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Effect of low temperature stress on field performance of highland sorghum (*Sorghum bicolor* (L.) Moench) at flowering stages

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Sorghum is a C4 grass native in the semi-arid environments of the African sub-Saharan and consequently chilling stress can affect the performance of the crop, especially at the reproductive stages. Moreover, a significant delay of flowering and maturity was observed when sorghum grows under low temperatures regions, and consequently farmers in highland areas of Uganda face yield penalties. Forty genotypes were evaluated in 2017B and 2018A seasons under non-stress (Kabanyolo) and cold stress (Kachwekano and Zombo) field conditions. Data were recorded on: Days to 50% flowering, days to physiological maturity, culm height, panicle length, panicle weight, kernel weight per panicle, and thousand grain weight. Mean comparison of most agronomic traits recorded indicated high significant differences for season-by-genotype, location-by-genotypes, and the three-way interaction (GxLxS). This indicates that cold stress significantly affects yield components. Significant positive correlation was obtained between days to 50% flowering, days to maturity, and culm height, which suggested that simultaneous improvement of these traits is possible. Some genotypes (IESV 91003LT, IESV 91105LT and IS 29376) were best ranked in normal environment but poorly performed in cold environments, which indicates lack of adaptation in highland. BM6, Cytanobe, IESV 91018, IESV 91609, IS 25563 showed generally good performance and stability in all locations. Therefore, these genotypes can be used as parental lines for further breeding process.

Key words: Sorghum, cold stress, flowering, maturity, yield component.

INTRODUCTION

Sorghum (*Sorghum bicolor* L. Moench) is among the most important food and animal feed grain crop wordwide and can be considered as the best bioenergy source in this era of global climate change (Reddy et al., 2008), owing to various merits in terms of tolerance to abiotic stresses (Tari et al., 2013). As a C4 grass native in the As a C4 grass native in the semi-arid environments of the African Sub-Saharan regions, the crop is well adapted to hot and dry conditions. However, its gradual introduction into regions characterized by low temperatures has led to

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the evolution of adapted cold tolerant sorghum (Maulana and Tesso, 2013). Although some progress has been made, numerous abiotic stresses, including cold stress, continue to present challenges in most sorghum producing areas.

Cold stress is a major determinant in the rate of plant growth and development, as well as distribution of plant genotypes in various regions of the planet (Sharma and Solanke and Sharma, 2008; Ramankutty et al., 2008; Yadav, 2009). Sorghum genotypes differ in their growth and development at the threshold temperature of around 15°C (Singh, 1985; Maiti, 1996). Therefore, a genotype can mature faster in non-stress environment, while in cold environment maturity is delayed. This is because gene expression patterns responsible for growth and development are altered under cold environment, and therefore protein stability is compromised which impairs stem and leaf growth (Rymen et al., 2007; Janmohhamadi et al., 2015). Chilling stress was found to cause a significant decline in key cellular functions and photosynthetic activity (Allen and Ort, 2001; Rapacz et al., 2008).

The effect of cold stress on plant growth rate and days to flowering varies among sorghum genotypes (Maulana and Tesso, 2013). However, earliness was found to be affected by both genetic background, environmental conditions, or the interaction of both. Recent studies reported six maturity genes and 40 QTL with small additive effects on flowering time (Rooney and Aydin, 1999; Mace et al., 2013). Hence, development of early maturing sorghum genotypes is a paramount goal for numerous breeding programs due to the fact that harvest can be done before the new season of cold and rainy weather resumes, thereby allowing famers to increase productivity and as well reduce yield penalties.

In Uganda, sorghum is grown in almost all agricultural regions, including the higher altitude regions that cover 25% of the arable land with high population density compared to the national density (Kasozi et al., 2005). To avoid the effects of seasonal cold temperatures, farmers in highland regions of Uganda plant sorghum 4 to 6 weeks before the beginning of the cold period that usually start from February to July. However, farmers are still using unimproved varieties with a longer maturity period of about eight months. Therefore, farmers would benefit from having genotypes with reduced maturity period for production twice per annum in order to alleviate issues of malnutrition and food insecurity. The objective of this study was to evaluate the effect of cold temperatures on plant development, flowering, maturity and yield components of sorghum genotypes in order to identify genetic sources of early maturity under cold stress.

MATERIALS AND METHODS

Genetic plant materials

The forty highland sorghum genotypes used in this research study were acquired from International Crops Research Institute for Semi-Arid Tropics (ICRISAT, Nairobi – Kenya), including various breeding lines, released varieties and local landraces. The names, origins and characteristics of sorghum genotype used in the present study are given in Table 1.

Experimental design

Sorghum genotypes were evaluated during two consecutive seasons (2017B and 2018A) at three locations: Kachwekano field farm (1° 15'S, 29° 57'E, 2,200 m.a.s.l.), located in the highland of South Western region of Uganda, is characterized by a bi–modal rainy season with an annual average rainfall of 1,300 mm, and has a sandy clay loam soil; Zombo (2° 40'S, 30° 54'E; 1,705 m.a.s.l.) situated in the northern region of the country, has heavy clay loam soil with an annual temperature and cooler temperature amplitude; while Kabanyolo (0° 32’N, 32°37’E, 1,240 m.a.s.l) is mid-altitude region characterized by relative optimum temperature ranges (19 - 28°C) for sorghum growth (Table 2).

A 4 × 10 alpha lattice design was used for this experiment with three replications. Plots of 3 m by 2.25 m were laid with spacing of 30 cm within row, and 75 cm between rows. Seeds were planted at 2 cm depth and agronomic practices were applied when necessary. Insecticides (Cypermethrin) were also applied regularly in order to control stem borer and shoot flies.

Data collection and statistical analysis

Data collection included: days to 50% flowering, days to physiological maturity, culm height, panicle length, number of leaves, panicle weight, kernel weight per panicle and thousand kernel weight. Days to 50% flowering were determined as the mean number of days from planting to half-bloom stage. Days to maturity was measured as the average number of days from planting to when the grains on the lower one-third section of the panicles have reached physiological maturity (formed black layer called aleuron). Culm height was recorded as the length of the plant from the ground to the beginning of the panicle, while the panicle length was measured as the length from the beginning to the tip of the panicle. After completion of physiological maturity, panicles were detached, dried and kernel threshed to measuring yield components. Panicle weight was measured as the weight of panicles from individual plants. Kernel weight per panicle was determined as the mean weight of kernels threshed from the individual panicle. A thousand kernel weight was measured and determined from each panicle.

A Restricted Maximum Likelihood (ReML) analysis was used to generate analysis of variance (ANOVA) for single site analysis, using Genstat 18th edition (VSN International, England). For multiple interactions (Genotype x Location x Season), data were analyzed as Randomized Complete Block Design (RCBD) in which replications, locations and seasons were considered as random and genotypes as fixed effects. Means were separated by Fisher’s protected least significance difference at 5% probability level. Pearson correlation was used to determine relationship among traits recorded in this experiment.

RESULTS

Growth and phenological parameters

The pooled analysis of variance including genotype, locations and seasons and their interactions, is presented in Table 3a and b. Genotypes, locations and seasons

Table 1. List of sorghum accessions, origins and characteristics used the study.

Accession name	Origin	Status	Subspecies	Seed color
ABALESHYA	Rwanda	Fixed line	Caudatum	Red
AMASUGI	Rwanda	Fixed line	Durra	Red
BM 16	Uganda	Fixed line	Caudatum	Red
BM 21	Uganda	Fixed line	Bicolor-caudatum	Red
BM 27	Kenya	Fixed line	Caudatum	Red
BM 29	Kenya	Fixed line	Bicolor-caudatum	Red
BM 6	Kenya	Fixed line	Caudatum	Red
CYTANOBE	Uganda	Fixed line	Bicolor	Red
NYUNDO	Rwanda	Fixed line	Caudatum	Red
E 1291	Kenya	Fixed line	Bicolor-caudatum	Red
IESV 90015 LT	Kenya	Breeding line	Bicolor	Red
IESV 90042 LT	Kenya	Breeding line	Caudatum	Red
IESV 91003 LT	Kenya	Breeding line	Caudatum	White
IESV 91018 LT	Kenya	Breeding line	Kafir	Red
IESV 91054 LT	Kenya	Breeding line	Kafir	Red
IESV 91069 LT	Kenya	Breeding line	Caudatum	Red
IESV 91071 LT	Kenya	Breeding line	Bicolor	Red
IESV 91073 LT	Kenya	Breeding line	Bicolor-caudatum	Red
IESV 91075 LT	Kenya	Breeding line	Caudatum	Red
IESV 91105 LT	Kenya	Breeding line	Caudatum	White
IKINYARUKA	Rwanda	Fixed line	Caudatum	Red
IS 11141	Kenya	Breeding line	Bicolor	Red
IS 11612	Kenya	Breeding line	Bicolor	Red
IS 11721	Kenya	Breeding line	Caudatum	Red
IS 11838	Kenya	Breeding line	Bicolor-caudatum	Red
IS 25546	Kenya	Breeding line	Caudatum	Red
IS 25547	Kenya	Breeding line	Caudatum	Red
IS 25557	Kenya	Breeding line	Bicolor-caudatum	Red
IS 25558	Kenya	Breeding line	Bicolor	Red
IS 25561	Kenya	Breeding line	Caudatum	Red
IS 25562	Kenya	Breeding line	Durra	Red
IS 25563	Kenya	Breeding line	Kafir	Red
IS 29415	Kenya	Breeding line	Kafir	Red
IS 25545	Kenya	Breeding line	Bicolor	Red
MB 30	Kenya	Fixed line	Caudatum	Bright orange
N 12	Uganda	Fixed line	Bicolor-caudatum	Red
N 2	Uganda	Fixed line	Bicolor	Red
NDAMOGA	Uganda	Fixed line	Caudatum	Red
S 87	Kenya	Breeding line	Caudatum	Red
IS 11442	Kenya	Breeding line	Bicolor	Red

significantly affected culm height and panicle length. Although, the average reduction of culm height was about 12 cm and 17 cm at Zombo and Kachwekano compared to the optimal growth condition of Kabanyolo, respectively, there was marked variation among sorghum lines. Results showed that late maturing genotypes such as IS 11442, IS 25545, IS 11612 and IS 11721, recorded the tallest culm height (> 250 cm) across environments (Appendix 2). Generally, culm height was greatly affected by cold temperatures, since the non-stress environment of Kabanyolo (Mean: 180.9 cm; range: 100.8 to 323 cm) recorded the higher average compared to Zombo (Mean: 168.5 cm; range: 89.6 to 295.7 cm) and Kachwekano (Mean: 163.3 cm; range: 85.3 to 281.3 cm) (Table 4).

Days to 50% flowering and maturity period were both affected by cold stress, as indicated by the significant interaction of genotype x location x season (Table 3a). As expected, Kachwekano had the longest days to 50%

Table *2*. Data on climatic conditions of the field experiments at three locations.

Location	Season	Trial date (sowing-harvest)	Mean temp. (°C)	Mean max temp. (°C)	Mean min. temp. (°C)	Precipitations (mm)
Kachwekano	2017B	August-April	16.4	23.1	11.6	543
	2018A	February-October	15.3	21.9	10.8	466
Zombo	2017B	August-February	18.4	25.7	14.4	572
	2018A	February-September	19.1	25.5	13.8	508
Kabanyolo	2017B	August-January	22.4	29.2	16.6	612
	2018A	February-July	21.7	28.7	15.3	487

flowering (Mean: 138.5 days; range: 117.8 to 167.3 days) followed by Zombo (Mean: 113.2 days; range: 88.6 to 153.5 days) while the non-stress environment of Kabanyolo recorded the shortest days to flowering (Mean: 75.8 days; range: 58.2 to 108.3 days). A significant genotype x season interaction indicated that flowering took slightly longer in the second season as compared to the first season. A similar trend was observed in days to physiological maturity, since additional 56 days at Zombo, and 73 days at Kachwekano were required to complete this stage, as compared to the non-cold stress environment of Kabanyolo. Generally, genotypes IESV 90015 LT, IESV 90042 LT and IESV 91003 LT flowered earlier than others across environments, while AMASUGI, IS 255545 and IS 11442 matured later (Appendix 2). Moreover, sorghum lines such as IESV 91054 LT, and IS 29415 failed to reach their reproductive stages due to their cold susceptibility under Kachwekano and Zombo environment.

Yield components

As expected, highly significant differences on all yield components evaluated in this study were observed and the genotypes and locations contributed significantly as sources of variation (Table 3a and b). Except at Kabanyolo, the season 2018A recorded relatively inferior yield components values because of extended periods of lower temperatures that occurred from March to August 2018 at Kachwekano and Zombo (Table 4). Overall, the cold weather of Kachwekano reduced 3 to 31.6% across sorghum genotypes, as compared to Kabanyolo. Except IESV 91105 LT that ranked first in the non-cold stress environment (Mean panicle: 144.8 g) and failed to reach maturity in the cold environments of Kachwekano and Zombo, results showed that AMASUGI, BM 6, CYTANOBE and IESV 91018 LT expressed higher panicle weight across environments, however, variation among other sorghum lines were marked.

Thousand kernel weight (TKW) and kernel weight per panicle averaged 25.2 and 73.2 g, respectively, at Kabanyolo, while it decreased at Zombo (TKW: 23.3 g; Kernel weight: 63.2 g) and Kachwekano (TKW: 22.6 g; Kernel weight: 60.8 g). As expected, highest kernel weight per panicle was recorded at MUARIK (IESV 91105 LT: 121.5 g), while the maximum at Zombo and KAZARDI was 102.3 g for IESV 91105 LT and 82.6 g for BM 6, respectively. Although there was marked variation in sorghum lines across locations and seasons (significant genotype x location x season), IESV 91105 LT recorded the highest kernel weight per panicle (Mean: 121.5 g), while the maximum at Zombo and Kachwekano was 102.3 g for IESV 91105 LT and 82.6 g for BM 6, respectively. Although there was marked variation in sorghum lines across locations and seasons (significant genotype x location x season), IESV 91003 LT and IESV 91105 LT expressed a higher TKW but were partially tolerant to cold, since they were unable to survive the weather conditions of Kachwekano in the season B. However, three sorghum genotypes recorded the lowest TKW, less than 17 g, at Kachwekano (BM21, IESV 91071 LT, IS 25561), Zombo were (BM16, IS 11721, IS 29376), while AMASUGI, IS 11612, and IS 11721 were ranked as the last at Kabanyolo.

Relationship among observed traits in the field trials

At Kachwekano, days to flowering was positive and highly significantly correlated to days to maturity (r = 0.95), culm height (r = 0.63), but negatively significant correlated to thousand kernel weight (r = -0.57) and slightly correlated to panicle weight (r = -0.29) (Table 5). Days to maturity was also highly significant correlated with culm height (r = 0.65) and thousand kernel weight (r = -0.54), and slightly correlated with panicle weight (r = -0.29) but non-significant with panicle length (r = 0.12) and kernel weight (r = -0.29). Moreover, panicle weight was also highly correlated to kernel weight (r = 0.96).

A similar trend was observed at both Kabanyolo and

Table 3. (a) Mean squares of recorded traits and their interactions across all locations and seasons; (b) Mean squares of the evaluated sorghum traits and their interactions partitioned into 2017B and 2018A seasons.

Source of variation	d.f.	Days to 50% Flowering	Days to Maturity	Culm Height (cm)	Panicle Length (cm)	Panicle Weight (g)	Kernel Weight (g)	T KW (g)
Location (L)	2	239,321.2***	332,489.2***	23,827***	698.2***	14,481.9***	12,140***	354.8***
Season (S)	1	6,076.9***	10,351.5***	14.3ns	27.7*	9.3ns	190.8ns	203.8***
L x S	2	765.8***	525.6***	511.5ns	2.3ns	624.4**	424.4*	81.2***
L x S/Rep	12	21.41	19.42	138.14	4.4	76.64	66.06	3.43
Genotype (G)	39	1,758.96***	1,779.43***	55,845.01***	343.23***	3,305.36***	2,240.98***	267.51***
G x L	76	140.19***	225.41***	463.90*	14.10ns	143.27*	132.16*	13.89*
G x S	39	29.02ns	51.71ns	488.84*	10.32ns	96.51ns	102.00ns	24.94***
G x L x S	72	49.62***	51.30***	285.45***	12.21***	90.82***	87.07***	9.42***
Pooled error	452	12.48	7.54	77.57	3.98	24.66	17.55	2.53

Source	d.f.	Days to 50% Flowering	Days to Maturity	Culm Height (cm)	Panicle Length (cm)	Panicle Weight (g)	Kernel weight (g)	TKW (g)
				2017 (Season B)				
Location (L)	2	120,707.82***	175,535.33***	9,071.24***	293.07***	5,925.23***	6,295.18***	62.08*
Rep/L	6	11.25	13.7	239.88	5.6	82.07	54.57	6.88
Genotype (G)	39	1,166.68***	997.11***	27,198.13***	161.52***	2,000.21***	1,383.22***	249.16***
G x L	73	122.46***	147.25***	308.35***	14.69***	144.59***	120.97***	9.70***
Error	224	11.92	5.76	59.74	3.23	26.28	18.07	2.63
s.e.d.		2.82	1.96	6.31	1.47	4.18	3.47	1.32
CV (%)		3.34	1.65	4.52	6.05	6.29	6.52	7.09
				2018 (Season A)				
Location (L)	2	154,288.36***	210,705.73***	1,6140.15***	377.703***	11,287.35***	8,392.96***	652.59***
Rep/L	6	31.75	19.22	101.9	3.7	142.17	117.24	1.968
Genotype (G)	49	1,170.87***	1,052.39***	29,552.40***	161.97***	2,498.08***	1,762.67***	343.93***
G x L	63	134.52***	186.87***	393.36***	10.47***	85.79***	75.75***	17.63***
Error	224	11.39	8.76	77.39	4.593	25.91	19.66	2.71
s.e.d.		2.75	2.41	7.18	1.75	4.15	3.62	1.34
CV (%)		3.1	1.94	5.14	7.27	6.18	6.64	6.73

*, **, *** Significant at P ≤ 0.05, P ≤ 0.01, and P ≤ 0.001, respectively; TKW= Thousand Kernel weight.

Zombo, where days to flowering was significantly correlated to days to maturity (r = 0.90 and r = 0.93, respectively), culm height (Kabanyolo: r = 0.53; Zombo: r = 0.56) and thousand kernel weight (Kabanyolo: r = -0.46, Zombo: r = -0.37). Days to maturity was significantly correlated to culm height (Kabanyolo: r = 0.53, Zombo: r = 0.56). Panicle length was only significant correlated to culm height (Zombo: r = 0.28; Kabanyolo: r= 0.36) and thousand kernel weight (Kabanyolo: r = -0.35; Zombo: r = -0.31).

Panicle weight was highly significant correlated

Table 4. Descriptive statistics of phenological parameters and yield related traits at three locations.

Phenological parameter	Statistics	Kabanyolo		Zombo		Kachwekano	
		2017B	2018A	2017B	2018A	2017B	2018A
Days to 50% flowering	Min	55.33	61.00	86.33	91.00	112.67	122.95
	Max	112.00	104.67	145.33	161.67	162.33	172.33
	Mean	74.85	76.78	109.94	116.49	134.11	143.06
	SD	10.93	8.51	11.56	13.51	10.55	9.91
Days to maturity	Min	93.67	101.00	129.67	135.33	158.67	166.83
	Max	151.00	141.67	190.67	218.00	208.33	219.33
	Mean	109.29	113.46	154.06	163.28	180.13	189.49
	SD	10.78	8.20	12.82	15.47	10.12	9.94
Culm height (cm)	Min	105.67	101.00	86.00	93.33	84.67	84.32
	Max	317.00	329.00	297.00	294.33	278.00	284.67
	Mean	192.28	195.67	180.23	180.07	175.83	173.44
	SD	56.29	61.32	55.26	56.55	53.89	56.31
Panicle length (cm)	Min	22.57	21.00	20.17	17.63	19.07	16.67
	Max	45.93	46.33	42.80	38.60	43.83	41.17
	Mean	31.95	31.78	29.38	28.85	28.98	28.50
	SD	4.80	5.34	4.90	4.51	4.56	4.23
Panicle weight (g)	Min	54.40	58.23	47.37	48.70	50.10	44.53
	Max	137.80	151.93	123.33	107.00	101.57	96.64
	Mean	84.87	88.29	76.72	75.31	72.78	70.08
	SD	16.58	17.23	15.08	13.13	12.74	12.21
Kernel weight (g)	Min	46.07	48.90	33.77	39.83	40.10	34.07
	Max	113.70	129.40	102.83	90.20	83.20	80.02
	Mean	69.43	71.99	58.24	60.81	58.52	56.48
	SD	13.43	14.74	13.28	11.29	10.19	10.42
Thousand kernel weight (g)	Min	15.59	16.38	14.53	16.34	16.11	16.13
	Max	38.87	40.77	37.29	38.72	35.64	34.57
	Mean	21.81	24.09	20.88	21.83	20.59	20.55
	SD	4.26	4.58	4.35	4.70	4.01	4.00

to kernel weight (Zombo: r = 0.96; Kabanyolo: r= 0.97), and thousand kernel weight (Zombo: r = 0.53; Kabanyolo: r = 0.54), but non-significant to panicle length (Table 5). Moreover, kernel weight per panicle was significantly correlated to thousand kernel weight at Kabanyolo (r = 0.54) and Zombo (r = 0.55).

DISCUSSION

Effect of cold stress to flowering time

Being a C4 plant native in the tropical regions, sorghum is sensitive to temperature below 15°C at all growth and developmental stages (Solanke and Sharma, 2008). Delays in both flowering time and days to physiological maturity are the most frequent phenomena found in cool weather environments (Kapanigowda et al*.,* 2013), especially in the African highland regions. In the present study, we noted that sorghum grown under cool weather (Kachwekano and Zombo) delayed significantly to reach days to 50% flowering and physiological maturity, even for the cold tolerant lines. This is because cold stress acts on key cellular functions, metabolism and photosynthetic activity (Rymen et al., 2007; Zhu et al*.,* 2007; Liu et al., 2019). Therefore, plants responded by slowing the growth rate during the vegetative stage, except for susceptible sorghum lines that died at early developmental stages.

Flowering time and physiological maturity are

Table 5. Phenotypic correlation among observed traits for 40 sorghum lines across locations.

Trait	Location	Days to flowering	Days to maturity	Culm height	Panicle length	Panicle weight	Kernel weight
Days to maturity	Kachwekano	0.95***					
	Zombo	0.93***					
	Kabanyolo	0.90***					
Culm height	Kachwekano	0.63***	0.65***				
	Zombo	0.64***	0.55***				
	Kabanyolo	0.70***	0.53***				
Panicle length	Kachwekano	0.19^{ns}	0.12^{ns}	0.24^{ns}			
	Zombo	0.06^{ns}	0.05^{ns}	0.28*			
	Kabanyolo	0.27^{ns}	0.28	0.36*			
Panicle weight	Kachwekano	-0.29*	-0.29*	-0.20^{ns}	-0.14^{ns}		
	Zombo	0.10^{ns}	0.11^{ns}	-0.17^{ns}	-0.21^{ns}		
	Kabanyolo	0.09^{ns}	0.12^{ns}	-0.15^{ns}	-0.19^{ns}		
Kernel weight	Kachwekano	-0.25^{ns}	-0.26^{ns}	-0.17^{ns}	-0.15^{ns}	0.96***	
	Zombo	0.04^{ns}	0.05^{ns}	-0.19^{ns}	-0.21^{ns}	0.96***	
	Kabanyolo	0.05^{ns}	0.09^{ns}	-0.13^{ns}	-0.21^{ns}	0.97***	
Thousand kernel weight	Kachwekano	-0.57***	-0.54***	-0.52***	-0.14^{ns}	0.30*	0.28*
	Zombo	-0.37**	-0.28*	-0.54***	-0.31*	0.53***	0.55***
	Kabanyolo	-0.46***	-0.32*	-0.61***	-0.35*	0.54***	0.54***

ns=non-significant, *, **, *** Significant at 0.05, 0.01 and 0.001 levels, respectively.

characteristics controlled by the genetic make-up of the plant and other environmental factors, especially temperatures (Andres and Coupland, 2012). Therefore, different sorghum genotypes can show variable responses under different temperature regime. Since the beginning of 20th century, maturity has been an important trait and one of the main focus for sorghum breeding programs (Quinby et al., 1974). This focus is because knowledge about genetic mechanism that regulate flowering and environmental factors that affect this trait (Murphy et al*.,* 2011), especially temperatures that are responsible for the plasticity in different environments (Marais et al*.,* 2013), could play an important role in the optimization of sorghum production in the highland regions.

Kabanyolo (non-stress environment) was the best environment to identify early maturing sorghum lines, since both cold tolerant and susceptible genotypes were able to reach the final maturity stages. IESV 91003 LT, IESV 91054 LT, and IESV 91105 LT showed early maturity attributes, but showed partial tolerance to cold stress at Kachwekano. This indicates that those sorghum lines could possess recessive alleles for genes responsible for maturity, since they reduce days to flowering (Wang et al*.,* 2015). However, this hypothesis needs to be tested through molecular and genetic analyses.

Generally, sorghum lines delayed by 37 and 63 days, at Zombo and Kachwekano, respectively, compared to non-stress weather conditions of Kabanyolo. Towards the end of the raining period, temperatures rose and cold stress was relieved, thus plants were able to reach their final plant height and complete maturity stage. Although all growth and phenological parameters decreased in all sorghum lines, cold-sensitive sorghum lines were seriously affected compared to tolerant variants. Moreover, physiological maturity was also affected since the grain filling period was longer in both cold environments, whereby the delay caused by this abiotic stress averaged 47 days at Zombo, and 73 days at Kachwekano.

Effects of cold stress on yield components

In tropical native plants like sorghum and maize, low temperature stress cause significant reduction in photosynthetic activity and biomass accumulation, which are the main sources of grain yield (Tari et al., 2013; Fiedler et al., 2014; Ortiz et al., 2017). In fact, cold stress negatively affects chlorophyll function, and consequently photosynthetic activities are significantly decreased (Allen and Ort, 2001; Tari et al., 2013). Furthermore, reproductive organs of plants grown cool environments can be seriously damaged and consequently cause reduction in the yield and yield components, when cold stress coincides with the grain filling period (Pereira da Cruz et al., 2006; Maulana and Tesso, 2013). In case where cold temperatures coincide with male and female organs formation, it may cause irreversible damages such as reduction anthesis rate, failed fertilization, reduced grain filling, which lead to the insufficient grain number per panicle and consequently low grain yield (Clarke and Siddique, 2004; Thakur et al*.,* 2010; Maulana and Tesso, 2013).

The comparison between the non-stress (Kabanyolo) and cold stressed environments (Kachwekano and Zombo) indicated that yield related components were reduced for all evaluated genotypes, although some marked differences were identified whereby some genotypes could only yield a half of their actual performance as compared to Kabanyolo. However, cold tolerance is mainly determined by the levels of expression of cold tolerant responsive genes in the line *per se* (Janmohammadi et al*.,* 2015). Cold tolerant genotypes have developed adaptation strategies to withstand cold stress through cold acclimation, whereby plants adjust to cold tolerance by exposing them to low but non-freezing temperatures (Thomashow, 1999, Chinnusamy et al*.,* 2007). Genetic variability exists in sorghum adapted to high altitude areas of Africa, including the Eastern-African highland regions, which are considered as an important source of cold tolerant sorghum gene pool (Balota et al*.,* 2010).

Conclusion

Low temperatures that coincide with vegetative period can affect various metabolic pathways, slowing growth rate and reduce photosynthetic activities. Consequently, susceptible plants would not survive, while tolerant genotypes with taller plant height can reach flowering and physiological maturity later. In the present study, sorghum genotypes with shorter stature coupled with tolerance to coldness were best ranked as early maturing in the cold environments of the highlands regions of Uganda, and thus can be used as parental lines for future breeding research based on line *per se* performance. Therefore, sorghum breeders need to constantly improve the genetic materials as far as flowering and grain filling period are concerned, as well as other agronomic traits based on farmer's preferences, since this strategy would result in reducing yield penalty and contribute to enhancement of food security.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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