

*Full Length Research Paper*

# Photosynthate remobilization capacity from drought-adapted common bean (*Phaseolus vulgaris* L.) lines can improve yield potential of interspecific populations within the secondary gene pool

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Interspecific lines obtained from crosses between common bean (*Phaseolus vulgaris* L.) and other species from its secondary gene pool have a tendency for excessive vegetative growth and low grain yield. Contrariwise, drought-adapted common bean lines have been observed to produce high yields despite low shoot biomass production. This was attributed to greater remobilization of photosynthates to grain development. The objective of the present study was to investigate whether F<sub>2</sub>-families derived from crosses between an interspecific line and drought-adapted *P. vulgaris* lines have improved ability to remobilize greater proportion of photosynthate from shoot biomass to grain yield and subsequently obtain higher yield potential. Seven F<sub>2</sub>-progenies derived from crosses of an interspecific hybrid line of *P. vulgaris* × *Phaseolus dumosus* with seven drought-adapted lines reflecting a range of photosynthate remobilization and partitioning were evaluated under irrigated and rainfed field conditions along with their eight parent lines and one drought-tolerant check at the International Center of Tropical Agriculture (CIAT) at Palmira, Colombia. Although no single parent trait led to higher yield potential in progenies, the mean yield potential of the progenies, as well as mean yield under drought was significantly higher than yields of the interspecific parent, indicating that crosses with drought-adapted bean lines with greater plant efficiency constitute a promising breeding approach for yield improvement of interspecific crosses in both drought stressed and favorable environments.

**Key words:** Drought adaptation, interspecific crosses, dry matter partitioning, *Phaseolus*, remobilization, yield.

## INTRODUCTION

"It is not always easy to distinguish between wild and cultivated plants in South America, for there are many intermediate stages between the utilization of plants in their wild state and their true cultivation", noted the ethnologist and anthropologist Claude Lévi-Strauss in 1950 (Smithsonian Institution Bureau of American Ethnology, 1950). Even today this is true for common

bean (*Phaseolus vulgaris* L.) and the species from its secondary gene pool (Harlan and de Wet, 1971). Cultivated *P. vulgaris* seems to have inherited survival mechanisms from its wild ancestor expressed as excessive viney growth and a lack of clear transition between the vegetative and reproductive growth stages, leading to a suppression of reproductive growth under a range of environments and a poor response to favorable conditions (Kelly et al., 1999; Beebe et al., 2008, 2009; Butare et al., 2011). Analogous growth habits, with low harvest indices (HI) and suboptimal yields are also

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adopted by species within common bean's secondary gene pool such as wild and cultivated forms of *Phaseolus coccineus* L. and *Phaseolus dumosus* Macfady and wild *Phaseolus costaricensis* Freytag and Debouck (Debouck, 1999; Singh, 2001). Nevertheless, common bean is the world's most important grain legume for direct human consumption (Broughton et al., 2003), with 20.3 million tons of dry bean harvested from 27.9 million ha worldwide in 2008 (FAOSTAT, 2010). Almost 80% of dry bean (*P. vulgaris*) is produced by small landholders in the developing countries of tropical Latin America and Africa (Rao, 2001), particularly in eastern and southern Africa and Central America. In these regions, beans constitute an important source of plant protein and micronutrients in human diets (Broughton et al., 2003).

Common bean is often grown on marginal lands under unfavorable environmental conditions (Rao, 2001; Broughton et al., 2003) with minimal soil and crop management inputs (Rao, 2001; Beebe et al., 2008, 2009). Low soil fertility due to phosphorus (P) deficiency or aluminum (Al) toxicity (Beebe et al., 2009) and high risk of intermittent or terminal drought (White and Izquierdo, 1991; Muñoz-Perea et al., 2006) are among the most common abiotic stresses. These production constraints explain why average yields in many countries of Africa and Latin America did not exceed 700 kg/ha in 2008 (FAOSTAT, 2010), although experimental dry bean yield potential exceeds 3000 kg/ha (Beebe et al., 2006). Regarding breeding efforts to improve grain yields, it has been estimated that up to 90% of genetic variability in common bean and its sister species remains un- or underutilized (Singh, 2001). Therefore, species in the secondary gene pool are considered easily accessible potential sources not only for tolerance to abiotic stresses, but also for agronomic and nutritional traits: Year-long bean (*P. dumosus*) and scarlet runner bean (*P. coccineus*) have been identified as sources of resistance to important fungal pathogens (Singh, 2001) and high iron (Fe) and zinc (Zn) content in grain in common bean (Beebe et al., 2006; CIAT, 2008). Scarlet runner bean also features resistances to viral and bacterial pathogens (Singh, 2001) and to damage caused by the bean fly (*Ophiomyia phaseoli* Tryon) (Kornegay and Cardona, 1991), as well as tolerance to low temperatures (Singh, 2001) and Al toxicity in soils (Beebe et al., 2009). *P. costaricensis* holds yet unutilized potential for common bean breeding (Singh et al., 1997). In fact, breeding programs have mainly concentrated on *P. coccineus* cultigens for gene introgression and the development of advanced lines with acceptable yield from interspecific hybrids with the secondary gene pool, particularly with wild forms has been limited (Debouck, 1999; Singh, 2001).

Difficulties to capitalize on variability in these sister species are attributable to excessive vegetative growth and poor partitioning of dry matter to grain which are inherent to all of them. However, efficient development patterns with a clear transition to reproductive growth allowing for higher grain yields under both drought and

favorable environments have been observed in drought-adapted bean lines (Beebe et al., 2008). This was associated with greater plant efficiency and remobilization of photosynthates to grain (Rao, 2001; Beebe et al., 2006, 2008; Rao et al., 2007, 2009). However, such remobilization capacity is needed in interspecific lines within the secondary gene pool to capitalize on their excessive vegetative growth under favorable conditions. Therefore, the present study was conducted to assess whether the photosynthate remobilization and the subsequent yield potential, of an interspecific advanced bean line resulting from a cross between *P. vulgaris* and *P. dumosus* can be improved by crossing it with drought-adapted bean lines possessing higher photosynthate remobilization capacity. An expected outcome of this study is to draw initial conclusions for the implementation of respective crosses in breeding programs aiming for the introgression of desirable traits from the secondary gene pool into *P. vulgaris*.

## MATERIALS AND METHODS

### Experimental site and meteorological conditions

The experiment was conducted during the dry season from June to September 2009 at the main experimental station of the International Center for Tropical Agriculture (CIAT) in Palmira, Colombia, located at latitude 3° 29' N, longitude 76° 21' W and an altitude of 965 m. The site has an average relative humidity of 74%, 896 mm of annual rainfall and an annual potential evaporation of 1834 mm. The soil is fine-silty, mixed, isohyperthermic Aquic Hapludoll, having no major fertility problems (pH = 7.7). The trials were managed according to standard practices to assure normal growth of the crop (Beebe et al., 2010). During the crop growing season, the mean maximum and minimum air temperatures were of 29.9 and 19.3°C in June, 32.2 and 19.1°C in July, 32.1 and 19.7°C in August and 33.1 and 19.5°C in September, respectively. The total potential pan evaporation of 574 mm during crop growth exceeded total rainfall, amounting to 86 mm. With 21 mm of rainfall in June, 8 mm in July, 29 mm in August and 28 mm in July, the rainfall distribution pattern corresponded to terminal drought stress conditions (Ludlow and Muchow, 1990).

### Plant material

The interspecific [*P. vulgaris* × (*P. vulgaris* × *P. dumosus*)] advanced inbred line MIB 755 was crossed with seven other advanced inbred CIAT bean lines. MIB 755 was selected for high Fe content in the grain from a backcross of an interspecific hybrid of a Carioca-type common bean line (FEB 226) with a *P. dumosus* accession, with FEB 226 as recurrent parent. Despite its valuable Fe content, it lacks wide acceptance with farmers due to its viney growth and low grain yields (S. Beebe, unpublished results), according to the growth pattern described earlier. MIB 755 was a suitable elite line to study the typical, viney growth pattern of interspecific bean lines with the secondary gene pool and to use as a common parent in further crosses for the study. The seven parent lines crossed with MIB 755 resulted from breeding programs aiming to produce drought-adapted beans from germplasm originating from the Mesoamerican gene pool (Kwak and Gepts, 2009), but were nevertheless chosen to test a range of productivity and photosynthate remobilization capacity under rainfed conditions based on earlier experience at CIAT. The only advanced line which

**Table 1.** Description of bean lines used as parents or as drought-resistant check.

Advanced line	Market class	Inter-specific	Breeding objectives
MIB 755	Carioca-type	Yes	High mineral content, particularly iron.
ALB 49	Red	Yes	Tolerance to Al toxicity, some drought tolerance.
SEN 46	Black	No	Drought adaptation.
SEN 74	Black	No	Drought adaptation.
SER 155	Red	No	Drought adaptation.
SER 16	Red	No	Drought adaptation.
SMR 4	Red	No	High iron content and drought tolerance.
SXB 743	Red	No	Drought resistance.
SER 118	Red	No	Drought resistance, associated with greater ability for remobilizing photosynthates.

had not resulted directly from a drought-breeding program was ALB 49, which was selected from a backcross of a scarlet runner bean (*P. coccineus*) accession with SER 16, a drought-adapted line, also used in the present study. A brief description of the advanced lines used in crosses or as check (SER 118) is given in Table 1. In the crosses with SEN 46, SER 16 and SXB 74, MIB 755 was employed as female parent. In the crosses with ALB 49, SEN 74, SER 155 and SMR 4, MIB 755 was employed as male parent. Seven F<sub>1</sub>-progenies resulted from these crosses. One F<sub>2</sub>-population was derived from each F<sub>1</sub>-progeny by self-fertilization, resulting in seven genetically segregating F<sub>2</sub>-progeny populations. These F<sub>2</sub>-populations, the eight parent lines and one drought-resistant check (SER 118) were included in the field trial, resulting in a total of 16 genotypes. All of these had indeterminate bush-type growth habits with little climbing ability [(categories IIa to IIIa according to the classification as described in van Schoonhoven and Pastor-Corrales (1987)].

The CIAT advanced line SER 118 was used as drought-resistant check having better dry matter partitioning ability to produce grain. Later, the term 'genotype' is used for the genetic materials included in this study, be they homozygous advanced lines or F<sub>2</sub>-progenies. For statistical analysis, genotype categories were formed. The term 'drought-adapted parents' further on designates the seven advanced lines which represent a range of drought adaptation and all were crossed with MIB 755 while 'progenies' designate the F<sub>2</sub>-populations resulting from these crosses.

### Experimental design

Two field experiments were planted as 4 × 4 lattice designs with three replications. The 16 genotypes were sown in six-row plots with 60 cm between rows, using rows of 3.72 m long with a plant to plant spacing of 7 cm within the row. The progeny of the cross between MIB 755 and ALB 49 was an exception, as only four rows of 1.86 m long were sown in each replication because of insufficient seed that was harvested from the difficult cross between two interspecific bean lines. The field with irrigated treatment received eight gravity irrigations of 35 mm of water each during plant growth to create favorable growth conditions. The field with drought treatment was irrigated only twice for the establishment of the crop and then left rainfed to create water-deficit conditions. In the irrigated environment, two supplementary sowing dates were needed to fill rows which dropped out because of technical incidents. The second sowing date had six days of delay compared to the first date. Rows sown on the third date were not used for sampling.

All samples for estimation of yields were taken from rows sown on the first sowing date, while samples for physiological measurements were taken from rows sown on the first or second

sowing date, when the plants reached the desired developmental stage.

### Yield measurements and phenological assessment

In the irrigated plots, grain was harvested from two rows (from an average of 73.6 plants) after discarding end plants. In the rainfed plots, grain was harvested from four rows (from an average of 174.2 plants) to compensate for spatial effects on plant growth. For the progeny of the MIB 755 × ALB 49 cross, grain from only two rows was harvested in both the irrigated and rainfed plots. Mean yields per hectare were corrected for 14% moisture in grain. The drought intensity index (DII) was calculated according to Fischer and Maurer (1978). Days to flowering (DF) and days to physiological maturity (DPM) were determined for each plot. DF is defined as the number of days after planting until 50% of the plants have at least one open flower. DPM is the number of days after planting until 50% of plants have at least one pod losing its green pigmentation.

### Assessment of leaf chlorophyll content, dry matter partitioning and seed P concentration

Foliar greenness was measured from each leaflet of the youngest fully expanded leaf of six plants in all plots by using a SPAD (soil plant analysis development) chlorophyll meter (SPAD-502 Chlorophyll Meter, Minolta Camera Co., Ltd., Japan) at mid-pod filling (MPF) (growth stage code 75 according to the BBCH scale for beans) under irrigated and rainfed conditions. Dry matter partitioning was assessed at MPF growth stage and also at harvest. Plants growing in 1 m of row, chosen to be representative of the growth on the respective plot were cut at the base. These samples correspond to an area of 0.6 m<sup>2</sup> and averaged 15 plants. Plants were counted and separated into plant organs which were then oven-dried for at least two days at 60°C and weighed. At MPF, dry weights (DW) of leaves, stems and pods and reproductive structures were determined. Leaf area was measured using a leaf area meter (model LI-3000, LI-COR, NE, USA) and the leaf area index (LAI) was calculated. At harvest, DW of stems, pod walls and seeds, as well as the number of seeds were quantified. Pod partitioning index (PPI), pod harvest index (PHI) and stem biomass reduction (SBR) were calculated as defined previously (CIAT, 2009; Beebe et al., 2010):

PPI (%) =

$$\frac{\text{Pod biomass dry weight at harvest}}{\text{Total shoot biomass dry weight at mid-pod filling}} \times 100$$

$$\text{PHI (\%)} = \frac{\text{Seed biomass dry weight at harvest}}{\text{Pod biomass dry weight at harvest}} \times 100$$

SBR (%) =

$$\frac{\text{Stem biomass DW at MPF} - \text{stem biomass DW at harvest}}{\text{Stem biomass dry weight at MPF}} \times 100$$

Economic growth rate (EGR), that is, grain yield formed per day of active plant growth up to physiological maturity was calculated according to Ramirez-Vallejo and Kelly (1998). Whereas, PHI and EGR were calculated for each genotype and replication and thus underwent an ANOVA, PPI and SBR were calculated from means of genotypes in the respective environment. Total seed P concentrations were determined according to the procedures described by Walinga et al. (1989).

### Statistical analysis

One plot of ALB 49 was very heavily affected by *Macrophomina phaseolina* and therefore was excluded from statistical analyses to avoid inclusion of an unplanned diverging factor in the crop environment caused by spatial differences in soil inoculum. Due to missing data, the ANOVA could not be calculated for the planned lattice design and was run as for a design of complete randomized blocks, as suggested by Thomas (2006), by SAS generalized linear model procedure (SAS Proc GLM), (SAS Institute, 2004). Combined analyses of drought and irrigated conditions were conducted with replication, moisture treatment, genotype and genotype\*moisture treatment interaction as fixed factors. Separate analyses for drought and irrigated conditions were conducted with replications, genotypes, and a classification into the four genotype categories 'common parent' (that is, MIB 755), 'drought-adapted parents' (that is, ALB 49, SEN 46, SEN 74, SER 155, SER 16, SMR 4 and SXB 743), 'progenies' (that is, the F<sub>2</sub>-populations resulting from the crosses between the drought-adapted parents and the common parent MIB 755) and 'check' (that is, SER 118) on one hand and genotypes among 'drought-adapted parents' and among progenies on the other as factors. Least square means were generated and pairwise differences analyzed by Tukey's range test, in the case of equal sample sizes, or Tukey-Kramer method, for variables with missing data. Honestly significant differences (HSD) were computed for a level of probability of 5%. Differences between genotype categories were estimated and tested using orthogonal contrasts in the generalized linear model procedure. Pearson's product-moment correlation coefficients and respective significance levels were calculated using SAS Correlation procedure (SAS Proc CORR). Traits of F<sub>2</sub>-progenies were regressed on traits of drought-adapted parents using the SAS regression procedure (SAS Proc REG).

In the following, values marked with \*, \*\* or \*\*\* are statistically significant at probability levels of 5, 1 and 0.1%, respectively.

## RESULTS

Grain yields ranged between 1372 and 3364 kg/ha under irrigated conditions and between 130 and 1928 kg/ha under terminal drought (Table 2). The DII, reflecting average yield reduction under drought, amounted to 0.57. The drought-adapted parent SER 16 yielded highest in both environments, out-yielding the drought-resistant check. The interspecific lines MIB 755 and ALB 49 had

lowest yields. Although genotype-by-treatment interaction for yield was non-significant (Table 3), the ranking of genotypes according to yields differed between the two environments when taking all genotypes into account and when considering drought-adapted parents and progenies separately. Nevertheless, yields under well-watered and drought conditions were positively correlated. No genotype yielding more than the treatment mean under drought stress yielded less than the mean under irrigation. Although significant yield differences were found among drought-adapted parents in both environments, none were found among the progeny populations (Table 3). The mean yield of progenies was, however, significantly higher than that of the common interspecific parent (Table 2). Significant differences were also found concerning the time to flower and maturity. Progeny populations flowered significantly earlier than the common interspecific parent, but not as early as the mean value of drought-adapted parents. Drought-adapted parents and the drought-tolerant check matured earlier than the interspecific parent and the progeny populations. On average, the F<sub>2</sub>-populations matured significantly earlier than their common interspecific parent under irrigated conditions (Table 2). DF (Table 4) and DPM (Figure 1) related negatively with yields regardless of moisture treatments. The resulting EGR was highest for the drought-resistant check and the mean of drought-adapted parents in both environments. The mean EGR of progeny populations was significantly higher than that of the interspecific parent (Table 2). At MPF, no significant differences in shoot biomass were found between genotypes under irrigated conditions. Under drought, drought-adapted parents and progeny populations produced significantly more shoot biomass than the interspecific MIB 755 and the check genotype (Table 2).

Regarding the values on dry matter distribution among plant structures, the DW of vegetative plant organs at MPF, that is, stems and leaves, did not significantly correlate with grain yield in either of the two environments, whereas the DW of pods did ( $r_{\text{irrigation}} = 0.7^{**}$ ;  $r_{\text{drought}} = 0.83^{***}$ ). The following results were found for LAI and SPAD chlorophyll meter readings (SCMR). As for total shoot biomass DW, mean LAI at MPF was significantly higher under irrigated conditions (3.38) than under drought (2.35). In both environments, the progeny populations produced the highest mean LAI values of 3.81 for irrigated and 2.54 for drought, differing significantly from the mean value of 3.02 for drought-adapted parents under irrigated conditions and from MIB 755 (1.74) and the check (2.01) under drought stress. Mean SCMR at MPF were significantly higher under drought (44.5) than under irrigation (42.5). Genotype  $\times$  treatment interaction was significant. Under irrigation and drought treatments, the mean SCMR of progenies (43.9 and 45.4, respectively) were significantly higher than for drought adapted parents (41.4 and 44.0, respectively). MIB 755 scored 44.1 and 43.6 under irrigation and drought, respectively. Significant differences were found

**Table 2.** Least square means of yield (kg/ha), DF (d), DPM (d), EGR (kg/ha/d) shoot biomass DW at MPF (kg/ha), stem DW at harvest (kg/ha), PHI (%) and seed P concentration (%) and respective honestly significant difference (HSD<sub>0.05</sub>) values under irrigated conditions (ir) and terminal drought stress conditions (td) for individual genotypes and the genotype categories 'drought-adapted parents' and 'F<sub>2</sub>-progenies'.

	Yield		DF		DPM		EGR		Shoot DW <sub>MPF</sub>		Stem DW <sub>harvest</sub>		PHI		Seed P conc.	
	ir	td	ir	td	ir	td	ir	td	ir	td	ir	td	ir	td	ir	td
<b>MIB 755</b>	<b>1382</b> c	<b>130</b> c	<b>39.0</b> a	<b>36.7</b> a	<b>78.0</b> a	<b>65.7</b> a	<b>17.7</b> d	<b>2.0</b> c	<b>4169</b> a	<b>1719</b> b	<b>1673</b> a	<b>997</b> b	<b>59.6</b> c	<b>35.6</b> c	<b>0.638</b> a	<b>0.628</b> a
SER 16	3364	1928	32.0	32.7	64.3	61.3	52.3	31.4	4214	2714	908	435	80.7	79.3	0.461	0.394
SXB 743	3004	1882	34.0	33.7	68.0	62.7	44.2	30.0	5430	3488	1171	732	79.1	79.1	0.559	0.412
SEN 46	3175	1745	35.3	35.0	69.7	62.7	45.6	27.8	4310	3615	923	643	82.4	78.0	0.469	0.386
SEN 74	2732	1380	38.0	36.3	67.3	65.7	40.6	21.0	4322	2468	1502	825	79.1	77.8	0.533	0.429
SMR 4	2905	1332	38.3	36.0	70.0	64.3	41.5	20.7	3467	3165	1503	784	74.7	71.3	0.586	0.487
SER 155	2881	1299	32.0	33.0	62.3	58.0	46.2	22.4	4004	2944	709	657	79.9	76.9	0.519	0.432
ALB 49	1372	557	39.0	35.9	76.7	69.4	17.9	8.1	2837	2035	1096	1094	73.1	65.2	0.551	0.549
<b>Mean</b>	<b>2776</b> b	<b>1446</b> a	<b>35.5</b> c	<b>34.6</b> c	<b>68.3</b> c	<b>63.1</b> b	<b>43.9</b> b	<b>23.1</b> a	<b>4083</b> a	<b>2918</b> a	<b>1116</b> b	<b>739</b> b	<b>78.4</b> a	<b>75.9</b> a	<b>0.526</b> c	<b>0.441</b> bc
<b>F<sub>2</sub>-Progenies from cross:</b>																
MIB 755 x SER 16	2900	1210	34.7	34.7	73.0	65.0	39.7	18.6	4735	2600	1130	955	73.5	67.6	0.603	0.406
MIB 755 x SXB 743	2777	1098	35.7	35.0	74.7	64.7	37.3	17.0	4881	3109	1603	867	73.9	69.5	0.591	0.470
MIB 755 x SEN 46	2665	1055	35.7	35.0	72.7	66.3	36.7	16.0	4844	2847	1388	1336	68.3	66.7	0.607	0.421
SEN 74 x MIB 755	2704	1052	38.3	36.7	73.0	67.0	37.1	15.7	4727	2906	1744	1211	75.5	66.8	0.563	0.484
SMR 4 x MIB 755	2449	860	37.3	36.0	76.0	66.0	32.2	13.0	3992	2838	1361	1011	71.1	62.8	0.583	0.516
SER 155 x MIB 755	3067	848	34.3	34.3	72.0	63.7	42.6	13.3	4928	2606	1608	847	76.0	61.8	0.529	0.498
ALB 49 x MIB 755	2686	936	41.3	36.3	79.0	65.7	34.0	14.2	3736	2143	1157	1144	72.0	63.3	0.518	0.456
<b>Mean</b>	<b>2750</b> b	<b>1008</b> b	<b>36.8</b> b	<b>35.4</b> b	<b>74.3</b> b	<b>65.5</b> a	<b>37.1</b> c	<b>15.4</b> b	<b>4549</b> a	<b>2721</b> a	<b>1427</b> a	<b>1053</b> a	<b>72.9</b> b	<b>65.5</b> b	<b>0.571</b> b	<b>0.464</b> b
<b>SER 118 (check)</b>	<b>3361</b> a	<b>1508</b> a	<b>36.0</b> bc	<b>35.3</b> b	<b>67.7</b> c	<b>63.0</b> b	<b>49.7</b> a	<b>23.9</b> a	<b>3800</b> a	<b>2263</b> b	<b>974</b> b	<b>640</b> b	<b>81.0</b> a	<b>81.2</b> a	<b>0.471</b> c	<b>0.395</b> c
<b>Treatment mean ***</b>	<b>2714</b>	<b>1176</b>	<b>36.3</b>	<b>35.2</b>	<b>71.5</b>	<b>64.4</b>	<b>38.4</b>	<b>18.4</b>	<b>4275</b>	<b>2716</b>	<b>1278</b>	<b>886</b>	<b>75.0</b>	<b>68.9</b>	<b>0.549</b>	<b>0.460</b>
HSD <sub>0.05</sub> genotypes	1283	596	4.3	1.6	2.3	3.7	17.5	9.3	ns	1119	894	479	6.4	15.9	0.136	0.137

<sup>a, b, c, d</sup> Means within one column marked with different letters have statistically significant differences at a probability level of 5%. \*\*\*Differences between treatment means were statistically significant at a probability level of 0.1% for all traits shown. Conc.: concentrations. ns: result was not statistically significant.

among drought-adapted parents and progenies regardless of irrigated or drought stress treatments. Under irrigation, SCMR readings at MPF correlated negatively with grain yield ( $r = -0.65^{**}$ ) and EGR ( $r = -0.77^{***}$ ). Among the plant structures weighed at harvest, stem DW under drought correlated negatively with grain yields under drought ( $r = -0.67^{**}$ ) and irrigation ( $r = -0.56^*$ ). The PHI of the common interspecific parent was

significantly lower than that of any other genotype category, whereas the progeny mean was below that of the drought-adapted parents and drought-resistant check (Table 2).

Note that the common interspecific parent MIB 755 showed by far the lowest PPI (Figure 2) and increased its shoot biomass DW between MPF and harvest under drought, as reflected by a negative SBR value (Figure 3). Under drought

conditions, positive correlations of SBR with PHI ( $r = 0.65^{**}$ ) and PPI ( $r = 0.5^*$ ) were found while correlations with seed P concentration ( $r = -0.58^*$ ) and stem DW at harvest ( $r = -0.76^{***}$ ) were negative. In the irrigated environment, SBR correlated positively with shoot biomass DW at MPF ( $r = 0.56^*$ ) but negatively with PPI ( $r = -0.58^*$ ). The mean P concentration in seeds at harvest was significantly lower for the progeny populations

**Table 3.** Degrees of freedom (DFr) and type I sums of squares of main effects for yield (kg/ha) and days to physiological maturity (d) in the combined ANOVA of traits observed on 9 advanced bean lines and 7 F<sub>2</sub>-progenies grown under irrigation and drought stress in Palmira, Colombia.

Source	DFr	Sum of squares (Type I)	
		Yield	DPM
Treatment	1	54960192.6*	1224.4*
Genotype	15	22613051.3*	1092.7*
Genotype category	3	11518819.7*	498.5*
Among drought-adapted parents	6	10518011.8*	519.6*
Among progenies	6	576219.9	74.6*
Genotype x treatment interaction	15	2096739.6	228.4*
Replication (within treatment)	4	702884.1	5.5
Error	59	5566988.8	56.0

\* Statistically significant at a probability level of 5%.

**Table 4.** Correlation coefficients (r) between grain yield, DPM and P concentration in seeds and yield components and biomass and partitioning traits observed on 9 advanced bean lines and 7 F<sub>2</sub>-progenies grown under irrigation (ir) and terminal drought stress (td) in Palmira, Colombia.

Variable		Grain yield (kg/ha)		DPM (d)		Seed P conc. (%)	
DF (d)	ir	-0.58	*	0.78	***	0.32	
	td	-0.60	*	0.75	***	0.56	*
Seed P conc. (%)	ir	-0.58	*	0.56	*	.	
	td	-0.89	***	0.51	*	.	
Stem DW <sub>harvest</sub> (kg/ha)	ir	-0.32		0.51	*	0.64	**
	td	-0.67	**	0.78	***	0.44	
PPI (%)	ir	0.48		-0.39		-0.51	*
	td	0.80	***	-0.46		-0.86	***
PHI (%)	ir	0.75	***	-0.76	***	-0.81	***
	td	0.90	***	-0.47		-0.87	***
SBR (%)	ir	0.25		-0.10		-0.08	
	td	0.77	***	-0.63	**	-0.58	*

\*, \*\*, \*\*\* Statistical significance at a probability level of 5, 1 and 0.1%, respectively. conc.: concentration.

than for MIB 755 (Table 2). Yields were negatively correlated with seed P concentration, as were partitioning indices, regardless of irrigated or drought stress treatments (Table 4). SBR correlated negatively with seed P only under drought. Under irrigation, stem DW at harvest correlated with seed P concentration. The partitioning indices related more strongly with grain yield under drought. PHI was among the traits most strongly related with grain yields regardless of irrigated or drought stress treatments. The relation of partitioning indices PPI and PHI obtained under drought with grain yields produced under irrigation is illustrated in Figure 2. Whereas, SBR correlated with grain yield and early maturity under drought, it did not under irrigation (Figure 3). The

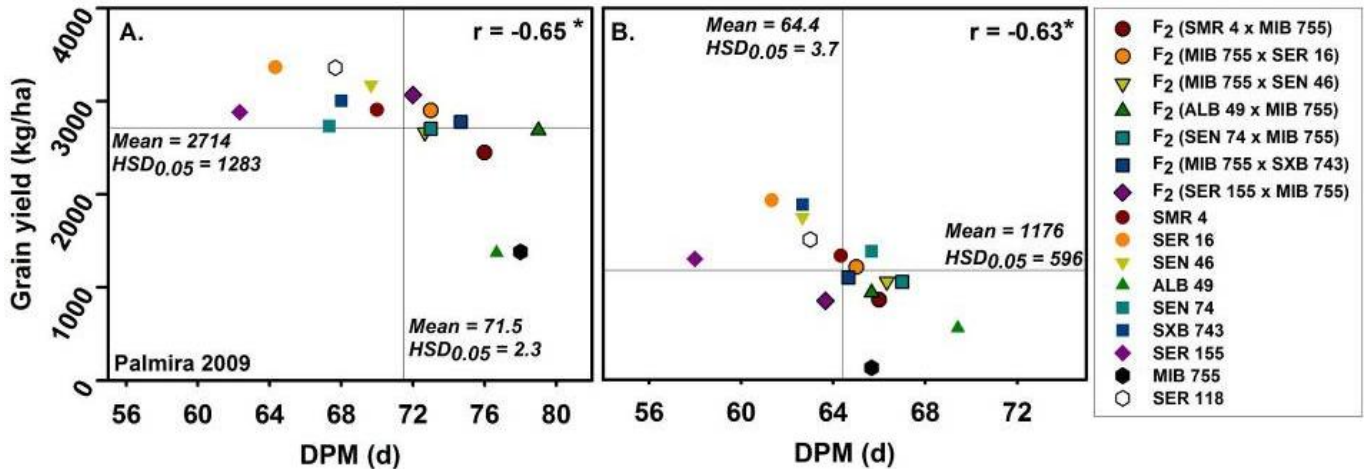
regression analysis of grain yields and DPM of the F<sub>2</sub> progenies under irrigated conditions on traits expressed by their respective drought-adapted parent line under drought and irrigated conditions revealed more parent traits with an effect on the time to maturity than on yield of progenies.

Regarding parent traits expressed under drought stress, DF and LAI at MPF were related negatively with progeny yield under irrigation (Table 5).

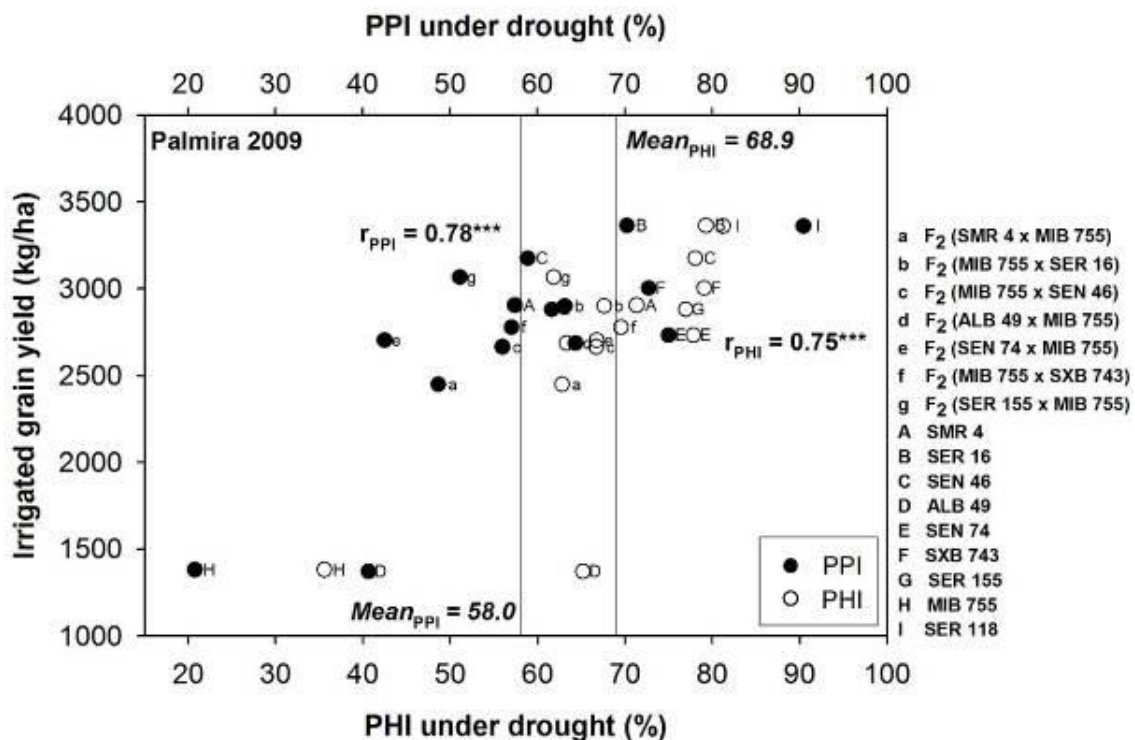
## DISCUSSION

Significant differences between irrigated and drought





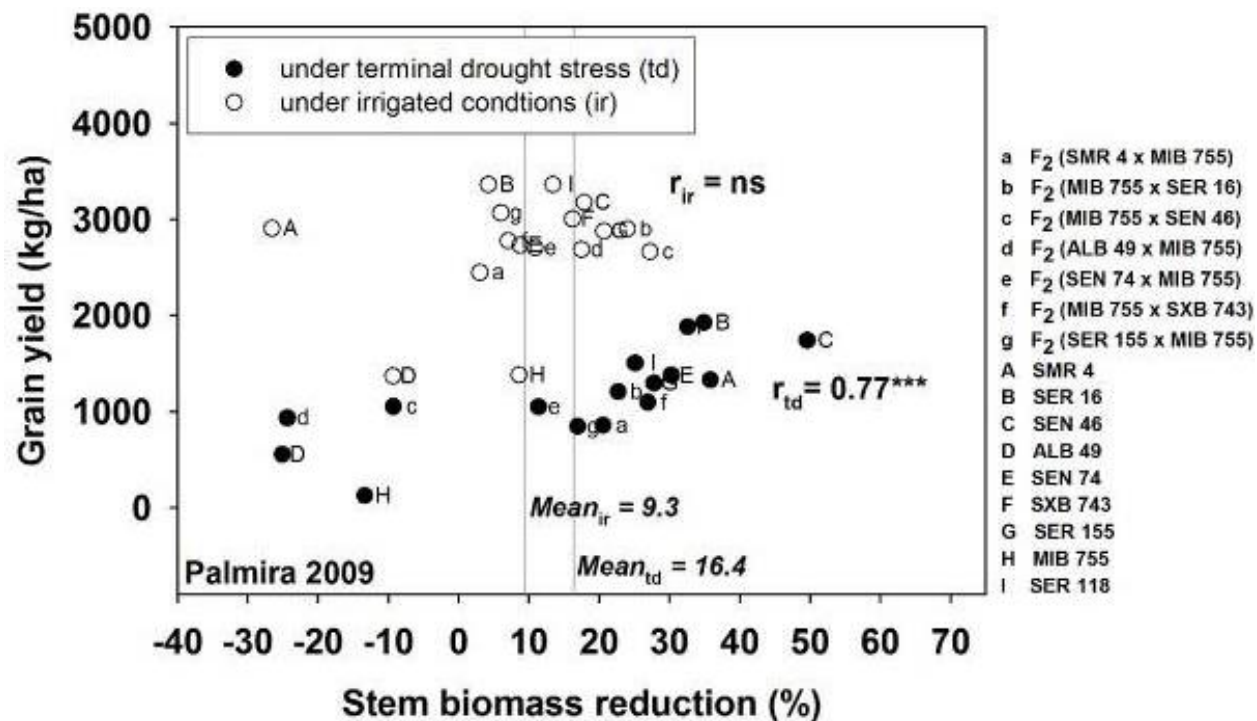
**Figure 1.** Days to physiological maturity (DPM) in days vs. grain yield (kg/ha) of nine advanced bean lines and seven F<sub>2</sub>-progenies grown under A) irrigated conditions and B) under terminal drought stress in Palmira, Colombia. \* indicates statistical significance at a probability level of 5%.



**Figure 2.** Pod partitioning and pod harvest indices (%) of nine advanced bean lines and seven F<sub>2</sub>-progenies under terminal drought stress vs. their grain yield (kg/ha) under irrigated conditions in Palmira, Colombia. \*\*\* indicates statistical significance at a probability level of 0.1%.

stress treatments of overall means for grain yield, phenological traits and total shoot biomass DW indicate severe drought stress conditions in the rainfed crop. It has been argued that DII values above 0.50 allow for identification of high levels of drought resistance, whereas genetic differences in germplasm may not result in significant differences under very severe terminal

drought stress (Singh, 2007). Hence, the observed DII of 0.57 should permit the determination of genetic differences of genotypes under severe terminal drought in the rainfed environment. Grain yields obtained in the favorable irrigated environment are considered as reflecting yield potential of the respective genotype (Beebe et al., 2008).



**Figure 3.** Stem biomass reduction (%) vs. grain yield (kg/ha) of nine advanced bean lines and seven F<sub>2</sub>-progenies grown under irrigated conditions and under terminal drought stress in Palmira, Colombia. \*\*\* indicates statistical significance at a probability level of 0.1%; ns indicates that a result was not statistically significant.

**Table 5.** Regression coefficients ( $b_1$ ) and coefficients of determination ( $R^2$ ) of yield and DPM of 7 F<sub>2</sub>-families irrigated conditions on selected traits expressed by the respective drought-adapted parents.

	Progenies, irrigated			
	Yield (kg/ha)		DPM (d)	
	$b_1$	$R^2$	$b_1$	$R^2$
<b>Parent traits under drought</b>				
Yield (kg/ha)	0.080	0.04	-0.004	0.49
EGR (kg/ha/d)	6.919	0.08	-0.230	0.54
DF (d)	-102.624	* 0.65	0.826	0.26
DPM (d)	-35.912	0.43	0.560	* 0.66
LAI at MPF	-377.911	* 0.74	1.110	0.04
Stem DW <sub>harvest</sub> (kg/ha)	-0.427	0.19	0.010	* 0.63
PHI (%)	16.498	0.20	-0.423	** 0.81
SBR (%)	0.061	0.00	-0.083	* 0.64
Seed P conc.	-1305.904	0.15	37.837	** 0.79
<b>Parent traits under irrigation</b>				
Yield (kg/ha)	0.057	0.04	-0.003	* 0.67
EGR (kg/ha/d)	6.088	0.12	-0.194	* 0.75
DF (d)	-53.565	* 0.67	0.569	0.47
DPM (d)	-28.435	0.45	0.472	** 0.78
SCMR at MPF	-53.361	0.42	0.800	* 0.59
Stem DW <sub>harvest</sub> (kg/ha)	-0.502	* 0.61	0.003	0.13
PHI (%)	29.303	0.25	-0.678	** 0.84

\*, \*\* Statistical significance at a probability level of 5 and 1%, respectively. conc.: concentration.



### The common interspecific parent

The common interspecific parent, MIB 755, presented growth patterns differing markedly from the drought-adapted common bean lines used in the trial. Low photosynthate partitioning and subsequent remobilization capacity, as reflected by low PPI and PHI under drought, led to low grain yield under irrigation despite similar shoot biomass production. High SCMR at MPF, reflecting high chlorophyll content in leaves, also indicate excessive vegetative growth and delayed senescence of leaves inhibiting a clear transition to reproductive growth and development. Consequently, maturity was reached more than 10 days after the check and EGR was extremely low. In fact, this poor response of MIB 755 to favorable growth conditions led its mean grain yield to be significantly lower than yields of the drought-resistant check and all drought-adapted parents with the exception of ALB 49, an interspecific line with *P. coccineus*. Congruent growth tendencies were observed under drought. Although total shoot biomass production was lowest of all, it did not differ significantly from the drought tolerant check. However, the mean yield of MIB 755 demonstrates a crop failure, whereas the check was among the highest-yielding lines. Apart from extremely poor dry matter partitioning towards grain yield, this is explained by a negative SBR value. Even after the onset of pod-filling, the MIB 755 crop continued storing of photosynthates in stems instead of remobilizing them to pods and seeds.

In conclusion, overlapping vegetative and reproductive phases inherited from *P. dumosus* seem to hamper drought-adaptation and also resulted in poor response to favorable conditions as recorded in MIB 755.

### Yields, phenology and economic growth rate

Acceleration of flowering and maturity have been identified as important traits in adaptation of common bean to terminal drought (White and Singh, 1991a; Rosales-Serna et al., 2004), but early maturity has generally been associated with lower yield potential in favorable environments (White and Singh, 1991b). Nevertheless, the correlation between irrigated grain yield and DPM was significant and negative. Congruent relationships were also found in interspecific RIL from crosses of *P. vulgaris* with *P. coccineus*, leading to the conclusion that traits inherited from *P. coccineus* may have dominated and subsequently led to late maturity, excessive vigor and inefficient partitioning of photosynthates to grain (Beebe et al., 2009), as observed in the interspecific lines (ALB 49 and common parent MIB 755) and progeny populations when compared with the drought-adapted common bean lines and the check. Two reasons thus explain the negative correlation of DPM and yield potential: Firstly, by simultaneous selection for grain

yield and early maturity (Wallace et al., 1993; Kelly et al., 1999) under drought, breeders might have indirectly selected for higher EGR in the drought-adapted lines.

Secondly, the inclusion of interspecific lines and populations means that longer maturity in those genotypes was attributed to excessive vegetative growth and hence low EGR.

### Photosynthate partitioning and remobilization

In both the drought and favorable environment, grain yields correlated with pod DW, but not with DW of vegetative plant structures, indicating that yields were generally limited more by the capacity to partition dry matter to reproductive growth than by lack of dry matter accumulation. In view of the stronger reliance of grain filling upon the remobilization of photosynthates within the plant (Egli and Leggett, 1976), the variation of photosynthate remobilization and partitioning capacity may be expressed more clearly under drought. In addition, the utilization of total shoot biomass at MPF for the calculation of PPI can lead to an underestimation of the maximal shoot biomass and overestimation of PPI for some genotypes: the total shoot biomass DW of bush-type bean crops commonly peak at the onset of rapid pod growth, but some genotypes obtain their maximum canopy DW near maturity (White and Izquierdo, 1991), particularly under irrigation (Rosales-Serna et al., 2005). For the interpretation of results, partitioning indices obtained under terminal drought were thus assumed to reflect the true potential of genotypes for photosynthate partitioning to seed, particularly in the case of PPI. The positive correlation of partitioning indices PHI and PPI with yield under drought highlight the importance of both steps of dry matter partitioning for yield production, that is i) from vegetative biomass to pods, indicated by the PPI, and ii) from pod wall to grain, indicated by the PHI. The remobilization of photosynthates stored first in stems, then in pod walls, to seeds has also been found to be important for drought tolerance in *Lupinus albus* and *Lupinus mutabilis* (Carvalho et al., 2004, 2005).

In the irrigated treatment, yield only directly correlated with PHI. This does not contradict the importance of the partitioning of photosynthates to pods, but indicates yields were limited by poor allocation of dry matter to seeds within pods rather than by pod formation. Beebe et al. (2009) have found significant variability among bean genotypes for mobilization of photosynthates from pod walls to seeds and termed the failure to fulfill this very last step of grain production as “lazy pod syndrome”. Of all traits, PHI showed strongest correlations with yield regardless of the irrigated or drought treatment. Confirming its poor photosynthate remobilization capacity, the PHI of MIB 755 was significantly below that of any other genotype examined. Yield, partitioning indices and EGR were negatively correlated with grain P

concentration, suggesting that some genotypes utilize acquired P more efficiently for grain production (Rao et al., 2007). Yields related more strongly with low seed P concentrations under drought than under irrigation. The strong correlation of SBR values observed under drought conditions with yields obtained under drought and irrigated conditions indeed corroborates the importance of the capacity to efficiently remobilize stem reserves to pods for improving yield potential under favorable, irrigated conditions as well as under drought conditions. However, the physiological processes linked to this remobilization seem to differ between plants grown under drought stress and under favorable conditions. SBR under irrigation and drought were in fact unrelated, indicating that differences in stem reserve remobilization, unlike other traits conducive to efficient reproductive growth and earliness, were environmentally induced.

Under drought, SBR correlated negatively with seed P concentration and stem DW at harvest and positively with PHI and PPI. This indicates that superior performers remobilize greater amounts of photosynthates from stems to seed per unit amount of P mobilized to seed (CIAT, 2005, 2006). In contrast, under favorable conditions, SBR correlated positively with shoot biomass DW at MPF and negatively with PPI, suggesting that genotypes having accumulated much dry matter in canopy, remobilized more photosynthates from stems, but did not mobilize them to pods. Such genotypes may have remobilized photosynthates to leaves to favor vegetative growth instead of making a clear transition to reproductive growth. This was particularly observed for the common interspecific parent and, to a lesser extent, the F<sub>2</sub>-progenies. Although, there was no direct relation to yield, stem DW at harvest correlated negatively with PHI and positively with seed P concentration and DPM in the favorable environment. No such correlations with PHI and seed P concentration were observed for SBR in the favorable environment. One may conclude that stem reserve remobilization is a crucial stage of plant efficiency for reproductive growth under drought, but it alone does not ensure plant efficiency under favorable conditions. In contrary, remobilized photosynthates in some cases seem to be used for non-reproductive purposes such as the maintenance of “stay-green” vegetative structures. In fact, efficient partitioning and good response to favorable conditions are associated with the ability to harness vegetative growth independently of the ability to later remobilize stem reserves, as indicated by low stem DW at harvest.

Harnessing the vegetative growth may thus be related with a clear transition from vegetative to reproductive growth under favorable conditions.

### F<sub>2</sub>-populations

The mean score of the progenies was between that of the drought-adapted parents and the common interspecific

parent for most of the traits discussed. Under favorable conditions, this was not obvious at first glance in the field, as most progenies were actually more vigorous than MIB 755, as indicated by shoot biomass DW and LAI. Nevertheless, mean stem DW of progenies at MPF and harvest were below that of MIB 755, indicating that they did not accumulate as much excessive stem reserves as MIB 755. The significant negative relation of progeny yields under irrigation with DF of respective parents, as well as their stem DW at harvest under irrigation indicates that parents having ability of harnessing vegetative growth under favorable conditions and generally making an early transition to reproductive growth resulted in progenies with a better response to the favorable environment. The LAI of parents under drought related negatively with progeny yield potential, suggesting that even under water-stress, some drought-adapted parents were overly vigorous and passed on this trait to progenies. However, yield differences among progenies were non-significant. The selection of drought-adapted parents with a range of remobilization and partitioning capacities according to past experience was expected to lead to a range in progeny yields. In fact, the PHI, which correlated strongly with yields when including all genotypes was similarly high for all drought-adapted parents in this trial: Only SMR 4 and ALB 49 significantly differed from other drought-adapted parents under irrigation and no significant differences were found under drought.

Crossing MIB 755 with the drought-adapted parents thus generally improved the dry matter partitioning within pods in the progenies, but the limited range of PHI represented did not allow for a strong differentiation among progenies concerning this trait. On the other hand, differences in plant efficiency of drought-adapted parents in both environments were reflected in progenies as earliness to mature under favorable conditions. Apart from DPM of parents in both environments, traits associated with efficient dry matter partitioning at all levels under drought related with earliness of progenies under favorable conditions. Early maturing progenies were also produced by drought-adapted parents beginning to senesce at MPF, as indicated by lower SCMR, and having a strong capacity to remobilize photosynthates to seeds within pods and produce high yields under favorable conditions. Thus, those drought-adapted parents that were able to counterbalance MIB 755's excessive vegetative growth under favorable conditions and “lazy pod syndrome” in both environments produced more efficient progenies, although this efficiency was expressed more by earliness than in grain yields. The progeny of SER 16 stood out for its above-mean yields in both environments, in line with the yields and the remobilization and partitioning capacities of SER 16, particularly concerning PHI. Except for ALB 49, it is the only advanced line in the trial having race Durango parentage, known for its rapid and complete transition to reproductive growth with rapid seed filling and high HI (Kelly et al., 1999). Race Durango germplasm has been

identified as an important source of drought resistance in interracial crosses (Beebe et al., 2008; Porch et al., 2009).

ALB 49 is a selection from an interspecific cross including SER 16 as recurrent parent. Under irrigation, its progeny yielded well above the best yielding parent. On one hand, the significant result found in this particular cross may be explained by the wide genetic distance between parents, which resulted from interspecific crosses with different *Phaseolus* species. On the other, it may indicate that SER 16 produces efficient progenies even when operating indirectly through offspring containing SER 16 germplasm. The PPI and PHI of ALB 49 under drought were not high, but certainly acceptable compared to the values obtained for MIB 755. The comparatively high partitioning efficiency for an interspecific bean line is attributable to the SER 16 parentage of ALB 49. The negative SBR values in both environments constitute an inconsistent transition to the reproductive phase inherited from the *P. coccineus* parent, although overall vigor was low. Hence, the combination of ALB 49 and MIB 755 germplasm entailed the combination of acceptable dry matter partitioning with vigor, leading to the compensation of reciprocal unfavorable traits. Interestingly, SER 155 combined very well with MIB 755 concerning yield potential, but poorly regarding drought resistance, despite SER 155's intermediate performance in both environments. The parent's yield limitations under favorable conditions can be explained by the extremely short growing cycle of SER 155, restricting the genotype from producing high grain yield despite high EGR. However, in its progeny, a significantly longer duration of growth and maturity was inherited from MIB 755, although it remained earliest to mature among progenies. Combined with the highest PHI and EGR among progenies, this led to the highest-yielding progeny. As found for the progeny of ALB 49, it seems that the combination SER 155 and MIB 755 led to the compensation of reciprocal unfavorable traits for yield potential. Low yields of the SER 155 progeny under drought may be attributed to a shallow rooting system inherited from SER 155, as detected on the parent in a greenhouse trial.

In contrast, SMR 4 produced the lowest yielding progeny. The shoot dry matter accumulation of the SMR 4 progeny was among the lowest under irrigation, but above that of high-yielding drought-resistant check SER 118. So, vigor was not a limiting factor, but PHI below the progeny mean indicates "lazy pod syndrome". SMR 4 indeed had below average PHI and lacked seed filling in the favorable environment as did MIB 755. Crossing the two bean lines thus led to a similarly inefficient, low-yielding progeny. Given their dry matter partitioning traits, the black-seeded lines SEN 46 and SEN 74 combined with interspecific MIB 755 in an unexpected manner. Although the yield of the progeny of SEN 74 corresponded with the intermediate performance expected

from the intermediate remobilization and partitioning capacity of SEN 74, the patterns of dry matter partitioning within the progeny were quite different than that of SEN 74. Conversely, the progeny of SEN 74 had the lowest PPI of all progenies under drought, although SEN 74 produced highest PPI. In contrast to the efficiency observed in both the irrigated and drought environment for the other black-seeded drought-adapted parent SEN 46, its progeny lacked efficiency to exploit the high amount of dry matter accumulated in shoots despite very high SBR. This progeny was, however, among the earliest to mature under favorable conditions, again indicating that plant efficiency inherited from drought-adapted parents can be expressed more as earliness than as yield potential in some progenies. On one hand, SEN 46 and its progeny may indicate that high remobilization and partitioning capacities as recorded by high SBR and PHI values are not sufficient to counterbalance inefficiencies inherited from MIB 755 in progenies. On the other hand, the traits of progenies of SEN 46 and SEN 74 with MIB 755 suggest that black-seeded (SEN) lines do not combine well with MIB 755 as do red-seeded (SER) lines.

Indeed, differences in combining abilities have been found between the market classes. For example red-seeded Mesoamerica lines have been found to combine better with race Durango than black-seeded ones for enhanced drought resistance (Beebe et al., 2008).

## Conclusions

The results of the present study highlight problems that are inherent in interspecific crosses of common bean with its secondary gene pool. The evolution of species such as *P. dumosus* or *P. coccineus* has favored a vigorous vegetative growth at the expense of efficiency in grain production. We have referred to the many attempts to utilize these species to improve common beans, especially as sources of disease resistance and in spite of the number of attempts, very few common bean cultivars carry genes derived from these species. We suggest that the problems of poor photosynthate remobilization that were documented in MIB 755 are symptomatic of the poor quality of such interspecific progenies. Using parents with enhanced photosynthate remobilization capacity should be part of the strategy to tap the vast genetic diversity of the secondary gene pool. Under scenarios of climate change in which some regions of the tropics are expected to receive significantly more rainfall, these species may become more attractive as sources of traits for humid environments, in which case their use in breeding programs may be more frequent (Beebe et al., 2011). For further investigation, it is recommended that corresponding field trials be repeated with a higher number of drought-adapted parents and various interspecific parents to verify relations found

in this study. Maternal effects involved when the interspecific or drought-adapted parent is used as maternal parent also need to be further examined.

Finally, the combining ability of black-seeded lines with interspecific lines should be investigated.

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**Abbreviations:** **Al**, Aluminum; **CIAT**, International Center for Tropical Agriculture; **DF**, days to flowering; **DII**, drought intensity index; **DPM**, days to physiological maturity; **DW**, dry weight; **EGR**, economic growth rate; **Fe**, iron; **HI**, harvest index; **HSD**, honestly significant difference; **LAI**, leaf area index; **MPF**, mid-pod filling; **P**, phosphorus; **PHI**, pod harvest index; **PPI**, pod partitioning index; **SCMR**, SPAD chlorophyll meter reading; **SBR**, stem biomass reduction; **Zn**, zinc.

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