Comparison of Sources and Lines Selected for Drought Resistance in Common Bean

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ABSTRACT

Drought is a major constraint to common bean (*Phaseolus vulgaris* L.) production worldwide. Our objectives were to (i) identify sources of drought resistant germplasm in common bean cultivars and (ii) compare drought resistant germplasm with lines selected from interracial and intergene pool populations. We included in this study 12 of the most promising drought resistant cultivars from race Durango and 11 from race Jalisco, nine drought resistant lines selected from interracial or intergene pool populations, and two drought resistant and two susceptible checks. The 36 genotypes were evaluated in drought-stressed (DS) and nonstressed (NS) environments in four cropping seasons between 1996 and 1998 at the International Center for Tropical Agriculture (CIAT), Palmira, Colombia. Drought stress reduced seed yield by 53%, 100-seed weight by 13%, and days to maturity by 3%. Race Durango cultivars had higher yield, larger seed weight, and earlier maturity than race Jalisco cultivars in DS and NS environments. Large variations within the two races were found for the three traits. Drought resistant selected lines out-yielded drought resistant checks by 44% in DS and 15% in NS and cultivars from race Durango by 48% in DS and 30% in NS and race Jalisco by 96% in DS and 46% in NS environments. Seed yield in DS was correlated negatively with the percent reduction (PR) because of drought stress and drought susceptibility index (DSI), whereas a positive correlation existed between PR and DSI. Drought resistant selected lines and race Durango cultivars had similar maturity. Mean 100-seed weight of selected lines (23 g) was less than race Durango (34 g) and race Jalisco cultivars (29 g). While new sources of drought resistance could be identified in races Durango and Jalisco, these drought resistant germplasm and selected lines derived from interracial and intergene pool populations should be utilized for improvement of drought resistance in common bean.

DROUGHT STRESS is a worldwide production constraint of common bean (Fairbairn, 1993; Wortmann et al., 1998). On the American continents, drought is endemic in northeastern Brazil (>1.5 million ha) and in the central and northern highlands of Mexico (>1.5 million ha). In Central America, moderate drought towards the end of the cropping season (November and December) is not uncommon. Moreover, in Chile, coastal Peru, and western and intermountain USA, rainfall is limited such that common bean cannot be grown without supplemental irrigations (five–eight). In tropical and subtropical Latin American bean growing environments, drought is often intermittent (Acosta et al., 1999; Schneider et al., 1997b) and complete crop failures are not uncommon. However, in dryland farming systems in intermountain regions of the USA, characterized by inadequate or no summer rainfall, terminal drought is more likely to affect bean production.

Moderate to high drought stress can reduce biomass, number of seeds and pods, days to maturity, harvest index, seed yield, and seed weight in common bean (Acosta-Gallegos and Adams, 1991; Ramirez-Vallejo and Kelly, 1998). A moderate drought stress has reduced yield by 41% without altering nitrogen (N) partitioning (Foster et al., 1995). However, severe drought stress has reduced yield by 92%, N harvest index, and N- and water-use efficiency in common bean. Severe drought during reproduction has reduced nodulation by an average of 43% and N_2 fixation to one sixth of a well-irrigated control (Castellanos et al., 1996). Root rots caused by *Macrophomina phaseolina* (Tassi) Goid., *Fusarium solani* f. sp. *phaseoli* (Burk.) Snyder & Hansen, and other fungi may aggravate drought stress. Similarly, DS bean crops may become prone to damage by leafhoppers (*Empoasca kraemeri* Ross & Moore) in the tropics and subtropics.

Genotypic differences for drought resistance have been reported for common bean (Abebe et al., 1998; Acosta et al., 1999). The most effective selection criterion, among various morphological, physiological, phenological, yield, and yield related traits, for identifying drought resistant genotypes was mean seed yield (the arithmetic and geometric) of DS and NS environments (Abebe et al., 1998; Ramirez-Vallejo and Kelly, 1998; White et al., 1994a). Narrow-sense heritability for seed yield under drought stress ranged from 0.09 ± 0.19 to 0.80 ± 0.15 (Schneider et al., 1997b; Singh, 1995; White et al., 1994b). Schneider et al. (1997a) reported four random amplified polymorphic DNA (RAPD) markers in one biparental population, and five in another population that were consistently associated with yield under DS or NS, and/or geometric mean (GM) yield of DS and NS environments. They concluded that the effectiveness of marker-assisted selection for drought resistance was inversely proportional to heritability of bean yield under drought stress.

Existence of useful genetic variation for specific traits related to drought resistance in parental germplasm is crucial for successful improvement of crop cultivars. At present, among *Phaseolus* species, the highest levels of drought resistance are found in the tepary bean, *P. acutifolius* A. Gray (Markhart, 1985; Rosas et al., 1991; Thomas et al., 1983) and probably in its closely related and sympatric species, *P. parvifolius* Freytag. However, despite repeated efforts of successful interspecific hybridization using embryo rescue (Mejía-Jiménez et al., 1994) and transfer of high levels of resistance to common

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Abbreviations: CIAT, Spanish acronym for International Center for Tropical Agriculture; D, race Durango; DII, drought intensity index; DS, drought-stressed; DSI, drought susceptibility index; GM, geometric mean; J, race Jalisco; M, race Mesoamerica; N, nitrogen; NS, nonstressed; PR, percent reduction; RAPD, random amplified polymorphic DNA marker.

bacterial blight [caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye] (Singh and Muñoz, 1999), and some indication of introgression of drought resistance (Thomas and Waines, 1982), unequivocal evidence of transfer of any significant level of drought resistance from tepary to common bean is still lacking (Rosas et al., 1991). For the immediate future, useful genetic variability for drought resistance must be identified and utilized from races and gene pools within *P. vulgaris*.

To find sources of drought resistance in common bean, one should consider its evolutionary origin and domestication. The wild populations of common bean (the immediate ancestors of cultivars) are distributed from the northern and central highlands of Mexico to northwestern Argentina (Toro et al., 1990). A noncentric domestication occurred along its distribution range (Gepts et al., 1986; Gepts and Debouck, 1991). Cultivars domesticated in the semiarid regions over millenia, namely those belonging to race Durango from the Mexican highlands, would be expected to possess high levels of drought resistance (Singh, 1989; Singh et al., 1991).

Recently, a diverse group of cultivars have been evaluated for drought resistance in Brazil (Silveira et al., 1981), Colombia (Laing et al., 1983; Singh and Terán, 1995), Mexico (Acosta-Gallegos and Adams, 1991; Acosta-Gallegos and Kohashi-Shibata, 1989; Acosta et al., 1999), the Rift Valley of East Africa (Abebe et al., 1998), and the USA (Acosta-Gallegos and Adams, 1991; Miller and Burke, 1983). Moreover, Rosales-Serna et al. (2000) and Schneider et al. (1997a,b) developed drought resistant lines from biparental populations using seed yield (the GM of DS and NS environments) and/or RAPD markers as selection criteria. Similarly, Singh (1995) used the arithmetic mean seed yield of DS and NS environments and percent reduction (PR) in yield due to drought stress as a selection criteria, and developed significantly ($P < 0.05$) higher yielding drought resistant lines from double-cross interracial (TR 7790) and intergene pool (TR 7791) populations. Our objectives in this study were to (i) identify sources of drought resistant germplasm in common bean cultivars and (ii) compare these cultivars with drought resistant lines previously developed from interracial and intergene pool populations.

MATERIALS AND METHODS

Twelve of the most promising drought resistant common bean cultivars from race Durango, 11 from race Jalisco, nine drought resistant selected lines from interracial and intergene pool populations, and two drought resistant and two susceptible checks were included in this study. Five cultivars of race Durango (Bayo Madero, Bayo Zacatecas, Bayo 400, Negro Durango, and Pinto Villa) and one of race Jalisco (Alteño) were developed from hybridization by the Mexican National Program (R. Lépiz, 2001, personal communication). All other genotypes were popular landraces that originated in the semiarid and semi-humid Mexican highlands (>1800 m elevation). These genotypes were selected from our previous evaluations in DS environments in Colombia (Singh and Terán, 1995). Although studied initially and exhibiting potential (Singh and Terán, 1995), cultivars from none of the Andean races could be included in this study because of their low levels of drought resistance. Eight drought resistant selected lines (with codes SEA 1 to SEA 13) were developed from an interracial population (TR 7790 = BAT 477/'San Cristobal 83'//'Guanajuato 31'/'Rio Tibagi') between races Durango and Mesoamerica, and one (SEA 14) was selected from an intergene pool population (TR 7791 = BAT 477/San Cristobal 83//BAT 93/'Jalo EEP 558') between races Mesoamerica and Nueva Granada (Singh, 1995). Of the four checks, BAT 477 was developed at CIAT, although not specifically for drought resistance, and was later identified as the most drought resistant genotype (Laing et al., 1983; White et al., 1994b). San Cristobal 83 is a drought resistant landrace cultivar from the Dominican Republic. Of the two susceptible checks, TR 7791-26 is a sister line of SEA 14, and A 750, possessing characteristics of race Jalisco, was bred for tolerance to low soil fertility at CIAT. It was subsequently identified as susceptible to drought stress. Nine drought resistant lines (with codes SEA 1–14) and three checks (BAT 477, San Cristobal 83, and TR 7791-26) possessed characteristics predominantly of small-seeded (<25 g 100-seed weight^{-1}) race Mesoamerica.

Table 1. Cumulative rainfall, mean growing season temperature, and drought intensity index for the four cropping seasons between 1996 and 1998 used to evaluate 36 common bean genotypes at CIAT-Palmira, Colombia.

Cropping season†	Cumulative rainfall	Mean growing season temperature	Drought intensity index‡
	mm	°C	
1996A	106	29	0.81
1997A	29.7	32	0.51
1998A	140.7	32	0.30
1998B	53.5	29	0.43

† Cropping season A = June to August and B = December to February.
‡ Drought intensity index (DII) = 1-Xds/Xns, where Xds and Xns are the mean of all genotypes in drought-stressed and nonstressed environments, respectively.

At CIAT-Palmira (Colombia), average annual rainfall is 1200 mm, but there are two relatively marked dry seasons: June to August (Season A), and December to February (Season B), the latter sometimes being less reliable for drought stress. By taking advantage of this situation, and by applying irrigation once 6 d before planting and then 10 to 12 d after emergence, a moderate to high level of terminal drought stress can be created in each cropping season. Thus, the 36 genotypes were evaluated during four relatively dry cropping seasons: in 1996A, 1997A, 1998A, and 1998B at CIAT-Palmira, Colombia. The soil was a fine silty, mixed isohypothermic, Aquic Hapludoll, with a pH of 7.5. Mean growing temperature, cumulative rainfall, and drought intensity index (DII, based on seed yield of 36 genotypes) were recorded for the four cropping seasons (Table 1). A 6-by-6 partially balanced lattice design with four replicates was used. Each plot consisted of four rows, spaced 0.6 m apart. The row length in 1996A and 1997A was 6.2 m, with 7.2 m^2 harvested from the two central rows (with head borders on either end) for seed yield measurements. For the trials conducted in 1998A and 1998B, the length of each row was 4.9 m, with 5.4 m^2 harvested for yield. All trials were grown in fields with residual soil fertility. Plots were kept free from weeds, diseases, and insect pests by means of a combination of preventive chemicals and hand labor. The DS and NS plots were grown adjacent to each other, both in a similar design and plot size (Singh, 1995). The DS plots received one gravity irrigation (approximately 35 mm of water) 6 d before planting, and an additional irrigation 10 to 12 d after emergence. The NS plots received four or five additional irrigations as required for normal crop growth and develop-

Table 2. Analysis of variance for seed yield, 100-seed weight, and days to maturity for sources of drought resistance from common bean races Durango and Jalisco and selected lines from interracial and intergene pool populations, and resistant and susceptible checks evaluated in drought-stressed (DS) and nonstressed (NS) environments at CIAT-Palmira, Colombia, in four cropping seasons between 1996 and 1998.

		Mean squares†					
Source	**df**	**Seed yield**	**PR**	**GM**	**DSI**	**100-seed weight**	**Days to maturity**
Cropping season (C)	3	2 806 419.6	53 048.6*	4 772 694.8**	6.4	1 563.0	2 598.3
Environments (E)	1	96 381 640.4**				5 072.8	1 205.4
C × E	3	5 177 983.5**				769.5**	2 104.5**
Rep/C	12		11 965.9	128 488.3	4.8		
Rep/C × E	24	478 820.6				18.2	4.98
Block/R × C	80		3 285.0	55 366.5	1.5		
Block/R × C × E	160	93 122.4				6.0	2.2
Genotypes (G)	35	1 705 833.6**	1 788.8	972 480.9**	1.8	1 392.5**	545.4**
G × C	105	188 372.9	1 675.3	93 391.3**	2.3**	38.0	45.1**
G × E	35	129 223.3				48.0	20.7
G × C × E	105	168 635.5**				35.9**	22.1**
Error	680	36 528.3				5.2	2.1
	340		1 407.9	18 941.0	0.7		

* Indicates significance at $P = 0.05$.
** Indicates significance at $P = 0.01$.
† PR = percent reduction in the DS in relation to the NS environment, GM (geometric mean) = $(NS \times DS)^{1/2}$, and DSI (drought susceptibility index) = (1 − Yds/Yns)/DII, where Yds and Yns are mean yields of a given genotype in DS and NS environments, respectively.

ment. Daily rainfall during each growing season was recorded (Table 1). In addition to seed yield (kg ha^{-1}), data were also recorded for 100-seed weight (g) and number of days to maturity. Values for the former two were adjusted to 14% moisture by weight. The DII for each growing season was calculated as DII = 1 − Xds/Xns, where Xds and Xns are the mean of all genotypes under DS and NS environments, respectively. Geometric mean (GM) was determined for seed yield, 100-seed weight, and days to maturity as GM = (NS × DS). Half percent reduction (PR) due to drought stress in relation to the NS environment was also determined for the three traits. Drought susceptibility index for seed yield for each genotype was calculated as follows: DSI = $(1 - Y_{ds}/Y_{ns})$/DII, where Y_{ds} and Y_{ns} are mean yields of a given genotype in DS and NS environments, respectively (Fischer and Maurer, 1978). Simple correlation coefficients among different traits were also determined. For data analysis, the cropping seasons and replications were considered as random effects and DS versus NS environments and common bean genotypes as fixed effects (McIntosh, 1983). All data were analyzed by a SAS PROC GLM statistical package (SAS, 1985).

RESULTS

The DII was comparatively high (0.81) in 1996A despite 106 mm rainfall during the growing season (Table 1). However, with much reduced rainfall in 1997A and 1998B cropping seasons, only moderate DII was recorded. Higher rainfall in 1998A resulted in the lowest DII. The effects of cropping seasons, replicates, and blocks within replicates were not significant ($P > 0.05$) for seed yield, 100-seed weight, and days to maturity (Table 2). Effects of DS versus NS environments for seed yield and differences among genotypes for all characters except PR and DSI were significant. The interactions between genotypes, cropping seasons, and DS versus NS environments were also significant for seed yield, 100-seed weight, and days to maturity.

Seed yield of all 36 genotypes in DS was significantly lower than its counterpart in NS environment (Table 3). Drought stress, on the average, reduced common bean yield by 53%, 100-seed weight by 13%, and days to maturity by 3%. The largest reduction in seed yield due to drought stress was in the susceptible checks (62%) and race Jalisco cultivars (59%), followed by the drought resistant checks (56%) and race Durango cultivars (52%). In contrast, the drought resistant selected lines showed comparatively less yield reduction (45%). Similarly, 100-seed weight and days to maturity of drought resistant selected lines and drought resistant checks were least affected by drought stress, whereas cultivars of races Durango and Jalisco exhibited the largest reduction in both traits (Table 3).

Drought resistant selected lines, on the average, significantly ($P < 0.05$) out-yielded all other groups of common bean genotypes under both DS and NS environments, followed by the drought resistant checks and race Durango cultivars (Table 3). As expected, drought susceptible checks had the lowest seed yield. Among drought resistant selected lines, SEA 5 exhibited the highest yield in both DS and NS environments (Table 3). All other selected lines were equal to or better than the highest yielding race Durango cultivars. Within race Durango cultivars, Bayo Los Llanos, Ojo de Cabra 24 MU, Negro Durango, Pinto Villa, and Zacatecano had comparatively higher seed yields in both environments. Similarly, in race Jalisco, Flor de Mayo IV, Apetito, Michoacan 89, Alteño, and Flor de Mayo had higher yields than other cultivars.

The DSI for seed yield was the lowest (0.6) for the race Durango cultivar Zacatecano and drought resistant selected line SEA 4 (Table 3). All drought resistant selected lines, except SEA 7, had relatively low DSI. Pinto Villa, Bayo Los Llanos, and Ojo de Cabra 24 MU in race Durango and Alteño in race Jalisco also had low DSI. Drought susceptible check A 750 and cultivars Bayo 400, Bayo Zacatecas, and Bayo Madero of race Durango and Rosa de Castilla, Michoacan 91-A, Garbancillo Zarco, and Frijola of race Jalisco had high DSI values ≥1.2.

Race Durango had the largest 100-seed weight (34 g), followed by race Jalisco cultivars (29 g) (Table 3). In race Durango, Morada de Agua, Bayo Zacatecas, and Bayo Madero had the largest seed weight. Cultivars

Table 3. Mean yield, 100-seed weight, and days to maturity for 36 common bean genotypes evaluated in drought-stressed and nonstressed environments at CIAT-Palmira, Colombia, in four cropping seasons between 1996 and 1998.

			Seed yield†					100-seed weight				Days to maturity		
Genotype	Origin	Seed color	NS	DS‡	GM	PR	DSI	NS	DS	GM	PR	NS	DS	GM
			kg ha^{-1}			%		g			%	d		
Race Durango cultivar														
Bayo Los Llanos	Mexico	Beige	1338	698	966	48	0.9	38	33	35	14	72	69	70
Ojo De Cabra 24 MU	Mexico	Brown	1311	679	943	48	0.9	31	27	29	14	66	66	66
Negro Durango	Mexico	Black	1302	626	903	52	1.0	31	28	29	8	75	73	74
Pinto Villa	Mexico	Pinto	1195	726	931	39	0.7	37	32	34	13	75	70	72
Ojo De Cabra Santa Rita	Mexico	Cream stripped	1265	595	868	53	1.0	34	28	31	19	67	65	66
Zacatecano	Mexico	Pinto	1071	719	878	33	0.6	35	30	32	14	69	67	68
Bayo Criollo Del Llano	Mexico	Beige	1109	484	733	56	1.1	37	34	35	7	74	71	72
Bayo 400	Mexico	Beige	1051	365	619	65	1.2	31	27	29	11	74	72	73
Guanajuato 31	Mexico	Beige	959	446	654	53	1.0	34	31	32	11	75	73	74
Morada De Agua	Mexico	Light purple	821	405	577	51	1.0	49	39	44	21	79	75	77
Bayo Zacatecas	Mexico	Beige	849	331	530	61	1.2	44	38	41	14	78	74	76
Bayo Madero	Mexico	Beige	769	240	430	69	1.3	41	35	38	15	78	77	77
Mean			1087	526	753	52	1.0	37	32	34	13	74	71	72
Race Jalisco cultivar														
Flor De Mayo IV	Mexico	Pink speckled	1170	493	759	58	1.1	32	27	29	15	80	77	78
Apetito	Mexico	Light purple	1094	506	744	54	1.0	26	23	24	14	74	71	72
Michoacan 89	Mexico	Pink	1089	452	702	58	1.1	22	20	21	10	73	73	73
Alteño	Mexico	Cream	967	573	744	41	0.8	28	27	27	4	75	73	74
Flor De Mayo	Mexico	Pink speckled	1049	438	678	58	1.1	33	26	29	19	80	78	79
Amarillo 153	Mexico	Yellow	1029	404	645	61	1.1	29	24	26	15	79	74	76
Rosa De Castilla	Mexico	Pink speckled	998	346	588	65	1.2	38	32	35	16	80	79	79
Chiapas 7	Mexico	Cream speckled	871	380	575	56	1.1	39	34	36	13	73	71	72
Michoacan 91-A	Mexico	Cream	992	255	503	74	1.4	34	27	30	21	79	78	78
Garbancillo Zarco	Mexico	Beige	745	272	450	63	1.2	30	25	27	15	82	78	80
Frijola	Mexico	Beige	707	263	431	63	1.2	39	26	32	32	82	77	79
Mean			974	398	620	59	1.1	32	26	29	16	78	75	77
Drought resistant line														
SEA 5	CIAT	Cream	1585	910	1201	43	0.8	28	24	26	14	72	70	71
SEA 8	CIAT	Cream speckled	1455	816	1090	44	0.8	22	20	21	6	74	73	73
SEA 2	CIAT	Cream	1432	812	1078	43	0.8	25	23	24	9	73	73	73
SEA 1	CIAT	Cream	1470	756	1054	49	0.9	27	24	25	8	74	72	73
SEA 13	CIAT	Cream	1392	786	1046	44	0.8	19	16	17	17	70	68	69
SEA 9	CIAT	Cream	1425	750	1034	47	0.9	24	23	23	4	75	73	74
SEA 14	CIAT	Cream	1373	770	1028	44	0.8	23	20	21	11	71	72	71
SEA 7	CIAT	Brown	1458	636	963	56	1.1	26	24	25	10	76	75	75
SEA 4	CIAT	Brown	1179	796	969	32	0.6	21	20	20	7	71	69	70
Mean			1419	781	1051	45	0.8	24	22	23	10	73	72	72
Drought resistant check														
BAT 477	CIAT	Cream	1296	603	884	53	1.0	20	19	19	4	74	74	74
San Cristobal 83	Dominican Republic	Red mottled	1169	478	748	59	1.1	27	24	25	10	75	77	76
Mean			1233	541	816	56	1.1	24	22	22	7	75	75	75
Drought susceptible check														
TR 7791-26	CIAT	Cream	731	328	490	55	1.0	19	15	17	18	81	78	79
A 750	CIAT	Purple speckled	359	115	203	68	1.3	25	20	22	21	85	85	85
Mean			545	221	347	62	1.2	22	18	20	20	83	81	82
Overall mean			1113	535	768	53	1.0	30	26	28	13	75	73	74
LSD (0.05)§			132	132	475	20	0.4	1.6	1.6	1.3	1.2	1.0	1.0	8
LSD(0.05)¶			38	38	47	2.0	0.03	0.5	0.5	1.3	1.2	0.3	0.3	0.8

† NS = nonstressed, DS = drought-stressed, PR = percent reduction in the DS in relation to the NS environment, GM (geometric mean) = (NS × ND)$^{1/2}$, and DSI (drought susceptibility index) = (1 − Yds/Yns)/DII, where Yds and Yns are mean yields of a given genotype in DS and NS environments, respectively.
‡ Paired values of NS and DS environments for each of 36 genotypes differ at $P = 0.05$.
§ To compare paired values among 36 genotypes.
¶ To compare means among races, selected lines, and checks.

Pinto Villa and Bayo Criollo del Llano also had large seeds. In race Jalisco, Rosa de Castilla and Chiapas 7 followed by Frijola and Flor de Mayo IV had the largest seed weight. Drought resistant selected lines generally had small seeds (<28 g 100-seed weight^{-1}). Nonetheless, SEA 1, SEA 5, and SEA 7 had relatively larger seeds (24 g 100-seed weight^{-1}), and SEA 13 had the smallest seeds among drought resistant selected lines.

The two drought susceptible checks (A 750 and TR 7791-26) followed by race Jalisco cultivars, namely Flor de Mayo IV, Flor de Mayo, Rosa de Castilla, Michoacan 91-A, Garbancillo Zarco, and Frijola were the latest to mature (77 d) (Table 3). Ojo de Cabra 24 MU and Ojo de Cabra Santa Rita were the earliest maturing genotypes requiring 67 d or less. Days to maturity of most drought resistant selected lines were similar to those of race Durango cultivars. Days to maturity of Ojo de Cabra 24 MU, Michoacan 91-A, SEA 2, BAT 477, and A 750 were not affected by drought stress. However, drought stress accelerated maturity of all other genotypes except San Cristobal 83. The latter matured 2 d later in DS compared with NS environment.

Correlation coefficients between the NS and DS environments were positive and highly significant ($P < 0.01$) for seed yield, 100-seed weight, and days to maturity (Table 4). Seed yield in DS environment was negatively correlated with PR for both seed yield and 100-seed weight and with DSI for seed yield. Seed yields in NS

Table 4. Correlation coefficients among nonstressed (NS), drought-stressed (DS), geometric mean (GM), percent reduction (PR), and drought susceptibility index (DSI) for seed yield, 100-seed weight, and days to maturity for 36 common bean genotypes evaluated in four cropping seasons between 1996 and 1998 at CIAT-Palmira, Colombia.

		Seed yield (kg ha^{-1})†				100-seed weight				Days to maturity			
		DS	GM	PR	DSI	NS	DS	GM	PR	NS	DS	GM	PR
Seed yield	NS	0.89**	0.95**	−0.29	−0.27	−0.38*	−0.25	−0.32	−0.54**	−0.68**	−0.61**	−0.66**	−0.23
	DS	–	0.98**	−0.56**	−0.51**	−0.40*	−0.28	−0.34*	−0.54**	−0.74**	−0.70**	−0.73**	−0.18
	GM		–	−0.48**	−0.40*	−0.43**	−0.29	−0.36*	−0.57**	−0.74**	−0.68**	−0.73**	−0.22
	PR			–	0.44**	0.15	0.04	0.10	−0.55**	0.54**	0.59**	0.58**	0.02
	DSI				–	−0.20	−0.27	−0.24	0.18	0.46**	0.57**	0.53**	−0.20
100-seed weight	NS					–	0.95**	0.99**	0.43**	0.19	0.03	0.12	0.46**
	DS						–	0.99**	0.16	0.06	−0.08	−0.01	0.37*
	GM							–	0.30	0.13	−0.02	0.05	0.41*
	PR								–	0.43**	0.31	0.38*	0.39*
Days to maturity	NS									–	0.92**	0.98**	0.35*
	DS										–	0.98**	−0.01
	GM											–	0.18

* Indicates significance at $P = 0.05$.
** Indicates significance at $P = 0.01$.
† GM (geometric mean) = $(NS \times DS)^{1/2}$. DSI (drought susceptibility index) = (1 − Yds/Yns)/DII, where Yds and Yns are mean yields of a given genotype in DS and NS environments, respectively (Fischer and Maurer, 1978).

and DS were negatively correlated with NS, DS, and GM values for days to maturity. A positive association was found between PR and DSI for seed yield and between PR and NS for 100-seed weight and days to maturity.

DISCUSSION

Several hundred germplasm accessions, breeding lines, and cultivars of common bean of diverse origins from the centers of origin and domestication of the crop in Latin America were systematically screened for drought resistance (Laing et al., 1983; Singh and Terán, 1995). However, as reported in this study, the highest level of drought resistance was found in race Durango cultivars from the Mexican highlands. Acosta-Gallegos and Adams (1991), Acosta-Gallegos and Kohashi-Shibata (1989), and Acosta et al. (1999) also reported high levels of drought resistance among cultivars from the same Mexican highland region. Cultivars from race Jalisco (e.g., Alteño, Flor de Mayo IV, and Apetito, among others) and Mesoamerica race (e.g., BAT 477, San Cristobal 83) also possessed significant levels of drought resistance.

Because of their evolutionary origins in semiarid and semi-humid regions in the Mexican highlands common bean cultivars from races Durango and Jalisco, respectively, would be expected to possess some degree of drought resistance (Singh, 1989; Singh et al., 1991). In this study, the former had significantly higher seed yield under drought stress than the latter group of cultivars. However, contrary to what was expected (Rosielle and Hamblin, 1981), the race Durango cultivars also consistently out-yielded race Jalisco cultivars in NS environments. In relatively cooler and semi-humid Mexican highlands, race Jalisco cultivars typically exhibit an aggressive climbing growth habit Type IV (Singh, 1982), and take approximately 150 d to maturity. In contrast, race Durango cultivars are of less aggressive growth habit Type III, and mature in approximately 120 d. As a result, the former is often higher yielding per unit of cropped area. At CIAT-Palmira, both groups of cultivars exhibited growth habit Type III, and matured in <90 d. A drastic change in growth habit and accelerated maturity, probably due to warmer temperatures and shorter day-length, affected race Jalisco more adversely than race Durango cultivars.

Even among a relatively small group of highly selected cultivars within races Durango and Jalisco, considerable variation existed for seed yield in DS and NS environments. Variation was also found for 100-seed weight, seed color, and days to maturity. Breeders and geneticists interested in developing drought resistant cultivars should therefore have ample opportunity to chose parents closely resembling to their choice of market class. Nonetheless, researchers in the USA, Canada, and in other higher latitude environments, should realize that landrace germplasm from races Durango and Jalisco are likely to be highly sensitive to long days (White and Laing, 1989). Consequently, a priori, a backcross conversion program (Bliss, 1993; Dudley, 1982; Urrea and Singh, 1995) or a two- or three-stage selection strategy (Kelly et al., 1998; Singh, 2001) may be required to introgress drought resistance and other traits successfully from these races into locally adapted cultivars.

Breeding crops for drought resistance is often considered to be a slow and difficult process (Blum, 1988; Hurd, 1976). For dryland or rain-fed environments, weather fluctuations, primarily the amount, duration, frequency, and timing of rainfall in relation to crop growth stages, are primary determinants of the levels of terminal or intermittent drought stress. Significant variation for these seasonal factors, and their interaction with genotypes, complicate the selection process in field-grown nurseries (Acosta et al., 1999). Therefore, for development of nine drought resistant lines, the F_2 to F_7 were grown under NS environment. The $F_{5:8}$ lines were evaluated in replicated yield trials for 3 yr in both DS and NS environments (Singh, 1995). Similarly, in this study, it was essential to conduct replicated trials for four cropping seasons in DS and NS environments to obtain reliable estimates for the three traits. Significant interactions among genotypes, cropping seasons, and DS versus NS environments occurred for most traits including seed yield. Moreover, drought at CIAT-Palmira may not be representative of that occurring in the major drought endemic regions of the world (Abebe et al., 1998; Miller and Burke, 1983; Rosales-Serna et al., 2000; Silveira et al., 1981). Thus, common bean genotypes identified or selected at CIAT-Palmira, Colombia, would need to be tested locally under drought stress before use in research and production programs elsewhere.

Drought resistant selected lines, as a group, significantly out-yielded cultivars from races Durango and Jalisco in both DS and NS environments. The specific adaptation in the environment in which they were developed and tested (i.e., CIAT-Palmira, Colombia) could have played a major role in their increased drought resistance. However, selected lines were derived from crosses between races Durango and Mesoamerica (population TR 7790 giving coded lines SEA 1 to SEA 13) and Mesoamerica and Nueva Granada (population TR 7791 giving line SEA 14) (Singh, 1995). CIAT breeding lines A 410 and A 422, derived from Mesoamerica × Durango interracial populations, also exhibited the highest levels of drought resistance in the Rift Valley of East Africa (Abebe et al., 1998). This indicates complementarity between and accumulation of favorable alleles from different common bean races for increased drought resistance. BAT 477 and San Cristobal 83, possessing characteristics of Mesoamerica race and used as parents in populations TR 7790 and TR 7791, were the most highly drought resistant germplasm in their group when these crosses were originally made (Laing et al., 1983; White et al., 1994b). However, as is evident from this study, Guanajuato 31 (with DSI = 1.0, indicating an average susceptibility to drought) apparently was not the most drought resistant germplasm from race Durango known at that time. For example, cultivars Bayo Los Llanos, Ojo de Cabra 24 MU, Pinto Villa, and Zacatecano had higher levels of drought resistance (with DSI <1.0, indicating below-average susceptibility to drought) than Guanajuato 31. Much larger genetic gains should be expected from the use of these cultivars in future breeding programs.

The race Jalisco cultivars, on the average, exhibited relatively lower levels of drought resistance (i.e., had a relatively higher DSI values) compared with race Durango cultivars. Nonetheless, in race Jalisco, cultivar Alteño had below-average susceptibility to drought stress. It is likely that Alteño and other such cultivars in race Jalisco also possess complementary and additive drought resistant alleles to those found in other races because of their distinct evolutionary origins (Singh, 1989; Singh et al., 1991). Use of drought resistant germplasm from races Durango and Jalisco and drought resistant selected lines reported in this study should therefore be maximized in cultivar development programs aimed at reducing water usage and production costs, and maximizing water-use efficiency and return for bean growers in a sustainable farming system.

Positive correlation between seed yield in DS and NS environments supported similar findings by Ramirez-Vallejo and Kelly (1998). Thus, genotypes that were high yielding in the DS were also high yielding in NS environment. The positive correlation between seed yield in DS and NS environments may have occurred because the mean yield in DS and NS environments, as well as PR due to drought stress, were taken into consideration for selecting drought resistant lines in both populations TR 7790 and TR 7791. From examining the performance of cultivars from races Durango and Jalisco it appears that a similar case, albeit unconsciously, might have happened during the domestication process, whereby genotypes that yielded well, both in years of drought stress and in favorable weather, were saved. Results of this study are similar to those reported by Rosales-Serna et al. (2000) and Schneider et al. (1997b), but contrary to those predicted by Rosielle and Hamblin (1981). The latter researchers predicted that high yielding genotypes in drought stress were likely to be low yielding in well-watered environments.

Negative association between seed yield in DS environment and PR and DSI would be expected because a higher yield in DS should result in lower PR and DSI values. However, its negative association with PR for 100-seed weight suggested that drought resistant genotypes, in general, had relatively smaller reductions in seed weight. Because of a positive association between PR and DSI for seed yield either trait could be used, in combination with the GM and/or arithmetic mean yield, to select drought resistant genotypes.

Days to maturity of drought resistant selected lines were comparable to those of cultivars from races Durango and Jalisco. Nonetheless, seed yields in NS and DS environments were correlated negatively with NS, DS, and GM values for days to maturity. Thus, terminal drought imposed during selection favored early maturing genotypes. Also, all drought resistant selected lines had comparatively smaller 100-seed weight, despite no selection being practiced for this or any other trait, except seed yield, during their development (Singh, 1995). This could be because of preferential adaptation (higher seed yield) of small-seeded beans in relatively warmer lowlands of tropical and subtropical Latin America, and that of medium-seeded race Durango and Jalisco cultivars in the cooler highlands as observed by Acosta-Gallegos et al. (1997), Singh (1989), and White et al. (1994b). Predominantly small seed size of selected drought resistant lines may also indicate that breeders interested in maintaining or improving 100-seed weight must select simultaneously for both yield and seed weight under drought stress.

CONCLUSIONS

For common bean, the highest levels of drought resistance were found in race Durango, followed by race Jalisco cultivars in field tests conducted at CIAT, Palmira, Colombia. Despite not having yet used most of the germplasm reported here in breeding and genetics studies, a systematic search for more drought resistant germplasm in these races would be justified. Because drought resistant selected lines from the interracial population Mesoamerica × Durango and intergene pool population Mesoamerica × Nueva Granada exhibited even higher levels of drought resistance than found in races Durango and Jalisco, further use of new sources of drought resistance in multiple-parent interracial and intergene pool populations should be maximized. This should assure sustained progress in breeding for drought resistance in common bean.

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