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Characterization of agronomic traits and markers of recombinant inbred lines from intra- and interracial populations of *Phaseolus vulgaris* L.

Abstract The value of intra- and interracial populations in common bean (*Phaseolus vulgaris* L.) needs to be determined in order to create useful genetic variation for maximizing gains from selection, broadening the genetic base of commercial cultivars, and making efficient use of available resources. Five large-seeded parents of race Nueva Granada (N), two small-seeded race Mesoamerica (M), and one medium-seeded race Durango (D) were hybridized to produce one intraracial (N × N) and three interracial (two N × M and one N × D) populations. Seventy-nine F_2-derived F_6 lines randomly taken from each population along with their parents were evaluated for agronomic traits and markers at Palmira and Popayán, Colombia, in 1990 and 1991. Variation for agronomic traits and for morphological, protein, and isozyme markers was larger in interracial populations than in the intraracial population. Mean seed yield of all lines as well as yield of the highest yielding line from two interracial populations were significantly higher than that of the intraracial population. The highest ($\geq 0.80 \pm 0.15$) heritability was recorded for 100-seed weight. Values for seed yield varied from 0.19 ± 0.17 to 0.50 ± 0.16. Gains from selection (at 20% selection pressure) for seed yield ranged from 3.9% to 11.4%. Seed yield was positively associated with biomass yield, pods/m^2, and days to maturity, but harvest index showed negative correlations with these traits and a positive value with 100-seed weight. Polymorphism was recorded for phaseolin, lectins, protein Group-1 and protein Group-2 fractions, and six isozyme loci. Lines with indeterminate growth habit had significantly ($P < 0.01$) higher seed yield than lines with determinate growth habit in a Redkloud × MAM 4 population. Also, 23 other associations of markers with agronomic traits other than seed yield were recorded. Of these associations, lines with T phaseolin, the $Diap1^2$ allele, and lilac flower color tended to possess greater seed weight.

Key words *Phaseolus vulgaris* · Common bean · Inter- and intraracial populations · Recombinant inbred lines · Agronomic traits · Markers

Introduction

Common bean (*Phaseolus vulgaris* L.) is a non-centric crop, originating in two major forms, Middle American and Andean South American (Gepts and Bliss 1985; Gepts et al. 1986; Sprecher 1988; Khairallah et al. 1990; Koenig and Gepts 1989a; Singh et al. 1991b,c). Middle American and Andean cultigens can be further divided into three races each (Singh et al. 1991a). While Middle American germ plasm is characterized as having smaller seed size (100-seed weight < 40 g) than its Andean counterpart (100-seed weight > 40 g) (Gepts and Bliss 1985; Singh and Gutiérrez 1984), indeterminate Middle American genotypes with growth habits II and III usually outyield their Andean counterparts (Singh 1989; White and González 1990; White et al. 1992).

There are several reasons for the growing interest in combining Andean and Middle American genotypes, not the least of which is to enlarge the genetic base for more durable and increased levels of resistance to both biotic and abiotic stress factors affecting bean production. Impetus for combining the higher yielding Middle American germ plasm with its large-seeded Andean counterparts also stems from a greater market demand for large-seeded beans in the Andes and Africa. In the Andes and Africa, there is an urgency to stabilize and improve yield because of limited resources available to farmers and increased diseases, low soil fertility, and drought problems.

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The value of increased genetic diversity for markers and agronomic traits resulting from interracial crosses of common bean is not well understood. Likewise, the value of interracial populations for improvement of large-seeded germ plasm is not presently known. Therefore, 79 randomly chosen F_2-derived F_6 recombinant inbred lines and their parents for one intraracial and three interracial populations were characterized for agronomic traits and markers. The objectives were to (1) determine the potentials of intra- and interracial populations for seed yield and other agronomic traits, (2) measure heritability and gains from selection, and (3) identify morphological, seed protein, and isozyme markers that could facilitate selection for seed yield and other agronomic traits.

Materials and methods

Eight common bean cultivars or lines of contrasting characteristics were used to develop four single-cross populations. Both parents of population 'Canadian Wonder' × 'A 486' had determinate type-I growth habit (Singh 1982), large seed size, and characteristics of Andean race Nueva Granada (Singh et al. 1991a). For the second population, large-seeded 'ICA L23' of race Nueva Granada was crossed with small-seeded 'Brazil 2' (G 3807) of race Mesoamerica. The two parents possessed determinate type-I growth habit. For the third population, 'Rio Tibagi' (G 4830) was crossed with 'ABA 58'. 'Rio Tibagi' is a widely grown small-seeded Brazilian cultivar of type-II growth habit and black seed coat color belonging to race Mesoamerica. 'ABA 58' possesses large white seeds, type-I growth habit, and other characteristics of Andean race Nueva Granada. The fourth population was obtained by crossing 'Redkloud' (G 76) with 'MAM 4'. Cultivar 'Redkloud' belongs to race Nueva Granada and possesses type-I growth habit. Line 'MAM 4' possesses medium-sized seeds of cream color, indeterminate type-III growth habit, and other characteristics of race Durango.

A random sample of 79 F_2-derived F_6 lines and the two parents from each population were used to analyze phaseolin proteins and isozymes. They were evaluated in a reps-in-set design at CIAT farms at Popayán (1750 m elevation) and Palmira (1000 m elevation), Colombia, in 1990 and 1991. In 1990, each plot consisted of a single row with two replications. Each row was 3 m long with a spacing of 0.6 m between rows at Palmira and 0.5 m at Popayán. The population density was 21 plants/m². The central 2 m of each row was harvested for yield. In 1991, field trials were repeated at both locations using a similar experimental design. However, each plot consisted of four rows, 5 m long. In both years, trials were protected from diseases and pests. Fields were kept free from weeds, and agronomic practices assured good crop growth and development. Seed yield was recorded on the two central rows, leaving head borders of 0.5 m on both ends. Data were also recorded for leaf shape, bracteole shape, bracteole size, flower color, growth habit, 100-seed weight (g), biomass (plant dry weight) yield of aerial parts, harvest index, number of pods/m², days to maturity, and the length of the fifth internode. When measuring biomass and harvest index, no attempts were made to collect fallen leaves.

A pooled analysis of variance for agronomic traits was conducted according to McIntosh (1983). Years and treatments (lines) were random and locations fixed. The Genstat package of statistical programs (Rothamsted Agricultural Experiment Station, UK) was used to analyze the data. Heritability (h^2) was calculated according to Hallauer and Miranda (1981). Percentage genetic gain (20% selection pressure) was calculated according to Frey and Horner (1957). Simple correlation coefficients were calculated among agronomic traits using the SAS (SAS Institute, Cary, North Carolina, USA) program.

Total seed proteins and phaseolin protein patterns were analyzed using sodium dodecyl sulphate polyacrylamide gel electrophoresis according to Brown et al. (1981a,b) and Gepts et al. (1986). Isozyme assays of young root and leaf samples were conducted according to

Hussain et al. (1986). Root samples were assayed for diaphorase (DIAP), malic enzyme (ME), malate dehydrogenase (MDH), and shikimic dehydrogenase (SKDH). Leaf samples were assayed for glutamate oxaloacetate transaminase (GOT), ribulose biphosphate carboxilase (rubisco or RBSC), and acid phosphatase (ACP). Isozyme loci and allozymes were designated as in Koenig and Gepts (1989a). The most common allele was designated 100, and all other allozymes were measured in millimeters from the standard. Lines were grouped according to the frequency distribution of markers: morphological, total protein, phaseolin, and allozymes. The means for agronomic traits were then compared pairwise using a Student's t-test (Steel and Torrie 1960).

Results

Agronomic traits

Significant differences ($P < 0.05$) were found for all agronomic traits among parents (Table 1). 'ABA 58', followed by 'MAM 4' and 'Rio Tibagi', had the highest seed yield. 'A 486' had the lowest yield of all the parents. All large-seeded parents of Andean origin (e.g., 'Redkloud', 'Canadian Wonder', 'ICA L23', 'A 486', and 'ABA 58') had a high 100-seed weight. Two parents of race Mesoamerica, 'Brasil 2' and 'Rio Tibagi', had the lowest seed weight.

'Canadian Wonder' and 'A 486' did not differ for agronomic traits, morphological markers, or proteins and allozymes, except for bracteole type and the MDH isozyme. 'ICA L23' and 'Brasil 2' differed for bracteole type, leaf shape, phaseolin, and all other proteins. They also showed differences for isozymes DIAP1, ME, MDH, SKDH, RBSC, and ACP. 'Rio Tibagi' and 'ABA 58' differed in terms of flower color, bracteole type, phaseolin, and all other proteins, as well as for isozymes DIAP1, ME, SKDH, and ACP. 'Redkloud' and 'MAM 4' differed in bracteole type, leaf shape, phaseolin type, other proteins, DIAP1, and ACP.

Effects of location, year, population, treatment (recombinant inbred lines), and interactions among them were significant for seed yield, 100-seed weight, pods/m², harvest index, and days to maturity (analysis not shown). All main effects, except that of location, and the first-order interactions were significant for fifth internode length and biomass yield.

Inbred lines from 'Rio Tibagi' × 'ABA 58' had the highest mean yield, followed by that from 'Redkloud' × 'MAM 4' (Table 2). On the other hand, 'ICA L23' × 'Brasil 2' had the lowest mean yield, even lower than the intraracial 'Canadian Wonder' × 'A 486' population. However, this was the only interracial population for which the highest yielding line ('TY 5578-45') significantly outyielded its highest yielding parent ('ICA L23'). The lowest yielding line yielded significantly less than the lowest yielding parent in all four populations. While 20 recombinant inbred lines of the intraracial population ('Canadian Wonder' × 'A 486') outyielded their highest yielding parent ('Canadian Wonder'), the highest yielding recombinant inbred lines from two out of three interracial populations outyielded the best line from the intraracial population.

Table 1 Characteristics of common bean parents used in intra- and interracial hybridization and development of recombinant inbred lines

Character	Canadian Wonder	A486	ICA L23	Brasil 2	Rio Tibagi	ABA 58	Redkloud	MAM 4
Yield (kg/ha)[a]	1737	1427	1833	1623	2287	2749	1780	2685
100-seed weight (g)[a]	45.6	47.3	45.8	22.2	17.4	49.2	51.5	37.6
Biomass (kg/ha)[a]	3318	2800	3336	2628	4329	4887	3208	4469
Harvest index[a]	0.63	0.59	0.61	0.53	0.55	0.62	0.59	0.64
Pods/m²[a]	165.3	120.6	134	263.5	278.8	266	159.2	253.2
Days to maturity[a]	71.7	74.5	84.2	81.8	84	79.9	73.8	75.2
Fifth internode length (cm)[a]	7.6	6.6	5.9	3.9	3.8	7.3	10.3	6.5
Growth habit	I	I	I	I	II	I	I	III
Flower color[b]	L	L	W	W	P	W	W	W
Bracteole shape[c]	O	Lt	Lt	C	C	O	O	Lt
Bracteole size[d]	S	S	S	L	L	S	S	L
Leaf shape[c]	O	O	O	C	C	C	C	O
Phaseolin	T	T	T	S	S	T	T	S
Lectin	1	1	2	1	2	1	1	2
Group 1 proteins	1	1	2	1	2	1	1	2
Group 2 proteins	1	1	2	1	2	1	1	2
DIAP1[e]	1	1	2	1	1	2	1	2
DIAP2[e]	1	1	2	2	2	2	2	2
ME	Me^{100}	Me^{100}	Me^{98}	Me^{100}	Me^{100}	Me^{98}	Me^{98}	Me^{98}
MDH	Mdh^{98}	Mdh^{100}	Mdh^{100}	Mdh^{98}	Mdh^{100}	Mdh^{100}	Mdh^{100}	Mdh^{100}
SKDH	$Skdh^{100}$	$Skdh^{100}$	$Skdh^{98}$	$Skdh^{100}$	$Skdh^{100}$	$Skdh^{100}$	$Skdh^{98}$	$Skdh^{98}$
RBSC	$Rbsc^{100}$	$Rbsc^{100}$	$Rbsc^{100}$	$Rbsc^{98}$	$Rbsc^{98}$	$Rbsc^{98}$	$Rbsc^{98}$	$Rbsc^{98}$
GOT	Got^{100}	Got^{100}	Got^{100}	Got^{100}	Got^{100}	Got^{100}	Got^{100}	Got^{100}
ACP	Acp^{100}	Acp^{100}	Acp^{100}	Acp^{98}	Acp^{100}	Acp^{98}	Acp^{98}	Acp^{100}

[a] Mean over 2 years at two locations
[b] L, Lilac; W, White; P, Purple
[c] O, Ovate; Lt, Lanceolate; C, Cordate
[d] S, Small; L, Large
[e] There are two banding patterns possible for both DIAP1 and DIAP2

'Rio Tibagi' × 'ABA 58' had the largest biomass and highest number of pods/m² and days to maturity while possessing the smallest seed size and fifth internode length of all populations. Comparatively lower biomass yields were recorded for the two populations ('Canadian Wonder' × 'A 486' and 'ICA L23' × 'Brasil 2') involving only determinate type-I growth habit parents. Also, the intraracial population had the smallest number of pods/m². 'Canadian Wonder' × 'A 486' and 'Redkloud' × 'MAM 4' were found to be earlier maturing than the remaining populations. 'Canadian Wonder' × 'A 486' had the highest value for harvest index (0.62). Mean harvest index for the three interracial populations ranged from 0.56 to 0.59.

Heritability and genetic gain

Of the seven agronomic traits studied, 100-seed weight had the highest heritability in all four populations (Table 3). This was followed by fifth internode length, number of days to maturity, and harvest index. Biomass and seed yield and pods/m² generally tended to have comparatively lower heritability values.

Genetic gain (at 20% selection pressure) for seed yield ranged from 3.9% for 'Redkloud' × 'MAM 4' to 11.4% for 'Rio Tibagi' × 'ABA 58' (Table 3). It was found that fifth internode length had the highest percentage genetic gain in interracial populations 'Rio Tibagi' × 'ABA 58'

(51.5%) and 'ICA L23' × 'Brasil 2' (45.6%). Days to maturity had the lowest overall percentage genetic gain, with a range of 2.5% ('ICA L23' × 'Brasil 2') to 5.0% ('Redkloud' × 'MAM 4').

Correlation coefficients among agronomic raits

Table 4 presents correlation coefficients among yield, its components, and other agronomic traits, using mean values across locations and years for recombinant inbred lines from all four populations. Days to maturity and pods/m² shared significant positive correlations ($P < 0.05$) with each other and with seed and biomass yields. The relationship of days to maturity and pods/m² with 100-seed weight, harvest index, and fifth internode length was negative. Biomass shared a positive association with yield but a negative association with harvest index. Fifth internode length demonstrated a positive association with 100-seed weight and negative correlations with pods/m² and days to maturity.

Markers

The occurrence and frequencies of markers: morphological, seed protein, and isozyme are presented in Table 5. The three interracial populations demonstrated a predominance of small- and medium-sized cordate-

Table 2 Mean, maximum, and minimum for yield and other agronomic traits for recombinant inbred lines from inter- and intraracial populations of common bean evaluated at two locations over 2 years in Colombia

Population, parents, and recombinant inbred lines	Yield (kg/ha)	100-seed weight (g)	Biomass (kg/ha)	Harvest index	Pods/m^2	Days to maturity	Fifth internode length (cm)
Canadian Wonder × A 486							
Canadian Wonder	1737	45.6	3318	0.63	165.3	71.7	7.6
A 486	1427	47.4	2800	0.59	120.6	74.5	6.6
Recombinant inbred lines							
Mean	1571	45.3	2900	0.62	144.6	73.5	6.8
Maximum	2073	54.9	3846	0.68	204.0	76.7	8.1
Minimum	1073	37.3	1926	0.55	109.1	69.2	5.2
ICA L23 × Brasil 2							
ICA L23	1833	45.8	3336	0.61	134.0	84.2	5.9
Brasil 2	1623	22.2	2628	0.53	263.5	81.8	3.9
Recombinant inbred lines							
Mean	1434	26.9	2609	0.56	199.9	81.7	5.6
Maximum	2314	42.2	4175	0.69	310.1	86.4	10.4
Minimum	916	17.0	1726	0.44	123.3	77.2	2.2
Rio Tibagi × ABA 58							
Rio Tibagi	2287	17.4	4329	0.55	278.8	84.0	3.8
ABA 58	2749	49.2	4887	0.62	266.0	79.9	7.3
Recombinant inbred lines							
Mean	1879	24.6	3508	0.56	265.6	81.9	5.3
Maximum	2667	37.5	5023	0.65	397.0	87.3	10.6
Minimum	1269	17.5	2165	0.43	156.3	74.2	2.3
Redkloud × MAM 4							
Redkloud	1780	51.5	3208	0.59	159.2	73.8	10.3
MAM 4	2685	37.6	4469	0.64	253.2	75.2	6.5
Recombinant inbred lines							
Mean	1727	33.2	3104	0.59	206.2	75.1	7.7
Maximum	2537	49.1	4161	0.71	269.2	82.9	14.4
Minimum	1263	26.7	1858	0.45	144.4	66.0	4.7
LSD (0.05)[a]	352	2.6	661	0.06	42.0	2.7	1.2
LSD (0.05)[b]	155	0.5	301	0.01	15.5	0.5	0.4

[a] For comparison of values for parents and maximum and minimum for recombinant inbred lines within and among populations
[b] For comparison of mean values of recombinant inbred lines among populations

Table 3 Heritability (h^2) and percentage genetic gain from selection[a] (GS) in recombinant inbred lines from intra- and interracial populations of common bean evaluated over 2 years at two locations in Colombia

Character	Canadian Wonder × A 486		ICA L23 × Brasil 2		Rio Tibagi × ABA 58		Redkloud × MAM 4	
	h^2 SE	GS	h^2 SE	GS	h^2 SE	GS	h^2 SE	GS
Yield	0.40 ± 0.16	7.8	0.31 ± 0.17	9.4	0.50 ± 0.16	11.4	0.19 ± 0.17	3.9
100-seed weight	0.80 ± 0.15	11.1	0.91 ± 0.15	26.6	0.94 ± 0.15	25.1	0.91 ± 0.15	20.6
Biomass	0.26 ± 0.17	4.6	0.37 ± 0.17	10.0	0.55 ± 0.16	12.5	0.36 ± 0.17	6.8
Harvest index	0.51 ± 0.15	3.0	0.51 ± 0.16	6.3	0.72 ± 0.21	7.7	0.69 ± 0.16	9.6
Pods/m^2	0.38 ± 0.16	6.3	0.61 ± 0.16	17.7	0.61 ± 0.16	15.1	0.38 ± 0.17	6.8
Days to maturity	0.72 ± 0.16	2.6	0.48 ± 0.16	2.5	0.63 ± 0.16	3.5	0.89 ± 0.16	5.0
Fifth internode length	0.30 ± 0.16	4.4	0.88 ± 0.16	45.6	0.91 ± 0.15	51.5	0.79 ± 0.15	29.6

[a] Calculated at 20% selection pressure and expressed as the percentage of the mean values of all recombinant inbred lines within each population

shaped bracteoles and ovate leaves, whereas the intraracial population demonstrated a mixture of lanceolate and other bracteoles of mostly medium-sized and ovate-shaped leaves. In all four populations, some lines were observed with non-parental flower colors.

Total-protein banding patterns constituted four groups: phaseolins, lectins, a group between the phaseolins and lectins (Group 1), and another group between the lectins and albumins (Group 2). The recombinant inbred lines from the intraracial population did not differ markedly from one another nor from either of

Table 4 Pearson correlation coefficients among some agronomic traits obtained from F_2-derived F_6 recombinant inbred lines from intra- and interracial populations of common bean evaluated at two locations over 2 years in Colombia

Character	Yield	100-seed weight	Biomass	Harvest index	Pods/m^2	Days to maturity
100-seed weight	−0.03					
Biomass	0.89**	−0.01				
Harvest index	0.03	0.34**	−0.18**			
Pods/m^2	0.55*	−0.70**	0.54**	−0.25**		
Days to maturity	0.17**	−0.60**	0.28**	−0.46**	0.47**	
Fifth internode length	0	0.37**	−0.06	0.03	−0.27**	−0.47**

**,* $P = 0.01$ and $P = 0.05$, respectively

the parents. In contrast, interracial populations demonstrated varying degrees of recombination among the four groups of proteins, indicating their separate genetic controls (unpublished).

Polymorphism for six isozymes (MDH, ME, SKDH, ACP, RBSC, GOT, and DIAP1) was observed (Table 5). It was found that DIAP1 displayed polymorphism only for the three interracial populations.

In the three interracial populations, distorted frequencies (i.e., values significantly different than the expected 50:50 ratios) were observed. Distorted frequencies were observed for DIAP1, MDH, and Group 2 fragments ('ICA L23' × 'Brasil 2'); DIAP1, ME, SKDH, ACP, and phaseolin ('Rio Tibagi' × 'ABA 58'); and ACP and Group 1 fragments ('Redkloud' × 'MAM 4').

Relationship between agronomic traits and markers: morphological, seed protein, and allozyme

The recombinant inbred lines from each population were grouped according to class frequencies for each of the markers: morphological, protein band, and allozyme. Those showing significant ($P < 0.05$) differences between the group mean values for agronomic traits are presented in Table 6. For 100-seed weight, recombinant lines with white flower color, $Diap1^1$, and S phaseolin had smaller seeds; and those with lilac flower, $Diap1^2$, and T phaseolin had higher seed weight. For biomass, lines with indeterminate growth habit, white flower color, and T phaseolin were found to yield more dry matter than their counterparts. Similarly, recombinant lines with large bracteole, Me^{100}, and S phaseolin had a significantly larger number of pods/m^2 than their counterparts. Mean values for fifth internode length were higher for groups of recombinant inbreds possessing determinate growth habit, cordate bracteole, Acp^{100}, and T phaseolin than for their counterparts. Lines with indeterminate growth habit, lilac flower in one population and white in the other, $Diap1^2$, and T phaseolin were relatively late maturing. Similarly, lines with determinate growth habit, Mdh^{98}, $Rbsc^{98}$, and S phaseolin had a relatively higher harvest index.

Indeterminate growth habit was positively associated with seed and biomass yields for 'Redkloud' × 'MAM 4'. Indeterminate growth habit also was associated with reduced harvest index, a longer maturing period, and shorter internode lengths.

Discussion

Contrasting growing conditions at Palmira and Popayán over 2 years and more precipitation at both locations in 1991 than in 1990 contributed to their significant effects on most agronomic traits. Large-seeded common beans from the Andes are usually better adapted to relatively cooler sites such as Popayán. Because all populations involved at least one large-seeded parent and because the crop took, on average, 2 weeks longer at Popayán due to lower temperatures, this may have helped improve their performance at Popayán over that at Palmira (unpublished).

The mean yield and yield of the highest yielding lines from two out of three interracial populations were higher than that of the intraracial population (Table 2). This demonstrated the greater usefulness of the interracial populations for increasing yield potential in common bean (Beaver and Kelly 1994; Singh et al. 1992b, 1993; Singh and Urrea 1994). Nonetheless, the lack of lines having a yield significantly higher than that of the highest yielding parents in these two interracial populations ('Rio Tibagi' × 'ABA 58' and 'Redkloud' × 'MAM 4') is worth discussing. Although higher genetic variation was created for morphological, allozyme, and protein markers, useful genetic variation for seed yield found in these interracial populations was not great. One reason could be zero or negative combining abilities for yield of 'Rio Tibagi' and 'Redkloud' (Nienhuis and Singh 1986, 1988a; Singh et al. 1992a). 'Canadian Wonder' and 'A 486' both had positive combining ability for yield (Nienhuis and Singh 1988a; Singh et al. 1992a), which may explain higher yields for 20 recombinant inbred lines than for their highest parent in this intraracial population. Moreover, it is possible that a threshold for genetic diversity among parents exists in order to create recombinants with potentially increased yields. For example, in interracial population 'ICA L23' × 'Brasil 2', 1 recombinant inbred ('TY 5578-45') outyield the highest yielding parent and had a large seed size. The two parents of this population differ principally

Table 5 Class frequencies (%) for markers: morphological, seed protein, and allozyme in recombinant inbred lines from intra- and interracial populations of common bean

Marker	Canadian Wonder × A 486	ICA L23 × Brasil 2	Rio Tibagi × ABA 58	Redkloud × MAM 4
Bracteole type				
Cordate	0	80.2	75.3	45.7
Lanceolate	49.4	7.4	11.1	19.8
Variable	50.6	12.3	13.6	34.6
Braceteole size				
Medium	87.7	46.9	70.4	44.4
Small	4.9	40.7	19.8	48.1
Large	7.4	12.3	9.9	7.4
Leaf type				
Cordate	7.4	23.5	38.3	30.9
Ovate	76.5	40.8	61.7	56.8
Variable	16.0	35.8	0	12.3
Flower color				
White	16.0	93.8	22.2	51.9
Lilac	82.7	6.2	40.7	4.9
Purple	0	0	37.0	37.0
Variable	1.2	0	0	6.2
Seed proteins				
Phaseolin				
S	0	39.5	74.1	56.8
T	100.0	37.0	25.9	29.6
Variable	0	23.5	0	13.6
Lectin				
Maternal-type	0 [a]	44.4	58.0	37.0
Paternal-type	0 [a]	46.9	38.3	59.3
Variable	0 [a]	8.6	3.7	3.7
Group-1 proteins				
Maternal-type	0 [a]	0 [a]	44.4	25.9
Paternal-type	0 [a]	0 [a]	53.1	74.1
Variable	0 [a]	0 [a]	2.5	0
Group-2 proteins				
Maternal-type	0 [a]	84.0	58.0	34.2
Paternal-type	0 [a]	16.0	33.3	56.2
Variable	0 [a]	0	8.6	9.6
Allozymes				
Diap 1				
Pattern 1	100.0	61.0	33.0	51.0
Pattern 2	0	39.0	67.0	49.0
Diap 2				
Pattern 1	100.0	0	0	0
Pattern 2	0	100.0	100.0	100.0
Mdh^{98}	58.0	39.0	0	0
Mdh^{100}	42.0	61.0	100.0	100.0
Me^{98}	0	47.0	7.0	100.0
Me^{100}	100.0	53.0	93.0	0
$Skdh^{98}$	0	52.0	35.0	51.0
$Skdh^{100}$	100.0	48.0	65.0	49.0
Got^{100}	100.0	100.0	100.0	100.0
Acp^{98}	0	49.0	33.0	25.0
Acp^{100}	100.0	51.0	67.0	75.0
$Rbsc^{98}$	0	58.0	44.0	56.0
$Rbsc^{100}$	100.0	42.0	56.0	44.0

[a] No differences (i.e., no polymorphism) between parents

for their seed size and evolutionary origins. In contrast, the parents of comparatively more divergent 'Rio Tibagi' × 'ABA 58' and 'Redkloud' × 'MAM 4' populations, in addition to differing in seed size and evolutionary origins, also differed for growth habit. Thus, excessive genetic distance between the parents and accumulation of some deleterious genes, whose effects could not be seen until brought together through hybridization, resulted in reduced yields for the recombinants compared with the highest yielding parent. Also, because yield is a quantitative trait controlled by many genes with relatively small effects, it is very likely that a

Table 6 Association among agronomic traits and morphological, seed protein and allozyme markers in recombinant inbred lines of common bean

Marker	Agronomic trait	Population
	Seed yield (kg/ha)	
Growth habit (determinate)	1642 **	Redkloud × MAM 4
Growth habit (indeterminate)	1835 **	
	100-seed weight (g)	
White flower	26.6*	ICA L23 × Brasil 2
Lilac flower	34.1*	
Diap1[1]	26.0*	ICA L23 × Brasil 2
Diap1[2]	28.7*	
S phaseolin	24.4**	ICA L23 × Brasil 2
T phaseolin	30.1**	
S phaseolin	24.0**	Rio Tibagi × ABA 58
T phaseolin	27.0*	
S phaseolin	32.0*	Redkloud × MAM 4
T phaseolin	36.9**	
	Biomass (kg/ha)	
Growth habit (determinate)	2853**	Redkloud × MAM 4
Growth habit (indeterminate)	3384**	
Growth habit (determinate)	3368**	Rio Tibagi × ABA 58
Growth habit (indeterminate)	3691**	
Lilac flower	3400**	Rio Tibagi × ABA 58
White flower	3989**	
S phaseolin	3445*	Rio Tibagi × ABA 58
T phaseolin	3792*	
	Harvest index	
Growth habit (determinate)	0.56**	Redkloud × MAM 4
Growth habit (indeterminate)	0.51**	
Growth habit (determinate)	0.53*	Rio Tibagi × ABA 58
Growth habit (indeterminate)	0.50*	
Mdh^{98}	0.59*	Canadian Wonder × A 486
Mdh^{100}	0.56*	
$Rbsc^{98}$	0.55*	Redkloud × MAM 4
$Rbsc^{100}$	0.52*	
S phaseolin	0.52*	Rio Tibagi × ABA 58
T phaseolin	0.49*	
S phaseolin	0.55*	Redkloud × MAM 4
T phaseolin	0.51*	
	Pods/m²	
Medium bracteole	198.0*	Redkloud × MAM 4
Large bracteole	211.1*	
$Skdh^{98}$	184.5**	ICA L23 × Brasil 2
$Skdh^{100}$	216.4**	
Me^{98}	189.1*	ICA L23 × Brasil 2
Me^{100}	209.9*	
S phaseolin	210.4**	ICA L23 × Brasil 2
T phaseolin	180.8**	
	Days to maturity	
Growth habit (determinate)	73 **	Redkloud × MAM 4
Growth habit (indeterminate)	77 **	
Growth habit (determinate)	80 **	Rio Tibagi × ABA 58
Growth habit (indeterminate)	84 **	
White flower	72.4*	Canadian Wonder × A 486
Lilac flower	73.7*	
White flower	75.1*	Redkloud × MAM 4
Purple flower	74.2*	
Diap 1[1]	81.3*	ICA L23 × Brasil 2
Diap 1[2]	82.3*	
S phaseolin	80.7**	ICA L23 × Brasil 2
T phaseolin	82.3**	
	Fifth internode length (cm)	
Growth habit (determinate)	5.8**	Rio Tibagi × ABA 58
Growth habit (indeterminate)	4.2**	
Lanceolate bracteole	6.1*	Redkloud × MAM 4
Cordate bracteole	7.4*	
Acp^{98}	5.2*	Redkloud × MAM 4
Acp^{100}	6.8*	
S phaseolin	4.7*	ICA L23 × Brasil 2
T phaseolin	6.5*	

*, ** Significantly different at $P = 0.05$ and $P = 0.01$, respectively

random sample of 79 recombinant inbred lines was not large enough to contain genotypes with all of the favorable genes from both parents.

The positive association between biomass and seed yield would justify development of larger plant size, but its negative association with harvest index suggests that independent selection for increased biomass should be avoided.

Because mean seed weight of lines from the three interracial populations was lower than the values for the intraracial population and none of the lines from interracial populations seemed to equal the seed weight of its large-seeded parent, recovery of large-seeded lines from biparental Andean × Middle American interracial populations would be problematic. It has been found that in crosses of Andean × Middle American parents, those from the Middle American genepools usually possess negative general combining abilities for seed size (Singh et al. 1992a). Nonetheless, the high heritability values and gains from selection for 100-seed weight found in this study (Table 3) and also reported by Motto et al. (1978), Nienhuis and Singh (1988b), and Singh et al. (1991d) should facilitate selection for larger seed size among and within interracial populations.

The inverse relationship of seed weight to seed yield, biomass yield, and pods/m^2 (Table 4) supports observations made by White and González (1990) on seed size effect. Pods/m^2 and biomass were significantly and negatively correlated with harvest index, which implies that greater non-economic yield results, at least in part, from diminished reproductive efficiency. An increased number of days to maturity produced more dry matter (biomass), pods/m^2, and seed yield. But its negative association with 100-seed weight and harvest index would suggest that large-seeded Andean beans achieve their maximum yields through different physiological phenomena than the small- and medium-seeded Middle American beans. Thus, earlier maturing cultivars, with fewer pods and larger seeds, would be expected to give higher yields in bush, determinate Andean beans in the tropics. On the other hand, genotypes that are late maturing have more pods/m^2 and yield a high biomass would be suitable for small- and medium-seeded beans of Middle America. This in essence conforms with the general characteristics of cultivated landraces from the two domestication regions. Because these genetic and developmental associations seem to have evolved over millennia, in order to create new recombinants with desirable traits from both germ plasm groups (i.e., large-seeded, high-yielding, indeterminate type-II and -III cultivars), the use of breeding schemes based on some form of recurrent mating and selection would be required. Recently, Beaver and Kelly (1994) were able to develop high-yielding lines with large seeds using recurrent selection from Andean American × Middle American interracial populations.

Both parents ('Canadian Wonder' and 'A 486') of the intraracial population had lilac flower color, but some recombinant inbreds were observed to have white flower color. This indicated the presence of different gene for lilac flower color in both parents, which permitted the expression of recessive gene coding for white flower color in some recombinant inbred lines. The fact that the same phenotype can be achieved by different genotypes was further supported by the occurrence of lilac and purple flower colors in population 'Redkloud' × 'MAM 4', both parents of which had white flowers. A similar phenomenon has been observed for seed coat color in common bean (M. J. Bassett, personal communication).

Several instances of distorted frequencies for seed protein and isozyme markers were recorded, especially in interracial populations (Table 5). Koenig and Gepts (1989b) also reported distorted ratios for specific alleles and suggested the action of some form of female/male-specific mechanism (nuclear-cytoplasmic interactions) that affects gene exchange between parental germ plasm. Distorted segregation ratios could also be caused by interactions between the embryo and endosperm of the maternal parent of interspecific crosses (Shii et al. 1982). Reversing the maternal/paternal roles in the populations used in this study could have possibly confirmed whether or not the distorted segregation ratios are attributed to female/male exchange mechanisms.

Gene exchange between parents from the same race should proceed without metabolical, hormonal, or physiological hindrance because of evolutionary similarity. In contrast, greater degrees of biochemical adaptation and modification would be necessary to accomodate gene exchange and adaptation among distantly related parents. The greater genetic distances between two parents that have evolved in separate ecological regions in response to different selection pressures would predicate greater degrees of biochemical/hormonal adaptation in order to allow successful crossing between the two genepools. Specifically, such biochemical adaptation would (depending upon genetic distance of the parents) necessitate potentially large-scale modifications of both major and minor metabolic and anabolic pathways in the viable progeny. This is probably affected by changes in genome expression, resluting in distorted segregation ratios among the progeny.

The use of morphological (bracteole shape, leaf shape, flower color, etc.), protein, and isozyme markers as indirect selection criteria is largely unknown in common bean. Breeders' preference toward using mostly intraracial populations in the past has resulted in reduced genetic variation and, hence, marker availability. Increased genetic variation among recombinant inbred lines from interracial populations increases the number of potential markers available as indirect selection criteria and for development of a linkage map. While no markers except growth habit (population 'Redkloud' × 'MAM 4') were found to be associated with seed yield, 23 associations were detected between several agronomic traits and morphological, seed protein and allozyme markers (Table 6). For example, associations were

found between T phaseolin protein and large seed size, and S phaseolin and small seed size, thus supporting earlier reports (Brown et al. 1981a). The statistically significant associations possibly infer a genetic linkage between the markers listed and the agronomic traits in the form of multilocus associations and/or pleiotropic effects of genes controlling these traits.

These associations can eventually be integrated, after mapping, into the existing genetic linkage map for common bean. Moreover, the potential usefulness of markers with more resolving power, such as the DNA-based random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP), and others, for indirect selection criteria for seed yield needs to be explored. Future studies should embark on determining the usefulness of the genetic variation generated through these and other interracial populations for resistance to diseases, drought, and other factors.

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