

Choice of parents to obtain common bean (*Phaseolus vulgaris*) cultivars tolerant to low temperatures at the adult stage*

Leonardo Cunha Melo, João Bosco dos Santos and Magno A. Patto Ramalho

ABSTRACT

We investigated the genetic control of low temperature tolerance and the interaction among the combining abilities for locations and generations in order to improve common bean plant tolerance to low temperatures at the adult stage. In the fall/winter of 1995, a complete diallel involving the F₃ and F₄ generations obtained from direct and reciprocal crosses among 11 parents was assessed in two locations (Lavras and Lambari, Minas Gerais). Data for grain yield (kg/ha), anthracnose incidence and flowering period (Lavras) were analyzed. The genetic variance and broad sense heritability for grain yield were estimated within the segregant populations. The diallel analysis was carried out using method III, described by Griffing (*Aust. J. Biol. Sci.* 9: 463-493, 1956). The parents differed in flowering period and grain yield under low temperature conditions at the adult phase. The line Small White was the earliest; A-488, Ouro and ESAL 591 were the most cold tolerant, and CNF-05, Rio Vermelho and ESAL 501 were the most cold sensitive. Additive, dominance and reciprocal effects were observed, with the predominance of the additive. The reciprocal effect explained only a small part of the variation, in a few populations. Only additive effects of the genes were observed for the flowering period. The general combining ability (GCA) interactions indicated that the populations should be assessed in several locations and generations in order to obtain reliable estimates. The A-488 x Ouro and Esal 591 x Ouro populations were the most promising for selection.

INTRODUCTION

Common bean cultivation is carried out in Minas Gerais in three distinct periods - the wet season, the dry season and the winter. Traditionally, the same cultivars have been used in all the planting periods, resulting in reduced crop yield mainly due to the low adaptation of these cultivars to the fall and winter climatic conditions. Low temperatures can reduce common bean seed yield by seed abortion, caused mainly by failure in the male and female reproductive organs, and also cause less branch growth (Farlow 1981;

Dickson and Boettger, 1984). A more efficient exploitation of the agricultural infrastructure has become feasible with the development of low temperature tolerant cultivars at the adult stage which allows harvesting at a more convenient time, given the rainfall patterns in the region.

There is wide genetic variability in the national and introduced germplasm. It may be possible to develop cultivars tolerant to low temperatures with the recombination of this variability (Kooistra, 1971; Von Pinho, 1990; Dias *et al.*, 1992; Otubo, 1994). Diallel crossing (Ramalho *et al.*, 1993) is a technique that helps in the choice of parents based on their genetic values. It takes into account their capacity to combine in hybrids, to produce promising segregant populations. However, this technique does not provide information about the

*Part of a thesis presented by L.C.M. to the Universidade Federal de Lavras, Lavras, MG, in partial fulfillment of the requirements for the Master's degree.

Departamento de Biologia, Universidade Federal de Lavras, Caixa Postal 37, 37200-000 Lavras, MG, Brasil. Send correspondence to J.B.S.

segregant loci, which are important to determine the chances of obtaining superior performing lines (Oliveira, 1995). Thus, besides diallel analysis it is important to know the genetic variance of the populations in order to be able to predict their true individual potential.

Interaction among genotypes and environments complicates the selection and the estimation of the combining ability of the parents (Ramalho *et al.*, 1988). The assessment of the populations in several environments and generations would allow a precise estimation of these interaction effects, resulting in more reliable estimates of the combining ability and permitting the correct choice of parents.

MATERIAL AND METHODS

During the fall and winter (April to August) of 1995, a complete diallel among 11 parents was assessed using the F_3 and F_4 generations in two locations in Southern Minas Gerais State. The parents Rio Vermelho, Small White, CNF-05, A-488, Carioca, Ouro, IPA-7419, ESAL 591, ESAL 609, A-354 and ESAL 501 were chosen based on the work of Von Pinho (1990).

Eight experiments were carried out using a partially balanced triple lattice design. Four experiments, two for the F_3 and two for the F_4 generations, were set up in each location. For each generation and location, one experiment involved a seven by seven (49 treatments) lattice and another involved a nine by nine (81 treatments) lattice, totalling 130 populations (parents, direct and reciprocal crosses). Each plot was made up of two three-meter rows, spaced at 50 cm. Sowing density was 15 seeds per linear meter of row. The grain yield, number of days from sowing to 50% of the plants opening the first flower (only in Lavras) and the incidence of anthracnose (*Colletotrichum lindemuthianum*) at 90 days after sowing were obtained. The assessment for anthracnose was performed according to the following scale of notes: 1 - no symptoms; 2 - slight symptoms; 3 - slightly severe symptoms; 4 - severe symptoms; 5 - very severe symptoms.

Initially, a variance analysis assuming the mean and treatments as fixed effects was carried out for each experiment separately. A joint analysis of variance of the two lattices (9×9 and 7×7), for each location and generation, was performed. This analysis was done by weighting the mean squares of each experiment by its respective degrees of freedom. Thus, a pooled error mean square was obtained: $MSe(ag) = [(MS1 \times DF1) + (MS2 \times DF2)] / (DF1 + DF2)$.

The diallel analysis was performed in mean data following Method III proposed by Griffing (1956),

which uses the direct and reciprocal crosses. Five reciprocal crosses did not produce enough seeds for use in the experiments. The quadratic components which express the genetic variability of the material were estimated in terms of general (ϕ_g) and specific (ϕ_s) combining ability (GCA, SCA), and the reciprocal effects (ϕ_{rc}). The ratio $\phi_g / (\phi_g + \phi_s)$ was estimated to provide information on the relative importance of the GCA and SCA effects (Maris, 1989). The ratio $\phi_g / (\phi_g + \phi_s + \phi_{rc})$ was also estimated to give an idea on the relative importance of the GCA effects relative to the total genetic variation. When this ratio is higher than 0.5 the GCA effects are more important in the genetic control of the trait, but if this ratio is lower than 0.5 the SCA and the reciprocal effects are more important. The parent effect was considered fixed in the diallel analysis. The calculation of the parameters of the model and of the sums of the square of the effects was done according to Cruz and Regazzi (1994). The sum of the squares of the interactions of the genetic effects with the locations and generations was calculated according to Vencovsky and Barriga (1992).

To identify the genetic variation within each segregant population, the broad sense heritability for grain yield was estimated from 15 and 10 randomly picked plants in each plot of the segregant populations and parents, respectively. As the number of segregant populations was very large, only the populations with promising parents (Ouro, Carioca and Rio Vermelho) were chosen, without considering the reciprocals. The phenotypic variance (σ_E^2) was obtained from the mean variances of the three replications of each population. The estimate of the phenotypic variance of the parents, which are pure lines, corresponds to the environmental variance (σ_E^2). In the segregant populations, the phenotypic variation contains both the environmental and genetic variances. However, since the parents and the descendant segregant population were assessed in different plots, the variances may have different environmental effects, leading to under or over estimation of the genetic variance (σ_G^2). The environmental variance of each segregant population was calculated from the mean of the coefficients of the environmental variation of the parents, according to the following expressions:

a) Estimation of mean CV_A of the parents:

$$CV_{Ai} = \frac{\sqrt{\sigma_{Ei}^2}}{m_i}; \quad CV_{Aj} = \frac{\sqrt{\sigma_{Ej}^2}}{m_j}; \quad CV_{Aij} = \frac{CV_{Ai} + CV_{Aj}}{2}$$

where: CV_{Ai} : environmental coefficient of variation of parental i ; σ_{Ei}^2 : phenotypic variance of parent i ; m_i : average of parent i ; CV_{Aj} : environmental coefficient of

variation of parental j ; σ_{Ej}^2 : phenotypic variance of parent j ; m_j : average of parent j ; CV_{Aij} : environmental coefficient of variation of population ij .

b) Estimation of σ_E^2 of segregant population ij :

$$\sigma_{Eij}^2 = (CV_{Aij} \times m_{ij})^2$$

where: σ_{Eij}^2 : environmental variance of population ij ;
 m_{ij} : average of population ij .

c) Estimation of σ_G^2 of segregant population ij :

$$\sigma_{Gij}^2 = \sigma_{Fij}^2 - \sigma_{Eij}^2$$

where: σ_{Gij}^2 : genetic variance of population ij ; σ_{Fij}^2 : phenotypic variance of population ij .

Accordingly, the broad sense heritability was estimated by the following expression:

$$h_{Aij}^2 = \frac{\sigma_{Gij}^2}{\sigma_{Fij}^2}$$

RESULTS AND DISCUSSION

Experimental conditions

One of the most important factors in the study of the genetic control of low temperature tolerance, and consequently in the choice of parents to be used in breeding programs for fall and winter conditions, is the minimum temperature at which the populations are assessed. In this study, the temperatures may be considered sub-optimum (minimum temperature was about 11°C and the maximum 24°C). The ideal temperatures for common bean cultivation vary from 18 to 30°C (Vieira, 1967; Camargo, 1972), and the best thermoperiod schedule is about 29.5/21.0°C (day/night) (Stobe and Hombord, 1966). Both Lavras and Lambari were suitable for tolerance to low temperature assessment (Figure 1). The main difference between the two locations was the lower minimum temperature in Lambari, especially from 55 days after sowing. This difference characterized Lambari as a more stressful location for plant development, especially during the flowering and grain-filling periods.

The generation and the experimental effects are confounded in this study because the two generations were assessed in different experiments. However, the environmental difference between the experiments must have been of low magnitude, due to the physical proximity of the two experiments. Furthermore, a diallel analysis was carried out taking into account only the parents whose hybrids and reciprocals were present in one same experiment, in order to identify if the joint analysis could have influenced the results. The results were similar in either case, indicating that the differences among the experiments were very small and did not influence the results decisively. From that analysis it may also be inferred that the experimental effects probably did not significantly influence the generation effect. Another factor which may have influenced the results is the incidence of anthracnose, which showed significant differences in all the experiments. However, preventive spraying with fungicides helped reduce the incidence of the disease in the population, which on average was 1.91 (scale of incidence 1 to 5), indicating a light attack. Thus the effect of anthracnose did not mask the effect of the low temperatures.

Number of days to flowering

Low temperatures delay the life cycle, altering the flowering period. Nevertheless, the number of days to flowering found in this study (Table I) was only slightly greater than that normally observed for the common bean plant (Ramalho *et al.*, 1993). The initial temperatures were not very low (Figure 1), compared with the ideal temperature. Differences among crosses were detected in the individual and joint analyses of variance. The mean number of days to flowering of the F_3 and F_4 generations (52.14 and 51.73, respectively) were not significantly different (Table I). These results

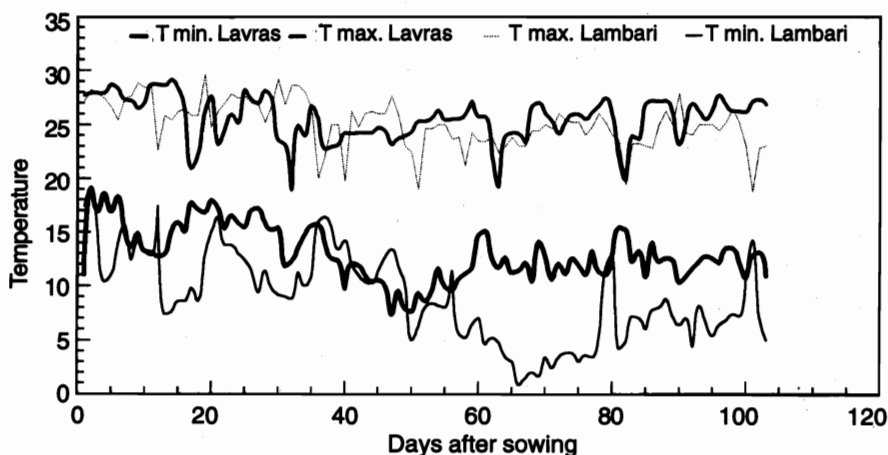


Figure 1 - Maximum (T max.) and minimum (T min.) temperatures (°C) during the trials in Lavras and Lambari in 1995.

Table I - Joint analysis of variance for number of days to flowering based on F₃ and F₄ generations evaluated in Lavras, 1995.

Source of variation (s.v.)	d.f.	Mean square (m.s.)
Replications/generations	4	4.14
Generations (G)	1	29.24
Treatments (T)	109	5.34**
GCA	10	42.44**
SCA	44	1.82
Rec.	55	1.40
T x G	109	1.66
GCA x G	10	2.57
SCA x G	44	1.46
Rec. x G	55	1.66
Error	428	1.90
Average		51.94
C.V. (%)		2.66
ϕ_g		0.36
ϕ_s		0.00
ϕ_{rc}		0.00
$\phi_g/\phi_s + \phi_{rc} + \phi_g$		1.00

**Significant at the 1% probability level based on F test.

ϕ_g = Quadratic component of GCA; ϕ_s = quadratic component of SCA; ϕ_{rc} = quadratic component of reciprocal (Rec.) effects.

are due to the significance of the GCA effects only, indicating the predominance of genes with additive action.

There are reports in the literature stating that the flowering period is controlled by few genes, with allele dominance towards earliness (Teixeira *et al.*, in press). However, there are also reports of polygenic control, either with a predominance of additive effects (White and Singh, 1991) or of dominance effects (Evans and Davis, 1978). These findings indicate that some genes must control the trait, associated with some modifiers. Depending on the parents and temperatures, the results vary. In our study, no early parent was used, and therefore, the dominant allele for earliness does not occur in the assessed populations. The differences found are probably due to modifying genes, with a predominantly additive action. The parents had very similar behaviors, but the line Small White was shown to reduce the number of days to flowering (Table II).

Grain yield

Yield is the most important trait in a bean breeding program. It is also the most complex as it depends

Table II - Estimates of general combining ability for days to flowering (GCA_i). Lavras, 1995.

Parents	GCA _i
Rio Vermelho	-0.16
Small White	-1.69
CNF-05	-0.31
A-488	0.28
Carioca	0.19
Ouro	0.13
IPA-7419	0.59
ESAL 591	0.29
ESAL 609	-0.08
A-354	0.60
ESAL 501	0.17

Days to flowering: LSD ($g_i - g_j$) = 0.37, based on *t*-test at 5% probability level.

on several other traits and several environmental factors. The populations differed for grain yield in this study, in all the experiments, indicating great variability among the populations (Table III). GCA effects were important in all the generations and locations, indicating a predominance of genes with additive action, under low temperature conditions at the adult stage. SCA was also significant, except in the F₄ generation in Lambari, and this suggests there are genes with non-additive effects in control of this trait. The reciprocal effect was significant, but less important, as it did not show consistent responses and only represented a significant part of the genetic variation in the F₄ generation in Lambari.

The joint analysis of variance (Table IV) involving the F₃ and F₄ generations and the two locations

Table III - Analysis of variance for grain yield (kg/ha) of the F₃ and F₄ populations, evaluated in Lavras and Lambari, 1995.

s.v.	d.f.	m.s.			
		F ₃ - Lavras	F ₃ - Lambari	F ₄ - Lavras	F ₄ - Lambari
Treatments	109	221615.62**	96709.72**	144865.09**	156585.85**
GCA	10	1166587.60**	298514.22**	745685.58**	517352.38**
SCA	44	147573.81**	86209.82*	111265.65**	103744.13
Rec.	55	109035.92*	68417.85	62504.52	133265.32**
Error	214	71433.79	59416.92	55055.89	80944.93
Average		1289.12	956.86	1199.05	949.42
C.V. (%)		19.67	24.17	18.56	28.43
ϕ_g		20280.59	4427.69	12789.41	8081.62
ϕ_s		12689.97	4465.47	9368.26	3799.81
ϕ_{rc}		6266.99	1500.19	1241.42	8720.05
$\phi_g/\phi_s + \phi_g$		0.61	0.498	0.58	0.68
$\phi_g/\phi_s + \phi_{rc} + \phi_g$		0.52	0.43	0.55	0.39

*, **Significant at 5% and 1% probability levels, respectively, based on F test.

ϕ_g = Quadratic component of GCA; ϕ_s = quadratic component of SCA; ϕ_{rc} = quadratic component of reciprocal (Rec.) effects.

(Lavras and Lambari) gave a global view of the behavior of the segregant populations. The significance of the location effect was expected because of the differences in minimum temperature. The generation effect was not significant, probably because the difference between the means of F_3 and F_4 generations was only 1/8 of the dominance deviation.

The population and component effects were significant, indicating genetic variability for low temperature tolerance at the adult stage. A significant dominance effect is not very common in studies involving bean yield, under normal cultivation. Absence of dominance has been reported in some situations (Santos *et al.* 1985; Nienhuis and Singh, 1988; Ramalho *et al.* 1993). However, Stushnoff *et al.* (1984) mentioned that in the genetic control of low temperature tolerance, dominant loci may be involved. The great diversity of results may be due to the differences in temperature and genotypes used in the various

Table IV - Joint analysis of variance for grain yield (kg/ha) based on F_3 and F_4 generations evaluated in Lambari and Lavras, 1995.

s.v.	d.f.	m.s.
Replications/generations/locations	8	903811.92**
Locations (L)	1	27934567.97**
Generations (G)	1	784249.87
L x G	1	563320.96
Treatments (T)	109	266736.89**
GCA	10	1697272.72**
SCA	44	148257.03**
Rec.	55	101424.64*
T x L	109	147067.06**
GCA x L	10	659184.59**
SCA x L	44	125940.81**
Rec. x L	55	70856.36
T x G	109	116469.89**
GCA x G	10	312208.20**
SCA x G	44	87543.80
Rec. x G	55	104014.59**
T x L x G	109	89501.54*
GCA x L x G	10	59474.37
SCA x L x G	44	87041.59
Rec. x L x G	55	96929.17*
Error	856	66712.89
Average		1098.62
C.V. (%)		23.51
ϕ_g		7548.85
ϕ_s		3397.71
ϕ_{rc}		1446.30
$\phi_g/\phi_s + \phi_g$		0.69
$\phi_g/\phi_s + \phi_{rc} + \phi_g$		0.61

*, **Significant at 5% and 1% probability levels, respectively, based on F test. ϕ_g = Quadratic component of GCA; ϕ_s = quadratic component of SCA; ϕ_{rc} = quadratic component of reciprocal (Rec.) effects.

studies. There are some possible explanations for dominance in the genetic control of this trait under low temperature conditions. The first is the possible existence of genes which are regulated and activated by low temperatures, so that they only manifest themselves when the temperature reaches critical values. The second explanation would be greater dominance when the plants are submitted to conditions of less competition (Hamblim and Morton, 1977). As the populations were cultivated during a period of low temperatures, which gave a reduced vegetative growth, and thus less competition, this may explain the dominance, even in the F_3 and F_4 generations. Another possible cause of the significance of the dominance effect may be the fact that the parents used in this study were very different, due to their different origins, although all were of meso-american origin.

The reciprocal effects, for grain yield, were also significant, which under normal cultivation is not very common (Ramalho *et al.*, 1993). Fowler *et al.* (1993) commented that although reciprocal effects are not usually significant in the composition of the variation of bean plant population under normal temperature conditions, they may be significant under low temperature conditions. Thus, cytoplasmic factors may influence in part the control of low temperature tolerance, although to a lesser extent than the nuclear effects.

The assessment of the populations in several locations and, if possible, in different generations is necessary to carry out a careful study of the population behavior. By this procedure, estimates of the genetic components free of interaction are obtained and allow a more accurate choice of the segregant populations. In the joint analysis of variance (Table IV) the populations interact with both locations and generations. When each component effect of the population is analyzed separately it can be seen that these do not interact homogeneously. The GCA and SCA effects had significant interactions with locations, differently from the reciprocal effect. Ramalho *et al.* (1988), assessing common bean plant populations in normal cultivation periods, found similar results for the interaction of GCA and SCA with locations.

The GCA and the reciprocal, but not the SCA effects interacted with generations (Table IV). A probable explanation for the interaction of the reciprocal effect with generations would be interaction among nuclear genes, in F_3 and F_4 generations, with cytoplasmic genes, which could interfere in the manifestation of this reciprocal effect. The interaction of GCA with generations possibly happened because of the presence of dominance effects for grain yield (Vencovsky, 1987), since with different generations

there were also changes in the amount of dominance for the trait. These differences are due to the different dominance effects contained in the populations, which are directly correlated to the diversity among the parents. Ramalho *et al.* (1988) did not find significant interaction among GCA and SCA with generation, when assessing populations under normal temperature conditions.

All of the partitioned population effects (GCA, SCA and reciprocal effects) were significant, and therefore, necessary in explaining the variation found among the segregant populations. The predominance of the GCA quadratic effects, however, indicated that the additive effects are the most important in the genetic control of low temperature tolerance at the adult stage of the common bean plant cultivation.

The interactions of GCA with locations and also with generations were present in populations with intermediate performance. When the calculations of GCA are analyzed in each experiment (Figure 2) it may be concluded that the parents which had the greatest estimates (A-488, Ouro and ESAL 591) had no negative GCA values in any of the locations or generations. Also, the parents with inferior performance (ESAL 501, CNF-05) had negative values in all the experiments. However, when the yield of the segregant population is assessed, the difference among parents is not always clear, and to assess low temperature tolerance at the adult stage of the common bean plant there should be estimates for various locations and generations. The interaction effect is removed from the estimated parameters, and more precise and reliable results are obtained, mainly when the difference among the parents is small.

The parents A-488, Ouro and ESAL 591 stand out in the estimates of the GCA for grain yield obtained from the mean values of all the experiments (Table V). This suggests that these lines have a greater number of favorable loci for low temperature tolerance at the adult phase, and that inbred lines (F_{00}) derived from the populations A-488 x Ouro, A-488 x ESAL 591 and ESAL 591 x Ouro will have a larger mean.

The hypothesis that high GCA is the same as a large number of favorable loci is confirmed by the greater yield reached by the populations which had A-488 or

Ouro as parent (Table V). Similarly, parents Rio Vermelho, CNF-05 and ESAL 501 must have the least number of favorable loci for this trait and will have the poorest performance as they had the lowest GCA estimates. Otubo (1994) found a different result for low temperature tolerance in the germination and emergence stages of the common bean plant. Using basically the same parents, the author reports that the lines Rio Vermelho and Small White are low temperature tolerant. Reciprocal and dominance effects were not observed. Thus, it seems that the genetic control of low temperature tolerance in different stages of bean plant development is carried out by different gene loci. This conclusion is based on the fact that lines considered more tolerant in the germination and emergence phases have been less tolerant in the adult phase, and also because there was no dominance or reciprocal effect for the tolerance trait at the juvenile stage. However, it must be pointed out that the parent A-488 was considered tolerant to low temperatures in two stages, showing that there may be loci in common in the genetic control of the two stages. These results credit the A-488 lines as promising material for use in breeding programs for common bean plant tolerance to low temperature. Kemp (1978) and Dickson and Petzoldt (1987) reported that low temperature tolerance at the different stages of common bean plant development is inherited independently.

The size of the SCA estimates gives an idea of the degree of complementation of the parents in a cross. Its significance indicates that the populations have heterogeneous performance and that their behavior cannot be predicted based only on the GCA as there are interactions among parents according to the degree of

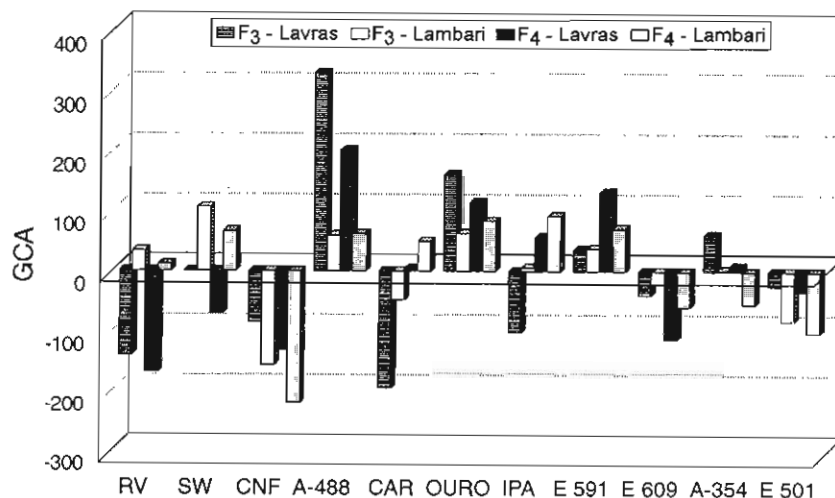


Figure 2 - Estimates of general combining ability per location (Lavras and Lambari) and per generation (F3 and F4) for grain yield (kg/ha). Lavras/Lambari, 1995. RV, Rio Vermelho; SW, Small White; CNF, CNF-05; CAR, Carioca; IPA, IPA-7419; E, ESAL 591, 609, 501.

Table V - Mean grain yield (kg/ha) of segregant populations (above diagonal) and of reciprocals (below diagonal), from two generations (F₃ and F₄) and two locations (Lavras and Lambari), and general combining ability for grain yield (GCA_y) of parents, 1995.

Parents ^{1/}	1	2	3	4	5	6	7	8	9	10	11
1 ^{2/}	-	*	1043.0	1157.6	955.6	1124.5	1055.0	997.5	1052.0	1009.7	901.9
2	941.8	-	1065.9	1235.9	1025.1	1195.7	1091.8	1210.1	1118.0	1125.4	1104.0
3 ^{2/}	946.3	1118.6	-	1200.7	867.8	1056.9	865.8	815.4	842.8	1100.3	*
4 ^{2/}	1324.0	1300.3	1056.7	-	1161.3	1481.3	1233.0	1307.2	*	*	1133.2
5	1025.0	1028.7	880.8	1233.0	-	1182.3	1342.3	1256.8	997.6	976.1	750.8
6 ^{2/}	1139.4	1134.2	1051.4	1169.2	1370.7	-	*	979.9	1142.8	1115.3	1203.0
7	965.5	1228.3	819.4	1250.9	845.9	1339.7	-	1359.3	1100.7	1029.9	965.0
8	1050.1	1155.3	908.2	1344.6	1194.0	1305.7	1235.3	-	1075.1	1210.0	1220.4
9	1031.4	1035.2	833.4	1327.7	920.8	1176.7	976.3	1122.5	-	1077.1	942.4
10	1088.8	1261.8	850.9	1258.3	1112.4	1191.4	1012.9	1269.4	1023.8	-	976.1
11	1034.9	1116.5	992.1	1139.5	996.8	1168.2	1151.8	1194.6	801.5	1102.2	-
GCA _y	-65.9	25.7	-148.0	162.5	-47.1	105.3	13.1	68.8	-58.3	4.3	0.17

1/: 1 - Rio Vermelho; 2 - Small White; 3 - CNF-05; 4 - A-488; 5 - Carioca; 6 - Ouro; 7 - IPA-7419; 8 - ESAL 591; 9 - ESAL 609; 10 - A-354; 11 - ESAL 501.

2/: * - Reciprocal mean value used for the diallel table being analyzed, because of the seeds that were not available.

LSD ($m_i - m_j$) = 103.3 kg/ha and LSD ($g_i - g_j$) = 48.71 kg/ha, based on *t*-test at 5% probability level.

divergence of the dominant loci. Oliveira (1995), however, used simulations to show that the SCA depends not only on the heterozygous loci, but also on the number of fixed loci with favorable alleles. It depends, therefore, on the proportion of homozygous loci with favorable and unfavorable alleles as it is a deviation from the mean. Thus, the greatest SCA value does not always mean a greater number of superior lines after complete homozygotes and neither a greater variance among the lines. Thus it will not always contribute to identify lines with better performance.

The SCA values (Table VI) show the great variation found, with amplitudes equivalent to those found in the GCA. It should be pointed out that the

population A-488 x Ouro, which had the highest grain yield, had negative SCA estimates, indicating that the two parents complemented each other more than with others, as for example A-488 x ESAL 501 and Ouro x IPA-7419, although this does not mean that these populations will produce a greater proportion of favorable lines. The population Ouro x Carioca had one of the greatest positive values for SCA, resulting in a considerable yield, in spite of the low GCA in the Carioca cultivar. Generally, the parents which had the highest GCA estimates had negative SCA when crossed with each other (Table VI), indicating a great difficulty in associating high GCA estimates with positive SCA values. Only the Ouro x IPA-7419 population had

Table VI - Estimates of reciprocal effect (above diagonal) and specific combining ability (SCA - below diagonal) for grain yield, based on generations mean (F₃ and F₄) and locations mean (Lavras and Lambari). Lavras/Lambari, 1995.

Parents ^{1/}	1	2	3	4	5	6	7	8	9	10	11
1	-	-	48.4	-83.2	-34.7	-7.4	44.7	-26.7	10.3	-39.6	-66.5
2	-116.6	-	-26.3	-32.2	-1.8	30.8	-68.3	27.4	41.4	-68.2	-6.2
3	110.0	116.0	-	72.0	-6.5	2.8	23.2	-46.4	4.7	124.7	-
4	45.6	-18.6	15.6	-	-35.8	156.0	-8.9	-18.7	-	-	-3.1
5	4.8	-50.2	-29.2	-16.8	-	-94.2	248.2	31.4	38.4	-68.1	-123.0
6	-6.0	-64.6	-1.8	-41.2	119.7	-	-	-162.9	-16.9	-38.0	17.4
7	-35.6	22.6	-121.1	-32.3	29.5	122.6	-	62.0	62.2	8.5	-93.4
8	-77.7	-10.4	-157.7	-4.0	105.1	-130.0	116.7	-	-23.7	-29.8	12.9
9	67.3	10.7	-54.2	123.2	-33.9	14.1	-14.9	-10.3	-	26.6	70.4
10	12.2	65.0	20.7	-7.1	-11.58	-54.9	-94.6	68.0	5.9	-	-63.0
11	-4.0	46.3	101.8	-64.4	-117.3	42.0	7.0	100.3	-108.0	-3.5	-

1/: 1 - Rio Vermelho; 2 - Small White; 3 - CNF-05; 4 - A-488; 5 - Carioca; 6 - Ouro; 7 - IPA-7419; 8 - ESAL 591; 9 - ESAL 609; 10 - A-354; 11 - ESAL 501.

Grain yield: Reciprocal effect values higher than 103.3 kg/ha are statistically different of zero, based on *t*-test at 5% probability level. LSD ($s_{ij} - s_{ik}$) = 137.79; LSD ($s_{ij} - s_{kl}$) = 128.89 kg/ha, based on *t*-test at 5% probability level.

positive SCA estimates, and the parents also had positive GCA estimates, which was reflected in a high yield mean (1339.7 kg/ha). This result probably happened because, although they are meso-americans, they are of different origins and are well adapted to the majority of the Brazilian cultivation regions.

Reciprocal effects, which are due to the cytoplasmic genes, were very inconsistent and heterogeneous, as only five populations displayed this effect (Table VI). The inconsistency of the reciprocal effect may be due to the interaction of nuclear and cytoplasmic genes, so that the parents do not express the cytoplasmic effects in all the crosses. However, it seems that the expression of the reciprocal effect is directly linked to the genetic nuclear constitution of the segregant population. Probably, for quantitative traits, the reciprocal effect is not characteristic of the parents, but of a specific segregant population. In spite of this, this effect is important as it directs the plant breeder in the choice of which parent will be the male or female. The mother cytoplasm is passed entirely to the embryo through the ovule and it is solely responsible for the cytoplasmic phenotypes of the descendants, as the pollen grain contributes practically no cytoplasm. Thus, the female parent of a given cross should be the parent which has the positive reciprocal effects. Population A-488 x Ouro, which had high GCA estimates, showed significant reciprocal effects. In this case the use of the parent A-488 as the mother may increase the grain yield by up to 312 kg/ha, in the mean of the segregant population.

Besides the mean components, the estimates of the genetic variance and broad sense heritability of each segregant population were also useful (Table VII). These estimates gave complementary information which allowed the careful choice of the most promising population for selection. A population with positive values for GCA and high genetic variance and heritability estimates is ideal, showing itself to be a carrier of a high frequency of favorable alleles and also genetic variability, which will guarantee success with a selection of lines tolerant to low temperatures at the adult stage. Genetic variance is only interesting if it is associated with a population with a high mean. The population with the highest grain yield (A-488 x Ouro) also had high heritability (Table VII), which is promising for selection. Populations with the same mean may be discriminated based on their heritability values. For example, the populations Ouro x ESAL 609 and Ouro x A-354 have similar means, but the first has a far higher heritability.

Table VII - Estimates of genetic variance (g^2 /plant)/heritability (%) and mean grain yield (kg/ha) of F₃ and F₄ populations. Lavras, 1995.

Parents	Rio Vermelho	Carioca	Ouro
Rio Vermelho	-	4.56/43 (1046.42)	9.83/59 (1266.05)
CNF-05	1.68/29 (949.72)	3.97/35 (1055.87)	7.42/43 (1221.72)
A-488	8.51/41 (1412.37)	6.51/34 (1474.65)	9.43/50 (1614.95)
Carioca	4.56/43 (1046.42)	-	3.20/20 (1388.19)
Ouro	9.83/59 (1266.05)	3.20/20 (1388.19)	-
IPA-7419	7.93/48 (1053.34)	4.68/20 (1174.29)	3.23/12 (1308.29)
ESAL 591	8.38/32 (1042.89)	5.25/28 (1300.02)	8.25/43 (1496.40)
ESAL 609	3.86/38 (1143.82)	3.97/28 (953.59)	14.11/35 (1320.72)
A-354	1.85/18 (1135.26)	2.73/13 (1208.89)	0.05/0.7 (1353.15)
ESAL 501	1.87/13 (1103.39)	3.49/26 (974.54)	2.42/20 (1377.82)
Average	5.39/36 (1128.14)	4.26/27 (1175.17)	6.44/31 (1371.92)

Populations with the Ouro parent had higher genetic variance estimates and broad sense heritabilities, among the populations. A good gain can be expected with selection and a higher probability of finding superior lines in the population, wherever the Ouro cultivar was one of the parents. One of the big problems in genetic improvement in the common bean plant for many Brazilian regions is the demand for a standard grain color characteristic of the Carioca cultivar. Thus, to attend the consumer market demand it could be recommended to use the segregant population ESAL 591 x Ouro, which besides having high grain yield, GCA, genetic variance and heritability, also has the greatest possibility of obtaining lines with the kind of grain commercially acceptable. With the parent A-488, which had great tolerance to cold, it is more difficult to obtain cultivars with Carioca type commercial grains because this material has black grains.

Although some populations were promising, it should be pointed out that this new cultivation period may be considered high risk, because of the great possibility of frosts during the cultivation period. Silva *et al.* (1986) reported that the period with the greatest incidence of low temperatures in the South of Minas Gerais was from May to August, July being the most probable month for frosts. In spite of some populations having been tolerant to low temperatures in the adult phase, none of them would withstand frost, as reported by Melo *et al.* (1995). Thus, even though promising populations are found for selection and cultivars better adapted to this new cultivation period may be found, one must be aware of the risk with the crop.

ACKNOWLEDGMENTS

The authors thank the Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Empresa de

Pesquisa Agropecuária de Minas Gerais (EPAMIG) and Fundação de Apoio à Pesquisa de Minas Gerais (FAPEMIG).

RESUMO

Visando melhorar o feijoeiro para tolerância ao frio na fase adulta, obtiveram-se informações sobre o controle genético da tolerância ao frio, a ocorrência de interações das capacidades combinatórias por locais e gerações e foram identificadas as populações mais promissoras para efetuar seleção. Para isso foram avaliados os cruzamentos e os recíprocos provenientes do intercruzamento de 11 genitores, no esquema dialélico completo, no outono/inverno de 1995, em duas gerações (F₃ e F₄) e em dois locais (Lavras e Lambari, Minas Gerais). Foram analisados dados relativos à produtividade de grãos (kg/ha), incidência de antracnose e época de florescimento (Lavras). Estimou-se a variância genética e herdabilidade no sentido amplo da produtividade de grãos, dentro das populações segregantes. A análise dialélica foi realizada utilizando o método III, descrito por Griffing (*Aust. J. Biol. Sci.* 9: 463-493, 1956). Os genitores diferiram com relação a época de florescimento e produtividade de grãos sob condições de baixa temperatura na fase adulta do feijoeiro. A linhagem Small White foi a mais precoce, A-488, Ouro e ESAL 591 as mais tolerantes e CNF-05, Rio Vermelho e ESAL 501 as mais sensíveis ao frio. Foi observada a presença de efeito aditivo, dominante e recíproco, com predominância dos efeitos aditivos. O efeito recíproco explicou uma pequena parte da variação, sendo ainda muito inconsistente e presente de forma significativa em poucas populações. Para época de florescimento foi observada somente a presença de efeito aditivo dos genes. As interações, principalmente com capacidade geral de combinação, indicam que para obtenção de estimativas precisas e confiáveis deve-se avaliar as populações em vários locais e várias gerações. As populações A-488 X Ouro e Esal 591 X Ouro mostraram-se promissoras para seleção.

REFERENCES

- Camargo, A.P. de** (1972). Esboço de zoneamento da aptidão agroclimática do feijão (*Phaseolus vulgaris*) no Brasil. In: *Simpósio Brasileiro de Feijão*, 1971, Universidade Federal de Viçosa, Viçosa, pp. 119-128.
- Cruz, C.D. and Regazzi, A.D.** (1994). *Modelos Biométricos Aplicados ao Melhoramento Genético*. UFV, Imprensa Universitária, Viçosa, pp. 390.
- Dias, D.A., Santos, J.B., Ramalho, M.A.P. and Abreu, A.F.B.** (1992). Seleção de progênes de feijoeiro adaptadas ao cultivo no inverno do sul de Minas Gerais, na população Rio Tibagi X Carioca 300 V. *Ciênc. e Prát.* 16: 68-73.
- Dickson, M.H. and Boettger, M.A.** (1984). Emergence, growth and blossoming of bean (*Phaseolus vulgaris*) at suboptimal temperatures. *J. Am. Soc. Hortic. Sci.* 109: 257-260.
- Dickson, M.H. and Petzoldt, R.** (1987). Inheritance of low temperature tolerance in beans at several growth stages. *Hortscience* 22: 481-483.
- Evans, A.M. and Davis, J.H.C.** (1978). Breeding *Phaseolus* beans as grain legumes for Britain. *Appl. Biol.* 34: 1-42.
- Farlow, P.J.** (1981). Effect of low temperature on number and location of developed seed in two cultivars of French beans (*Phaseolus vulgaris*). *Aust. J. Agric. Res.* 32: 325-330.
- Fowler, D.B., Limin, A.J., Robertson, A.J. and Gusta, L.V.** (1993). Breeding for low-temperature tolerance in field crops. In: *Crop Breeding for Low Temperatures* (Fowler, D.B., Limin, A.J., Robertson, A.J. and Gusta, L.V., eds.). University of Saskatchewan, Saskatoon, Canada, pp. 357-362.
- Griffing, B.** (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* 9: 463-493.
- Hamblin, J. and Morton, J.R.** (1977). Genetic interpretations of the effects of bulk breeding on four populations of beans (*Phaseolus vulgaris*). *Euphytica* 26: 75-83.
- Kemp, G.A.** (1978). Growth of primary leaves of beans (*Phaseolus vulgaris* L.) under suboptimal temperature. *Can. J. Plant Sci.* 58: 169-174.
- Kooistra, E.** (1971). Germinability of beans (*Phaseolus vulgaris*) at low temperature. *Euphytica* 20: 208-213.
- Maris, B.** (1989). Analysis of an incomplete diallel cross among three ssp. tuberosum variates and seven long-day adapted ssp. andigena clones of potato (*Solanum tuberosum*). *Euphytica* 41: 163-182.
- Melo, L.C., Santos, J.B., Ramalho, M.A.P. and Abreu, A.F.B.** (1995). Avaliação da capacidade de combinação de cultivares de feijoeiro sob baixas temperaturas. In: *Congresso Nacional de Genética*. Rev. Bras. Genet., Caxambu, 1995, pp. 104.
- Nienhuis, J. and Singh, S.P.** (1988). Genetics of seed yield and its components in common bean (*Phaseolus vulgaris*) of Middle-American origin. I. General combining ability. *Plant Breed.* 101: 105-106.
- Oliveira, L.B.** (1995). Alternativas na escolha dos parentais em um programa de melhoramento do feijoeiro. Master's thesis, Universidade Federal de Lavras (UFLA), Lavras, MG.
- Otubo, S.T.** (1994). Controle genético da tolerância do feijoeiro (*Phaseolus vulgaris*) a baixas temperaturas na fase de germinação. Master's thesis, Universidade Federal de Lavras (UFLA), Lavras, MG.
- Ramalho, M.A.P., Santos, J.B. and Pereira-Filho, I.** (1988). A choice of parents for dry bean (*Phaseolus vulgaris* L.) breeding. I. Interaction of mean components by generation and by localization. *Rev. Bras. Genet.* 11: 391-400.
- Ramalho, M.A.P., Santos, J.B. and Zimmermann, M.J.** (1993). *Genética Quantitativa em Plantas Autógamas*. 1st edn. UFG, Goiânia, pp. 271.
- Santos, J.B., Vencovsky, R. and Ramalho, M.A.P.** (1985). Controle genético da produção de grãos e seus componentes primários em feijoeiro. *Pesq. Agrop. Bras.* 20: 1203-1211.

- Silva, I., Castro Neto, P. and Silveira, J.V.** (1986). Época e probabilidade de ocorrência de temperatura mínima abaixo de dado valor, para região de Lavras, Minas Gerais. *Ciênc. Prát.* 10: 210-219.
- Stobe, F.H. and Hombord, D.P.** (1966). Blossoming and fruit set patterns in *Phaseolus vulgaris* as influenced by temperature. *Can. J. Bot.* 44: 813-819.
- Stushnoff, C., Fowler, D.B. and Brule-Babel, A.** (1984). Breeding and selection for resistance to low temperature. In: *Plant Breeding - A Contemporary Basis* (Stushnoff, C., Fowler, D.B. and Brule-Babel, A., eds.). Pergamon Press, Oxford, pp. 115-136.
- Teixeira, F.F., Ramalho, M.A.P. and Abreu, A.F.B.** Estimativa do número de genes envolvidos no início da floração do feijoeiro (*Phaseolus vulgaris*), usando a metodologia de Jinks e Towey. *Ciênc. Agrotec.* (in press).
- Vencovsky, R.** (1987). *Melhoramento e Produção do Milho*. 2nd edn. Fundação Cargill, Campinas, pp. 795.
- Vencovsky, R. and Barriga, P.** (1992). *Genética Biométrica Aplicada ao Fitomelhoramento*. Sociedade Brasileira de Genética, Ribeirão Preto, SP, pp. 496.
- Vieira, C.** (1967). *O Feijoeiro Comum: Cultura, Doenças e Melhoramento*. Imprensa Universitária, Viçosa, pp. 220.
- Von Pinho, R.G.** (1990). Tolerância do feijoeiro (*Phaseolus vulgaris* L.) a baixas temperaturas na fase de germinação e emergência. Master's thesis, Universidade Federal de Lavras (UFLA), Lavras, MG.
- White, J.W. and Singh, S.P.** (1991). Sources and inheritance of earliness in tropically adapted indeterminate common bean. *Euphytica* 55: 15-19.

(Received June 17, 1996)