beans were introduced, besides when, where and which human groups brought the cultivation of the species⁽²³⁾. Therefore, it is difficult to affirm or disprove that common genotypes were used during the development of commercial genotypes.

Inbreeding, or the likelihood of two randomly taken alleles, in a single locus, to be identical by descent, limits the possibility of new gene combinations in their offspring. The narrow genetic base and self-fertilization processes produce gene blocks that reduce the potential for recombination in offspring⁽²⁴⁾. Studies estimating recombination rates in Arabidopsis reported that the absence of differences between homologous chromosomes reduced the recombination rate potential⁽²⁵⁾. Likewise, the scant evidence about the difference between parents and progenies suggests the occurrence of additive gene activity for the trait root distribution.

Evidence of heterosis expression was only detected in progenies resulting from parents between gene pools (Table 4). In the selection of the parents for the composition of the crossing blocks, those presenting different agronomic

Table 7: Test of the inbreeding model $y = 0.6573 + 0.0192d + 0.0135h$ for the populations P_1 , P_2 , F_1 and F_2 of the BAF07 x IPR Uirapuru crossing, considering the parameters m -mean, d - deviation of homozygotes and h - deviation of heterozygotes

Sources of variation	DF	SS	MS	F	P > F
Model	1	0.0082	0.0082	3.2855	0.0763
Deviation	2	0.0002	0.0001	0.0522	0.9491
Experimental residue	47	0.1175	0.0025		

traits were chosen from the two existing bean gene groups, Middle American and Andean cultures. As stated by Shull in 1908, heterosis is regarded as the superiority of F_1 hybrid progenies over the mean of their parents. This phenomenon is proportional to the genetic dissimilarity among the parents used in the directed hybridization. This fact was actually verified in only 7% of the comparisons between offspring and parents (between gene pools). The suggested heterosis model explains the variation observed only for the BAF07 x BAF53 population. As exemplified by the BAF07 x Uirapuru progeny, an inbreeding model seems to clarify the root distribution behavior (Table 7).

The traits of agronomic interest since the beginning of the domestication process have undergone intense selection in constant search for individuals that provide superior products. The introduction of breeding programs intensified the targeted selection processes by promoting changes that impacted the crops, especially for grain yield and its primary components⁽²⁶⁾. In addition, the development of cultivars generally occurred in environments favorable for the development of plants (high amount of nutrients and water ad libitum). These conditions do not favor root growth, since these nutrients are available in the most superficial layer of the soil. In other words, there is a negative correlation between shoot growth and root growth. Thus, the selection pressure exerted on the aerial part of the bean may have reduced the genetic variability of the root. Besides, the two centers of domestication represent incipient species, and as such, each has evolved with their own coadapted complex of genes. When one crosses between centers, these coadapted complexes are broken up and the result is usually inferior progeny.

Insufficient evidence of significant differences between parents and offspring actually resulted in negative heterosis (Tables 4, 5), and only one case of superior performance for the parent was detected (Table 5). Gene interactions may be the genetic explanation for this phenomenon. Gene expression is given by the production of a certain protein, which results in the expression of the phenotype. When a change in the genetic constitution is detected, the protein produced and its function may change or not. In the heterozygous condition, the genes in activity in the root distribution expression can be masked by other genes, which hinders root growth - also known as epistasis⁽²⁷⁾, which has already been observed in *Arabidopsis thaliana*^(28,29). Evidence of epistatic interactions was found for grain yield and its primary components in beans^(27,30,31). In these studies, prog-

enies from bean crosses between gene pools were inferior to their parents.

Considering the common ancestry, the narrow genotype base used in breeding programs and the selection pressure exerted on shoot traits, the formation of gene blocks is one of the hypotheses for the absence of heterosis. One of the solutions to increase the genetic base for the trait root distribution is the adoption of cycles of recurrent crosses, besides the breaking of gene blocks to obtain a more comprehensive gene recombination. Recurrent selection cycles, together with the selection of the parents, seek to increase the frequencies of desirable alleles for quantitative traits, which results in phenotypic classes with superior performance for the specific trait. Genetic gains have already been obtained for bean culture through recurrent selection for agronomic traits and resistance to diseases^(32,33).

The results obtained in this study for the first segregant population (F_2) are in agreement with the findings for other progenies studied in complete diallel, also involving the parents BAF07 and IPR Uirapuru⁽⁷⁾. These authors verified the presence of heterosis for most F_2 progenies, but the most common occurrences involved highly contrasting genotypes. Further studies have revealed the superiority of F_2 and F_3 progenies, but it was observed in the occurrence of increased contribution of additive genes throughout the segregating generations⁽⁸⁾. Thus, to obtain satisfactory gains in root breeding and displace the mean of this trait, it will be necessary to promote hybridization between more contrasting parents.

CONCLUSIONS

Crosses between Middle American and Andean gene groups revealed significant estimates for genetic parameters (genetic variance, heritability, and average degree of dominance) compared to intra-pool crosses. The joining of alleles with identical provenance may be the main cause of the observed effects. The breeding strategy for root distribution should consider more divergent parents.

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REFERENCES

1. Ceccarelli S. Efficiency of Plant Breeding. *Crop Sci.* 2015;55(1):87–97.
2. Fess TL, Kotcon JB, Benedito VA. Crop breeding for low input agriculture: A sustainable response to feed a growing world population. *Sustainability.* 2011;3(10):1742–1772.
3. Bishopp A, Lynch JP. The hidden half of crop yields. *Nat Plants.* 2015;1:15117.
4. Topp CN, Bray AL, Ellis NA, Liu Z. How can we harness quantitative genetic variation in crop root systems for agricultural improvement? *J Integr Plant Biol.* 2016;58(3):213–225.
5. Slovak R, Ogura T, Satbhai SB, Ristova D, Busch W. Genetic control of root growth: From genes to networks. *Ann Bot.* 2016;117(1):9–24.
6. Yu P, Gutjahr C, Li C, Hochholdinger F. Genetic control of lateral root formation in cereals. *Trends Plant Sci.* 2016;21(11):951–961.
7. Toaldo D, de Moraes PP, Battilana J, Coimbra JL, Guidolin AF. Selection in early generations and the occurrence of heterosis for the character root distribution. *Euphytica.* 2013;190(1):335–344.
8. de Melo RC, Schmit R, Cerutti PH, Guidolin AF, Coimbra JL. Genetic variation in the trait root distribution over segregating generations of common bean. *Euphytica.* 2016;207(1):665–674.
9. Thompson R, Brotherstone S, White IM. Estimation of quantitative genetic parameters. *Philos Trans R Soc Lond B Biol Sci.* 2005;360(1459):1469–77.
10. Hill WG. Understanding and using quantitative genetic variation. *Philos Trans R Soc Lond B Biol Sci.* 2010;365(1537):73–85.
11. Rovaris SR, de Oliveira AL, Sawazaki E, Galo PB, Ayres ME, Paterniani GZ. Genetic parameter estimates and identification of superior white maize populations. *Acta Sci Agron.* 2017;39(2):157–164.
12. González AM, Rodiño AP, Santalla M, De Ron AM. Genetics of intra-gene pool and inter-gene pool hybridization for seed traits in common bean (*Phaseolus vulgaris* L.) germplasm from Europe. *Field Crops Res.* 2009;112(1):66–76.
13. Zeinab EG, Helal AG. Diallel analysis and separation of genetic variance components in eight faba bean genotypes. *Ann Agric Sci.* 2014;59(1):147–154.
14. Bárbaro IM, Di Mauro AO, Centurion MA, Machado PC, Junior LS. Análises genéticas em populações de soja resistentes ao cancro da haste e destinadas para áreas canavieiras. *Colloquium Agrariae.* 2011;5(1):8–24.
15. Vieira C. O feijão comum. Cultura, doenças e melhoramento. Viçosa: Imprensa Universitária da UFV; 1967.
16. Bohm W. Methods of studying root systems. v. 33. Berlin: Springer-Verlag; 1979.
17. Steel RGD, Torrie JH, Dickey DA. Principles and procedures of statistics: a biometrical approach. 3. ed. New York: McGraw-Hill, 1997.
18. Brummer EC, Barber WT, Collier SM, Cox TS, Johnson R, Murray SC, et al. Plant breeding for harmony between agriculture and the environment. *Front Ecol Environ.* 2011;9(10):561–568.
19. da Rocha F, Coan MM, Coimbra JL, Bertoldo JG, Guidolin AF, Kopp MM. Root distribution in common bean populations used in breeding programs. *Crop Breed Appl Biotechnol.* 2010;10(1):40–47.
20. Velho LP, de Melo RC, Bernardy JP, Grigolo S, Guidolin AF, Coimbra JL. Root distribution and its association with bean growth habit. *Ana Acad Bras Ciências.* 2018;90(2):1837–1844.
21. Bitocchi E, Nanni L, Bellucci E, Rossi M, Giardini A, Zeuli PS, et al. Mesoamerican origin of the common bean (*Phaseolus vulgaris* L.) is revealed by sequence data. *Proc Natl Acad Sci USA.* 2012;109(14):E788–E796.
22. Schmutz J, McClean PE, Mamidi S, Wu GA, Cannon SB, Grimwood J, et al. A reference genome for common bean and genome-wide analysis of dual domestications. *Nat Genet.* 2014;46(7):707–713.
23. Freitas FD. Evidências genético-arqueológicas sobre a origem do feijão comum no Brasil. *Pesq Agropec Bras.* 2006;41(7):1199–1203.
24. Canci PC, Barbosa JF Neto, Carvalho FI. Implementação da seleção recorrente no melhoramento de plantas autógamas através da macho-esterilidade. *Ciênc Rural.* 1997;27(3):505–512.
25. Salomé PA, Bomblies K, Fitz J, Laitinen RA, Warthmann N, Yant L. The recombination landscape in *Arabidopsis thaliana* F2 populations. *Heredity (Edinb).* 2012;108(4):447–455.
26. Bertoldo JG, Paz R, Favreto R. Consequências da domesticação em feijão-comum para o melhoramento de plantas. *Pesq Agropec Gaúcha.* 2012;18(1):17–23.
27. Borel JC, Ramalho MA, Abreu AF. Epistasis in intra- and inter-gene pool crosses of the common bean. *Genet Mol Res.* 2016;15(1):15017573.
28. Gärtner T, Steinfath M, Andorf S, Lisec J, Meyer RC, Altmann T, et al. Improved heterosis prediction by combining information on DNA- and metabolic markers. *PLoS One.* 2009;4:e5220.
29. Fiévet JB, Dillmann C, de Vienne D. Systemic properties of metabolic networks lead to an epistasis-based model for heterosis. *Theor Appl Genet.* 2010;120(2):463–473.
30. Johnson WC, Gepts P. The role of epistasis in controlling seed yield and other agronomic traits in an Andean x Mesoamerican cross of common bean (*Phaseolus vulgaris* L.). *Euphytica.* 2002;125(1):69–79.
31. Moreto AL, Ramalho MA, Bruzi AT. Epistasis in an Andean x Mesoamerican cross of common bean. *Euphytica.* 2012;186(1):755–760.
32. Amaro GB, Abreu AD, Ramalho MA, Silva FB. Phenotypic recurrent selection in the common bean (*Phaseolus vulgaris* L.) with carioca-type grains for resistance to the fungi *Phaeoisariopsis griseola*. *Genet Mol Biol.* 2007;30(3):584–588.
33. Leite ME, de Figueiredo IC, Dias JA, Alves FC, dos Santos JB. Reaction of common bean lines derived from recurrent selection for white mold resistance and aggressiveness of *Sclerotinia sclerotiorum* isolates. *Bioscience J.* 2017;33(5):1177–1187.