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Heritability of drought resistance in *Solanum aethiopicum* Shum group and combining ability of genotypes for drought tolerance and recovery

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ABSTRACT

Drought tolerance is a complex trait whose inheritance had not been investigated in *Solanum aethiopicum* L. Shum group. This is partly because of perceived cross incompatibilities in the crop. This study relied on 24 successful crosses from an incomplete 9 × 4 North Carolina II mating design, evaluated under five watering conditions based on plant growth stage and watering level in order to determine the heritability of drought resistance and combining ability. Subsequent data analyses were based on restricted maximum likelihood. Overall, specific combining ability (SCA) effects were significant across and within watering environments for all study traits. The most highly heritable traits (in the narrow-sense) were identified as leaves per plant, chlorophyll content (CHL), leaf fresh yield and leaf dry yield while leaf area (LA), leaf relative water content (LRWC) and leaf mass area (LMA) were least heritable. However, the broad sense heritability (H^2) was over 0.80 for seven of the traits, indicating that dominance gene action surpass additive gene effects for drought resistance in *S. aethiopicum* Shum. Further analysis showed that LA is suited for selection of best combiners under well-watered and drought-stress (DS) treatments. The LRWC served best in separating the SCA effects of crosses under DS. The CHL produced clear separations of SCA effects under both DS and drought recovery while LMA served best under the latter.

1. Introduction

African eggplant (*Solanum aethiopicum; family Solanaceae*) is the third most important *Solanum* species after tomato and potato (Gramazio et al., 2016, 2017a,b; Sseremba et al., 2017a). Of four recognized morphological groups of *S. aethiopicum*, the Shum is cultivated for its leaves (Gramazio et al., 2016, 2017a, b; Prohens et al., 2013; Sseremba et al., 2017b; Sseremba et al., 2018a,b). Thus, the crop yield directly deteriorates whenever a stress affects the foliage (Banik et al., 2016; Basu et al., 2016; Gramazio et al., 2016, 2017a,b; Kesiime et al., 2016; Kumar et al., 2012; Sseremba et al., 2018a,b). Drought is one of the most threatening constraints to crop productivity. Generally, crops respond to drought through escape, avoidance, tolerance and/or recovery mechanisms (Amelework et al., 2015; Beyene et al., 2015; Kumar et al., 2012; Yoshida et al., 2014). Drought escape strategies such as early flowering time and a short vegetative phase enable the completion of the plant's full life-cycle before a drought event sets in (Basu et al., 2016; Pucholt et al., 2015; Turyagyenda et al., 2013). According Shavrukov et al. (2017), plants employing drought escape strategies tend to exhibit very high metabolic rates with low water use efficiency (WUE).

A drought stress stimulus is signaled in the root leading to synthesis of abscisic acid (ABA); the chemical messenger for osmotic stress on the one hand (Yoshida et al., 2014). The signaling process for ABA-dependent osmoregulation is aided by calcium ions (Ca^{2+}), protein kinases, protein phosphatases and membrane trafficking components (Fita et al., 2015). On the other hand, ABA-independent regulation of ion channels by osmotic stress is also believed to occur in guard cells (Basu et al., 2016; Fita et al., 2015; Yoshida et al., 2014). The signaling of drought stress either through ABA or Ca^{2+} stimulate the closing of inward and opening of outward pores for potassium (K+) movement out of the guard cells, leading to stomatal closure (Basu et al., 2016; Kröber et al., 2015; Parry et al., 2014; Ramírez et al., 2014). Stomatal closure reduces the conductance for carbon dioxide (CO_2) and oxygen

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Abbreviations: CHL, chlorophyll content; DR, drought recovery; DS, drought stress; GCA, general combining ability; H^2, broad sense heritability; h^2, narrow sense heritability; LA, leaf area; LMA, leaf mass area; LPP, number of green leaves per plant; LRWC, leaf relative water content; LWS, leaf wilting score; LYD, leaf dry yield; LYF, leaf fresh yield; NCII, North Carolina II mating design; RE, re-watering treatment; SCA, specific combining ability

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Table 1
Description of hybrids studied and their parents.

F1 hybrid			Female parent			Male parent		
Code	Pedigree	Color	Code	Pedigree	Attributes	Code	Pedigree	Attributes
E1xE4	SAS168/G/2015 x SAS/163/P/2015	P	E1	SAS168/G/2015	DS, SLS, G	E4	SAS/163/P/2015	DT, SLS, P
E3SxE4	SAS163/2015.S x SAS/163/P/2015	P	E3S	SAS163/2015.S	DS, MLS, P	E4	SAS/163/P/2015	DT, SLS, P
E7HxE4	SAS163/G/2015.H x SAS/163/P/2015	P	E7H	SAS163/G/2015.H	DS, MLS, G	E4	SAS/163/P/2015	DT, SLS, P
E10xE4	SAS157/G/2015 x SAS/163/P/2015	P	E10	SAS157/G/2015	DS, SLS, P	E4	SAS/163/P/2015	DT, SLS, P
E11xE4	SAS/148/2015 x SAS/163/P/2015	P	E11	SAS/148/2015	DS, LLS, G	E4	SAS/163/P/2015	DT, SLS, P
E13xE4	SAS/168/P/2015 x SAS/163/P/2015	P	E13	SAS/168/P/2015	DS, MLS, P	E4	SAS/163/P/2015	DT, SLS, P
E1xE6	SAS168/G/2015 x SAS160/2015	GP	E1	SAS168/G/2015	DS, SLS, G	E6	SAS160/2015	DT, MLS, GP
E3SxE6	SAS163/2015.S x SAS160/2015	P	E3S	SAS163/2015.S	DS, MLS, P	E6	SAS160/2015	DT, MLS, GP
E7HxE6	SAS163/G/2015.H x SAS160/2015	GP	E7H	SAS163/G/2015.H	DS, MLS, G	E6	SAS160/2015	DT, MLS, GP
E13xE6	SAS/168/P/2015 x SAS160/2015	P	E13	SAS/168/P/2015	DS, MLS, P	E6	SAS160/2015	DT, MLS, GP
E1xE15	SAS168/G/2015 x SAS137/2015	P	E1	SAS168/G/2015	DS, SLS, G	E15	SAS137/2015	DT, SLS, P
E2xE15	SAS183/G/2015 x SAS137/2015	P	E2	SAS183/G/2015	DS, LLS, G	E15	SAS137/2015	DT, SLS, P
E3HxE15	SAS163/2015.H x SAS137/2015	P	E3H	SAS163/2015.H	DS, MLS, P	E15	SAS137/2015	DT, SLS, P
E7SxE15	SAS163/G/2015.S x SAS137/2015	P	E7S	SAS163/G/2015.S	DS, MLS, G	E15	SAS137/2015	DT, SLS, P
E7HxE15	SAS163/G/2015.H x SAS137/2015	P	E7H	SAS163/G/2015.H	DS, MLS, G	E15	SAS137/2015	DT, SLS, P
E10xE15	SAS157/G/2015 x SAS137/2015	P	E10	SAS157/G/2015	DS, SLS, P	E15	SAS137/2015	DT, SLS, P
E11xE15	SAS/148/2015 x SAS137/2015	P	E11	SAS/148/2015	DS, LLS, G	E15	SAS137/2015	DT, SLS, P
E13xE15	SAS/168/P/2015 x SAS137/2015	P	E13	SAS/168/P/2015	DS, MLS, P	E15	SAS137/2015	DT, SLS, P
E1xE20	SAS168/G/2015 x SAS185/P/2015	P	E1	SAS168/G/2015	DS, SLS, G	E20	SAS185/P/2015	DT, SLS, P
E3SxE20	SAS163/2015.S x SAS185/P/2015	P	E3S	SAS163/2015.S	DS, MLS, P	E20	SAS185/P/2015	DT, SLS, P
E7SxE20	SAS163/G/2015.S x SAS185/P/2015	P	E7S	SAS163/G/2015.S	DS, MLS, G	E20	SAS185/P/2015	DT, SLS, P
E10xE20	SAS157/G/2015 x SAS185/P/2015	P	E10	SAS157/G/2015	DS, SLS, P	E20	SAS185/P/2015	DT, SLS, P
E11xE20	SAS/148/2015 x SAS185/P/2015	P	E11	SAS/148/2015	DS, LLS, G	E20	SAS185/P/2015	DT, SLS, P
E13xE20	SAS/168/P/2015 x SAS185/P/2015	P	E13	SAS/168/P/2015	DS, MLS, P	E20	SAS185/P/2015	DT, SLS, P

DS, drought susceptible female; DT, drought tolerant male; SLS, small leaf size; MLS, medium leaf size; LLS, large leaf size; G, green stem and leaf lamina; GP, pale purple stem and leaf lamina; P, purple stem and leaf lamina. All crosses between green stem females and purple stem males produced purple stem F_1 hybrids.

(O_2) gases (Galmés et al., 2013; Yoshida et al., 2014). The consequence is reduced internal CO_2 concentration and increased O_2 concentration that favors photorespiration at the expense of photosynthesis, leading to accumulation of free radicals of oxygen or peroxides which are referred to as reactive oxygen species (ROS) (Amelework et al., 2015; Anjum et al., 2011; Banik et al., 2016; Beyene et al., 2015). The free oxygen radicals cause oxidative stress that bleaches the chlorophyll membranes "the thylakoids" where light reactions of photosynthesis take place (Fita et al., 2015; Kesiime, 2014; Yoshida et al., 2014). Morphologically, osmotic stress impairs various traits including plant height, leaf size, leaf yield (Nakanwagi et al., 2018; Sseremba et al., 2018a,b), grain yield and tuber yield. The crop of focus in this study is a leafy vegetable, the *S. aethiopicum* Shum; thus only leaf traits (leaf wilting score, number of green leaves per plant, leaf yield, leaf area, leaf relative water content, leaf mass area and chlorophyll content) were measured.

In leafy vegetables such as the *S. aethiopicum* Shum, it is desirable to have a variety having a long vegetative phase if maximum production with optimum WUE is to be realized (Sseremba et al., 2018a,b). This provides vegetable breeders with options of breeding for drought avoidance, tolerance, recovery or a combination of strategies. Drought avoidance strategies (such as high WUE) involve slow plant growth which is associated with small/closed stomata, resulting in reduced photosynthesis thereby preparing plants for a coming drought (Shavrukov et al., 2017). Desired vegetable genotypes are those which can tolerate drought stress to produce appreciable leaf yield (Galmés et al., 2013) and quality traits such as leaf relative water content (Banik et al., 2016; Ramírez et al., 2014; Sseremba et al., 2018a,b), leaf mass area and chlorophyll content (Galmés et al., 2013; Shavrukov et al., 2017; Yoshida et al., 2014). If it was a short drought period that clears to normalcy (resumption of water availability after a period of drought stress), plants tend to recover to productivity levels depending on genotype (Fita et al., 2015).

Improvement approaches such as cross breeding are commonly used to enhance crops' ability to perform under a stress like drought. Cross breeding explores hybrid vigor; a common concept that has been extensively applied for yield and other traits' improvement in major food crops particularly maize (Pioneer Hi-Bred, n.d.; Sprague, 1936). The International Crops Research Institute for Semi-Arid Tropics also explores the combining ability of sorghum lines; with results indicating convincing heterotic potential of sorghum hybrids (Ben-Israel et al., 2012; Mindaye et al., 2016). In vegetables, hybridization leads to significant yield increases in crops like tomato (Sharma et al., 2015) and cabbage (Kibar et al., 2015; Saeki et al., 2016). In *S. aethiopicum*, the notion of hybridization and possible heterosis for performance under drought had not been extensively investigated especially in the leafy morphological group, the Shum (Lester and Thitai, 1989; Meier, 2011).

Aside heterotic advantage of hybrids with good specific combining ability (SCA), controlled crossing helps in trait introgression into farmer-preferred varieties using parental material of known general combining ability (GCA) since not all variation is heritable (Ahsan et al., 2015). Hybridization for estimation of variance components is a widely studied subject where various mating designs are applied (Bu et al., 2015; Murtadha et al., 2016; Nduwumuremyi et al., 2013; Stuber, 1980).

Among the *S. aethiopicum* morphological groups, reports on successful production of hybrids in the Gilo group are available (Lester and Thitai, 1989; Meier, 2011). Hybridization potentials within other *S. aethiopicum* groups namely Shum, Kumba and Aculeatum had not been investigated. The Shum group was the focus for this study. The main objective was to determine the combining ability of *S. aethiopicum* Shum under different watering conditions. Specifically, we aimed to determine the heritability of drought resistance in *S. aethiopicum* Shum across watering treatments, and identify suitable traits for selecting genotypes for combining ability effects under particular watering environments.

2. Materials and methods

2.1. Plant material

Thirteen accessions were obtained in 2015 from Department of Agricultural and Biological Sciences, Uganda Christian University (DABS/UCU), Mukono, Uganda. The accessions were then self-

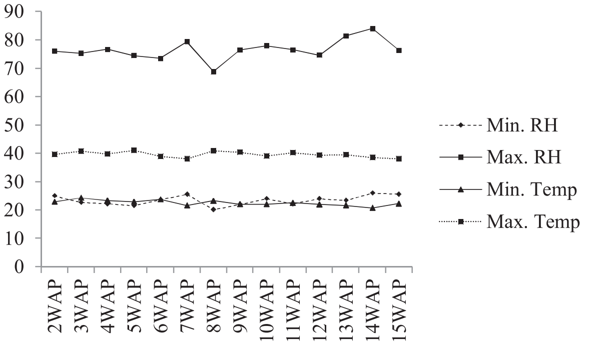

Fig. 1. Variation in relative humidity and temperature within screen house over time during the experiment. Min., minimum value; Max., maximum value; RH, relative humidity in percentages; Temp, temperature in degrees celcius; WAP, weeks after planting.

Table 2
Heritability estimates of different traits across watering conditions.

Trait	VA	VD	VE	H^2	h^2
Leaves per plant	411.23	66.97	205.15	0.92	0.79
Chlorophyll content	57.50	10.27	86.04	0.80	0.68
Leaf dry yield	49.16	20.05	66.65	0.84	0.60
Leaf fresh yield	5248.33	2642.60	8231.39	0.83	0.55
Leaf area	1626.07	6869.11	4872.00	0.90	0.17
Leaf relative water content	8.62	36.72	58.13	0.80	0.15
Leaf mass area	30.60	124.07	282.11	0.73	0.14
Leaf wilting score	0.01	0.14	0.18	0.81	0.06

VA, additive variance; VD, dominance variance; VE, environmental variance; H^2, broad sense heritability; h^2, narrow sense heritability; GCA, general combining ability; SCA, specific combining ability. The traits are ranked by *narrow sense heritability*.

pollinated for three generations under screen house conditions in order to ensure that they are pure lines. Filial 1 generation (F_1) hybrids were made by crossing four drought tolerant accessions with nine drought susceptible accessions (Table 1). In a traditional 9 × 4 North Carolina II (NCII) design, the resulting number of crosses would be 36 but only 24 crosses (67%) were realized and evaluated; making it an incomplete North Carolina II mating design. The evaluation was carried out in the screen house under during which temperature and relative humidity largely remained constant throughout the experiment (Fig. 1). The daylight intensity of the screen house during the experiment was about 90% of the outdoor daylight intensity around the equator.

2.2. Experimental design

A 9 × 4 NCII mating design (with missing crosses) that produced 24 F_1 hybrids was evaluated in 2017 in a randomized complete block design with two replications under three different watering conditions namely well watered (WW), drought tolerance (DT) and recovery (DR) in one screen house at the DABS/UCU. The blocking was made along the direction of sunrise. Plastic pots of uniform size (10 kg of potting substrate each) were used with steam-sterilized 3 parts of clay-loam soil in 1 part of cow dung manure. Sowing was done directly with three seeds into each pot on 23rd May 2017, and six pots per genotype per replication were sown. Thinning was then carried out at 4-leaf stage to retain one most healthy seedling per pot. Fertilizer application was carried out at a rate of 5 g/pot, once every month.

Well-watered experiment: Watering to 100% field capacity was carried out routinely to ensure optimum soil water availability throughout the well-watered experiment, right from sowing up to 8 weeks. The duration of the well-watered experiment was 8 weeks after planting (WAP). The procedure applied for estimation of field capacity of the soil is the same as that described in detail by Sseremba et al. (2018a).

Drought tolerance experiment: From the well-watered experiment, half the number of the plants per genotype per replication was maintained under field capacity (100% FC) watering while for remaining plants the watering was ceased at 8 WAP for 2 weeks in a split-plot arrangement. The drought tolerance experiment last 10 weeks (8 weeks of well-watering + 2 weeks of drought).

Drought recovery experiment: In the recovery experiment, 100% FC watering was similarly continued for well-watered controls, and the watering was resumed to rest of plants which had been exposed to drought stress for 2 weeks (during the drought tolerance experiment). The recovery of plants from drought stress was allowed to occur for 2 weeks since the start of re-watering. The drought recovery experiment last 12 weeks (8 weeks of well-watering + 2 weeks of drought + 2 weeks of re-watering).

2.3. Data collection

2.3.1. Time of data collection

Data collection for the well-watered, drought stressed and re-watered (drought recovery) experiments was carried out at 8, 10 and 12 WAP, respectively. Eight traits were considered, five of which were morphological and three physiological traits.

2.3.2. Morphological variables

The morphological variables measured include leaf wilting (score), leaves per plant (number of green leaves per plant), leaf area (cm^2), leaf fresh yield (g/plant) and leaf dry yield (g/plant). The leaf fresh yield and leaf dry yield was measured by weighing all the freshly harvested green leaves per plant and the oven-dried leaves (oven temperature was set at 105 °C for 24 h), respectively. Leaf wilting was scored according to a modified 0–5 scale earlier used by Banik et al. (2016) where 0 = no leaf is wilted, 1 = 25% of leaves are wilted, 2 = 50% of leaves are wilted, 3 = 75% of leaves are wilted, 4 = 100% of leaves are wilted, and 5 = 100% leaf plus stem wilting. Leaf area (LA) was measured on the most fully open leaf from top of plant using a portable leaf area meter, model AM350 (ADC Bioscientific Ltd, Global House, Geddings Road, Hoddesdon, Herts, EN11 0 N T, UK).

2.3.3. Physiological variables

The physiological variables measured include leaf mass area (mg/cm^2), leaf relative water content (LRWC%) and chlorophyll content on the most fully open leaf from top of individual potted plants. Leaf mass area (LMA) was calculated by dividing leaf dry mass by LA as described by Galmés et al. (2013). The LRWC% was estimated using the formula: $LRWC\% = \frac{FW - DW}{TW - DW} * 100$; where FW = fresh weight of a leaf sample disc, TW = turgid weight of the leaf sample disc, and DW = dry weight of the leaf sample disc as earlier applied by Banik et al. (2016) and Ramírez et al. (2014). The chlorophyll content (CHL) was measured as a chlorophyll content index (CCI) using CCI-200 plus chlorophyll content meter (Opti-Sciences inc., 8 W in. Avenue, Hudson, NH 03051, USA). The CCI measurement is a fast and non-destructive assay that relies on optical absorbance in two different wavebands (653 nm and 931 nm), and it is designed to measure CHL albeit compensating for leaf thickness (Parry et al., 2014).

2.4. Statistical analysis

2.4.1. Effect of watering condition on combining ability

For each experiment and across experiments, we applied multivariate linear mixed modeling approach (general model form: $y = X\beta + Zu + \varepsilon$) using the R sommer package to estimate the GCA and SCA variance components for an incomplete North Carolina II mating design (Covarrubias-Pazaran, 2016). From the model, y is the observed measurement, X is an incidence matrix for fixed effects such as grand mean, Z is an incidence matrix for random effects such as GCA and SCA, β is the vector for best linear unbiased estimates (BLUEs) of fixed

Table 3
Significance of combining ability effects for measured traits under well-watered, drought tolerance and recovery experiments.

Variable	Source of variation	WW experiment	Drought tolerance (DT) experiment			Drought recovery (DR) experiment			Across experiments
			DT-AT	DT-CT	DT-DS	DR-AT	DR-CT	DR-RE	
Leaf wilting	GCA_{Males}	0.000	0.007	0.000	0.026	0.013	0.000	0.051	0.002
	$GCA_{Females}$	0.000	0.000	0.000	0.000	0.020	0.000	0.079	0.000
	SCA	0.000	0.087*	0.000	0.384**	0.062*	0.000	0.284*	0.036*
	Error	0.000	0.222***	0.000	0.233***	0.260***	0.000	0.313***	0.182***
Leaves per plant	GCA_{Males}	72.314	81.220	389.100	5.345	73.080	389.100	1.508	76.880
	$GCA_{Females}$	9.582	40.900	142.800	0.101	38.390	142.800	3.880	25.920
	SCA	11.586*	11.750	112.000*	3.034*	15.320	112.000*	18.342*	16.740*
	Error	48.479***	275.640***	270.800***	2.609***	289.640***	270.800***	15.039***	205.150***
Leaf fresh yield	GCA_{Males}	3534.925	314.500	1176.000	53.537	208.750	859.500	184.443	744.700
	$GCA_{Females}$	1.891	897.100	3638.000	0.194	705.930	2388.600	5.691	567.400
	SCA	1998.698*	1789.700	8514.000*	24.757*	91.010	1014.600	59.118*	660.700*
	Error	4159.612***	11,724.900***	12,197.000***	18.723***	3509.900***	4724.100***	118.285***	8231.400***
Leaf dry yield	GCA_{Males}	49.129	5.452	24.880	1.845	0.285	1.992	2.201	5.893
	$GCA_{Females}$	5.317	8.372	34.280	0.000	3.641	9.884	0.121	6.397
	SCA	27.122*	9.449	41.930*	0.976**	1.404	10.653*	1.087*	5.013*
	Error	57.276***	73.164***	95.720***	0.546***	23.551***	32.141***	1.265***	66.647***
Leaf area	GCA_{Males}	3378.000	0.000	0.000	0.000	2.559	2.242	3.078	406.500
	$GCA_{Females}$	0.000	0.000	0.000	0.000	0.772	2.916	0.000	0.000
	SCA	6418.000**	20,180.000**	1649.000*	2741.000**	0.937*	1.953*	1.010*	1717.300**
	Error	7553.000***	2555.000***	3071.000***	1686.000***	3.999***	3.794***	1.660***	4872.000***
Leaf mass area	GCA_{Males}	0.136	0.147	0.020	0.261	63.730	0.686	238.400	7.650
	$GCA_{Females}$	0.010	0.000	0.036	0.000	0.000	0.000	0.000	0.000
	SCA	0.103*	0.223*	0.353*	0.630*	297.300*	4.030*	1341.000**	31.020*
	Error	0.245***	0.760***	0.478***	0.498.000***	614.150***	6.143***	405.800***	282.110***
Leaf relative water content	GCA_{Males}	2.370	24.014	4.706	158.064	0.160	0.000	0.510	0.000
	$GCA_{Females}$	5.386	1.871	0.000	2.526	0.000	0.739	0.000	2.155
	SCA	31.640**	21.895*	21.234**	80.957*	4.530*	2.797*	20.685*	9.181*
	Error	14.077***	88.506	11.316***	64.436***	23.533***	5.426***	26.144***	58.133***
Chlorophyll content	GCA_{Males}	3.516	0.000	5.106	0.000	5.582	2.263	9.372	0.376
	$GCA_{Females}$	8.633	7.385	22.660	0.000	11.230	6.775	4.867	13.998*
	SCA	7.748*	32.157*	26.535*	110.140**	12.545	42.169*	53.762*	2.568
	Error	34.108***	106.695***	42.519***	73.080***	79.552***	61.484***	37.606***	86.040***

*, **, ***significance of effects at alpha (α) = 5%, α = 1% and α = 0.1%, respectively. WW, well-watered; AT, across treatments; CT, control; DS, drought-stressed; RE, re-watered; GCA, general combining ability; SCA, specific combining ability.

Table 4
GCA of parents for different traits measured across watering environments.

Parent	Role	LWS	LPP	LYF	LYD	LA	LRWC	CHL	LMA
E11	Female	0.2	0.2	50.3	4.5	18.3	2.0	6.8	8.2
E1	Female	0.0	−0.8	2.5	−0.7	7.0	6.6	5.7	0.9
E7S	Female	−0.1	−1.1	−10.5	−1.4	−7.5	3.9	4.0	−1.0
E2	Female	0.2	2.1	49.3	5.1	14.6	4.0	3.9	−2.6
E10	Female	0.0	7.9	−23.4	−3.2	27.6	6.7	3.8	3.2
E4	Male	0.1	−2.7	−35.2	−2.7	−23.2	−1.4	1.3	5.0
E20	Male	0.1	9.7	0.7	−0.5	−3.9	0.1	1.2	−2.7
E15	Male	0.0	3.2	−1.0	−0.3	−16.5	−0.8	0.7	−2.6
E13	Female	0.0	10.7	31.3	3.0	−2.3	6.7	−0.1	−1.1
E7H	Female	0.0	−1.6	8.9	2.7	24.1	3.2	−0.6	−0.4
E6	Male	−0.2	−10.2	35.4	3.6	43.5	2.1	−3.2	0.3
E3S	Female	0.3	−4.5	−27.5	−1.8	−13.6	3.2	−5.0	−1.9
E3H	Female	−0.4	−12.9	−80.8	−8.3	−68.2	−36.4	−18.4	−5.2

LWS, leaf wilting score; LPP, leaves per plant; LFY, leaf fresh yield; LYD, leaf dry yield; LA, leaf area; LRWC, leaf relative water content; CHL, chlorophyll content; LMA, leaf mass area; GCA, general combining ability.

effects, u is the vector for best linear unbiased predictions (BLUPs) of random effects, and ε are residuals (Bu et al., 2015; Covarrubias-Pazaran, 2016).

Accordingly, any observed performance was considered predictable from the model: $y = X\beta + Zu_{GCA_{males}} + Zu_{GCA_{females}} + Zu_{SCA} + \varepsilon$ where y is the measurement of any morphological or physiological trait. Then X and Z refer to incidence matrix for fixed effects (grand mean, replication and moisture condition) and incidence matrix for random effects (GCA due to males, GCA due to females and SCA due to crosses). The β, u and ε stand for vector for BLUEs of the fixed effects, vector for BLUPs of the random effects and the residuals (environmental variance, V_E), respectively. In the well-watered experiment, the fixed effects included grand mean and replication. In the drought tolerance and drought recovery experiments, the fixed effects included the grand mean, replication and moisture condition. Across environments, the fixed effects were grand mean and watering condition.

Significance of combining ability effects was decided basing on critical values of Z-ratio; 1.64, 2.33 and 3.09 for probability of difference by chance (α) being set at 0.05, 0.01 and 0.001, respectively. The GCA and SCA variance estimates were generated and used to calculate additive (V_A) and dominance genetic variance (V_D), respectively as follows: $V_A = 4 * V_{GCA}$ and $V_D = 4 * V_{SCA}$ where $V_{GCA} = V_{GCA_{males}} + V_{GCA_{females}}$. Genotypic variance ($V_G$) was thus calculated as follows: $V_G = V_A + V_D$. The measured or phenotypic variance

Table 5
SCA of crosses for different traits across watering environments.

Cross	LWS	LPP	LYF	LYD	LA	LRWC	CHL	LMA
E3HxE15	0.3	18.5	73.7	7.7	60.6	35.5	13.1	6.2
E11xE20	0.1	−3.4	47.2	4.3	−7.3	−4.2	−4.3	−8.0
E7HxE4	0.0	2.3	36.8	3.0	11.9	−5.6	−0.5	−6.5
E13xE6	0.0	−4.5	23.3	1.3	13.2	−6.0	0.2	0.3
E10xE4	0.0	0.6	19.1	2.1	−49.0	−4.3	−2.8	3.3
E10xE15	−0.1	−3.0	17.7	0.9	−52.1	−4.1	−1.9	−2.8
E7SxE20	−0.2	−6.1	16.3	2.1	−9.2	−2.6	−2.8	2.2
E1xE6	0.0	−3.3	11.4	0.3	37.8	−2.6	−0.6	4.5
E1xE15	0.1	−4.1	0.1	−0.1	−5.8	−4.1	−1.9	0.3
E3SxE20	−0.1	−1.8	−0.6	−1.1	−24.9	−5.2	−2.4	2.5
E11xE15	−0.2	−4.4	−1.4	−0.1	13.4	−1.8	−3.3	−8.4
E2xE15	−0.1	−5.5	−6.8	−0.4	9.4	−4.0	−2.7	1.8
E13xE15	−0.2	−4.4	−14.5	−0.2	4.9	−3.1	−2.0	1.4
E3SxE6	0.2	0.3	−18.6	−1.9	−28.4	−8.8	−2.7	−2.2
E7HxE6	−0.4	−0.8	−19.1	−1.6	−17.8	−1.5	1.8	1.0
E13xE20	0.1	5.9	−19.6	−0.9	−35.3	−6.2	−3.8	0.3
E1xE4	0.0	−3.2	−20.0	−2.1	−14.4	−6.4	−5.8	−7.2
E13xE4	−0.1	−6.4	−20.5	−3.1	−11.2	−3.6	−2.1	−5.4
E1xE20	−0.1	1.1	−22.8	−1.1	−46.0	−5.8	0.5	−1.1
E10xE20	−0.2	−14.9	−24.8	−1.7	123.3	−3.7	−4.2	−2.7
E7SxE15	0.0	−11.5	−31.7	−2.7	15.3	−6.2	−2.9	1.5
E11xE4	−0.2	−9.4	−33.8	−2.8	16.1	−6.2	−1.4	14.2
E7HxE15	0.3	1.1	−40.4	−4.1	−19.3	−7.0	−6.0	0.2
E3SxE4	−0.1	−9.1	−82.2	−6.5	−12.8	−1.8	−8.8	−4.9

Genotype performance is ranked by LYF. LWS, leaf wilting score; LPP, leaves per plant; LYF, leaf fresh yield; LYD, leaf dry yield; LA, leaf area; LRWC, leaf relative water content; CHL, chlorophyll content; LMA, leaf mass area; SCA, specific combining ability.

(V_P) was then estimated as: $V_P = V_A + V_D + {}^{V_E}\!/_{n}$; on the assumption of negligible epistatic effects (Falconer and Mackay, 1996; Kang, 2002), in order to enable calculation of study traits heritability. For across watering environments, n = 5; for within environment analysis, n = number of blocks = 2. Traits that produced non-significant effects (GCA or SCA) were eliminated from calculations of values for each study genotype.

2.4.2. Calculation of combining ability effects

The GCA effect of any male genotype was calculated by subtracting the mean of progeny from all males from the mean performance of progeny of a given male. Similarly, the GCA effect of any female genotype was estimated by subtracting the mean of progeny from all females from the mean performance of progeny of a given female. On the other hand, SCA effect was computed by subtracting expected mean from observed mean performance; whereby $\textit{Expected mean} = \textit{overall mean} + \textit{GCA for a given male} + \textit{GCA for a given female}$ (Falconer and Mackay, 1996; Kang, 2002).

2.4.3. Heritability of drought resistance

The broad- (H^2) and narrow-sense (h^2) heritability was also consequently calculated: $H^2 = \frac{V_G}{V_P}$ and $h^2 = \frac{V_A}{V_P}$. To estimate heritability, 5 environments namely well-watered at 8 WAP, well-watered at 10 WAP, drought-stressed at 10 WAP, well-watered at 12 WAP and re-watered at 12 WAP) were used in the model.

2.4.4. Selection of traits for separating combining ability effects

In addition to elimination of traits based on significance, a boxplot on means of combining ability effects for each genotype within environment were used to indicate the appropriateness of selected variables for discerning the genotypes. The boxplot provides a visual spread among data, and it was on this basis that particular traits were qualified for discerning the combining ability effects under specified watering conditions.

3. Results

3.1. Effect of watering condition on combining ability

3.1.1. Across experiments

The GCA effects were significant among females ($p < 0.05$) for CHL but non-significant for the rest of traits (Table 3). Based on CHL, parent E11 had the best (highest positive) GCA effect followed by E1 and E7H. The GCA effects of E11 were also positive for all other measured traits though a positive effect for LWS is not desired (Table 4). On the other hand, E3H had the lowest negative GCA effect for CHL. The GCA effect of E3H was also negative for rest of traits.

The SCA effects were significant for LWS, LPP, LYF, LYD, LMA, LRWC and CHL; and highly significant ($p < 0.01$) for LA. Cross E7HxE6 had the best (negative) SCA effect for LWS followed by E11xE15 and E7SxE20 (Table 5) while E3HxE15 had the worst (highest positive) effect. For LPP, E3HxE15 had the best SCA effect followed by E13xE20 while E10xE20 had the worst effect. The SCA effects for E3HxE15 were also positive for LYF (LYD), LA, LMA, LRWC and CHL.

3.1.2. Well-watered

There were non-significant GCA effects ($p > 0.05$) for all measured traits (Table 3). The SCA effects were also non-significant for LWS. However, the SCA effects were significant ($p < 0.05$) for LPP, LYF, LYD, LMA and CHL; and highly significant ($p < 0.01$) for LA and LRWC.

3.1.3. Drought tolerance

Across and within watering treatments, the GCA effects were non-significant for all measured (Table 3). The SCA effects across watering treatments were significant for LWS, LMA, CHL and LRWC and highly significant for LA. Within the control, the SCA effects were significant for LPP, LYF, LYD, LA, LMA and CHL; and highly significant for LRWC. Within drought-stressed plants, the SCA effects were significant for LPP, LYF, LMA and LRWC; and highly significant for LWS, LYD, LA and CHL.

Table 6
Pearson's correlation coefficients and significance of correlation between study traits.

Variate		1	2	3	4	5	6	7	8
LWS	1	–	< 0.001	< 0.001	< 0.001	< 0.001	0.8208	< 0.001	< 0.001
LPP	2	−0.4495	–	< 0.001	< 0.001	0.1426	0.5295	< 0.001	< 0.001
LYF	3	−0.4263	0.5652	–	< 0.001	< 0.001	< 0.001	< 0.001	0.3183
LYD	4	−0.4164	0.5116	0.886	–	< 0.001	< 0.001	< 0.001	0.0103
LA	5	−0.1427	−0.0349	0.3966	0.4899	–	< 0.001	0.043	< 0.001
LMA	6	−0.0054	0.015	−0.2096	−0.1658	−0.3555	–	< 0.001	< 0.001
LRWC	7	−0.4985	0.5417	0.4483	0.4201	0.0481	0.3772	–	< 0.001
CHL	8	−0.097	0.114	−0.0238	−0.061	−0.2831	0.1827	0.3772	–
		1	2	3	4	5		7	8

LWS, leaf wilting score; LPP, leaves per plant; LFY, leaf fresh yield; LYD, leaf dry yield; LA, leaf area; LRWC, leaf relative water content; CHL, chlorophyll content; LMA, leaf mass area.

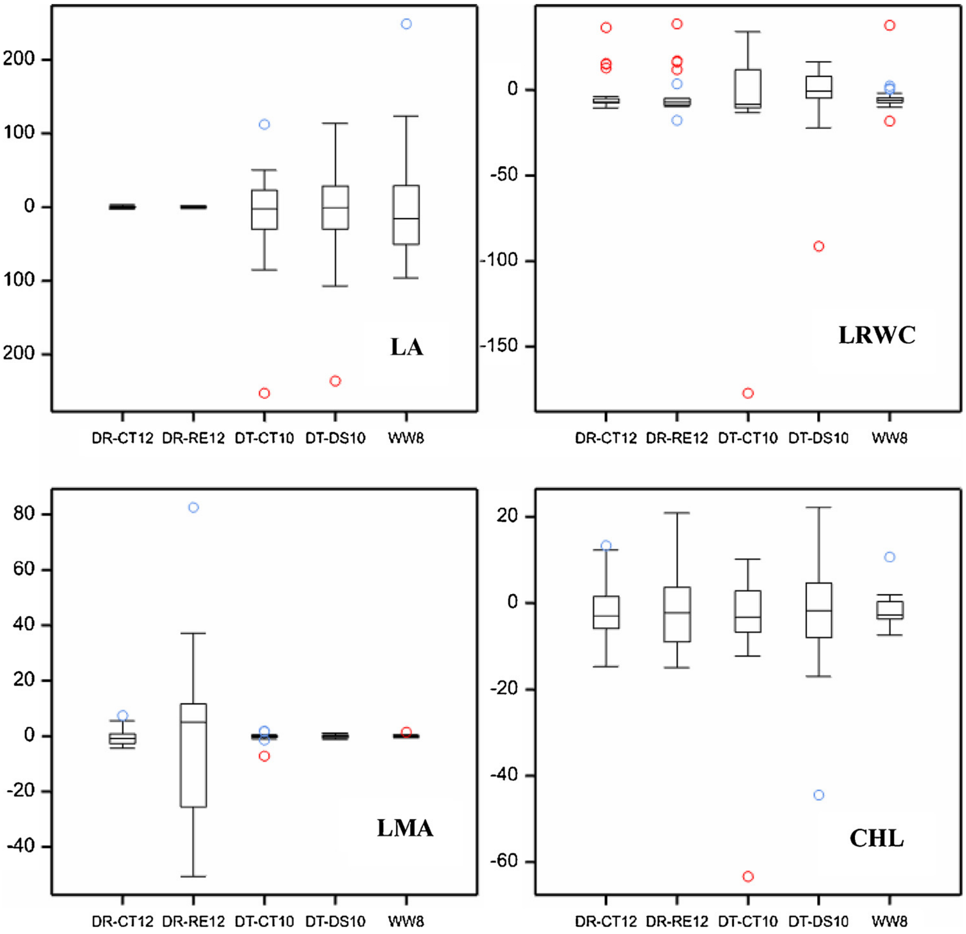

Fig. 2. Spread in SCA effects of crosses for selected traits at different watering conditions LA, leaf area; LRWC, leaf relative water content; LMA, leaf mass area; CHL, chlorophyll content.

3.1.4. Drought recovery

Non-significant GCA effects were exhibited for all measured traits across and within watering treatments (Table 3). Across treatments, SCA effects were significant ($p < 0.05$) for LWS, LA, LMA and LRWC but non-significant ($p > 0.05$) for LPP, LYF, LYD and CHL. Within control, the SCA effects were significant for LPP, LYD, LA, LMA, LRWC and CHL. Within re-watered plants, the SCA effects were significant for all measured traits and highly significant for LMA.

3.2. Heritability of drought resistance

3.2.1. Morphological traits

All morphological traits had H^2 value of > 0.80. The highest and lowest H^2 values were obtained for LPP (0.92) and LWS (0.81), respectively (Table 2). The h^2 was highest for LPP at 0.79 followed by LYD, and the lowest h^2 was obtained for LWS at 0.06.

3.2.2. Physiological traits

The H^2 was highest for CHL and LRWC at 0.80 and lowest for LMA (0.73). The h^2 was highest for CHL at 0.68. The h^2 was relatively low for LRWC and LMA at 0.15 and 0.14, respectively.

3.3. Traits for separating hybrids for SCA effects

The pearson's correlation analysis indicated that LPP, LYF, LYD, LWS and LRWC are correlated (Table 6). The LYD is also positively correlated with LA. Therefore, LA, LRWC, CHL and LMA were considered for selecting best hybrids. Further, boxplots revealed that the widest spread in LA was revealed under well-watered experiment at 8 WAP (WW8) and drought stress treatment under drought tolerance experiment at 10 WAP (DT-DS10) followed control treatment under drought tolerance experiment at 10 WAP (DT-CT10), control treatment under drought recovery experiment at 12 WAP (DR-CT12) and the narrowest spread was observed with re-watered treatment under drought recovery experiment (DR-RE12) (Fig. 2). There was wider spread in LRWC for DT-DS10 and DT-CT10 than for DR-CT12 and DR-RE12. The spread in LMA was very wide for DR-RE12 but it was very narrow the rest treatments. Based on CHL, the spread among hybrids was widest for both DT-DS10 and DR-RE12 followed by DR-CT12, DT-CT10 and WW8.

Consequently, under optimum growth conditions (WW8), the hybrids were discriminated for SCA effects using LA. The ranking of genotype SCA effects for drought tolerance was based on LA, LRWC and CHL. Similarly, the ranking of genotype SCA effects for recovery from drought stress (RE) was based on LMA and CHL.

Under WW8, cross E10xE20 had the best SCA effects on LA followed by E3HxE15 while E10xE4 had the worst effect (Table 7). Based on LA, cross E10xE20 had the best SCA effects for drought tolerance (DT) followed by E1xE6 while E11xE4 had the worst effect. The LRWC measured under DT produced E3HxE15 with the best SCA effects followed by E11xE15 while E11xE4 had the worst effect. Based on CHL, the best SCA effects under drought stress were obtained for E7HxE6 followed by E1xE20 while E11xE4 performed the worst. When plants were re-watered after drought stress exposure, SCA effects for LMA were highest on E11xE4 followed by E1xE6 while E11xE20 had lowest effect. Based on CHL, the SCA effects for RE were most favorable for E3HxE15 followed by E7HxE4 while E3SxE20 had the worst effect.

Table 7
SCA effects of crosses under well-watered, drought-stressed and re-watered treatments.

Cross	Leaf area (cm^2)		LRWC (%)	Chlorophyll content (CCI)		LMA (mg/cm^2)
	WW8	DT-DS10	DT-DS10	DT-DS10	DR-RE12	DR-RE12
E3HxE15	123.6	47.2	16.4	7.3	20.9	22.2
E11xE15	26.7	−8.1	13.1	6.1	−14.1	−49.6
E1xE4	−39.9	1.3	11.3	5.2	−12.3	−33.8
E13xE15	10.5	−18.7	9.0	4.2	−9.4	5.3
E1xE6	72.8	80.0	8.7	−2.3	−11.8	37.2
E7SxE20	−14.1	−27.0	8.4	−3.0	−14.8	11.6
E7HxE6	−61.7	33.4	7.5	22.2	3.7	7.4
E10xE20	248.6	113.9	7.2	4.1	−8.2	−20.3
E7HxE4	31.0	26.0	0.4	3.0	14.9	−30.9
E7HxE15	−35.7	16.0	0.3	−17.0	10.0	10.7
E13xE4	−24.8	−11.0	−0.2	−7.2	−7.5	−34.9
E2xE15	25.8	−4.8	−0.2	−4.0	−4.0	9.3
E1xE15	−9.0	3.3	−1.1	−6.4	−4.8	11.7
E10xE4	−96.3	−67.1	−1.2	−10.5	0.3	21.4
E11xE20	−18.9	−2.9	−1.4	−13.7	3.7	−50.7
E1xE20	−84.2	−32.7	−2.2	15.0	0.6	4.4
E10xE15	−89.4	−60.0	−2.6	3.8	−8.5	−18.8
E3SxE6	−30.8	−107.1	−4.2	−11.3	6.3	−10.3
E3SxE4	−17.3	51.7	−5.1	8.1	−0.5	−34.9
E7SxE15	46.0	6.9	−7.8	−1.2	1.8	6.3
E13xE20	−62.0	−54.6	−10.7	−8.7	0.1	4.2
E3SxE20	−62.0	6.6	−14.7	−4.2	−14.9	15.4
E13xE6	15.9	30.8	−22.3	0.3	3.8	4.9
E11xE4	55.0	−236.1	−91.4	−44.5	−6.0	82.6

Genotype performance is ranked by LRWC. LRWC, leaf relative water content; CCI, chlorophyll content index; WW8, well-watered plants at 8 WAP; DT-DS10, drought-stressed plants at 10 WAP; DR-RE12, re-watered plants at 12 WAP.

4. Discussion

The significance of GCA effects for CHL among females rather than males points to maternal inheritance (Day, n.d.; Lester and Thitai, 1989; Meier, 2011). Chloroplast organelles are located in the cytoplasm, and it is known that chloroplasts contain DNA (Ohmiya et al., 2014). The NCII mating design involves no reciprocals (Nduwumuremyi et al., 2013; Stuber, 1980) and this study recommends a diallel analysis (Griffing, 1956; Stuber, 1980) to validate the assertion that CHL in *S. aethiopicum* Shum is maternally controlled. Nonetheless, the higher the chlorophyll content of a genotype, the better the health of that genotype. Female parent E11 had the highest positive GCA effects, indicating that the accession can be used to breed for increased health and light interception potential for optimum photosynthetic rates (Parry et al., 2014). However, female E3H had the worst GCA effects for CHL.

Across and within watering environments, SCA effects were significant while GCA effects were largely non-significant for most traits. Such observation indicates the predominance of dominance over additive gene action (Falconer and Mackay, 1996; Golparvar, 2012) in influencing phenotypic expression in *S. aethiopicum* Shum. To emphasize, the H^2 was favorably very high (above 0.80) for all traits except LMA. Notwithstanding high h^2 estimates (above 0.50) for LPP, CHL and leaf yield which support selection methods for self-pollinated crops (Kang, 2002), an overriding approach should be cross-breeding for high gains in drought tolerance and recovery (Amelework et al., 2015; Banik et al., 2016; Blum, 2005; Sharma et al., 2015). Across watering environments, the best performing hybrid on the basis of positive SCA effects for LYF was E3HxE15 while the worst was E3SxE4. A study into produce ability of commercial hybrids of *S. aethiopicum* groups is necessary for the benefit of smallholder farmers in many developing countries in Africa, Asia and South America.

It was also realized that some traits were highly correlated and not all traits were offering opportunity to select crosses on the basis of SCA effects in each watering environment. Because LPP, LYF, LYD, LWS and LRWC were correlated to each other in a favorable direction, only the LRWC was selected among them. Specifically, genotypes with high LPP, LYF, LYD and low LWS (on a scale of 0–5; 0 for no wilting at all) also had high LRWC. The LRWC is considered the most preferred indicator of drought tolerance in *S. aethiopicum* Shum group (Sseremba et al., 2018a). It was also revealed that LYD is positively correlated with LA. The CHL and LMA did not show strong correlation with the other traits. The candidate traits recommended from this study when exploring diversity for SCA effects under drought tolerance experimentation in the Shum group include LA, LRWC, CHL and LMA. These have previously been applied to select for drought tolerance in the *S. aethiopicum* Shum (Sseremba et al., 2018a) as well as other crops like potato and tomato (Banik et al., 2016; Galmés et al., 2013; Ramírez et al., 2014; Tuberosa et al., 2007).

Differences in data spread for each candidate trait among watering environments, as earlier applied by Sseremba et al. (2018a), implied that each trait is suited differently when discerning SCA effects of crosses. The LA is suited under both well-watered (WW) and drought stress conditions. The LRWC and LMA are suited for drought stress (DS) and drought recovery (DR) screening, respectively. The CHL is however, suited for both DS and DR screening. Based on LA under WW, LRWC under DS and CHL under RE, the best performing crosses in terms of SCA effects were E10xE20, E3HxE15 and E3HxE15, respectively. The worst performers for LA under WW, LRWC under DS and CHL under RE were E10xE4, E11xE4 and E3SxE20, respectively.

5. Conclusion

Across watering environments, all study traits had high broad-sense heritability while it was only leaves per plant, chlorophyll content (CHL) and leaf yield with high narrow-sense heritability. Apart from GCA effects among females for CHL, the predominant combining ability type across and within environments was specific (SCA) in nature. The importance of SCA- over GCA effects show potential for heterosis in hybrids of the *S. aethiopicum* Shum; offering an opportunity for the crop's performance improvement across various water availability conditions through hybridization. Further, the traits suited for selection of crosses based on SCA effects under particular watering environments were identified as LA (for well-watered and drought-stressed), LRWC (for drought-stressed), LMA (for drought recovery) and CHL (for both drought-stressed and drought recovery). Drought directly affects the performance of leafy vegetables (particularly, *S. aethiopicum* Shum in this case) but the results from this study offer remedy breeding options for improving crop resilience to unreliable water supply in drought-prone areas.

Conflict of interest

The authors have declared that no conflict of interest exists.

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