Potential of wild common bean for seed yield improvement of cultivars in the tropics

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Singh, S. P., Molina, A. and Gepts, P. 1995. **Potential of wild common bean for seed yield improvement of cultivars in the tropics.** Can. J. Plant Sci. **75**: 807–813. Thirty nine wild or weedy common bean (*Phaseolus vulgaris* L.) accessions, representing the two extremes of geographical range of distribution and domestication of cultigens in the Americas, were crossed to a high-yielding, small-seeded cultivar, ICA Pijao. The resulting F_1, F_2, and F_3 population bulks, along with ICA Pijao, were evaluated for seed yield, days to maturity, and 100-seed weight under favorable growing conditions at two locations in Colombia. The F_3 and F_4 bulks were tested separately under soil-fertility and moisture stresses. Thirty random F_5-derived F_8 lines from the highest yielding population involving both Andean and Middle American wild beans, along with the parents and a control cultivar, were also evaluated for 2 yr, under favorable conditions. No F_1 hybrid, population bulk, or F_5-derived F_8 line significantly outyielded ICA Pijao in any test environment. The mean yield of F_1 hybrids, population bulks, and F_5-derived F_8 lines involving wild and weedy beans of Middle America was higher than that involving Andean South American wild beans. Heritability for seed yield, seed weight, and days to maturity, as well as gains from selection were comparable to those obtained in crosses among cultivars. The small seed of the progenies and the positive correlation between seed size and seed yield suggest that alternative mating schemes that increase the recovery of progenies with a cultivated phenotype should be investigated. Until this research is done, it would be premature to draw conclusions about the yield improvement potential of wild beans.

Key words: *Phaseolus vulgaris*, common bean (wild), yield, heterosis, heritability, selection gain

Singh, S. P., Molina, A. et Gepts, P. 1995. **Potentialités de l'utilisation des formes sauvages du haricot pour améliorer le rendement grainier des cultivars dans les Tropiques.** Can. J. Plant Sci. **75**: 807–813. Trente-neuf obtentions de haricot (*Phaseolus vulgaris* L.) vivant à l'état sauvage ou adventice et représentatives des deux extrêmes de l'aire géographique de répartition et de domestication de cette espèce cultivée dans l'Amérique latine, ont été croisées avec un cultivar à petits grains, de rendement élevé ICA Pijao. Les populations résultantes F_1, F_2 et F_3 (en mélange) ainsi que le cultivar testeur étaient évaluées sur le rendement grainier, sur la précocité de maturation et sur le poids de 100 grains dans de bonnes conditions de culture, à deux endroits en Colombie. Les populations mélangées F_3 et F_4 étaient évaluées séparément en conditions de fertilité médiocres et en condition de stress hydrique. Trente lignées F_8 aléatoires issues de F_5 ($F_{5.8}$) provenant de la population la plus productive comportant des lignées sauvages mésoaméricaines et andennes, ainsi que les progéniteurs et un cultivar témoin étaient également évalués pendant deux ans dans de bonnes conditions de végétation. Aucun F_1, mélange de populations et lignée $F_{5.8}$ n'avait un rendement significativement supérieur à celui de Pijao, quelles que soient les conditions de culture. Le rendement moyen des hybrides F_1, des mélanges de populations et des lignées $F_{5.8}$ comportant des obtentions sauvages ou adventices d'Amérique centrale était supérieur à celui des lignées provenant de la région andéenne de l'Amérique du Sud. Les valeurs d'héritabilité pour le rendement grainier, le poids du grain et la précocité de maturation ainsi que les gains réalisés par la sélection étaient semblables à ceux observés dans les croisements entre cultivars. La faible grosseur du grain dans les descendances et la corrélation positive entre la grosseur du grain et le rendement grainier semblent indiquer qu'il faudrait envisager d'autres protocoles de croisement susceptibles de produire davantage de descendances possédant un phénotype de haricot cultivé. En attendant ces recherches, il serait prématuré de tirer des conclusions sur les possibilités d'amélioration du rendement des formes sauvages du haricot.

Mots clés: *Phaseolus vulgaris*, haricot (sauvage), rendement, hétérosis, héritabilité, gain de sélection

Wild species related to most major field crops have been evaluated for identification and transfer of useful genes for resistance to diseases, insects, and adverse edaphic and moisture conditions and for yield potential and other traits. In the past several years, there has been an increased emphasis on exhaustive and systematic collection, preservation, characterization, and use of the biodiversity available within the cultigens and their wild progenitors. The progeny of crosses between crop plants' wild progenitors and their cultivated descendants usually do not exhibit the viability and fertility problems characterizing interspecific crosses. This should facilitate the transfer of useful traits from the wild progenitors to the cultivated descendant. In addition, both theoretical considerations and empirical results suggest that domestication has often produced a bottleneck in genetic diversity (Ladizinsky 1985; Doebley 1992). Wild progenitors could thus, represent a reservoir of additional genetic diversity for crop improvement.

Wild common bean (*Phaseolus vulgaris* L.) populations are distributed from northern Mexico to northwestern Argentina (Nabhan et al. 1986; Toro et al. 1990). Contrasting differences for morphological (Gepts and Debouck 1991), molecular (Gepts et al. 1986; Koenig et al. 1990), physiological (Lynch et al. 1992), and reproductive isolation traits (Koinange and Gepts 1992) between wild populations from the two extremes of their range and parallel geographical distributions of some similar traits in the cultivated counterparts from the respective regions (Gepts et al. 1986; Singh et al. 1991b) strongly suggest that this divergence in wild bean populations of Middle and Andean America probably occurred prior to domestication (Singh et al. 1991a; Koinange and Gepts 1992). The cultivated common bean of Andean origin has a greater seed weight (≥40 g 100-seed weight^{-1}) than its Middle American counterparts (Gepts and Bliss 1985; Singh et al. 1991b). Also, Andean cultivars appear to be physiologically less efficient and yield less seed than their Middle American counterparts (White et al. 1992).

Both wild and cultivated common beans possess $2n = 2x = 22$. Although some exceptions occur (Wells et al. 1988), both wild populations and cultigens are predominantly self-pollinating (Tucker and Harding 1975; Pereira Filho and Cavariani 1984). Moreover, wild beans cross easily with cultigens, producing normal, fertile progenies (Motto et al. 1978) and, hence, form part of the primary gene pool of *P. vulgaris*.

The level of polymorphism for phaseolin seed protein (Gepts et al. 1986; Koenig et al. 1990) in wild bean, compared with cultivars of common bean, may suggest a reduction in genetic diversity upon domestication. This is indicated by the discovery of higher levels of polymorphism for phaseolin seed protein in wild than in cultivated landraces of common bean (Gepts et al. 1986; Koenig et al. 1990). Useful genes may be present in wild bean populations. For example, the arcelin gene (*Arl*), which confers high levels of resistance to storage insect bruchids, *Zabrotes subfasciatus* Boheman (van Schoonhoven et al. 1983; Cardona et al. 1989), is found in wild beans from Mexico but is not found in cultivated landraces.

Consequently, all available wild beans in the germplasm bank at the International Center for Tropical Agriculture (CIAT), Cali, Colombia, are being systematically evaluated for reaction to principal diseases and pests and for other traits. Because wild beans have extremely small seeds that often shatter when pods mature and are poorly adapted, meaningful evaluations of the accessions per se for yield and other traits dependent on yield measurements, such as tolerance of drought and low soil fertility, could not be made. These traits could, however, be studied by crossing representative wild and weedy bean populations to tester cultivars and studying the performance of their hybrid populations and (or) derived lines.

Our objectives were to determine 1) whether similar differences in yielding ability, as in cultigens, existed between wild beans from the two regions, and 2) what the potential of wild beans would be for the improvement of yield and other traits in cultivars in the tropics.

MATERIALS AND METHODS

Thirty-nine wild and weedy accessions (Toro et al. 1990) were selected on the basis of their diversity for phaseolin seed protein (Gepts 1988) and their geographical distribution in Latin America (Table 1). Weedy accessions are wild-growing beans that show phenotypic signs of introgression from, or some similarities with, cultivated beans, such as larger seeds and modified seed colors. Five were from Argentina, 1 was from Peru, and 33 were from Mexico. More accessions were chosen from Middle America (Mexico), because of their proportionately larger number in the germplasm bank and prior reports of the presence of useful genes in them. All 39 wild and weedy bean accessions were crossed to the tropically adapted, small-seeded (<25 g 100-seed weight^{-1}), high-yielding cultivar ICA Pijao. This cultivar is a noncarrier of the complementary dominant, dosage-dependent, lethal DL_1 and DL_2 genes which cause hybrid weakness, dwarfism, or incompatibility in some Middle American × Andean common bean crosses (Singh and Gutiérrez 1984; Gepts and Bliss 1985). These incompatibility genes are also known to occur in wild populations (Koinange and Gepts 1992). In all cases, ICA Pijao was used as the female parent and hybridizations were made by hand emasculation and pollination in 1987–1988. In most cases, repeated plantings of parents were made to obtain an adequate quantity of F_1 seed. Part of the seed of each F_1, along with ICA Pijao, was grown at CIAT, Palmira (1000 m elevation; mean temperature, 24°C; and Mollisol soil with pH 7.5), to check for its hybrid origin and to produce selfed (F_2) seed.

Experiment 1

Thirty-nine F_1 hybrids, their F_2 populations, and ICA Pijao were evaluated on CIAT farms at Palmira and Popayán (1750 m elevation; mean temperature, 18°C; and Inceptisol soil with pH 4.5) in 1989. The F_1 and F_2 of each wild bean accession, along with ICA Pijao, were grown together in paired plots. A randomized complete-block design, with two replications, was used. Each plot consisted of four rows, 5 m long. Spacing between rows at Popayán was 50 cm; at Palmira, 60 cm. Trials were kept free from weeds, diseases, and insects during the entire growing season. Soil corrections were made at Popayán and fertilizers were applied at both Palmira and Popayán to ensure normal growth and development. Also, irrigation was applied at Palmira whenever required. Data were recorded on days to maturity, 100-seed weight (g), and seed yield (kg ha^{-1}). The latter two were converted to 14% moisture by weight. F_1 heterosis (%

Table 1. Geographical and phaseolin-type origin of wild and weedy common bean used in crosses with cultivar ICA Pijao

Geographical origin	Number of accessions	Phaseolin type[z]
Middle America		
Mexico		
Wild	23	S(12), M(11)
Weedy	10	S (6), M (4)
Andean America		
Peru		
Weedy	1	T (1)
Argentina		
Wild	5	C (2), H (2), T (1)
Cultivated tester		
ICA Pijao (Colombia)	1	S

[z]According to Gepts et al. (1986)

Table 2. Morphological and other characteristics of cultivar ICA Pijao, wild Andean and Middle American bean with the highest seed yield in early-generation bulk population tests used for line development, and check cultivar Carioca

Identification	Growth habit[z]	Bracteole		Stripe-of-flower standard	Seed color	Disease score[y]	
		Shape	Size			BCMV	Anthracnose
ICA Pijao	II	Lanceolate	Large	Present	Black	R	9
G 12864	IV	Cordate	Medium	Present	Gray speckled	S	3
G 19898	IV	Triangular	Small	Absent	Brown striped	S	6
Carioca	III	Cordate	Large	Present	Cream striped	R	5

[z]II, indeterminate erect; III, indeterminate prostrate; IV, indeterminate climbing.
[y]For BCMV: R, resistant; and S, susceptible. For anthracnose: 1–3, resistant; 4–6, intermediate; 7–9, susceptible.

over ICA Pijao) and inbreeding depression in the F_2 were calculated for seed yield.

Experiment 2

The same 39 F_2 and their F_3 populations, along with ICA Pijao, were grown on CIAT Farms at Palmira (March to May) and Popayán (May to August) in 1990. A randomized complete-block design, with four replications, was used. Each plot consisted of four rows, 7 m long. Spacing between and within rows, agronomic management of the trial, and data recordings were similar to those of exp. 1.

Experiment 3

The 39 F_3 and their F_4 populations, along with ICA Pijao, were evaluated under moisture stress from June to August 1990 at CIAT, Palmira. One irrigation was applied before sowing, and two additional irrigations were applied during the first 3 wk after sowing. A similar trial was conducted at CIAT, Quilichao (990 m elevation; mean temperature, 24°C; Oxisol soil with pH 4.5 and moderately deficient in nitrogen and phosphorus). A randomized complete-block design, with four replications, was used at both locations. Plot size, spacings between and within rows, and data recordings were similar to those of exp. 2.

Data from exp. 1, 2 and 3 were used to calculate heritability by parent–offspring regression (Smith and Kinman 1965). Also, expected and realized gains from selection (20% selection pressure) were calculated according to Frey and Horner (1955).

Experiment 4

One high-yielding population involving a wild bean accession (G 12864) from Mexico (GX 8166 = ICA Pijao × G 12864) and another involving a wild bean accession (G 19898) from Argentina (GX 8191 = ICA Pijao × G 19898) were selected on the basis of their mean seed yield in F_1, F_2, F_3, and F_4 population bulks across environments. Characteristics of ICA Pijao, G 12864, and G 19898 are listed in Table 2.

A representative sample of the F_5 seed of both populations was space-planted at Popayán in a plot with four rows, 7 m long. Before sowing, all extremely small seeds (<10 g 100-seed weight^{-1}) resembling the wild parents and requiring scarification of the seed coat were discarded. Approximately 250 plants were harvested individually from each population. They were grown in plant-to-progeny rows in the F_6. All plants within a row were harvested in bulk, and their seed was increased in the F_7. Thirty F_5-derived F_8 lines taken randomly from each of two populations, along with ICA Pijao, G 12864, G 19898, and the control cultivar, Carioca (Table 2), were tested for 2 yr (1992 and 1993) at Popayán. Carioca is a small-seeded cultivar of race Mesoamerica and is extensively grown in Brazil and other

Table 3. Mean seed yield (kg ha^{-1}), 100-seed weight (g), and maturity (days) of F_1, F_2, F_3, and F_4 population bulks involving wild common beans of Andean and Middle American origin and a tester parent, ICA Pijao, grown in different environments in Colombia

	Seed yield					Maturity					100-seed weight			
	Nonstressed			Stressed		Nonstressed			Stressed		Nonstressed			Stressed
	Exp. 1		Exp. 2	Exp. 3	Exp. 4	Exp. 1		Exp. 2	Exp. 3	Exp. 4	Exp. 1		Exp. 2	Exp. 4
				Moisture	Soil fertility				Moisture	Soil fertility				Soil fertility
	F_1	F_2	F_2 & F_3	F_3 & F_4	F_3 & F_4	F_1	F_2	F_2 & F_3	F_3 & F_4	F_3 & F_4	F_1	F_2	F_2 & F_3	F_3 & F_4
Middle American														
Mean	2750	2211	1921	535	692	81.4	80.4	80.0	76.5	72.0	14.1	12.6	10.8	11.5
GX 8166	3682	2780	1910	736	868	83.0	82.5	80.5	78.5	74.0	14.0	13.7	11.1	11.3
Andean American														
Mean	2053	1722	1773	377	771	79.2	80.9	80.0	77.0	71.0	15.4	15.1	12.4	12.7
GX 8191	2368	1326	1954	366	987	82.0	83.0	81.5	79.0	71.5	14.2	14.2	11.8	12.3
ICA Pijao	3020	2849	2026	983	1396	81.3	81.3	77.0	72.0	73.0	22.5	22.5	17.2	20.0
$LSD_{0.05}$[z]	981	981	342	261	315	4.4	4.4	2.4	2.8	3.3	1.8	1.8	1.2	1.3
$LSD_{0.05}$[y]	611	611	107	82	100	2.7	2.7	0.7	0.9	1.0	1.1	1.1	0.4	0.4

[z]For comparison of values between GX 8166 and GX 8191.
[y]For comparison of mean values between the Middle American and Andean American populations.

Table 4. Heterosis (%) over a tester parent, ICA Pijao, and inbreeding depression (%) for seed yield in crosses with wild and weedy common bean of Andean and Middle American origin grown at two locations in Colombia in 1989

	F_1 heterosis			Inbreeding depression in F_2		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Andean	-71.6	-17.1	-34.0	-44.0	33.5	-11.0
Middle American	-36.8	18.4	-12.9	-47.0	18.1	-14.9

countries. An 8 × 8 lattice design, with three replications, was used. Each plot consisted of 4 rows, 3.4 m long. Spacing between rows was 0.5 m. Plots were kept free from diseases, insects and weeds throughout the entire cropping season. Two central rows with head borders of 20 cm on either end, were harvested for yield measurements (kg ha^{-1}, adjusted to 14% moisture by weight). Data were also recorded for days to maturity and 100-seed weight (g). Data were subjected to a standard statistical analysis whereby populations were considered fixed and years random effects.

RESULTS

Table 3 presents mean values for yield for different generations and environments. In general, yields in the F_1 were higher than in the F_2 and subsequent generations, thus showing inbreeding depression. The sharpest reduction in yield in nonstressed environments occurred between the F_1 and F_2. When populations were grouped on the basis of their evolutionary origin (Middle American vs. Andean), the mean values for F_1 hybrids involving Middle American wild beans were significantly higher ($P < 0.05$) than those involving Andean types. Similarly, mean seed yields of F_1 hybrids and F_2 bulk populations of GX 8166 (Mexican) were significantly higher than those of its Andean counterpart, GX 8191 (Table 3).

The percentage heterosis for seed yield (averaged over Palmira and Popayán) over ICA Pijao in the F_1 ranged from -71.6 to 18.4%, and values ranged from -47.0 to 33.5% for inbreeding depression in the F_2 (Table 4). Only six values for both heterosis and inbreeding depression were significant ($P < 0.05$), all of which were negative (data not shown). Thus, none of the F_1 or F_2 generations significantly outyielded ICA Pijao.

Marked reductions in yield were observed when the F_3 and F_4 generations were tested under moisture stress at Palmira and soil-fertility stress at Quilichao (Table 3). Although differences among populations were significant, none of the populations bulk yields were equal to or higher than that of ICA Pijao under either stressed environment.

Heritability calculated on the basis of the parent–progeny regression (Smith and Kinman 1965) for seed yield under favorable conditions was 0.32 ± 0.14 (Table 5). Values under moisture and soil-fertility stresses, respectively, were 0.40 ± 0.12 and 0.40 ± 0.16. Expected selection gains (at 20% selection pressure) ranged from 4.8 to 16.6%; actual gains, from 2.2 to 11.8% (Table 5). The heritability values for 100-seed weight and days to maturity were higher (≥0.64) in nonstressed than stressed environments (<0.50). Gains from selection for 100-seed weight were ≥17.0%; for days to maturity, <2.5%. These values are comparable to those obtained in crosses among cultivars (Singh et al. 1990; Singh and Urrea 1994).

Table 5. Heritability obtained from parent–offspring regression and expected and actual gains from selection for seed yield, 100-seed weight, and days to maturity in wild and weedy populations of common bean grown in stressed and nonstressed environments in Colombia

Character and environment	Heritability	Gains from selection[z] Expected	Actual
Seed yield			
Nonstressed (F_3 on F_2)	0.32±0.14	4.8	2.2
Stressed (F_4 on F_3)			
Moisture	0.40±0.12	16.6	9.8
Soil fertility	0.40±0.16	15.7	11.8
100-seed weight			
Nonstressed	0.65±0.07	18.0	17.0
Stressed			
Moisture	—	—	—
Soil fertility	0.50±0.09	32.1	31.6
Days to maturity			
Nonstressed	0.64±0.03	2.5	2.4
Stressed			
Moisture	0.33±0.13	1.7	1.4
Soil fertility	0.40±0.11	2.5	1.6

[z]Determined at 20% selection pressure and expressed in % over the mean of all bulk populations.

Table 6 presents correlation coefficients between filial generations for seed yield, 100-seed weight, and days to maturity. All values were positive and significant ($P < 0.01$).

The mean value for 30 F_5-derived F_8 lines from population GX 8166 involving Middle American wild bean was significantly higher than for GX 8191, the Andean counterpart (Table 7). But differences for the highest and lowest yielding lines were not significant ($P > 0.05$). None of the lines in either population significantly outyielded ICA Pijao. Population GX 8166, on average, matured later than GX 8191. No differences were recorded for 100-seed weight between the mean values for the two groups of lines. The check cultivar, Carioca, had slightly greater 100-seed weight than ICA Pijao. But its seed yield and days to maturity were similar to those of ICA Pijao.

DISCUSSION

The genetic potential of any germplasm bank accession can be determined by 1) its performance per se, 2) the performance of its hybrid bulks, and 3) the performance of advanced generation lines derived from its hybrid populations. Because they have to aggressively compete for light, nutrients, moisture, and other resources with shrubs, trees,

Table 6. Simple correlation coefficient between generations for seed yield, 100-seed weight, and days to maturity

	No stress		Stress: Moisture	Stress: Soil fertility
	F_1–F_2	F_2–F_3	F_3–F_4	F_3–F_4
Yield (kg ha^{-1})	0.50*	0.47*	0.59*	0.42*
100-seed weight (g)	0.89*	0.90*	—	0.76*
Days to maturity	0.54*	0.95*	0.61*	0.62*

*Significance at $P = 0.01$.

Table 7. Minimum, maximum, and mean for seed yield (kg ha^{-1}), 100-seed weight (g), and maturity (days) for parents and 30 F_5-derived F_8 lines from the highest yielding population involving both Andean and Middle American wild bean, grown in different environments in Colombia

	Yield			100-seed weight			Maturity		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean
F_8 line									
Andean (GX 8191)	1720	2921	2312	12.1	17.4	14.7	83.0	88.0	85.8
Middle American (GX 8166)	2096	3318	2768	12.8	16.1	14.6	87.0	91.0	88.8
Parent									
G 19898		840			7.4			77.9	
G 12864		1053			2.3			119.0	
ICA Pijao		2973			19.0			87.0	
Check									
Carioca		2889			21.0			86.0	
$LSD_{0.05}$	491	491	90	1.8	1.8	0.3	2.7	2.7	0.5

and other plants in their natural habitat, wild bean plants display extensive vegetative development, such as climbing growth habit and profuse branching (Smartt 1988). Hence, the fitness of wild beans in their natural habitat is conditioned by their vegetative as much as by their reproductive development. This is reflected in the lower harvest index displayed by wild beans. In addition, wild and weedy common beans have much smaller seeds than cultigens, have seeds that require scarification before sowing (a time- and labor-consuming task), are rarely used for human consumption, have undesirable traits (including seed shattering when pods mature), and are often poorly adapted. It is thus usually not possible to objectively assess the potential value of wild bean accessions for increasing yield potential based on their yield performance per se. Therefore, the performance of hybrid bulks and (or) lines derived from them was the criterion used to assess the potential of 39 wild and weedy accessions of common bean from their extreme domestication regions in the Americas.

The first indication of a wild or weedy accession's potential is the performance of its F_1 with a common tester parent. Even in crops where commercial use of F_1 heterosis is not currently feasible, the magnitude and sign of F_1 heterosis indicate the genetic diversity and complementarity between the parents and the upper limits of potential performance of homozygous lines that could be derived from the cross in subsequent generations. Although none of the positive heterotic values that varied from 0.5 to 18.4% over ICA Pijao were significant ($P > 0.05$), all eight accessions involved in those crosses were from Mexico and possessed M or S phaseolin seed protein (Gepts et al. 1986). Furthermore, seven of these were wild, and only one (G 12925) was a weedy type. Because most of these accessions continued to perform well in subsequent generations, they likely possess complementary genes useful for yield potential not present in ICA Pijao. Thus, individual lines derived from the population bulks showing performances similar to ICA Pijao and possessing the complementary useful genes from both parents might outyield ICA Pijao in advanced generations.

In general, early generations of populations involving Mexican wild and weedy beans outyielded those involving Peruvian and Argentinean accessions (Table 3). Similar tendencies were observed for the F_5-derived F_8 lines from the highest yielding populations from each of the respective regions (Table 7). This suggests that Andean wild bean populations are inherently inferior in yield potential and are physiologically inefficient compared with their Mexican counterparts. Similar conclusions were arrived at by Lynch et al. (1992), who reported that Mexican wild and weedy accessions have high photosynthetic rates, low soluble-protein content, and the highest instantaneous photosynthetic nitrogen-use efficiency. Argentinean accessions had low values for these leaf-photosynthesis-related parameters. As noted earlier, similar patterns and differences in yielding ability are observed in small- and medium-seeded Middle American compared with large-seeded Andean cultivated beans (White et al. 1992). Furthermore, Nienhuis and Singh (1988) and Singh et al. (1992) reported that cultivated germplasm from Mexican highland races Jalisco and Durango (Singh et al. 1991a) possessed positive general combining ability for seed yield and could be used as parents for yield improvement of germplasm belonging to other races and gene pools (Singh et al. 1989; Singh and Urrea 1994). This also suggests that diversification among Middle American and Andean common beans predates domestication from wild beans to cultigens (Koinange and Gepts 1992; Singh et al. 1991b). An alternative explanation for the superiority of Mexican wild beans is that they belong to the same gene pool(s) as the tester cultivar ICA Pijao. The crosses between ICA Pijao and Andean wild beans may be subject to the same poorly understood yield-reducing factors that characterize crosses involving Middle American and Andean cultivars (Kornegay et al. 1992; Singh and Gutiérrez 1984; Singh and Urrea 1994).

Within Mexican wild versus weedy accessions, mean yield differences were significant in the F_2 in nonstressed environments and in the F_3 and F_4 generations at Quilichao under soil-fertility stress. In each case, the mean yield of populations involving weedy types was higher than that involving wild types. When wild beans were grouped on the basis of their phaseolin type, that is, M versus S types, the mean differences were significant only in the F_1; those with M type, on average, had higher heterotic values and were superior to those involving accessions with S type (unpublished).

Because differences among population bulks within and across generations were highly significant ($P < 0.01$) in all test environments, narrow-sense heritability and expected and realized gains from selection were calculated for seed yield (Table 5). Heritability values for seed yield were similar to those reported earlier for populations derived from crosses within cultivated common bean (Singh et al. 1990; Singh and Urrea 1994). The expected gains from selection (20% selection pressure) were usually higher than the realized gains. Furthermore, genetic gains for seed yield were higher under moisture or fertility stress than under optimum conditions. This occurred because the heritability values in stressed environments were higher. Also, it is likely that the range of variation among populations in stressed environments was smaller. Positive association between filial generations existed for all traits (Table 6). Thus, it should be possible to identify high- and low-yielding populations on the basis of bulk yield performance in early generations (Hamblin and Evans 1976; Singh et al. 1990; Singh and Urrea 1994). Low-yielding populations could be discarded early on.

Although mean values of 30 random F_5-derived F_8 lines from GX 8166 (Middle American) were significantly higher than those from GX 8191 (Andean), it is not understood why none of the lines, even those from GX 8166, did not significantly outyield ICA Pijao. It is likely that occurrence of exceptionally high-yielding lines, even from promising populations, is infrequent in common bean, and a sample of 30 random lines was not large enough to contain lines higher yielding than ICA Pijao because of the increased genetic distance between the wild populations and the cultivars and because seed yield is a quantitatively inherited trait with moderate to low heritability (Singh et al. 1990; Singh and Urrea 1994). Alternative mating and selection strategies, such as congruity backcrossing (Urrea and Singh 1995) and recurrent selection (Beaver and Kelly 1994), for maximizing recombination between and transfer of favorable alleles from wild common beans to cultivars might be required.

The number of Andean wild and weedy accessions used in this study was less than the number of accessions from Mexico. Also, more and different wild beans from both the Andes and Middle America have been collected since this study was undertaken (Toro et al. 1990). Therefore, there is a need to systematically study more wild and weedy accessions from different areas. In addition, there may be a need to evaluate several mating and selection systems to identify the system that will provide the highest frequency of superior recombinants in wild × cultivated crosses. The relative superiority of weedy accessions, which probably arose from wild × cultivated crosses or were partially domesticated, suggests that mating systems involving some form of backcrossing (e.g., inbred backcross, congruity backcross, and convergent backcross) may be more useful than the mating systems used in this study. These backcross-based systems may help the recovery of progeny with a cultivated phenotype, in which complementary useful genes from the wild parent may be better expressed. The small seed size of the F_2, F_3, and F_4 generations, compared with that of the cultivated parent, ICA Pijao (Table 3), indicates that their average phenotype did not resemble that of the cultivated parent. Because of the numerous phenotypic differences between wild and cultivated beans (Gepts and Debouck 1991), very large F_2 populations would have to be raised to recover progeny with a cultivated phenotype. The positive correlation between seed size and yield (Table 6) also suggests that limited backcrossing may be useful for speeding up the recovery of cultivated phenotypes, although the actual number of backcrosses and mating schemes remain to be determined. Until these experiments have been performed, it would be premature to draw a definitive conclusion about the potential of wild beans for improving the yield of cultivated beans.

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