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Homeostasis of common bean populations with different genetic structures

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ABSTRACT – Eight lines of common bean, a mixture in equal proportions (MP) and the F_2 generation of the multiple hybrids (MH) between them were analyzed to verify whether they differ in homeostasis and phenotypic plasticity. The experiments were conducted in 20 environments (seasons and locations) from November 2004 to December 2005, in Alto Paranaíba and the south of Minas Gerais state. Based on the mean yield of the environments the stability was evaluated by the ecovalence values (W_i^2). To estimate the repeatability of the stability parameters the 20 environments were separated in two groups of 10, simulating 1000 possibilities. The MH and MP were the most stable. Nevertheless, high stability was also identified in some pure lines. The repeatability of mean grain yield ($r_k^2=0.73$) was higher than W_i^2 ($r_k^2=0.18$). The chances of success of selection for the smallest contribution to the $G \times E$ interaction are small.

Key words: Individual buffering, population buffering, repeatability.

INTRODUCTION

The cultivation conditions for common bean in the state of Minas Gerais differ greatly, ranging from subsistence farmers who make practically no use of technology, to large rural entrepreneurs, who exploit all techniques available. It must be emphasized as well that common bean is presently being grown practically all year long, in three growing seasons, under very distinct climatic conditions. In these conditions the cultivar performance is not expected to coincide in the different environments, i.e., a cultivars \times environments interaction is likely.

For the recommendation of new cultivars, evaluations in the largest number of environments

possible are therefore indispensable. Moreover, it is not enough to only state the presence of interaction, but it is also necessary to identify the cultivars with greatest homeostasis, that is, with highest phenotypic plasticity under environmental variations (Allard and Bradshaw 1964). In this context, literature is full of reports on methods that allow the identification of these cultivars with greater homeostasis (Kang and Gauch Jr. 1996, Cruz et al. 2004). In the case of common bean, the recommended cultivars normally consist of a pure line. On the other hand, the cultivars used by farmers are mixtures of a large number of lines. It is known that this results in greater yield stability. Furthermore, the use of multilines has been suggested as a mechanism to establish a more durable resistance

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against different pathogens races, that is, lines with greater homeostasis over the course of time. There is little information of this kind on common bean in Brazil.

The objective of this study was to verify whether populations that consist of a single pure line, a mixture of pure lines or a population with most loci in heterozygosis differ in stability and how this information could be used in common bean improvement programs.

MATERIAL AND METHODS

The experiments were conducted in 20 environments (seasons and locations) in the period from November 2004 to December 2005, on states of farmers in the region who traditionally grow common bean and at experimental stations in the regions South and Alto Paranaíba of Minas Gerais (Table 1). Eight common bean lines were used, all carioca grain lines, to make

comparisons of the different origins in terms of improvement programs, plant type and grain size possible (Table 2). Furthermore, the lines differed in resistance alleles to pathogens, mainly of angular leaf spot (*Phaeoisariopsis griseola*) and anthracnose (*Colletotrichum lindemuthianum*). An equal proportion mixture between lines (MP) was used as well as the F₂ generation of the multiple hybrid (MH) between the pure lines.

Multiple hybrids were obtained by artificial crosses in a greenhouse, with a methodology similar to that used by Carneiro et al. (2002). Four distinct single-cross hybrids were obtained in four biparental crosses. These were crossed pairwise to generate two double cross hybrids, which were crossed again to create the multiple hybrid.

A 4 x 4 triple lattice was used to obtain higher experimental efficiency. Since there were altogether eight

Table 1. Main traits of the experimental sites of evaluation of common bean populations with different genetic structures, from November 2004 to December 2005, in Alto Paranaíba and in the south of Minas Gerais

Locations	Sowing Dates	Latitude	Longitude	Altitude (m)
LAVRAS	Nov/04, Mar/05, Jul/05	21° 14' S	44° 59' W	919
IJACI	Mar/05, Jul/05	21° 10' S	44° 75' W	832
SÃO VICENTE DE MINAS	Nov/04	21° 42' S	44° 26' W	1057
ALTEROSA	Nov/04	21° 14' S	46° 08' W	843
CANA VERDE	Nov/04, Mar/05	21° 01' S	45° 10' W	867
ALFENAS	Nov/04, Mar/05	21° 25' S	45° 56' W	881
PATOS DE MINAS	Nov/04, Mar/05, Jul/05	18° 34' S	46° 31' W	832
LAMBARI	Mar/05	21° 58' S	45° 21' W	887
IBIÁ	Jul/05	19° 28' S	46° 32' W	895

Table 2. Traits of the lines used in the experiments

Lines	Origin	Grain type ¹	Growth habit ²
(1) TALISMÃ	UFLA	Carioca	III
(2) PÉROLA	EMBRAPA	Carioca	II/III
(3) CARIOCA-MG	UFLA	Carioca	II
(4) MAGNÍFICO	FT	Carioca	II/III
(5) ESAL 693	UFLA	Carioca	I
(6) IAPAR 81	IAPAR	Carioca	II
(7) OP-S-16	UFLA	Carioca	II/III
(8) MA-I-25	UFLA	Carioca	II/III

¹ Cream-colored grains with brown stripes. ² I- determinate growth habit type I; II- indeterminate growth habit type II; III- indeterminate growth habit type III;

lines, the mixture between the lines and the multiple hybrid, the populations MH and MP were artificially replicated in four different treatments (totalizing 16) to improve the experimental planning and reliability. This separation was undone for the analyses. Plots consisted of two rows of four meters, along which 15 seeds per meter were sown.

For the individual analyses per environments based on grain yield (kg ha⁻¹) as well as the joint analysis involving all environments we used SAS software, proc GLM (SAS 2000). The population's means were compared by the test of Scott & Knott (1974). The contribution of each population to the genotype-by-

environment interaction was obtained by the ecovalence values (W_i^2) by the following expression:

$W_i^2 = \sum (Y_{ij} - \bar{Y}_i - \bar{Y}_j + \bar{Y}_{..})^2$ where: Y_{ij} measurement of population i in environment j , \bar{Y}_i : mean of population i , \bar{Y}_j : mean of environment j and $\bar{Y}_{..}$: overall mean (Wricke and Weber 1986).

The homogeneity of the ecovalence of the populations was compared using the ratio of the pairwise variances by the expression $H = \frac{W_i^2}{W_i'^2}$ where: H : ratio of the variances of the contribution to the interaction, W_i^2 : sum of squares of the contribution to the interaction of population i , $W_i'^2$: sum of squares of the contribution to the interaction of population i . It is worth mentioning that in spite of using sums of squares, this procedure is equivalent to the ratio of the variances, since the degrees of freedom are the same in the numerator and denominator.

The risk of adoption of the populations was estimated by the method Annicchiarico (1992). For this method, the means of each population were transformed into percentages of environmental means. Then the standard deviation (s_i) of the percentages of each population was estimated. The reliability index (I_i) was estimated by the expression $I_i = Y_i - Z_{(1-\alpha)} \cdot s_i$. Where $Z_{(1-\alpha)}$ is the value in the normal standardized distribution, and α a level of pre-fixed significance ($P \leq 0.25$).

To estimate the repeatability of the stability parameters the 20 environments were separated in two groups of 10. Due to the high number of possibilities 1000 situations were simulated with the combinations of these environments. The means (m) and the contribution of the populations to the interaction ($W_i^2\%$) were estimated for each simulation. These estimates obtained by simulation were subjected to analysis of variance. Based on the E (MS) the repeatability of k simulations (r_k^2) of $W_i^2\%$ and of m was estimated, in a procedure similar to the one proposed by Corte et al. (2001).

RESULTS AND DISCUSSION

A coefficient of variation (CV) of 18.7% was stated in the joint analysis involving the 20 environments. Considering that most experiments were conducted on farms, under difficult experimental conditions and

without irrigation, it may be concluded that the experimental precision was good. The CV estimate was of similar magnitude to that obtained with common bean in the region, in conditions of an experimental station (Marques Júnior et al. 1999). The source of population variation was highly significant (Table 3). The yield mean varied from 1557 kg ha⁻¹ (Magnífico) to 1947 kg ha⁻¹ (OP-S-16) (Table 4). This latter line was derived in the genetic improvement program of common bean of the UFLA from a cross between two well-adapted cultivars, 'Pérola' and 'Ouro Negro' with a good resistance level to common bean angular leaf spot, *Phaeoisariopsis griseola*, and anthracnose, *Colletotrichum lindemuthianum*. This must have contributed to the good yield performance. It is worth

Table 3. Summary of the joint analysis of variance for grain yield (kg ha⁻¹) obtained in the evaluation of common bean populations with different genetic structures between November 2004 and December 2005

Sources of variation	df	MS
Populations (P)	9	798342.03**
Enviroments (E)	19	21426625.81**
P x E	171 (92) ¹	238153.85**
Error	540 (284) ¹	108664.90
CV (%)		18.70
Mean		1759

** Significant by the F test at 1% probability ($P \leq 0.01$).

¹ Values adjusted by the method of Cochran (1954) due to the heterogeneity of the residual MS.

Table 4. Estimate of the Reliability index (RI %) and mean yield (kg ha⁻¹) of common bean populations with different genetic structures

Populations	RI (%)	Mean Yield
PÉROLA	90.16	1756 b ¹
IAPAR 81	76.34	1672 d
ESAL 693	83.00	1604 d
MA-I-25	90.89	1826 b
TALISMÃ	84.87	1705 c
CARIOCA-MG	81.85	1703 c
OP-S-16	103.70	1947 a
MAGNÍFICO	66.36	1557 d
MH	98.00	1840 b
MP	91.13	1754 b

¹ Means followed by the same letter belong to the same group by the test of Scott and Knott (1974) at 5% probability

mentioning that the yield means of MH and MP were also good.

The existence of variation among the populations together with the significant environmental effect were the main cause of the highly significant populations x environments interaction ($P \leq 0.01$). The sum of squares (SS) attributed to interaction was 5.75 times higher than SS owing to the source of population variation (Table 3). This evidenced that the population performance did not coincide in the evaluation of the 20 distinct environments. This result agrees with those of Corte et al. (2001) and Pirola et al. (2002), in experiments conducted with common bean in different environments.

It was observed that population MP and MH contributed less to the interaction (Tables 5 and 6). In the literature there are some studies that stated that heterogeneous populations or populations with most loci in heterozygosity were more stable (Patanothai and Atkins 1974, Schnell and Becker 1986, Corte et al. 2001, Hausmann et al. 2001, Helland and Holland 2001). These results support the theory of genetic homeostasis proposed by Allard and Bradshaw (1964) which says that genotypes with most loci in heterozygosity and/or populations represented by a mixture of genotypes are more stable since they have individual and population buffering, that is, individual and population homeostasis, respectively.

But some of the cultivars that consist of pure lines such as 'Pérola', 'ESAL 693', 'MA-I-25' and 'Carioca-

MG' contributed equally to the interaction as the two above-cited populations (Table 5). Becker and León (1988), Corte et al. (2001) and Hausmann et al. (2001) made the same observation: that it is possible to identify lines that are as stable as the heterogeneous populations and/or populations with most loci in heterozygosity.

A criterion apart from mean yield breeders can use when recommending cultivars is the estimate of the risk of the choice of a particular cultivar (Annicchiarico 1992). Note that line OP-S-16 presented the lowest risk, since at worst the yield would exceed the overall mean of the environment by 3%. It is also noteworthy that the populations MH and MP presented low risks as well (Table 4).

The use of hybrid cultivars in common bean can therefore be indicated as a valuable strategy, in view of the possibility of high stability associated to good yield mean. Nevertheless, the great difficulty to obtain hybrid seed of common bean must be stressed, once the crosses are made by hand, which possibly impedes large-scale seed production.

In the literature there are reports on the difficulty of obtaining mixtures of lines that all have high yields, which affects the use of line mixtures. Normally, the mean of the mixture would therefore be lower than in some lines. This was the case here in the comparison of population MP and line OP-S-16. Nevertheless, the performance of the mixture was similar to some pure lines that were already recommended for cultivation, as for example 'Pérola', and even higher superior to that of 'Talismã'.

With these results the probability for success for the use of multilines of carioca common bean cultivars in Brazil can be predicted. This is possible in view of the large number of lines available on the market with very similar color standards, which could be mixed without affecting the commercial aspect. This population, as shown above, will certainly have greater stability and, if lines with good grain yield, are involved, high means can be expected.

A frequently asked question is the possibility of selecting for greater stability. The answer depends on the heritability (h^2) of the trait. It is not easy to obtain h^2 estimates; a representative genotype sample of random effect is required, evaluated in a large number of environments. Since in most cases a previously selected group of cultivars (lines and/or populations) is used, with fixed effect, it is usually the repeatability (r_i^2) that is estimated instead.

Table 5. Estimate of the contribution of the populations to the genotypes x environments interaction (W_i^2) obtained for common bean populations with different genetic structures evaluated in the period from November 2004 to December 2005

Populations	W_i^2	W_i^2 (%)
(1) PÉROLA	2184108.48	5.36
(2) IAPAR 81	5924262.63	14.54
(3) ESAL 693	2071453.08	5.08
(4) MA-I-25	3923350.68	9.63
(5) TALISMÃ	6168802.83	15.14
(6) CARIOCA-MG	3725198.28	9.14
(7) OP-S-16	4236010.83	10.40
(8) MAGNÍFICO	6205992.03	15.23
(9) MH	2437355.88	5.98
(10) MP	3848183.28	9.44
TOTAL	40724718.07	100

Table 6. Test of homogeneity of the ecovalence value (W_i^2)

Populations	2 ¹	3	4	5	6	7	8	9	10
1 ¹	2.71*	1.05	1.79	2.82*	1.70	1.93	2.84*	1.11	1.76
2		2.85*	1.51	1.04	1.59	1.39	1.04	2.43*	1.53
3			1.89	2.97*	1.79	2.04	2.99*	1.17	1.85
4				1.57	1.05	1.07	1.58	1.60	1.01
5					1.65	1.45	1.00	2.53*	1.60
6						1.13	1.66	1.52	1.03
7							1.46	1.73	1.10
8								2.54*	1.61
9									1.57

* Significant by the F test at 10% probability.

¹ Values from Table 5

Table 7. Estimate of the repeatability (r_k^2) for adaptability and stability considering 1000 simulations of the environments separated in groups of 10

	Adaptability	Stability
Minimum	0.21	-0.43
1 st Quartile	0.54	-0.02
Intermediate	0.63	0.13
Mean	0.73	0.18
3 rd Quartile	0.72	0.29
Maximum	0.91	0.80

The results obtained for the repeatability of the ecovalence varied from -0.43 to 0.80 (mean of 0.18) (Table 7). The ecovalence value evaluates what Lin et al. (1986) classified as “type 2 or agronomic stability”, with a similar performance to the method of Plaisted and Peterson (1959). As mentioned above, the $W_i^2\%$ estimate represents the contribution of each population to the interaction. This is a measure of stability, in other words, populations with lower $W_i^2\%$ magnitudes are more stable.

For the mean estimate, measure of adaptability, the mean repeatability was 0.73 varying from 0.21 to 0.91 (Table 7). Note that these values are similar to those normally reported for the heritability estimate of the trait grain yield of common bean (Carneiro et al. 2002, Silva et al. 2004).

In some studies in the literature the repeatability of the stability parameters was estimated analogously to this research, that is, using groups of environments. The repeatability was evaluated by Spearman's rank order correlation between the estimates. Highest magnitudes were obtained for the coefficient of linear

regression, by the method of Eberhart and Russel (1966), and for mean yield. For the other parameters the estimates were low (Leon and Becker 1988, Jalaluddin and Harrinson 1993).

When the experiments have a greater number of replications - four, for example - another strategy has been used to estimate the repeatability of stability parameters, to separate the replications in groups and obtain the estimate of the stability parameter for each group. Later, the variances are analyzed with these estimates. In most of these studies the repeatability estimates for mean grain yield and stability parameters and mainly the coefficient of linear regression were considerably higher than those obtained here (Soares and Ramalho 1993, Farias et al. 1998, Corte et al. 2001). Nevertheless, one must bear in mind that a drawback of this r_i^2 estimate is that the numerator of the expression does not contain the genetic deviation only. The permanent environmental effects are included as well, which are equal in a group of replications. These effects are, i.e., precipitation, soil type and temperature, which is certainly common to all replications in the same experiment. This could be the reason for the greater magnitude of the r_i^2 estimates. Our results allow the conclusion that the probability of success for selection for mean yield and greater adaptability is higher than for the contribution of the populations to the interaction.

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REFERENCES

- Allard RW and Bradshaw AD (1964) Implications of genotype-environmental interactions in applied plant breeding. **Crop Science** **5**: 503-508.
- Annicchiarico P (1992) Cultivar adaptation and recommendation from alfalfa trials in Northern Italy. **Journal of Genetics and Breeding** **1**: 269-278.
- Becker HC and Léon J (1988) Stability analysis in plant breeding. **Plant Breeding** **1**: 1-23.
- Cruz CD, Regazzi AJ and Carneiro PCS (2004) **Modelos biométricos aplicados ao melhoramento genético**. Editora UFV, Viçosa, 480p.
- Carneiro JES, Ramalho MAP, Abreu AFB and Gonçalves FMA (2002) Breeding potential of single, double, and multiple crosses in common bean. **Crop Breeding and Applied Biotechnology** **2**: 515-524.
- Corte HR, Ramalho MAP and Abreu AFB (2001) Estabilidade de populações segregantes e respectivos genitores. **Ciência e Agrotecnologia** **4**: 900-908.
- Eberhart SA and Russel WA (1966) Stability parameters for comparing varieties. **Crop Science** **1**: 36-40.
- Farias FJC, Ramalho MAP, Carvalho LP, Moreira JAN and Cosata JN (1998) Repetibilidade dos parâmetros de estabilidade na cultura do algodoeiro herbáceo. **Pesquisa Agropecuária Brasileira** **4**: 457-461.
- Hausmann BIG, Obilana AB, Ayiecho PO, Blum A, Schipprack W and Geiger HH (2001) Yield and yield stability of four population types of grain sorghum in a semi-arid area of Kenya. **Crop Science** **40**: 319-329.
- Helland SJ and Holland JB (2001) Blend response and stability and cultivar blending ability in oat. **Crop Science** **41**: 1689-1696.
- Jalaluddin M and Harrison SA (1993) Repeatability of stability estimators for grain yield in wheat. **Crop Science** **4**: 720-725.
- Kang MS and Gauch Jr HG (1996) **Genotype-by-environment interaction**. CRC Press, New York, 416p.
- Leon J and Becker HC (1988) Repeatability of some statistical measures of phenotypic stability – Correlations between single year results and multi years results. **Plant Breeding** **2**: 137-142.
- Lin CS, Binns MR and Lefrovitch LP (1986) Stability analysis: where do we stand? **Crop Science** **5**: 894-899.
- Marques Júnior OG, Ramalho MAP and Ferreira DF (1999) Emprego do látice no programa de melhoramento do feijoeiro. **Ciência e Agrotecnologia** **3**: 753-759.
- Patanothai A and Atkins RE (1974) Yield stability of single cross and three-way hybrids of grain sorghum. **Crop Science** **2**: 287-290.
- Pirola LH, Ramalho MAP, Carneiro JES and Abreu AFB (2002) Natural selection and families x locations interaction in the common (dry) bean. **Genetics and Molecular Biology** **3**: 343-347.
- Plaisted RL and Peterson LC (1959) A technique for evaluating the ability of selections to yield consistently in different locations or seasons. **American Potato Journal** **11**: 386-389.
- SAS Institute (2000) **SAS/STAT User's Guide, Version 8**. SAS Institute, Cary.
- Silva NO, Ramalho MAP, Abreu AFB and Carneiro JES (2004) Performance of common bean families after different generations under natural selection. **Revista Brasileira de Genética** **4**: 574-578.
- Scott AJ and Knott M (1974) A cluster analysis method for grouping means in the analysis of variance. **Biometrics** **3**: 507-512.
- Schnell FW and Becker HC (1986) Yield and yield stability in a balanced system of widely differing population structures in *Zea mays* L. **Plant Breeding** **1**: 30-38.
- Soares AA and Ramalho MAP (1993) Repetibilidade do rendimento de grãos e dos parâmetros de estabilidade na cultura do arroz. **Ciência e Prática** **1**: 64-70.
- Wricke G and Weber WE (1986) **Quantitative genetics and selection in plant breeding**. Walter de Gruyter, Berlin, 406p.