RESEARCH

Selection for Drought Resistance in Common Bean Also Improves Yield in Phosphorus Limited and Favorable Environments

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ABSTRACT

An estimated 60% of common bean (*Phaseolus vulgaris* L.) production worldwide is at risk of drought. A breeding program was developed at the International Center of Tropical Agriculture (CIAT) to create drought resistant breeding lines with varietal potential in the small red, small black, cream (mulatinho) and cream-striped (carioca) grain classes. Breeding populations were created from triple or double crosses. Field screening under terminal drought was performed at Palmira, Colombia in the dry season in F_2, $F_{3:5}$, and $F_{6:8}$ generations over two cycles of recurrent selection in the small red and small black classes, and one cycle in the mulatinho and carioca classes. Drought resistant lines yielded significantly more than commercial check cultivars under drought in all color classes. Some outyielded the respective checks by 15 to 25% (depending on color class and trial) in one or more of three favorable environments, or in the combined analysis across favorable environments, and were also earlier to mature. Drought resistant lines presented up to 36% greater yield d^{-1} in favorable environments. Some also expressed superior yields in a phosphorus-limited environment. Thus, selection for drought resistance has improved yield potential and plant efficiency across different environments. It is suggested that selection under drought stress reveals genes that correct inefficiencies inherited from the wild *Phaseolus vulgaris*, and are key to yield improvement of common bean.

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Cᴏᴍᴍᴏɴ ʙᴇᴀɴ (*Phaseolus vulgaris* L.) is a small-farmer crop in Latin America and eastern and southern Africa, where it is often cultivated in unfavorable conditions and with minimal inputs. It is estimated that 60% of the bean crop is cultivated under the risk of either intermittent or terminal drought (White and Singh, 1991a; Thung and Rao, 1999). The effects of drought on common bean are dependent on the intensity, type, and duration of the stress (White and Izquierdo, 1991; Terán and Singh, 2002a, b; Muñoz–Perea et al., 2006). In Africa as much as 300,000 Mg of beans are lost to drought annually (Wortmann et al., 1998). Highland Mexico, Central America, northeast Brazil, and much of eastern and southern Africa are bean producing areas where drought is endemic.

Cultivated common bean has two major gene pools and several races within pools (Beebe et al., 2000; Singh et al., 1991). Mesoamerican race Durango from dryland Mexico has been an important source of useful drought-resistance genes (Acosta–Gallegos and Kohashi–Shibata, 1989; Acosta–Gallegos and Adams, 1991; Singh, 1995; Acosta–Gallegos et al., 1999; Terán and Singh, 2002b), although local adaptation is an important component of drought resistance (White, 1987). Race Mesoamerica is native to the warm lowlands of Central America (Singh et al., 1991).

Combining races Durango and Mesoamerica has been a consistent source of improved drought resistance for lowland tropical environments (Terán and Singh, 2002b; Frahm et al., 2004; Ishitani et al., 2004).

Genetic improvement of drought resistance in crops is a slow and difficult process (Blum, 1988; Subbarao et al., 1995). Multiple variables are usually involved in influencing the impact of drought on crop performance (Sinclair and Purcell, 2005). Many drought adaptation traits, such as phenology, root size and depth, hydraulic conductivity, and the storage of reserves, are associated with plant development and structure and are constitutive rather than stress induced (Chaves et al., 2003). Greater root length in lower soil strata is an important drought resistance mechanism of common bean (Sponchiado et al., 1989). BAT 477, a drought-resistant race Mesoamerica line identified in CIAT-Colombia, possesses deep rooting ability (White et al., 1994a,b) with greater water absorption efficiency (Guimaraes et al., 1996). Greater mobilization of photosynthate to seed under stress is another important trait that is found in G 21212, another landrace of race Mesoamerica (Rao, 2001). In Australia, Dowkiw et al. (2000) compared "indirect" (trait) selection with the conventional "direct" (yield) selection method to improve drought resistance in navy bean. They concluded that seed yield shows more genotype × environment interaction than the functional yield components such as the transpiration, water use efficiency, and harvest index but that several negative correlations between these traits may limit genetic progress using the indirect selection method.

Furthermore, other production constraints are also endemic to regions subject to drought. Soil fertility in tropical soils is often poor, especially with regard to phosphorus availability, and can limit vegetative development and root growth (Lynch and Beebe, 1995; Thung and Rao, 1999). A Brazilian landrace, Carioca (CIAT accession G 4017), was recognized as superior in tolerance to low soil fertility (Thung, 1990). Although improving common bean for tolerance to infertile soil has been difficult (Singh et al., 1989), progress has been registered in recent years (Singh et al., 2003). Poor soil fertility often occurs in combination with drought in farmers' fields, but combining tolerance to these two constraints may represent a particular challenge. Ho et al. (2005) suggest that a shallow and abundant root system is more effective in absorption of nutrients in the top 20 cm of soil where nutrients are concentrated, while deeper rooting favors accessing moisture and drought resistance.

Yet another question is the relationship of stress resistance to yield potential under favorable conditions (Blum, 2005). Breeding under high–yielding, non-stressed conditions may not be the best approach to increasing yields where severe abiotic stresses are encountered in the target environments (Rosielle and Hamblin, 1981; Simmonds,

1991). On the other hand, Bänziger et al. (1999) found that selection for resistance to midseason drought stress in maize (*Zea mays* L.) has increased yields in four lowland tropical maize populations of different genetic backgrounds when grown across a wide range of nitrogen levels. Yields of corn and soybeans in the United States have increased as a result of tolerance to high plant densities (Specht et al., 1999; Tollenaar and Wu, 1999), which could be an expression of stress tolerance. Thus, yield potential in stressful environments and yield potential in non-stressful environments may not be mutually exclusive.

Much breeding for drought resistance in common bean for the warm tropics has until now focused on developing improved sources of drought resistance without regard for other varietal traits (Singh et al., 2001; Terán and Singh, 2002a). The objective of the research presented here was to obtain drought-resistant genotypes in commercial classes of common bean, with regard to grain type, disease resistance, and yield response of drought resistant lines to other environments, especially those with low soil P availability. Furthermore, we wished to test the hypothesis that selection for drought resistance does not imply a yield penalty in other environments, especially in favorable environments that are not limited by either drought or soil fertility.

MATERIALS AND METHODS
Development of Populations
Parental materials were selected from among lines in CIAT's bean breeding program. Seven had been developed specifically for drought resistance. For example, SEA 15 which is a progeny of breeding line SEA 5 (Singh et al., 2001; Terán and Singh, 2002b), was used frequently. Besides SEA 5, SEA 15 has another race Durango parent, Apetito, a Mexican landrace in its pedigree. Another eleven parental lines such as red-seeded RAB's 609 and 651 had no previous selection for drought during their development, and had no race Durango parentage, but had expressed a level of resistance when evaluated as advanced lines. Ten lines were included as parents due to their superior performance in conditions of low soil phosphorus. G 21212, a landrace from Colombia, had presented tolerance to low soil P availability and subsequently was recognized as possessing some resistance to drought. Nine lines were included as sources of resistance to bean golden yellow mosaic virus (BGYMV), especially red-seeded lines obtained from the Pan-American School in Zamorano, Honduras. Among the four parents in a double cross, normally two parents had some recognized drought resistance. All crosses included parental materials with preferred regional grain types: small red and small black types for Central America; and cream striped (carioca) and cream (mulatinho) for Brazil. In the first cycle of selection, 125 multiple crosses were created. In the second cycle, 50 crosses were created using 19 drought selected lines, seven low fertility selections, and four sources of resistance to BGYMV. Two cycles of crossing and selection were completed for the red- and black-seeded types, and one cycle for the carioca and mulatinho types.

Table 1. Characteristics of the four field sites in Colombia and average annual meteorological conditions.

Variable	Field sites			
	Palmira	Popayán	Quilichao	Darién
Altitude (m)	965	1750	990	1523
Latitude and Longitude	3 ° 29′ N; 76 ° 21′ W	2 ° 25′ N; 76 ° 40′ W	3 ° 06′ N; 76 ° 31′ W	3 ° 55′ N; 76 ° 28′ W
Soil type	Mollisol (fine-silty, mixed, isohyper-thermic Aquic Hapludoll)	Inceptisol (medial, isothermic Typic Dystrandept)	Oxisol (very fine, kaolinitic, isohyper-thermic Plinthidic Kandiudox)	Inceptisol (typic Dystrandept)
Mean temperature (°C)	24.3	20.1	24.1	20
Minimum	18.8	13.8	17.7	16.2
Maximum	28.4	23.8	28.4	25.6
Relative humidity (%)	74	74	78	–
Annual rainfall (mm)	896	2124	1756	1650
Annual potential evapotranspiration (mm)	1834	1530	1563	–

Selection Environments

Selection was practiced in three different environments in Colombia in successive generations, seeking broad adaptation. Basic characteristics of the field sites and annual climatic conditions are listed in Table 1. Drought resistance was evaluated in Palmira in the dry season from June to September. The soil presented no major fertility problems (pH = 7.7), and was estimated to permit storage of 130 mm of available water (assuming 1.0 m of effective root growth with −0.03 MPa and −1.5 MPa as upper and lower limits for soil matric potential) (White and Castillo, 1992). During the crop-growing season, average maximum and minimum air temperatures in 2004 were 30.5 and 18.7°C, and in 2005 were 31.2 and 19.3°C, respectively. The incident solar radiation ranged from 10.3 to 22.7 MJ m^{-2} d^{-1} in 2004 and 11.7 to 22.8 MJ m^{-2} d^{-1} in 2005. The total rainfall during active crop growth was 110.4 mm in 2004 and 130.1 mm in 2005. The potential pan evaporation was of 390 mm in 2004 and 472.5 mm in 2005, far exceeding rainfall after irrigation was suspended. Fields for drought nurseries were furrow irrigated (approximately 35 mm of water per irrigation) 6 d before planting and twice more at 12 and 25 d after planting before suspending irrigation. Drought treatment resulted in incipient wilting at midday during flowering, and stress increased throughout the pod filling period until physiological maturity. Measurements of soil moisture tension revealed values of −70 kPa or lower as plots were approaching physiological maturity, confirming severe terminal stress.

Selection for cool-temperature adaptation and moderate P stress was practiced in Popayán. Soil is of volcanic origin with very low native soil P availability and very high P fixation capacity, although continuous cultivation over a 25-year period has resulted in a residual soil P availability of 6 to 8 mg kg^{-1} (Bray II). Additional P was supplied to segregating populations at a rate of 15 kg ha^{-1} to get a moderate level of P stress. Plots were inoculated with local isolates of the anthracnose pathogen (*Colletotrichum lindemuthianum*) by aspersion of inoculum over the canopy twice during the growing season. Reaction to anthracnose was evaluated on a scale of 1 (immune) to 9 (totally susceptible) (Schoonhoven and Pastor-Corrales, 1987).

Selection for tolerance to a moderate level of soil acidity was practiced in Quilichao. Soil was classed as an Oxisol but with relatively high organic matter (about 60 g kg^{-1}). Here, too,

native soil P availability was very low but residual P availability was 5 to 10 mg kg^{-1} (Bray II). Lime was applied as needed to correct extreme soil acidity and relieve severe aluminum (Al) toxicity. Segregating populations received an additional 10 kg ha^{-1} P to create a moderate level of P stress. Segregating populations were inoculated twice in the growing season with local isolates of the ALS pathogen (*Phaeoisariopsis griseola*). Reaction to ALS was evaluated on a scale of 1 (immune) to 9 (totally susceptible) (Schoonhoven and Pastor-Corrales, 1987).

Selection Procedures

F_2 populations were managed by gamete selection as described by Singh et al. (1998). In this system complex crosses result in F_1 plants each with a unique genetic composition. F_1 plants were harvested individually to create F_1-derived F_2 populations. These were planted and selected visually for pod load in the drought nursery, seeking families that matured normally under terminal drought with well filled pods indicative of superior mobilization of photosynthates (good translocation). Selected families were mass selected based on productivity. F_3 populations were planted under moderate P stress and anthracnose pressure in Popayán, where individual plant selections were made within superior populations. $F_{3:4}$ families were planted as single rows in Quilichao and evaluated for ALS resistance under moderate P stress and soil acidity. Selected $F_{3:5}$ families were subsequently evaluated again under drought conditions at Palmira as described above, in a series of lattice design experiments of either 7 × 7 or 6 × 6 plots with three replications. Small lattice designs were preferred to maintain a relatively more compact sub-plot and results across trials were compared in relation to common checks. The experimental unit consisted of two 3.72 m rows 60 cm apart, with plants approximately 10 cm apart within the row. Individual F_6 plants were selected from superior families to develop lines. In each generation selection pressure was applied for well filled grain, assessed visually. Individual plants, families and lines with poorly filled seed were discarded. It was expected that such selection pressure would favor genes for better photoassimilate remobilization. A second cycle of selection was initiated by crossing $F_{3:6}$ families among each other and with additional parents for disease resistance. Results of drought yields from the second cycle of selection are reported for $F_{3:5}$ families in 2004 (out of a total of 244 tested)
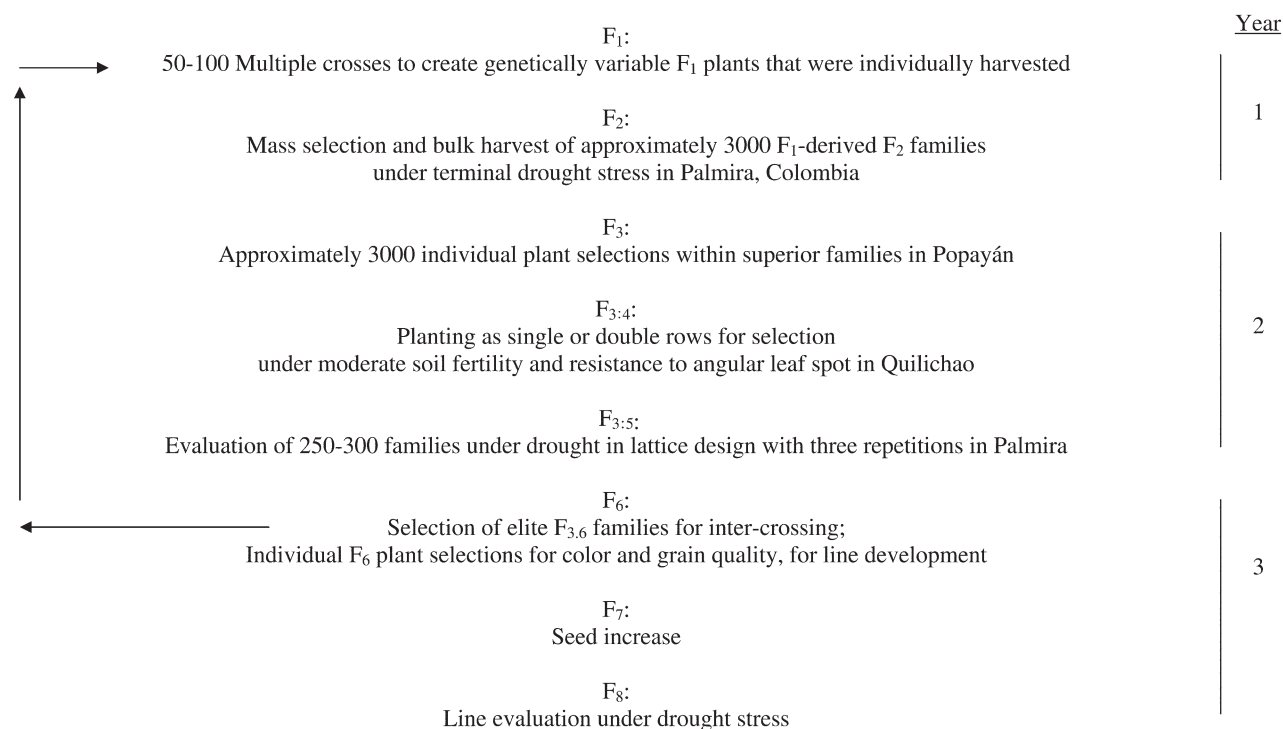
Year

F_1:
50-100 Multiple crosses to create genetically variable F_1 plants that were individually harvested

F_2:
Mass selection and bulk harvest of approximately 3000 F_1-derived F_2 families
under terminal drought stress in Palmira, Colombia

1

F_3:
Approximately 3000 individual plant selections within superior families in Popayán

$F_{3:4}$:
Planting as single or double rows for selection
under moderate soil fertility and resistance to angular leaf spot in Quilichao

2

$F_{3:5}$:
Evaluation of 250-300 families under drought in lattice design with three repetitions in Palmira

F_6:
Selection of elite $F_{3.6}$ families for inter-crossing;
Individual F_6 plant selections for color and grain quality, for line development

3

F_7:
Seed increase

F_8:
Line evaluation under drought stress

Figure 1. The breeding scheme used to develop drought resistant common bean lines.

which produced the ten most promising $F_{6:8}$ or $F_{7:9}$ lines in the respective color class in 2005 (see below). For purposes of this article, drought resistance is defined as higher yield under drought conditions compared to drought sensitive commercial check cultivars. The selection scheme is summarized in Fig. 1.

Line Evaluation

A total of 362 $F_{6:8}$ (red- and black-seeded) and $F_{7:9}$ (mulatinho and carioca types) lines were evaluated under drought in 2005 to confirm drought resistance. Lines were organized by color class into eleven yield trials in lattice design (5×5 or 7×7) and planted in the drought nursery in June 2005 as described above. Commercial checks for each color class were the cultivars Tio Canela (red-seeded), DOR 390 (black-seeded), and Perola (carioca type). These are standard cultivars in the respective commercial classes and are representative of the yield potential in these classes at present. Given the objective of cultivar improvement within commercial classes, these were utilized as controls in yield trials both in drought stressed and unstressed environments. No attempt was made to include all parental material of the lines in the trials, which was not practical considering the large number of parental stocks (more than 30) that contributed to these lines.

Additionally, we wished to know if drought-selected lines would respond to favorable environments. Therefore elite drought lines from the 2005 trials were selected for multilocational trials in Palmira, Popayán and Quilichao in the 2005 September–December planting season. Ninety-four lines plus checks were organized in three trials in 6×6 lattice design with three replications, and each trial was sown at all three locations. Four row plots with 60 cm between rows were planted, 5 m long in Popayán and Quilichao and 3.72 m long in Palmira, with 7 cm between plants in the row. Grain was harvested from the central two rows after discarding end plants. Common checks

were included in all three trials to facilitate comparison across trials. Diseases were controlled opportunely, and rainfall at all sites was fully adequate for the crop's needs. Fertilizer was applied as N-P-K at the rate (kg ha^{-1}) of 74N-32P-61K in Popayán and 69N-30P-57K in Quilichao, and lime was applied as needed. No soil amendments or fertilizers were required in Palmira.

Finally, we were concerned that the lines should have at least an average response under low fertility, especially low P, such that expression of drought resistance would not be limited by a poor response to low P. Thus two trials were established at a fourth site, Darién. The climate in Darién is favorable for beans, and rainfall is not limiting. The only major abiotic stress is low soil P availability, and the trial at this site focused on the response to this constraint. The first trial, planted in October 2005 was established with 177 elite drought-selected lines as an informal observation nursery in two unrandomized replicates of two 4 m rows per plot. Soil testing revealed less than 2 mg kg^{-1} of available P (Bray II), and fertilizer was banded manually to the rows at a rate of 10 kg ha^{-1} P. A commercial check sensitive to low soil P availability, cultivar Tio Canela, was planted after every ten materials throughout the field for comparison. End plants were discarded and plots were harvested for grain yield. A t test was used to compare yields of populations of drought-selected lines by color group, versus the population of Tio Canela checks intercalated within those lines. Fourteen high yielding lines were selected from this trial and subsequently planted in April 2007 with two checks [Tio Canela and landrace Carioca (G 4017)] in the same site in 4-row 4-m plots, in a 4×4 lattice, with 10 kg ha^{-1} P so as to induce P deficiency in sensitive lines. Yield was measured on the central two rows of each plot after discarding end plants.

Lines were also evaluated in a greenhouse test for resistance to BGYMV, using a local isolate of the virus and mechanical inoculation of 10 plants per family. Resistance is quantitative

Table 2. Yields of ten red-seeded, drought resistant common bean lines that yielded best in favorable environments compared to the 'Tio Canela' check, including drought stressed yields as $F_{3:5}$ and $F_{6:8}$ families, unstressed yields in three sites, days to maturity and yield per day.

Line	Drought treatment, $F_{3:5}$ Palmira			Drought treatment, $F_{6:8}$ lines Palmira				Unstressed treatments, $F_{6:9}$ lines Palmira			Quilichao		Popayán		Average, 3 sites		
	Tr†	Yield‡, kg ha⁻¹ (% check§)	YD¶	Tr	Yield, kg ha⁻¹ (% check)	YD	g-100 seed⁻¹	Tr	Yield, kg ha⁻¹ (% check)	YD¶	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	DTM#
SER 43	1	1895 (123)	29.2	1	1589** (250)	24.9**	25	1	3395 (114)	46.0	1087 (115)	17.1	2041** (176)	22.9*	2127** (123)	28.1*	76
SER 48	1	1851 (120)	29.3	1	1607** (253)	26.8**	28	1	3653* (123)	54.1*	1159 (122)	19.2	1939** (167)	23.3*	2220** (128)	31.9**	70**
SER 51	1	1946 (127)	31.5*	2	946** (210)	15.1**	23	1	3254 (109)	49.4*	1113 (117)	17.9	1758* (151)	20.3*	2082* (120)	29.8**	72**
SER 94	2	2284** (161)	36.1**	4	1196** (230)	19.9**	24	2	3326 (108)	48.5	3074** (123)	47.0*	2258* (139)	27.5*	2893** (119)	41.0**	72**
SER 95	2	2284** (161)	36.1**	4	946* (181)	15.9*	24	2	3525 (114)	49.2	3058* (122)	47.0*	1982 (122)	24.0	2834** (117)	39.8**	73**
SER 96	2	2284** (161)	36.1**	4	997* (191)	16.8*	24	2	3388 (110)	49.8	3216** (128)	48.9*	2258* (139)	27.8*	2934** (121)	41.9**	71**
SER 102	2	2258** (159)	37.2**	5	888* (255)	14.9*	24	2	3252 (106)	47.8	3069** (123)	48.0*	2035 (125)	25.0*	2807** (116)	40.6**	71**
SER 112	2	1814 (128)	28.2	5	913* (263)	14.5*	31	2	3636* (118)	51.0*	2818 (112)	42.9	2062 (127)	24.4	2918** (120)	40.4**	74**
SER 113	2	2040* (143)	31.1*	5	1025** (295)	15.9**	28	2	3710* (120)	53.9*	3195** (128)	47.8*	2253* (139)	26.7*	3009** (124)	42.3**	73**
SER 118	3	1616 (98)	24.8	1	1534** (241)	24.6**	24	2	3437 (112)	49.6	3280** (131)	49.4*	1849 (114)	21.3	2824** (116)	39.8**	74**
Tio Canela	1	1531	23.5	1	634	9.7	21.7	1	2978	41.7	948	14.7	1163	13.1	1730	23.7	75
LSD (0.05)	1	499	7.5	1	615	9.8	2.1	1	503	7.0	398	6.2	527	6.0	287	3.8	1
Tio Canela	2	1417	21.8	2	450	6.9	20.6	2	3081	43.6	2505	36.8	1626	18.5	2425	33.2	76
LSD (0.05)	2	528	7.9	2	349	5.5	2.1	2	490	6.7	420	6.2	514	6.0	278	3.7	1
Tio Canela	3	1645	25.3	4	520	8.3	19.8										
LSD (0.05)	3	399	6.0	4	424	6.9	2.3										
Tio Canela				5	347	5.4	22.7										
LSD (0.05)				5	490	7.9	2.7										

*Statistical significance at the 0.05 probability level in relation to check.

**Statistical significance at the 0.01 probability level in relation to check.

†Trial number.

‡Adjusted mean from lattice design with three replications.

§Yields are derived from several parallel trials. Therefore yields are calculated as percent of yield of Tio Canela in each respective trial to facilitate comparisons.

¶Yield per day calculated for each of three replications and adjusted as per lattice design.

#Days to physiological maturity, averaged over three sites and three replications per site.

and under intense inoculation conditions, symptoms can be induced even in resistant lines. Therefore, families with even two plants expressing symptoms were considered resistant.

RESULTS
Yield in Drought Stressed and Favorable Environments
Reds

Since data are derived from several different trials, we present yields as relative to the Tio Canela check to facilitate comparison (Table 2). Among the check cultivars in the three color classes, Tio Canela was the best yielding, thus the relative values comparing the advantage of advanced lines over the checks appear less dramatic in the red lines, although in fact the greatest absolute yields were found mostly among these lines. Selected $F_{6:8}$ lines produced 2 to 3 times more than Tio Canela under severe terminal drought (Table 2). Furthermore, seed filling and seed quality were excellent in most elite lines, as seen in the data on seed size in the drought treatment that ranged from 23 to 31 g 100 seed⁻¹, compared to Tio Canela with

22 g 100 seed⁻¹. This represents a great advantage in terms of the commercial value of the harvested grain that is not reflected in the yield data alone.

Among the unstressed trials across sites, all red–seeded trials gave acceptable yield levels except one of the trials in Quilichao (Trial 1) for which yields were reduced by soil compaction. However, yields from this trial are included for comparison and completeness (Table 2). Trial averages at Popayán were likewise acceptable (1500 to 2000 kg ha⁻¹) but somewhat less than historical averages at that site due to heavy rains. Yield of most of the 47 red–seeded lines did not differ significantly from that of the respective commercial Tio Canela check (data not shown), and thus selection for drought resistance did not reduce yield potential. However, some lines yielded significantly more than the check in one or more environments (Table 2). For example, SER 96 yielded 110, 128, and 139% of the check yield over the three unstressed environments (Palmira, Quilichao, and Popayán, respectively), significantly outyielding the check in two environments. All ten elite lines presented in Table 2 yielded significantly more than Tio Canela in the combined

analysis across sites. However, in spite of yielding as well or better than the check, many lines were earlier to mature than Tio Canela, for example, SER 96 that matured in 72 d versus 75 d for Tio Canela, or SER 48 that matured in 70 d. SER 113 had greater yield d^{-1} in all three environments, and SER's 48, 51, 94, 96, and 102 in two environments (Table 2). Thus, several drought-selected lines presented better yield efficiency under unstressed conditions than the check.

Blacks

Given the very poor yield of the DOR 390 check under drought, the relative yields of the $F_{6:8}$ elite lines were from 4 to 6 times greater than the check (Table 3). However, absolute yields of the black-seeded lines were in general lower than those of the red-seeded lines. On the other hand, DOR 390 was the highest yielding check in unstressed conditions, and only one drought resistant line (SEN 36) outyielded DOR 390 in the unstressed trials across sites. SEN 36 matured in 76 d versus 78 d for DOR 390. Although most lines did not exceed DOR 390 in absolute yield, several have similar yields with much earlier maturity, suggesting better yield efficiency (for example, SEN's 43, 44, 52, and 56 that were 5 to 7 d earlier than DOR 390). About 50% of the elite black-seeded lines presented greater yield d^{-1} compared to DOR 390 in the combined analysis across unstressed environments (Table 3). Most lines with improved drought resistance presented grain size under drought that is normal for black beans (18–22 g 100 $seed^{-1}$) (Table 3).

Brazilian Grain Types

Similar to the case with black beans, the check cultivar Perola yielded very poorly under drought, leading to very high relative yields of the $F_{7:9}$ test lines, as high as 689% of the Perola yield (Table 4). In Palmira without stress, yields of the lines were frequently greater than the check yield. For example, cream-seeded SXB 403 yielded 132, 104, and 149% of the Perola check yield in Palmira, Quilichao, and Popayán, while carioca-type SXB 410 yielded 143, 115, and 108%, respectively. Pink seeded (rosinha type) SXB 418 was also outstanding. Based on yield d^{-1} most lines were more efficient than the check in Palmira (Table 4), which was the highest yielding environment. Grain size under drought stress in the carioca and mulatinho types was as high as 35 g 100 $seed^{-1}$, compared to the check Perola with 31 g 100 $seed^{-1}$.

Yield in Phosphorus Limited Environment

When the several color groups of advanced lines were compared using a *t* test with the Tio Canela checks that were intercalated every ten materials, three of the six groups of lines outyielded the check significantly, and by a wide margin: the red beans selected for drought resistance (SER lines), by 221 kg ha^{-1}; the black beans selected for drought and BCMNV resistance (NCB lines), by 336 kg ha^{-1}; and the

Brazilian types selected for drought resistance (SXB lines), by 684 kg ha^{-1}. SEN (black-seeded drought lines), RCB (red-seeded BCMNV resistant) and MIB (selected for high mineral concentration in grain) lines did not differ from the check. The promising yield levels in the SER, NCB, and SXB lines led us to establish a replicated yield trial under P stress to validate these results with selected lines.

In the subsequent trial of fourteen selected lines, most yielded marginally better than the low-P tolerant Carioca check (Table 5), suggesting that they possessed a moderate level of low P tolerance comparable to 'Carioca.' Most lines were also 3 or 4 d earlier to mature than Carioca. Two lines, however, yielded significantly more than Carioca: SER 118, which yielded 34% more, and NCB226, which outyielded Carioca by 41%. Thus, although the margin over the checks was not as wide as in the previous trial, these results confirmed the potential of some lines to yield well under a moderate level of low P stress, and better than a long-standing low P check, Carioca. Furthermore, both NCB 226 and SER 118, together with SER 119, presented greater yield d^{-1} than Carioca. Thus, the tendency for greater yield efficiency was also observed in conditions of P limitation.

Although it is not our primary purpose to report on the selection of disease resistance of the advanced lines, data suggested that recovery of resistance to anthracnose, ALS or BGYMV in drought resistant lines was totally feasible (data not shown). Among the red-seeded lines that yielded more than the check, 23% were resistant or intermediate to ALS, and 58% were resistant to BGYMV. Among black-seeded lines in Table 3 about 20% expressed resistance to BGYMV, but only one line had intermediate resistance to ALS. The Brazilian grain types were only evaluated for ALS but all lines in Table 4 expressed an intermediate or resistant reaction. Anthracnose evaluation was not practiced on advanced lines but 89% of the red and 100% of black-seeded early generation families that produced the advanced lines expressed a majority of resistant plants.

DISCUSSION

Yield under drought improved significantly compared to commercial check materials in three color classes of common bean. While detailed physiological analysis is in progress, preliminary evidence based on vigor, pod load, seed yield, seed size, and root development suggests that selection has recovered both favorable root traits as well as efficient mobilization of photosynthate to grain (Rao, 2001; Ishitani et al., 2004; Beebe et al., 2007). Pedigrees of many advanced lines included SEA 15, which is a progeny of SEA 5, which in turn was derived from an interracial cross including races Durango and Mesoamerica of the Middle American gene pool (Terán and Singh, 2002b). SEA 15 also has Apetito (G 1759), a race Durango landrace, in its pedigree. Improved drought resistance in interracial crosses combining Durango and Mesoamerican races was also reported before (Singh, 1995;

Table 3. Yields of ten black-seeded, drought resistant common bean lines that yielded best in favorable environments compared to the 'DOR 390' check, including drought stressed yields as $F_{3:5}$ and $F_{6:8}$ families, unstressed yields in three sites, days to maturity and yield per day.

Line	Drought treatment, $F_{3:5}$ Palmira			Drought treatment, $F_{6:8}$ lines Palmira				Unstressed treatments, $F_{6:9}$ lines									
									Palmira		Quilichao		Popayán		Average, 3 sites		
	Tr[†]	Yield[‡], kg ha⁻¹ (% check[§])	YD[¶]	Tr	Yield, kg ha⁻¹ (% check)	YD	g-100 seed⁻¹	Tr	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	DTM[#]
NCB 226	5	2641** (255)	40.5**	7	1240** (244)	18.7**	33	1	3814 (106)	50.7	1236 (101)	19.3	1726 (111)	19.8	2265 (105)	30.0	75**
NCB 229	5	2641** (255)	40.5**	7	1508** (297)	21.6**	35	1	3914 (109)	51.6	1052 (86)	16.7	1530 (98)	17.5	2164 (100)	28.6	75**
SEN 36	6	1449* (167)	22.2*	8	712* (384)	11.1*	22	3	3821 (114)	52.8	2910 (109)	44.4	1810 (126)	20.2	2805* (115)	38.7*	76**
SEN 38	5	1986** (192)	32.2**	8	1055** (570)	17.2**	21	3	3443 (103)	50.9	2760 (103)	44.3	1241 (86)	14.4	2477 (102)	36.5	72**
SEN 43	5	1986** (192)	32.2**	8	974** (526)	16.3**	21	3	3132 (94)	48.2	2740 (102)	44.9	1684 (117)	19.6	2537 (104)	37.8*	71**
SEN 44	5	1986** (192)	32.2**	8	891** (481)	14.8**	20	3	3299 (99)	49.8	2829 (105)	46.4*	1354 (94)	15.7	2586 (106)	38.4*	71**
SEN 46	5	1914** (185)	31.7**	8	928** (501)	15.7**	19	3	3050 (91)	44.0	2565 (96)	41.9	1603 (112)	18.7	2421 (99)	35.1	72**
SEN 48	7	1832 (129)	30.0*	8	854** (461)	14.2**	21	3	3190 (95)	46.2	2482 (92)	40.5	1622 (113)	19.0	2483 (102)	35.9	72**
SEN 52	5	1872** (181)	30.4**	8	908** (490)	15.5**	22	3	3731 (112)	58.0*	2723 (102)	44.4	1335 (93)	15.8	2606 (107)	39.6**	70**
SEN 56	5	1872** (181)	30.4**	8	1191** (643)	20.3**	23	3	3518 (105)	53.3*	3031 (113)	48.1*	1367 (95)	16.2	2618 (107)	38.9**	71**
DOR 390	5	1033	16.1	7	507	7.5	19	1	3585	47.9	1216	18.7	1549	16.7	2164	28.3	77
LSD (0.05)	5	485	7.2	7	453	6.9		1	583	8.5	688	10.4	436	5.0	287	3.8	1
DOR 390	6	864	13.5	8	185	2.9	16	3	3330	44.4	2669	38.8	1430	15.7	2436	32.4	78
LSD (0.05)	6	543	8.0	8	397	6.6		3	503	7.0	398	6.2	527	6.0	354	4.9	2
DOR 390	7	1411	21.3														
LSD (0.05)	7	539	8.0														

*Statistical significance at the 0.05 probability levels in relation to check.

**Statistical significance at the 0.01 probability levels in relation to check.

[†]Trial number.

[‡]Adjusted mean from lattice design with three replications.

[§]Yields are derived from several parallel trials. Therefore yields are calculated as percent of yield of DOR 390 in each respective trial to facilitate comparisons.

[¶]Yield per day calculated for each of three replications and adjusted as per lattice design.

[#]Days to physiological maturity, averaged over three sites and three replications per site.

Schneider et al., 1997). Thus, interracial combinations continue to produce drought-resistant lines in common bean.

The red-seeded Central American types combined especially well with race Durango genes for enhanced drought resistance. Among race Mesoamerica types, more superior red-seeded lines were recovered than black-seeded after two cycles of crossing and selection. Furthermore, it was particularly difficult to recover good grain quality in a black-seeded type II growth habit (upright indeterminate bush; Schoonhoven and Pastor-Corrales, 1987) under severe terminal drought. Nielsen and Nelson (1998) reported that seed weight was the only yield component that was significantly reduced by water stress in reproductive and grain filling stages in black bean cultivar Midnight, confirming the sensitivity of seed weight in an upright black bean cultivar. Although both the black and red-seeded materials derive from race Mesoamerica (Singh et al., 1991), red-seeded landraces (Beebe et al., 2000) and red-seeded bred lines (Beebe et al., 1995) can both be discriminated from the type II black-seeded materials based on DNA polymorphisms. The type II accessions were designated sub-race M1, while the red- and black-seeded accessions of growth habit type III (prostrate bush with well developed branches; Schoonhoven

and Pastor-Corrales, 1987), were designated sub-race M2 (Beebe et al., 2000). It is possible that these two sub-races are distinguished by an inherent difference in drought resistance. However, this is not an insurmountable difference, as we did recover type II black-seeded lines with good drought resistance such as SEN 36, as did Frahm et al. (2004) working in Central America. Black-seeded NCB 226 which displayed resistance to both drought and low P would appear to be another exception, but in fact it is derived from accession G 21212, which morphologically pertains to sub-race M2.

There are theoretical reasons to suggest that a root system that is advantageous under drought (deep rooting) might be contrary to a root system for adaptation to low P (shallow and abundant) (Ho et al., 2005). In spite of this, some drought-selected lines, especially NCB 226 and SER 118, also yielded well in low P. The accession G 21212 had also expressed combined stress resistance (drought and low P) in previous experiments (Rao, 2001; Beebe et al., 2007). For many years the Brazilian landrace Carioca was used as the standard of low P tolerance. In prior studies, the most promising line bred for low fertility tolerance, A 774, presented an advantage over Carioca of up to 27% (Singh et al., 2003). However, lines selected under drought outyielded Carioca

Table 4. Yields of ten drought resistant common bean lines in Brazilian grain classes that yielded best in favorable environments compared to the 'Perola' check, including drought stressed yields as $F_{4:6}$ and $F_{7:9}$ families, unstressed yields in three sites, days to maturity and yield per day.

| Line | Drought treatment, $F_{4:6}$ | | | Drought treatment, $F_{7:9}$ lines | | | | Unstressed treatments, $F_{7:10}$ lines | | | | | | | | | |
| | Palmira | | | Palmira | | | | | Palmira | | Quilichao | | Popayán | | Average, 3 sites | | |
	Tr[†]	Yield[‡], kg ha⁻¹ (% check[§])	YD[¶]	Tr	Yield, kg ha⁻¹ (% check)	YD	g-100 seed⁻¹	Tr	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	Yield, kg ha⁻¹ (% check)	YD	DTM[#]
SXB 398	8	1551 (130)	25.2*	9	1022** (549)	15.0**	35	3	3141 (120)	44.9*	2845 (113)	45.5	1832 (119)	21.3	2606* (119)	37.2**	73**
SXB 399	8	1551 (130)	25.2*	9	998** (536)	14.9**	32	3	3421** (131)	48.7*	2277 (91)	35.6	1874 (121)	21.4	2523 (115)	35.2*	74**
SXB 403	8	1735* (145)	25.8*	9	1217** (654)	18.5**	29	3	3458** (132)	47.6*	2601 (104)	40.3	2305** (149)	26.6*	2720** (124)	37.3**	74**
SXB 409	8	1735* (145)	26.8*	9	1023** (550)	15.2**	30	3	3047 (116)	42.1	2610 (104)	41.1	1734 (112)	19.8	2542 (116)	35.2*	75*
SXB 410	8	1720* (144)	26.2*	9	937** (503)	14.3**	30	3	3745** (143)	49.4*	2895 (115)	42.8	1660 (108)	18.3	2738** (125)	36.4**	78
SXB 412	8	1658 (139)	25.9*	9	1283** (689)	20.2**	25	3	3266* (125)	45.3*	3172 (126)	50.6*	1210 (78)	13.4	2471 (112)	35.5*	75*
SXB 414	8	1820** (152)	29.0**	9	884** (475)	13.6**	26	3	3106 (119)	44.8*	2828 (113)	44.9	2118* (137)	24.0*	2670** (122)	37.8**	73**
SXB 415	8	1820** (152)	29.0**	9	863** (463)	13.0**	28	3	3457** (132)	47.7*	2818 (112)	45.4	1207 (78)	14.2	2519 (115)	36.0**	73**
SXB 416	8	1804** (152)	27.6**	9	1125** (604)	17.5**	25	3	3322* (127)	45.2*	2446 (98)	37.7	1955 (127)	22.1	2587* (118)	35.1*	76
SXB 418	8	1804** (152)	27.6**	9	1121** (602)	17.3**	26	3	3417** (131)	47.7*	2911 (116)	44.2	1726 (112)	19.6	2675** (122)	37.0**	75*
Perola					186	2.5	31	3	2617	35.3	2504	36.2	1544	17.2	2197	29.3	77
LSD (0.05)					481	7.5		3	583	8.5	688	10.4	436	5.0	354	4.9	2
DOR 390		1190	18.2														
LSD (0.05)		450	6.8														

*Statistical significance at the 0.05 probability levels, in relation to DOR 390 in the $F_{3:5}$ families, and to 'Perola' in $F_{6:8}$ and F_9 lines.

**Statistical significance at the 0.01 probability levels, in relation to DOR 390 in the $F_{3:5}$ families, and to Perola in $F_{6:8}$ and F_9 lines.

[†]Trial number.

[‡]Adjusted mean from lattice design with three replications.

[§]Yield calculated as percent of yield of DOR 390 in the $F_{3:5}$ families, and as percent of yield of Perola in $F_{6:8}$ and F_9 lines.

[¶]Yield per day calculated for each of three replications and adjusted as per lattice design.

[#]Days to physiological maturity, averaged over three sites and three replications per site.

under P stress by as much as 41% in the case of NCB 226. Although the data of Singh et al. (2003) with A 774 reflected adaptation to multiple edaphic stresses (low P among them), the fact of recovering a highly significant yield advantage over Carioca without intense directed selection for this trait is noteworthy. This suggests that some effects of drought resistance genes are expressed in other stress environments and/or that there is a positive interaction among stress resistance mechanisms. In particular, these factors seem to be associated with greater plant efficiency. Photosynthate mobilization to seed might be a common stress resistance mechanism under both types of stress (Rao, 2001; Beebe et al., 2007). The importance of remobilization of both carbon and nitrogen for seed filling in grain legumes in general and chickpeas in particular under terminal drought stress was highlighted by Turner et al. (2005).

Selection for drought resistance did not reduce yields in favorable conditions; almost no lines yielded significantly less than the respective checks in any environment. To the contrary, several lines significantly outyielded the respective checks in the red and Brazilian grain classes, as well as one line (SEN 36) in the small black class. Yield gains were registered in materials with similar or even earlier maturity, such as SER 48 with a 5 d advantage over 'Tio Canela' resulting in greater yield d⁻¹. This is a biologically signifi-

cant result, since early maturity is usually associated with lower yield potential; White and Singh (1991b) found that each day of reduction in growth cycle resulted in a loss of 74 kg ha⁻¹ of yield. While evaluation for resistance to terminal drought in the present study may have led to selection of early maturing materials, the fact that yield d⁻¹ increased as a result of selection suggests more fundamental physiological changes associated with greater plant efficiency.

Suboptimal yield efficiency of common bean might have its origin in the evolution of wild *Phaseolus vulgaris*. Wild ancestors of cultivated crops typically have lower harvest index than their cultivated counterparts (Evans, 1993), and many survival mechanisms of wild plants tend to reduce economic yield (Richards, 1997). Wild *P. vulgaris* is a viney annual plant that germinates among small trees and shrubs in forest clearings or in disturbed environments with the onset of seasonal rains. Intense competition for light makes rapid shoot development necessary for survival, and requires suppression of seed production until the wild bean can climb up and over the surrounding canopy. The original viney habit with profuse branching, seen in most wild species, was selected against to obtain an early harvest (Debouck, 1999), but even the cultivated common bean is prone to excessive vegetative growth, low harvest index, and occasionally reduced seed yields under high soil fertility and abundant

Table 5. Yields of selected elite drought resistant common bean lines under phosphorus stress in Darién, Colombia.

Line	Color	Yield[†], kg ha^{-1} (% tolerant check[‡])	g 100 seed^{-1}	YD[§]	DTM[¶]
NCB 226	Black	2077* (141)	28	25.8*	81
NCB 280		1694 (115)	23	22.3	77**
RCB 273	Red	1465 (100)	22	19.4	75**
SER 47		1680 (114)	29	21.2	79
SER 78		1116 (76)	22	14.6	76**
SER 109		1200 (82)	25	16.0	76**
SER 118		1964* (134)	24	25.6*	77**
SER 119		1842 (125)	26	23.5*	78*
SER 125		1470 (100)	28	19.2	76**
SER 128		1548 (105)	26	20.1	77**
SXB 405	Cream	1705(116)	29	21.8	78*
SXB 409	Cream striped	1736 (118)	27	22.0	79
SXB 412	Cream	1682 (114)	22	22.0	76**
SXB 418	Pink	1480 (101)	22	19.0	78*
'Tio Canela' (sensitive check)	Red	1317 (90)	21	16.2	81
'Carioca' (tolerant check)	Cream striped	1469 (100)	23	18.0	81
LSD (0.05)		439	1.5	5.5	2.8

*Statistical significance at the 0.05 level in relation to Carioca check.

**Statistical significance at the 0.01 probability level in relation to Carioca check.

[†]Adjusted mean from lattice design with three replications.

[‡]Yield calculated as percent of yield of low P tolerant check Carioca.

[§]Yield per day calculated for each of three replications and adjusted as per lattice design.

[¶]Days to physiological maturity, averaged over three replications.

water supply. This response is exacerbated by low photosynthetically active radiation, suggesting that it is related to the wild bean survival mechanism in its native, shady environment. These observations provoked the comment that the bean crop is only partially domesticated (J.W. White, personal communication, 2006). Bean seems to have a delicate physiological balance between vegetative and reproductive phases, and is prone to suppressing reproductive development and reverting to a vegetative state under a range of environmental conditions.

Why might selection for drought resistance be conducive to improving yield efficiency of common bean—even in favorable environments? One response to drought observed in some bean genotypes is a delayed reproductive development, the plants remain green and vegetative. For example, Terán and Singh (2002b) found that the genotype 'San Cristobal 83' (G 17722) lengthened its growth cycle under drought. Some drought-sensitive genotypes produce abundant biomass with low yield (Rao, 2001; Rao et al., 2006). This response may be associated with a coping mechanism of the wild *Phaseolus vulgaris* under drought. The growth cycle of the wild *P. vulgaris* is from 8 to 10 mo in length, and in tropical environments with bimodal rainfall, a mid-season dry period occurs that can last 2 to 4 wk near the sub-tropics, to as long as 3 mo on the equator. In response to this mid-cycle drought the wild *P. vulgaris* enters a survival mode of slow growth and reduced physiological activity, until rainfall resumes and flowering occurs. Such a survival response was associated with lower harvest index values of wild relatives of several field crops (Evans, 1993). Although effective for wild *P. vulgaris* with a growth cycle that bridges the two peaks of rainfall, if such a response persists in cultivated bean, this could decrease plant efficiency for a crop of only 60 to 80 d duration. Such a survival response may be reflected in observations of Amede and Schubert (2003), who found that bean cultivar Brilliant reduced its rate of photosynthesis by 75% after one week of moderate drought due to stomatal closure, compared to only 20% in chickpea. White et al. (1994a) also found that drought sensitive bean genotypes tended to conserve water, resulting in high water use efficiency but low yield. A survival response to drought that slows reproductive development may be another negative characteristic that is inherited from the wild *Phaseolus vulgaris*. Intense selection of populations under drought permits discarding genotypes with this survival response, resulting in better mobilization of photosynthates to grain and improved yield (Rao, 2001; Rao et al., 2006). Although we did not practice selection for a specific physiological trait during line development, the selection pressure that we exercised for well-filled grain under severe stress may have favored genes for enhanced sink strength (Trouverie and Prioul, 2006; Yang and Zhang, 2005). Such genes may have a favorable effect across environments, including P stressed environments, and may explain why plant efficiency improved as reflected in greater yield day^{-1} and greater yield potential in favorable conditions.

As noted above, bean race Durango has been an important source of drought resistance in common bean. In the present study SEA 15 was the most frequent source of Durango genes. Race Durango has been subjected to selection under drought for centuries in the dry highlands of Mexico. Nienhuis and Singh (1986) found that race Durango and materials derived from it also presented positive general combining ability for yield potential in favorable environments, and Singh et al. (1991) attributed high harvest index to race Durango. Thus, in race Durango, we also see that drought resistance coincides with yield potential, as is suggested in the genotypes reported here. It is possible that these traits of race Durango result from the same factors of sink strength that we hypothesize above, and that came to characterize race Durango as a result of selection for drought resistance. Furthermore, in our experience Mesoamerica sub-race M2 (both black-seeded G 21212 and small-seeded red beans) may also possess genes that contribute to drought resistance, grain filling, and possibly better sink strength (Rao, 2001; Beebe et al., 2007).

In light of the above hypothesis that retarded reproductive development reflects an active plant response to the environment, low yield under drought may also be in part a reflection of plant responses and not entirely a result imposed by environmental limitations. This perspective has important implications for studies of drought resistance. For example, some plant genes that are expressed under drought may be deleterious to yield, while their nonexpression is more favorable to yield. In such cases, genomic studies of differential gene expression in drought-resistant materials might consider genes that do not express under drought stress as well as those that do. Advances in the molecular biology of stress response in tolerant organisms are raising a number of possibilities concerning the regulatory genes that may be used in crop improvement programs, not only to ensure survival under water deficit but also to guarantee a reasonable productivity under reduced water availability (Chaves and Oliveira, 2004).

Typically it has been difficult to improve yield potential of grain legumes compared with cereals (Hall, 2004). This was mainly attributed to the inherent differences that constrain photosynthate production in grain legumes, in comparison with cereals, such as the metabolic costs of fixing atmospheric nitrogen and producing grain with protein or oil (Hall, 2004). Grain legume breeders have not been as successful as cereal breeders in achieving increases in grain yield by enhancing the partitioning of photosynthates to grain and thereby increasing the harvest index. Although it is encouraging to find a positive response to drought selection being expressed as yield potential in a grain legume, this strategy might not work for all grain legumes. For example, chickpeas and lentils evolved under relatively dry conditions, and these species might already have maximized the potential that can be gained from selection under drought. Even within the species, much less progress in breeding for yield has been registered with common bean of the Andean gene pool, and it remains to be seen if the same principles can be extended to the large seeded Andean types.

We conclude that selection for resistance to drought may lead to constitutional changes that are also of adaptive advantage under low P availability in soil and also in favorable conditions. Results from this work are relevant to ongoing common bean breeding programs that are aimed at developing stress-adapted beans for the drought-prone areas of the tropics where drought and low soil P availability are the two major abiotic constraints for improving bean yields in farmer's fields.

Acknowledgments

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