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Response of stay-green quantitative trait locus (QTL) introgression sorghum lines to post-anthesis drought stress

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An experiment was carried out to evaluate the response of sorghum stay-green quantitative trait locus (QTL) introgression lines under induced post-flowering drought stress. The QTL introgression was done in 2006 to 2008 from known stay-green lines to the locally adapted varieties through marker assisted backcrossing. The field experiment was carried out in 2009/2010 and involved two irrigation levels and 14 genotypes organized in a split plot design with three replications. Analysis of variance showed significant difference among the genotypes for all the measured nine morpho-physiological quantitative characters. Significant differences were also observed in leaf area, head exsertion, grain yield and hundred seed weight for irrigation indicating that the two irrigation levels were able to differentiate the genotypes for these characters. Genotype-by-irrigation interaction was significant only for head weight and 100 seed weight. In general, a yield reduction of up to 49% was observed in an induced post-flowering moisture deficit. Grain yield had strong positive correlation with head weight (r=0.66) and hundred seed weight (r=0.52) under conditions of moisture deficit. Most of the stay-green introgression lines included in this experiment maintained at least 25% of their green leaf area until maturity though some showed early leaf senescence, but there was no associated increase in grain yield. Possible reasons are discussed.

Key words: Drought, introgression, post-anthesis, QTL, stay green, sorghum.

INTRODUCTION

Drought is the single greatest problem limiting crop productivity in the semi-arid tropics (SAT) where most of the production systems are rain-fed (Serraj et al., 2005). The trade-offs between the trends of increased population size and the associated increased demand for food on one hand and the decrease in availability of water on the other hand call for the development of more water efficient (climate smart) crops (Balota et al., 2008). Sorghum is one of the most important food, feed and bio-energy crops in the world, which tolerates drought stress better than most other cereals. It is also an important food crop in sub-Sahara Africa including Ethiopia on which millions of poor people depend. In Ethiopia, it grows in a wide range of agro-ecological zones, but it is more important in the dry lowlands where crop failure due to recurrent drought stress is common (Adugna, 2007). Cates (1922) has applied the name "crop camel" to kafir (one of the grain sorghums) because the plants can stand for considerable dry periods without apparent suffering from a deficiency of moisture. Since the crop is

both drought tolerant and highly responsive to added water, it is adapted to both dryland and irrigated conditions (Eck and Musick, 1979).

Drought may occur at any stage during the growth cycle of the sorghum crop. Sorghum exhibits two distinct responses to drought stress (Rosenow et al., 1983). One occurs when plants are stressed during the head development stage prior to flowering, called *preflowering,* and the second occurs when plants are stressed after anthesis and during grain development, called post-flowering (Walulu et al., 1994). When it occurs as preflowering during the first growth stage (GS1), the period between seedling emergence and panicle initiation (Quinby, 1974), it affects the vegetative growth and the time of floral initiation. Drought at second growth stage (GS2), the period between panicle initiation and anthesis, affects the number of seeds that will be produced, whereas at the third growth stage (GS3), the period between floral anthesis and physiological maturity, it affects seed weight as the grain does not fill well. Therefore, grain yield reduction becomes relatively worse when drought occurs at the last two growth stages (GS2-pre flowering and GS3-post-flowering) than at GS1 since seed number and weight are the most important grain yield components in sorghum. The reason why terminal drought stress might cause yield reduction is that, the affected plants mature early as a result of the induction of premature leaf senescence (forced maturity) (Gregersen et al., 2013). Genetic variation for resistance to drought at each stage has been observed in sorghum germplasm (Walulu et al., 1994). Hence, many genotypes with a high level of resistance at one stage were found to be susceptible at the other stage (Rosenow et al., 1983). Until recently, the global sorghum improvement approach towards alleviating the effect of drought has been focused on the development of short duration varieties, those that can escape drought occurs late during the season (terminal drought). Based on this approach a number of early maturing varieties have been released and are still being produced globally including Ethiopia. However, even these early maturing types can fail to produce if drought occurs at the critical stages. For example, in pearl millet, Mahalakshmi et al. (1987) found that when drought occurred during the midseason, early genotypes, which were proved to effectively escape a terminal drought stress suffered greater grain yield reduction than the later flowering genotypes.

Recently, the focus of research has been changed to the development of drought tolerant varieties helped by marker assisted selection. The best example of marker assisted selection against drought in sorghum is for the stay-green trait (Rosenow et al., 1983). The term stay-green refers to delayed senescence, which is associated with post-flowering drought tolerance irrespective of the maturity of the genotype (Ejeta and Knoll, 2007). It focuses mainly on alleviating the effect of drought at grain filling as drought stress during this stage in sorghum usually results in rapid premature plant senescence (Stout and Simpson, 1978). Sorghum genotypes with functional stay-green continue to fill their grain normally under drought (Rosenow and Clark, 1981; Borrell et al., 2014). Such stay green trait, producing healthier stems on plants, may indirectly contribute to higher crop performance by providing disease resistance, standability, resistance to lodging, and higher seed quality characteristics (Cukadar-Olmedo and Miller, 1997; Cattivelli et al., 2008).

Moreover, previous reports suggest that the Stay-Green trait in sorghum and rice might contribute to increased post-anthesis biomass production under drought stress (Borrell et al., 2000; 2001). Therefore, stay-green has been suggested as an indirect selection criterion for post-flowering drought tolerance (Rosenow et al., 1983). Molecular markers linked to the already mapped sorghum stay green QTLs are available (Hash et al., 2003; Harris et al., 2007) and with which marker assisted backcrossing has been undertaken (Kassahun et al., 2010). This study was, thus intended to evaluate the response of stay-green QTL introgression sorghum lines developed using marker assisted backcrossing and their parents for induced post-anthesis drought stress.

MATERIALS AND METHODS

Plant materials

Sorghum varieties adapted to the dry lowlands of Ethiopia; 76T1#23, Teshale, Gambella 1107, and Meko were selected for the backcrossing program. All of them, except Gambella 1107 were selections from ICRISAT introduced regional trials. Gambella 1107 is a selection from landraces in Gambella area, Ethiopia. These varieties have maturity days ranging from 90 to 130 days. So far, the sources of the stay-green QTLs that are widely used in sorghum have been B35 and E36-1 lines, which were originally obtained from Ethiopia (Reddy et al., 2009). B35 is a BC_1 derivative of landrace germplasm accession IS 12555, which is a durra sorghum (Rosenow et al., 1983). A Marker assisted backcrossing program was held in Ethiopia between 2006 and 2008 and carried out at Melkassa Agricultural Research Center in collaboration with ICRISAT, Nairobi to introgress stay-green QTLs from B35 and E36-1 to the locally adapted early maturing, but senescent sorghum varieties (76T1#23, Teshale, Gambella 1107, and Meko). Starting from the first backcrossing, all plants in a 5 m nursery plot were tagged and leaf samples were taken from each of them and sent to the Bio-Sciences for East and Central Africa (BECA) laboratory in Nairobi, Kenya for marker assisted selection of the stay green QTLs. Based on the marker information, those plants which had one or more stay-green QTLs from the donor parents were backcrossed to the respective locally adapted lowland sorghum varieties used as recurrent parents. In total, six stay-green QTLs conferring post-anthesis drought stress tolerance: *StgA*, *Stg1*, *Stg2*, and Stg4 from B35 and *SBI-01* and *SBI-10* from E36-1 were introgressed into the four elite local varieties in three molecular marker (SSRs) assisted backcrosses and the resulting populations were self-pollinated three times. Thus, all of the introgression lines used in this study had one or more of the stay-green quantitative trait loci (QTLs) (Table 1). Hence, eight backcross populations (BC_3F_3) here after referred to as stay-green QTL introgression lines resulted from the four lowland sorghum

Table 1. Genotype means for the measured quantitative characters (in parenthesis are stay-green QTLs).

Genotype	HL	HW	LA	PE	GY	HW	HSW
Teshale x B35 (*Stg2*)	19.8	11.0	368.6	13.86	316.0	65.8	3.1
Meko x B35 (*Stg1, Stg4*)	23.3	11.4	423.3	2.08	438.0	115.2	3.9
Gambella 1107 x B35 (*StgA*)	22.5	9.6	582.3	1.74	490.4	116.3	3.5
76T1#23 x B35 (*StgA*)	20.4	9.3	357.5	10.10	307.5	78.5	3.1
Teshale x E36-1 (*SBI-01*)	21.4	11.5	483.4	11.48	443.0	92.7	3.1
Meko x E36-1 (*SBI-01*)	23.7	12.5	517.1	1.24	626.3	128.7	3.8
Gambella 1107 x E36-1 (*SBI-01*)	21.1	10.3	604.6	4.49	588.5	117.0	3.7
76T1#23 x E36-1 (*SBI-10*)	19.2	9.7	393.8	7.74	392.8	91.9	3.0
Teshale	19.9	13.3	417.8	10.57	486.9	108.6	3.4
Meko	21.4	10.8	570.1	2.91	611.5	121.9	3.6
Gambella 1107	21.1	10.5	585.0	2.17	554.5	122.9	3.4
76T1#23	20.6	9.7	371.1	7.84	417.5	89.7	3.2
B35 (*Stg1, Stg2, Stg4, StgA*)	23.2	9.6	393.1	18.11	317.5	89.7	2.8
E36-1 (*SBI-01, SBI-10*)	21.9	12.7	449.8	6.76	469.0	118.4	3.9
Mean	21	11	466	7.22	461.4	104.1	3
LSD (0.05)	1.1	1.5	68.1	2.70	58.5	10.5	0.2

PH, plant height recorded at physiological maturity; LA, leaf area; HL, head length, HW, head width; PE, Peduncle exsertion; HWT, head weight; GY, grain yield; HSW, 100 seed weight.

varieties and the two stay green source lines (B35 and E36-1) were included in the experiment. Moreover, the 6 parents (donor and recurrent) were included in the experiment for comparison (Table 1).

Experimental setup

The field experiment was carried out during the off-season (from 16 December 2009 through 24 April 2010) at Melkassa Agricultural Research Center located in the Central Rift Valley of Ethiopia (39°21′E, 8°24′N, altitude=1550 m) by inducing drought at the post-anthesis stage. The soil at the experimental site is silty clay loam Andosol with a pH of ~7.8. It was a split plot design with three replications. The main plot factor was irrigation with two levels (I_0 = irrigation withheld after anthesis and I_1 = irrigation continued after anthesis until maturity) and the sub-plot factor was the genotypes with 14 levels (consists of 8 introgression lines, 2 donor, and 4 recurrent parents). The two groups of the irrigation (flood) treatments differed in three frequencies during the post-flowering stage. In the first case (I_1), all of the 14 genotypes were irrigated every seven days throughout their growth stages. In the second (I_0), however, the replicas of all of the genotypes did not receive irrigation after anthesis (the last irrigation was given just at anthesis). Hence, the total number of treatments was 2 × 14 = 28. The border of each block was sown to the variety Melkam to avoid border effect. Each plot had a single row of 4 m length and the inter-row space was 75 cm. the space between the two main plots was 1.5 m. The treatments were randomized within each main plot. The seeds were sown by hand drilling and later thinned to 15 cm between plants to give a total population density of 88 888 plants per hectare. The management practices including fertilizer and weeding except irrigation were done as per the recommendation for sorghum. Accordingly, DAP fertilizer was applied at the rate of 100 Kg/ha during planting in the seed furrow and Urea was applied at the rate of 50 Kg/ha as top dressing before booting. The field was kept free from weeds throughout the experiment. To control shoot flies and stem borers, Karate 5% EC was applied at the rate of 320 mm/ha two weeks after emergence.

Data recording and statistical analysis

As there is heavy weaver bird (*Quelea quelea*) pressure at Melkassa during the off-season, it was difficult to measure plot yield. Therefore, five plants were bagged with cloth bags from each row plot after anthesis and used for data recording. Data on days to flowering (DTF), plant height (PH) recorded at physiological maturity, leaf area (LA), head length (HL), head width (HW), Peduncle exsertion (PE), head weight (HWT), grain yield (GY) (Kg per plot, in this case mean of 5 plants), and 100 seed weight (HSW) at 12% moisture content, were measured from the five plants based on the new key access and utilization of sorghum descriptors (Bioversity International, 2010). In addition, the visual leaf senescence data scoring was modified from the descriptors for sorghum (IBPGR/ICRISAT, 1993) as 0 = ~100% green leaf area; 1=75% green leaf area; 2= 50% green leaf area; 3= 25% green leaf area; 4 = 100% leaves and stalk dead. This data were recorded at physiological maturity. Leaf area was calculated as Leaf length × Leaf width × 0.71 following Krishnamurthy et al. (1974). The data were subjected to analysis of variance to see individual treatment and interaction effects for all the measured quantitative characters using SPSS Release 17 Software. Moreover, paired t-test was performed in all means of the measured characters to evaluate the trend of the differences between irrigated and non-irrigated treatments using the protected LSD procedure at P = 0.05 (Carmer and Swanson, 1973).

RESULTS

The result of this study showed a high significant difference in the genotypes for all the traits measured; indicating that the tested genotypes were diverse. Analysis of variance (ANOVA) showed highly significant difference (p<0.01) for genotypes factor for all the traits measured, which indicated that the tested genotypes were diverse. Highly significant differences were also

Table 2. Mean values of the measured characters for irrigation.

Irrigation	DTF	PH	HL	HW	LA	PE	GY	HW	HSW
I_0	79.04	159.08	20.99	10.67	423.39	8.28	433.40	94.33	3.28
I_1	79.81	161.37	21.79	11.04	507.68	6.17	489.37	113.84	3.48
LSD (0.05)	2.68	5.89	1.94	0.68	104.36	1.01	32.35	7.43	0.06

DTF, flowering; PH, plant height recorded at physiological maturity; LA, leaf area; HL, head length, HW, head width; PE, Peduncle exsertion; HWT, head weight; GY, grain yield; HSW, 100 seed weight.

Table 3. Genotype × irrigation interaction means of the stay-green QTL introgression lines and their parents for the different characters measured after harvest.

Genotype	HWT		GY		HSW	
	I_1	I_0	I_1	I_0	I_1	I_0
Teshale × B35	71.48	60.07	337.00	295.00	3.10	3.00
Meko × B35	119.20	111.23	449.00	427.00	3.90	3.80
Gambella 1107 × B35	134.44	98.11	524.33	456.50	3.57	3.47
76T$_1$#23× B35	82.13	74.81	368.00	247.00	3.15	3.13
Teshale × E36-1	118.67	66.64	463.00	423.00	3.55	2.65
Meko × E36-1	144.08	113.35	629.50	623.00	3.90	3.65
Gambella 1107 × E36-1	122.23	111.82	599.50	577.50	3.60	3.70
76T$_1$#23 × E36-1	95.69	88.03	419.00	366.67	3.13	2.90
Teshale	130.67	86.55	507.33	466.50	3.63	3.10
Meko	137.54	106.30	607.00	616.00	3.87	3.33
Gambella 1107	122.37	123.40	625.50	483.50	3.20	3.50
76T$_1$#23	99.40	79.94	451.50	383.50	3.30	3.03
B35	93.30	86.11	333.00	302.00	2.87	2.80
E36-1	122.60	114.28	537.50	400.50	3.97	3.83
Mean	113.84	94.33	489.37	433.40	3.48	3.28
SE± mean differences	4.372		12.573		0.079	
CV (%)	8.7		11		6.1	
Paired t test of the differences	4.46		4.45		2.57	
p(≤0.05) two-tail	0.001		0.001		0.023	

observed among the genotypes for leaf area, head length, head weight, grain yield, and hundred seed weight in response to the induced post-anthesis drought stress, which was further confirmed by paired t-test (Table 1). In these characters, the stressed plots showed reduced mean values. Although, significant differences were observed between mean grain yield, panicle exsertion and head weight of irrigated and non-irrigated sets of genotypes with higher values being in the former (Table 2), genotype-by-irrigation interaction was not significant for these traits except head weight (Tables 3 and 4).

Effect of induced post-anthesis drought stress on individual traits

Grain yield had significant positive correlation (p<0.05)

with head weight (r=0.66) and hundred seed weight (r=0.52) under moisture stressed condition. The reduction in leaf area was significant and ranged from 8.3% (B35) to 45.6% (Gambella 1107 × B35) in response to the changed irrigation levels. Genotype-by-irrigation interaction was significant for head weight indicating differential response of the genotypes in response to irrigation levels for this trait. There was a wide range of head weight reduction between 0 and 78%. Head weight had positive correlation (r=0.66) with grain yield under non-irrigated condition and even the correlation was stronger (r= 0.87) under irrigated condition. Even though there is significant difference among the mean grain yield and panicle exsertion of irrigated and non-irrigated sets of genotypes, the absence of genotype-by-irrigation interaction in these traits may indicate that moisture stress at the post-anthesis stage affects these traits regardless of genotype. In a well-watered condition, Gambella 1107

Table 4. Genotype × irrigation interaction means of the QTL introgression lines and their parents for the different characters measured during pre-harvest

Genotype	DTF		PH		HL		HW		LA		PE	
	I_1	I_0	I_1	I_0	I_1	I_0	I_1	I_0	I_1	I_0	I_1	I_0
Teshale × B35	81.00	81.00	179.20	178.20	19.20	20.33	10.00	12.07	416.66	320.52	13.86	13.87
Meko × B35	77.67	77.00	153.73	151.07	23.87	22.80	11.33	11.53	481.35	365.15	0.97	3.20
Gambella 1107 × B35	86.00	84.33	164.18	167.73	23.00	22.07	10.60	8.67	690.42	474.10	0.78	2.70
76T₁#23 × B35	74.33	72.00	142.20	140.40	21.33	19.40	9.27	9.27	398.66	316.32	7.63	12.58
Teshale × E36-1	82.67	81.67	215.93	215.93	21.27	21.53	11.47	11.53	561.69	405.14	10.84	12.13
Meko × E36-1	80.67	80.00	157.20	158.28	24.07	23.40	12.93	12.13	553.61	480.66	0.78	1.70
Gambella 1107 × E36-1	84.50	83.67	176.07	171.43	22.07	20.20	10.67	9.87	632.01	577.23	2.87	6.11
76T₁#23 × E36-1	77.00	75.00	139.13	139.93	19.80	18.53	9.87	9.47	432.20	355.34	5.02	10.47
Teshale	80.33	79.67	209.87	203.40	19.93	19.80	14.80	11.80	439.26	396.37	9.23	11.92
Meko	81.33	80.33	166.20	146.93	21.80	20.93	10.67	10.93	603.57	536.58	3.33	2.50
Gambella 1107	82.67	82.50	162.00	160.13	21.40	20.73	10.60	10.47	626.24	543.78	2.72	1.63
76T₁#23	73.33	72.00	137.13	136.40	21.07	20.13	10.07	9.33	387.49	354.66	6.75	8.93
B35	78.33	79.00	90.07	87.10	24.27	22.20	9.53	9.60	408.79	377.36	16.13	20.10
E36-1	77.50	78.33	166.30	170.22	22.00	21.73	12.73	12.73	475.51	424.18	5.47	8.07
Mean	79.81	79.04	161.37	159.08	21.79	20.99	11.04	10.67	507.67	423.38	6.17	8.28
SE± mean differences	0.243		1.510		0.234		0.307		13.550		0.524	
CV (%)	3.17		5		4.6		12.1		12.6		32.3	
Paired t test of the differences	3.53		1.52		3.45		1.19		6.22		-4.03	
p(≤0.05) two-tail	0.007		0.153		0.004		0.254		0.000		0.001	

gave the highest and B35 the lowest yield of all the parental lines. Meko × E36-1 gave the highest yield of all the introgression lines under both water regimes. Meko and its introgression line, Meko × E36-1 gave comparative grain yield under both well watered and water deficit conditions. On the contrary, B35 and its introgression lines with 76T1#23 and Teshale gave relatively lower grain yield (Figure 1). Irrigation factor was significant (p<0.05) for hundred seed weight. When the data were pooled for all the genotypes, the range of reduction of hundred seed weight in response to the induced post-flowering drought was 0.5% (76T1#23 × B35) to 34.0% (Teshale × E36-1). All of the introgression lines, except Teshale × E36-1 and crosses of Gambella 1107, had lower sensitivity to the simulated drought stress response to seed weight than their recurrent parents (Table 3). Hundred seed weight had strong positive correlation (r=0.52) with leaf area. It had also very high positive correlation (r=0.79) with head weight under moisture stress and even higher positive correlation (r=0.84) under irrigated condition. Conse-quently, withholding irrigation during post-anthesis stage significantly reduced weight of the seeds by affecting grain filling (Table 2).

Genotype-by-irrigation interaction was also significant for hundred seed weight indicating differential response of the genotypes to the varying irrigation levels for this trait. However, hundred seed weight in the introgression lines alone had no correlation with leaf area (r=0.427, p=0.164) under stressed condition. It had also very high

positive correlation with head weight under both moisture stress (r=0.887, p=0.003) and well watered (r=0.876, p=0.004) conditions. Irrigation factor was also significant (p<0.05) for peduncle exsertion. Twelve of the 14 introgression lines showed an increase in peduncle exsertion in response to moisture stress. The highest increase was observed in 76T₁#23 × E36-1 followed by 76T₁#23 × B35, both introgression lines of 76T1#23 with the two stay green source lines.

Leaf senescence is the most pertinent trait so far as this study was concerned. Five of the 14 genotypes, viz., Meko and Gambella 1107 and their introgression lines Meko × E36-1, Gambella 1107 × E36-1, Gambella 1107 × B35 showed early leaf senescence in one or more of the stressed plots. However, high level of average leaf senescence was visually observed in Gambella 1107 × B35, Meko, and Gambella 1107. The stay-green source line, B35 and its introgression lines 76T1#23 × B35 and Meko × B35 (Figure 2) maintained their green leaves until maturity.

DISCUSSION

Effect of induced post-anthesis drought stress on performance of the genotypes

Leaf characters

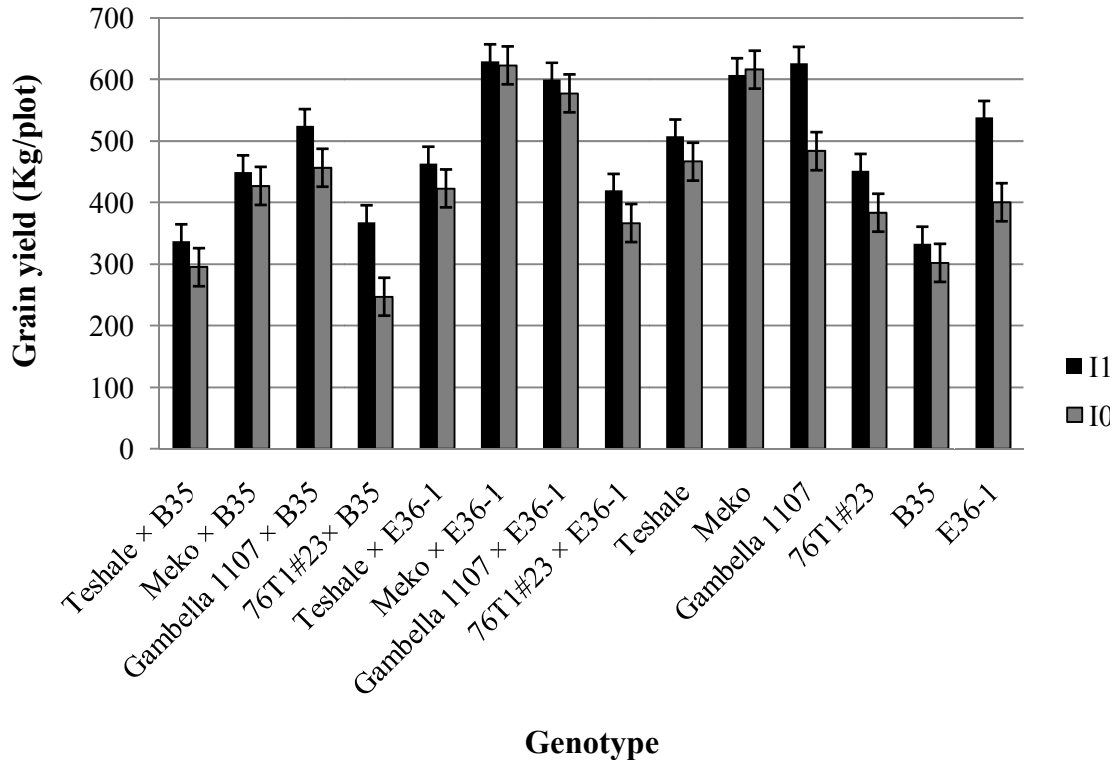Even though no leaf size increase is generally expected

Figure 1. Comparison of the sorghum genotypes for grain yield under well watered (I_1) and water deficit (I_0) conditions (bars are standard error of means).

Figure 2. Differences in leaf senescence in the stay-green introgressed line, Meko × B35 (Left) and its recurrent parent Meko (Right) under water deficit condition (to the extreme left is a border row).

beyond flowering, the reduction in leaf area in this experiment was probably due to contraction of the full sized leaves in response to the induced moisture deficit. However, leaf area was highly and positively correlated with grain yield (r=0.885, p=0.004) under moisture deficit. It has been reported that decreasing leaf area reduces crop water use and results in reduced grain yield (Borrell et al., 2014; Vadez et al., 2014). Early studies by Swanson (1941) and Blum et al. (1989) showed that early maturing varieties having a small leaf area are the most efficient in the production of grain per unit of leaf area whereas later varieties have a higher biomass, higher daily transpiration and a longer transpiration period and are likely to suffering dry seasons. In the present study, most of the introgression lines showed higher sensitivity to moisture stress with respect to the change in leaf area. Perhaps that was one mechanism of drought tolerance beyond the maintenance of green leaf area that the stg QTLs are contributing. In their recent study aiming at investigating the positive effect of *Stg* QTLs on grain yield under drought, Borrell et al. (2014) concluded that leaf area and transpiration per unit leaf area could be some of the mechanisms that Stg loci have impacts to regulate transpiration on the demand for water. Although, the reduction in the mean values in the remaining characters is a disadvantage, the reduction in leaf area could be considered as an important adaptive physiological mechanism expressed in response to the changed osmotic potential contributing to drought tolerance. In agreement with this finding, Swanson (1941) reported that leaf area was the greatest when there was an abundant moisture supply and the influence of drought on leaf development was shown by the results when the rainfall was deficient throughout the growing season. The same study showed that leaf area per acre in droughty season was 73 to 81% less than when there was abundant moisture and very heavy leaf development.

Inheritance study of Walulu et al. (1994) suggested that the stay green traits in one of the known source lines, B35 is influenced by a major gene but, later, it has been mapped as a quantitative trait and four QTLs controlling the stay-green (*Stg1* through *Stg4*) were identified (Xu et al., 2000). Moreover, the effect of environment on expression of the stay-green trait in sunflower was suggested by Cukadar-Olmedo and Miller (1997). Therefore, these show that multi-location testing of the introgression lines would have helped the evaluation complete. The stay-green (non-senescence) trait in sorghum is reported to be often associated with good plant health and increased plant resistance to insects and diseases (Cukadar-Olmedo and Miller, 1997). Moreover, as it results in greater functional leaf area during grain filling and reduces the need for translocation of stored assimilates from the stem during grain filling, non-senescent sorghum accumulates more soluble sugars in the stem than does senescent sorghum, both during and after grain filling (McBee et al., 1983), which in turn

improves the digestible energy content of the Stover (van Oosterom et al., 1996). In addition, stay-green QTLs may improve Stover digestibility by 3 to 5% units without negatively affecting grain and Stover yields (Reddy et al., 2012). This is also a very important trait in places like in Ethiopia where sorghum Stover is equally valued for cattle feed.

Yield and yield attributes

Although grain yield is a function of head weight and hundred grain weight, the significance of genotype × irrigation interaction in these characters in this experiment was not adequate to bring about a parallel significance in this major trait of importance. Eck and Musick (1979) found that a 27-day stress period (with average afternoon leaf water potential, - 22.7 bars) beginning at early grain filling reduced yields by 12% only. Similarly, in the present experiment whereby the non-irrigated treatments were exposed to a month of drought stress, the range of yield reduction in all the genotypes was from 1.0% (Meko × E36-1) to 49.0% (76T$_1$#23 × B35) with an average of 12.9%. The variety Gambella 1107 was the most sensitive local variety that showed a yield reduction of 29.4%. On the other hand, the variety Meko was the least sensitive, which performed similarly in both water regimes. Unexpectedly, the stay green source line, E36-1 showed 34.2% yield reduction under drought stress. However, B35 had very low yield reduction indicating its low sensitivity (stability) to the induced drought, which in turn confirms its tolerance to drought stress. The introgression line Gambella 1107 × E36-1 showed better grain yield than its recurrent parent, Gambella 1107 under moisture stress. Meko × E36-1 was the highest yielding of all the genotypes included in the experiment, but had no advantage over its recurrent parent, Meko (Figure 1). Earlier reports showed that yield increases in stay-green types have been directly associated with maintenance of photosynthetic capability during the grain filling period (McBee, 1984; Wolfe et al., 1988) and longevity of a leaf is intimately related to its nitrogen status or water availability (Thomas and Rogers, 1990; Borrell et al., 2001). In the present preliminary experiment, although 76T$_1$#23 × B35 maintained >50% of its green leaves until maturity, its yield reduction by 49% was probably because it possessed a cosmetic type (types C and D) of stay-green (Borrell et al., 2014).

Reduction in yield components as a result of drought stress was previously reported. For instance, similar to the present study (Table 4), Hooker (1985) found a decrease in head weight and weight of the 100 seeds associated with reduction in soil moisture by affecting grain filling. In their comparative study of senescent and non-senescent sorghum genotypes, Duncan et al. (1981) also found that the non-senescent (stay-green) genotypes

had higher test weight. However, genotypic differences do exist for the period they take to fill their grain due to their efficiency in using the available moisture during post anthesis deficit. For instance, in the present study the variety Meko and its introgression line with E36-1 showed more or less similar grain yield in both moisture regimes. Kassahun et al. (2010) reported the low yield potential of B35 due to its small panicle size, non-tillering and small number of seeds per panicle. The lower grain yield in B35 and its introgression lines than their respective elite recurrent parents was in agreement with the findings of Kassahun et al. (2010) and may be an indication of yield drag caused by one or more of the stay-green QTLs of B35. Gambella 1107 × B35 had the same stay-green QTL (*StgA*) as that of 76T$_1$#23 × B35, but it senesced earlier, which is an indication of the possibility of existence of QTL × Genotype or QTL × Genotype × Environment interaction for phenotypic expression of the trait, which calls for multilocation testing.

Previous reports showed that increased peduncle exsertion in rice was found to be associated with drought resistance and is controlled genetically (O'Toole and Cruz, 1983). This was in agreement with the present study and can be considered as an indirect selection criterion for drought tolerance in sorghum.

Conclusion

The scarcity of water associated with the impending climate change demands introduction and development of climate smart crops. Sorghum is one of these crops due to its adaptation to survive in severely stressed environments. Among the cope up strategies that sorghum as a climate smart crop possesses are drought and heat tolerance. Stay-green is a post-anthesis drought tolerance mechanism. In this experiment, stay-green QTLs were introgressed from known sources to the farmer preferred Ethiopian local sorghum varieties. Eight of the resulting introgression lines those possessed at least one *Stg* QTL were organized in an experiment to observe their performance under well watered and water deficit conditions. The result of this single season and single location experiment has indicated that most of the introgression lines maintained their green leaf area until maturity under conditions of post anthesis moisture deficit. However, most of them did not show better grain yield than their recurrent parents probably because the introgressed stay-green was cosmetic type. The reduction in leaf area was significant in the *Stg* QTL introgression lines under moisture stress perhaps because the QTLs play significant role in leaf area dynamics. Multienviroment testing of the performance of the introgression lines may give better understanding of the effect of the introgressed QTLs on the various characters.

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