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## EFFECT OF INTERMITTENT DROUGHT ON PHENOTYPIC TRAITS OF F5 RIL ANDEAN INTRA-GENE CROSS POPULATION (BRB 191 X SEQ 1027) OF COMMON BEAN

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### ABSTRACT

Drought is a major constraint to common bean (*Phaseolus vulgaris* L.) production in East Africa, where irrigation for the crop is very uncommon. The objective of this study was to identify drought tolerant lines and phenotypic traits underlying drought tolerance among 128 F5 recombinant inbred lines (RILs), derived from intra gene pool population, between drought tolerant BRB 191 (source of *bc-3*) and SEQ 1027. The population was evaluated with eight experimental checks that included BAT 477, CAL 96, DAB 441, DAB 494, and Diacol Calima, NABE 4, SCR 9 and SEQ 1003. A total of 20 phenological, morphological and physiological shoot traits were evaluated, under drought and non-stress conditions, in the field for 2 years (2014 and 2015) at Kawanda in Uganda. New sources of drought tolerance, and previously identified sources of drought tolerance in common bean (BAT 477, DAB 441 and DAB 494), were confirmed based on their superior geometric means and low drought susceptibility. Drought stress in the field significantly affected all measured traits, except harvest index and stem dry weight reduction ( $P < 0.001$ ). Drought significantly reduced yield, yield components and pod harvest index ( $P < 0.01$ ). However, chlorophyll content, canopy temperature, stem dry mass reduction, and 100 seed weight remained stable under season by genotype by water regime treatment interactions (S x G x T). The stability of these traits highlighted their usefulness in selecting for drought tolerance across different environments. Furthermore, pod partitioning index (PPI), harvest index (HI), chlorophyll content and stem dry weight reduction also remained stable under G x T effects. Significant correlations ( $P < 0.001$ ) were maintained between HI and PPI with seed yield under drought stress in field conditions, indicating that photosynthate remobilisation increases yield under drought stress conditions.

**Key Words:** *Phaseolus vulgaris*, photosynthate remobilisation

### RÉSUMÉ

La sécheresse est une contrainte majeure à la production du haricot commun (*Phaseolus vulgaris* L.) en Afrique de l'Est, où l'irrigation pour la culture est très rare. L'objectif de cette étude a été d'identifier les lignées tolérantes à la sécheresse et les traits phénotypiques contrôlant la tolérance à la sécheresse parmi les 128 F5 de lignées consanguines recombinantes, dérivées d'une population intra-gène de la région andine, entre la lignée tolérante à

la sécheresse BRB191 (source du *bc-3*) et SEQ 1027. La population a été évaluée avec huit contrôles expérimentaux comprenant BAT 477, CAL 96, DAB 441, DAB 494, et Diacol calima, NABE 4, SCR 9 et SEQ 1003. Un total de 20 traits phénologiques, morphologiques et physiologiques a été évalué, sous les conditions de stress hydrique, dans le champ pour 2 ans (2014 et 2015) à Kwanda en Uganda. De nouvelles sources de tolérance, et des sources de tolérance précédemment identifiées dans le haricot commun (BAT 477, DAB 441 et DAB 494), ont été confirmées sur la base des moyens de supériorité géométriques et de susceptibilité de faible sécheresse. Le stress hydrique dans le champ a significativement affecté tous les traits mesurés, à l'exception de l'indice de récolte et la réduction du poids sec de la tige ( $P < 0,001$ ). La sécheresse a significativement réduit le rendement, les composantes du rendement et l'indice de la récolte de la gousse ( $P < 0,01$ ). Toutefois, la température de la canopée, la réduction du poids sec de la tige, et le poids de 100 graines sont restés stables sous le traitement de l'interaction entre la saison x génotype x régime d'eau de même que l'interaction entre le génotype x le traitement (G X T) ( $P < 0,001$ ). La stabilité de ces traits a montré leur utilité dans la sélection pour la tolérance à la sécheresse à travers les différents environnements. De plus, l'indice du partitionnement de la gousse (PPI), l'indice de récolte (HI), la teneur en chlorophylle et la réduction du poids sec de la tige sont restés également stables sous les effets de G x T. Des corrélations significatives ( $P < 0,001$ ) ont été maintenues entre HI et PPI avec le rendement en graine sous le stress hydrique dans les conditions de champ, indiquant la viabilité de la remobilisation de la photosynthate dans l'augmentation du rendement potentiel sous les conditions de stress hydrique.

*Mots Clés:* *Phaseolus vulgaris*, remobilisation de la photosynthate

## INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is the most important food legume crop for direct consumption in the world (Harvest Plus, 2009). The crop is recognised as the second most important source of dietary protein (Blair *et al.*, 2010), and is particularly suitable for food security due to its short growing cycle (2.5 to 3 months) and adaptability to different cropping systems (Wagara and Kimani, 2007).

Drought is an endemic abiotic constraint in the major producing areas, affecting over 60% of dry bean production worldwide (Beebe *et al.*, 2013; Lasley, 2013). Bean production in Africa is greatly exposed to the risk of drought, with only 7% of the bean-growing area receiving adequate rainfall (Sofi *et al.*, 2017). In Uganda, drought has been reported to cause serious dry bean yield losses in nearly all agro-ecological zones (NEMA, 2001; Okonya *et al.*, 2013). Drought stress limits expression of the full genetic potential of crops (Taiz and Zeiger, 2006), causing large effects at all growth stages, especially at grain filling (Rao, 2001).

Several adaptation and mitigation strategies are required to cope with drought stress in crops, however development of drought-adapted cultivars is the most effective control

measure for mitigating the effects of drought on common bean yields (Darkwa *et al.*, 2016). Improving tolerance to drought in common bean has been a challenge for a number of reasons; one being the multi-faceted nature of this production constraint as it may be expressed in four different scenarios, namely: (i) low total rainfall throughout the season, (ii) intermittent drought, (iii) terminal drought and (iv) late initiation of rains (Katungi *et al.*, 2011; Beebe *et al.*, 2013). Furthermore, drought hardly occurs in the absence of other stress factors such as pests, diseases and heat stress (Sadras, 2002; Sinclair *et al.*, 2008); which have further made the study of drought tolerance, complex. Identification of key plant traits and mechanisms that contribute to improved drought adaptation may increase the proficiency of breeding programmes in selecting drought tolerant genotypes. However, the process is both labour intensive and time consuming (Beebe *et al.*, 2013; Trapp *et al.*, 2015).

Several studies over the past two decades have identified traits underlying drought tolerance in the common bean. Progress in improving drought tolerance has been more advanced in the Mesoamerican gene pool (majorly small seeded) and intergene populations compared to the Andean gene pool,

probably because the former are most widely grown around the world and are found in areas where drought stress has been on the increase (Blair *et al.*, 2012). However, the genetics and mechanisms of these traits are still not fully understood (Beebe *et al.*, 2013). This study focused on an Andean derived cross to explore additional diversity for drought resistance alleles, and to analyse the effect of genetic backgrounds on the alleles that have already been identified. The specific objective of the study was to identify key traits underlying drought tolerance in the Andean cross of (BRB 191 x SEQ 1027) RIL population.

## MATERIALS AND METHODS

**Plant materials.** A F5 recombinant inbred line (RIL) population of 128 lines was evaluated with eight experimental checks at Kawanda during 2014 and 2015. The population was developed from BRB 191 (a source of the *bc<sub>3</sub>* gene) (Blair *et al.*, 2006) and SEQ 1027 (CIAT, 2008), a large red mottled cultivar with drought tolerance properties developed by CIAT (CIAT, 2008). Both parents are Andean cultivars with bush type growth habits. The BRB/SEQ F<sub>2</sub> population was developed at CIAT in Cali, Colombia, and was advanced to F5 generation

at Kawanda in Uganda. The F5 population was evaluated with eight checks that included BAT 477, CAL 96, DAB 441, DAB 494, Diacol Calima, NABE 4, SCR 9 and SEQ 1003 (Table 1).

SEQ lines are already widely used in many breeding programmes in Ethiopia, Kenya and Zimbabwe (Beebe, 2012; Simbarashe, 2013). DAB 441 and DAB 494 are part of the advanced drought Andean bean (DAB) nursery developed by CIAT. The DAB nursery has already been phenotyped under different drought conditions in several studies and breeding programmes in Africa (CIAT, 2008). NABE 4 is a red mottled large seeded commercial cultivar in Uganda, resistant to Halo blight, but susceptible to drought (Amongi *et al.*, 2014). SCR 9 is a red seeded cultivar that is tolerant to BCMV and drought (Amongi *et al.*, 2014).

**Field evaluation.** The field study was carried out in 2014 and 2015, in the off season (planting before the beginning of the rainy season) to target intermittent drought. In 2014, the experiment was carried out from July to October, while in 2015 the experiment was conducted between February and May. This is the short rain season in Uganda. Kawanda, the study site, is located in Uganda at an

TABLE 1. Principal characteristics and merits of bean parental genotypes and checks evaluated at Kawanda in Uganda

Genotype	Origin	Growth habit	Seed size	Merits
BAT 477	Mesoamerican	III	Small	Drought tolerant and Resistant to low soil phosphorous
CAL 96	Andean	I	Large	Drought susceptible and Tolerant to angular leaf spot
DAB 441	Andean	I	Medium	Drought tolerant
DAB 494	Andean	I	Medium	Drought tolerant
Diacol Calima	Andean	I	Large	Drought susceptible
NABE 4	Andean	I	Large	Resistant to Halo blight
SCR 9	Andean	I	Large	Drought tolerant
SEQ 1003	Andean	I	Large	Drought tolerant
BRB 191	Andean	I	Large	Has <i>bc3</i> gene for BCMV
SEQ 1027	Andean	I	Large	Drought tolerant

I = Determinate habit (Bush); III = Indeterminate bush with weak stem and branches, BCMV = Bean Common Mosaic Virus

elevation of 1193 masl on latitude 0° 24' 49" N and longitude 32° 31' 60" E.

During each experiment, the germplasm was evaluated under field conditions in two water regimes treatment i.e., non-stress (NS) where the plants were irrigated when there was no rain, and drought stress (DS) where there was no irrigation. However, two irrigations of 35 mm of water using a vehicle water tank were applied in both DS and NS plots, 1 day before planting, and 10 days after planting (DAP) to allow plant germination and initial vegetative growth. The drought intensity was exceptionally high in 2014 that, to avoid complete senescence of the plants, DS treatment received three additional irrigations at 30, 50 and 65 DAP that year. During the first season, the two treatments were in separate fields due to limited land size. However, in 2015, both treatments were run in the same field, separated by a 6 m buffer zone in order to prevent lateral movement of water between the two regimes.

Plots consisted of two rows of 2.5 m long, of which one row was used for destructive sampling. The spacing between rows was 80 cm; while between plants in each row was 7.5 cm. Genotypes were replicated three times in each treatment, for each season, in an alpha lattice design comprising of 10 blocks with 14 genotypes per block.

A mixture of fungicides (Ridomil, Dithane M 45 and Amathane) was applied at intervals of 14 days in all plots to reduce disease incidence. Fertiliser (NPK, 17:17:17) was applied at the reproductive and flowering stage to address poor soil fertility. Hand weeding was carried out once a month throughout the experiment.

**Response variables.** Environmental data, including daily rainfall (mm), relative humidity (%) and temperatures (°C) were obtained from a satellite system by the Uganda National Meteorological Authority (UNMA). To evaluate effects of drought stress on crop growth and yield, 20 traits consisting of phenological, morphological and physiological shoot

characteristics were recorded. Phenological traits included days to flowering (DF) and days to physiological maturity (DPM). DF was measured individually for each plot when 50% of the plants were in a fully flowered state; while DPM was measured individually for each plot when 50% of the plants had developed fully-matured and dry pods.

Morphological traits measured in this study included growth vigour (GV), growth habit (GH), flower colour (FLCOL), and pods per plant (PDPL) (Corrales and van Schoonhoven, 1987). GV was visually scored at reproductive phase 5, when plants had reached maximum development (Corrales and van Schoonhoven, 1987). The scale use was as follows 1: excellent, 2: good, 3: intermediate, 4: poor and 5: very poor. GH was measured during the reproductive stage 6 based on visual classification of Corrales and van Schoonhoven, (1987). The evaluation scale was as follows: I: determinate bush; strong and erect stem and branches, II: indeterminate bush habit (erect stems and branches); with guides and ability to climb, III: indeterminate bush habit with weak mainstream and prostrate stem and branches, IV: indeterminate climber habit with weak, long and twisted stem and branches and V: determinate climber. For FLCOL, the prominent colour of freshly opened flowers was recorded at reproductive phase 6, using the CIAT scale of five categories namely: 1: white 2: pink 3: red 4: lavender 5: purple (Hannan, 1983).

For PDPL, the total number of pods was counted at harvest on five randomly selected plants in each plot. Then the average was computed to determine the PDPL for each genotype.

The study also measured a number of physiological traits that were collected and measured destructively or non-destructively. Non-destructive measurements included SPAD Chlorophyll Meter Readings (SCMR) or chlorophyll content and canopy temperature (CT). SPAD (Soil Plant Analysis Development) values were measured once at mid-pod filling (45 DAP), using a non-destructive, hand-held

chlorophyll meter (SPAD-502 Chlorophyll meter) on a fully expanded young leaf of a randomly chosen plant.

Canopy temperature was also taken at mid-pod filling on a fully expanded leaf (the same leaf where SCMR was measured) using an infrared thermometer (Telatemp model AG-42D, Telatemp, Fullerton, CA, USA). The infrared thermometer was held at 50 cm from the canopy surface in a 45° angle to record CT.

Destructive sampling was done at mid-pod filling and harvest to collect data on canopy dry mass components, namely leaf dry weight, stem dry weight and pod dry weight (Polania *et al.*, 2017). At both mid-pod filling and harvest, a row length of 0.5 m for the first plot was selected; the number of plants counted and the stems cut at the soil surface. Plants were then separated into leaves (without petioles), stems and reproductive structures (pods and flowers). Separated components were then placed in well labelled paper bags and oven-dried at 60 °C for 48 hours. Samples were then weighed and the dry weights of leaf, pod and stem dry weight recorded for each genotype.

Canopy dry mass was further used to calculate the following indices: Drought intensity index (DII) (Fischer and Maurer, 1978) was used to determine the intensity of drought stress in given environments and was calculated as:

$$1 - (X_s/X_i);$$

Where:

$X_s$  is the grand mean yield of all genotypes grown under drought stress,  $X_i$  is the grand mean yield of all genotypes grown under optimum conditions.

Drought susceptibility index (DSI) (Fisher and Maurer, 1978) was used to determine changes in grain yield of a specific genotype under two environments and was calculated as:

$$1 - Y_{ds}/Y_{ns}/DII$$

Where:

$Y_{ds}$  and  $Y_{ns}$  are mean yields of a given genotype in drought stress (ds) and no stress (ns) treatments respectively. Geometric mean (GM) was calculated as:

$$\sqrt{(Y_s \times Y_i)}$$

Where:

$Y_s$  is yield under the stressed treatment and  $Y_i$  is yield under the non-stress treatment.

Harvest index (HI) for each genotype was determined as the ratio of seed dry weight at harvest to total shoot dry weight at mid-pod filling. Pod Harvest Index (PHI) was calculated as the percentage of pod dry weight that was due to seed (ratio of seed dry weight at harvest to total pod dry weight at harvest).

Pod wall dry weight proportion (PWBP) for each genotype was calculated as the percentage of pod dry weight due to pod wall (ratio of pod wall dry weight at harvest to total pod dry weight at harvest). Also, pod partitioning index (PPI) for each genotype determined the percentage of total shoot dry weight that is transformed into pods and was calculated as the ratio of pod dry weight at harvest to total shoot dry weight at mid-pod filling.

Stem dry weight reduction (SBR) indicated the percentage of stem dry weight at mid-pod filling that was transformed into pods and was calculated as the ratio of the difference in stem dry weight at mid-pod filling and harvest to stem dry weight at mid-pod filling. Seed yield and 100 seed weight (100SW) for each genotype were also determined at harvest, after the seed was allowed to dry under ambient conditions to moisture content of 14%.

**Data analysis.** Statistical data analysis was done using GenStat, Discovery Edition Version 4 (Lawes Agricultural Trust, Rothamsted, UK).

A Restricted maximum likelihood (ReML) mixed model approach was used in GenStat computer package (Release 14.1, PC/Windows 7; VSN International Ltd., 2011) analysis of variance. Water regime treatment and genotype were considered as fixed effects; while replication and block were considered as random effects.

Pearson correlation analysis was done to determine the strength of linear relationship between various plant materials. Similarly, a multiple linear regression analysis was performed; with grain yield as dependent and all other measured traits as independent variables to assess the contribution of these to the RILs response to drought stress. Both correlation and regression analyses were done for each season and for the two water regime treatments using GenStat statistical package.

## RESULTS

**Field environmental conditions.** The two field trials experienced different levels of intra-seasonal droughts during various stages of development (Fig. 1).

The rainfall patterns at Kawanda in both growing seasons were irregular, subjecting the experiment to intermittent drought, rather than a more typical terminal drought. Accordingly, the drought stress was more severe in 2014 than in 2015 as revealed by the total cumulative rainfall per season and the drought intensity index (DII). Total cumulative rainfall received in the field experiments was 178 mm in 2014 and 325 mm in 2015. In contrast, DII was 0.775 and 0.415 in 2014 and 2015 respectively. Furthermore, high temperatures might also have augmented the effects of drought in 2014 and 2015. Average temperatures were higher than the optimum range for bean growth (15.6° - 21.1°C) in both seasons (22.2°C in 2014 and 24.5°C in 2015). Although the cumulative rainfall in 2015 was well within the optimum levels, most of the rainfall (65% in 2015 and 46% in 2015) was received after yield formation stages and therefore had minimal impact (Fig. 2).

**Response of drought related traits to drought stress in 2014 and 2015.** Interactions of season by genotype by water

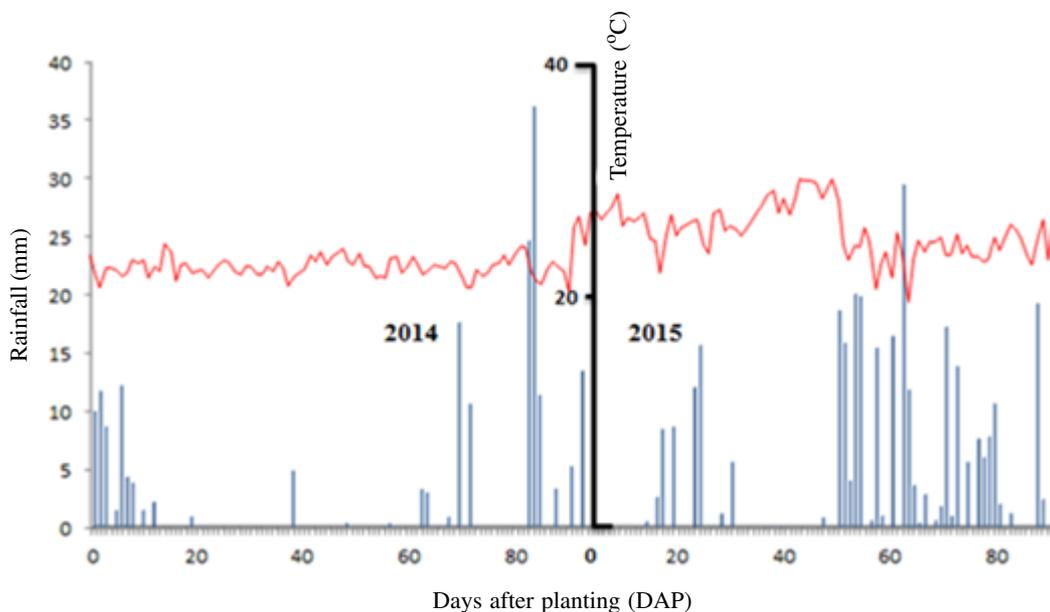


Figure 1. Rainfall (mm) and average temperature (°C) in the off-seasons of 2014 and 2015.

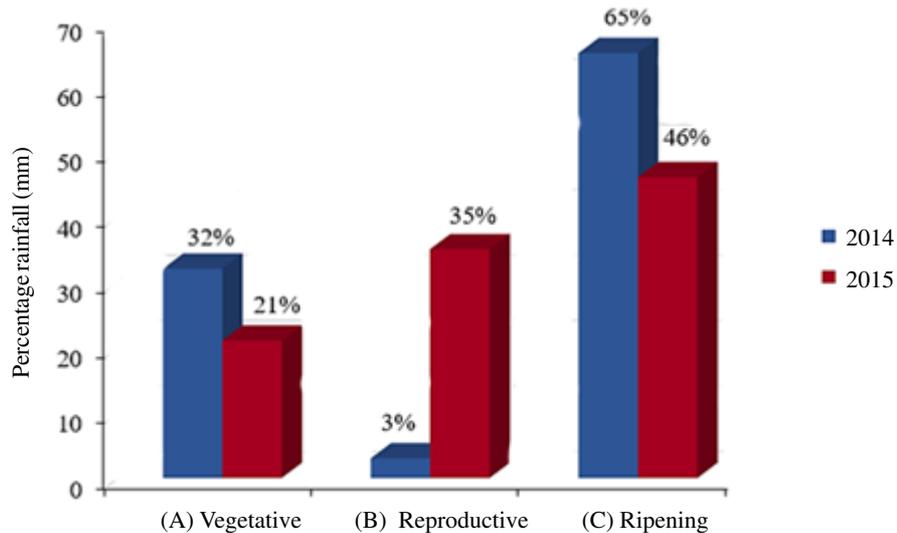


Figure 2. Distributions of percent rainfall (mm) during the growth phases, A: establishment and vegetative (0-30 DAPs), B: reproductive and yield formation (30-60 DAPs) and the ripening phase (60-90 DAPs) in 2014 and 2015 at Kawanda, Uganda.

regime treatment (S x G x T) significantly affected ( $P < 0.05$ ) all the traits, except chlorophyll content, canopy temperature, 100 seed weight and stem dry weight reduction (Table 2).

GxT interactions were insignificant for all traits, except for yield, pod harvest index (PHI) and pod wall dry weight proportion (PWBP) ( $P < 0.001$ ). Genotype by water regime treatment (G x T) interactions significantly ( $P < 0.05$ ) affected eight traits in 2014 and 13 traits in 2015 (Table 3). A number of traits were significantly affected by G x T interactions in 2015 and not in 2014; and *vice versa*. Partitioning indices were all significantly affected by G x T interactions in 2015. Nevertheless, pod harvest index, pod wall dry weight proportion and stem dry weight reduction were not significantly affected by G x T interactions in 2014.

Seven traits were significantly affected by genotype by irrigation effects in both 2014 and 2015 ( $P < 0.05$ ) (Table 3); these included seed yield, harvest index, pod partitioning index, leaf dry weight at MPF, stem dry weight at MPF and pod dry weight at MPF.

The effects of water regime treatment significantly ( $P < 0.05$ ) affected all traits evaluated in the field, except for harvest index, stem dry weight reduction and pod partitioning index (remained stable in 2014) (Table 2). Drought stress significantly reduced yield, 100 seed weight and number of pods per plant in both 2014 and 2015 ( $P < 0.01$ ) (Table 3). Mean yield reductions in the BRB/SEQ were 77.1 and 41.5% in 2014 and 2015, respectively. The reductions in 100 seed weight due to drought stress were 21.6 and 2.5% in 2014 and 2015, respectively; while number of pods per plant was reduced by 55.6% in 2014. Harvest index (HI) and pod partitioning index (PPI) were not significantly affected by drought stress, except PPI which remained stable in 2014. Average values for PPI were 92 and 92.2% in 2014, while it was increased by 14.2% under drought stress conditions of 2015.

Although all partitioning traits differentiated significantly amongst genotypes ( $P < 0.001$ ), harvest index was insignificantly different under genotypic effects in 2015 (Table 3).

Analysis of variance showed significant difference between seasons for all the traits,

TABLE 2. Combined means of squares and levels of significance for 17 traits evaluated at Kawanda in Uganda for two years (2014 and 2015)

SOV	Df	Yield	HI	PPI	YPE	SBH	PBH	LB	SBMP
Season (S)	1	478703.96*	54407.9**	42581.13 <sup>ns</sup>	5.4*	1820.8**	64704.7**	104.8 <sup>ns</sup>	6536.3***
S/Rep	4	267324***	2518 <sup>ns</sup>	5128 <sup>ns</sup>	0.25 <sup>ns</sup>	548.4***	14403.8***	214.4**	184.6**
Genotype (G)	139	13013264***	757719***	1338206.3**	75.8***	31590.7***	342323***	27810.1***	44880***
Treatment (T)	1	31391118***	110.9 <sup>ns</sup>	37528*	0.01 <sup>ns</sup>	34963.2**	1095808***	2308***	30522.5***
G x T	139	4966612.4***	614159 <sup>ns</sup>	1125098.6	61.4 <sup>ns</sup>	10720.4	217747*	10501.6 <sup>ns</sup>	13294.2 <sup>ns</sup>
S x G	139	7660204.8***	581632 <sup>ns</sup>	1035152.7 <sup>ns</sup>	58.2 <sup>ns</sup>	12741.5*	238353**	13342.8***	17898.7***
S x T	1	1155338.1***	25319**	39077.6*	2.5**	3.7	5266*	31422.5***	8123.1***
S x G x T	139	4262442.2*	718909**	1325674.6**	71.9**	13353*	241202**	11041.7**	17288.4***
Error	1062	11413	1823	3327	0.18	36.2	626.5	31.1	40.3
LEE	1080	23535.1	3696	6737.5	0.37	73.3	1272	63.5	81.2
SOV	Df	PWH	PHI	100SW	PWBP	SBR	PBMP	SCMR	CT
Season (S)	1	4830**	4236.28***	23032.2***	4236.82***	1135 <sup>ns</sup>	3803112***	207.4 <sup>ns</sup>	4095.3*
S/Rep	4	969.6***	124.14**	114.1 <sup>ns</sup>	124.11**	5165 <sup>ns</sup>	1525.3 <sup>ns</sup>	68.4**	449.7**
Genotype (G)	139	35070.6***	73.72***	297.8***	73.72***	4891**	164706**	13664***	38179.7 <sup>ns</sup>
Treatment (T)	1	34841***	12929***	12554.4***	12930.1***	13592 <sup>ns</sup>	1105544***	33071.1***	18334.5***
G x T	139	17377.8	51***	131.2 <sup>ns</sup>	50.98***	4347 <sup>ns</sup>	142607 <sup>ns</sup>	5534.7 <sup>ns</sup>	42682.5 <sup>ns</sup>
S x G	139	28601.1***	50.4***	140.6 <sup>ns</sup>	50.36***	4224 <sup>ns</sup>	142529.5 <sup>ns</sup>	6823.8**	37833.3 <sup>ns</sup>
S x T	1	399.2 <sup>ns</sup>	218.84**	7762.8***	218.72**	178751***	242336***	40955.3***	49770.1***
S x G x T	139	25945.8**	52.65***	133.1	52.65***	4146	167362.6**	5734.5 <sup>ns</sup>	41273.7
Error	1062	66.3	32.67	120.8	32.67	3713	420.4	17.1	72
LEE	1080	133.5	-	-	-	-	862.6	34.3	291.1

\*P<0.05; \*\*P<0.01, \*\*\* P<0.001, ns = non-significant, SOV = Source of variation; Rep = Replication, S = Season; G = Genotype; T = Water regime treatment; LEE = Lattice effective error

TABLE 3. Effect of drought stress on traits evaluated under field conditions at Kawanda in Uganda in 2014/ 2015

Trait	2014				2015			
	NS mean	DS mean	Treatment effects	G x T effects	NS mean	DS mean	Treatment effects	G x T effects
Yield	294	67.1	***	***	371.3	217.3	***	*
100 Seed weight	45.1	35.3	***	Ns	48.2	47.01	**	Ns
Pods per plant	18	8	***	Ns	—	—	—	—
Harvest index	69.2	64.2	Ns	*	73.2	79	Ns	*
Pod harvest index	75.3	69	***	Ns	77.7	72.89	***	***
Pod partitioning index	92.2	92	Ns	*	94.2	107.6	***	**
Pod wall dry weight proportion	24.74	31	***	Ns	22.3	27.11	***	***
Stem dry weight reduction	13.3	-13.1	***	Ns	-9	5.9	***	*
Yield production efficiency	0.7	0.6	Ns	*	0.7	0.79	Ns	*
SCMR (Chlorophyll content)	38.6	37.8	*	Ns	32.6	45.86	***	Ns
Canopy temperature	33.6	31.5	**	Ns	24.3	33	***	***
Leaf dry weight at MPF	14.8	7.1	***	**	9.7	14.11	***	Ns
Stem dry weight at MPF	16.6	7.5	***	*	19.5	16.6	***	**
Pod dry weight at MPF	33.1	14	***	*	89.9	37.27	***	*
Total shoot dry weight at MPF	64.5	28.6	***	*	119	67.8	***	*
Stem dry weight at Harvest	13.4	7.1	***	Ns	19.2	12.68	***	*
Pod dry weight at Harvest	55.6	22.6	***	Ns	99.9	61.5	***	***
Pod wall dry weight at Harvest	13.8	6.6	***	Ns	22.2	16.5	***	Ns
Days to flowering	39	34	***	***	—	—	—	—
Days to physiological maturity	80	80.9	***	*	—	—	—	—

\*P<0.05; \*\*P<0.01, \*\*\* P<0.001, ns = non-significant, (G x T) = Genotype by treatment interaction, MPF; mid-pod filling, NS =non stress, DS = drought stress, Irr = effects due to irrigation regime

Phenotypic traits underlying drought tolerance in Ardean common bean

except PPI, LB, SBR and SCMR suggesting that the overall mean performance of the genotypes was different for the two seasons (Table 2). Seasonal effects contributed more than 50% to variation (data not shown).

**Performance of the F5 RIL (BRB/SEQ) population.** Average yield reductions of the BRB/SEQ population were 76.6 and 37.4% in 2014 and 2015, respectively (Table 4). Similarly, the number of pods per plant was reduced by 55.6% in 2014. Geometric means (GM) for seed yield ranged from 0 to 358.6 and 33.9 to 491.5 grammes, with the averages of 132.7 and 277.3 grammes in 2014 and 2015, respectively (Table 4). However, average drought susceptibility indices were significantly different between seasons; 0.7 in 2014 versus 0.5 in 2015.

Seven better performing lines were identified based on their superiority in GM for seed yield, drought susceptibility index (DSI) and percentage reductions (PR) in yield under drought stress; these included RILs 114, 91, 41, 27, 9, 19 and 117 (Table 4). Parental lines (BRB 191 and SEQ 1027) performed better than the population average geometric means in both seasons, with BRB 191 having the highest geometric mean for seed yield in 2014 (Table 4). Furthermore, BRB 191 had an increase in yield under drought stress (25.7%) in 2014 unlike the season of 2015 when yield reduced by 43% (Table 4). Recombinant inbred lines 9, 114 and 117 had lower DSI than population average in both seasons. CAL 96 had the lowest seed yield geometric mean and highest percentage reductions in both seasons (Table 4).

**Parameter correlations.** There was a significant positive correlation between seed yield and 100 seed weight under drought stress treatment in both seasons ( $r=0.35$  and  $0.33$  in 2014 and 2015, respectively;  $P<0.001$ ) (Table 5). In general, highly significant correlations ( $r<0.3$ ,  $P<0.001$ ) were observed between yield

and all partitioning indices (except stem dry weight reduction (SBR) under non-stress conditions in 2014. Inconsistent correlations were observed between seed yield and partitioning indices across the two seasons (2014 and 2015). However, no significant correlations were observed between seed yield and all the partitioning indices under non-stress conditions of 2015 (Table 5).

Specially, harvest index (HI) and pod partitioning index (PPI) had the highest correlations with yield under non-stress conditions in 2014. Furthermore, significant correlations were observed between these traits (HI and PPI) with seed yield under drought stress conditions as well.

Correlations between yield and physiological traits; SCMR and canopy temperature were weak and insignificant. However, there was a highly significant positive correlation between yield and canopy temperature in 2015 ( $r=0.35$ ,  $P<0.001$ ) under drought stress conditions (Table 5).

**Linear regression analysis.** A multiple linear regression analysis was conducted to estimate the effects of selected traits on grain yield for each season and water regime treatment at Kawanda. Regression sums of squares were highly significant ( $P<0.001$ ) for both treatments in both seasons (Table 6). Overall, the regression model explained 33.3 and 62%, and 7.5 and 41.3% under non-stress and drought stress conditions in 2014 and 2015, respectively (Table 6).

Harvest index (HI), 100 seed weight (100SW), leaf dry weight, pod dry weight at harvest and stem dry weight at mid-pod filling contributed significantly ( $P<0.01$ ) to the regression model in three environments (Table 7). Leaf dry weight had the highest average contribution to the model with a percentage contribution of 22.8 and 10.7% in the drought stress trials in 2014 and 2015, respectively (Table 7).

TABLE 4. Geometric means for seed yield, 100 seed weight, pod harvest index and pod partitioning index, percentage yield reductions and drought susceptibility indices of selected cultivars at Kawanda in Uganda in 2014/ 2015

Genotype	2014						2015					
	Yield <sup>GM</sup>	PR (yield)%	DSI	100 SW <sup>GM</sup>	PHI <sup>GM</sup>	PPI <sup>GM</sup>	Yield <sup>GM</sup>	PR (yield)%	DSI	100SW <sup>GM</sup>	PHI <sup>GM</sup>	PPI <sup>GM</sup>
SEQ 1027	222.5	57.9	0.46	40.9	72.4	94.3	440.3	37.3	-0.49	45.9	73.2	95.9
BRB191	358.6	-25.7	-0.61	48.1	75.9	65.6	302.9	56.4	-0.04	59.3	76.3	82.4
BxS 114	252.9	49.5	0.35	45.2	70.1	97.3	372.1	19.1	-0.93	54.1	78.2	154.1
BxS 91	211.6	56	0.44	44.5	72.3	94.5	267.5	-46	-2.48	52.5	72.6	133.8
BxS 41	236	61.1	0.5	41.0	73.8	101.4	332.6	7.3	-1.21	50.4	77.1	81.9
BxS 27	187	49.6	0.35	47.1	76.6	75	183.1	18.9	-0.93	53.3	80.1	99.3
BxS 9	234.4	41.2	0.25	40.1	70.6	90.8	384.6	31.9	-0.62	44.4	76.6	119.4
BxS 19	173.8	60.5	0.49	44.3	68.0	86.0	383.6	50.2	-0.19	47.1	76.7	139.9
BxS 117	235.8	64.2	0.54	43.9	76.8	106.3	357.7	27.3	-0.73	51.5	79.0	101.7
Diacol Calima	140.2	62.1	0.51	40.3	77.4	85.4	197.9	78.7	0.49	47.4	78.5	100.7
DAB494	46	84.4	0.8	34.9	72.6	53.6	153.8	80.6	0.56	41.3	78.7	79.1
SEQ1003	67.1	81.2	0.76	30.9	73	96.7	179.2	21.7	-0.86	45.4	74.4	132.0
SCR9	129.9	88.5	0.85	44.4	75.4	50.7	222.2	-9.6	-1.61	49.7	73.5	41.4
DAB441	88.7	73	0.65	42.9	73.8	73.4	71.8	67.1	0.21	47.3	73.1	78.5
NABE4	141.4	79.5	0.73	40.9	77.7	105.4	113.5	56.5	-0.04	50.4	77.2	100.0
CAL96	0	100	1	28.9	73.6	88.1	33.9	26.7	-0.74	39.4	73.7	93.7
BAT477	227	57.9	0.46	21.4	75.2	71.1	380	61.9	0.09	28.9	70.3	94.5
Average	132.7	76.6	0.7	39.6	72.0	89.5	277.3	37.4	-0.49	47.5	75.2	97.3
Range	0 - 358.6	-26 - 100	-0.61 - 1	21.4 - 50.2	63.4 - 77.7	49.8 - 180.3	33.9 - 492	-119 - 91.4	-4.22 - 0.8	28.9 - 60.7	56.4 - 83.7	35.1 - 173.7

PR (yield) % = Percentage reduction in yield due to drought stress, Yield<sup>GM</sup> = Geometric mean for seed yield, 100 SW<sup>GM</sup> = geometric mean for hundred seed weight, PHI<sup>GM</sup> = geometric mean for pod harvest index, PPI<sup>GM</sup> = geometric mean pod partitioning index, DSI = Drought susceptibility index

Phenotypic traits underlying drought tolerance in Ardean common bean

TABLE 5. Pearson's correlation coefficients between seed yield and other traits evaluated under both non-stress and drought stress treatments at Kawanda in Uganda

Other traits	Seed yield			
	2014		2015	
	NS	DS	NS	DS
<b>Yield components</b>				
100 seed weight	0.09 <sup>ns</sup>	0.35 <sup>***</sup>	0.13 <sup>**</sup>	0.33 <sup>***</sup>
Pods per plant	0.27 <sup>***</sup>	0.10 <sup>ns</sup>	-	-
<b>Partitioning indices</b>				
Harvest index	0.30 <sup>***</sup>	0.12 <sup>***</sup>	0.04 <sup>ns</sup>	0.13 <sup>**</sup>
Pod harvest index	0.20 <sup>***</sup>	0.03 <sup>ns</sup>	0.09 <sup>ns</sup>	0.12 <sup>**</sup>
Pod partitioning index	0.25 <sup>***</sup>	0.11 <sup>*</sup>	0.02 <sup>ns</sup>	0.12 <sup>**</sup>
Pod wall dry weight proportion	-0.20 <sup>***</sup>	-0.03 <sup>ns</sup>	-0.09 <sup>ns</sup>	-0.12 <sup>**</sup>
Stem dry weight reduction	-0.07 <sup>ns</sup>	-0.04 <sup>ns</sup>	0.01 <sup>ns</sup>	0.01 <sup>ns</sup>
<b>Physiological traits</b>				
SCMR (Chlorophyll content)	0.14 <sup>**</sup>	0.03 <sup>ns</sup>	0.01 <sup>ns</sup>	-0.05 <sup>ns</sup>
Canopy temperature	-0.08 <sup>ns</sup>	-0.09 <sup>ns</sup>	0.001 <sup>ns</sup>	0.35 <sup>***</sup>
<b>Canopy Dry mass components</b>				
Leaf dry weight at MPF	0.11 <sup>*</sup>	0.21 <sup>***</sup>	0.08 <sup>ns</sup>	0.27 <sup>***</sup>
Stem dry weight at MPF	0.25 <sup>***</sup>	0.19 <sup>***</sup>	0.20 <sup>***</sup>	0.33 <sup>***</sup>
Pod dry weight at MPF	0.21 <sup>***</sup>	0.25 <sup>***</sup>	0.09 <sup>ns</sup>	0.20 <sup>***</sup>
Total shoot dry weight at MPF	0.23 <sup>***</sup>	0.25 <sup>***</sup>	0.12 <sup>*</sup>	0.29 <sup>***</sup>
Seed dry weight at harvest	0.53 <sup>***</sup>	0.34 <sup>***</sup>	0.18 <sup>***</sup>	0.42 <sup>***</sup>
Stem dry weight at harvest	0.33 <sup>***</sup>	0.22 <sup>***</sup>	0.17 <sup>***</sup>	0.31 <sup>***</sup>
Pod dry weight at harvest	0.51 <sup>***</sup>	0.33 <sup>***</sup>	0.17 <sup>***</sup>	0.41 <sup>***</sup>
Pod wall dry weight at harvest	0.32 <sup>***</sup>	0.30 <sup>***</sup>	0.06 <sup>***</sup>	0.31 <sup>***</sup>

\*P<0.05; \*\*P<0.01, \*\*\* P<0.001, <sup>ns</sup> = non-significant, NS = non stress, DS = drought stress

TABLE 6. Sums of squares of regression models for drought stress and non-stress conditions at Kawanda in Uganda

Water regime	2014		2015	
	s.s	% explained	s.s	% explained
Non-stress	1918923 <sup>***</sup>	33.3	1001402 <sup>***</sup>	7.5
Drought stress	11815629 <sup>***</sup>	62.0	3520985 <sup>***</sup>	41.3

s.s = sums of squares for the regression model, % explained = percentage contribution by the regression model, \*P<0.05; \*\*P<0.01, \*\*\* P<0.001

TABLE 7. Percentage contribution of selected traits to the total variation of the regression model under non-stress and drought stress conditions at Kawanda in Uganda

Trait	Contribution to variation (%)			
	2014		2015	
	NS	DS	NS	DS
Harvest index	8 <sup>***</sup>	2.4 <sup>***</sup>	0.1 <sup>ns</sup>	1.8 <sup>***</sup>
Pod harvest index	2.4 <sup>***</sup>	-	-	-
Pod partitioning index	0.2 <sup>ns</sup>	-	0.9 <sup>ns</sup>	0.8 <sup>*</sup>
100 seed weight	-	9.9 <sup>***</sup>	1.8 <sup>**</sup>	10.9 <sup>***</sup>
Leaf dry weight at MPF	5.3 <sup>***</sup>	22.8 <sup>***</sup>	-	10.7 <sup>***</sup>
Stem dry weight at MPF	0.5 <sup>ns</sup>	0.6 <sup>***</sup>	1.9 <sup>**</sup>	1.5 <sup>***</sup>
Stem dry weight at harvest	0.8 <sup>*</sup>	0.4 <sup>**</sup>	0.4 <sup>ns</sup>	0.2 <sup>ns</sup>
Pod dry weight at MPF	0.1 <sup>ns</sup>	0.7 <sup>***</sup>	-	0.1 <sup>ns</sup>
Pod dry weight at harvest	0.4 <sup>ns</sup>	16 <sup>***</sup>	1.9 <sup>**</sup>	4.8 <sup>***</sup>

\*P<0.05; \*\*P<0.01; \*\*\*P<0.001; ns = not significant, - = not measured, NS = non-stress, DS = drought stress

## DISCUSSION

**Field environmental conditions.** The kind of drought stress expressed in the field was mainly intermittent drought stress. The amount of rainfall received in both growing seasons (2014 and 2015) at Kawanda was below optimum levels for bean production (350-500 mm). As such, the drought intensity induced in the field was sufficient to evaluate the common bean RIL population for tolerance to drought stress. The population was exposed to a wide range of water deficits that are representative of the conditions bean crops are likely to encounter during growing seasons in Uganda (Mulinde, 2013).

**Response of drought related traits to drought stress in 2014 and 2015.** Variations in drought induced in the field caused contradictions in the response of evaluated traits to drought related interactions between seasons (Table 3). However, some of the sensitivity of bean traits to environmental stress is not necessarily imposed by the environment, but rather is an active survival response of the plant to stress (Beebe *et al.*, 2008).

This study also helped to identify some key phenotypic traits associated with drought

tolerance in Andean bean germplasm. Chlorophyll content, canopy temperature, 100 seed weight and stem dry weight reduction were found to be the most stable traits/parameters across the highest level of interactions (season by genotype by irrigation regime interactions) (Table 2). Furthermore, these four traits were significantly differentiated amongst genotypes. Genetic diversity is of paramount importance in crop improvement because it determines the selection intensity and effectiveness, and the genetic gain. Thus every breeding programme aims to have a substantial genetic diversity in the breeding population. The significant differences observed among genotypes' means (Table 2) suggest that there was genetic diversity among the RILS. As a result, selection can be made among these RILS for breeding for tolerance to drought stress in Andean Bean. The genetic differentiation and stability of chlorophyll content, canopy temperature, 100 seed weight and stem dry weight reduction across a wide range of interactions proved these characteristics as stable tools for selection for drought tolerance under drought stress (Talebi, 2011; Asfaw *et al.*, 2012). Findings on 100 seed weight in this study are important because the common bean breeding

programmes have focused on grain size to meet the consumer market, which has preferred larger grains with high seed weight (Carbonell *et al.*, 2010). Therefore, seed weight could be a more efficient and stable tool in selection compared to seed yield (Schneider *et al.*, 1997).

Canopy temperature has been proposed as potential surrogate tools for selecting genotypes with higher WUE in several legumes (Siddique *et al.*, 2001; Condon *et al.*, 2002; Ainsworth and Rogers, 2007; Blum, 2009). According to Guendouz *et al.* (2012), higher CT leads to flaccidity or looseness of stomata which in turn causes lower carbon fixation efficiency. Consequentially, this results into lower dry matter accumulation and low seed yield. In this study, although canopy temperature was stable under G x T, it was non-significantly differentiated among genotypes. This indicated that CT is highly dependent on external environmental factors which could mask genetic variation. Nevertheless, cooler temperatures in the field were associated with increased seed yield as found in other studies (Blum, 2009; Beebe *et al.*, 2013).

Chlorophyll content was significantly differentiated among genotypes (Table 2). The better performing line 114 and drought tolerant experimental checks BAT 477, DAB 441 and DAB 494 contained higher chlorophyll under drought stress conditions in this study. Similar results have been reported by several authors where values of chlorophyll contents in drought tolerant cultivars were significantly higher than those in drought sensitive genotypes under drought stress (Khayatnezhad, 2011; Alaei, 2011). Accordingly, chlorophyll content could be considered as a reliable indicator in screening germplasm for drought tolerance as other studies have reported (Li *et al.*, 2006; Zaefyzadeh *et al.*, 2009). Nonetheless, selection using a combination of traits like canopy temperature, chlorophyll content, and seed weight would produce more stable drought tolerant lines.

Leaf dry weight at mid pod-filling, pod partitioning index, chlorophyll content and stem dry weight reduction remained significantly stable across seasons (Table 2) despite extreme variations in drought intensity across seasons. Additionally, PPI and HI were also stable under G x T interactions. These results suggested that drought tolerance in this population could be due to the ability of genotypes to remobilise photosynthates into yield during drought stress. Photo-assimilate remobilisation is one of the characteristics indirectly selected during the development of drought resistant cultivars (Rosales-Serna *et al.*, 2004; Miklas *et al.*, 2006). The outstanding performance of stem dry weight reduction and pod partitioning index in this study were important because they confirmed increased reservation of photosynthates as measured by SBR; and the successful transformation of these photosynthates into pod as measured by the PPI. However, some studies have reported increased photosynthate remobilisation without direct effect on yield; a phenomenon known as the 'lazy pod syndrome' (Beebe *et al.*, 2009). Nevertheless, the importance of increased pod partitioning index (PPI) and stem dry weight reduction (SBR) in maintaining yield potential under drought was confirmed as other previous studies had postulated (Klaedtke *et al.*, 2012; Rao *et al.*, 2013; Rao, 2014; Assefa, 2015; Polania *et al.*, 2016). Overall, selection using a combination of drought related traits such as photosynthate remobilisation, seed weight, canopy dry weight, and chlorophyll content will positively impact drought breeding programmes especially in the Andean studies.

**Performance of the F5 RIL (BRB/SEQ) population.** The impact of drought on yield was evident on number of pods per plant, 100 seed weight and dry matter accumulation (Table 3). It should, however, be noted that reduction in grain yield was greater in 2014 than in 2015 due to the higher drought intensity expressed in 2014. These findings agree with those from other studies where there was

increased yield under non-stress conditions (Razinger *et al.*, 2010; Darkwa *et al.*, 2016; Polania *et al.*, 2017). As a whole, the BRB 191 x SEQ 1027 RIL population was moderately susceptible to drought stress in 2014 and tolerant in 2015. This was probably because of differences in DSI that resulted from the changes in intensity and duration of drought stress between seasons. Some negative values of DSI were observed (Table 4) indicating higher yield under drought stress compared to non-stress environments; something very uncommon in drought studies of the common bean. Multiple trials in different locations will help ascertain drought susceptibility levels in this population.

According to Porch *et al.* (2009), duration and intensity of drought stress in common bean significantly determines the level of grain yield reduction. Major reductions in yield and its components due to drought in the common bean have been reported in other studies (Rosales-Serna *et al.*, 2004; Lizana *et al.*, 2006; Emam *et al.*, 2010; Mukeshimana *et al.*, 2014). However, the extent of yield reductions between different studies is controlled by both environmental and genetic factors (Rao and Hodgkin, 2002). According to Farooq *et al.* (2009), yield reductions in drought studies are inevitable especially when there is a decrease in fresh and dry weights. As observed earlier with yield, reductions in canopy dry weight components were also more pronounced in 2014. Besides, incidence of disease observed in the field such as Angular leaf spot, Anthracnose, Common bacterial blight and Rust could have masked the real potential of drought stress on both canopy dry weight and yield reduction. Diseases mask the expression of the desired drought tolerance traits making it difficult for breeders to identify superior genotypes under drought stress. Therefore, breeding for multiple constraint resistance including disease-drought interaction studies would produce more stable drought resistant genotypes in common bean (Beebe *et al.*, 2008; Makunde, 2013). New sources of

drought tolerance were identified among the BRB/SEQ population, which included RILs 9, 91 and 114 (Table 4). Previously identified drought tolerant cultivars such as BAT 477, DAB 441, and DAB 494 were also confirmed based on their outstanding performance (Table 4). Most importantly, BRB 191, the female parent used in this study, was affirmed as a viable source of drought tolerance. It was the highest yielding cultivar in 2014 and 2015.

**Parameter correlations.** The most stable traits identified in the study namely; chlorophyll content, canopy temperature, 100 seed weight and stem dry weight reduction, also had significant positive correlations with seed yield in different field environments. This further proved them as useful tools for selection for drought tolerance under drought stress (Talebi, 2011; Asfaw *et al.*, 2012). Positive correlations between seed yield and seed weight in both seasons were deemed as important in this study. Negative linkages of SW and seed yield potential in common bean has been a challenge for bean breeders (Beaver and Osorno, 2009); however, results from our study provide an opportunity for simultaneous selection for these two traits in Andean intragene crosses. Highly significant correlations were observed between seed yield and partitioning.

**Linear regression analysis.** According to the linear regression model, harvest index and 100 seed weight contributed significantly in three environments (Table 7). Selection using harvest index and 100 seed weight in breeding programmes could indirectly increase yield under both drought stress and non-stress environments for the common bean and other legumes. In the past, harvest index (HI) has proved to be an important trait to breeders in identifying genotypes that are adapted to drought stress through better photosynthate mobilisation (Beebe *et al.*, 2008; Beebe *et al.*, 2013; Rao *et al.*, 2013).

## CONCLUSION

This study has demonstrated the potential of using better performing RILs in the BRB/SEQ population as sources of drought tolerance to improve Andean cultivars in Uganda. Also, selection for photosynthate remobilisation characterised by HI and PPI would indirectly increase yield potential in Andean genotypes in breeding programmes. Nevertheless, considering the complexity of seed yield under drought stress, selection using a combination of drought related traits would produce more stable and high yielding genotypes. Thus, findings from this study will permit studies to focus on specific genetic regions that control photosynthate acquisition, accumulation and remobilisation for yield improvement under drought stress.

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