



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

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ARTICLE INFO

Keywords:

Specific combining ability
Optimum watering
Drought tolerance mechanisms
Breeding traits
Hybridization
African eggplant

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

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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<https://doi.org/10.1016/j.scienta.2018.06.028>

Received 19 March 2018; Received in revised form 26 May 2018; Accepted 11 June 2018
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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 F₁ hybrids.

(O₂) gases (Galmés et al., 2013; Yoshida et al., 2014). The consequence is reduced internal CO₂ concentration and increased O₂ 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-

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