CAN TEPARY BEAN BE A MODEL FOR IMPROVEMENT OF DROUGHT RESISTANCE IN COMMON BEAN?

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ABSTRACT

Common bean (*Phaseolus vulgaris* L.) is the most important grain legume for human consumption and drought stress affects over 60% of dry bean production worldwide. Field studies were conducted over two seasons at Centro Internacional de Agricultura Tropical (CIAT), Palmira, Colombia to (i) evaluate phenotypic differences in drought resistance; and (ii) identify adaptive traits that can be used in on-going breeding programmes of common bean for developing drought resistant genotypes. A total of 36 genotypes, including elite inbred and interspecific lines and landraces of common bean and tepary bean were evaluated under field conditions with two levels of water supply (irrigated and rainfed). Results showed that two accessions of tepary bean, *P. acutifolius* (G 40159 and G 40068) and two elite lines (RAB 650, SEA 23) of common bean were outstanding in their adaptation to terminal drought stress. The superior performance of these genotypes under drought stress was associated with their ability to mobilise photosynthates from leaves and stems to developing grain. Tepary bean was superior to common bean in combinig several desirable traits that contribute to greater level of adaptation to terminal drought stress. Canopy biomass, pod partitioning index, stem biomass reduction and pod harvest index could serve as useful traits to improve the efficiency of breeding programmes to select superior genotypes of common bean under terminal drought stress.

Key Words: Abiotic stress, harvest index, water stress

RÉSUMÉ

Le haricot common (*Phaseolus vulgaris* L.) est une légumineuse la plus importante pour la consummation humaine don't la sécheresse affecte plus de 60% de bean production mondiale. Des études en champs étaient conduits en deux saisons au Centro Internacional de Agricultura Tropical (CIAT), Palmira, Colombia afin de (i) évaluer les différences phénotypiques pour la résistance à la sécheresse; et (ii) identifier les traits adaptifs pouvant être utilisés dans les programmes en cours d'amélioration du haricot commun pour le développement des génotypes resistant à la sécheresse. Trente six génotypes incluant des hybroides élites et interseptiques ainsi que des haricot de races locales et haricot *tepary* étaient évalués au champs avec deux niveaux d'approvisionnement en eau (irrigation et pluvial). Les résultats ont montré que deux accessions du haricot *tepary, P. acutifolius* (G 40159 et G 40068) et deux lignées élites (RAB 650, SEA 23) de haricot commun s'étaient distinguées de par leur adaptation au stress hydrique. La performance supérieur de ces génotypes sous stress hydrique était associée avec leur capacité de mobiliser les photosyntates des feuilles et tiges pour le développement de grains. Le haricot *tepary* était supérieur au haricot commun en terme de combinainson de plusieurs taits désirables qui contribuent au niveau plus élevé d'adaptation au stress hydrique. La biomasse de canopée, l'indice de la repartition des gousses, la réduction de la biomasse des tiges et l'indice de récolte de gousses pourrainet servir comme des traits utiles pour améliorer l'efficacité des programmes d'amélioration pour pour sélectionner les génotypes supérieurs de haricot commun sous stress hydrique.

Mots Clés: Stress abiotique, indice de récolte, stress hydrique

INTRODUCTION

Drought is a recurrent problem of rainfed agriculture throughout the world. Since 84% of the world´s cultivated lands are rainfed, drought stress has major implications for global economy and trade. Some of the most important impacts of global climate change and the associated drought and heat stress will be felt among "subsistence" or "smallholder" farmers in developing countries (Morton, 2007). Drought resistance is defined as the relative yield of a genotype compared to other genotypes subjected to the same drought stress. Blum (2009) indicated that plant breeders should consider plant constitutive and adaptive traits, which drive the effective use of water and the resultant dehydration avoidance as major traits for yield improvement in drought prone environments. Salekdeh *et al.* (2009) developed a conceptual framework for drought phenotyping in a molecular breeding programme. This framework emphasizes the importance of identification of plant traits and mechanisms that contribute to superior adaptation to drought stress.

Common bean (*Phaseolus vulgaris* L.) is the most important grain legume for human consumption as it provides an important source of protein (~22%), vitamins (folate), and minerals (Ca, Cu, Fe, Mg, Mn, Zn) for human diets, especially in developing countries (Beebe, 2012). It is cultivated largely by resource-poor farmers in the tropics; and compared to other grain legumes such as cowpeas, beans are less adapted to extreme environments of very low rainfall, high temperatures, or low fertility soils (Thung and Rao, 1999; Beebe *et al.*, 2011). Drought affects over 60% of dry bean production worldwide (Rao, 2001; Beebe *et al.*, 2008). Bean producing areas where drought is endemic include highland Mexico, Central America, northeast Brazil, and much of eastern and southern Africa (Beebe, 2012).

The effects of drought on common bean are dependent on the intensity, type and duration of the stress (Beebe *et al.*, 2013). Development of drought adapted bean varieties is an important strategy to minimise crop failure and improve food security in bean growing regions in the face of climate change (Beebe *et al.*, 2011).

Since common bean is grown over a wide range of habitats where it can be exposed to seasonal droughts and wide fluctuations in soil moisture availability between years, it has evolved several mechanisms of maintaining plant water status within reasonable limits for normal metabolic functioning under drought stress (Beebe *et al.*, 2013). Moderate to severe drought stress in common bean is known to reduce canopy biomass and seed yield, harvest index, number of pods and seeds, seed weight, and days to maturity (Nunez-Barrios *et al.,* 2005; Beebe *et al.*, 2013). Earliness, deep rooting and greater ability to partition photosynthates to grain have been identified as key mechanisms contributing to improved drought resistance in common bean (Rao, 2001; Rao *et al.*, 2009; Beebe *et al.*, 2013).

Combining races Durango and Mesoamerica has been a consistent source of improved drought resistance in common bean for lowland tropical environments (Beebe, 2012). Beebe *et al.* (2008) found that selection for drought resistance improves yield potential and plant efficiency across different environments (e.g., non-stress, low phosphorus stress) and suggested that selection under drought stress reveals genes that correct inefficiencies (excessive vegetative growth) inherited from the wild *Phaseolus vulgaris*, and that are key to yield improvement of common bean.

However, intraspecific crosses with sister species of the genus *Phaseolus* offer prospects of further progress. Tepary bean (*P. acutifolius* A. Gray) originated on dry subtropical slopes in the deserts of Mexico and the south-western United States and is well adapted to drought stress. Drought resistance mechanisms in tepary include deep rooting to avoid dehydration; small leaves for reduced water use; and stomatal control but not with osmotic adjustment (Mohamed *et al.*, 2005; Beebe *et al.*, 2013). Greenhouse evaluation under drought stress using soil cylinders, revealed that it has fine, profusely branched roots that access limited water reserves rapidly (Butare *et al.*, 2011).

Sexual crosses of tepary with common bean require embryo rescue to obtain F_1 plants (Waines *et al.*, 1988). Tepary was used as a source of genes for the improvement of common bean through the congruity backcross system (Mejía-Jimenez

et al., 1994) for resistance to disease and insect (Singh 1992) and drought (Beebe, 2012). DNA markers suggested introgression of up to 25% of the tepary genome into common bean (Muñoz *et al.*, 2004).

Different domesticated species within the *Phaseolus* genus express contrasting degrees of harvest index. For example, interspecific lines derived from crosses between common bean and species from its secondary gene pool (*P. dumosus*, *P. coccineus*) tend to present excessive vegetative growth and low grain yield; while drought adapted common bean lines produce lower shoot biomass but high grain yield. This was attributed by Beebe *et al.*, 2008 and Klaedtke *et al.*, 2012 to greater mobilisation of photosynthates to grain development, concluding that differences in biomass partitioning to grain play a key role in improving drought resistance of common bean.

Tepary bean has much less tendency to excessive vegetative growth than common bean, but there is limited comparative analysis of biomass partitioning differences between these two species under drought stress. But quantifying genotypic differences in harvest index in common bean has been difficult due to leaf fall during grain filling. Developing methodology to dissect harvest index into successive components to track the photosynthate mobilisation from vegetative organs to pod and grain could help the breeders to identify genotypes that are better adapted to drought stress.

The objectives of the present study were to: (i) evaluate phenotypic differences in drought resistance; and (ii) identify adaptive traits that can be used in on-going breeding programmes of common bean for developing drought resistant genotypes.

MATERIALS AND METHODS

Germplasm. Three landraces of common bean (*P. vulgaris*) G 21212, G 1977 and Apetito, two landraces of tepary bean (*Phaseolus acutifolius*) G 40068 and G 40159, five commercial cultivars of common bean (ICA Pijao, ICA Quimbaya, Tio Canela, Pinto Villa and DOR 390), five interspecific lines between tepary bean and common bean

(INB 35, INB 36, INB 37, INB 38, INB 39 developed from five cycles of congruity backcrossing of tepary with ICA Pijao) and twenty one elite lines of common bean (RAB 608, RAB 609, RAB 618, RAB 636, RAB 619, RAB 620, RAB632, RAB 650, RAB 651, RJB 7, SEA 5, SEA 15, SEA 16, SEA 17, SEA 18, SEA 19, SEA 20, SEA 21, SEA 22, SEA 23, BAT 477) were included in this study. SEA 5, BAT 477 and Pinto Villa were included as drought resistant checks and Tio Canela 75 and DOR 390 were included as drought sensitive checks based on previous evaluations. All the genotypes except ICA Quimbaya, belong to Mesoamerican gene pool. Details on seed colour, 100 seed weight (SW), days to physiological maturity (DPM), growth habit, type of germplasm, genus, species and origin are listed in Table 1.

Crop environment. Two field trials were conducted at CIAT-Palmira, Colombia in 2001 and 2002 during dry season (June to September). Basic characteristics of this field site were already described (Beebe *et al.*, 2008). Climatic conditions including rainfall distribution, pan evaporation, maximum and minimum temperatures during the two seasons are shown in Figure 1. The soil is a Mollisol (Aquic Hapludoll) with adequate nutrient supply and is 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 upper and lower limits for soil matric potential) (White and Castillo, 1992). During the crop-growing season, maximum and minimum air temperatures in 2001 were 30.5 °C and 18.7 °C and in 2002 were, 30.6 °C and 19.2 °C, respectively. The maximum and minimum temperatures during the dry season were similar to normal seasonal temperatures in the study area (Beee *et al.*, 2008).

The incident solar radiation ranged from 4.6 to 25.0 MJ m^{-2} d^{-1} in 2001 and 11.2 to 24.7 MJ m^{-2} d^{-1} in 2002. Total rainfall during the active crop growth was 122.7 mm in 2001 and 83.9 mm in 2002. The potential pan evaporation was of 432 mm in 2001 and 441 mm in 2002.

Both trials included 36 genotypes mentioned above. Trials were grown in dry seasons to induce drought stress. Two levels of water supply (irrigated and rainfed) were applied to simulate control and drought stress treatments. Trials were furrow irrigated (approximately 35 mm of water

TABLE 1. Characteristics of common bean (*P. vulgaris*) and tepary bean (*P. acutifolius*) genotypes used in the field studies

Genotype	Seed colour	100 seed weight (g)	Days to physiological maturity	Growth habit	Type of germplasm	Origin
P. vulgaris elite lines						
RAB 608	Red	16.6	75	II	Inbred line	Colombia
RAB 609	Red	15.8	76	II	Inbred line	Colombia
RAB 618	Red	22.7	72	II	Inbred line	Colombia
RAB 636	Red	23.7	74	II	Inbred line	Colombia
RAB 619	Red	23.1	72	II	Inbred line	Colombia
RAB 620	Red	18.8	72	II	Inbred line	Colombia
RJB 7	Red	22.3	76	II	Inbred line	Colombia
RAB 632	Red	17.2	74	II	Inbred line	Colombia
RAB 650	Red	18.7	72	II	Inbred line	Colombia
RAB 651	Red	19.6	71	II	Inbred line	Colombia
SEA 15	Purple	26.1	71	III	Inbred line	Colombia
SEA 16	Yellow	21.2	76	II B	Inbred line	Colombia
SEA 17	Cream	18.8	75	II B	Inbred line	Colombia
SEA 18	Black	16.2	74	II	Inbred line	Colombia
SEA 19	Black	19.4	74	II	Inbred line	Colombia
SEA 20	Red	15.7	76	II	Inbred line	Colombia
SEA 21	Red	21.2	72	II	Inbred line	Colombia
SEA 22	Red	20.9	71	II	Inbred line	Colombia
SEA 23	Pink	20.4	71	II	Inbred line	Colombia
P. vulgaris x *P. acutifolius* interspecific lines						
INB 35	Variable	16.0	79	II	Line	Colombia
INB 36	Black	15.4	78	II	Line	Colombia
INB 37	Variable	17.1	76	II	Line	Colombia
INB 38	Black	16.0	80	II	Line	Colombia
INB 39	Black-brown	17.5	80	II	Line	Colombia
P. acutifolius germplasm accessions						
G 40068	Brown	12.6	68	IV	Landrace	USA
G 40159	White	11.5	68	IV	Landrace	Mexico
P. vulgaris germplasm accessions and checks						
G 21212	Black	20.1	75	II	Landrace	Colombia
G 1977	Black	17.3	75	II	Landrace	Guatemala
SEA 5	Cream	21.6	75	II	Inbred line	Colombia
BAT 477	Cream	16.1	79	III	Inbred line	Colombia
Tio Canela 75	Red	17.3	74	II	Inbred line	Honduras
DOR 390	Black	14.5	76	II	Inbred line	Colombia
Pinto Villa	Cream-brown	30.3	71	III	Inbred line	Mexico
Apetito	Pink	19.2	77	III	Landrace	Mexico
ICA Pijao	Black	15.8	80	II	Commercial	Colombia
ICA Quimbaya	Red	34.6	75	I	Commercial	Colombia

RAB = shiny red bush bean for monoculture; RJB = red bush bean; SEA = advanced drought resistant line; INB = interspecific cross derivatives; G = germplasm accession; BAT = bean adapted to tropics; DOR= bean golden mosaic virus; ICA = instituto colombiano agropecuario. Growth habit I (bushy, erect and determinate; II (bushy, erect and indeterminate); IIb (bushy, erect and indeterminate with a terminal guide); III (prostrate, viny and indeterminate); IV (strong climbing and indeterminate)
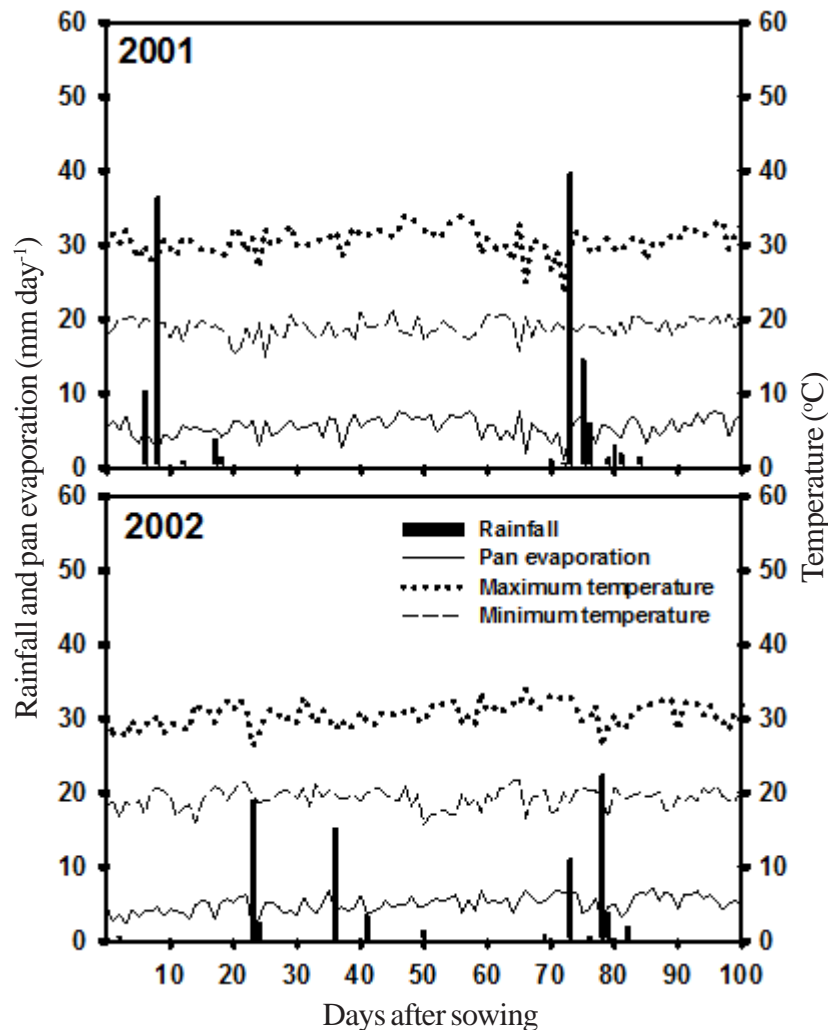
Figure 1. Rainfall distribution, pan evaporation, maximum and minimum temperatures during crop growing period at Palmira in 2001 and 2002.

per irrigation). Drought stress treatment under rainfed conditions in 2001 received irrigation at 6 days before planting and at 5 and 26 days after planting. In 2002, irrigation was provided at 6 days before planting and at 11 and 21 days after planting. In both years, irrigation was suspended after the third irrigation to induce terminal drought stress (less water availability from flowering to physiological maturity) conditions. The irrigated control treatment received 6 irrigations to ensure adequate soil moisture for crop growth and development.

Drought treatment resulted in incipient wilting at mid-day during flowering, and stress increased throughout the pod filling period until physiological maturity.

Measurements of soil moisture tension at 15 cm soil depth revealed values of -70 kPa or lower as plots were approaching physiological maturity, confirming severe terminal stress conditions.

A 6 x 6 partially balanced lattice design with 3 replications was used. Details on planting and management of the trial were similar to those reported before (Beebe et al., 2008). Experimental units consisted of 4 rows, 5 m long by 0.6 m wide with 7 cm between plants in the row. Trials were not fertilised but were weeded and sprayed with insecticides and fungicides. Fungicide

applications included weekly applications of 1.25 g l^{-1} benomyl (methyl 1-(butylcarbomoyl) 2-benzimidazolecarbamate) at the base of plants to reduce infection of root pathogens during the first 2 to 3 weeks after planting. Growth habit was recorded during flowering and verified at the end of physiological maturity. Days to maturity was recorded when 90% of the pods changed from green to yellow or beige colour.

Agronomic and physiological measurements. A 50 cm row length from each plot with about 7 plants was used for destructive sampling to measure leaf area index (LAI), canopy biomass (CB) and dry matter distribution between leaves, stems and pods. Leaf chlorophyll content of fully expanded leaves was measured using a non-destructive, hand-held chlorophyll meter (SPAD-502 Chlorophyll Meter, Minolta Camera Co., Ltd., Japan). The principle is based on the difference in light attenuation at wavelengths 430 and 750 nm. From the difference in light attenuation, a numerical SPAD (Soil Plant Analysis Development) unit, ranging from 0 to 80 is calculated by the microprocessor in the SPAD-502 Chlorophyll Meter. The results are expressed as SPAD chlorophyll meter reading (SCMR).

At the time of harvest, dry weights of stem biomass, pod biomass, and seed biomass, number of pods per plant, dry weight of pod wall biomass, seed number per pod, 100 seed dry weight (SW), seed number per area (SNA), and pod number per area (PNA) were measured. The two central rows of each plot were used after discarding end plants to determine grain yield (YLD). The following attributes were determined:

i.   harvest index (HI) (%): seed biomass dry weight at harvest/total shoot biomass dry weight at mid-pod filling x 100;

ii. pod harvest index (PHI) (%): seed biomass dry weight at harvest/pod biomass dry weight at harvest x 100;

iii. pod partitioning index (PPI) (%): pod biomass dry weight at harvest/total shoot biomass dry weight at mid-pod filling x 100;

iv. Stem biomass reduction (SBR) (%): (stem biomass dry weight at mid-pod filling – stem biomass dry weight at harvest)/stem biomass dry weight at mid-pod filling x 100;

v.   pod production efficiency (PPE) (no. g^{-1}): pod number per area/total shoot biomass dry weight at mid-pod filling per area (adapted from Board and Maricherla, 2008);

vi. seed production efficiency (SPE) (no. g^{-1}): seed number per area/ total shoot biomass dry weight at mid-pod filling per area, all adapted from Board and Maricherla, 2008; and

vii. drought intensity index (DII): the DII for each growing season was calculated as DII = 1 – X_{ds}/X_{ns}, where X_{ds} and X_{ns} are the mean of all genotypes under drought stress (ds) and no stress (ns) treatments, respectively (Fischer and Maurer, 1978).

Statistical analysis. All data were analysed using the SAS (v 9.0) PROC MIXED and PROC CORR (SAS, 2004). The adjusted means for each genotype and the environment (irrigated and rainfed) were obtained using the mixed models theory together with the MIXED procedure considering the effects of the replications and blocks within replications as random and genotypes as fixed.

RESULTS

The data on rainfall distribution and pan evaporation in both years (2001 and 2002) indicated that the crop suffered high level of terminal drought stress during active growth and development (Fig. 1). The extent of terminal drought stress was greater in 2002 than in 2001 as reflected by the drought intensity index of 0.37 and 0.21, respectively. The maximum temperatures were about 32 °C while the minimum temperature was about 19 °C.

Grain yield. The analysis of YLD showed significant differences (P<0.01) for all sources of variation, except the year x environment (Y x E)

interaction. The analysis indicated that 21.6% of the total sum of squares was attributable to year (Y), 20.5% to environment (E), and 4.9% to year x environment (Y x E) interaction. It also indicated 25.6% to genotype (G), 4.4% to genotype x year (G x Y) interaction and 6.2% genotype x environment (G x E) interaction. The traits including YLD, SW and DPM showed significant differences for G x E, G x Y and G x E x Y interactions.

The mean value of YLD under rainfed conditions decreased by 31% compared with irrigated conditions (Table 2). Under rainfed (water stress) conditions in the field, YLD of 36 genotypes ranged from 416 to 1147 kg ha^{-1} (Table 2). Among the genotypes tested, two accessions of *P. acutifolius* (G 40159 and G 40068) and two elite lines (RAB 650 and SEA 23) were outstanding in their adaptation to rainfed conditions. There was response to irrigation in most of the genotypes, but not in all genotypes as evident from the mean values (Table 2, Fig. 2).

A high incidence of a leafhopper pest (*Empoasca kraemeri*) during reproductive development in the rainfed treatment and attack of a pod-boring insect (*Epinotia opposita*) in the irrigated treatment affected the performance of several genotypes including G 21212 in 2001 season. The relationship between YLD of rainfed and irrigated treatments indicated that G 40159, RAB 650, SEA 23 and SEA 15 were not only adapted to drought stress but are also responsive to irrigation (Fig. 2). Geometric mean (GM) values of grain yield of these genotypes were higher than the other genotypes (Table 2). Among the 36 genotypes tested, the interspecific line between tepary bean and common bean, INB 36 was the most poorly adapted elite line under rainfed conditions. All five INB lines tested were less adapted to drought stress conditions.

Leaf and canopy traits. The effects of drought stress on leaf traits including LAI and SCMR are shown in Table 2. The mean value of LAI decreased by 13% under rainfed conditions compared with 31% reduction in grain yield to that of irrigated conditions. The highest values of LAI corresponded to the interspecific line INB 35 under irrigated conditions and to SEA 16 under rainfed conditions. ICA Pijao had greater value of LAI under rainfed conditions than several elite lines but it was the lowest grain yielder among the 36 genotypes tested. Drought stress did not affect SCMR although the genotypic differences were significant within rainfed or irrigated conditions. The drought adapted tepary bean accession G 40159 showed a decrease in SCMR under rainfed conditions compared with irrigated conditions. Several drought adapted elite lines showed no effect on SCMR under rainfed conditions.

Photosynthate partitioning and mobilisation. The mean value of CB under irrigated conditions was 2,536 kg ha^{-1}; while it was 2160 kg ha^{-1} under rainfed conditions (Fig. 3a, b). The accumulation of biomass in the rainfed treatment was facilitated by the fact that adequate moisture was supplied during the vegetative phase, and water deficits were induced during the reproductive phase. Thus, much of the biomass was accumulated before drought effects set in, and this narrowed the difference between the rainfed and irrigated treatments for this parameter.

The relationships between CB production and YLD, and HI and YLD under irrigated or rainfed conditions are shown in Figure 3. Under irrigated conditions, the interspecific line INB 35 was the most vigorous genotype in terms of CB (Fig. 3a), but its YLD was only at the mean value of the 36 genotypes tested, mainly due to its lower value of HI (Fig. 3c). Under rainfed conditions, at the same level of CB of about 2,400 kg ha^{-1}, there was marked difference in YLD of several genotypes showing the importance of HI or partitioning of photosynthates to grain (Fig. 3b). SEA 15 was the most vigorous elite line under rainfed conditions (Fig. 3b), but SEA 23 which showed lower CB value than SEA 15 had similar yield due to its higher HI value (Fig. 3d). Highest values of HI under rainfed conditions were observed with the two accessions of the tepary bean (G 40159 and G 40068), while ICA Pijao showed the lowest value of HI. Among the RAB lines tested RAB 651 was superior in CB production and YLD under irrigated conditions, while RAB 650 was superior under rainfed conditions and was comparable to tepary in HI (Fig. 3a, b).

The relationships of YLD to SBR, to PPI, and to PHI under irrigated or rainfed conditions are

TABLE 2. Differences in grain yield (YLD), grain yield geometric mean (GM), leaf area index (LAI) and SPAD chlorophyll meter reading (SCMR) of 36 genotypes of common bean and tepary bean grown under irrigated or rainfed conditions in a Mollisol at Palmira

Genotype	Yield (kg ha^{-1})			Leaf area index (m^2 m^{-2})		SPAD chlorophyll meter reading	
	Irrigated	Rainfed	GM	Irrigated	Rainfed	Irrigated	Rainfed
RAB 608	735	463	577	1.84	1.77	39.5	41.3
RAB 609	1074	583	778	1.87	1.77	45.6	38.7
RAB 618	898	624	728	1.61	1.41	36.1	33.1
RAB 636	722	590	644	1.82	1.55	35.0	33.7
RAB 619	970	641	783	2.00	1.72	39.5	41.4
RAB 620	901	567	706	1.40	1.67	37.5	42.8
RJB 7	902	550	684	2.12	1.71	39.4	31.4
RAB 632	929	722	808	1.69	1.63	44.9	42.2
RAB 650	1125	945	1011	1.81	1.83	35.9	35.3
RAB 651	1202	790	961	2.21	2.07	39.2	38.7
SEA 15	1340	890	1070	1.94	1.30	38.9	36.9
SEA 16	1078	783	902	2.89	2.39	36.9	39.2
SEA 17	872	621	731	2.68	2.29	39.5	38.1
SEA 18	970	835	895	1.82	1.93	44.2	43.6
SEA 19	1036	667	826	2.10	1.92	38.5	35.7
SEA 20	713	605	643	1.92	1.69	40.5	38.3
SEA 21	1052	670	820	1.81	1.24	41.6	41.8
SEA 22	1076	625	813	1.93	1.50	35.5	38.0
SEA 23	1186	907	1026	1.79	1.34	38.8	42.5
INB 35	984	566	740	2.88	2.14	36.0	37.1
INB 36	808	392	550	2.10	1.71	37.6	35.8
INB 37	883	522	671	2.17	1.82	43.7	39.2
INB 38	857	514	659	2.55	1.92	40.3	38.1
INB 39	1018	551	735	2.16	1.78	43.7	43.4
G 40068	943	1115	952	1.15	1.37	42.9	37.4
G 40159	1463	1147	1262	1.06	0.78	41.7	34.9
G 21212	723	638	659	1.79	2.04	42.7	38.1
G 1977	534	604	554	2.13	2.07	39.6	40.3
SEA 5	917	724	801	2.44	2.00	37.7	43.5
BAT 477	1085	693	862	1.82	2.05	38.8	36.9
Tio Canela 75	1087	671	848	1.67	1.70	42.3	42.6
DOR 390	842	475	611	2.00	1.44	40.6	40.2
Pinto Villa	1250	681	914	1.57	1.30	40.6	34.2
Apetito	662	558	597	1.94	1.71	40.0	36.0
ICA Pijao	1043	416	644	2.75	2.17	43.8	40.3
ICA Quimbaya	676	454	540	1.44	1.25	36.7	34.1
Mean	960	661	778	1.97	1.72	39.9	38.5
LSD$_{0.05}$	261	189	162	0.75	0.69	6.8	6.3

GM = Geometric mean

shown in Figure 4. Under rainfed conditions genotypes with higher YLD also showed higher values of SBR at maturity; while there was no relationship between SBR and YLD under irrigated conditions (Fig. 4b). Higher values of SBR are considered to reflect greater ability to mobilise photosynthates from stems to developing grains. The elite line, SEA 15 showed the highest value of SBR under rainfed conditions (Fig. 4b), while the interspecific bred line, INB 37
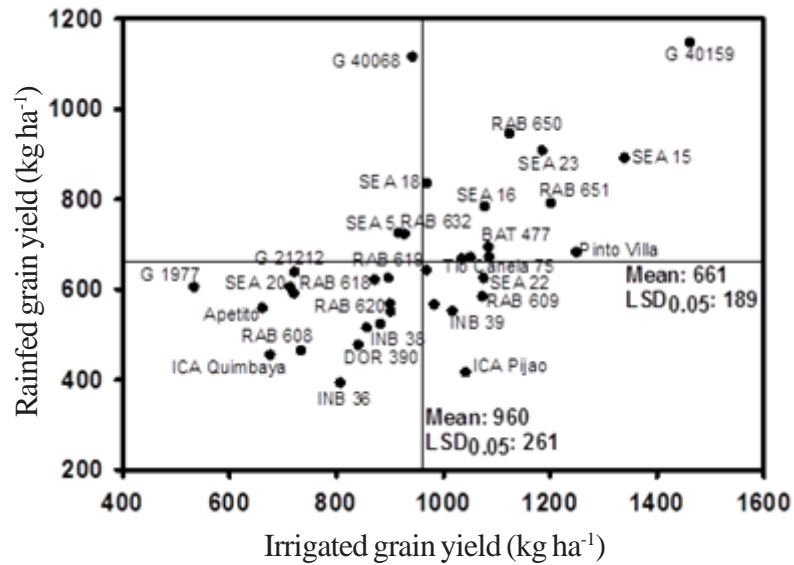
Figure 2. Identification of genotypes that are adapted to rainfed conditions and are responsive to irrigation on a Mollisol at Palmira. Genotypes that yielded superior with drought and were also responsive to irrigation were identified in the upper, right hand quadrant.
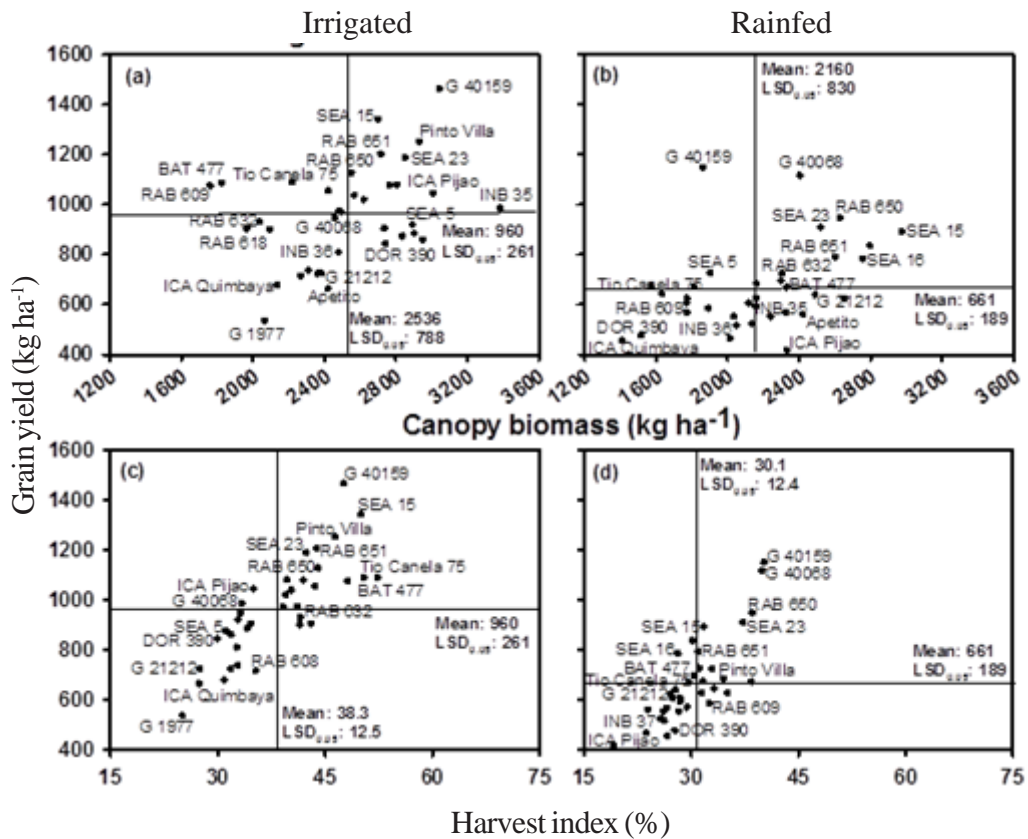

Figure 3. Identification of genotypes with greater values of grain yield and canopy biomass (a, b) and grain yield and harvest index (c, d) under irrigated or rainfed conditions on a Mollisol at Palmira. Higher yielding genotypes with greater values of canopy biomass and harvest index were identified in the upper, right hand quadrant.

showed negative value of SBR indicating that the stems continue to accumulate photosynthates during grain filling process. PPI is a measure of mobilisation of photosynthates from leaves and stems to pod development. The relationship between PPI and YLD under irrigated and rainfed conditions showed that the two accessions of *P. acutifolius* (G 40159 and G 40068)

and two bred lines (RAB 650 and SEA 23) presented higher and comparable values of PPI under rainfed conditions (Fig. 4d). Under irrigated conditions, BAT 477 showed the highest value of PPI (Fig. 4c). PHI value, which is a measure of the ability to set and fill seed was markedly higher with the two accessions of *P. acutifolius* (G 40159 and G 40068) and four bred lines (RAB 650, SEA
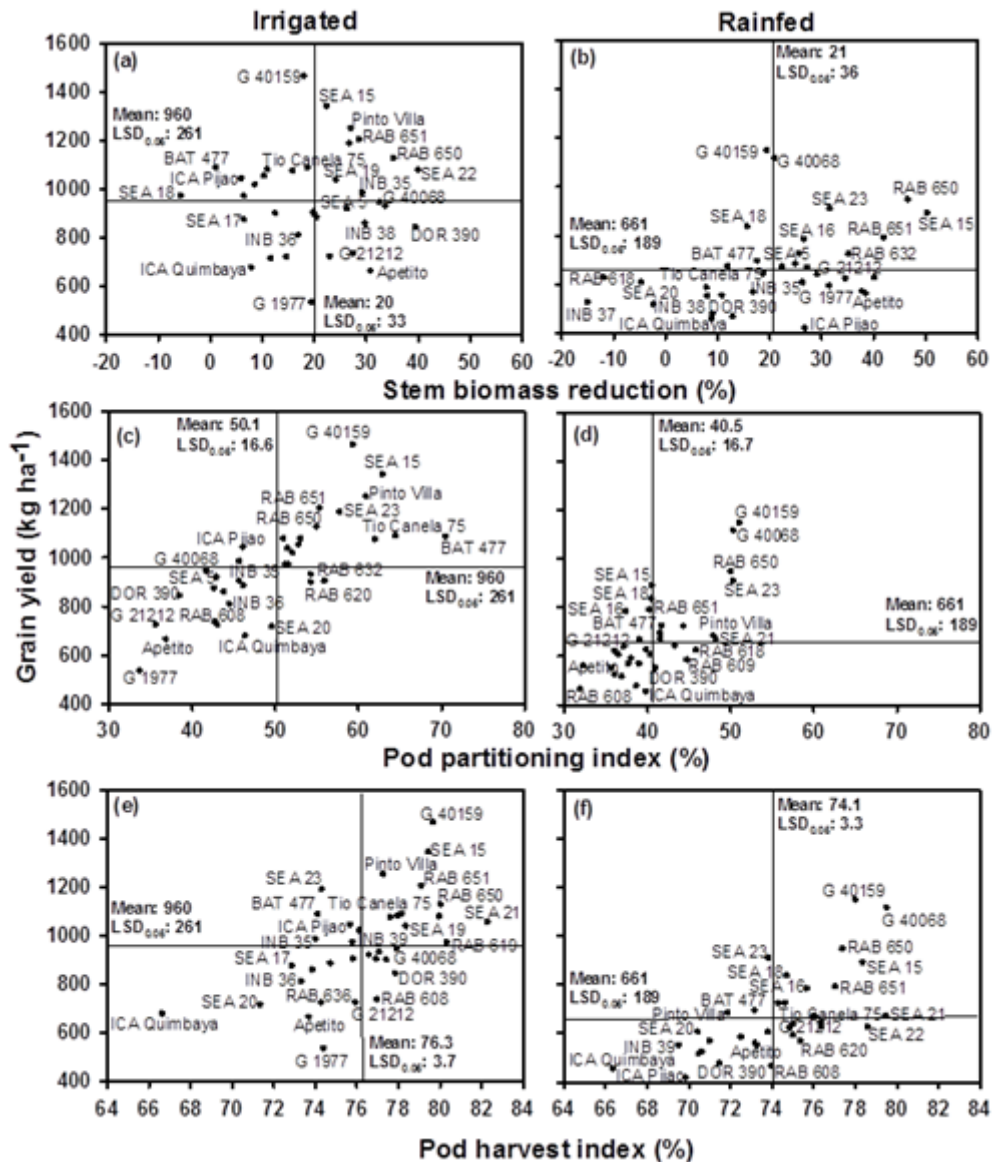

Figure 4. Identification of genotypes with greater values of grain yield and stem biomass reduction (a, b), grain yield and pod partitioning index (c, d) and grain yield and pod harvest index (e, f) under irrigated or rainfed conditions on a Mollisol at Palmira. Higher yielding genotypes with greater values of stem biomass reduction, pod partitioning index and pod harvest index were identified in the upper, right hand quadrant.

15, SEA 21, SEA 22) under rainfed conditions (Fig. 4f). ICA Quimbaya, a large seeded Andean cultivar showed the lowest values of PHI under both irrigated and rainfed conditions (Fig. 4e). Drought stress decreased mean values of PPI compared with irrigated conditions (Fig. 4c, d).

The relationships of YLD with SNA, PNA, and SW under irrigated or rainfed conditions are shown in Figure 5. As expected, the two very small seeded accessions of tepary bean showed the highest number of seeds and pods per unit area, while the large seeded Andean cultivar, ICA Quimbaya showed the lowest number of seeds and pods per unit area under rainfed conditions (Fig. 5b, d). Drought stress decreased the mean values of SNA, PNA and SW (Fig. 5a to f).
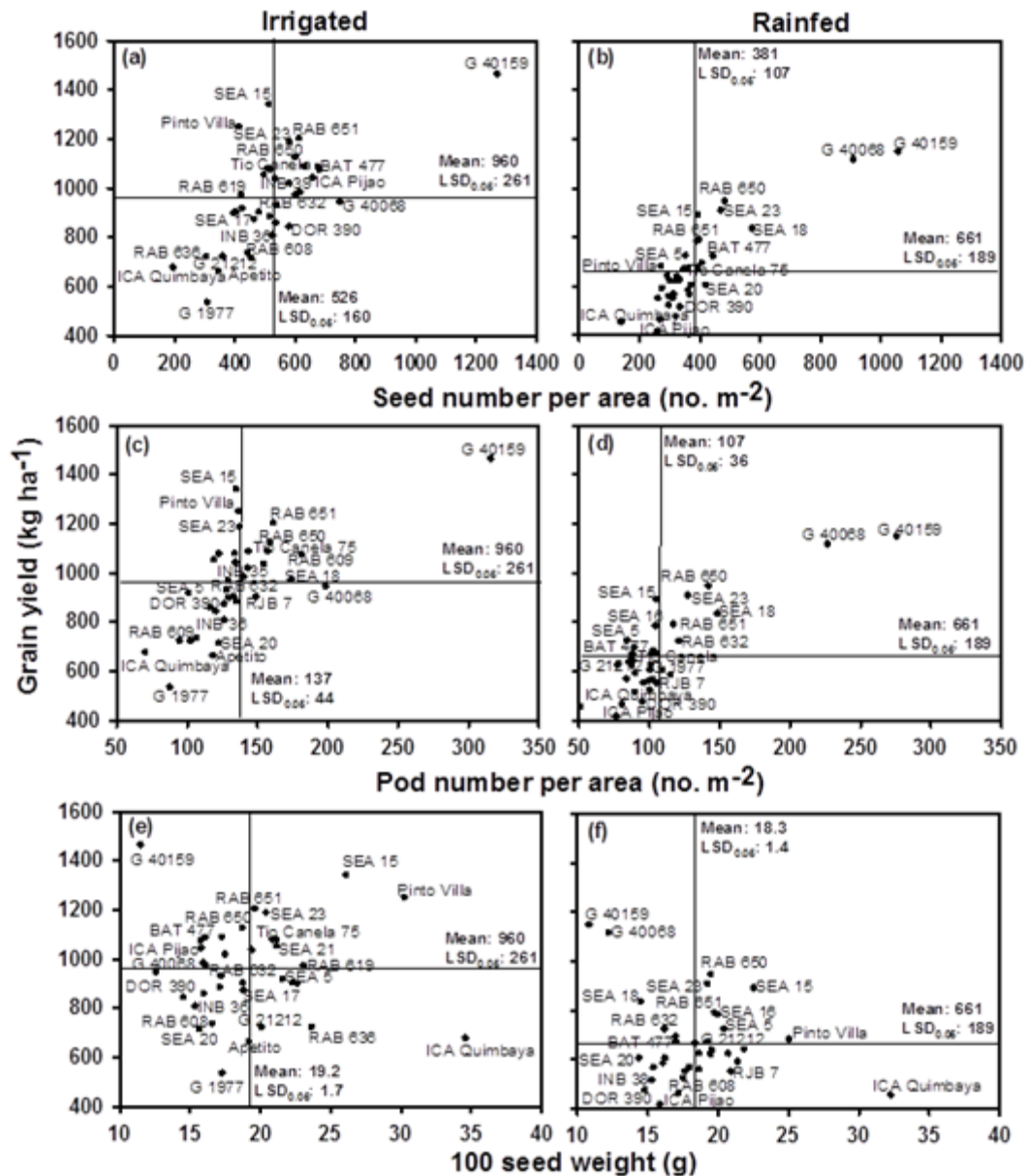

Figure 5. Identification of genotypes with greater values of grain yield and seed number per area (a, b), grain yield and pod number per area (c, d) and grain yield and 100 seed weight (e, f) under irrigated or rainfed conditions on a Mollisol at Palmira. Higher yielding genotypes with greater values of seed number per area, pod number per area and 100 seed weight were identified in the upper, right hand quadrant.

Correlations among shoot traits. Correlation matrix among LAI, CB, SBR, PPI, PHI and YLD under irrigated or rainfed conditions is shown in Table 3. Under rainfed conditions, YLD showed highly significant (P<0.001) correlation with HI (r = 0.71), PPI (r = 0.68) and PHI (r = 0.41); while its relationship with SBR was significant (P<0.05) but lower (r = 0.20). As expected, HI showed almost a linear correlation with PPI under both rainfed and irrigated conditions; while it showed highly significant (P<0.001) but lower values of correlation with PHI under both rainfed and irrigated conditions. Under rainfed conditions, SBR was closely associated with CB and LAI and CB was closely associated with LAI. CB was also highly correlated with LAI under irrigated conditions.

Correlation matrix among YLD, SNA, PNA, SPE and PPE under irrigated or rainfed conditions is shown in Table 4. Under rainfed conditions, YLD was highly correlated (P<0.001) with SNA (r = 0.85) while with PNA the correlation was highly significant but lower. Under irrigated conditions, YLD was highly correlated with both SNA (r = 0.83) and PNA (r = 0.79). As expected, SPE was highly correlated with PPE under both rainfed and irrigated conditions.

DISCUSSION

Traits for drought resistance. Previous research on common bean identified earliness and deep rooting are useful plant traits for drought avoidance in common bean (Beebe *et al.,* 2013). This study identified three additional plant attributes that could be useful to analyse the physiological basis of drought resistance. These include PPI, SBR and PHI. Genotypic differences in these three traits could indicate the extent of photosynthate mobilisation as assessed by sink strength (PPI), stem reserve mobilisation (SBR) and grain filling (PHI). We measured PPI using the value of pod biomass at harvest relative to canopy biomass value at mid-pod filling growth stage, which is assumed to be the time that reflects the maximum vigor of the genotype. This measurement is useful to assess the genotypic differences in sink strength. The measure of SBR at harvest relative to stem biomass at mid-pod

filling indicates the extent of stem reserve mobilisation to grain filling. The measure of PHI (measured at harvest) indicates the extent of photosynthate mobilisation from pod wall to seed. Pod wall is the source of carbon for the developing seed (Turner *et al.*, 2005). These traits could also contribute to greater yield potential under optimum (nonstress) conditions (Beebe *et al.*, 2008). Thus, an accelerated photosynthate (products of photosynthesis) partitioning towards the reproductive structures could be an important mechanism for improved grain yield under both stress and nonstress conditions (Rao, 2001; Rosales-Serna *et al.*, 2004; Rao *et al.*, 2006, 2009; Beebe *et al.*, 2008).

Genotypes that combine these three plant attributes with greater values of shoot vigour, should outperform the other genotypes under drought stress conditions. In rainfed conditions, many common bean lines were equal or superior to *P. acutifolius* in canopy biomass; although in the irrigated treatment, G 40159 was second only to INB 35. Most common beans were superior to *P. acutifolius* in LAI in both irrigated and rainfed conditions. Therefore, common bean tends to be superior in variables associated with plant size.

Drought resistant genotypes. Among the 36 genotypes tested, two accessions of *P. acutifolius* (G 40159 and G 40068) and two elite lines (RAB 650 and SEA 23) were outstanding in their adaptation to rainfed conditions. Among the common bean lines in the rainfed trial, RAB 650, SEA 23, SEA 15, SEA 18 and SEA 16, were the highest yielding, in that order. Six genotyoes (G 40159, SEA 15, SEA 23, RAB 650, RAB 651 and G 40068) showed greater values of geometric mean of grain yield than other genotypes. Among those, RAB 650, SEA 23 and SEA 15 were not only adapted to drought stress but were also responsive to irrigation. The responsiveness to irrigation is important because these genotypes could also perform better under optimal growing conditions (i.e., less yield penalty). Several of the best performing common bean lines also presented high expression of traits associated with photosynthate mobilisation. RAB 650, SEA 23 as well as Pinto Villa presented HI values similar to that of *P. acutifolius*. Compared to tepary bean,

TABLE 3. Correlation matrix of leaf area index (LAI), canopy biomass (CB), stem biomass reduction (SBR), pod partitioning index (PPI), pod harvest index (PHI), harvest index (HI) and grain yield (YLD) of 36 genotypes of common bean and tepary bean grown under irrigated (IR) or rainfed (RF) conditions on a Mollisol in Palmira over two seasons

		LAI (m² m⁻²)		CB (kg ha⁻¹)		SBR (%)		PPI (%)		PHI (%)		HI (%)		YLD (kg ha⁻¹)	
		IR	RF	IR	RF	IR	RF	IR	RF	IR	RF	IR	RF	IR	RF
LAI	IR	1													
	RF	0.14*	1												
CB	IR	0.81***	-0.08	1											
	RF	0.03	0.54***	-0.03	1										
SBR	IR	-0.07	0.18**	-0.04	0.14*	1									
	RF	0.13*	0.29***	0.13	0.53***	0.04	1								
PPI	IR	-0.35***	-0.07	-0.29***	-0.004	-0.16*	-0.08	1							
	RF	0.10	-0.51***	0.18**	-0.41***	-0.18**	-0.14*	0.08	1						
PHI	IR	0.14*	-0.10	0.30***	0.02	0.004	0.12	0.05	0.14*	1					
	RF	-0.06	-0.09	0.07	0.14*	0.03	0.24**	0.08	0.14*	0.42***	1				
HI	IR	-0.31***	-0.10	-0.23***	0.0006	-0.17*	-0.05	0.98***	0.11	0.24***	0.16*	1			
	RF	0.08	-0.51***		0.18***	-0.37***	-0.17*	-0.11	0.09	0.99***	0.19**	0.27***	1		
YLD	IR	0.43***	-0.22***	0.65***	-0.05	-0.17*	0.12	0.39***	0.27***	0.50***	0.26***	0.47***	0.13	1	
	RF	0.09	-0.16*	0.29***	0.15*	-0.10	0.20**	0.11	0.68***	0.31***	0.41***	0.18*	0.71***	0.43***	1

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively

TABLE 4. Correlation matrix of grain yield (YLD), seed number per area (SNA), pod number per area (PNA), seed production efficiency (SPE) and pod production efficiency (PPE) of 36 genotypes of common bean and tepary bean grown under irrigated (IR) or rainfed (RF) conditions in a Mollisol in Palmira over two seasons

		YLD (kg ha⁻¹)		SNA (no. m⁻²)		PNA (no. m⁻²)		SPE (no. g⁻¹)		PPE (no. g⁻¹)	
		IR	RF	IR	RF	IR	RF	IR	RF	IR	RF
YLD	IR	1									
	RF	0.43***	1								
SNA	IR	0.83***	0.43***	1							
	RF	0.32***	0.85***	0.56***	1						
PNA	IR	0.79***	0.46***	0.90***	0.54***	1					
	RF	-0.14*	0.24***	-0.01	0.29***	-0.03	1				
SPE (no. g⁻¹)	IR	0.31***	0.37***	0.48***	0.53***	0.34***	0.53***	1			
	RF	0.22***	0.29***	0.37***	0.42***	0.33***	-0.45***	0.48***	1		
PPE (no. g⁻¹)	IR	0.23***	0.41***	0.36***	0.52***	0.40***	-0.01	0.89***	0.45***	1	
	RF	0.17*	0.13	0.27***	0.26***	0.31***	-0.45***	0.39***	0.87***	0.43***	1

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively

RAB 650, SEA 23, Pinto Villa and SEA 21 were only slightly lower in PPI, while RAB 650, SEA 15, SEA 21 and SEA 22 were comparable in PHI.

Under irrigated conditions, BAT 477 showed the highest value of PPI (Fig. 4c). ICA Quimbaya, a large seeded Andean cultivar showed the lowest values of PHI under both irrigated and rainfed conditions. Some genotypes of common bean, notably RAB 650 and SEA 15, mobilised nearly 50% of stem biomass, considerably more than tepary bean, although this trait was one of the most variable among common bean lines.

Commercial cultivars, ICA Pijao, DOR 390 and Tio Canela, all of race Mesoamerica (Singh *et al.*, 1991), tended to present average to low values of traits associated with photosynthate mobilisation, and/or to express even lower values in the rainfed treatment. Common bean lines with higher values of photosynthate mobilisation traits had been included in this study based on previous selection for drought resistance. This indicates that previous selection had resulted in improved mobilisation of photosynthates, and had led to enhancement of traits similar to those that confer drought resistance to *P. acutifolius*.

Tepary versus common bean. Under rainfed conditions, the two accessions of *P. acutifolius* (G 40159 and G 40068) yielded more than any elite line or accession of *P. vulgaris*. This demonstrated the advantage that this species continues to display over *P. vulgaris* under terminal drought stress, thus justifying our on-going breeding efforts in interspecific crosses. Data obtained in these trials revealed traits that are associated with its high yield.

The advantage of *P. acutifolius* was not due to greater biomass accumulation since YLD was not related to LAI under rainfed conditions (Table 3). Several genotypes (e.g., ICA Pijao, SEA 17) had greater LAI (Table 2), and comparable or greater biomass (Fig. 3) than two accessions of tepary bean under rainfed conditions. The superior performance of these two accessions could be due to better transport system for mobilising photosynthates to developing grains as revealed by the highest values of HI under rainfed conditions (Fig. 3). Similarly, the two accessions of *P. acutifolius* maintained greater values of PPI under rainfed conditions (Fig. 4d).

PHI was markedly higher with the two tepary beans. Tepary bean also mobilised substantial amounts of photosynthates from stems for grain filling (SBR), although proportionally less than several common bean entries.

The relationships of YLD with SNA, PNA and SW under irrigated and rainfed conditions indicated that the two very small seeded tepary beans had the highest number of seeds and pods per area under rainfed conditions, far greater than any common bean line. The two tepary bean genotypes yielded more not because of their small seed size but because of other traits related to photosynthate mobilisation. Smaller seed size could have an advantage in grain filling and greater number of seeds or pods could have an advantage for compensation if seed or pod abortion occurs during drought stress. Thus, smaller seed size could also contribute toward greater phenotypic plasticity. Perhaps because of small seed size, the two accessions of tepary bean showed higher values of SPE under both moisture regimes.

The large number of pods in tepary bean could be interpreted as part of a compensation mechanism, whereby more pods compensate for small seed size. However, in the ontogeny of yield components, one would expect that pod number is determined before seed size. Can these two yield components be uncoupled?

Legumes typically abort a high percentage of flowers that fail to form pods (Hall, 2004), and apparently have the potential to form far more sink capacity than what they do. If pod number were increased in common bean as it is in tepary bean, it remains to be seen if further improvement capacity as documented in these trials could serve to fill additional pods and seeds for greater yield.

Multiple adaptive traits. Multiple traits play a role in improved drought resistance (Beebe *et al.*, 2013). *P. acutifolius* appears to combine high levels of the traits evaluated in these trials. The superiority of tepary bean in drought resistance could be exploited in two ways for the improvement of common bean. On the other hand, tepary could be a model for common bean, employing common bean sources that are superior for specific traits that contribute to drought resistance in tepary, and combining these traits through intraspecific common bean crosses. Some potential sources of traits within common bean have been highlighted in this study, and other sources could be identified through analysis of other advanced lines (Beebe *et al.*, 2008). Additionally, tepary could be a source of genes for the improvement of common bean through the congruity backcross system (Mejía-Jimenez *et al.*, 1994). Tepary has been employed to improve resistance to some disease and insect limitations of common bean including common bacterial blight (caused by *Xanthomonas axonopodis*), *Empoasca kraemerii*, and *Acanthocelides obtectus* (Singh, 1992). However, the INB lines used in this study were not promising for their drought reaction, perhaps because the common bean parent used in their creation (ICA Pijao) was especially poor in photosynthate remobilisation capacity, and diluted the contribution of tepary. Also, these INB lines had no previous selection for drought. However, recent experience with interspecific crosses for drought resistance is encouraging (S. Beebe, CIAT, personal communication). Although introgression to common bean of a quantitative trait such as drought resistance will be especially challenging due to poor chromosome pairing, a large number of interspecific families and lines exist with significant introgression from tepary, and could be tapped for multiple traits (Muñoz *et al.*, 2004).

CONCLUSION

Tepary bean is superior to common bean in combining several desirable traits that contribute to a greater level of adaptation to terminal drought stress. Breeding efforts in the tropics for increase in drought resistance in common bean should aim to combine high CB production with greater photosynthate mobilisation to grain within the acceptable maturity. Our data indicate that CB, PPI, SBR and PHI are four important traits for improving the efficiency of breeding programmes to select superior genotypes of common bean under drought stress. Because of the simplicity in measurement, PHI should be particularly useful as a selection criterion for improving both yield potential and drought resistance, if the breeder combines it with visual evaluations of CB (shoot

vigour) and pod load. Higher values of CB at mid-pod filling under drought stress could be related to greater root vigour and deeper rooting ability that facilitates canopy cooling and moderate crop growth rate. Further research work is needed to test these relationships under different type (intermittent or terminal), intensity (moderate or severe) and duration of drought stress.

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