


Stability of *Solanum aethiopicum* Shum accessions under varied water deficit stress levels and identification of pertinent breeding traits for resistance to water shortage

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Abstract Drought is a major constraint to productivity of *Solanum aethiopicum* ‘Shum’ group due to loss in market and nutrient value of stressed plants. This study evaluated *S. aethiopicum* Shum group accessions to identify genotypes (G) that excel across moisture deficit stress levels (WLs). A split-plot arrangement composed of four WLs and twenty accessions of *S. aethiopicum* as main plot and sub-plot factors, respectively, was implemented in a greenhouse, and repeated for two experiments. In each experiment, there was a highly significant effect of at least two WLs on mean performance among at

least two accessions for most of the traits at $p < 0.05$. Further, very highly significant $WL \times G$ interactions were obtained for leaf relative water content (LRWC), leaves per plant (LPP) and plant height (PH), and non-significant for leaf blade length and leaf blade width. The order of priority as breeding traits for stability superiority across WLs was suggested as $LRWC > PH > LPP$. Consequently, based on LRWC, the most superiorly stable accessions were identified as accession 160 followed by accessions 145, 137, 108P and 184G while the least stable ones were identified as accessions 163G, 141, 163 and 108. The broad sense heritability (H^2) for each of the three recommended traits for drought resistance breeding was above 0.9 thus supportive for a good response to selection. Drought stress negatively affected the performance of *S. aethiopicum* Shum group but the exhibited variation allowed for selection of superiorly stable genotypes.

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Introduction

Solanum aethiopicum Shum group is one of the four morphological groups of *S. aethiopicum* ($2n = 24$) (Adeniji et al. 2013; Plazas et al. 2014; Prohens et al.

2013). The other groups include the Gilo, Kumba (Bationo-Kando et al. 2015) and Aculeatum (Plazas et al. 2014). The Shum group is a leafy vegetable and an important nutrient security crop in Uganda (Sseremba et al. 2017a, b) and various other countries in sub-Saharan Africa (Bationo-Kando et al. 2015; Osei et al. 2010; Şekara et al. 2007). The leafy vegetable crop's productivity is however, constrained by many factors including drought (Anjum et al. 2011; Kumar et al. 2012). The crop cultivation under constant irrigation for year-round production has been practiced in urban and peri-urban areas (Bahadur et al. 2009). However, the water resource is increasingly becoming either inadequate or unreliable in supply; as one of the effects of climate change (A&N Technical Services 2015; Bahadur et al. 2009). The most sustainable way of ensuring a continued and improved production of the crop is the identification of superior varieties that are stable amid reductions in soil moisture (Kumar et al. 2012; Şekara et al. 2007). The *S. aethiopicum* has for long been a research-neglected and under-utilized crop species (Abukutsa-Onyango et al. 2010; Anjum et al. 2011), although recent molecular tools have become available and the relationships among the different cultivar groups studied (Acquadro et al. 2017; Gramazio et al. 2016, 2017; Plazas et al. 2014; Prohens et al. 2013); and its germplasm had not been characterized for drought tolerance (Abukutsa-Onyango et al. 2010; Blum 2009; Kumar et al. 2012). In leafy vegetables, drought stress reduces leaf quality as a result of unfavorable leaf-water status (Kumar et al. 2012; Ssekabembe and Odong 2008).

In general, it is understood from studies in other crops that water deficit stress is signaled in the roots leading to increased abscisic acid (ABA) synthesis which results in modification of the root system architecture, leaf relative water content, chlorophyll content, leaf temperature, photosynthetic rate, and stomatal conductance (Pucholt et al. 2015). Drought response mechanisms are broadly categorized as escape, avoidance, tolerance and recovery; which occur at morphological, physiological, biochemical, cellular and molecular levels (Amelework et al. 2015; Yoshida et al. 2014). For instance, according to Singh et al. (2015), at physiological level, plants use osmotic adjustment (through osmolytes such as ammonium compounds, sugars, sugar alcohols and amino acids) as an adaptive mechanism to maintain turgor pressure

under drought (and salt) stress conditions. This osmotic adjustment protects plants from damaging effects of free radicals of oxygen (Kumar et al. 2012; Singh et al. 2015; Yoshida et al. 2014). The measurement of plant traits such as stem (or leaf) water potential, leaf relative water content or even morphological attributes can give a good indication of plant water status and genotypes' response to water deficit stress (Amelework et al. 2015; Blum 2005, 2009; Kesiime 2014; Kumar et al. 2012; Mwale et al. 2017). The most important indicator of plant- (or leaf-) water status is the leaf relative water content (LRWC) (Anjum et al. 2011; Fang and Xiong 2015; Kesiime 2014; Kumar et al. 2012). The higher the LRWC above 80%, the better the drought tolerance of the plant; and vice versa (Kesiime 2014). Until now however, no particular traits had been recommended for effective breeding of *S. aethiopicum* Shum group for resistance to drought.

Stability superiority analysis that considers identification of high performing genotypes across environments (Mendes de Paula et al. 2014; de Oliveira et al. 2014) was used in this study. The measure has severally been applied in selection of superior and stable genotypes (Altaye 2015; Eberhart and Russell 1966; Kamidi 2001). Studies indicate that the various statistical techniques, whether additive main effects and multiplicative interaction (AMMI) or genotype-by-genotype-by-environment interaction (GGE), provide similar genotype ranking (Mendes de Paula et al. 2014); and thus can be used concurrently for 'internal check' or validation purposes (Kamidi 2001; Mendes de Paula et al. 2014; de Oliveira et al. 2014). The AMMI and GGE interaction analyses that variously employ stability coefficients to rank genotypes and environments for multi-site and/or multi-year data (de Oliveira et al. 2014) were applied in this study. The different moisture deficit levels were applied as the testing environments in order to execute the study in the screen house. Our focus was to evaluate *S. aethiopicum* accessions in order to identify genotypes that excel across drought stress levels. Specifically, the study was aimed at: determining the effect of drought stress on physiological (leaf relative water content) and selected morpho-agronomic traits (i.e., leaf blade length, leaf blade width, number of leaves per plant and plant height) of *S. aethiopicum* Shum, identifying superiorly stable accessions for the drought tolerance related traits across moisture deficit

levels, and identifying pertinent breeding traits for resistance to water shortage in *S. aethiopicum* Shum. The results from this study are expected to guide the design of drought tolerance improvement programs for farmer-preferred varieties.

Materials and methods

Accessions and experimental site

The germplasm used in this study was obtained from the Department of Agricultural and Biological Sciences, Uganda Christian University (UCU); followed by two seasons of purification through self pollination. The accessions (Table 1) differed in various morphological attributes such as stem color, plant height and growth habit (Sseremba et al. 2017a, b). All the accessions belong to the Shum group of *Solanum aethiopicum*. The study was carried out in a screen house at UCU.

Experimental design

A split-plot design composed of drought stress factor (main plot) with four (4) levels, and accessions of *Solanum aethiopicum* Shum (sub-plot factor) with 20 levels, was used. Three (3) pots per sub-plot treatment and two (2) replications were used. The seeds of each accession were sown in dedicated pots on 10th April 2016 and raised into seedlings before transplanting into individual pots. Plastic pots each filled with 10 kg of potting mixture were used. The potting mixture consisted of loam soil and cow dung manure in a ratio of 3:1, respectively. The transplanting of seedlings was

carried out at 3–4 leaf stage on 1st May 2016. The transplanted seedlings were watered optimally for two (2 weeks) to ensure proper establishment. The water stress was imposed at end of the 2nd week after transplanting. Thereafter, four different watering levels were impressed based on field capacity of the potting soil mixture. The optimum amount of water (field capacity, FC) for watering the individual pots was pre-determined as earlier applied by Kesiime (2014). Briefly, the FC was determined as follows; 10 kg of the potting soil mixture was oven dried at 105 °C for 24 h to get rid of moisture. The heated soil was cooled followed by assembling a set-up of a plastic mesh fitted on top of a transparent bucket, and the cooled soil returned in the plastic pot was placed on top of the bucket. The potted soil was then uniformly wetted until a first drop of water was received in the transparent bucket. The set-up was left to stand till no more drops of water were received in the bucket. The amount of water retained in the potted soil (field capacity) was then calculated by subtracting the volume of water seeped into the bucket from the quantity of water delivered to wet the potted soil. The drought stress levels used were determined based on the FC such that four levels namely: 100% FC or optimum watering (3 litres), 75% FC (2.25 litres), 50% FC (1.5 litres) and 25% FC (0.75 litres) were obtained. The water deficit stress levels were applied to individual pots over a period of 3 weeks, from the 2nd week after transplanting onwards (WAT) till 5 WAT stage; coinciding with the vegetative or harvest maturity stage. The second experiment was established in November 2016 under the same procedure as for the first experiment; and the 100%FC, 75%FC, 50% and 25%FC were estimated at 2.4, 1.8, 1.2 and 0.6 litres of

Table 1 List of accessions used in this study

	No.	Acc. code	Pedigree	No.	Acc. code	Pedigree
	1	168G	SAS168/G/2015	11	148	SAS148/2015
	2	183G	SAS183/G/2015	12	145	SAS145/2015
	3	163	SAS163/2015	13	168P	SAS168/P/2015
	4	163P	SAS163/P/2015	14	184G	SAS184/G/2015
	5	157P	SAS157/P/2015	15	137	SAS137/2015
<i>SAS Solanum aethiopicum</i>	6	160	SAS160/2015	16	184P	SAS184/P/2015
Shum; P and G are color	7	163G	SAS163/G/2015	17	141	SAS141/2015
codes for purple and green	8	183P	SAS183/P/2015	18	108P	SAS108/P/2015
stem, respectively; as	9	108	SAS108/2015	19	185G	SAS185/G/2017
originally described by	10	157G	SAS157/G/2015	20	185P	SAS185/P/2015
UCU at the time of						
obtaining the germplasm						

water, respectively. During each experiment, soil moisture content (SMC), relative humidity and temperature were monitored. The percentage SMC was monitored using a digital soil moisture meter, Model MO750 (Extech® Instruments Corporation, USA) and the meter measurements were verified with the oven (thermogravimetric) method to enable maintenance of set water levels as earlier demonstrated by Ogbu et al. (2016). In this study, the soil water content monitoring was carried out from the 3rd to 5th WAT stage of the experiment, during which, the soil moisture was kept as close to possible to the desired respective treatments (i.e., 100, 75, 50 and 25% FC). The relative humidity and temperature were recorded on a daily basis using a Thermo-Hygrometer, Model 13307 (DeltaTrak, Pleasanton, CA 94566, USA). The mid-day temperature ranged between 26.0 to 37.2 °C and 25.8 to 36.9 °C for 1st and 2nd experiments, respectively. The mid-day relative humidity ranged between 35.0 to 69% and 36.5 to 73.8% for the 1st and 2nd experiments, respectively. The screen house daylight intensity during both experiments was ~ 90% of outdoor daylight intensity around the equator.

Data collection

Data collection was carried out at 5 WAT stage. A potted plant was the observational unit. Leaf relative water content (LRWC, %), a physiological trait was measured according a formula:

$$\%LRWC = \frac{FW - DW}{TW - DW} \times 100;$$

where FW = fresh weight of leaf sample, TW = Turgid weight of leaf sample, and DW = Dry weight of leaf sample (Kesiime 2014). Four morphological traits which tend to vary under drought stress were measured: leaf blade length (centimeters, cm), leaf width (cm), number of green leaves (herein simply referred to as leaves per plant (LPP) and plant height in cm (Amelework et al. 2015; Kesiime 2014; Mwale et al. 2017).

Data analysis

Effect of moisture deficit stress on leaf relative water content and morphological traits

A generalized linear model that considers replication, water deficit stress, water deficit stress-by-accession

and accessions as random effects was analyzed following a split-plot arrangement within an experiment. The GenStat Release 12.1 edition (VSN International) was used to implement the following split-plot model in which the water deficit stress level and accessions were the main plot and sub-plots, respectively:

$$y_{ijkl} = \mu + R_i + W_j + W * G_k + G_l + \varepsilon_{ijkl};$$

where μ was the grand mean, y_{ijkl} was the measured observation due to the i th replication (R), j th water deficit stress level (W), k th water deficit stress-by-accession interaction ($W * G$), l th accession (G) effects, and random error (ε_{ijkl}).

Variance components and genotypic coefficient of variation estimates

For each experiment (Table 2) and for each trait measured, variance components, obtained from variance analysis (ANOVA), were partitioned out using the mean squares method in order to estimate the broad sense heritability and genotypic coefficient of variation, as elaborated in Falconer and Mackay (1996). Any further analysis and reporting of results was then based on data from only one of the experiments in case the results from both experiments were similar.

The following formulae were used to estimate the genetic variance, broad sense heritability and genetic coefficient of variation:

Genotypic variance (V_G):	$V_G = \frac{(rw\sigma_g^2 + rw\sigma_{wg}^2 + \sigma_e^2) - (rw\sigma_{wg}^2 + \sigma_e^2)}{r * w}$
Broad sense heritability (H^2):	$H^2 = \frac{\sigma_g^2}{\sigma_p^2}$
Phenotypic variance (V_P):	$V_P = \sigma_g^2 + \frac{\sigma_{wg}^2}{w} + \frac{\sigma_e^2}{rw}$
Genotype by water deficit stress interaction (V_{WG}):	$V_{WG} = \frac{(r\delta_{wg}^2 + \delta_e^2) - \delta_e^2}{r}$
Genetic coefficient of variation ($GCV\%$):	$GCV\% = \frac{\sqrt{\sigma_g^2}}{\mu} \times 100$

$r, w, g, \varepsilon, \mu$ refer to number of replications (blocks), water deficit stress levels, number of genotypes (accessions), pooled error and grand mean, respectively

Stability estimates

Stability superiority coefficients were estimated for each trait by implementing a model published earlier by Eberhart and Russell (1966), and modified by Linn

Table 2 ANOVA table showing expected mean squares for each experiment

Source of variation	Degrees of freedom	Mean squares (MS)	Expected mean squares	F test
Replications (R)	$r - 1$	MSR	$wg\sigma_r^2 + g\sigma_{rw}^2 + \sigma_\epsilon^2$	$\frac{MSR}{MSM}$
Watering regime (W)	$w - 1$	MSW	$rg\sigma_w^2 + g\sigma_{rw}^2 + r\sigma_{wg}^2 + \sigma_\epsilon^2$	$\frac{MSW + MSE}{MSM + MSS}$
Main plot error (M)	$(r - 1)(w - 1)$	MSM	$g\sigma_{rw}^2 + \sigma_\epsilon^2$	$\frac{MSM}{MSE}$
Accessions (G)	$g - 1$	MSG	$rw\sigma_g^2 + r\sigma_{wg}^2 + \sigma_\epsilon^2$	$\frac{MSG}{MSS}$
Subplot error (S)	$(rw - 1)(g - 1)$	MSS	$r\sigma_{wg}^2 + \sigma_\epsilon^2$	$\frac{MSS}{MSE}$
Error (E)	$(rwg - 1)(p - 1)$	MSE	σ_ϵ^2	
Total	$rwgp - 1$			

and Binns (1988). The model is based on the differences between a given accession performance and the maximum response observed, across all water stresses. The stability superiority coefficient (P_i) of the i th accession is calculated as:

$$P_i = \sum_{j=1}^n (X_{ij} - M_j)^2 / (2w)$$

where X_{ij} is the performance of the i th accession grown under the j th water deficit stress level, M_j is the maximum response among all accessions under the j th water deficit stress level, and w is the number of water deficit levels. The stability superiority models have been widely applied in superior genotypes selection (Kamidi 2001; Mendes de Paula et al. 2014; de Oliveira et al. 2014). The stability superiority coefficients analysis was implemented in GenStat (Breeding View) Release 18.0 (VSN International Ltd, Hemel Office).

Identification of drought tolerance breeding traits

From ANOVA, traits with significant difference for $WL \times G$ interaction each at 99% confidence were considered as potential breeding traits for drought resistance. The candidate traits were further scrutinized for uniqueness through correlation analysis in order to eliminate any redundancy. When its $WL \times G$ interaction is significant, the LRWC was not subjected to the correlation analysis scrutiny because it is a widely accepted drought tolerance breeding trait in comparatively well-researched crops such as cassava (Turyagyenda et al. 2013), potato (Banik et al. 2016) and tomato (Zhu et al. 2014).

Results

Effect of drought stress and accession on leaf relative water content and morphological traits

There was a highly significant difference among the water deficit stress levels and genotypes for all measured traits in each experiment. For instance, for both experiments the mean leaf relative water content (LRWC) of plants, together with mean performance for all morphological traits namely leaf blade length (LBL), leaf blade width (LBW), leaves per plant (LPP) and plant height (PH), decreased steadily with increasing drought stress from 100% (W1) to 25% of field capacity (W4) (Fig. 1). Water stresses (W2, W3, W4), compared to field capacity (W1), increase data dispersion of LRWC (Fig. 1), but not of morphological traits, which display even a decreased dispersion in the second experiment for W3 and W4 (Fig. 2). Both experiments produced similar results, thus further analysis was based on data from 1st experiment. The results of ANOVA from 1st experiment are summarized in Table 3 (ANOVA table for 2nd experiment is not presented). Broad sense heritability is very high for all variables measured (variation from 0.89 to 0.97) and the GCV is much higher for PH than for LRWC, LBL, LBW and LPP (Table 3).

Stability superiority of accessions and traits for drought tolerance breeding

Stability estimates

The accessions having the highest and most stable LRWC across drought stress levels were 160, 145, 157P and 108P while those with the lowest and

Fig. 1 Boxplot for leaf relative water content at increasing water deficit stress levels (W1–W4): **a** 1st experiment; **b** 2nd experiment

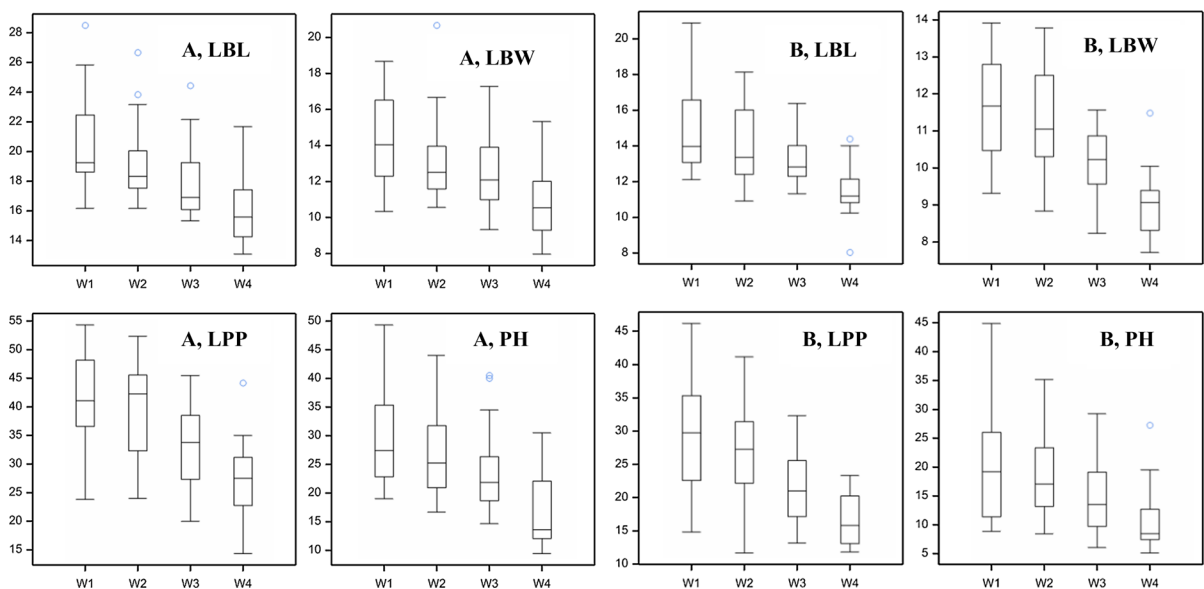
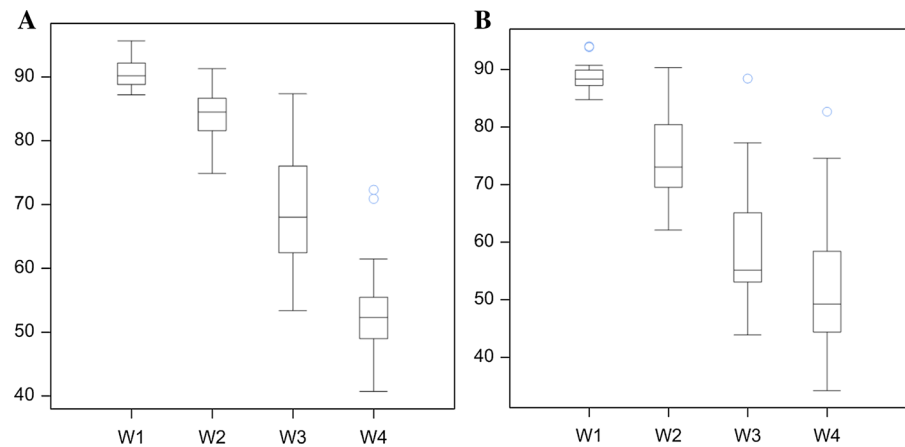


Fig. 2 Boxplot for morphological traits: **A** 1st experiment; **B** 2nd experiment; **LBL** leaf blade length, **LBW** leaf blade width, **LPP** leaves per plant, **PH** plant height

least stable values were 163G, 141, 163 and 108 (Table 4). For morphological traits, four accessions namely 160, 145, 148 and 108P had largest and most stable leaf blade length (LBL) and leaf blade width (LBW) across water deficit stress levels but generally the most inferior for leaves per plant (LPP). Accessions having the highest and most stable LPP were 185P followed by 185G, 163P and 157G. Accessions 163P, 163G, 168G and 163 maintained the tallest plants while accessions 137, 160, 183G and 108P had the shorted plants across drought stress levels.

Drought tolerance breeding traits

There were very highly significant $WL \times G$ interactions for LRWC, LPP and PH, each at 99.9% confidence level. The very highly significant $WL \times G$ interactions enabled differentiation of superiorly stable from unstable genotypes based on, for instance, LRWC (Fig. 3) and PH (Fig. 4). Taking an example from Table 4 and Fig. 3, the most superiorly stable genotypes for LRWC (like 145) maintained high performance irrespective of moisture stress deficit level (WL) while the least stable genotypes

Table 3 Mean squares, variance components and genotypic coefficient of variation across moisture stress levels

Source of variation	d.f	LRWC	LBL	LBW	LPP	PH
Replications (R)	1	9.60	1.51	0.28	20.83	15.05
Watering regime (W)	3	33,059.10***	494.96**	244.18*	5255.39***	4193.97***
Main plot error (M)	3	0.97	9.18	7.06	28.90	23.17
Accessions (G)	19	764.43***	135.34***	92.26***	1195.84***	1453.96***
W × G interaction	57	112.60***	12.76	12.07	89.84***	48.95***
Subplot error (S)	76	13.15	10.31	9.07	18.03	14.97
Error (E)	320	12.17	3.78	4.07	11.10	9.95
Variance components, broad sense heritability and genotypic coefficient of variation						
V_G		88.58	15.50	10.24	143.38	178.05
V_{WG}		21.80	3.79	3.14	18.85	9.79
V_P		95.55	16.92	11.53	149.48	181.75
$H^2(\%)$		92.70	91.61	88.78	95.92	97.97
$GCV\%$		12.67	21.29	25.11	34.02	54.71

*, ** and *** significant at $p \leq 0.05$, 0.01 and 0.001, respectively

df degrees of freedom, LRWC leaf relative water content (%), LBL leaf blade length (cm), LBW leaf blade width (cm), LPP leaves per plant, PH plant height (cm)

(like 163G) greatly declined in performance as water deficit stress increased.

However, the WL × G interactions was non-significant for LBL and LBW. Further, the Pearson's correlation analysis produced very strong and very highly significant correlations between LBL and LBW ($r = 0.8$, $p < 0.001$, two-tailed t test). The two traits, LBL and LBW are thus similar and are both inferior to LRWC, LPP and PH when selecting for stability superiority among genotypes. A significant correlation was also observed between LRWC and each of the study traits; LRWC v LBL ($r = 0.5$, $p < 0.001$), LRWC v LBW ($r = 0.4$, $p < 0.001$), LRWC v LPP ($r = 0.4$, $p < 0.001$) and LRWC v PH ($r = 0.2$, $p < 0.001$). Weak but very highly significant correlation was observed between LPP and PH ($r = 0.2$, $p < 0.001$).

Discussion

There were very highly significant water deficit stress-by-genotype (WL × G) interaction for LRWC, LPP and PH, indicating the importance of these traits in selecting for stability superiority of variety performance under drought stress. Conversely, LBL and

LBW which are correlated and exhibiting non-significant WL × G interaction, are poised as non-essential in breeding for stability superiority across water deficit stress levels. In addition, larger dispersion in data (mean performance of genotypes) was observed for LRWC than for morphological traits under drought stress suggesting that *S. aethiopicum* Shum genotypes can best be distinguished from each other under drought stress using the LRWC. Such observation emphasizes the importance of LRWC as a drought tolerance breeding trait, which is already applied in other crops like tomato (Zhu et al. 2014), potato (Banik et al. 2016) and cassava (Turyagyenda et al. 2013).

Notably further, there was a significant correlation of LRWC with most of the morphological traits studied (one-tailed test, $r > 0.4$); suggesting that by selecting genotypes with superiorly stable LRWC alone, a breeder would have indirectly selected for increased stability superiority for LBL, LBW and LPP. However, since the estimated correlation between LRWC and PH was very weak (one tailed, $r = 0.2$), it is deemed essential to consider the superiority stability of a genotype for both LRWC and PH. Although LRWC is considered the most important indicators of plant-water status (as related to

Table 4 Stability superiority coefficients for study traits across moisture deficit stress levels

ACC	Code	LRWC		LBL		LBW		LPP		PH	
		SSC	Mean (%)	SSC	Mean (cm)	SSC	Mean (cm)	SSC	Mean (#)	SSC	Mean (cm)
6	160	0.0	86.6	0.0	25.2	0.2	17.7	375.4	21.8	324.8	15.8
12	145	0.5	85.9	2.5	23.4	2.7	16.4	259.6	26.5	178.9	22.2
15	137	37.9	78.8	36.2	16.8	21.3	11.6	45.4	41.6	344.8	15.0
18	108P	42.0	78.6	13.7	20.2	3.7	15.5	236.6	27.6	290.1	17.1
14	184G	65.7	78.0	34.4	17.2	18.6	12.4	43.4	40.2	211.8	21.2
5	157P	70.2	77.2	37.1	17.2	20.9	11.9	71.6	37.5	246.1	19.0
10	157G	74.2	76.0	28.2	18.1	22.9	11.4	36.5	43.3	206.0	20.9
4	163P	89.9	75.5	44.1	16.2	22.3	11.6	24.8	42.6	4.5	39.6
1	168G	116.8	72.6	37.6	16.8	17.3	12.4	81.1	37.3	11.9	37.1
11	148	118.3	73.8	11.2	20.7	8.2	14.4	347.0	22.8	131.1	25.5
13	168P	122.3	73.1	21.3	19.1	16.9	12.4	124.2	33.5	55.6	31.3
2	183G	125.1	72.0	39.8	16.6	15.7	12.7	110.3	34.5	297.6	17.0
20	185P	127.2	73.0	36.9	16.8	36.1	9.6	20.9	44.4	181.3	22.3
8	183P	127.4	72.3	31.6	17.4	20.6	11.7	127.8	33.2	174.5	22.4
16	184P	144.4	72.1	37.3	16.7	24.2	11.1	149.4	31.9	238.7	19.6
19	185G	145.3	71.7	26.9	18.1	19.6	12.1	24.4	44.7	150.2	23.8
9	108	155.0	71.0	23.8	18.7	17.8	12.7	60.8	40.3	157.5	23.4
3	163	212.0	67.8	26.4	18.1	20.3	12.3	95.0	35.9	13.1	37.0
17	141	294.2	65.3	36.2	16.9	24.3	11.1	75.1	37.3	224.8	20.0
7	163G	296.4	64.5	16.5	19.7	8.6	14.1	237.8	27.3	9.0	37.7

Accessions with smaller values are more stable across the different moisture deficit stress levels. The accessions are ranked by SSCs for LRWC.

SSC stability superiority coefficient; LRWC leaf relative water content, LBL, leaf blade length, LBW leaf blade width, LPP leaves per plant, PH plant height

drought tolerance stability, in this case), stability in PH should be considered as well. In leafy vegetables like the crop in this study, superiorly stable varieties under drought stress are desired for yield assurance (Kumar et al. 2012; Yoshida et al. 2014).

Upon further scrutiny however, it was established that very tall accessions like 163P, 163G, 168G and 163 retained their tallness across moisture deficit stress levels yet majority of them suffered significant reductions in LRWC. Only accession 163P was relatively superiorly stable for both PH and LRWC. It is therefore suggested that prioritization of choice for drought resistance breeding traits in *S. aethiopicum* Shum should consider LRWC (1st choice), PH (2nd choice) and LPP (3rd choice). The chosen traits are strategic in that LRWC directly influences postharvest deterioration and market value because high LRWC

indicates high quality (non-wilted and freshy) leaves which are of high market value (Kumar et al. 2012; Ssekabembe and Odong 2008). The PH and LPP usually influence leaf yield (Kumar et al. 2012; Sseremba et al. 2017a, b), i.e., the higher the PH/LPP, the higher the yield potential of the genotype of a leafy vegetable.

Favorably, the H^2 for all the three priority traits (LRWC, PH and LPP) was above 90%, indicating that the observed genotypic variation is heritable (Ogunniyan and Olakojo 2014). The GCV % was also favorably high especially for PH and LPP. Traits with relatively high GCV % indicate a good response to selection (Falconer and Mackay 1996; Roychowdhury and Randrianotahina 2011). The accession set used in this study can be used to effectively select for stability superiority across drought stress levels based on PH

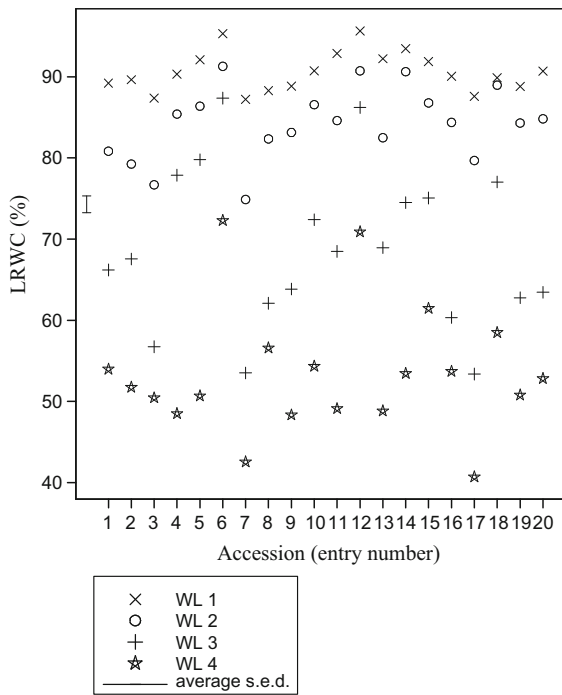


Fig. 3 Variation in LRWC of accessions at different moisture deficit levels. 1–20, entry numbers for study accessions; 1, 168G; 2, 183G; 3, 163; 4, 163P; 5, 157P; 6, 160; 7, 163G; 8, 183P; 9, 108; 10, 157G; 11, 148; 12, 145; 13, 168P; 14, 184G; 15, 137; 16, 184P; 17, 141; 18, 108P; 19, 185G; 20, 185P. WL moisture deficit level, WL1 100%FC, W2 75%FC, WL3 50%FC, WL4 25%FC, FC field capacity of potting soil mixture

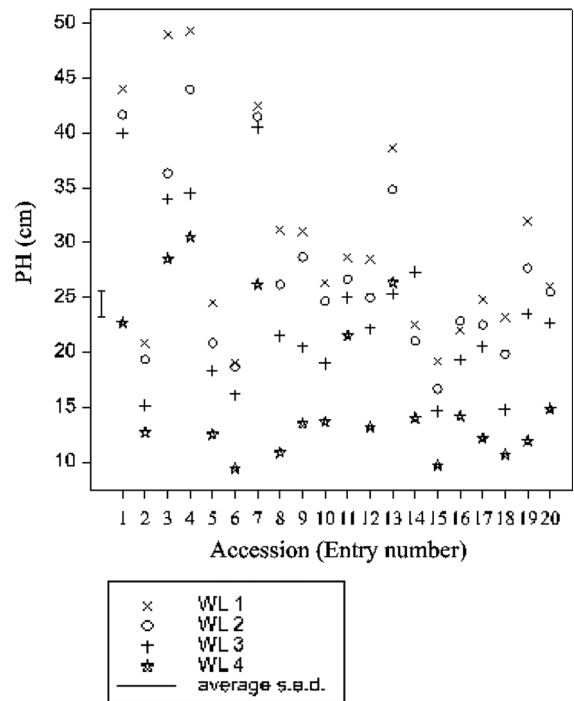


Fig. 4 Variation in PH of accessions at different moisture deficit levels. 1–20, entry numbers for study accessions; 1, 168G; 2, 183G; 3, 163; 4, 163P; 5, 157P; 6, 160; 7, 163G; 8, 183P; 9, 108; 10, 157G; 11, 148; 12, 145; 13, 168P; 14, 184G; 15, 137; 16, 184P; 17, 141; 18, 108P; 19, 185G; 20, 185P. WL moisture deficit level, WL1 100%FC, W2 75%FC, WL3 50%FC, WL4 25%FC, FC field capacity of potting soil mixture

(very high likelihood) followed by LPP, leaf size and LRWC (lowest likelihood). The LRWC % had an intermediate GCV % suggesting a moderate response to selection (Ahsan et al. 2015; Al-Tabbal and Al-Fraihat 2011; Ogunniyan and Olakojo 2014; Roychowdhury and Randrianotahina 2011). However, since results indicated positively and significant correlation between LRWC and LPP, stability superiority for the former can be indirectly selected for using the latter (Falconer and Mackay 1996).

Ultimately, the order of preference as selecting criteria for superiority stability across water deficit levels is recommended as: LRWC is greater than PH is greater than LPP. Further, because LRWC influences leaf quality (leaves being the harvestable part in leafy vegetables) under drought stress (Kumar et al. 2012; Ssekabembe and Odong 2008), the trait was relied on for selecting the most superiorly stable accessions. Thus, accession 160 was the most superiorly stable followed by 145, 137, 108P and 184G. On the lower

extreme, accessions 163G was the least superiorly stable followed by 141, 163 and 108.

Conclusion

Drought stress negatively affects the performance of *Solanum aethiopicum* Shum group but the exhibited variation allows for selection of drought tolerant accessions. Of the five traits studied (LRWC, LBL, LBW, LPP and PH), it was established that LRWC, PH and LPP provided the best possibility to select for stability superiority across drought stress levels. The order of preference as drought stress breeding traits is such that LRWC > PH > LPP. Based on LRWC which is a physiological trait, the accessions 160, 145, 137, 108P and 184G are considered to be the most superiorly stable across moisture deficit stress levels while the accessions 163G, 141, 163 and 108 are unstable. Based on the high heritability of the priority

traits, it is possible to achieve good response to selection and potential genetic advance on stability superiority of performance across moisture deficit stress levels if appropriate breeding methods are used.

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