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Heterosis for the root distribution trait in common bean

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ABSTRACT. Heterosis has been one of the most studied phenomena since genetic studies were conceived. Knowledge of this phenomenon for the root distribution trait in beans (*Phaseolus vulgaris* L.) can favour the development of genotypes that are more tolerant to abiotic stresses. This study aimed to verify the occurrence of heterosis for the root distribution trait in hybrid F₁ populations of common bean derived from crosses within and between gene groups. Thirty-six populations (six parents and 30 hybrids) were evaluated under field conditions in the agricultural years 2016/17 and 2017/18. The root distribution was assessed with the adapted Bohm method. The genotypes responded similarly to environmental changes (absence of an interaction). However, the root distribution differed significantly between the agricultural years. Comparisons between the mean of hybrids from crosses within each gene pool and the mean of parents did not reveal heterosis. The comparisons between gene groups showed significant differences only between BRS Embaixador x IPR Uirapuru, CBS 14 x IPR Uirapuru, and BAF 53 x IPR Uirapuru and the mean of parents. The absence of heterosis in the root trait can be explained by the degree of kinship between the gene groups, as well as some epistatic interactions.

Keywords: *Phaseolus vulgaris* L.; hybrid vigor; gene pools; genetic hypotheses.

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Introduction

Common bean (*Phaseolus vulgaris* L.) is extremely sensitive to adverse environmental conditions (Reynolds-Henne et al., 2010; Seidel, Rachmilevitch, Schutze, & Lazarovitch, 2016). To mitigate the unpredictability of such uncontrolled factors, plant breeding programmes must obtain full knowledge of genotypes, including their root system (Topp, Bray, Elis, & Liu, 2016). Despite the crucial role of roots in tolerating the main abiotic stresses, the selection of this trait, mainly under field conditions, has not been routinely performed in plant breeding programmes. Due to this lack of selection, combined with labourious phenotyping, little is known about the genetic mechanisms involved in the expression of this trait.

Heterosis has been one of the most studied phenomena since genetic studies were conceived (Khotyleva, Kilchevsky, & Shapturenko, 2017). The subject has been addressed in publications for more than 100 years, and early studies (East & Hayes, 1912; East, 1936; Shull, 1908) provided the basis for the creation of hybrids, not only in maize but also in other valuable crops. Compared to allogamous species, heterosis in autogamous plants is rarely explored due to the high cost of hybrid seed production on a commercial scale, which is the case for common bean. However, in a breeding programme, hybrid vigor must be assessed for the selection of superior genetic constitutions. Thus, heterosis can be used to promote the selection of genotypes with a greater root distribution.

Three theoretical models have been proposed to explain heterosis, namely, the dominance hypothesis, the overdominance hypothesis and the epistasis hypothesis (Birchler, Yao, Chudalayandi, Vaiman, & Veitia, 2010; Chen, 2013; Schnable & Springer, 2013). Generally, the greater the distance between the parents, the greater the chance of heterosis (East & Hayes, 1912). Crosses between distinct gene pools may increase the effects of this phenomenon.

In the case of beans, there are two main centres of domestication, which gave rise to the so-called Andean and Mesoamerican gene groups (Freitas, 2006; Gioia et al., 2013; Koenig & Gepts, 1989). These two groups present high genetic variability for several traits. However, the effects of hybridization within and between gene groups on heterosis for the root distribution remain unknown. Therefore, the present work

aimed to verify the occurrence of heterosis for the root distribution trait in F_1 populations of common bean derived from crosses within and between gene groups.

Material and methods

Determination of the genetic constitutions and description of the experiment

Six genotypes of beans were selected for the development of artificial hybrids. Three of them belonged to the Mesoamerican group, and the other three belonged to the Andean group. Table 1 provides a description of the gene group, colour, type of growth habit, and origin of the seeds of the genotypes.

Table 1. Description of the parents used to obtain F_1 hybrids in beans.

Genotype	Gene group	Colour	Type†	Origin
BAF 07	Mesoamerican	Black	III	Accessions CAV/UDESC
BAF 35	Mesoamerican	Carioca	III	Accessions CAV/UDESC
IPR Uirapuru	Mesoamerican	Black	II	Cultivar
BAF 53	Andean	Colour (beige)	I	Accessions CAV/UDESC
CBS 14	Andean	Colour (white)	I	Accessions UFSC
BRS Embaixador	Andean	Colour (red)	I	Cultivar

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

The six parents were hybridized in a complete diallel scheme with their reciprocals. The procedure was performed in a greenhouse in June 2016, under controlled temperature and humidity. Five-litre plastic containers filled with ready-to-use substrate containing peat, vermiculite, limestone, gypsum, and NPK fertilizer were used. Due to the differences in cycles among the genotypes, the seeds of the genotypes were sown on different dates so that flowering would occur on the same day and crosses could be performed.

After the hybrid seeds (F_1) were obtained, the experiment began under field conditions in Nov. of the 2016/17 crop year and Oct. of the 2017/18 crop year. The experiment was conducted in Lages, Santa Catarina State, Brazil (27°48' S and 50°19' W). The area is located at an altitude of 950 m, with a temperate climate (cfb) (moist mesothermic and mild summer) according to Köppen and soil classified as a Udepts Humudepts Inceptisol with a moderate A horizon, clayey texture, and wavy relief.

The six parental and 30 hybrid populations (36 populations) were evaluated using a completely randomized experimental design with two replicates. The plots were composed of four lines four metres in length with 0.45 m spacing between them. A 0.90 m spacing between the experimental units was used to enable assessment of the root distribution.

Because it is unfeasible to produce large-scale hybrid bean seeds for assessment under field conditions, the respective maternal parent of the cross (A) was sown on the inner lines of the evaluation plots of F_1 (A x B) hybrids. When the experimental unit was composed of the cultivars IPR Uirapuru and BRS Embaixador and the accessions BAF 07, BAF 35, BAF 53, and CBS 14 (parents), the four lines were composed of the same seeds, with differences only in seed density between the inner and outer lines. The outer lines of each experimental unit were sown with a spacing of 0.50 m between the seeds, totalling eight seeds per line. In the inner lines of each experimental unit, a seeding density of 12 seeds per linear metre was used.

Following the establishment of the experiment, when the plants were in full bloom (stage R6 of the International Center for Tropical Agriculture - CIAT scale), a plant from each outer line was randomly selected for root distribution analysis. For the selected plants, profiles perpendicular to the sowing line on the outside were opened, 0.05 m away from the plants, and the roots were exposed with pointed stems, according to the method adapted from Bohm (1979). In the open profile, with roots properly exposed, a rectangle measuring 0.50 m in width, 0.30 m in height, and subdivided into 0.05 m grid cells (for a total of 60 squares) was placed. Using a photographic camera positioned at an average distance of 0.60 m from the grid, the profile was photographed for later evaluation. The root distribution in each square were determined in the binary system (presence – 1 or absence – 0) by digital photography.

Statistical analysis

All analyses were performed using the GLM procedure in Statistical Analysis System [SAS] (Cary, NC: SAS Institute Inc.). The data obtained were evaluated according to the following statistical model:

$$y_{ijk} = \mu + population_i + year_j + population * year_{ij} + \varepsilon_{ijk}$$

where: y_{ijk} refers to the observation obtained for the root distribution trait; μ is the effect of the general mean; $population_i$ is the effect of the i -th population; $year_j$ is the effect of the j -th year; $population * year_{ij}$ is the effect of the interaction between the level of the i -th population and the level of the j -th year; and ε_{ijk} is the residual effect.

Comparisons of interest were performed using the univariate contrast technique to quantify the effects of heterosis. Heterosis was determined by the difference between the mean of the F_1 population minus the mean of the respective parents, using the following formula:

$$h = F_1 - \left(\frac{P_1 + P_2}{2} \right)$$

The following comparisons were performed for the direct and reciprocal crosses: a) F_1 hybrids vs the mean of the parents involved in the hybridization within the gene groups and b) F_1 hybrids vs the mean of the parents involved in the hybridization between the gene groups.

Results and discussion

The joint analysis of variance revealed no significant differences between the studied populations. In addition, it was evident that the root distribution was significantly affected by year (Table 2). However, the population x year interaction was not significant. This result agrees with the results found by Velho et al. (2018), who reported no interaction between the years and genotypes evaluated for the root distribution trait. The evaluated populations probably responded similarly to changes in the environment and revealed the same root distribution pattern in both years (2016/17 and 2017/18). There were no changes in their classification because both the parents and their F_1 progenies generally exhibited lower means for the root distribution in 2016/17 than in 2017/18.

Table 2. Analysis of joint variance and its respective degrees of freedom corresponding to the root distribution trait.

Source of variation	Degrees of freedom	Mean square	Pr > F
Population	32	0.0095	0.2222
Year	1	2.5176	< 0.0001
Population*year	31	0.0110	0.1101
Residual	62	0.0076	
Total	126		

Although the analysis of variance did not reveal significant differences between the populations, it is important to investigate the means in detail, since analysis of variance is an overall analysis of variation and its region of inference is not always the same as that of a means test (Cardellino & Siewerdt, 1992). Thus, since plant breeders are usually interested in specific combinations, every effort to separate genetic variation from random variation is important. Thus, comparisons were carried out through contrasts between and within gene groups for each agricultural year.

In the Mesoamerican gene group, when the accessions BAF 07 and BAF 35 and the cultivar IPR Uirapuru were hybridized, the resulting progenies were not significantly different from their parents. This result was verified for all genetic constitutions in both agricultural years (Table 3). Similarly, the results can be expanded to crosses between the parents belonging to the Andean gene group (accessions BAF 53 and CBS 14 and cultivar BRS Embaixador). Hybridization within each gene pool did not cause heterosis.

The genetic basis of heterosis has been explained mainly by theories of dominance and overdominance, in which the presence of divergent alleles at the same locus resulting from hybridization between contrasting parents can lead to heterosis. The dominance theory was proposed by Bruce (1910), Davenport (1908), and Keeble and Pellew (1910). These authors sought to explain heterosis by the complementary action of the superior dominant alleles of both parents. Concurrently, East (1908) and Shull (1908) proposed the overdominance theory to explain heterosis. The overdominance theory was proposed based on the heterozygous condition of the loci that control the trait. The presence of contrasting alleles at each locus triggers the activation of biochemical routes that, when associated, allow better performance than that displayed by individuals with a single type of allele at each locus.

Table 3. Estimates of heterosis for the root distribution trait between hybrids and the mean of their respective parents within each gene group. Comparisons were conducted for two agricultural years (2016/17 and 2017/18).

Gene group	Hybrid combination†	2016/17	2017/18
Mesoamerican	BAF 07 x IPR Uirapuru	-0.0292	0.0125
	BAF 35 x BAF 07	0.0833	0.0938
	BAF 35 x IPR Uirapuru	0.1291	0.0500
	IPR Uirapuru x BAF 07	0.0209	-0.0002
	IPR Uirapuru x BAF 35	0.0792	-0.0291
Andean	CBS 14 x BAF 53	0.0167	-0.0229
	CBS 14 x BRS Embaixador	0.0834	-0.1520
	BAF 53 x CBS 14	0.0584	0.0189
	BAF 53 x BRS Embaixador	-0.0082	-0.0625
	BRS Embaixador x CBS 14	0.0166	-0.0229
	BRS Embaixador x BAF 53	-0.3320	-0.1083

† The hybrid combination was compared to the respective parents.

In early studies on the heterosis phenomenon, East and Hayes (1912) reported that the "amount of heterosis" expressed in an F_1 plant was approximately proportional to the genetic disparity between the parents used in the hybridization. This fact was confirmed by East (1936) in studies on plants of several genera, including *Capsicum*, *Fragaria*, *Linum*, *Phaseolus*, *Nicotiana*, *Oxalis*, *Solanum*, *Zea*, *Cucurbita*, and *Begonia*, provided that ontogeny was normal. Over the years, other lines of research conducted by Allard (1999), Hallauer, Carena, and Miranda Filho (1988), Smith and Lee (2016), and Zhou et al. (2012) have corroborated the previous theories and revealed a negative relationship between the level of genetic kinship and heterosis. The more alleles two inbred lines share in common, the lower the observed heterosis. Therefore, it is assumed that the genotypes do not present genetic divergence for the root distribution trait within the gene groups.

Bitocchi et al. (2012), through studies on DNA samples from different wild bean genotypes, identified the common ancestry of bean. Other studies estimated the genetic divergence for traits of agronomic interest in bean cultivars from different Brazilian locations and demonstrated the existence of specific alleles from the black group in the carioca group, which indicated kinship between these commercial groups. There may be a common genealogy between the genotypes used within each respective gene group. Under such conditions, since the hybrids did not show the expected contrasting heterozygous loci, heterosis was not observed.

With respect to the contrasts carried out between the hybrids originating from crosses between parents from the Mesoamerican vs Andean gene groups and the means of the parents, in the two agricultural years, the results observed were similar to those found within the gene groups (Table 4). Regarding the contrasts carried out between Andean and Mesoamerican parents, three significant differences were observed (10% of the contrasts). Most of the hybrids were similar to their parents for the root distribution trait and showed no heterosis. In the 2016/17 agricultural year, only the BRS Embaixador x IPR Uirapuru combination differed significantly from the mean of the parents. In contrast, in the year 2017/18, the combinations CBS 14 x IPR Uirapuru and BAF 53 x IPR Uirapuru differed significantly from the mean of the parents. Among the significant contrasts, CBS 14 x IPR Uirapuru exhibited a greater root distribution than the mean of the parents, with approximately 16% more filled squares than observed in the parents. In contrast, the hybrid BAF 53 x IPR Uirapuru presented 17% fewer filled squares than its parents (Table 4).

Similar to other autogamous species, beans show a low frequency of heterozygous loci in the population since the heterozygous loci are reduced by half in each generation of self-fertilization. Nevertheless, since this species has two main centres of domestication (the Andean and Mesoamerican regions), geographic isolation, combined with different soils, biotic and abiotic factors associated with different climatic conditions, and human intervention, led these two gene pools to develop genotypes with different traits (Schmutz et al., 2014). Under these conditions, there is a hypothesis that the divergence between the genotypes for some traits already studied may result in an increased root distribution.

In 1948, Shull published an article entitled *What is Heterosis?*, which reported that the genes of a given organism, because of their coevolution and coexistence for a long period of time, have developed metabolic processes adjusted to function effectively due to the process of natural selection. According to this theory, due to the evolution of bean genotypes from Mesoamerica and the Andes, each gene pool developed gene blocks and/or epistatic combinations that facilitated adaptation. Since the root distribution trait is controlled by several genes (Beebe et al., 2006), in addition to gene action between alleles, interactions between genes (epistasis) may affect the phenotypic expression.

Table 4. Estimates of heterosis for the root distribution trait between hybrids and their respective parents for different gene groups. Comparisons were carried out in two agricultural years (2016/17 and 2017/18).

Gene group	Hybrid combination†	2016/17	2017/18
Mesoamerican vs Andean	BAF 07 x BRS Embaixador	0.1528	-0.0542
	BAF 35 x CBS 14	-0.1666	0.1062
	BAF 35 x BAF 53	0.0292	-0.0833
	BAF 35 x BRS Embaixador	0.1125	-0.1042
	IPR Uirapuru x CBS 14	0.0665	-0.0896
	IPR Uirapuru x BAF 53	0.0751	0.0666
	IPR Uirapuru x BRS Embaixador	0.0333	-0.1041
Andean vs Mesoamerican	CBS 14 x BAF 07	-0.0138	-0.0545
	CBS 14 x BAF 35	-0.0208	0.0354
	CBS 14 x IPR Uirapuru	0.1083	0.1642*
	BAF 53 x BAF 35	0.0126	-0.0708
	BAF 53 x IPR Uirapuru	0.1084	-0.1708*
	BRS Embaixador x BAF 07	-0.1041	-0.0875
	BRS Embaixador x BAF 35	0.0125	-0.0668
	BRS Embaixador x IPR Uirapuru	0.2419*	-0.1084

* Significant at the 0.05 level of error probability. † The hybrid combination was compared to the respective parents.

When the epistatic combinations conferring adaptation of a species to its region of origin are disrupted (in the artificial hybridization process), the adaptation is lost. This loss may explain the absence of heterosis for the root distribution trait. In fact, some studies have demonstrated that epistasis may be the cause of the poor performance of segregating progenies in crosses between subgroups of the same species (for example, in the case of beans, the Andean and Mesoamerican groups). Sometimes, the performance of the population resulting from some crosses is poor compared to the mean performance of the parents (Johnson & Gepts, 2002).

Epistasis has been observed for traits evaluated in other species, such as grain yield in wheat (Singh & Singh, 1976), some agronomic traits in rice (Subbaraman & Rangasamy, 1989), and fava beans (Bakheit, El-Hifny, Eissa, & Ragheb, 2002) and yield and its components in sesame (Bakheit, Ismail, El-Shiemy, & Sedek, 2001). The positive and negative effects of epistasis on common bean crops remain controversial. Moreto, Ramalho, and Bruzi (2012) detected epistasis for all components of bean yield in hybrids between Andean and Mesoamerican gene groups. Other studies have shown that populations obtained by hybridization between gene groups - when exempt from incompatibility - present equal or inferior performance in terms of grain yield compared to their parents (Bruzi, Ramalho, & Abreu, 2007; Johnson & Gepts, 2002). This finding was corroborated by Borel, Ramalho, and Abreu (2016) for grain yield and 100-seed weight. These authors emphasized the marked effect of epistasis when Andean and Mesoamerican genotypes were used.

In the present study, two explanations involving epistasis can be given for the absence of heterosis for the root distribution trait in beans: i) among the numerous genes that control the expression of the root distribution, one or more heterozygous genes suppress the expression of other genes that could be related to an increased root distribution; and ii) a gene unrelated to the expression of the root distribution in the hybrid combination inhibits one or more genes that control the expression of the trait, as found by Chalyk (2000) for plant height and productivity in corn hybrids. Thus, the expression of heterosis is compromised since not all genes help maximize the expression of the trait.

In addition, since approximately 93% of the hybrid combinations from crosses between parents from different gene pools did not express heterosis, the discrepancy or divergence of the parents raises some questions. Schmutz et al. (2014), while studying wild bean genotypes through molecular tools, suggested that a few thousand individuals belonging to the Mesoamerican group gave rise to the wild Andean genotype. Furthermore, Rossi et al. (2009) pointed out that besides of the common ancestry of bean, genetic bottleneck effects prior to Andean group domestication may have produced equal homozygous loci between the two gene pools. In addition, the selection pressure exerted since the domestication of the species has mainly focused on the aerial part of the plant (yield and number of pods), which may have reduced variability in the root trait. This reduction may increase the similarities between the genotypes for the root distribution trait, thus increasing the degree of kinship and consequently the endogamous effect.

The absence of heterosis for the root distribution trait may be related to the number of genes and the complexity of their interactions, which are directly proportional to the difficulty in recovering new constitutions of complementary genes, as proposed by Johnson and Gepts (1999). In addition, since the trait

is quantitative, the contribution of the environment to its phenotypic value is high and may obscure the estimates of genetic parameters such as heterosis (Abreu, Ramalho, Santos, & Pereira Filho, 1990).

In conclusion, for most contrasts performed, non-significance indicated the similarity between the progenies and the mean of the parents (Tables 3 and 4). However, the occurrence of heterosis coincided with hybridization between parents from different gene groups. In addition, when subjected to different environmental conditions (different agricultural years), the hybrids were similar to their parents; in other words, the expression of heterosis did not change according to the environment. The hypotheses raised may still receive further clarification, for example, from the selection of contrasting genotypes for the root distribution for diallel schemes. Methodologies that allow the estimation of other genetic parameters involved in the expression of the trait will also be helpful.

Conclusion

The root distribution in beans does not exhibit heterosis when parents in the same gene group are involved, but combinations between distinct gene groups can lead to hybrid vigor, regardless of the environmental conditions.

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