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Full Length Research Paper

Introgression of root protein and yield traits from backcross hybrids between cassava and its wild progenitor (*Manihot esculenta* ssp *flabellifolia*)

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***Manihot esculenta* spp *flabellifolia* is a potential progenitor for cassava root protein content and yield improvement. Storage roots of cassava landraces are low in protein content due to the fact that past breeding objectives concentrated mainly on yield and resistance to diseases. The improvement of cassava through its wild progenitor is of importance for the full utilization of the potential of the wild progenitor. An interspecific F_1 was crossed to a cultivated variety (MTAI - 8) to generate a backcross population. Root protein, yield and other quality traits were evaluated. High root protein content of 9.61%; fresh root yield of 60.00 ton ha^{-1}; dry root yield of 34.75 ton ha^{-1}; and dry matter content of 59.45% was found in this population. High broad-sense heritability was obtained for all the traits evaluated which is a good indicator that genetic improvement can be achieved in this population. This first backcross population had protein values higher than the earlier documented values in the landraces.**

Key word: Cassava, *Manihot esculenta* ssp *flabellifolia*, interspecific, protein and yield.

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) has enormous potential to reduce hunger and malnutrition for millions of people that thrive on it as a food security crop. Wild relatives of cassava have become a source of improving the crop by introgressing useful genes from it (Fregene et al., 2007). One of the drawbacks of cassava root is its low protein content (Fregene et al., 2006).

In general, breeding programmes seek to improve crop productivity and quality, widen the genetic base, and maintain its adaptation to specific agro-ecologies. The potential for genetic improvement of cassava has been demonstrated and progress made in increasing yield potential and stability (Ngoan et al., 1995; Kawano, 1998; Ojulong et al., 2008; Okechukwu and Dixon, 2009). However, world mean yield (12.2 ton ha^{-1}) for cassava is still far below the yield potential (90 ton ha^{-1}) from the experimental field evaluations of the released varieties across growing regions (Fermont et al., 2009; Lebot, 2009; Ziska et al., 2009).

Despite the progress already made by breeders,

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additional gains in productivity are demanded at a faster pace because of demographic pressures, changes in agricultural practices, consumer preferences, biotic and abiotic stresses. Other root quality traits relevant to different cassava breeding programmes world-wide are the cyanogenic potential in the root (Dixon et al., 1994a; Balyejusa-Kizito et al., 2007), early bulking capacity (Okogbenin and Fregene, 2002; Olasanmi, 2010), and high protein content in the roots (Fregene et al., 2006). Unfortunately, the genetic variability for the latter two traits is relatively small in *M. esculenta*, therefore, inter-specific crosses with other *Manihot* species are necessary to introgress useful alleles from them (Ceballos et al., 2004).

In an earlier study reported by Asiedu et al. (1992), the introgression of root protein from its wild progenitor was not successful. Wild relatives of cassava are known sources of resistant genes to virtually all cassava pests and diseases as well as high root protein content (CIAT 2002; Fregene et al., 2006; Ojulong et al., 2008; Carabali et al., 2010).

Cassava cultivars are sometimes deficient in some economically important characters such as resistance to pests and diseases, drought tolerance and have low protein content in the root (Nassar and Dorea, 1982; Nassar and Grattapaglia, 1986; Okogbenin et al., 1998) due to the selection that occurred during domestication. Lost genes can be restored to the gene pool of the cultigen by inter-specific hybridization with wild relatives which possess these genes (Nassar et al., 1986). Wild species of cultivated crops have been frequently used as an important source of genetic diversity and have been employed effectively in a variety of breeding programmes (Tanksley and McCouch, 1997; Hajjar and Hodgkin, 2007; Okogbenin et al., 2007). The objective of this study was to introgress genes from wild progenitors of cassava for increased root protein yield and quality traits into commercial cassava.

MATERIALS AND METHODS

Population development

An inter-specific F_1 hybrid CW 198 - 11 was earlier developed at the International Centre for Tropical Agriculture (CIAT), Cali, Colombia (CIAT, 2002). Genetic crosses of open pollinated seeds from *M. esculenta* ssp *flabellifolia* OW230 - 1 (Morantes et al., 2002) and CW30 - 65, (an inter-specific hybrid between an improved cassava variety SG427 - 87 and an accession of *M. esculenta* ssp *flabellifolia* (MESCFLAX - 80)). The inter-specific cross was 'backcrossed' to MTAI 8 to generate a B_1P_2 family with 225 individuals. The male parent (MTAI 8) is a successful elite Thailand cultivar with high dry matter content, good tuber formation, and cream coloured roots from the breeding programme at the Thailand Agricultural Research Centre.

Geographical location of the experiment and evaluations

Embryo axes of sexual seeds from the B_1P_2 family were cultured *in vitro* and micro-propagated to produce six to eight plantlets per genotype (Akinbo et al., 2010). The plantlets were transferred to the screen house in 2005 for hardening. After 60 days of hardening in the screen house, the seedlings were transplanted to the field at CORPOICA field experiment station, Palmira, Colombia. At 10 months after planting (MAP), one to two roots were 'milked' from each genotype and used to evaluate the genotype for protein content. At 10 MAP, matured stem cuttings from the plants harvested were used to establish a preliminary yield trial, of 225 genotypes in a randomized complete block design, three replicates and eight plants per row, with border plants on the edges. Planting was on ridges at a spacing of 0.7 m (within rows) x 1.4 m (between rows). The plants were not fertilised or sprayed with insecticide, but weeded when necessary. The field trial was conducted at CIAT - Palmira in 2006/2007 season, at Palmira in Valle del Cauca Department (elevation 965 m, 3°49'N, 76°36'W), located in the mid altitude tropics of Colombia, and repeated in CIAT and Quilichao in the 2007/2008 season for second year evaluation. The sites have bimodal rainfall, although there are yearly variations, with peaks usually between March - June and October – December (Table 1). Yield and quality traits were evaluated using the six middle plants to minimize border effects and means were calculated. MTAI 8 was used as the national check over a period of two years.

Data collection

The 6 internal plants in each row were harvested and their storage roots were weighed to determine root yield. Samples of roots from 6 plants of each genotype were collected for dry matter content (DMC) determination. DMC assessment was done by peeling of the fresh roots, chopping them into small pieces, mixing uniformly in a petri dish and oven dried at 60°C for 48 h after which the weight difference between the fresh weight and dry weight was measured and the percentage dry matter was calculated. Percentage dry matter content was determined using the formula:

$$\%DMC = \frac{\text{Weight of the oven dried sample}}{\text{Weight of the fresh sample}} \quad X \quad 100$$

The dry root yield was calculated as follows: %DMC x fresh root yield.

Harvested plants were assessed for number of storage roots per plant. The aerial part (stems and leaves) of the plants were weighed to determine fresh shoot weight. Harvest index was computed as the ratio of root yield to the total harvested biomass per genotype on fresh basis.

For protein analysis, all samples were analysed at the plant tissue analytical laboratory at CIAT. Nitrogen determination was based on a modification of the Kjeldahl method (Skalar, 1995). The digestion of the samples began with hydrogen peroxide and with this step, the larger part of the organic matter was oxidised. After decomposition of the excess of H_2O_2, the digestion was completed by concentrated sulphuric acid at elevated temperature (330°C) with selenium as catalyst (Novozamsky et al., 1983; Walinga et al., 1989). The root samples were digested with a mixture of sulphuric acid, selenium and salicylic acid. The salicylic acid formed a compound with the nitrates present to prevent losses of nitrate-nitrogen. The supernatant was then 'coloured' using the salicylate (molarity), nitroprusside (catalyst) and active chlorine were added to form a green colour complex with the ammonium ion. Nitrogen was quantified based on colorimetric measurement of the supernatant on a segmented flow analyzer. The absorption was measured at 660 nm (Krom 1980; Searle 1984).

Hock-Hin and Van-Den (1996) reported that, in the case of cassava roots, the conversion factor for protein contents based on N concentrations should probably range between 4.75 and 5.87. An

Table 1. Meteorological data at Palmira and Quilichao in 2006/2007 and 2007/2008 seasons.

Climatic factors	Palmira		Quilichao	
	2006-2007	2007-2008	2006-2007	2007-2008
Precipitation (mm)	104.5	82.85	-	171.42
Evaporation (mm)	135.73	135.08	-	117.35
Radiation (MJ m^{-2})	17.68	16.86	-	14.87
Maximum temperature (°C)	30.14	30.23	-	28.90
Minimum temperature (°C)	19.32	18.94	-	18.51
Mean relative humidity (%)	76.79	76.72	-	79.69
Mean wind velocity (m/sec.)	56.58	58.96	-	30.62

Table 2. Range of values for agronomic traits of 225 progenies of a cassava backcross population grown in CIAT 2006/2007, and CIAT and Quilichao 2007/2008 season.

Variables	CIAT 2006-2007				CIAT 2007-2008				Quilichao 2007-2008			
	[a]Min	[b]Max	[c]Aver	[d]SD	Min	Max	Aver	SD	Min	Max	Aver	SD
[e]Rt/plt	1.87	16.50	6.67	2.33	0.50	30.00	4.07	2.03	0.33	25.00	4.33	2.28
[f]ComRt	0.00	9.00	1.63	1.63	0.00	12.00	0.69	0.96	0.00	8.62	1.21	1.48
[g]FRY	18.75	58.75	45.88	9.28	16.66	60.00	37.82	10.38	15.71	58.75	37.83	11.42
[h]DRY	5.18	19.39	11.88	2.78	3.66	21.05	9.53	2.97	4.23	34.75	10.17	3.45
[i]HI	0.30	0.88	0.42	0.08	0.29	0.91	0.41	0.09	0.27	0.80	0.50	0.12
[j]DMC	27.01	47.04	39.03	4.01	25.01	59.45	40.24	5.43	23.57	50.01	37.82	4.50
[k]PC	0.84	9.61	3.02	1.21	1.10	8.13	2.91	1.26	0.69	7.75	2.13	0.86

[a]Minimum; [b]Maximum; [c]Average; [d]Standard Deviation; [e]Roots per plant; [f]Commercial Roots; [g]Fresh root yield (ton ha^{-1}); [h]Dry root yield (ton ha^{-1}); [i]Harvest Index (0-1); [j]Dry matter content (%); [k]Protein content (%).

average of 5.31 was the standard being established and used for the cassava roots procedure at CIAT.

Data analysis

SAS (2002) statistical programmes were used for analysis of variance, correlation and frequency distributions of phenotypic classes. Only genotypes which had complete data from the three replications were used. Since roots per plant, root weight and fresh and dry root yield data were not normally distributed, data sets were transformed by the square root method using the formula: $y = \sqrt{(x+0.5)}$. The percentage of dry matter content and protein content were transformed by the square root method using the formula: $y = \sqrt{(x)}$, where y is the resulting transformation and x is the data point. The SAS correlation (proc corr.) procedures were used to estimate correlation and regression coefficients between different parameters. Analyses of variance (ANOVA) of yield, yield components and quality traits across environment were performed using the general linear model procedure in the SAS software. Genotypes and environments were considered fixed and random effects, respectively (Griffing, 1956). The following model was used for the combined data:

$$Yij = \mu + G_i + E_j + GE_{ij} + e_{ij}$$

Where μ is the general mean, G_i, E_j and GE_{ij} represent the effect of the genotype, environment and G x E interaction respectively; e_{ij} is the average of random errors associated with r^{th} plot that receives the i^{th} genotype in the j^{th} environment (Crossa, 1990).

Estimates of broad sense heritability were determined using Agrobase (2005). Principal component analysis (Iezzoni and Pritts, 1991) was used to investigate the relevant traits contributing to the phenotypic variation among genotypes.

RESULTS

A relatively high number of roots per plant was obtained (average = 5.02), with genotype B_1P_2 - 6 having the highest number of 30. The average number of commercial sized storage roots (5 to 10 cm in diameter at the top and 15 cm to 30 cm long) was 1.17 with genotype B_1P_2 - 6 having the highest number of 12 commercial sized roots. The highest fresh root yield was recorded in B_1P_2 - 252 (60.00 ton ha^{-1}) while highest dry root yield was recorded in B_1P_2 - 62 (34.75 ton ha^{-1}). Recorded dry matter content ranged from 23.57% in B_1P_2 - 77 to 59.45% in B_1P_2 – 247 (Table 2).

Dry root yield was highly significantly correlated with number of commercial sized storage roots, roots per plant, harvest index, root weight, and fresh root yield (Table 3). Fresh root yield was highly significantly correlated with roots per plant, commercial roots and harvest index. Harvest index was highly significantly correlated with number of commercial sized storage roots

Table 3. Simple correlation coefficient matrix of yield components and quality traits for a cassava backcross population evaluated in CIAT 2006-2007, CIAT and Quilichao 2007-2008 season.

Variables	Root per Plant	Commercial Root	Harvest Index	Fresh Root Yield	Dry Root Yield	Dry Matter Content
Commercial Root	0.40**					
Harvest Index (0-1)	0.17**	0.38**				
Fresh Root Yield (ton ha^{-1})	0.99**	0.40**	0.17**			
Dry Root Yield (ton ha^{-1})	0.91**	0.41**	0.21**	0.91**		
Dry Matter Content (%)	0.09	-0.07	-0.12	0.09	-0.30**	
Protein Content (%)	-0.04	-0.13	0.26**	-0.04	-0.12	0.19**

**P<0.0001.

Table 4. Principal component coefficients of the various traits with principles of the various yield and quality related traits evaluated in a cassava backcross population at CIAT 2006/2007, and CIAT and Quilichao 2007/2008 seasons.

Traits	PC1[a]	PC2	PC3
Roots per plant	0.52	0.23	-0.02
Commercial Root	0.33	-0.22	0.37
Harvest Index (0-1)	0.20	-0.49	0.49
Fresh Root Yield (ton ha^{-1})	0.52	0.23	-0.02
Dry Root Yield (ton ha^{-1})	0.52	0.01	-0.30
Dry Matter Content (%)	-0.05	0.52	0.71
Protein Content (%)	-0.10	0.55	-0.05
Eigenvalue	3.23	1.43	0.98
Percent total variance	46.21	20.50	14.03
Cumulative	46.21	66.71	80.74

[a]Principal component.

and roots per plant. Protein content was highly significantly correlated with harvest index and dry matter content and negatively correlated with number of commercial sized roots, roots per plant, and dry matter content.

The relative contribution of the various traits to the genotype performance was explained by principle component analysis (Table 4). The first three principal components explained most of the variation and accounted for 80.74% of the total variation. The first principal component accounted for 46.21% of the total variation. Most of the variables were positively correlated which is an indication that they all contributed to total variation, except protein content. Based on the PC1 coefficients, four variables made a major contribution to variation (roots per plant, commercial roots, fresh root yield, and dry root yield). PC2 explained 20.50% of the total variation, with major contribution from harvest index, dry matter content, and protein content. PC3 explained 14.03% of the total variation with major contribution from commercial roots, harvest index and dry matter content.

Combined analysis of variance in CIAT and Quilichao trial sites over two years indicated that genotype was highly significant for roots per plant, root weight, harvest index, fresh root yield, dry root yield, protein content and for dry matter content of the traits evaluated (Table 5). Year was highly significant for all traits evaluated. Genotype by year interaction was highly significant for fresh root yield, dry root yield; root weight and root per plant.

The combined analysis of variance in two locations of CIAT trial sites is presented in Table 6. There were highly significant differences in the genotype main effects for root per plant, harvest index; fresh root yield, dry root yield and dry matter content. Interaction between genotype and location was significant for only dry matter content. After the yield and protein data were transformed, all the traits showed a good coefficient of determination (R^2) of 0.99 across the three environments. There was a highly significant location effect for all the traits.

DISCUSSION

Despite the world-wide importance of cassava, cassava

Table 5. Combined general linear model (GLM) sum of squares of yield parameters and quality traits in a cassava backcross population at CIAT, Colombia in 2006/2007 and Quilichao in 2007/2008 season.

Source of variation	Sum of squares						
	df[a]	RtpIt[b]	HI[c]	FRY[d]	DRY[e]	DMC[f]	PC[g]
Genotype	208	233.42	3.57	23342.65	2033.66	5834.09	245.43
Year	1	37.79	0.83	3779.48	173.63	173.16	26.09
Replication	2	12.80	0.13	1280.96	31.52	361.43	6.59
Year*Geno	76	69.61	0.52	6961.80	572.23	1138.21	63.34
Year*Geno*Rep	24	28.41	0.13	2841.76	191.84	275.99	22.20
Error	552	733.15	7.67	73315.62	5752.30	11113.45	618.36

[a]Degree of freedom; [b]Roots per plant; [c]Harvest index (0-1); [d]Root weight (kg); [e]Fresh root yield (ton ha^{-1}); [f]Dry root yield (ton ha^{-1}); [g]Dry matter content (%); [h]Protein content (%).

Table 6. Combined general linear model (GLM) table of protein and yield parameters evaluated in three environments in 2006-2008 in CIAT and CIAT and Quilichao, Colombia.

Source of variation	Mean squares							
	df[a]	RtPlt[b]	[c]ComRt	FRY[d]	DRY[e]	HI[f]	DMC[g]	PC[h]
Genotype (G)	220	0.14^{ns}	0.19**	1.68^{ns}	0.45^{ns}	0.01**	0.20**	0.16*
Environment (E)	2	3.73***	2.18****	41.93***	11.62**	0.36****	2.77****	1.70***
Rep (R)	2	0.65^{ns}	0.11*	7.52^{ns}	1.04^{ns}	0.01*	3.47****	0.13^{ns}
E x G	303	0.09^{ns}	0.10*	1.10^{ns}	0.30^{ns}	0.002^{ns}	0.10*	0.05^{ns}
R x G	334	0.09^{ns}	0.09*	1.09^{ns}	0.28^{ns}	0.002^{ns}	0.09*	0.03^{ns}
E x R	4	0.46^{ns}	0.75***	5.32^{ns}	2.00**	0.02^{ns}	0.58**	0.28*
E x R x G	137	0.09^{ns}	0.10*	1.04^{ns}	0.24^{ns}	0.001^{ns}	0.09*	0.03^{ns}
Error	1045	0.07	0.02	0.88	0.23	0.001	0.02	0.036
CV[i]		13.28	13.65	14.87	14.72	3.53	2.65	12.64

[a]Degree of freedom; [b]Roots per plant; [c]Commercial Root; [d]Fresh root yield (tonha^{-1}); [e]Dry root yield (tonha^{-1}); [f]Harvest index (0-1); [g]Dry matter content (%); [h]Protein content (%); [i]Coefficient of variance; ns=not significant at P<0.05; * P<0.05; ** P<0.01; ***P<0.001; **** P<0.0001.

cultivars have low protein content (Anonymous, 1968; Nassar and Dorea, 1982). Efforts have been made in the past to introgress root protein trait from wild progenitors but failed during the backcross phase (Asiedu et al., 1992). The low protein content in the roots of cassava can be attributed to the selection methods adopted by the cassava breeders where emphasis has not been placed on protein content as a part of the selection criteria (CIAT, 2004). Recently, storage root proteins have proved to be an increasingly important target for cassava breeders and geneticists who are now using marker-assisted selection and genetic engineering because of the role of protein in determining the nutritional quality of storage roots (Zhang et al., 2003).

The two parents (CW 198 - 11 and MTAI 8) that were used to generate this B_1P_2 population had large differences in their protein and dry matter content values of 11.20 (CW 198 - 11) and 2.30 (MTAI 8) for protein content, 33.24% (CW 198 - 11) and 44.96% (MTAI 8) for dry matter content. In the wild relative *M. esculenta* ssp *flabellifolia* (OW 230), the dry matter content and protein content were 46.12 and 10.50% respectively. The use of wild progenitors is part of the development at the CIAT breeding programme partly reported by Ojulong et al. (2008) of a new selection scheme, where the root protein content is a priority.

The results of this study differ from those reported by Ceballos et al. (2006) from another population with highest protein content of 7.20% in an unreplicated trial of a wide range of local neo-tropical varieties and higher than the value reported by Chávez et al. (2005) with the highest protein content of 8.72% of the same materials in an un-replicated trial. Efforts are ongoing in the National Root Crops Research centres in Africa where materials with high protein content introduced from Latin America are being utilised in the breeding activities to combine both protein and beta carotene (C. Egesi, NRCRI, Umudike, Nigeria, personal communication). Selection based on one breeding goal for the target environment is being implemented in the Nigerian cassava breeding community to meet a specific nutritional and agro-ecological and industrial goal (Nigeria Presidential initiative on Cassava).

Results from simple statistics showed that the potential

percentage dry matter content in this introgression (50.51%) was higher than the past documentations (Ojulong et al., 2008; Ceballos et al., 2006; Jaramillo et al., 2005; Iglesias., 1994; Magoon et al., 1973). Ceballos et al. (2006) reported negative correlation between dry matter and protein contents in the roots, suggesting that clones with higher protein content tended to have lower levels of dry matter content. This is contrary to what was found in this study, where it was not significant.

Simple correlation analysis in this population showed that all traits (commercial roots, roots per plant, harvest index, root weight, and fresh root yield) contributed to economic yield, which is by implication, an improvement over the previous studies reported by Kawano et al. (1998) and Ojulong et al. (2008) that association was detected between dry matter content and fresh root yield at the early stage, this might be as a partial result of other genes affecting this stage of introgression.

The use of Genotype by environment interactions is a means by which clones are tested for a wide adaptation to a range of environments with higher yield (Ngeve et al., 2003; Aina et al., 2007; Egesi et al., 2007; Okechukwu and Dixon, 2009). The contribution of genotype sum of squares to total sum of squares in yield and quality traits was significant, which indicated a large genetic component. This is in agreement with a report by Ceballos et al. (2006) which provides strong evidence to support the hypothesis of a genetic origin of protein content in the cassava root. The possibilities of further increasing the protein content in the root are therefore encouraging (Steel and Torrie 1960; Dudley, 1974; Gomez and Gomez, 1984; CIAT, 2003; Ceballos et al., 2006).

High broad-sense heritability was reported for fresh root yield, dry root yield, dry matter content, root weight, harvest index, roots per plant, commercial roots and protein content, which is in agreement with the findings of Pérez et al. (2002), Okogbenin (2004), Ceballos et al. (2004) and Ojulong et al. (2008).

There have been wide variation ranges of other qualitative traits from both wild and landraces of cassava roots (Asiedu et al., 1992; Sánchez et al., 2009; Rolland-Sabaté et al., 2012). However, studies have been carried out on other root quality traits of cassava at CIAT, the International Institute of Tropical Agriculture (IITA), National Roots Crops Research Institute (NRCRI), and other root crops research institutes around the world (Egesi, personal communication; Nuwamanya et al., 2009; Njoku et al., 2011). Other efforts have also been made in the use of genetical engineering to incorporate root quality traits into cassava to improve the health of cassava root consumers around the world (Sayre et al., 2011).

Results from this study are indeed very promising. Perhaps the most relevant benefit from these introgressions would be in improving the nutritional status of millions of people who depend heavily on cassava as a food security crop. The novelty of this finding is in the addition of higher protein content with higher dry matter content in the roots of cassava. The genotypes with the combination of these two traits have been pre-selected for further backcrossing to other cassava genotypes with other root quality traits so as to pyramid these genes from various sources and select the best for the benefit of the end users (farmers and consumers). These pre-selected genotypes for the second backcross are presently being evaluated in root crops research institutes in Nigeria, Ghana, Uganda and Tanzania.

Conflict of Interest

The authors have not declared any conflict of interest.

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Correlation analysis for maize grain yield, other agronomic parameters and *Striga* affected traits under *Striga* infested/free environment

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Evaluation of 15 F_1 hybrids and six parents obtained from partial diallel crosses was carried out during 2011 rainy season at Institute of Agricultural Research (IAR) Samaru, Zaria *Striga* infested field and *Striga* free field (2 environments). Interrelationships of grain yield and its components under *Striga* infestation revealed that character ear height had positive and highly significant phenotypic correlation with grain yield (r_{ph} = 0.55). While the remaining six characters recorded no significant correlation with grain yield. Similarly, *Striga* related parameters with *Striga* affected traits indicated high and highly significant positive correlation between *Striga* count one with *Striga* count two (r_g= 0.79, r_{ph} = 0.92 and r_e = 0.96)** and *Striga* rating (r_g = 0.84, r_{ph} = 0.71 and r_e = 0.77)** and also had highly significant positive genotypic correlation with number of leaves per plant (r_g = 0.79**) *Striga* count two exihibited high and highly significant positive phenotypic and environmental correlation with the traits *Striga* rating (r_{ph} = 0.78**and r_e = 0.71**) and number of leaves per plant (r_{ph} = 0.64** and re = 0.55**). While *Striga* rating recorded highly significant positive genotypic correlation (r_g = 0.89**) coefficient r_{ph} = 0.78** and r_{ph}= 0.97** respectively. At *Striga* free environment grain yield was positively significantly correlated with 1000 grain weight (r_{ph} = 0.43* and r_e = 0.45*), highly significantly positively correlated at genotypic level (r_g= 0.69)**, phenotypic level (r_{ph} = 0.52)* and environmental level (r_e = 0.43)* with number of leaves per plant. Furthermore, plant height with grain yield recorded highly significant positive correlation genotypically, phenotypically and environmentally with the following coefficients (r_g = 0.86, r_{ph}= 0.67 and r_e = 0.58)**, and likewise ear height and grain yield revealed significantly positive correlation with the following coefficients r_g = 0.45*, r_{ph} = 0.48* and r_e = 0.49*. Thus characters such as ear height, plant height, number of leaves per plant and 1000 grain weight should be taken into cognizance when selecting high yielding genotypes. Hybrids TZEEI 11 x TZEEI 3, TZEEI 11 x TZEEI 7 are outstanding in performance, especially grain yield and TZEEI 11 is good for hybrid formation.**

Key words: correlation, *Striga* parameters, grain yield and *Striga* affected traits.

INTRODUCTION

Maize (*Zea mays* L.) is one of the principal agricultural crops in many countries along with wheat and rice (FAO, 1982). In most of the developing countries of the world, maize constitutes the principal food for the majority of the

people. Demand for maize globally and sub-Saharan Africa has been predicted to increase by 54 and 93% in 1995 to 2020 (Pingali and Pandey, 2001), while that of Nigeria is predicted to increase by about 84% by the year 2020 (Shaibu et al., 1997). This is because in Nigeria maize is a major staple food and makes an important contribution to the diet of the majority of the people constituting about 80 to 90% of the dietary profile of adults and over 80% of that of infants (Doswell et al., 1996). It is also a dependable cash for farmers in northern Nigeria (Ado et al., 1999).

Industrially wise maize is used as corn bread, corn chips, paper, insulator, card board pipe, chemicals, plastics, methanol, baby food, greencorn, starch, glucose and oil (Nuhu and Showemimo, 2008). The parasitic witch weed *Striga hermonthica* infestation is one of the most serious constraints to cereal production by small holder farmers in sub-Saharan Africa (Olaoye and Bello, 2008) infestation result in substantial yield losses usually more than 70% (Kim, 1994). Much of the damage occurs before the *Striga* emerges from the ground. The degree of damage depends on the susceptibility of the cultivar, the *Striga* species, the level of infestation and any additional stress imposed by the environment (Shinde and Kulkarni, 1982; Vasudeva Rao, 1982). Kim (1994) in a study conducted on genetics of maize tolerance to *S. hermonthica* reported that genetic control in the maize inbreds tested was inherited quantitatively and thus expected to be durable. It was concluded that, two different types of gene action are responsible for the inheritance of the traits studied. Additive gene action plays a major role in inheritance of *Striga* tolerance and non additive gene action plays a major role in *Striga* emergence (Kim, 1994). Correlation studies between yield and yield components are pre – requisite to plan a meaningful breeding programme (Muhammad et al., 2004). Many researchers studied association of characters for the selection of high yielding varieties. Khatun et al. (1999) studied that grain yield per plant was positively and significantly correlated with 1000 grain weight, number of kernels ear $^{-1}$ and ear height. Orylan et al. (1999) studied that most important traits influencing grain yield were number of grains per row and number of grains per ear. Akanvou and Doku (1998) reported that, genetic correlation (r_g) for characters studied showed that yield was negatively correlated with *Striga* count one (r_g = - 0.22), *Striga* rating one (r_g = - 0.92) and with ear *Striga* rating (r_g= 0.88). They further stated that, the negative association obtained were expected since *Striga* reduces yield through its adverse effects on the physiology of the infested plants.

In another investigation under *Striga asiatica*, Olakojo and Olaoye (2011) reported that, at phenotypic level, *Striga* count was negatively and significantly correlated with *Striga* rating (r_p = - 0.30)*, ear height (r_p = - 0.74)*and maize grain yield (r_p = 0.57)* indicating that the two traits are probably controlled by different genes. They further affirmed that, *Striga* syndrome rating was however positively count, was positively correlated with *Striga* genes and significantly correlated with ear height (r_p = 0.31)*, days to silking (r_p = 0.60)* and grain yield (r_p = 0.33)*. Phenotypic correlation of ear height and grain yield was however negatively significantly correlated suggesting that, the two traits were not closely associated. Similarly, genotypic correlation coefficients shows that, *Striga* rating, plant height, days to silking, days to tasselling and kernel rows per cob had the following coefficients of 0.91*,0.30*, 0.44** and 0.85** respectively. *Striga* rating on the other hand was positively correlated with plant height (r_g = 0.36) and days to tasselling (r_g = 0.50)** as compared with ear height which was negative and significantly correlated with *Striga* rating (r_g = 0.72)**. The objectives of this study therefore, were (1) to determine the association of some maize agronomic traits to grain yield under *S. hermonthica* infestation and free environment. (2) to determine the association of *Striga* related parameters to *Striga* affected traits in maize plant.

MATERIALS AND METHODS

The study was conducted during 2011 rainy season (May to October) at the Institute for Agricultural Research (IAR) Farm Samaru, Zaria (Northern guinea savanna 11° 11'N 7° 38'E, 686 m above sea level). The genetic materials used comprised six *Striga* resistant inbred lines that are extra-early maturing developed by International Institute of Tropical Agriculture (IITA) Ibadan. Paired parents mating according to Stuber (1980) was used to intermate the six inbred lines. The six inbred lines were crossed in a partial diallel mating. 15F_1 hybrids were obtained, processed and stored prior to field evaluation. The field study was carried out at *Striga* sick plot of Institute for Agricultural Research Samaru, Zaria and *Striga* free field at the same Institute. Entries which included the hybrids and the parents were planted on 9th July 2011 under *Striga* infested field and 10th July, 2011 under *Striga* free field. Planting was done in a row plot of 5 x 1.5 m each and planted at inter row spacing of 75 cm and within row spacing of 50 cm to enhance a plant population of 53, 333 plant per hectare. The experiment was laid out using 5 x 5 incomplete lattice design pattern with three replications. *Striga* inoculum was prepared by thoroughly mixing *Striga* seeds with sieved sand at a ratio of 1:39 by weight which can be translated as approximately 2000 germinable seeds per 2.5 g of sand to seeds mixture (Kim, 1994). Uniform artificial inoculation was mixing *Striga* seeds with sieved sand at a ratio of 1:39 by weight which can be translated as approximately 2000 germinable seeds per 2.5 g of sand to seeds mixture (Kim, 1994). Uniform artificial inoculation was accomplished using one full coca cola bottle cap of *Striga* inoculum per planting hill of 3cm deep and 5cm wide. In the Striga infested trial, three seeds were sown per hole and later

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thinned to two seedlings per stand, at two weeks after planting (WAP). The same trial was repeated at the Striga free field. NPK fertilizer was applied at the rate of 60 kgN ha^{-1}, 30 kg P205 ha^{-1} and 30 kg K20 ha^{-1} in split- doses, half of the N and all of the P205 and K20 were applied at two WAP, while the remaining half of N was applied six WAP. In the *Striga* inoculated plot, *Striga* shoot counts at eight and 10 WAP and *Striga* syndrome rating at 10 WAP were recorded using scale 1-9 described by Kim (1994). For the rating, 1 = normal plant growth, no visible symptom; 9 = complete scorching of leaves causing premature death or collapse of the host plant and no ear formation. At both the *Striga* inoculated and the non-inoculated fields, agronomic parameters recorded were: Days to 50% tasseling (number of days from planting till the time 50% have tasseled), days to 50% silking (number of days from planting to when 50% of the population have silked), plant height measured from soil level to the base of the tassel, Ear height from the soil level to the node bearing the top most ear, number of leaves per plant, 1000 grain weight (weight of 1000 grains randomly taken from each plot after shelling) and grain yield per plot transformed to kilograms per hectare.

Genotypic, phenotypic and environmental correlations were estimated using the formula described by Singh and Chaudhary (1985):

$$\text{Genotypic correlation (rg)} = \frac{\sigma_g^2 X.Y}{\sqrt{(\sigma_g{}^2 X)(\sigma_g^2 Y)}}$$

Where: $\sigma_g{}^2$ X.Y = genotypic covariance between two traits X and Y, $\sigma_g{}^2$ X = genetic variance of trait X, $\sigma_g{}^2$y = genetic variance of trait Y.

$$\text{Phenotypic correlation } (r_{ph}) = \frac{\sigma_{ph}^2 X.Y}{\sqrt{(\sigma_{ph}^2 X)(\sigma_{ph}^2 Y)}}$$

Where: σ^2_{ph} X.Y = Phenotypic covariance's between two traits X and Y, σ^2_{ph} X = Phenotypic variance of traits x, σ^2_{ph}Y = phenotypic variance of traits y.

$$\text{Environmental correlation } (r_e) = \frac{\sigma_e^2 X.Y}{\sqrt{(\sigma_e^2 X)(\sigma_e^2 Y)}}$$

Where: $\sigma_e{}^2$ X.Y = environmental covariance between traits X and Y, σ^2_e X = Environmental variance of traits X, σ^2_eY = Environmental variance of traits Y.

RESULTS

Mean performance of parents and crosses are shown in Table 1 under *Striga* infested environment inbred parent TZEEI 4 (57 days) x TZEEI 4 (52 days) had the least number of days to 50% tasselling respectively. For days 50% silking inbred parent TZEEI 6 and TZEEI 4 (59 days each) and hybrid TZEEI 6 x TZEEI 3 (59 days) are the least for the trait. TZEEI 8 (9.89) plant and TZEEI 11 x TZEEI 7 (10.11) hybrid had the highest mean value for number of leaves per plant. For the trait plant height TZEEI 6 (86.78 cm) is the shortest parent however for crosses TZEEI 11 x TZEEI 7 (137.11) is the tallest plant while the smallest hybrid was TZEEI 8 x TZEEI 4 (69.89 cm). TZEEI 4 (28.22) parent had the lowest ear placement. For grain yield TZEEI 8 (1413 kg/ha) inbred parent had the highest mean value while hybrid TZEEI 11 x TZEEI 7 (1093.33 kg/ha) had the highest mean value. 1000 grain weight TZEEI 8 (130.96 g) recorded the highest mean value, TZEEI 11 x TZEEI 3 (128.17 g) hybrid recorded the highest mean value for the trait.

Under *Striga* free environment (Table 2) TZEEI 7 and TZEEI 6 (52 days each) together with the hybrid TZEEI 11 x TZEEI 3 (49 days) recorded the least number of days to 50% tasselling respectively for days to 50% silking inbred parent TZEEI 7 (57 days) and cross TZEEI 11 x TZEEI 4 (55 days) had the least mean value respectively. TZEEI 8 (9) parent had the highest number of leaves per plant, while hybrid TZEEI 6 x TZEEI 3 (9) recorded the highest mean value for the trait. TZEEI 6 (69.89 cm) and cross TZEEI 8 x TZEEI 6 (27.22 cm) had the lowest mean respectively. TZEEI 6 (18.11 cm) had the lowest mean value respectively for ear placement. For grain yield TZEEI 8 (737.77 kg/ha) is the highest inbred parent for the trait and hybrid TZEEI 11 x TZEEI 3 (1111.10 kg/ha) is the highest. For 1000 grin weight parent TZEEI 8 (114.53 g) is the highest for the trait, while cross TZEEI 7 x TZEEI 3 (115.7 g) had the highest mean value for the trait.

The genotypic (r_g), phenotypic (r_{ph}) and environmental (r_e) correlations measured in *Striga* infested environment and *Striga* free environment are presented in Tables 3, 4 and 5. All the correlation coefficient determined in this study were either positive or negative correlation coefficients. Under *Striga* infestation (Table 3) 1000 grain weight had significant positive genotypic correlation with days to 50% tasselling (r = 0.44). The trait also indicated highly significant positive phenotypic association with plant height (r = 0.66) and ear height (r = 0.55). Highly significant positive environmental correlation between the trait and days to 50% tasseling were observed (r = 0.88). Days to 50% tasseling exhibited highly significant negative environmental correlation with plant height (r = -0.78). Number of leaves per plant showed highly significant positive genotypic (r = 0.98) phenotypic (r = 0.75) and environmental (r = 0.72) association with ear height. Plant height showed highly significant positive phenotypic (r = 0.75) and environmental correlation (r = 0.98) with ear height. Ear height showed highly significant positive phenotypic association with grain yield (r = 0.55) (Table 3). For *Striga* parameters and *Striga* affected traitsin maize (Table 3). *Striga* count one showed highly significant positive genotypic correlation with *Striga* count two (r = 0.76), *Striga* rating (r = 0.84) and number of leaves per plant (r = 79). The trait also indicated highly significant positive phenotypic association with *Striga* count two (r = 0.92) and *Striga* rating (r = 0.71) *Striga* count one showed highly significant positive environmental correlation with *Striga* count two (r = 0.96) and *Striga* rating (0.77). *Striga* count two exhibited highly significant positive association with ear height (r =

Table 1. Mean performance of parents, four checks and fifteen crosses evaluated under *Striga* infestation in Samaru (2011).

Genotypes	Days to 50% Tasselling	Days to 50% Silking	Number of leaves per Plant	Plant height (cm)	Ear height (cm)	Grain yield kg/ha	1000 grain weight (g)	STR C01 8WAS	STR C02 10 WAS	STRR 10 WAS
TZEEI 11	58^{ab}	62^{a}	9^{bc}	116.89^{ab}	36.97^{b-d}	506.7^{a-d}	111.41^{ab}	0.30^{c}	1.00^{ab}	2.00^{c-e}
TZEEI 8	58^{ab}	62^{a}	10^{bc}	113.11^{ab}	41.67^{b-d}	1413.33^{ab}	130.96^{a}	2.33^{ab}	4.00^{ab}	4.67^{a}
TZEEI 7	61^{a}	63^{a}	9^{bcd}	122.11^{ab}	37.23^{b-d}	711.13^{a-d}	94.40^{ab}	2.67^{ab}	7.00^{a}	3.67^{a-c}
TZEEI 6	58^{ab}	59^{a}	7^{b-e}	86.78^{a-c}	32.23^{cd}	702.23^{a-d}	114.82^{ab}	0.30^{c}	1.33^{ab}	2.00^{c-e}
TZEEI 4	57^{ab}	59^{a}	8^{b-e}	109.45^{a-c}	28.22^{cd}	791.10^{a-c}	96.70^{ab}	0.30^{c}	0.66^{c}	1.33^{c-f}
TZEEI 3	59^{ab}	64^{a}	9^{bc}	118.21^{ab}	38.77^{b-d}	577.77^{a-d}	96.65^{ab}	1.67^{ab}	3.00^{ab}	3.00^{cd}
SAMMAZ 13	62^{a}	67^{a}	7^{b-e}	84.11^{a-c}	40.57^{b-d}	311.57^{a-e}	98.57^{ab}	2.00^{ab}	4.00^{ab}	1.33^{c-f}
SAMMAZ 28	51^{a-c}	58^{a}	9^{bc}	108.55^{a-c}	28.10^{cd}	711.16^{a-e}	113.93^{ab}	3.00^{ab}	4.00^{ab}	3.00^{ab}
SAMMAZ 29	55^{a}	66^{b}	10^{b}	109.22^{a-b}	27.67^{b}	915.57^{a-c}	88.93^{bc}	3.67^{ab}	4.67^{ab}	4.00^{ab}
OBA SUPE 7	62^{a}	67^{a}	13^{a}	164.11^{a}	64.11^{cd}	1711.10^{a}	101.94^{ab}	1.00^{c}	2.33^{ab}	2.00^{c-e}
SE ±	1.49	3 .29	0.74	7.12	3.99	254.94	8.44	1.30	3.07	0.97
TZEEI 11 x TZEEI 8	56^{a}	64^{a}	8^{b-e}	108.89^{a-c}	37.77^{b-d}	631.13^{a-d}	89.80^{bc}	1.67^{ab}	2.00^{ab}	2.33^{c-e}
x TZEEI 7	62^{a}	64^{a}	10^{bc}	137.11^{ab}	26.33^{d}	1093.33^{ab}	120.95^{ab}	0.00	2.00^{ab}	2.67^{c-e}
x TZEEI 6	57^{a}	65^{a}	9^{bc}	125.34^{ab}	29.63^{cd}	711.11^{a-d}	120.17^{ab}	0.00	1.00^{ab}	1.67^{c-f}
x TZEEI 4	52^{a}	63^{a}	8^{b-e}	115.66^{ab}	34.57^{b-d}	446.67^{a-d}	118.83^{ab}	1.33^{c}	1.00^{ab}	1.33^{c-f}
x TZEEI 3	55^{a}	65^{a}	9^{b-e}	117.27^{ab}	55.97^{ab}	951.13^{a-c}	128.17^{ab}	0.67^{c}	1.33^{ab}	1.67^{c-f}
TZEEI 8 x TZEEI 7	56^{a}	60^{a}	9^{bc}	120.89^{ab}	48.90^{a-c}	888.90^{a-c}	122.80^{ab}	2.00^{ab}	3.67^{ab}	4.33^{ab}
x TZEEI 6	60^{a}	62^{a}	7^{b-e}	93.73^{a-c}	41.32^{b-d}	312.57^{a-e}	93.33^{ab}	0	0.33^{d}	1.00^{c-f}
x TZEEI 4	57^{a}	60^{a}	9^{b-e}	69.89^{a-e}	47.43^{a-d}	241.50^{a-f}	101.00^{ab}	0.00	0.00	0.63^{c-f}
x TZEEI 3	54^{a}	57^{ab}	8^{b-e}	88.67^{a-c}	40.87^{b-d}	539.63^{a-d}	98.53^{ab}	0.00	0.33^{d}	1.33^{c-f}
TZEEI 7 x TZEEI 6	65^{a}	68^{a}	9^{b-e}	96.45^{a-c}	34.13^{b-d}	225.61^{a-f}	87.87^{bc}	6.33^{a}	6.67^{ab}	4.00^{ab}
x TZEEI 4	64^{a}	67^{a}	9^{b-e}	106.22^{a-c}	27.44^{cd}	546.90^{a-d}	109.67^{ab}	2.67^{ab}	4.00^{ab}	4.33^{ab}
x TZEEI 3	56^{a}	64^{a}	6^{e}	75.31^{a-d}	49.47^{a-c}	234.04^{a-f}	110.23^{ab}	0.30^{c}	0.33^{d}	1.33^{c-f}
TZEEI 6 x TZEEI 4	57^{a}	67^{a}	8^{b-e}	102.56^{a-c}	38.90^{b-d}	533.33^{a-d}	97.20^{ab}	1.33^{c}	2.67^{ab}	2.00^{c-e}
x TZEEI 3	56^{a}	59^{a}	8^{b-e}	84.22^{a-c}	38.23^{b-d}	391.73^{a-e}	98.81^{ab}	0.00	0.00	1.33^{c-f}
TTZEEI 4 x TTZEEI 3	57^{a}	63^{a}	8^{b-e}	101.33^{a-c}	37.13^{b-d}	582.83^{a-d}	89.42^{bc}	2.67^{ab}	3.67^{ab}	3.00 ^{cd}
S.E ±	3.31	10.40	1.90	18.55	11.25	294.16	18.92	2.12	2.67	0.71

Where DYAT< = days to 50% tasselling, DYSLK, = Days to 50% silking, EARHT = Ear Height, PLTHT = Plant height, 1000GWT = 1000 Grain weight, STR CO1 = striga count one, STR CO2 = striga count two and STRR = striga rating.

0.48). The trait also showed highly significant positive phenotypic correlation with Striga rating and number of leaves per plant. The trait had highly significant positive environmental correlation with Striga rating and number of leaves per plant. Striga rating showed highly significant positive genotypic correlation with plant height (r = 0.89). The trait also had highly positive genotypic correlation with ear height (r = 0.67) and

Table 2. Mean performance of six parents, four checks and fifteen crosses evaluated under *Striga* free environment in Samaru (2011).

Genotypes	Days to 50% Tasselling	Days to 50% Silking	Number of leaves per plant	Plant height (cm)	Ear height (cm)	Grain yield (kg/ha)	1000 grain weight (g)
TZEEI 11	54^{a-d}	59^{b-d}	8^{a-c}	89.45^{b-d}	29.33^{b-d}	257.80^{a-d}	79.07^{bc}
TZEEI 8	57^{ab}	61^{a-e}	9^{a-c}	108.55^{b}	35.33^{b-d}	737.77^{b}	114.53^{ab}
TZEEI 7	52^{b-d}	57^{b-e}	9^{a-c}	99.66^{b}	29.78^{b-d}	328.30^{a-d}	99.27^{ab}
TZEEI 6	52^{b-d}	59^{b-e}	7^{bc}	69.89^{a-c}	18.11^{de}	562.73^{c}	85.03^{bc}
TZEEI 4	54^{a-d}	59^{b-e}	8^{a-c}	82.22^{bc}	35.22^{b-d}	202.27^{a-d}	86.07^{bc}
TZEEI 3	52^{b-d}	58^{b-e}	8^{a-c}	87.77^{b}	29.22^{b-e}	323.70^{a-d}	86.93^{bc}
S.E ±	1.96	2.78	1.25	21.43	6.36	257.73	24.42
SAMMAZ 13	52^{b-d}	59^{b-e}	6^{a-c}	42^{a-f}	37.11^{b-d}	213de	104.10^{ab}
SAMMAZ 28	49^{dc}	54^{c-e}	7^{a-c}	77.11^{a-c}	37.11^{b-d}	223.44^{b-e}	81.40^{bc}
SAMMAZ 29	52 b-d	58^{b-d}	10^{a}	97.48^{b}	97.48^{b}	314.10^{b-d}	93.33^{ab}
OBA SUPER 7	57^{ab}	61^{a-d}	10^{a}	131.45^{a}	131.45^{a}	1517.89^{a}	102.83^{ab}
SE±	12.52	14.09	1.88	11.19	7.30	262.92	29.04
TZEEI 11 x TZEEI 8	52 $^{b-d}$	58^{b-e}	8^{a-c}	89.33^{b}	22.44^{b-e}	315.07^{a-d}	95.9^{ab}
x TZEEI 7	59^{a}	66^{a}	9^{a-c}	94.33^{b}	40.67^{ab}	426.67^{a-d}	73.96^{c}
x TZEEI 6	51^{dc}	56de	9^{a-c}	109.55^{b}	28.56^{b-d}	533.33^{c}	108.83^{ab}
x TZEEI 4	52^{b-d}	55^{c-e}	8^{a-c}	95.44^{b}	31.44^{b-d}	353.93^{a-d}	107.9^{ab}
x TZEEI 3	49^{dc}	64^{ab}	8^{abc}	115.44^{ab}	34.34^{bcd}	1111.10^{ab}	112.2^{ab}
TZEEI 8 x TZEEI 7	56^{a-c}	61^{a-e}	7^{abc}	89.55^{b}	35.67^{b-d}	333.23^{a-d}	102.3^{ab}
x TZEEI 6	56^{a-c}	59^{b-e}	6^{a-c}	74.22^{a-c}	34.50^{b-d}	280^{a-d}	69.75^{ab}
x TZEEI 4	54^{a-d}	60^{b-e}	7^{a-c}	82.66^{b}	28.22^{b-d}	366^{a-d}	135.17^{a}
x TZEEI 3	54^{a-c}	62^{a-c}	7^{a-c}	79.77^{a-c}	25.22^{b-e}	254.57^{a-d}	109.07^{ab}
TZEEI 7 x TZEEI 6	55^{a-c}	62^{a-c}	7^{a-c}	71.00^{a-c}	20^{c-e}	230.24^{a-d}	81.93^{bc}
x TZEEI 4	56^{a-c}	58^{b-e}	8^{a-c}	85.11^{b}	27.57^{b-d}	480^{a-d}	108.23^{ab}
x TZEEI 3	54^{a-d}	59^{b-e}	6^{c}	35.67^{a-f}	28.67^{b-d}	215.90^{a-d}	115.7^{ab}
TZEEI 6 x TZEEI 4	54^{a-d}	61^{a-e}	7^{a-c}	70.00^{a-c}	30.87^{b-d}	248.93^{a-d}	85.20^{bc}
x TZEEI 3	52^{b-d}	59^{b-e}	9^{a-c}	74.00^{a-c}	22.00^{b-e}	223.90^{a-d}	76.13^{ab}
TZEEI 4 x TZEEI 3	55^{ab}	60^{a-e}	7.00^{bc}	72.33^{a-c}	31.11^{b-d}	216.73^{a-d}	101.77^{ab}
S.E±	2.78	3.24	4.78	22.89	10.13	292.03	15.40

significant positive genotypic correlation with number of leaves number per plant (r = 0.47). The trait also showed significant positive phenotypic association with ear height (r=0.44) and grain yield (r=0.43) and significant positive significant positive phenotypic correlation with ear height (r=0.78) and grain yield (r = 0.97). For *Striga* free environment (Table 5) 1000 grain weight indicated highly significant environmental correlation between the

Table 3. Correlation among the seven traits of Maize grown under *Striga* infested environment in Samaru (2011).

Traits		1000 GWT	DYAT	DYSLK	L/N/PLANT	PLTHT	EAR HT	GRY
1000 GWT	(g)		0.44*	-0.60**	-0.13	0.21	0.11	0.45*
	(p)		0.42	-0.20	-0.23	0.66**	0.55**	0.26
	(e)		0.88**	-0.40	-0.10	0.45*	0.44*	0.19
DYAT	(g)			1.00**	-0.08	-0.56**	-0.14	-0.14
	(p)			0.18	-0.10	-0.22	-0.01	-0.01
	(e)			0.82**	-0.04	-0.78**	0.42	-0.15
DYSLK	(g)				0.34	-0.23	0.05	0.33
	(p)				-0.01	0.29	0.23	0.44*
	(e)				-0.18	0.27	0.24	0.11
L/N/PLANT	(g)					0.28	0.98**	0.15
	(p)					-0.23	0.75**	0.15
	(e)					-0.51*	0.72**	-0.34
PLTHT	(g)						0.82**	0.21
	(p)						0.53*	0.40
	(e)						0.98**	0.19
EARHT	(g)							0.19
	(p)							0.55**
	(e)							0.36

1000 GWT = 1000 Grain weight, DYAT = Days to 50% Tasselling, DYSLK = Days to 50% silking, L/N/plant = number of leaves per plant, PLT HT = Plant height, EAR HT = Ear height and GRY = Grain yield *, **, Significant at 5%, 1% level of probability respectively.

Table 4. Correlation of *Striga* Parameters and *Striga* affected traits in maize under *Striga* infested environment in Samaru (2011).

TRAITSTRCO1		STRCO2	STRR	N/L/PLANT	PLT.HT	EAR HT	GRY	
STR CO1	(g)		0.79**	0.84**	0.79*	0.22	0.14	-0.41
	(p)		0.92**	0.71**	0.15	0.10	0.09	0.04
	(e)		0.96**	0.77**	0.05	0.08	0.08	0.20
STR CO2	(g)			0.07	0.09	0.83**	-0.48*	0.15
	(p)			0.78**	0.64**	0.21	-0.15	0.17
	(e)			0.71**	0.55**	0.08	-0.08	0.13
STRR	(g)				0.02	0.89**	0.69**	0.06
	(p)				0.28	0.23	0.78**	0.97**
	(e)				0.16	-0.07	-0.10	0.91**

*, ** Significant at 5%, 1% level of probability respectively. STRC01 = *Striga* count one, STRC02 = *Striga* Count Two, STRR =*Striga* Rating.

Table 5. Correlation among the seven traits of Maize grown under *Striga* free environment in Samaru (2011).

		1000 GWT	DYAT	DYSLK	N/L/PLANT	PLT HT	EAR HT	GRY
1000GWT	(g)		0.10	0.69**	0.47*	0.33	0.67**	0.42
	(p)		0.25	0.92**	0.32	0.41	0.44*	0.43*
	(e)		0.15	0.23	0.30	0.08	0.40	0.45*
DYAT	(g)			0.40	0.24	0.13	0.07	0.75**
	(p)			0.43*	0.34	0.25	0.15	0.89**
	(e)			0.03	0.10	0.12	-0.02	0.14
DYSLK	(g)				0.28	0.35	0.26	0.33
	(p)				0.35	0.44*	0.33	0.06
	(e)				0.07	0.09	0.12	-0.13
No of Leaves/Plant	(g)					0.26	0.96**	0.69**
	(p)					0.88**	0.71**	0.52*
	(e)					0.62**	0.63**	0.43*
PLT HT	(g)						0.82**	0.86**
	(p)						0.71**	0.67**
	(e)						0.67**	0.58**
EAR HT	(g)							0.45*
	(p)							0.48*
	(e)							0.49*

*, ** Significant at 5%,1% level of probability respectively.1000 GWT = 1000 grain weight, DYAT = days to 50% tasselling, DYSLK = days to 50% silking, L/N/PLANT = number of leaves per plant,PLTHT=plant height, EARHT=ear height and GRY=grain yield.

trait and grain yield (r = 0.45) was also observed.

Days to 50% silking showed significant positive phenotypic correlation with plant height (r = 0.44). Number of leaves per plant exhibited highly significant positive genotypic association with ear height (r = 0.96) and grain yield (r = 0.69). The trait also had highly significant positive phenotypic correlation with plant height (r = 0.88) and ear height (r = 0.71) and highly significant positive genotypic correlation(r = 0.69) and significant phenotypic correlation (r=0.52) with grain yield and highly significant positive environmental correlation with plant height (r = 0.62) and ear height (r=0.63) and significant positive environmental association with grain yield (r =0.43).

Plant height showed highly significant positive genotypic correlation with grain yield (r = 0.86) and highly significant positive phenotypic association with ear height (r = 0.71) and grain yield (r = 0.67). The trait also showed highly significant positive environmental correlation with ear height (r = 0.67) and grain yield (r = 0.58). Ear height showed significant positive genotypic correlation with grain yield (r = 0.45) and significant positive phenotypic correlation between the trait and grain yield (r =0.48). The trait also had significant positive environmental correlation with grain yield (r = 0.49).

DISCUSSION

Correlation result under *Striga* infested environment indicated that 1000 grain weight was positively and significantly correlated with days to 50% tasseling genotypically (rg = 0.44)* and environmentally (re =0.88)**. 1000 grain weight also have positive and significant association with plant height (r_{ph} = 0.66)** and ear height (r_{ph} = 0.55)** at phenotypic level. Similar result was reported by Ibitome (2010) where he indicated

that 1000 grain weight increases with increase in plant and ear height which indicates more leaves, photosynthesis and heavier grains. Days to 50% tasselling have negative but significant environmental correlation with plant height (r_e = 0.78)**. This indicates that the two traits are probably controlled by different genes. Days to 50% silking had the same effect as days to 50% tasselling on plant height, ear height and grain yield which showed that the longer the days to 50% tasseling and days to 50% silking, the taller the plant and ear heights the more the number of leaves and the more the assimilates for grain yield (Ibitome, 2010; Devi et al., 2001). Number of leaves per plant have positive and significant correlation with ear height at genotypic, phenotypic and environmental level with the following coefficients 0.98**, 0.75** and 0.72** respectively. The physiological implication of this association is the more the number of leaves the greater the ability of the plant to photosynthesize and consequently the production of assimilates for grain yield. Plant height had highly positive significant association with ear height at phenotypic (r_p = 0.75)** and environmental level (r_e = 0.98)** and this signifies that increase in plant height may increase grain yield (Hallauer and Miranda, 1988). Ear height also had positive significant phenotypic correlation with grain yield (r_p = 0.55)** indicating that increase in ear height contributed to increase in grain yield as reported by Ibitome (2010) and Rahman et al. (1995). Correlation on *Striga* parameters was carried out taking into cognizance of the affected portion of the plant that were use to assess the damage caused by *S. hermonthica* as reported by Berner et al. (1997) the plant parts are leaves, stalk and cobs and it is on this note that correlation studies were carried out on number of leaves per plant, plant height, ear height and grain yield.

The trait *Striga* count one had positive significant correlation with *Striga* count two at genotypic (r_g = 0.79)** phenotypic (r_p = 0.92)** and environmental level (r_e = 0.96)** and it also had positive association with *Striga* rating with following coefficients r_g = 0.84**, r_p = 0.71** and r_e = 0.77**. The positive and significant correlation between *Striga* count one, count two and *Striga* rating concur with the findings of Gethi and Smith (2004) where they suggested that one could use one of these traits to select for the others. Similarly, *Striga* count one had significant and positive genotypic correlation with the number of leaves per plant (r_g = 0.79)**. *Striga* count two had positive significant correlation with *Striga* rating (r_p = 0.78** and r_e = 0.71**), number of leaves per plant (r_p = 0.6** and r_e = 0.55**) plant height (r_g = 0.83)**. This finding is almost in agreement with that of Olakojo and Olaoye (2011) where they reported significant positive correlation of *Striga* count on *Striga* rating and plant height under *Striga lutea* infestation. Furthermore, there is significant but negative correlation between *Striga* count two and ear height at genotypic level (r_g = -0.48)* this indicate that according to Akanvou and Doku (1998) negative association were expected since *Striga* reduces yield through its adverse effects on the physiology of the infested plants. For *Striga* rating there are significant positive association with plant height at genotypic level (r_g = 0.89)**, ear height and grain yield at phenotypic level with coefficient 0.78** and 0.97** respectively. This result concur with that of Olakojo and Olaoye (2011) in which they affirmed that *Striga* syndrome rating being positively counted was however positively correlated with *Striga* genes and significantly correlated with ear height and grain yield and positively significantly correlated with plant height.

Under *Striga* free environment 1000 grain weight had positive significant genotypic correlation with number of leaves per plant (r_g = 0.47)* and positive significant genotypic and phenotypic correlation with ear height (r_g = 0.67** and r_p = 0.44*). It is similarly had an association with grain yield at environmental level (r_e = 0.45*). The data agree with the findings of Rafique et al. (1999) and Orylan et al. (1999). Days to 50% silking had positive significant association with plant height at phenotypic level (r_p0.44)* number of leaves per plant had positive significant phenotypic and environmental correlation with plant height (r_p = 0.88** and r_e = 0.62**) and similarly, also had positive significant association with ear height (r_g = 0.96)**, (r_p = 0.71)** and (r_e = 0.63)** and grain yield (r_g = 0.69)**(r_p = 0.52)* and (r_e = 0.43)* genotypically phenotypically and environmentally. For plant height there is significant positive phenotypic and environmental correlation with ear height (r_p = 0.71** and r_e = 0.67**). It also had significant positive association genotypically (r_g = 0.86)**, phenotypically (r_p = 0.67)** and environmentally (re = 0.58)** with grain yield. Furthermore, the trait ear height recorded significantly positive correlation to grain yield at genotypic, phenotypic and environmental level with following coefficients 0.45*, 0.48* and 0.49* respectively. The physiological implication of days to 50% silking to plant height, ear height and grain yield was reported by Mohan et al. (2002) as days to 50% tasselling increases with days to 50% silking and had an inverse association with plant height, ear height and grain yield. Ibitome (2010) and Devi et al. (2001) indicated that days to 50% silking had the same effect as days to 50% tasselling on plant height, ear height and grain yield which showed that, the longer the days to 50% tasselling and 50% silking the taller the plant and ear heights, the more the number of leaves and the more the assimilate for grain yield. Also Troyer and Larkins (1985) observed that plant height was strongly associated with the flowering dates, both morphologically and ontogenically, because internode formation stops at floral initiation which means that earlier flowering maize is usually shorter.

Conclusion

From the result of this study it is concluded that effective selection for superior genotypes is possible taking into

cognizance of days to 50% tasselling, days to 50% silking, number of leaves per plant, ear height, plant height and 1000 grain weight.

Conflict of Interest

The authors have not declared any conflict of interest.

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Genetics of drought tolerance in common bean genotypes adapted to Ugandan conditions

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Common bean (*Phaseolus vulgaris* L.) is an important source of food and income for majority of households in Sub-Saharan Africa. However, bean production in Uganda is being affected by drought which has resulted from recent changes in climate. Developing high-yielding and drought-tolerant bean cultivars would significantly contribute to increased and stable yields in drought-prone environments. However, prior research was not focused on breeding for drought tolerance in bean in Uganda. Thus, this study sought to elucidate the genetics governing the inheritance of drought tolerance in Ugandan bean genotypes, through establishing the mechanism of inheritance of this trait in the genotypes relevant to Uganda. Five drought-tolerant and three drought-sensitive genotypes were hybridized using a NCII mating design. The findings of the study indicated that drought tolerance is controlled by both additive and non-additive gene action with more predominance of additive gene effects for seed yield, pod weight, seed and pod and number. Further findings also revealed that the genotypes SEN 99 and NABE 15 are good combiners for drought tolerance.

Key words: *Phaseolus vulgaris*, drought, screening, combining ability, inheritance

INTRODUCTION

Climate change and food security are important issues challenging Uganda (NAPA, 2007) and Sub-Saharan Africa. Production of food crops is mainly dependent on natural rainfall and as such variety improvement for drought tolerance is key in coping with the negative impact of climate change on food security. Common bean is the most important crop legume in Uganda (Haggblade and Dewina, 2010), providing both food and income especially for the poor (Katungi et al., 2009) and it accounts for 7% of the national agricultural gross domestic product (CIAT, 2008). Thus, the crop's adaptation to climate change requires immediate action.

Drought is becoming particularly more frequent and prolonged (NAPA, 2007) and is expected to have increasing negative effects on common bean production in Uganda (Kiwuka et al., 2012). It has been reported that

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the dry spells being experienced during the rainy season are sufficient to reduce agricultural production but these dry spells are expected to result into prolonged droughts in the future (NAPA, 2007) and this will have devastating effects on the yield of drought sensitive crops such as common bean.

According to Nielsen and Nelson (1998) yield reductions in common bean resulting from drought depend mainly on the severity and the period of drought occurrence. Reports by White and Singh (1991) have indicated overall common bean yield reductions in most production regions in the world as a result of drought. Singh (2007) quantified reductions in common bean seed yields to be as high as 88% depending on the cultivar and severity of the drought. In addition, Thornton et al. (2009) predicted that higher temperatures will affect the altitudinal range of adaptation of bean genotypes, reduce root growth and accelerate decomposition of soil organic matter, thereby aggravating drought stress.

With the present climate change, drought will continue to threaten the stability of Ugandan bean production (NAPA, 2007; Hepworth and Goulden, 2008) considering that less than 1% of the total arable land is irrigated (Kiiza, 2001). These effects are more profound with resource poor producers living in drought prone areas, who cannot afford to use irrigation (Wortmann et al., 1998). The development of high-yielding and drought-tolerant bean cultivars should significantly increase and stabilise yield in drought-prone environments. Considering the significant role that common bean plays in human nutrition and livelihood (CIAT, 2008), failure to address drought constraints might impact negatively on the livelihoods of the people living in drought prone areas of Uganda.

Previous attempts to improve the market-preferred Ugandan common bean genotypes for tolerance to drought were made by the National Bean Breeding Program in Uganda. Five drought-tolerant genotypes were obtained from CIAT and screened together with three market-preferred Ugandan bean genotypes. Results of the screening indicated possible existence of drought-tolerance in CIAT genotypes SEN 98, SEN 99 and SCR 48. However, there was no evidence for drought tolerance in the screened Ugandan genotypes (Amongi, 2013). Considering that these drought-tolerant genotypes are not adapted to Uganda's agro-ecological zones, there exists a need to introgress drought tolerance into the Ugandan genotypes and also understands the inheritance of drought tolerance in these genotypes.

Common bean has a wide genetic base (Beebe et al., 2013; Kiwuka et al., 2012) with genetic differences reported in traits such as seed weight, leaf proline content, stay-green, root spread and depth, all of which play major roles in drought tolerance (Thomas, 1983; Badr, 2005). Previous studies have shown that drought tolerance in this crop is controlled by quantitative traits (Blum, 2002; Acquaah, 2007; Beebe et al., 2008, Mukeshimana et al., 2014). According to Thomas (1983) and Badr (2005), seed weight in bean is controlled by a large number of genes with both additive and dominance effects. In addition, Badr (2005) reported the role of partial dominance for total yield/plant where relatively low narrow sense heritability (< 60) estimates were obtained on a single plot basis. Similarly, Ramirez and Kelly (1998) found higher heritability (> 60) estimates on family mean basis for seed yield in a segregating population. In other drought related research on common bean, both additive and non-additive effects for seed yield and pod number per plant under drought stress have been reported (Asadi et al., 2010). Also, Makunde et al. (2007) found predominance of non-additive genes for seed yield. In this study, Ugandan market-preferred genotypes were crossed with the non-adapted drought-tolerant genotypes from CIAT to specifically, establish the mechanism of inheritance of drought tolerance in these crosses. The information generated will in turn be used to facilitate planning of an efficient breeding program for the improvement in the level of drought tolerance in common bean in Uganda.

MATERIALS AND METHODS

Study area

The study was conducted in a screen house at the National Crops Resources Research Institute (NaCRRI) located in Namulonge, Wakiso District, 28 km north of Kampala (32° 34'E, 0° 32'N). The Institute's elevation is 1150 m above sea level and it receives mean annual precipitation of 1300 mm. Its mean annual temperature is 22°C with annual minimum and maximum temperatures of 16 and 28°C, respectively. The temperature and humidity in the screen house ranged from 20 to 34°C and 45 to 96%, respectively. The water holding capacity of soil used in the study was 29 ml/100 g fresh soil.

Developing a breeding population

Eight genotypes were crossed in order to create a breeding population. Five exotic genotypes, three of which were confirmed as drought tolerant were obtained from CIAT, while the three market-preferred genotypes were provided by the National Bean Program in Uganda. The hybridization program utilized adapted (local) and non-adapted (exotic) drought-tolerant parents. Thus, a full North Carolina II (NC II) mating design, adapted to include reciprocals was used to produce 30 F_1 families (Table 1). Wide application of NCII mating design is in studies of combining ability, heterosis and in estimating additive and non-additive gene effects. The NCII mating design is commonly used to estimate both general and specific combining ability of inbred lines (Acquaah, 2007).

Population advancement and screening for drought tolerance

The F_1 plants for each of the 28 out of 30 successful NC II progenies were selfed to derive F_2 seed. However, eight out of the 10 crosses of K132 with the five CIAT genotypes did not produce F_2 seed because of inter gene pool incompatibilities. The successful crosses shown in Table 1 and the eight parents were phenotypically

Table 1. Successful **c**rosses used in the study.

Forward cross	Reciprocal cross
NABE 4/SCN9	SCN9/NABE 4
NABE 4/SEN98	SEN98/NABE 4
NABE 4/SEN99	-
NABE 4/SCN6	SCN6/NABE 4
NABE 4/ SCR48	SCR48/NABE 4
NABE 15/SCN9	SCN 9/NABE 15
NABE 15/SEN98	SEN98/NABE 15
NABE 15/SEN99	SEN99/NABE 15
NABE 15/SCN6	SCN6/NABE 15
-	SCR48/NABE 15

SCN = Drought tolerant black bean with recessive BCMV gene; SCR = Drought tolerant small red bean with recessive BCMV gene; SEN = Black drought tolerant beans, NABE 4 = Red mottled medium-sized bean with tolerance to halo blight, NABE 15 = Small cream seeded early maturing bean with anthracnose resistance.

screened for drought tolerance for the following traits: leaf rolling, primary leaf lamina drooping, number of trifoliate leaves, dry pod and seed weights, number of pods per plant and number of seed per pod.

The genotypes were subjected to drought conditions in the screen house to determine their reactions to moisture stress using two watering regimes of either daily watering or watering after every four days. The critical watering interval was estimated based on the yield reduction observed by Amongi (2013). The water-stressed treatment was fully watered until 18 days after planting and thereafter, it was supplied with one litre of water in the late morning hours on the appropriate day. The well watered treatment was irrigated daily with one litre of water until physiological maturity. The experimental design used for this evaluation was a randomised complete block design in a split plot arrangement with only two replications due to limited seed. An experimental unit consisted of sixty Ten-litre dishpans each containing six plants, that is, four plants per cross and their two parents. Stress treatment was duplicated within a replication. Twenty (20) of the 60 dishpans were therefore well watered and 40 were imposed to drought stress. The stressed treatment was duplicated to increase the number of stressed plants in order to obtain reliable information on drought stress. Each dishpan contained 10 kg of sandy-clay-loam soil. Moisture meter that records a value of 1 to 5 when inserted in the soil was used in managing fluctuations of soil water.

Data collection

Data on potential drought stress indicators on growth and yield associated parameters were collected on a single plant basis. For growth parameters, data were collected on leaf rolling, primary leaf lamina drooping and number of trifoliate leaves. A 5-point scale where 0 = Not rolled / drooped leaf; 1 = shallow V-shaped leaves; 3 = deep V-shaped leaves; 5 = fully capped leaves / lamina fully collapsed and wrinkled, and 7 = tightly rolled leaves / lamina fully collapsed and dried was used to score for leaf rolling and laminate drooping (Amongi, 2013). When 90% of the pods had reached physiological maturity identified as a change in colour from green to yellow (Munoz-Perea et al., 2006), the number of pods per plant, seed number per pod, pod dry weight, and seed dry weight (g/plant) were recorded. The seeds were oven dried at 30°C for 3 weeks before recording seed weight (g). In addition, plants were also closely monitored for root rot infection caused by *Fusarium solani* f. sp. *phaseoli* through visual inspection of the stem base for necrosis.

Data analyses

Means of individual plant values for the 18 F_2 populations and their seven parents were computed per replication for statistical analyses using the GenStat computer package (Release 14.1, PC/Windows 7; VSN International Ltd., 2011). Individual replication data were entered and subjected to general analysis of variance using the linear model shown:

$$Y_{ijk} = \overline{Y} + GCA_i + GCA_j + SCA_{ij} + B_k + e_{ijk}$$

Where, $\overline{Y}_{ijk}$, Mean of a specific cross; Y, Grand mean; GCA, general combining ability; Effect of the parent in the phenotypic mean of its crosses, i = female, j = male; SCA, specific combining ability; Phenotypic value of a specific cross compared to the value predicted from parental GCA values; $B_{k,}$ Block effect; $e_{ijk,}$ Error effect.

The error variance obtained from individual replication data analysis was used to test the significance of the sources of variations. The means of F_2 progenies were subjected to general ANOVA and regression analysis using Genstat (Release 14.1 PC/Windows 7; VSN International Ltd., 2011) to determine the variance of general combining ability (GCA), specific combining ability (SCA), reciprocal and direction effects. SCA effects were calculated by subtraction of predicted means from observed means. In addition, the significance of SCA and GCA effects were tested using a standard t-test [t = effect / (standard error of the effect)]. Within watering regimes analyses were performed and to provide more understanding on the importance of the GCA, and SCA for the variables, their variance components which exclude the extraneous effect of replication unlike mean squares (variance) were estimated. These estimates were then used to calculate Baker's ratio according to Baker (1978) and coefficients of genetic determination (estimate of heritability). Baker's ratio which estimates the relative significance between additive and non-additive effects (Baker, 1978) was calculated as:

$$(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)}) / (\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA})$$

Where, σ^2, Sample variance; $(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)})$, Additive gene effect; $(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA),}$ Total genetic effect. Narrow sense coefficient of genetic determination (NS CGD ≈ h^2), a

Table 2. Variances for the response of 18 F_2 populations and seven parents to drought stress in varying watering regimes.

Source of variation	d.f.[a]	Growth drought stress indicators			Yield associated drought stress indicators			
		Leaf rolling	Primary leaf lamina drooping	Number of trifoliate leaf	Dry pod weight	Dry seed weight	Pod number per plant	Seed number per pod
Replication(R)	1	3.06***	1.09	5.9	5.2	2.0	0.15	0.06
Water[b]	1	3.93***	8.91***	98.4***	262.8***	212.4***	129.10***	21.64***
R x Water	1	0.13	2.57**	22.8*	0.8	1.4	0.11	0.03
Entry	24	0.21*	1.37***	21.3***	6.9***	12.6***	8.06***	3.22***
Entry x Water	24	0.15	0.60*	3.0	7.5	5.3	2.82	0.61
Error	48	0.11	0.32	3.4	4.2	3.2	2.36	0.66
Total	99							

[a]Degree of freedom, [b]Watering regime, ***, **,* = significant levels at P ≤ 0.001, 0.01, 0.05, respectively.

proportion of the phenotypic variation attributed only to additive gene effects (Falconer and Mackay, 1996) was calculated as:

$$(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)}) / (\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA+} \sigma^2_{e)}$$

Where, e, Sample error; $(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)})$, Additive gene effect; $(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA+} \sigma^2_{e)}$, Phenotypic effect. Broad sense coefficient of genetic determination (BS CGD ≈ H), a proportion of the phenotypic variation due to all genetic effects (Falconer and Mackay, 1996) was calculated as:

$$(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA)} /(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA+} \sigma^2_{e)},$$

Where, $(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA),}$ Total genetic effect; $(\sigma^2_{GCA(Exotic)} + \sigma^2_{GCA(Local)+} \sigma^2_{SCA+} \sigma^2_{e),}$ Phenotypic effect.

Drought intensity index (DII) was calculated as 1 - (Mean yield from stressed environment / Mean yield from well watered environment) (Ramirez-Vallejo and Kelly, 1998). Values of DII exceeding 0.70 indicates severe drought.

RESULTS

Phenotypic performance of F_2 populations and parents

The analysis of variance of 18 F_2 populations and their seven parents in varying watering regimes showed that their response to watering were significantly different (P ≤ 0.001) for all the parameters. However, their interactions with watering regimes were only significantly different (P ≤ 0.05) for primary leaf lamina drooping (Table 2).

The populations and parents were significantly different (P ≤ 0.05) for all variables under water stress (Table 3). The F_2 population, NABE 4 x SCN 9, had the lowest leaf lamina drooping and low leaf rolling but also the lowest number of trifoliate leaves and no pod production under water stress. However pod number per plant and seed biomass for the F_2 populations, SEN 98 x NABE 15 and SCR 48 x NABE 15 were not only the highest but also greater than the mean of all F_2 populations under water stress (Table 3). The F_2 populations namely; NABE 15 x SEN 98, NABE 15 x SEN 99, SEN 99 x NABE 15 and SCR 48 x NABE 15 produced the highest number of trifoliate leaves, greater than the mean of all F_2 populations. In addition, the F_2 populations, NABE 15 x SEN 98 and SCR 48 x NABE 15 also produced high dry pod and seed weight, pod and seed number greater than the mean of all the crosses, unde water stress (Table 3).

Contribution of the exotic verses local parent

The analysis of variance for the performance of F_2 populations in each watering regime revealed that the F_2 populations expressed more variation under water stress. It further showed that the variance of general combining ability (GCA) for both exotic and local parents differed significantly (P ≤ 0.01) for primary leaf lamina drooping (LD-P), seed weight, pod and seed number under drought stress (Table 4). The GCA variance for leaf rolling, trifoliate leaf number and pod weight were only significantly different (P ≤ 0.05) for local parents. No significant differences were observed for variance of specific combining ability (SCA) and reciprocal effect for yield associated variables.

However, direction effect was significant (P ≤ 0.01) for seed number and reciprocal effect on laminate drooping under water stress (P ≤ 0.05) (Table 4). The comparison of variance components of GCA revealed that GCA for local parents were higher than the GCA for exotic parents for leaf rolling, trifoliate leaf number and pod weight under water stress. The reverse is true for primary leaf lamina drooping, seed yield, pod and seed number (Table 4).

Table 3. Means of growth and yield associated parameters in F_2 populations and their parents.

Entries	Leaf rolling		Primary leaf lamina drooping		Number of trifoliate leaf		Dry pod Weight (g/p)		Dry seed weight (g/p)		Pod number per plant		Seed number per pod	
F_2 populations	**DS**	**WW**	**DS**	**WW**	**DS**	**WW**	**DS**	**WW**	**DS**	**WW**	**DS**	**WW**	**DS**	**WW**
NABE 15/SEN 98	1.4^{abc}	0.8^{bc}	4.5^{a}	2.3^{efg}	5.7^{bcde}	3.9^{fgh}	1.4^{bcd}	2.5^{efgh}	1.3^{bcdef}	1.6^{defg}	1.5^{bcde}	3.4^{bcdefg}	1.9^{cde}	0.9^{ef}
SEN 98/NABE 15	1.5^{ab}	1.4^{ab}	4.7^{a}	3.4^{abcdef}	5.3^{bcde}	8.2^{bcde}	4.9^{a}	4.1^{bcdefgh}	1.6^{bcde}	3.9^{bcdefg}	1.7^{bcd}	4.0^{abcdefg}	1.8^{def}	1.9^{abcdef}
SCR 48/NABE 15	1.3^{abcd}	0.5c	4.1^{abc}	3.5^{abcde}	5.7^{bcde}	9.8^{bcd}	1.5^{bcd}	6.0^{abcdefg}	1.4^{bcde}	5.2^{abcdefg}	1.9^{bc}	5.3^{abcde}	2.1^{bcde}	2.9^{abcde}
NABE 15/SEN 99	1.7^{a}	1.6^{a}	4.3^{ab}	4.2^{ab}	6.0^{abcde}	6.1^{defg}	1.2^{cd}	0.9^{gh}	1.1^{defg}	0.2^{g}	1.4^{cdef}	1.3^{defg}	1.6^{defgh}	2.6^{abcde}
SEN 99/NABE 15	1.3^{abcd}	0.9^{abc}	4.5^{a}	4.4^{a}	6.5^{abcd}	7.4^{cdef}	1.4^{bcd}	6.7^{abcdef}	1.2^{cdefg}	6.0^{abcde}	1.4^{cdef}	4.5^{abcdefg}	2.5^{bcd}	3.2^{abc}
NABE 15/SCN 6	1.5^{ab}	0.9^{abc}	4.1^{abc}	2.9^{cdefg}	5.1^{cdef}	6.4^{defg}	0.4^{cd}	2.2^{efgh}	0.1^{h}	2.4^{cdefg}	0.8^{efgh}	1.7^{defg}	0.7^{fghi}	1.6^{cdef}
SCN 6/NABE 15	1.7^{a}	1.0^{abc}	4.7^{a}	4.0^{ab}	5.4^{bcde}	9.0^{bcde}	1.5^{bcd}	8.9^{abcd}	0.8^{efgh}	7.1^{abc}	0.8^{efgh}	6.5^{abc}	1.2^{efghi}	3.0^{abcd}
NABE 15/SCN 9	1.5^{ab}	1.4^{ab}	3.7^{abc}	3.4^{abcdef}	5.0^{cdef}	6.5^{defg}	0.1^{cd}	3.0^{efgh}	0.1^{h}	3.1^{bcdefg}	0.2^{h}	2.2^{cdefg}	0.6^{ghi}	1.7^{bcdf}
SCN 9/NABE 15	1.0^{bcd}	1.1^{abc}	2.6^{de}	3.9^{abc}	5.4^{bcde}	6.8^{def}	0.1^{cd}	3.6^{defgh}	0.0^{h}	2.4^{cdefg}	0.4^{gh}	3.1^{cdefg}	0.5^{hi}	1.1^{def}
NABE 4/SEN 98	1.1^{bcd}	1.4ab	4.7^{a}	3.0^{bcdefg}	4.1^{def}	6.3^{defg}	1.0^{cd}	3.8^{cdefgh}	1.1^{defg}	4.2^{abcdefg}	1.3^{cdefg}	3.0^{cdefg}	1.8^{def}	3.7^{ab}
SEN 98/NABE 4	0.9^{bcd}	0.7^{bc}	3.4^{bcd}	3.0^{bcdefg}	3.3^{ef}	7.0^{cdef}	0.3^{cd}	5.1^{bcdefgh}	0.2^{h}	3.9^{bcdefg}	0.3^{h}	2.7^{cdefg}	0.5^{hi}	2.1^{abcdef}
NABE 4/SEN 99	1.5^{ab}	0.4^{c}	3.2^{cd}	2.2fg	3.0^{ef}	5.0^{efgh}	0.4^{cd}	3.0^{efgh}	0.5^{fgh}	3.8^{bcdefg}	0.7^{fgh}	2.4^{cdefg}	1.1^{efghi}	3.0^{abcd}
NABE 4/SCR 48	1.3^{abcd}	0.9^{abc}	4.7^{a}	4.0^{ab}	5.5^{bcde}	7.7^{cdef}	1.0^{cd}	6.6^{abcdef}	0.9^{efgh}	6.1^{abcde}	1.1^{defg}	5.5^{abcd}	2.0^{bcde}	3.2^{abc}
SCR 48/NABE 4	1.5^{ab}	0.6^{c}	4.1^{abc}	3.4^{abcdef}	4.8^{cdef}	7.3^{cdef}	0.2^{cd}	1.4^{fgh}	0.0^{h}	1.3^{efg}	0.3^{h}	0.8^{fg}	0.4^{i}	2.4^{abcde}
NABE 4/SCN 6	1.1^{bcd}	0.8^{bc}	4.2^{abc}	2.7^{defg}	3.1^{ef}	6.4^{defg}	0.0^{d}	0.0^{h}	0.1^{h}	0.7^{fg}	0.1^{h}	0.3^{g}	0.2^{i}	0.9^{ef}
SCN 6/NABE 4	1.0^{bcd}	0.9^{abc}	2.8^{de}	3.4^{abcdef}	4.4^{cdef}	5.8^{defg}	0.0^{d}	1.9^{efgh}	0.1^{h}	0.7^{fg}	0.2^{h}	1.2^{defg}	0.6^{ghi}	2.3^{abcde}
NABE 4/SCN 9	1.1^{bcd}	0.4^{c}	2.1^{e}	2.0^{g}	2.1^{f}	1.3^{h}	0.0^{d}	0.6^{gh}	0.1^{h}	1.0^{efg}	0.1^{h}	0.3^{g}	0.1^{i}	0.2^{f}
SCN 9/NABE 4	0.8^{d}	0.8^{bc}	3.2^{cd}	3.4^{abcdef}	3.3^{ef}	2.5^{gh}	0.4^{cd}	0.0^{h}	0.4^{gh}	0.1^{g}	0.3^{h}	1.0^{efg}	0.2^{i}	2.0^{abcdef}
Mean	1.3	0.9	3.9	3.3	4.6	6.3	0.9	3.3	0.6	2.9	0.8	2.7	1.1	2.1
Parents:														
SEN 98	1.3^{abcd}	0.7^{bc}	4.4^{ab}	3.8^{abc}	8.3^{ab}	12.0^{ab}	1.8^{bcd}	7.0^{abcdef}	1.9^{bcd}	6.5^{abcd}	1.9^{bc}	4.6^{abcdefg}	2.6^{abcd}	3.5^{abc}
SCR 48	1.7^{a}	0.8^{bc}	4.4^{ab}	3.7^{abcd}	7.4^{abc}	8.5^{bcde}	2.2^{bcd}	4.2^{bcdefgh}	1.9^{bcd}	3.9^{bcdefg}	1.9^{bc}	3.1^{cdefg}	3.0^{abc}	2.9^{abcde}
SEN 99	1.4^{abc}	1.0^{abc}	4.2^{abc}	2.8^{defg}	8.3^{ab}	9.7^{bcd}	3.6^{ab}	11.6^{a}	3.1^{a}	9.2^{a}	2.8^{a}	7.5^{ab}	3.7^{a}	3.2^{abc}
NABE 15	1.6^{a}	0.7^{bc}	4.5^{a}	4.2^{ab}	6.7^{abcd}	9.2^{bcde}	2.4^{abc}	7.4^{abcde}	2.1^{b}	5.8^{abcdef}	2.2^{ab}	5.1^{abcdef}	2.1^{bcde}	2.7^{abcde}
SCN 6	1.1^{bcd}	1.0^{abc}	4.5^{a}	2.7^{defg}	9.1^{a}	11.3^{abc}	1.9^{bcd}	9.4^{abc}	1.8^{bcd}	9.2^{a}	1.9^{bc}	8.2^{a}	3.1^{ab}	3.8^{a}
NABE 4	1.0^{bcd}	0.7^{bc}	4.2^{abc}	4.4^{a}	5.2^{bcdef}	7.8^{bcdef}	2.2^{bcd}	9.6^{ab}	2.0^{bc}	8.1^{ab}	2.0^{bc}	5.1^{abcdef}	1.7^{defg}	3.2^{abc}
SCN 9	0.8^{d}	0.9^{abc}	4.3^{ab}	4.3^{a}	9.1^{a}	15.4^{a}	1.0^{cd}	3.5^{defgh}	0.8^{efgh}	2.5^{cdefg}	0.6^{gh}	1.9^{defg}	1.1^{efghi}	2.5^{abcde}
Mean	1.3	0.8	4.4	3.7	7.7	10.6	2.2	7.5	1.9	6.5	1.9	5.1	2.5	3.1
SE^{c}	0.2	0.3	0.4	0.4	1.1	1.5	0.8	1.9	0.3	1.8	0.3	1.5	0.4	0.7
LSD^{d} (5%)	0.6	0.8	1.1	1.3	3.2	4.3	2.4	5.7	0.9	5.2	0.8	4.4	1.2	2.1

Drought intensity index for the experiment = 0.76, ^{a}DS = Intermittent drought stress, ^{b}WW=Well watered, ^{c}Standard error of the mean, ^{d}Least significance difference, ^{c,d}Obtained from analysis of both F_2 populations and parent.

Table 4. Variances, variance components, Baker's ratio and coefficients of genetic determination on entry mean basis for response of 18 F_2 populations to drought stress within a watering regime.

Source of variation	d.f[a].	Growth indicators of drought stress						Yield associated indicators of drought stress							
		Leaf rolling		Primary leaf lamina drooping		Number of trifoliate leaf		Dry pod weight (g/p)		Dry seed weight (g/p)		Pod number per plant		Seed number per pod	
		DS[b]	WW[c]	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW
Variance															
GCA[d] (Exotic)	4	0.09	0.068	1.28***	0.33	1.25	7.03*	1.57	4.72	0.458**	3.45	0.799***	2.61	1.26***	1.86*
GCA (Local)	1	0.306*	0.375*	1.41**	1.34*	17.55***	15.70*	3.42*	17.33*	0.706**	7.27	1.678***	13.43*	1.87**	0.01
SCA[e]	4	0.071	0.216*	0.2	0.64*	0.68	3.17	0.81	2.42	0.118	2.11	0.143	1.28	0.06	0.41
Reciprocal	8	0.049	0.12	0.40*	0.32	0.41	1.78	0.81	5.76	0.07	3.68	0.112	3.51	0.32	0.54
Direction	1	0.033	0.059	0.28	1.00*	0.18	5.3	0.01	9.44	0.001	5.5	0.149	2.55	1.60**	0.88
Error	24	0.04	0.069	0.13	0.89	1.18	2.18	0.69	3.76	0.09	3.12	0.084	2.27	0.16	0.5
Variance component															
GCA (E)	4	0.013	0	0.29	0.04	0.02	1.21	0.22	0.18	0.092	0.06	0.179	0.08	0.27	0.34
GCA (L)	1	0.027	0.031	0.07	0.12	1.64	1.35	0.27	1.36	0.062	0.42	0.16	1.12	0.17	-0.05
SCA	4	0.031	0.157	0.13	0.45	-0.5	0.99	0.19	-1.34	0.028	-1.01	0.059	-1	-0.1	-0.09
Genetic determination on entry mean basis															
Baker's ratio		0.56	0.17	0.86	0.25	0.77	0.72	0.81	0.53	0.85	0.32	0.85	0.55	0.82	0.81
NS CGD[f]		0.36	0.12	0.67	0.19	0.5	0.45	0.38	0.23	0.57	0.1	0.7	0.27	0.64	0.4
BS CGD[g]		0.64	0.72	0.78	0.76	0.65	0.62	0.47	0.43	0.67	0.32	0.83	0.49	0.77	0.49

[a]Degree of freedom; [b]DS = Intermittent drought stress; [c]WW = Well watered; [d]GCA = General combining ability; [e]SCA = Specific combining ability; [f]NS CGD = Narrow sense coefficient of genetic determination; [g]BS CGD = Broad sense coefficient of genetic determination; ***, **,* = significant levels at P ≤ 0.001, 0.01, 0.05, respectively.

Heritability and Baker's ratio

Baker's ratios for genetic determination greater than 0.8 and 0.5 were reported under water stress treatment for yield associated variables and growth parameters, respectively. Under water stress, the NS-CGD ranged from 0.36 to 0.7 while BS-CGD ranged from 0.47 to 0.83 for all parameters (Table 4).

Combining ability effects

The parents with positive significant GCA effects for number of trifoliate leaf, dry pod and seed weight, pod number per plant and seed number per pod were defined as good combiners, whereas those with negative significant and non-significant GCA effects for these traits were designated poor combiners. This is because high values for these variables are desirable in a well performing progeny, whereas the opposite was true for leaf rolling, and primary leaf lamina drooping since lower values for these variables could imply less drought stress on a progeny. Genotype SCN 9 had the lowest significant (P ≤ 0.05) GCA effect for leaf rolling, primary leaf lamina drooping, seed weight, pod and seed number and it was followed by NABE 4 for all growth parameters under water stress. On the other hand, SCR 48 had high significant (P ≤ 0.05) GCA effect for primary leaf lamina drooping and on number of pod per plant and seed per pod. It also had high GCA effects pod and seed yield. The genotype, SEN 98 had the highest GCA effect for seed yield and pod weight and also a high significant (P ≤ 0.05) GCA effect for pod number (Table 5).

Considering the specific combining ability, F_2 individuals of NABE 15 and SEN 98 had high positive SCA effects for trifoliate leaf number, pod weight (significant at P ≤ 0.05) and pod number

Table 5. Effect of general combining ability for growth and yield associated parameters in common bean genotypes under contrasting water regimes.

Genotype	Growth parameters						Yield associated variables							
	Leaf rolling		Primary leaf lamina drooping		Trifoliate leaf number per plant		Dry pod weight		Dry seed weight		Pod number per plant		Seed number per pod	
	DS[a]	WW[b]	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW
SEN 98	-0.09	0.20	0.45*	-0.30	-0.02	-0.07	1.03*	0.47	0.42*	0.36	0.38*	0.43	0.35	-0.07
SCR 48	0.07	-0.25	0.42*	0.33	0.81	2.22**	0.18	1.61	0.28	1.44	0.45*	1.38	0.50*	0.64
SEN 99	0.20*	-0.04	-0.06	0.04	-0.02	-0.52	-0.06	-0.02	0.24	0.41	0.19	-0.18	0.41	0.69*
SCN 6	0.02	0.05	0.11	0.02	-0.09	0.50	-0.42	-0.14	-0.39*	-0.31	-0.39*	-0.43	-0.48*	-0.27
SCN 9	-0.21*	0.05	-0.92***	-0.08	-0.67	-2.13**	-0.73	-1.92	-0.55***	-1.9	-0.62**	-1.19	-0.80**	-0.99**
NABE 15	0.13	0.16	0.29	0.31	0.96	0.98	0.51	0.98	0.27	0.67	0.34*	0.89	0.36	-0.04
NABE 4	-0.13	-0.16	-0.29	-0.31	-0.96	-0.98	-0.51	-0.98	-0.27	-0.67	-0.34*	-0.89	-0.36	0.04
SE[c] (Exotic)	0.07	0.15	0.17	0.25	0.50	0.74	0.13	1.19	0.14	1.12	0.16	0.82	0.19	0.32
SE (Local)	0.07	0.14	0.15	0.22	0.45	0.66	0.12	1.07	0.12	1.0	0.14	0.74	0.17	0.29

[a]DS = Intermittent drought stress; [b]WW = Well watered; [c]Standard error of the effects; ***, **,* = significant levels at P ≤ 0.001, 0.01, 0.05, respectively.

under water stress. High positive SCA effects were in turn recorded for pod and seed weight and pod number for the cross SEN 99 x NABE 15. Furthermore, the cross NABE 15 x SCR 48, had relatively high SCA effects for trifoliate leaf number, and seed number under drought stress. The SCA effect was high for most drought stress indicators under well watered condition (Figure 1).

DISCUSSION

In any breeding strategy, germplasm diversity is of paramount importance when creating a breeding population (Kiwuka et al., 2012). Knowledge of the sources of resistance/tolerance and the gene action governing the trait of interest is particularly important in the improvement and selection of desired traits. This study was performed to investigate the mechanism of inheritance of drought tolerance in the crosses of Ugandan genotypes and CIAT drought-tolerant genotypes as a prerequisite in planning an efficient breeding program for drought tolerance in common bean in Uganda.

Phenotypic performance of F_2 populations and parents

The drought intensity index (DII) for the experiment calculated basing on seed yield was 0.76 implying the water stress was high. Values of DII exceeding 0.70 indicates severe drought (Ramirez-Vallejo and Kelly, 1998). Nonetheless, high differences occurred between parents and crosses for all parameters suggesting diversity among genotypes. Generally, the parents performed better than the crosses for most yield associated indicators of drought stress because many F_2 plants did not produce seed. Thus, there were not many elite recombinants. In addition, analysis of variance showed more contribution from the exotic genotypes for yield and associated parameters and more for growth parameters from the local genotypes.

Contribution of the exotic verses local parent

The relative magnitude of GCA and SCA variance or variance component provides information on the predominant type of gene controlling the inheritance of a trait (Baker, 1978). On the other hand, the relative magnitude of variance component of GCA male (exotic) and GCA female (local) provides information on the relative genetic contribution of the different categories of parents used in a cross. The significant differences reported in both GCA variance for exotic parents and GCA variance for local parents under water stress implies that gene action is additive and both exotic and local parents contributed towards

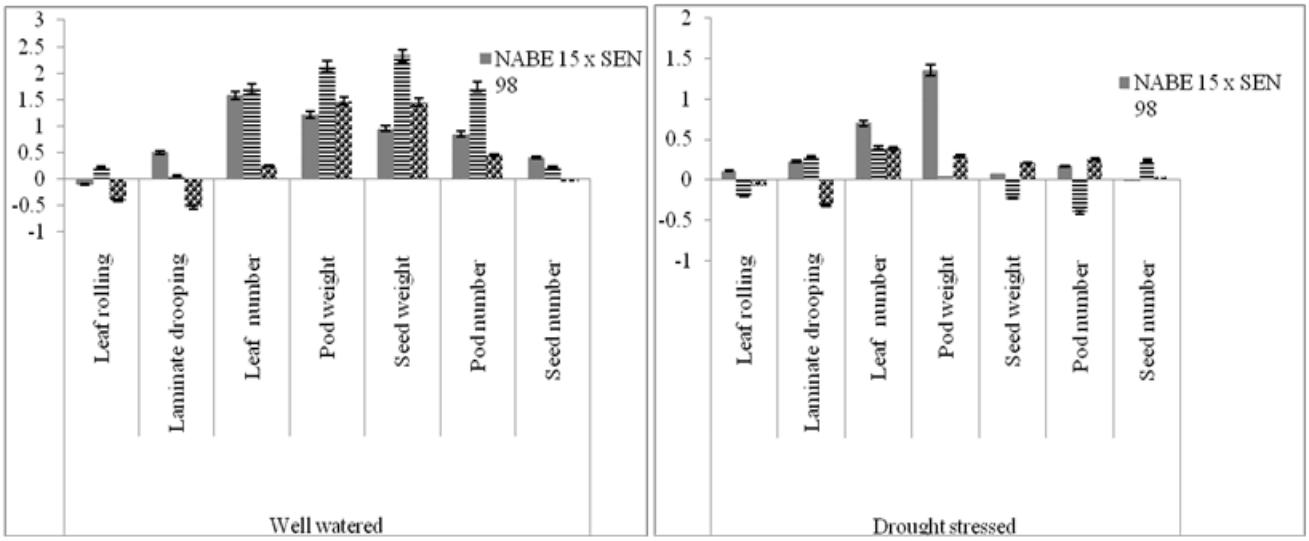

Figure 1. Effect of specific combining ability for growth and yield associated parameters in the crosses of NABE 15 by SEN 98, SEN 99 and SCR 48. These crosses were selected basing on positive significant SCA effects observed in most yield attributes.

drought tolerance or sensitivity for primary leaf lamina drooping (LD-P), seed weight, pod number per plant and seed number per pod.

In addition, the GCA variance for local parents were not only significant but also had the highest variance components for pod weight under water stress, implying that accumulation of assimilates in pod wall was mainly contributed by the local parent. There was more contribution by the exotic parents for LD-P, seed weight, seed number per pod and pod number per plant basing on the relative magnitude of variance components under water stress.

Heritability and Baker's ratio

The predominant role of additive genes in the inheritance of seed yield under water stress is supported by previous studies (Venkatraman et al., 2007; Badr, 2005; Asadi et al., 2010). However, contrary to the findings of these studies, the SCA variance of parents for seed biomass yield was not significant although its variance component was high, possibly implying statistical inadequacy due to small sample size. High SCA variance like that obtained in leaf rolling (LR) indicates presence of non-additive genes (Baker, 1978) which results in low heritability and thus delayed selection till advanced generations at F_6 or F_7. Seed weight exhibited high estimates for narrow sense (≥ 0.50) and broad sense (≥ 0.72) coefficients of genetic determination on entry mean basis as did LD-P, number of trifoliate leaves, pod and seed weight, pod and seed number. The result on seed weight is supported by findings of Ramirez and Kelly (1998). Despite the high narrow sense heritability reported in these traits, increased replication and multi-location testing would be necessary to effectively select for drought tolerance because it is quantitative inherited (Teran and Singh, 2002; Beebe et al., 2008) and high genotype x environment has been reported (Beebe et al., 2013). In addition, these traits also recorded a high Baker's ratio (≥ 0.77) under drought stress implying predominance of additive genes. The genetic superiority observed in one generation would, therefore, be largely passed on to subsequent generations. It also means that the value of the F_2 individuals can be predicted from the mid parent. Baker's ratio of 1 implies total influence of additive genes (Baker, 1978). For a self-pollinated crop like bean, a trait with high Baker's ratio means that the genes controlling that trait can be fixed by the breeder in advanced generations, a time when non-additive genes have been lost.

Combining ability effect

Combining ability effects are effective genetic information used in planning the next phase of breeding programs. From this study, the lowest negative significant GCA effects recorded for SCN 9 with respect to LR and LD-P under water stress are desirable indicators of drought tolerance. Genotype SCN 9 has the potential to produce more progenies that can withstand high levels of water stress before showing LR and leaf lamina drooping signs. Similarly, the low negative non-significant GCA effect for LR and LD-P recorded for SEN 98 and SEN 99 respectively, the high positive significant GCA effects for pod and seed biomass, and pod number per plant recorded for SEN 98 in addition to the high positive GCA effects for seed weight, pod number per plant and seed number per pod obtained for SEN 99 are the desirable

effects for producing more drought-tolerant progenies. This is in agreement with Franco et al. (2001) findings where they reported that crosses involving parents with higher estimates of general combining ability for traits where high values are desirable should be potentially superior for the selection of lines in advanced generations.

Given the high SCA effects recorded in F_2 individuals of NABE 15 and SEN 98 for trifoliate leaf number and pod weight and in SEN 99 x NABE 15 for pod and seed dry weight and pod number per plant would indicate that the means of these F_2 individuals were higher than predicted for the mentioned indicators of drought stress. These effects imply that genotypes SEN 99 and NABE 15 could be considered as good combiners for use in future drought breeding programs in common bean.

Conclusions

This study generated knowledge on the genetic inheritance of drought tolerance in a chosen set of common bean parents. The role of additive genes was noted to be greater than non-additive gene action in most parameters under drought stress. This implies that weight and number of seeds and pods, number of trifoliate leaves and laminate drooping can be fixed in advanced generations. In comparison, it is worth noting that non-additive genes; dominance or epistasis played a significant role in the inheritance of leaf rolling under water stress which suggests that this trait would be lost in advanced generations. Genotypes SEN 99 and NABE 15 were noted to be good combiners because they had a high SCA effect resulting from a higher mean for seed yield, pod weight and pod number than predicted.

In addition, genotypes SEN 98, SEN 99 and SCR 48 had high positive GCA effects for yield associated variables. Thus, these genotypes should be useful donors to improve drought tolerance. The best progenies from the cross made between NABE 15 x SEN 99, SEN 98 x NABE 15 and SCR 48 x NABE 15 (Figure 1) will be further screened and advanced and could possibly be released as new drought tolerant bean genotypes with traits that are preferred in Ugandan markets by local consumers.

Conflict of Interest

The authors have not declared any conflict of interest.

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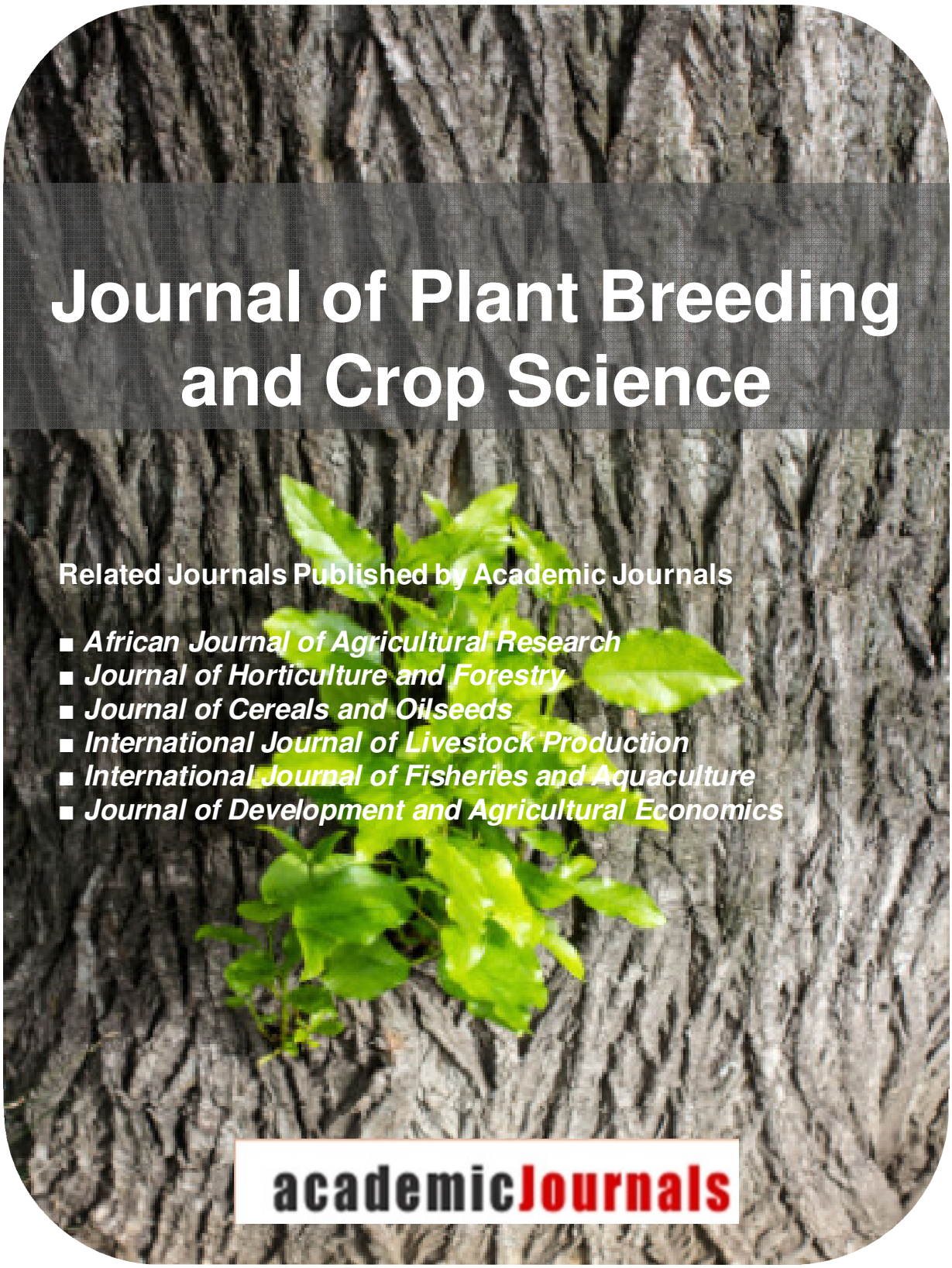

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