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GENERAL COMBINING ABILITY IN 80 SMALL-SEEDED CULTIVARS OF COMMON BEAN (*PHASEOLUS VULGARIS* L.) FOR SEED YIELD AND ITS COMPONENTS

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Abstract

Increase in yield potential of dry common bean (Phaseolus vulgaris L.) cultivars has been either imperceptible or small and gradual, in spite of large variation of most traits, including seed yield. Therefore, general combining ability (GCA) of 80 cultivars and lines was investigated. Eight sets of 10 entries each were used, with five parents each as females and males in a Design II mating system. The resulting 200 F_2 populations, excluding parents, were evaluated in a replicates-in-sets design for yield and its components at two locations in Colombia. GCA was calculated by Griffing's Method 4, Model I.

Sixty-two parents, including high yielding and widely grown small-seeded Latin American cultivars ('Aete 3,' 'Carioca,' 'Catu,' 'ICA Pijao,' 'IPA 74-19,' 'Jamapa,' 'Moruna 80,' 'Porrillo Sintetico,' 'Rio Tibagi'), new releases, and many sources of diseases, insect pests, and drought resistance, had zero or negative GCA for yield and its components at one or both locations. The 18 parents that had positive GCA for yield at one or both locations were all bred lines. At least nine of these resulted from a cross between a small-seeded cultivar with zero or negative GCA for yield, on one hand, and a landrace from the highlands of Mexico, on the other. Two such landraces, 'Guanajuato 31' and 'Ojo de Liebre,' contributed positive GCA for seed yield and seed weight to all their lines studied, suggesting a major gene control. Breeding implications are discussed.

Key words: Common bean - Phaseolus vulgaris - yield components - general combining ability - breeding - Mexican highland germplasm

HAMBLIN and EVANS (1976) reported that cross potential in common bean (Phaseolus vulgaris L.) could be predicted based on performance of parents or early generation progeny. In tropical and subtropical environments of Latin America, high-yielding bean lines are often derived from crosses involving only high-yielding parents, but it has been difficult to surpass the yield of the highest-yielding parent. To increase yield we must, therefore, develop a more complete understanding of the range of available variation and its inheritance, the combining ability of parents, and the relative effectiveness of different criteria and methods of selection.

Yielding potential of dry common bean cultivars is determined by growth habit, seed size, maturity, growing environment, cropping system, agronomic management, and inputs applied. Among these, the first three are intrinsic characteristics of each bean cultivar. Within and across bean production regions, these three traits and, hence, yield, vary greatly among commercial cultivars and landraces (NIENHUIS and SINGH 1985; SINGH 1987; SINGH and GUTIERREZ 1984). In Latin America, for example, small-seeded indeterminates of growth habits II and III of intermediate maturity predominate in Brazil, Cuba, Venezuela, most Central American countries, and the south-central coasts of Mexico; approximately 5 million ha, i.e., 50% of total world hectarage under dry common bean, are planted yearly with these beans. In contrast, large-seeded, early maturing determinate of growth habit I (< 2000 meters above sea level) and late-maturing indeterminate of growth habit IV climbing bean cultivars (> 2000 meters above sea level) predominate in the highlands of Colombia, Ecuador, and Peru. Similarly, in the highlands of Mexico, medium-seeded indeterminate growth habits III (semi-arid areas) and IV (humid regions) predominate. Late maturing type IV climbing bean cultivars generally possess the highest yield potential ($\geq$ 5000 kg/ha) when grown on trellises or stakes, and early maturing type I cultivars have the lowest yield ($\leq$ 3000 kg/ha). In a sole cropping system without artificial support the highest-yielding cultivars in tropical and subtropical environments often are those with small seeds (< 26 g/100 seed) and indeterminate growth habits II and III.

The primary centers of domestication and evolution of small- and large-seeded cultivated common bean are located in Middle and South America, respectively (EVANS 1973; GEPTS and BLISS 1985; GEPTS et al. 1986). Patterns of morphological variation and characteristics of major gene pools of common cultivated bean from both Middle and South American centers of domestication were described recently by SINGH (1987). Breeding and genetic studies based on knowledge of gene pools should facilitate proper management and exploitation of germplasm, expedite progress from selection, and save bean breeders from misdirected efforts.

FOOLAD and BASSIRI (1983) found that the specific combining ability (SCA) was more important than general combining ability (GCA) for yield, number of pods, and seeds/plant in dry bean. But GCA was more important than SCA for 100-seed weight and days to flowering. CHUNG and STEVENSON (1973) also reported that the dominance component was more important than the additive component, and over-dominance was observed for number of pods and yield. Although genetic effects varied according to cross and cropping system, additive effects generally were small compared with dominance and epistatic effects for yield and harvest index in bean (ZIMMERMANN et al. 1985). In contrast, KORNEGAY and TEMPLE (1986) found that under leafhopper pressure, only SCA was important for bean yield. But in insect-protected conditions, both GCA and SCA were significant and the magnitude of GCA was greater than that of SCA. MITRANOV (1983) and SINGH and SAINI (1983) found both GCA and SCA to be important in the F_1 and the variance due to the former was greater than the latter. From analysis of 6x6 diallel crosses, VAID et al. (1985) concluded that in dry bean both GCA and SCA were important in F_1 and F_2 for days to flowering, days to maturity, plant height, branch number, pod number, pod length, seeds/pod, 100-seed weight, seed protein, and yield/plant. Moreover, for all traits except seeds/pod, GCA variances were higher than SCA variances. Similarly, based on a study of 9x9 diallel crosses involving three parents of different seed sizes of each of three bush growth habits (determinate I, indeterminate upright II, and indeterminate, prostrate semiclimbing III), NIENHUIS and SINGH (1986) reported that GCA was more important than SCA in tropical and subtropical environments of Colombia not only for yield and its components but also for most architectural traits in dry common bean. Further, the SCA variance in the F_2 (NIENHUIS and SINGH 1986) and the F_3 (HARTANA 1986) analyses for yield was not significant.

High positive F_1 heterosis in bean is often associated with increasing divergence (genetic distance) among parents for growth habit, seed size, maturity, and other traits (EVANS 1970; FOOLAD and BASSIRI 1983; GHADERI et al. 1984; GUTIERREZ and SINGH 1985; NIENHUIS and SINGH 1986). But EVANS (1970) and SINGH and GUTIERREZ (1984) found that crosses among diverse parents, especially between small-seeded forms of Middle American centers and large-seeded types of South

American centers of domestication, result in unbalanced segregates of poor performance or negative heterosis in the F_2 and subsequent generations. Further, genetic incompatibility and F_1 hybrid dwarfism, controlled by two complementary dominant genes (SHII et al. 1980), has been reported in some crosses between small- and large-seeded types (GEPTS and BLISS 1985; GUTIERREZ and SINGH 1982; SINGH and GUTIERREZ 1984).

Of nine parents utilized in our earlier study (NIENHUIS and SINGH 1986), only two lines ('A 375' and 'A 457'), characterized by indeterminate growth habit III and medium-sized seeds, had positive GCA for bean yield in both F_1 and F_2 at both locations; none of the small- or large-seeded types had similar positive GCA values. However, the number of materials tested was too small to draw any definite conclusions. This warranted further studies involving more parents, preferably grouped according to seed size and evolutionary origins. Thus, in order to identify parents with high positive GCA for seed yield and its components and to determine likely sources of such desirable germplasm, separate studies for small- and large-seeded types were initiated. The latter study involving 64 parents is still in progress. For the former, 80 parents were selected, including most of the commercial cultivars from tropical and subtropical Latin America and donors of desirable genes to overcome some production constraints. Estimates of genetic variance, heritability, and expected gain from selection will be reported subsequently. GCA for yield and its components for 80 parents is reported here.

Materials and Methods

Eighty dry bean cultivars and experimental lines adapted to tropical and subtropical environments of Latin America were selected for the study. These are commonly utilized in breeding programs at CIAT and by national programs in Latin American countries and elsewhere. Of these, 61 parents were small-seeded (< 26 g/100 seed) and 19 lines were medium-seeded (26 to 40 g/100 seed). The latter group was composed of 13 lines developed from crosses between small-seeded tropical and subtropical cultivars with medium-seeded germplasm bank accessions from the highlands of Mexico, one bank accession from Zaire, and five experimental lines developed from germplasm from Andean South America. Because of their extreme susceptibility to bean common mosaic virus, majority of landraces and cultivars were excluded, except for the resistant 'Jamapa' (Mexico), 'ICA Pijao' (Colombia), 'Porrillo Sintetico' (El Salvador), 'Aete 3,' 'Aroana 80,' 'Catu,' 'Carioca,' 'Carioca 80,' 'CENA 164,' 'IPA 7419,' 'Moruna 80,' 'RAI 54,' and 'Rio Tibagi' (Brazil). We had known based on our field experience that BCMV grossly affects plant development and yield and was recently reported to affect general performance and heterosis for protein, yield, and yield components (SARRAFI and ECOCHARD 1986).

Of the 80 parents, three lines -- one each of determinate growth habit I ('A 132'), indeterminate upright II ('A 359'), and indeterminate prostrate and semiclimbing III ('A 375')--were of known combining ability from our previous study (NIENHUIS and SINGH 1986). Eighty parents were randomly assigned to eight blocks of 10 lines each and crossed in a Design II mating scheme (COMSTOCK and ROBINSON 1948). Within a set, five parents were used as males, and each was crossed to five other parents, used as females, to obtain a total of 25 crosses per set, giving a total of 200 F_1 crosses from the eight sets. The 25 F_2 populations without parents from each block were planted in a replicates-in-sets design with 2 replications at CIAT farms at Palmira (1,000 m above sea level, mean temperature 23.6 C) and Santander de Quilichao (980 m a s l, mean temperature 23.8 C), Colombia, in 1983. The soil in Palmira is a fertile Mollisol with pH of approximately 7.5, whereas Santander de Quilichao has an Ultisol with a pH of 4.5. The latter soil is deficient in phosphorus and has toxic levels of magnesium and aluminum. Before sowing necessary dosages of fertilizer were applied at both sites and lime only at Santander de Quilichao to correct for soil problems. The experimental unit was 4-m long rows, spaced 60 cm apart. A density of 22 plants/m^2 was established by planting excess seed and thinning. Regular applications of insecticides and fungicides were used to control insects and diseases, and supplemental irrigation was used as needed at both locations. After the plants had matured in the field, pods were harvested from 2.25 m of bordered plants in the two center rows (harvested area 2.7 m^2). Pod number was determined for each plot, and the seeds were threshed, counted, and weighed. Yield was expressed as g/m^2 and adjusted to a moisture content of 14% by weight. The mean number of seeds/pod was calculated by dividing the number of seeds/plot by the number of pods/plot. Seed weight was calculated by dividing yield by the number of seeds/m^2.

Mean squares due to locations (L), sets (S), LxS, and replications/S/L were nonsignificant (our unpublished data). The general combining ability effects associated with each parent based on the average performance of their F_2 progeny in each location were estimated separately for each set according to Griffing's method 4, model 1 (1956). The GCA values >1.96 standard error (SE) and >2.57 SE were significant at P=0.05 and P=0.01, respectively.

Results

Table 1 presents GCA estimates of 62 cultivars, sources of desirable traits and other experimental lines for yield and its components. All 62 had zero or negative GCA values for yield at both locations. These included essentially all sources of resistance (e.g., 'EMP 84,' 'XAN 87,' 'BAT 85,' 'BAT 841,' 'EMP 110,' 'DOR 60,' 'A 63,' 'A471,' 'A 176,' 'A 339,' 'A 297,' and 'A 210') for leafhoppers, common bacterial blight, drought, bean golden mosaic virus, rust, anthracnose, and angular leaf spot included in the study; commercial bean cultivars grown extensively in Latin America ['Carioca' (Brazil), 'ICA Pijao' (Guatemala, Cuba, Bolivia, Argentina), 'Jamapa' (Mexico), 'Porrillo Sintetico' (El Salvador), and 'Rio Tibagi' (Brazil)]; and newly released improved cultivars of Brazil, Costa Rica, and Argentina (e.g., 'Aete 3,' 'Aroana 80,' 'BAT 58,' 'BAT 304,' 'Carioca 80,' 'Catu,' 'CENA 164,' 'IPA 7419,' 'Moruna 80,' and 'RAI 54'). All traditional and newly released cultivars were small-seeded, of indeterminate growth habits II or III, and of intermediate maturity. In spite of differences in growth habit, maturity, seed weight, and origin, 35 other lines also had zero or negative GCA for yield and most of its components.

Eighteen parents had positive GCA for yield at one or both locations (Table 2). These were 'A 213,' 'A 246,' 'A 252,' 'A 259,' 'A 310,' 'A 373,' 'A 375,' 'A 445,' 'A 457,' 'A 462,' 'BAT 477,' 'BAT 1510,' 'BAT 1573,' 'BAT 1617,' 'BAT 1670,' 'G 825' (Wulma), 'RIZ 11,' and 'XAN 105.' ~~They were~~ all except 'G 825' were bred lines which differed in seed size, growth habit, and maturity. Most lines were derived from crosses involving traditional, high-yielding cultivars (e.g., 'Jamapa', 'Porrillo Sintetico', 'ICA Pijao', and 'Carioca') or their derived lines, which are characterized by zero or negative GCA. Thus the positive GCA of these lines was attained inadvertently and was contributed by other parents involved in their crosses. This led us to examine further the pedigree of 18 lines that had positive GCA for yield at one or both locations. From the analysis of 9x9 diallel crosses (NIENHUIS and SINGH 1986), we had known that two lines ('A 375' and 'A 457') that had positive GCA for bean yield in both F_1 and F_2 across locations were derived from crosses between small-seeded types of Middle or South America and medium-seeded accessions, such as 'Guanajuato 31' ('G 2618') and 'Ojo de Liebre' ('G 2910') from the highlands of Mexico. Of 18 lines with positive GCA for bean yield at one or both locations, seven medium-seeded ('A 213,' 'A 310,' 'A 373,' 'A 375,' 'A 445,' 'A 457' and 'A 462') and two small-seeded ('A 252' and 'A 259') were each derived from similar crosses between small-seeded types of Middle or South American origin, and medium-seeded accessions 'G 879,' 'G 2337,' 'Garrapato' ('G 2402'), 'Guanajuato 31' ('G 2618') and 'Ojo de Liebre' ('G 2910') from the highlands of Mexico. The cross 'Carioca' x 'Guanajuato 31' deserves special mention because lines 'A 252,' 'A 259,' 'A 373,' 'A 375' and 'A 445' were derived from that. The fact that 'Carioca' had negative or zero GCA values and all lines involving 'Guanajuato 31' as parent in this and our earlier study (NIENHUIS and SINGH 1986) had positive GCA, suggests that a major gene(s) was responsible for the positive GCA contributed by 'Guanajuato 31.' Similarly, two lines, 'A 457' and 'A 462,' derived from the cross 'Ojo de Liebre' x 'A 27' had positive GCA for seed yield and seed weight at one or both locations.

Positive estimates of GCA were found for pods/plant for 14 parents, for seeds per pod for 22 parents, and for seed weight for 22 parents at one or both both locations. Of these, 14 had positive GCA values for both yield and seed weight, one for yield and seeds per pod, and two for yield and pods/plant.

Of five lines of medium-sized seeds (26 to 40 g/100 seed) bred from germplasm from Andean highlands of South America and included in the present study ('A 471,' 'A 488,' 'BAT 1256,' 'BAT 1407' and 'BAT 1617'), only 'BAT 1617' had positive GCA for seed yield at CIAT-Palmira.

Three parents, one each of determinate growth habit I ('A 132'), indeterminate upright II ('A 359'), and indeterminate prostrate semiclimbing III ('A 375') from an earlier study of combining ability analysis (NIENHUIS and SINGH 1986) involving F_1 and F_2 generations of a 9 x 9 diallel crosses, were included in the present GCA analysis. The magnitude and sign of GCA estimates for bean yield and its components for the three lines in the present study (Tables 1 and 2) are similar to those reported previously (NIENHUIS and SINGH 1986).

Discussion

The general lack of positive GCA for yield in small-seeded dry bean parents utilized in the present study was very discouraging. Actual causes for the lack of positive GCA for yield in small-seeded germplasm in general and in high-yielding, widely grown commercial cultivars in particular are not understood. It is possible that parents within this group of germplasm have a common evolutionary origin (GEPTS et al. 1986) and are genetically very similar for yield in spite of differences in seed color, growth habit, maturity, and other traits, and might have attained a unique and balanced genetic constitution necessary for adaptation and fitness in tropical and subtropical environments. Further yield increases from crosses among parents within this group of germplasm would not be expected because of their similar genetic behavior. Moreover, their genic balance would be disrupted when crossed to low yielding, poorly adapted parents or to those likely to possess different developmental pathways, such as large-seeded types from Andean South America (SINGH and GUTIERREZ 1984). Although a few small-seeded accessions possessing different phaseolin patterns from South America have been reported, a large majority carry 'S' patterns and originated in Middle America from a common wild relative in which considerably large variation in phaseolin patterns has been found (GEPTS et al. 1986).

Germplasm from the semi-arid highlands of Mexico generally is characterized by an indeterminate prostrate growth habit III with short leaves, internodes, and pods but medium-sized seeds (gene pool 5, SINGH 1987). This developmental characteristic of the germplasm from the Mexican highlands constitutes an exception to the usual association between small seed size, small foliage, and short internodes (characteristic, for example, of the germplasm from lowland tropical Central America) and large seed, large foliage, and long internodes (characteristic of the germplasm from Andean South America). Because both the small-seeded (Middle American) and medium-seeded (Mexican highlands) cultivars and landraces exhibited an 'S' phaseolin type, GEPTS and BLISS (1985) and GEPTS et al. (1986) concluded that the two groups of germplasm had a common evolutionary origin. The common origin, on one hand, could explain the absence of any known genetic incompatibility found, for example, between small- (Middle America) and large-seeded types of South America (GEPTS and BLISS 1985; GUTIERREZ and SINGH 1982; SINGH and GUTIERREZ 1984). The genetic divergence between Middle American and Mexican highland groups, reflected, for example, in their contrasting morphology, on the other hand, could explain their genetic complementarity resulting in high positive GCA for seed yield, seed size, and productivity potential. However, further studies should be conducted to test this hypothesis and assess the specific value of germplasm from highlands of Mexico for yield improvement of small-seeded cultivars. The specific characteristics of bean cultivars, 'Konstantin 1026' (MITRANOV 1983) and 'IC 7808' (SINGH and SAINI 1983), which were reported to have positive GCA for seed yield and its components, are not known to us, but cultivar 'Pinto UI III' (FOOLAD and BASSIRI 1983) which showed positive GCA for seed yield belongs to the same gene pool 5 as landraces 'Guanajuato 31' and 'Ojo de Liebre' from the highlands of Mexico. Since all five lines derived from the cross 'Carioca' x 'Guanajuato 31' and both lines 'Ojo de Liebre' x 'A27' that were included in this study had positive GCA for seed yield and seed weight, this may suggest that the inheritance of these traits is controlled by major genes or gene families in these landraces from the Mexican highlands.

Since the magnitude and sign of GCA estimates for seed yield and its components for 'A 132,' 'A 359' and 'A 375' were similar (Tables 1 and 2) to those reported previously (NIENHUIS and SINGH 1986), in large breeding programs of self-pollinated crops such as common bean, the Design II mating system should be preferred over diallel crosses for estimation of GCA, because a comparatively large number of parents can be studied from relatively few crosses.

Because most small-seeded parents, including high yielding commercial cultivars, had negative GCA and because the narrow sense heritability of yield was reported to be low (CHUNG and STEVENSON 1973; COYNE 1968; MUTSCHLER and BLISS 1981; FOOLAD and BASSIRI 1983; NIENHUIS and SINGH unpublished; PANIAGUA and PINCHINAT 1976; ZIMMERMANN et al. 1984), serious problems arose for devising an effective breeding strategy to increase dry bean yield. Selection for morphological traits positively associated with yield did not increase yield in dry bean of growth habits I, II, and III in tropical environments (NIENHUIS and SINGH 1985). Also, recurrent selection (DUARTE 1966; TOLLA 1978), recurrent mass selection based on a desired gain index (SULLIVAN and BLISS 1983), and simple phenotype selection for bean yield (COYNE 1968) were not effective. How then could yield potential of small-seeded dry bean cultivars be improved?

The 18 experimental lines identified with positive GCA for yield are of special interest, because they vary in growth habit, seed size, and maturity as well as in other traits, and most of them were derived from crosses involving high-yielding cultivars adapted to tropical environments. Thorough evaluation and in-depth genetic study of these lines and their parents and pedigree should help find clues as to how both GCA and yield of small-seeded commercial cultivars could be improved. Also, other sources of germplasm from both Middle and South

American centers of domestication and elsewhere, that are likely to combine well with the existing small-seeded traditional and improved cultivars should be searched out. In the meantime, the 18 lines and those identified by other researchers (FOOLAD and BASSIRI 1983; MITRANOV 1983; SINGH and SAINI 1983) possessing positive GCA for yield should be utilized in crossing programs for improvement of small-seeded cultivars, especially for tropical and subtropical Latin America.

Apparently there is an urgent need for introgressing genes from other gene pools (SINGH 1987) to broaden the base of small-seeded cultivars. If parents to be utilized in crosses vary in maturity, seed size, growth habit, and ecological adaptation, their combinations should be determined carefully to assure involvement of at least one parent with high positive GCA for yield in each cross. When crossing among extreme types (e.g., growth habit I x growth habit IV, small- x large-seeded, and extremely early x late-maturing types), their single crosses should be utilized in subsequent crosses (SINGH 1982) or in backcrosses or subjected to selective intermating in segregating generations, or recurrent selection should be employed to increase the frequency of desirable genes. All resulting F_2, F_3, and F_4 generations should be yield-tested in replicated trials at commercial cropping densities within target environments. High-yielding populations and families could then be identified for each maturity and growth habit for single plant selection and progeny tests from F_5 on. This proposed method of mass selection based on replicated yield tests in early segregating generations should also facilitate stabilization and selection of other desirable agronomic traits, including seed color, size, shape, and brilliance (SINGH 1988).

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Table 1. Parental characteristics and general combining ability of commercial cultivars, sources of resistance, and other common bean lines for seed yield and its components at two locations, CIAT-Palmira (Pal.) and CIAT-Quilichao (Quil.) in Colombia in 1983.

Parental characteristics							General combining ability							
Identification	Set[†] No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
Old and new cultivars														
Aete 3	4F	Cream	III	75	Small	Brazil	0	0	0	0	0	0	0	0
Aroana 80	3M	Brown	II	77	Small	Brazil	0	0	0	0	-*	0	0	0
BAT 58	3F	Black	II	73	Small	Brazil	-**	0	-*	0	0	0	-**	0
BAT 304	3F	Black	III	68	Small	Brazil[‡]	0	0	0	0	0	0	0	0
Carioca	7M	Cream striped	III	76	Small	Brazil	-**	0	-**	0	0	0	0	0
Carioca 80	8F	Cream striped	III	75	Small	Brazil	0	0	-**	0	+*	0	+**	0
Catu	8M	Cream	II	74	Small	Brazil	0	0	-*	0	+**	+*	-**	0
CENA 164	6F	Cream striped	II	76	Small	Brazil	0	0	+*	0	-**	0	0	0

Table 1 (continued):

Parental characteristics							General combining ability							
Parent identification	Set† No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
EMP 84	1F	Black	II	73	Small	Argentina	0	0	0	0	0	0	0	0
ICA Pijao	2M	Black	II	70	Small	Guatemala‡	0	0	0	0	+**	0	0	0
IPA 74-19	8F	Cream	III	74	Small	Brazil	-*	0	0	0	0	0	-**	0
Jamapa	8M	Black	II	70	Small	Mexico	-**	0	0	0	0	0	-**	-*
Moruna 80	6F	Black	II	73	Small	Brazil	0	0	0	0	0	-*	0	0
Porrillo Sintetico	1M	Black	II	74	Small	El Salvador	0	-**	0	0	0	0	0	0
RAI 54	7F	Brown	III	73	Small	Brazil	-*	0	0	0	0	0	-**	0
Rio Tibagi	6F	Black	II	75	Small	Brazil	0	0	0	0	+**	+*	0	-**
Sources of resistance														
A 59	3F	Gray	III	64	Medium	Earliness	0	0	0	0	0	0	+**	+*
A 63	7F	Beige	III	78	Small	Angular leafspot	0	0	+*	+*	0	0	-**	-**
A 176	8F	Beige	III	72	Small	Angular leafspot	0	0	0	0	-**	-*	0	0
A 210	8M	Black	II	72	Small	Anthracnose	0	0	0	0	0	0	-**	0

Table 1. (continued)

	Parental characteristics						General combining ability							
Identification	Set[†] No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2) Pal.	Yield (g/m^2) Quil.	Pods/m^2 Pal.	Pods/m^2 Quil.	Seeds/pod Pal.	Seeds/pod Quil.	Seed weight Pal.	Seed weight Quil.
A 297	1F	Beige	II	71	Small	Angular leafspot	0	0	0	0	0	+**	-**	-**
A 339	8F	Cream	II	73	Small	Angular leafspot	0	0	0	0	-**	-*	0	0
A 430	5F	Pinto	II	79	Small	BGMV	0	0	0	0	0	0	0	0
A 433	5F	Pinto	II	76	Small	BGMV	0	0	0	-*	0	0	0	0
A 471	7F	Purple mottled	I	75	Medium	Angular leafspot	-**	0	0	0	-*	-**	0	0
BAT 85	2M	Cream	II	75	Small	Drought	0	0	0	0	0	+*	0	0
BAT 841	5F	Beige	III	71	Small	Anthracnose	0	0	0	0	0	0	0	0
DOR 60	6M	Black	II	74	Small	BGMV	0	0	0	0	+*	+**	0	-*
EMP 110	5F	Cream	II	73	Small	Leafhopper	0	-*	0	-*	+*	0	-**	0
EMP 117	7M	Cream striped	III	70	Small	Leafhopper	0	0	0	0	0	+**	-**	0
XAN 87	2F	Black	II	72	Small	Common blight	0	0	0	0	0	0	0	0
XAN 94	2M	Red	II	68	Small	Common blight	-**	0	0	0	0	+*	-**	-**
XAN 110	1M	Red	II	73	Small	Common blight	0	0	0	0	+*	0	-**	0

Table 1. (continued)

	Parental characteristics						General combining ability							
Identification	Set† No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
Other lines														
A 57	6F	Cream	I	73	Small	Architecture	0	0	0	0	0	-*	+*	0
A 126	7M	Cream	II	73	Small	Architecture	0	0	+**	0	-*	-**	0	0
A 132	6M	Cream	I	69	Small	Dwarf	-**	-**	0	0	-**	-**	0	0
A 140	1F	Cream	III	79	Small		0	-*	0	0	0	-**	0	0
A 156	4M	Cream	II	75	Small	High node numbers	0	0	+*	+**	0	-**	-**	0
A 205	5M	Gray speckled	III	71	Small		0	0	0	0	0	0	0	0
A 218	4M	Black	II	69	Small		-*	0	0	0	-**	0	0	0
A 282	3F	Cream striped	II	75	Small		0	0	0	0	0	+*	-**	0
A 287	4F	Cream striped	II	75	Small		0	0	0	0	+**	+**	-**	-**
A 293	4M	Cream	II	76	Small		0	0	0	0	0	+**	0	0

Table 1. (continued)

Parental characteristics							General combining ability							
Identification	Set[†] No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
A 317	1F	Cream	III	70	Medium		-**	0	-**	0	0	-*	0	0
A 348	2F	Cream	III	79	Small		0	0	0	-*	+**	+**	0	0
A 354	5M	Cream	III	79	Small		0	0	0	0	0	0	-**	0
A 359	6M	Cream	II	77	Small		0	0	0	0	0	+**	-**	-*
A 367	2M	Gray	III	71	Small		0	0	0	0	0	0	+*	0
A 387	3M	Beige	II	79	Small		0	0	0	0	0	-**	0	0
A 395	2F	Cream	II	78	Medium		-**	0	0	0	-*	-**	0	0
A 409	5M	Pink speckled	III	78	Small		0	0	0	0	0	0	+**	0
A 488	3M	Red mottled	III	75	Medium	Andean region	-*	0	0	0	-*	-*	0	0

Table 1. (continued)

Parental characteristics							General combining ability							
Identification	Set† No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
BAT 1256	4F	Purple mottled	I	72	Medium	Andean region	-*	0	0	0	-**	-**	+**	+**
BAT 1301	1M	Brown mottled	II	79	Small		0	0	+**	+**	-**	-**	-**	-**
BAT 1407	7M	Purple mottled	I	72	Medium	Andean region	0	0	0	0	-**	-**	+**	0
BAT 1449	5M	Red	III	70	Small		0	-*	0	0	0	0	-**	-**
BAT 1458	3M	Pink	III	71	Small		0	0	0	0	0	0	0	0
BAT 1514	4M	Red	II	69	Small		0	0	0	0	0	0	0	0
BAT 1550	1M	Cream	II	79	Small		-**	0	-*	0	0	0	-**	-**
BAT 1658	4F	Red	II	76	Small		0	0	0	+*	0	0	-**	-*
BAT 1659	8F	Red	II	70	Small		0	0	+**	0	0	0	-**	-*
BAT 1671	2F	Cream speckled	III	79	Small		0	-*	+*	0	0	0	-**	0

Table 1. (continued)

Parental characteristics							General combining ability							
Identification	Set[†] No.	Seed color	Growth habit	Days to maturity	Seed size	Observation	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
Location Mean							137	157	145	166	4.1	4.0	23.3	23.7
Standard error of GCA effects							7	11	7	10	0.2	0.1	0.4	0.7

[†] Set in which the parent was crossed either as male (M) or female (F).

[‡] Also, cultivated in other countries.

*, ** Significant at P=0.05 and P=0.01, respectively.

Table 2. Characteristics of bean lines with positive general combining ability for seed yield at CIAT-Palmira (Pal.) and/or CIAT-Quilichao (Quil.) in Colombia in 1983.

Parental Characteristic							General Combining Ability							
Identification	Set† No.	Seed color	Growth habit	Days to maturity	Seed size	Pedigree	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
A 213	2M	Black	III	74	Medium	BAT 76 x (G 879 x Garrapato)	+**	0	+**	+*	-**	-**	+**	+**
A 246	7M	Cream striped	II	68	Small	Carioca x BAT 76	+*	0	0	0	+**	0	-**	-*
A 252	1F	Cream striped	III	70	Small	Carioca x Guanajuato 31	+**	0	+*	0	0	0	+**	+**
A 259	8M	Cream striped	III	66	Small	Carioca x Guanajuato 31	+*	0	0	0	0	0	+**	0
A 373	3F	Brown	III	67	Medium	Carioca x Guanajuato 31	+**	0	0	0	0	0	+**	0
A 375	1M	Brown	III	72	Medium	Carioca x Guanajuato 31	+**	+*	0	0	0	+*	+**	+**
A 445	7F	Brown striped	III	79	Medium	Carioca x Guanajuato 31	+**	0	0	0	0	0	+**	0

Table 2 (continued):

		Parental Characteristic					General Combining Ability							
							Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
Identification	Set[†] No.	Seed color	Growth habit	Days to maturity	Seed size	Pedigree	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
A 457	7F	Brown striped	III	70	Medium	Ojo de Liebre x A 27	+**	0	-*	-**	0	+*	+**	+**
A 462	4F	Brown striped	III	71	Medium	Ojo de Liebre x A 27	+*	0	0	-**	0	0	+**	+**
A 310	2F	Cream	III	79	Medium	BAT 561 x (G 879 x G 2337)	0	+**	0	+**	-*	0	+**	+*
BAT 477	3M	Cream	II	69	Small	(G 3834 x G 4493) x (G 4792 x G 5694)	+**	+*	0	0	+**	+**	0	0
BAT 1510	5F	Purple	III	76	Small	BAT 93 x BAT 821	0	+*	0	+**	0	0	0	0
BAT 1573	6F	Red	II	70	Small	BAT 896 x BAT 1040	+*	0	0	0	+*	0	+**	0
BAT 1617	8M	Brown mottled	I	73	Medium	Pompadour x ICA Tundama	+**	0	+*	0	-**	-**	+**	+**
BAT 1670	5M	Red	III	70	Small	BAT 1225 x BAT 1200	0	+**	0	0	0	0	+**	0
G 825	6M	Black	III	75	Medium	Wulma, Zaire	+**	0	0	-*	0	0	+**	+**
RIZ 11	6M	Black	III	74	Small	(G 4482 x G 5711) x (G 5711 x G 5694)	0	+**	0	+**	0	0	0	0
XAN 105	4M	Beige	III	76	Medium	G 11509 x BAT 93	+*	0	0	0	0	0	+**	+**

Table 2 (continued):

Parental Characteristic							General Combining Ability							
Identification	Set[†] No.	Seed color	Growth habit	Days to maturity	Seed size	Pedigree	Yield (g/m^2)		Pods/m^2		Seeds/pod		Seed weight	
							Pal.	Quil.	Pal.	Quil.	Pal.	Quil.	Pal.	Quil.
Location Mean							137	157	145	166	4.1	4.0	23.3	23.7
Standard error of GCA effects							7	11	7	10	0.2	0.1	0.4	0.7

[†] Set in which the parent was crossed either as male (M) or female (F).

*, ** Significant at P=0.05 and P=0.01, respectively.