Received: 8 May 2020 | Accepted: 17 September 2020 | Published online: 18 November 2020

DOI: 10.1002/csc2.20363

Crop Science

SPECIAL ISSUE: ADAPTING AGRICULTURE TO CLIMATE CHANGE: A WALK ON THE WILD SIDE

Assessment of the potential of wild *Ipomoea* spp. for the improvement of drought tolerance in cultivated sweetpotato *Ipomoea batatas* (L.) Lam

Stella E. C. Nhanala[1,2] | **G. Craig Yencho**[1]

[1] Department of Horticultural Science, North Carolina State University, 2721 Founders Dr., Raleigh, NC 27607, USA

[2] Instituto de Investigação Agrária de Moçambique (IIAM), Av. das FPLM, No. 2698, Caixa, Maputo Postal 3659, Mozambique

Correspondence
G. Craig Yencho, Department of Horticultural Science, North Carolina State University, 2721 Founders Dr., Raleigh, NC 27607, USA.
Email: craig_yencho@ncsu.edu

Assigned to Associate Editor Hannes Dempewolf.

Funding information
Global Crop Diversity Trust, Grant/Award Number: GS14028

Abstract

Sweetpotato [*Ipomoea batatas* (L.) Lam] is cultivated worldwide, and it is a staple food in many developing countries. In some regions (e.g., Africa) drought is a major production constraint that results in significant yield loss. Climate change is predicted to result in even greater losses due to long periods of drought and elevated temperatures. The goal of this study was to assess the potential of wild *Ipomoea* spp. as a source of drought tolerance in cultivated sweetpotato. We evaluated the drought tolerance of *I. batatas*, *I. cynanchifolia*, *I. leucantha*, *I. trifida* and *I. triloba* in a randomized complete block design, with five levels of simulated drought: control (daily irrigation), and no irrigation for 7, 9, 21 and 50 days. We observed that post drought re-irrigation of the wild species subjected to 21 days of stress resulted in plant recovery and an increase of the stomatal conductance of up to 99% in *I. leucantha*. However, under extreme stress (50 d) the wild plants did not respond to re-irrigation, resulting in up to 89% (*I. leucantha*) plant mortality. The wild species did not produce storage roots, while the *I. batatas* cultivars produced storage roots. Under 50 days of stress *I. batatas* had a survival rate between 44% (cv. Tanzania) and 89% (cv. Beauregard). We concluded that the wild genotypes screened may not be a valuable source of germplasm for drought tolerance and that significant levels of drought tolerance may exist in cultivated sweetpotato.

1 | INTRODUCTION

Sweetpotato [*Ipomoea batatas* (L.) Lam] is a crop grown worldwide, and its storage roots and foliage provide a source of calories, vitamins and minerals for humans and animals (Mohanraj & Sivasankar, 2014; Padmaja, 2009; Pochapski et al., 2011). Being a good source of energy and nutrients, sweetpotato is a staple food in many Asian, sub-Saharan Africa and South Pacific countries (Grüneberg, Manrique, Zhang, & Hermann, 2005; Hotz et al., 2012; Low et al., 2020; Minot, 2010; Mwanga et al., 2017). Sweetpotato is also thought to be a drought tolerant crop, and due to this, it is grown in drought-prone areas (Hahn, Alvim, & Kozlowski, 1977; Kays & Bouwkamp, 1985).

Drought tolerance in plants is a complex phenomenon, and the response of a plant to drought varies according to a wide range of physiological and physical factors related to

Abbreviations: CWR, Crop wild relatives; NCSU, North Carolina State University.

genotype (Andrade et al., 2016; Gajanayake, Reddy, Shankle, & Arancibia, 2014a; Hahn et al., 1977). In a scenario of climate change, with extended periods of drought being one of the impacts of environmental changes in agriculture, it is important to increase our basic knowledge of drought resistance in crop plants to prevent reduced yield in food crops.

Understanding how drought stress impacts stomatal conductance is critical to our understanding of how photosynthetic activity is affected by drought in plants. Stomatal conductance regulates plant gas exchange and plant water relations, and it is correlated with photosynthesis (Farquhar & Sharkey, 1982; Kusumi, Hirotsuka, Kumamaru, & Iba, 2012; Medrano, Escalona, Bota, Gulías, & Flexas, 2002; Wong, Cowan, & Farquhar, 1979). Therefore, studies of stomatal conductance may provide valuable insights into how plants survive when the uptake of carbon dioxide is reduced.

Taiz and Zeiger (2006) have noted that, in addition to stomatal conductance, leaf area plays an import role in photosynthesis, with a large leaf area implicating a high photosynthesis. Therefore, it can be speculated that leaf loss reduces the photosynthetic capacity of a plant. The opening or closure of stomata may also be as important as the ability of a plant to keep or lose its leaves when the plant is under stress. If a plant only wilts and then recovers after the period of stress, the plant may still be able to resume its normal photosynthetic capacity. However, if a plant loses a substantial portion of its leaves, probably, it will have its uptake of carbon dioxide reduced.

The yield of sweetpotato is evaluated mainly by the biomass of the storage roots (Kays & Bouwkamp, 1985; Kivuva, Githiri, Yencho, & Sibiya, 2015; Meyers et al., 2017). The formation of storage roots includes three growth stages: initiation, induction and development (Du Plooy, Van den Berg, Hammes, & Holtzhausen, 1992; Kays & Bouwkamp, 1985; Gajanayake, Reddy, Shankle, & Arancibia, 2013; Gajanayake, Reddy, Shankle, Arancibia, & Villordon, 2014b; Meyers et al., 2017; Ravi, Naskar, Makeshkumar, Babu, & Krishnan, 2009; Solis, Villordon, Baisakh, LaBonte, & Firon, 2014; Villordon, LaBonte, & Firon, 2009). Typically, sweetpotato storage root initiation occurs within 30 days after the crop has been planted and is characterized by the differentiation of young and thick adventitious roots that develop into storage roots. The induction of storage roots is the beginning of the storage root formation process and the development of the storage roots is largely the result of starch accumulation. Starch is the major carbohydrate of storage roots (Kays & Bouwkamp, 1985) and it is a moderately heritable trait (Amankwaah, 2019; Oloka, 2019). Sweetpotato yield can be greatly reduced when grown under deficient irrigation. Limited water uptake affects the formation of storage roots, and under these conditions, pencil roots may be formed instead of storage roots, resulting in reduced yield (Kays & Bouwkamp, 1985; Low et al., 2020; Meyers et al., 2017). Regular irrigation appears to be very important for all of the storage root developmental stages of sweetpotato, but some stages may be more critical than others and each stage can be compromised if any of them are affected by irregular or no irrigation (Meyers et al., 2017).

Core Ideas

- Sweetpotatoes are cultivated worldwide and they are a staple food in many developing countries.
- We compared the drought resistance of cultivated varieties and four crop wild relatives (CWR).
- We found that cultivated and CWR of sweetpotato respond differently to drought.
- We concluded that the cultivated genotypes may be more tolerant to drought than the CWR.
- Drought tolerance in cultivated sweetpotato may be related to storage root development.

Climate scientists predict that drought events will become prolonged and more erratic due to climate change (Dai, 2013; McDowell et al., 2008; Schlaepfer et al., 2017; Trenberth et al., 2014). These periods of water stress will undoubtedly lead to decreased yields of many of the staple crops such as sweetpotato. To prevent the reduction of yield due to extended and/or erratic periods of drought in sweetpotato it is crucial for us to develop germplasm that can serve as a source of improved drought tolerance. The utilization of crop wild relatives (CWR) of sweetpotato for improved drought tolerance could be a means to adapt its cultivated counterpart to long periods of drought.

The improvement of cultivated plants to abiotic and biotic stress via the utilization of CWR has been evaluated in many crops. Many of these studies show evidence that CWR are a valuable source of genetic diversity for breeding programs. The exploitation of CWR as a source of genetic diversity for drought tolerance purposes has been studied in food crops such as wheat (Placido et al., 2013; Zaharieva, Gaulin, Havaux, Acevedo, & Monneveux, 2001), soybean (Chen, Chen, & de los Reyes, 2006), bean (Porch et al., 2013), barley (Honsdorf, March, Berger, Tester, & Pillen, 2014; Suprunova et al., 2004) and peanut (Brasileiro et al., 2015). Zaharieva et al. (2001) identified accessions of *Aegilops geniculata*, a wild relative of wheat that has the potential to be used in cultivated wheat breeding programs to improve drought and heat stresses through improved leaf area and biomass production. Chen et al. (2006) identified the wild *Glycine soja* (PI 407155) as more tolerant to drought stress than its cultivated counterpart 'Essex' soybean. Honsdorf et al. (2014) evaluated introgression lines of wild barley, in order to select drought tolerant materials. They identified the line S42IL-121 as drought tolerant and suggested that S42IL-I21 could be used as a source of drought tolerant genes to improve barley. Brasileiro

TABLE 1 Genotypes evaluated in the study, breeding program or country origin, and years evaluated

Species	Genotype	Origin	Year(s)
I. batatas	Beauregard	USA – Louisiana State University	2018/2019
I. batatas	Tanzania	Uganda – East African Landrace	2018/2019
I. batatas	Resisto	USA – USDA Agricultural Research Service	2019
I. batatas	Hatteras	USA – North Carolina State University	2019
I. cynanchifolia	PI 549093	Peru	2018/2019
I. leucantha	PI 518481	Mexico	2018/2019
I. trifida	PI 540724	Mexico	2018/2019
I. triloba	PI 618966	Mexico	2018/2019

et al. (2015) did transcriptomic profiling of two wild relatives of peanut that resulted in the identification of drought-tolerant candidate genes such as expansin, nitrilase, NAC, and *bZIP*.

Khoury et al. (2015) used geographic and ecological habitat criteria to identify the CWR of *I. Cynanchifolia, I. lacunosa, I. leucantha, I. littoralis, I. splendor-sylvae, I. trifida* and *I. triloba* with potential adaptation to drought-prone areas. The identification of genotypes of wild *Ipomoea* spp. that are tolerant to drought could be a step towards to the improvement of drought tolerance in sweetpotato.

We assessed the potential of four wild relatives identified by Khoury et al. (2015) to be exploited as a source of germplasm to improve drought tolerance in sweetpotato. We hypothesized that these wild relatives would be more tolerant to drought than the cultivated sweetpotato. The drought tolerance of eight genotypes belonging within the series *Batatas* was compared by comparing stomatal conductance, leaf loss, plant survival and biomass accumulation of wild and cultivated *Ipomoea* spp. under different levels of irrigation stress.

2 | MATERIALS AND METHODS

2.1 | Location

The study was performed during two years (May–October 2018, May–October 2019) under greenhouse conditions at the Horticulture Field Laboratory greenhouses at North Carolina State University, Raleigh, NC (35.7847° N, 78.6821° W).

2.2 | Plant materials

The first study was conducted during May to October 2018. We evaluated six genotypes of *Ipomoea* spp. (Table 1). One of these genotypes, PI618966, was identified as *I. trifida* in the U.S. National Plant Germplasm System (NPGS) GRIN-Global database. However, phenotypic studies conducted by members of the senior author's team at NCSU and unpublished molecular genetic studies conducted by Jan Kreuze at the International Potato Center (CIP) using 13 diagnostic SSR primers have determined that this accession, which was originally donated to the US NPGS by the CIP germplasm bank, is actually an *I. triloba* accession. In 2019, we studied eight *Ipomoea* spp. genotypes in total, and to better evaluate the yield (storage roots) of sweetpotato, we added two more cultivars of sweetpotato, Hatteras and Resisto (Table 1).

The wild species (*I. cynanchifolia*, *I. leucantha*, *I. trifida* and *I. triloba*) were identified as having the potential to be adapted to drought-prone areas based on their eco-geographic distribution by Khoury et al. (2015). To date, several *I. batatas* cultivars have been evaluated in drought-related studies: Beauregard (Gajanayake et al., 2014a; Lewthwaite & Triggs, 2012; Taduri, Lone, Meyers, Shankle, & Reddy, 2017), Resisto (Andrade et al., 2016; Laurie, Laurie, Du Plooy, Finnie, & Van Staden, 2015; Van Heerden & Laurie, 2008) and Tanzania (Andrade et al., 2016; Kivuva et al., 2015). Heat tolerance has been positively correlated with drought tolerance in plants (Bouslama & Schapaugh, 1984; Havaux, Ernez, & Lannoye, 1988; Zaharieva et al., 2001). *I. batatas* cv. Hatteras was identified as a drought and heat tolerant cultivar by Taduri et al. (2017), and it has also been regarded as a heat and drought tolerant cultivar by the Sweetpotato Breeding and Genetics Program at NCSU, who developed this cultivar (G.C. Yencho, personal observation).

Seed of the wild *Ipomoea* spp. were acquired from the U.S. National Plant Germplasm System (GRIN, 2018). Plants (~15 cm in length) of the cultivated genotypes were obtained from the Sweetpotato Breeding and Genetics Program at NCSU. The seed was germinated at 22 °C in germinating mix substrate (Fafard Germinating Mix, Sun Gro Horticulture, Agawam, MA, USA). Germinated wild *Ipomoea* spp. plantlets and 15 cm cuttings of sweetpotato were transplanted into 1 L (one liter) pots containing a 1:1 sand/soil mix. Each pot contained 1.3 kg of soil, and the dosage of irrigation per day was 125 ml. Plants were fertigated once a week, and after one month after transplanting they were fertigated twice a week.

2.3 | Experimental design

The study was established as a randomized complete block design. In 2018, the plants were assigned to four blocks and three treatments: Treatment 1, control (daily irrigation); Treatment 2, moderate (non-irrigated for 7 days [7 d]); and Treatment 3, severe (non-irrigated during 21 days [21 d]). Within each block three plants of each genotype per treatment were established. However, six plants of *I. trifida* representing two control plants, two moderate (7 d) plants, and two severe (21 d) plants, did not survive after the transplantation making this study an unbalanced design with a population size of 210 individuals. In 2019, the plants were established with three blocks and three treatments, under the following treatments: Treatment 1, control (daily irrigation); Treatment 2, moderate (non-irrigated for 9 days [9 d]); and Treatment 3, extra severe (non-irrigated for 50 days [50 d]). Within the three blocks of each treatment, three plants of each genotype were planted, resulting in an experiment with 216 individuals.

The treatments were applied four weeks after the plants were transplanted. Due to a general lack of information regarding drought stress on wild *Ipomoea* spp., the drought treatments were established based on visual observation of signs of drought (e.g., wilted leaves, and leaf loss) observed during the initial experiment. These observations resulted in the following drought treatments: moderate (7–9 d); severe (21 d); and extra severe (50 d). The moderate treatment was established as 7–9 d, based on the phenotypic observation of "complete" wilt status of the plant; the severe treatment was identified as the point where the wild species had completely lost their leaves and appeared totally dry to the observer; and the extra severe treatment, was defined based on the results observed in 2018, and was identified as a point where all genotypes (wild and cultivated) were completely desiccated in order to evaluate the ability of the cultivated genotypes to recover when completely dry and leafless. After the imposition of the respective drought treatment, the plants were re-irrigated until harvest.

The plants were irrigated using an automatic drip irrigation system programmed to supply 125 ml of water/day over a 3 minute interval at 09:00 AM. The irrigation drippers were manually adjusted for each of the assigned treatments of moderate (7–9 d), severe (21 d) and extra severe (50 d). Plants were fertigated once a week from transplantation up to four weeks old, and later on the plants were fertigated twice a week.

2.4 | Data collection

The following traits were measured during the experiments in 2018: 1) leaf loss – one week after re-irrigation of the severe treatment the fallen leaves were collected and weighed using an SP401 Ohaus Scout Pro Portable Electronic Balance (400 g; Ohaus Corporation, Pine Brook, NJ, USA); 2) survival rate and recovery capacity – the percentage of plants surviving the treatments, and the percentage of plants that developed (recovered) new leaves from the stems of the leafless and/or dry plants under the 21 d and 50 d treatments (the plants that did not become completely dry were not recorded); 3) stomatal conductance – a fully expanded young leaf of each plant was recorded using an SC1-Leaf Porometer (Decagon Devices, Inc. Pullman, WA, USA) (stomatal conductance was recorded from: 11:00 AM to 4:00 PM); 4) plant biomass – the fresh weight of the above and belowground parts of the plant; 5) storage root count per plant – the number of storage roots for each plant; and 6) dry weight of the storage roots.

In 2019 we did not measure leaf loss, and based on the plant survival results from 50 d, we did not evaluate plant recovery in these plants. Instead we evaluated the plant status by associating the visual physiological status with a subjective scale where: 1 = at least 2/3 of the plant appeared to be dry; 2 = at least 2/3 of the plant had a wilted appearance; and 3 = normal plant appearance, similar to the control.

2.5 | Data analysis

Analysis of variance (ANOVA) of the data was conducted using SAS version 9.4 (SAS Institute Inc., Cary, NC) by determining the least significant means at $P \leq .05$ of the traits that were analyzed, using the Tukey method. A mixed model (proc mixed), with the statistical model:

$$Y = X\beta + Z\gamma + \varepsilon$$

where Y is the response variable; X is the design matrix; β is the fixed-effects parameter; Z is the design matrix; γ is the random-effects parameter; and ε is the residual error term.

The percentage change of the traits evaluated were calculated using:

$$\text{Stress treatment}(\%) = \frac{\text{mean of the stress treatment}}{\text{mean of the control treatment}} \times 100$$

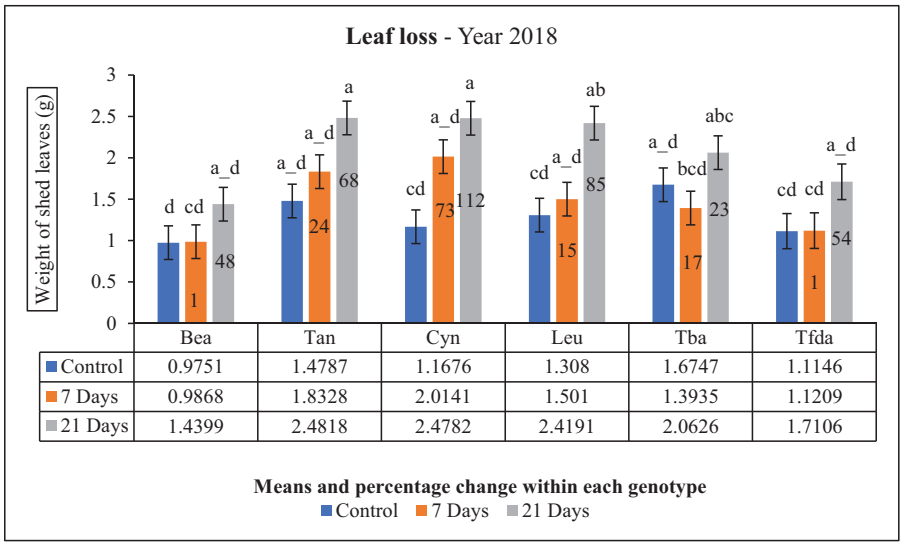
and

$$\text{Change}(\%) = 100\% - \text{Stress treatment}(\%)$$

3 | RESULTS

3.1 | Survival rate and recovery capacity

The moderate treatments (7 d and 9 d without irrigation) resulted in some leaf loss (Figure 1); however, none of the plants grown under these levels of stress became completely dry. In the 21 d stress treatment, all of the cultivated genotypes survived, while 20% of the *I. cynachifolia* and 8% of the *I. leucantha* plants survived. These results reflected a recovery capacity from the 21 d (severe) treatment of: 80%



	Bea	Tan	Cyn	Leu	Tba	Tfda
Control	0.9751	1.4787	1.1676	1.308	1.6747	1.1146
7 Days	0.9868	1.8328	2.0141	1.501	1.3935	1.1209
21 Days	1.4399	2.4818	2.4782	2.4191	2.0626	1.7106

Common letters within genotypes represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Leu = *I. leucantha*; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.

FIGURE 1 Leaf loss of *Ipomoea* spp. studied. The figure shows the averages calculated for the control, 7 d, and 21 d treatments. The results include observations of the shed leaves for the control, 7 d, and 21 d treatments

(*I. cynachifolia*), 92% (*I. leucantha*), and 100% (remaining wild *Ipomoea* spp.)

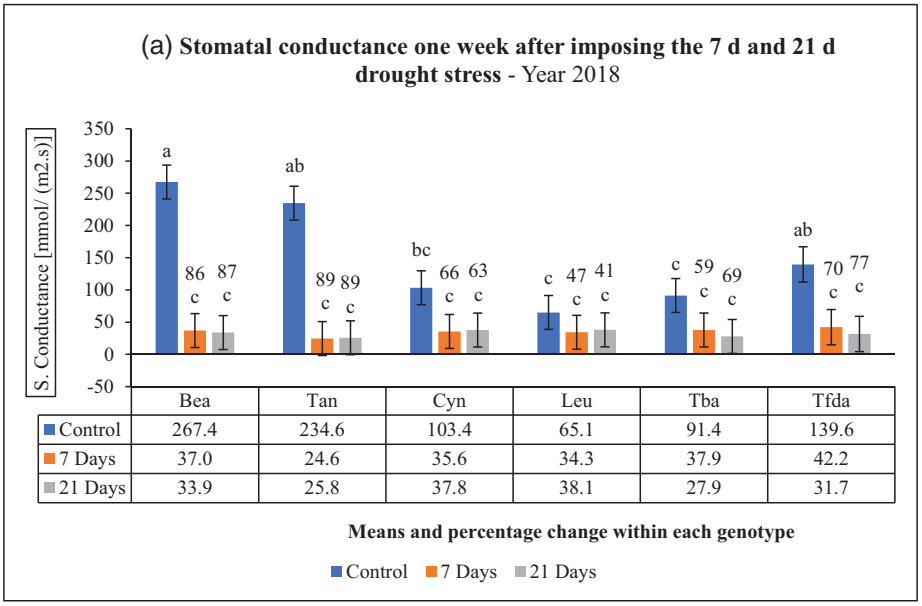
In terms of the 50 d stress treatment applied in 2019, all of the *I. cynachifolia*, 89% of the *I. leucantha*, 44% of the *I. trifida* and 67% of the *I. triloba* plants died; while the wild species *I. leucantha* (11%), *I. trifida* (56%), and *I. triloba* (33%) exhibited some recovery. Even after the 50 d of stress, most of the cultivated genotypes never became completely desiccated unlike the CWR, with survival rates for Beauregard, Hatteras, Resisto and Tanzania of 89%, 78%, 33%, and 44%, respectively. Due to the high rate of death of wild *Ipomoea* spp., and due to the fact that some cultivated genotypes never achieved a death status, we did not evaluate the recovery capacity of the plants under 50 d stress.

3.2 | Leaf loss

In 2018, all the genotypes were negatively affected by the 21 d treatment (Figure 1), with significant leaf shedding occurring in each of the genotypes compared to the control treatment. In general, there was a greater percentage change between the control and the 21 d treatments, but that difference was not always observed between the control and the 7 d treatments. For instance, Beauregard lost only 1% of its leaves when comparing the control and 7 d treatments, while there was a difference of 48% between the control and the 21 d treatment. Similarly, *I. trifida* exhibited minimal leaf loss between the control and 7 d treatment at 1%, while leaf loss between the control and the severe treatment amounted to 54%. *I. triloba* had a 17% decrease of leaf loss between the control and moderate stress treatment and had the lowest difference (23%) between the control and the 21 d treatments. For *I. cynachifolia*, the severe treatment caused more than the double (112%) of the leaf loss when compared with the control treatment. *I. cynachifolia* was the genotype that was the most affected by the leaf loss for both treatments: moderate (73%) and severe (112%). In general, based on leaf loss, *I. triloba* was more tolerant to long-term (21 d) drought than all other genotypes evaluated. In 2019, it was pre-determined that the third treatment would be when all the cultivated genotypes completely lost their leaves in order to evaluate their recovery ability. In 2018, the severe treatment proved to be statistically different from the control and moderate treatments. Therefore, in 2019, we inferred that the amount of leaf loss representing the extra severe treatment, i.e. complete dry and leafless plants of wild and cultivated genotypes, would also be statistically different from the other two treatments evaluated.

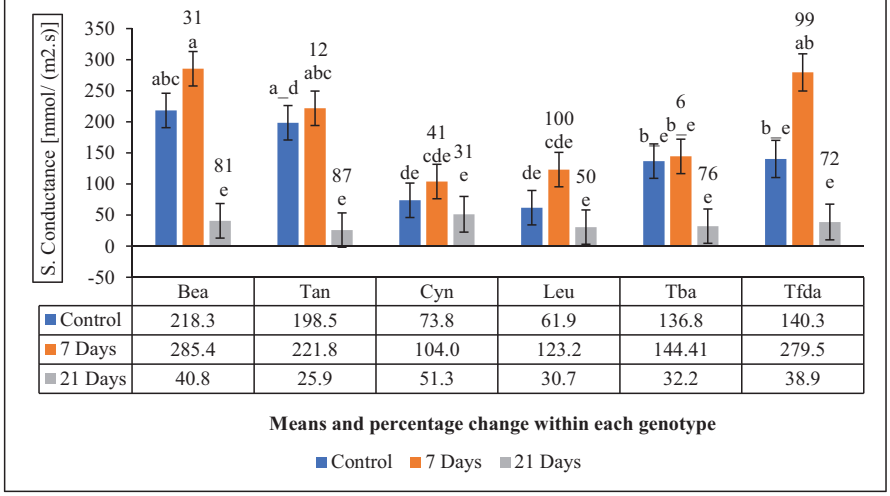
3.3 | Stomatal conductance

Stomatal conductance was reduced both moderate and severe water stress after 7 d and 21 d of no irrigation (Figure 2a, b). None of the genotypes presented significant differences between the moderate and severe treatments. *Ipomoea leucantha* and *I. triloba* did not exhibit statistically significant



	Bea	Tan	Cyn	Leu	Tba	Tfda
Control	267.4	234.6	103.4	65.1	91.4	139.6
7 Days	37.0	24.6	35.6	34.3	37.9	42.2
21 Days	33.9	25.8	37.8	38.1	27.9	31.7

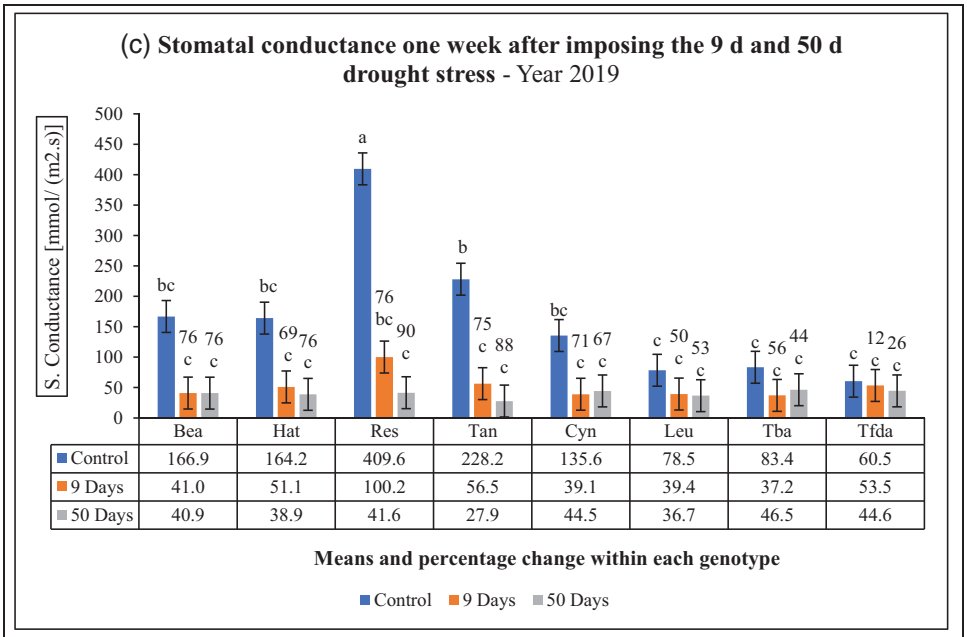
Common letters represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Leu = *I. leucantha*; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.



	Bea	Tan	Cyn	Leu	Tba	Tfda
Control	218.3	198.5	73.8	61.9	136.8	140.3
7 Days	285.4	221.8	104.0	123.2	144.41	279.5
21 Days	40.8	25.9	51.3	30.7	32.2	38.9

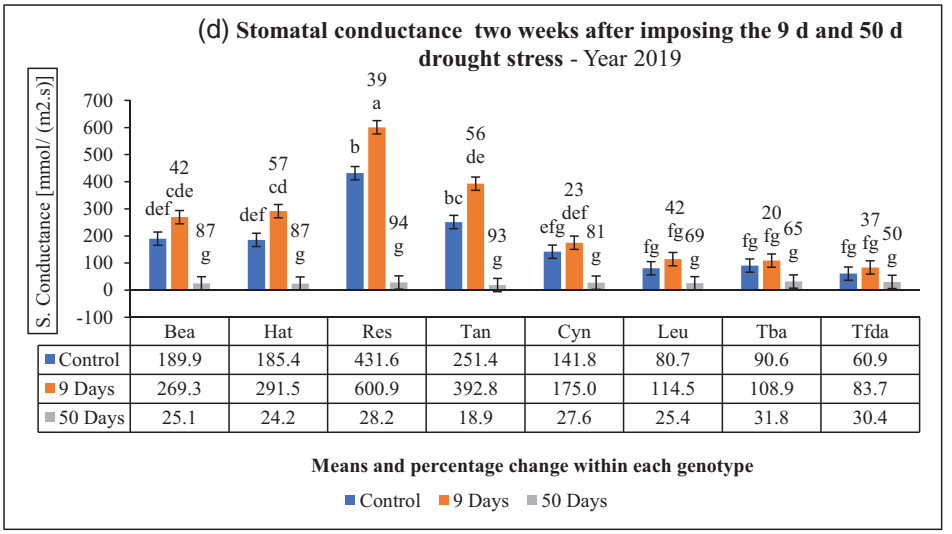
Common letters represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Leu = *I. leucantha*; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.

FIGURE 2 Stomatal conductance of *Ipomoea* spp. studied. Averages of stomatal conductance at different time points of the study are provided for the control, 7 d, 9 d, 21 d and 50 d treatments. The results include observation of the stomatal conductance one week after imposing the 7 d and 21 d stress (a); two weeks after imposing the 7 d and 21 d stress (b); one week after imposing the 9 d and 50 d stress (c); two weeks after imposing the 9 d and 50 d stress (d); and stomatal conductance of the plants recovered from 21 d stress (4e)



	Bea	Hat	Res	Tan	Cyn	Leu	Tba	Tfda
Control	166.9	164.2	409.6	228.2	135.6	78.5	83.4	60.5
9 Days	41.0	51.1	100.2	56.5	39.1	39.4	37.2	53.5
50 Days	40.9	38.9	41.6	27.9	44.5	36.7	46.5	44.6

Common letters represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Hat = Hatteras; Leu = *I. leucantha*; Res = Resisto; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.



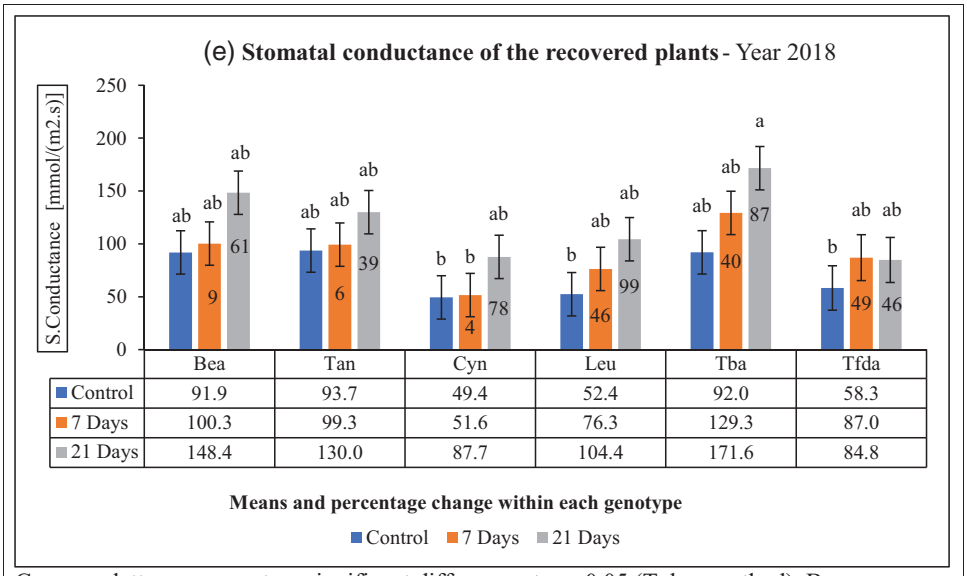
	Bea	Hat	Res	Tan	Cyn	Leu	Tba	Tfda
Control	189.9	185.4	431.6	251.4	141.8	80.7	90.6	60.9
9 Days	269.3	291.5	600.9	392.8	175.0	114.5	108.9	83.7
50 Days	25.1	24.2	28.2	18.9	27.6	25.4	31.8	30.4

Common letters represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Hat = Hatteras; Leu = *I. leucantha*; Res = Resisto; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.

FIGURE 2 Continued

differences in stomatal conductance between all three treatments. Upon application of re-irrigation after the 7 d drought treatment, the stomatal conductance of all the genotypes under the 7 d drought treatment exhibited increased stomatal conductance (Figure 2b). *Ipomoea leucantha* had almost the double (99%) of the stomatal conductance of the control treatment. *Ipomoea triloba* had an increase of approximately 6% of the percentage when the plants received the moderate treatment.

As in 2018, one week after applying the 9 d drought treatment in 2019 the stomatal conductance of all the genotypes were reduced, with a percentage decrease ranging 11–75% (Figure 2c). Statistical differences were observed between the control and moderate treatments within Beauregard, *I. cynachifolia*, Hatteras, Resisto and Tanzania. Upon re-irrigation of the 9 d treatment stomatal conductance increased 20–56% (Figure 2d). The plants exposed to drought stress had a percentage decrease in an order of 50–93%.



Common letters represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Leu = *I. leucantha*; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.

FIGURE 2 Continued

Except for *I. triloba* and *I. trifida*, we observed a significant difference within the 9 d and 50 d treatments for all genotypes.

In terms of stomatal conductance of the recovered plants, after 21 d of water stress, all of the CWR had dropped their leaves and their stems appeared to be desiccated. However, roughly one month after the re-irrigation of the plants under stress for 21 d, the wild *Ipomoea* spp. produced new leaves from the seemingly desiccated stems (Figure 2e). The stomatal conductance of the recovered plants increased, with a percentage change between 30–99%. Compared with the 21 d treatment, the plants under the 50 d of stress did not recover their leaves after the re-irrigation.

3.4 | Plant status

The imposition of drought in all genotypes elicited phenotypic changes that were scorable in our greenhouse-based studies. One week after applying treatment, the 9 d treatment plants began to exhibit wilting stress (Table 2a, b). The extension of the period of drought resulted in more pronounced changes in plant phenotypic appearance in all genotypes.

3.5 | Plant biomass

3.5.1 | Biomass aboveground

The fresh weight of the aboveground biomass was negatively affected by all the drought stress treatments (Table 3a, b). *Ipomoea trifida* was the genotype least affected by the 7 d treatments, while *I. cynachifolia* (11%) was the most affected by the 21 d stress (70%). *Ipomoea cynachifolia* was negatively affected by the 50 d treatment, and none of the *I. cynachifolia* plants survived in the extra severe treatment. *Ipomoea triloba* had the lowest survival rate under the 50 d treatment (82%).

3.5.2 | Biomass belowground

Belowground biomass was reduced by all the drought stress treatments (Table 3c, d). In 2018, *I. trifida* was the genotype least affected by the 7 d treatment with an increase of 41%, while *I. cynachifolia* was the most affected by the 21 d stress (94%). *Ipomoea cynachifolia* was severely affected by the 50 d treatment, with none of the plants surviving this treatment.

3.6 | Yield of cultivated sweetpotato

3.6.1 | Storage root count per plant

None of the wild *Ipomoea* spp. produced storage roots. For Beauregard, there was not a statistical difference between the control, 7 d and 21 d treatments (Table 4a) in terms of storage root numbers. The same results were observed for Tanzania. Tanzania storage root number was reduced in the 7 d (27%) and 21 d (91%) treatments. Beauregard was negatively affected almost to the same extent by the 7 d and 21 d treatments, with a decrease of about 16% (Table 4a). Tanzania

TABLE 2 Frequency of the status of the Ipomoea spp. plants studied. Each numerical value was assigned to a specific plant status: Normal (3), wilted (2) and, dry (1). The data include the frequency of the status of the plants for control, 9 d and 50 d treatments during the first week (a); and the frequency during the second week (b). Values were derived from a sample of 216 individuals

a. Frequency of the status of the plants one week (8–10 days) after treatment; Year 2019									
	Status 3 = Normal			**Status 2 = Wilted**			**Status 1 = Dry**		
Genotype	**Control**	**9 d**	**50 d**	**Control**	**9 d**	**50 d**	**Control**	**9 d**	**50 d**
Beauregard	9	2	0	0	7	9	0	0	0
I. cynachifolia	9	2	0	0	6	6	0	1	3
Hatteras	9	3	0	0	6	8	0	0	1
I. leucantha	9	0	0	0	7	8	0	2	1
Resisto	9	3	0	0	6	9	0	0	0
Tanzania	9	3	0	0	6	9	0	0	0
I. triloba	9	2	0	0	6	9	0	1	0
I. trifida	9	3	0	0	6	8	0	0	1
Total	72	18	0	0	50	66	0	4	6
Percentage	33%	8%	0%	0%	23%	31%	0%	2%	3%
b. Frequency of the status of the plants two weeks (16–18 days) after treatment; Year 2019									
	Status 3 = Normal			**Status 2 = Wilted**			**Status 1 = Dry**		
Genotype	**Control**	**9 d**	**50 d**	**Control**	**9 d**	**50 d**	**Control**	**9 d**	**50 d**
Beauregard	9	8	0	0	1	7	0	0	2
I. cynachifolia	9	8	0	0	1	0	0	0	9
Hatteras	9	9	0	0	0	8	0	0	1
I. leucantha	9	8	0	0	1	4	0	0	5
Resisto	9	8	0	0	1	6	0	0	3
Tanzania	9	7	0	0	2	7	0	0	2
I. triloba	9	9	0	0	0	4	0	0	5
I. trifida	9	9	0	0	0	5	0	0	4
Total	72	66	0	0	6	41	0	0	31
Percentage	33%	31%	0%	0%	3%	19%	0%	0%	14%

Bea = Beauregard; Cyn = *I. cynachifolia*; Hat = Hatteras; Leu = *I. leucantha*; Res = Resisto; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.

was highly affected the by the 9 d and 50 d treatments, with the number of roots per plant being reduced to 0% when the plant was under stress for 50 d (Figure 3; Table 4b). Hatteras and Resisto, two clones known for their drought tolerance had fewer storage roots at 9 d compared to the 50 d treatment. For Hatteras, the percentage decrease was of 44% (9 d) and 33% (50 d), while Resisto's productivity was reduced by half when grown under 9 d of stress, and 40% when exposed to severe stress.

3.6.2 | Dry weight of the storage roots

Tanzania yield, as measured by dry weight, was less than all of treatments, with 21 d and 50 d treatments resulting in the most yield loss (Table 4c, d). The 50 d treatment reduced yield in all genotypes, with a percentage ranging from 92–100% (Table 4d).

4 | DISCUSSION

Our results suggest that the wild species studied were more sensitive to water stress than their cultivated counterparts and they responded to water stress differently. In response to severe drought stress *I. leucantha*, *I. trifida*, and *I. triloba* dropped their leaves, and their stems desiccated to the point that the plants were seemingly dead. However, after the drought was ended, they produced new foliage from seemingly dead tissue and exhibited some recovery.

Tanzania, *I. cynachifolia* and *I. leucantha* wilted and lost their leaves faster than Beauregard, *I. trifida*, and *I. triloba* (Figure 1). The effects of 7 d of stress resulted in a 24% leaf loss in Tanzania, 73% in *I. cynachifolia* and 15% in *I. leucantha*, while the other genotypes Beauregard, *I. trifida*, and *I. triloba* increased 1%, 1%, and 17%, respectively. Taiz and Zeiger (2006) recognized leaf loss due to water stress as a mechanism to adjust a plant's leaf area to prevent water loss

TABLE 3 Mean ± standard error of aboveground and belowground fresh biomass of the Ipomoea spp. studied. Tables present averages calculated for the control, 7 d, 9 d, 21 d and 50 d treatments. The results include observation of the aboveground weight of the 7 d and 21 d stress (a); aboveground weight of the 9 d and 50 d stress (b); belowground weight of the 7 d and 21 d stress (c); and the belowground weight of the 9 d and 50 d of stress (d). Percentage of change was calculated based on the means of the control treatment for the respective genotype

a. Biomass aboveground; Year 2018					
	Control	**7 d**		**21 d**	
Genotype	**Mean**	**Mean**	**Change**	**Mean**	**Change**
	g		%	g	%
Beauregard	46.16 ± 2.47 cd	38.94 ± 2.47 cde	15.63	36.20 ± 2.47 cdef	21.57
Tanzania	77.89 ± 2.47 a	59.68 ± 2.58 b	23.37	46.21 ± 2.47 cd	40.66
I. cynachifolia	48.34 ± 2.47 bc	33.25 ± 2.47 defg	31.21	14.33 ± 2.47 hi	70.35
I. leucantha	48.29 ± 2.47 bc	32.76 ± 2.47 efg	32.16	14.82 ± 2.47 hi	69.30
I. triloba	36.55 ± 2.47 cdef	23.84 ± 2.47 fgh	34.78	10.21 ± 2.47 i	72.05
I. trifida	38.32 ± 2.65 cde	33.93 ± 2.67 defg	11.44	20.29 ± 2.67 ghi	47.03
b. Biomass aboveground; Year 2019					
	Control	**9 d**		**50 d**	
Genotype	**Mean**	**Mean**	**Change**	**Mean**	**Change**
	g		%	g	%
Beauregard	80.06 ± 5.02 bcd	72.70 ± 5.02 cde	9.20	41.29 ± 5.29 efg	48.42
I. cynachifolia	67.90 ± 5.02 cdef	48.86 ± 5.02 ef	28.03	NE	–
Hatteras	84.02 ± 5.29 abc	70.27 ± 5.29 cde	16.36	35.19 ± 5.64 fg	58.11
I. leucantha	67.84 ± 5.02 cdef	45.94 ± 5.02 efg	32.28	10.40 ± 14.17 fg	84.67
Resisto	75.25 ± 5.02 bcde	80.77 ± 5.02 bcd	7.34	39.16 ± 8.70 efg	47.95
Tanzania	108.61 ± 5.02 a	101.87 ± 5.02 ab	6.20	40.79 ± 7.42 efg	62.44
I. triloba	53.80 ± 5.02 def	45.36 ± 5.02 efg	15.67	9.76 ± 8.70 g	81.84
I. trifida	64.37 ± 5.64 cdef	59.83 ± 5.64 cdef	7.06	15.57 ± 6.57 fg	75.8
c. Biomass belowground; Year 2018					
	Control	**7 d**		**21 d**	
Genotype	**Mean**	**Mean**	**Change**	**Mean**	**Change**
	g		%	g	%
Beauregard	35.22 ± 5.54 a	16.42 ± 5.54 abc	53.38	11.02 ± 5.54 abc	68.72
Tanzania	13.13 ± 5.54 abc	5.25 ± 5.54 bc	60.03	2.35 ± 5.54 bc	82.13
I. cynachifolia	31.37 ± 5.54 ab	12.12 ± 5.54 abc	61.38	1.79 ± 5.54 c	94.30
I. leucantha	12.22 ± 5.54 abc	4.75 ± 5.54 bc	61.11	1.47 ± 5.54 c	87.94
I. triloba	10.07 ± 5.54 abc	2.60 ± 5.54 bc	74.16	1.42 ± 5.54 c	85.88
I. trifida	19.26 ± 5.64 abc	9.46 ± 5.58 abc	50.89	5.88 ± 5.71 abc	69.45
d. Biomass belowground; Year 2019					
	Control	**9 d**		**50 d**	
	Mean	**Mean**	**Change**	**Mean**	**Change**
Genotype	g		%	g	%
Beauregard	12.21 ± 5.51 d	13.27 ± 5.51 d	8.73	13.41 ± 5.78 d	9.81
I. cynachifolia	95.58 ± 5.51 ab	45.94 ± 5.51 cd	51.93	NE	
Hatteras	8.47 ± 5.78 d	8.98 ± 5.78 d	6.03	10.25 ± 6.16 d	20.90
I. leucantha	42.72 ± 5.51 cd	24.46 ± 5.51 d	42.73	7.40 ± 15.11 d	82.68
Resisto	13.14 ± 5.51 d	11.24 ± 5.51 d	14.45	8.86 ± 9.55 d	32.54
Tanzania	24.38 ± 5.51 d	29.83 ± 5.51 d	22.32	15.84 ± 8.07 d	35.01
I. triloba	44.35 ± 5.51 cd	22.64 ± 5.51 d	48.95	4.60 ±9.55 d	89.63
I. trifida	104.68 ± 5.51 a	70.36 ± 5.51 bc	32.78	16.65 ± 7.12 d	84.09

NE = Mean not estimated due to no survival of none of the plants grown under the treatment.
Common letters within columns represent no significant difference at α = .05 (Tukey method).

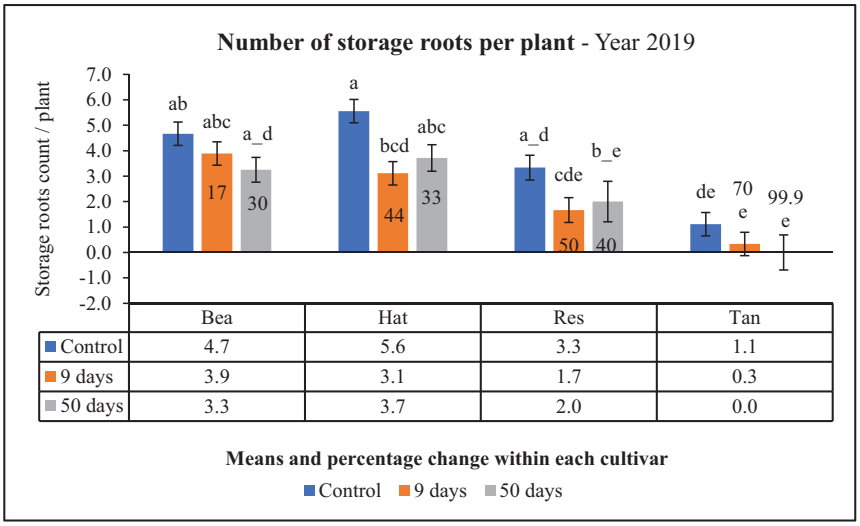
TABLE 4 Mean ± standard error of storage root yield of the cultivated I. batatas. The data include the storage root count per plant and dry weights for control, 7 d, 9 d, 21 d, and 50 d the treatments. Storage root count per plant for 7 d and 21 d (3a); storage root count per plant for 9 d and 50 d (3b); dry weight of the storage roots for 7 d and 21 d (3c); dry weight of the storage roots for 9 d and 50 d (3d). Percentage of change was calculated based on the means of the control treatment for the respective genotype

a. Storage root count per plant; Year 2018					
	Control	**7 d**		**21 d**	
Genotype	**Mean**	**Mean**	**% Change**	**Mean**	**% Change**
Beauregard	3.07 ± 0.31 a	3.08 ± 0.31 a	0.14	2.57 ± 0.31 a	16.31
Tanzania	0.91 ± 0.31 b	0.66 ± 0.31 b	27.42	0.08 ± 0.31 b	91.01
b. Storage root count per plant; Year 2019					
	Control	**9 d**		**50 d**	
Genotype	**Mean**	**Mean**	**% Change**	**Mean**	**% Change**
Beauregard	4.66 ± 0.45 ab	3.88 ± 0.45 abc	16.67	3.25 ± 0.48 abcd	30.36
Hatteras	5.55 ± 0.45 a	3.11 ± 0.45 bcd	44.00	3.71 ± 0.52 abc	33.14
Resisto	3.33 ± 0.48 abcd	1.66 ± 0.48 cde	49.99	2.00 ± 0.79 bcde	39.99
Tanzania	1.11 ± 0.45 de	0.33 ± 0.45 e	70.00	0.00 ± 0.68 e	100.00
c. Dry weight of the storage roots; Year 2018					
	Control	**7 d**		**21 d**	
Genotype	**Mean**	**Mean**	**Change**	**Mean**	**Change**
	g		%	g	%
Beauregard	22.6579 ± 1.1841 a	11.8751 ± 1.1841 b	47.59	6.5313 ± 1.1841 bc	71.17
Tanzania	1.6835 ± 1.1841 cd	1.3739 ± 1.1841 cd	18.39	0.03915 ± 1.1841 d	97.67
d. Dry weight of the storage roots; Year 2019					
	Control	**9 d**		**50 d**	
Genotype	**Mean**	**Mean**	**Change**	**Mean**	**Change**
	g		%	g	%
Beauregard	70.14 ± 8.21 ab	47.05 ± 8.21 abc	32.92	5.40 ± 8.41 c	92.29
Hatteras	83.61 ± 8.21 a	49.57 ± 8.21 abc	40.70	3.94 ± 8.81 c	95.28
Resisto	32.27 ± 8.41 bc	11.28 ± 8.41 c	65.02	1.43 ± 14.22 c	95.96
Tanzania	9.50 ± 8.21 c	0.45 ± 8.21 c	95.20	0.00 ± 11.24 c	100.00

Common letters within columns represent no significant difference at α = .05 (Tukey method).

(via transpiration) and improve the performance of the plant in a long-term drought event. Tanzania appeared to be more sensitive to drought than the other cultivated genotypes studied. *Ipomoea cynachifolia* and *I. leucantha*, which had 21% and 8% mortality, respectively, did not survive the 21 d stress while the other wild species recovered 100%. After 50 days of stress 100% of the *I. cynachifolia* plants died, followed by *I. leucantha* (89%); 44% of *I. trifida* and 67% of *I. triloba* that did not recover from the 50 days of stress.

Leaf loss in the CWR generally occurred from the bottom up (Figure 4). Kramer (1983) argued that the death of the older leaves, in terms of drought tolerance, has no effect in plants, as the rates of transpiration and photosynthesis of the old leaves contribute minimally to plant growth. Leaf loss as a plant survival strategy is undoubtedly complex. To understand this assumption with a bit more of detail, it is important to understand the role of stomatal conductance. The wild relatives studied here could have a mechanism that allows to them to mitigate drought through the reduction of stomatal conductance to prevent water loss via transpiration. The reduction of stomatal conductance inhibits photosynthesis, as stomatal conductance is positively correlated with photosynthesis (Farquhar & Sharkey, 1982; Kusumi et al., 2012; Medrano et al., 2002; Wong et al., 1979). With the closure of stomata, plants may suffer due to the reduction of the uptake of carbon dioxide, preventing photosynthesis. The recovery of the wild species after the 21 d stress, resulted in recovered plants with higher stomatal conductance than the control and moderate plants (Figure 2e) supports the hypothesis that leaf loss might not be a strategy to protect the plant. The reason is while the plants lost their leaves to prevent water loss, they also reduced the uptake of carbon dioxide, and once the plants sensed that water stress was not an issue anymore, stomatal conductance increased in order to uptake the carbon dioxide that was suppressed during the time the plant was under stress. Except for *I. trifida*, the stomatal conductance of the



Common letters within genotypes represent no significant difference at α = 0.05 (Tukey method). Bea = Beauregard; Cyn = *I. cynachifolia*; Hat = Hatteras; Leu = *I. leucantha*; Res = Resisto; Tan = Tanzania; Tba = *I. triloba*; Tfda = *I. trifida*.

FIGURE 3 Storage root yield of the cultivated *I. batatas* studied. The figure shows the storage root count per plant for control, 9 d, and 50 d treatments

FIGURE 4 Signs of drought stress of *I. batatas* studied. The figure shows *I. batatas* cultivars Tanzania and Hatteras, with signs of 15 days of drought stress

recovered plants had higher values than the stomatal conductance of the plants that were under the control and moderate treatments (Figure 2e).

All the wild species that were evaluated in our study have their origin in Latin America (Table 1; GRIN, 2018), where the environmental conditions are different from where the studies were conducted (North Carolina), and they naturally grow in uncultivated conditions. Tanzania, a medium maturity African released landrace adapted to dry areas (Mwanga, Odongo, Ocitti, Obwoya, Gibson, & Smit, 2001), was the first cultivated genotype showing signs of drought in our study, with a leaf loss of 24% after 7 d of stress (Figure 1), and the stomatal conductance at that same point, being reduced at about 90% of its normal capacity (Figure 4a). All the remaining cultivated genotypes were cultivars developed in the U.S. (Table 1). Tanzania has been used as a check cultivar in drought-prone environments and it is thought to be drought tolerant (Andrade et al., 2016; Grüneberg et al., 2015; Kivuva et al., 2015). However, it did not perform as well as the other cultivated genotypes. Probably an interaction between genotype and environment (G × E) is playing a role in the way how Tanzania responds to drought, as Tanzania is not adapted to the environmental and daylength conditions of North Carolina.

None of the CWR of *Ipomoea* spp. produced storage roots, and our general observations suggest that the *I. batatas* cultivars studied were more tolerant to drought than the CWR studied. Sweetpotato storage roots are mainly composed of starch (Amankwaah, 2019; Kays & Bouwkamp, 1985; Kitahara et al., 2017). It is possible that the storage roots served as a source/reserve of carbohydrate that allowed the plant to continue to perform its "normal" metabolic activities even under water stress. Thus, the cultivated genotypes when under stress, used the carbon from starch as a source of reserve for the plant. This hypothesis is supported by Huber (2000) and Taiz & Zeiger (2006). Starch and sucrose are the carbohydrate end products of photosynthesis (Huber, 2000; Taiz & Zeiger, 2006). Huber (2000) recognized the role of starch in plant metabolism as a reserve of carbon. The starch that is found in sink tissues (the storage roots of sweetpotato), are a source of reserve of carbon. The wild relatives, not having this source of reserve, once they sense drought, they begin to drop their leaves as a mechanism of defense against drought (Taiz & Zeiger, 2006). Beauregard is a cultivar that matures early (Rolston et al., 1987), Hatteras has an early to mid-cycle maturity (Yencho & Pecota, 2009), Resisto has a mid to late cycle (Kapinga et al., 2010), and Tanzania is a medium to late maturity cultivar (Mwanga et al., 2001). The initiation of storage roots begins around two to three weeks after transplantation (Gajanayake et al., 2013; Meyers et al., 2017), but this time can vary dramatically according to the cultivar. Our treatments were applied about two weeks after the early cultivars had started the initiation of storage roots. It is possible that the mid to late cultivars, began the initiation of storage roots a bit later, and the treatments (water stress) that we applied were a limiting factor in the initiation of the storage roots for those mid to late cultivars (Figure 3). Added to that, the genotype by environment interaction (G × E) also played a role in the storage root set. Thus, based on the results that we observed in terms of storage root set per plant (Figure 3), and the absence of storage roots within the wild genotypes, we interpreted that because the wild species did not have the source of carbohydrate reserves to cope with the drought tolerance they showed signs of drought earlier than the cultivated genotypes. Tanzania, a short-day adapted, drought tolerant land race from eastern Africa, that was grown under long-day conditions in these experiments, produced only a few small storage roots. Its lack of storage roots probably did not provide as much reserve as the other cultivated genotypes, and because of this it may have expressed earlier signs of drought such as leaf loss compared to the other cultivars (Figure 1). We assume therefore that storage roots play an important role in a plant's ability to tolerate water deficit stress, and that role can be even greater if the process of initiation of storage roots is not affected. Resisto, a mid to late cultivar, had the second lowest number of storage roots per plant and had the lowest survival (33%) rate under extra severe conditions, followed by Tanzania (44%), Hatteras (78%), and Beauregard (89%). These survival rates also support the hypothesis that the storage roots were a source of reserves or the plants under stress.

The wild genotypes that were evaluated in this study were diploids, while the cultivated genotypes were hexaploids. Polyploid plants are known for having certain advantages over diploid plants. Hybrid vigor and heterosis are some of the advantages of polyploids over the diploids (Beest et al., 2012; Comai, 2005; Sattler, Carvalho, & Clarindo, 2016). Zhang et al. (2015) observed that autotetraploid apples increased drought tolerance in apple. Yang, Huang, Qin, Zhao, and Zhou (2014) observed that autotetraploid lines of rice responded better to drought tolerance than the corresponding diploid lines. It could be that the cultivated genotypes (autoploid hexaploids) are taking advantage of their genome duplication over the diploid ones.

The role of leaf loss as a strategy to protect the plant against the stress is unclear. Based on our observation of near complete stem desiccations of some of the CWR, we speculate that the wild *Ipomoea* spp. could be resurrection plants. Resurrection plants are plants that can tolerate desiccation to 5% relative water content for extended periods and yet resume full metabolic activity on re-watering (Farrant, Brandt, & Lindsey, 2007). Transcriptomics studies have been done on resurrection plants and would help us to understand better the genetic mechanism behind the recovery of the wild species that were completely dry and recovered after they were irrigated. Yet, our studies suggest that in the case of sweetpotato, trying to study materials that produce storage roots may be a more

feasible and productive approach to understand drought tolerance in this crop.

In conclusion, at the phenotypic level, the cultivated genotypes evaluated in our study were more tolerant to drought than the wild species studied. Also, we speculate that the storage roots of sweetpotato may play an important role into the response of cultivated sweetpotatoes to environmental stresses. Last, in terms of the yield of sweetpotato, since none of the CWR of *I. batatas* produced storage roots and they did not appear to be more tolerant of drought in general compared to the cultivated sweetpotatoes, probably these species may not be the best option to improve drought tolerance in sweetpotato.

ACKNOWLEDGMENTS

This work was undertaken as part of the initiative "Adapting Agriculture to Climate Change: Collecting, Protecting and Preparing Crop Wild Relatives", which is supported by the Government of Norway. The project is managed by the Global Crop Diversity Trust with the Millennium Seed Bank of the Royal Botanic Gardens, Kew and implemented in partnership with national and international gene banks and plant breeding institutes around the world. For further information, see the project website: http://www.cwrdiversity.org/.

We thank Dr. Richard E. Miller for sharing his experience on the *I. batatas* series, and Chris Heim for his assistance with the irrigation system used in this study.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

ORCID

G. Craig Yencho https://orcid.org/0000-0001-6583-0628

REFERENCES

Amankwaah, V. A. (2019). Phenotyping and genetic studies of storage root chemistry traits in sweetpotato. PhD Dissertation, Raleigh, NC: North Carolina State University.

Andrade, M. I., Naico, A., Ricardo, J., Eyzaguirre, R., Makunde, G. S., Ortiz, R., & Grüneberg, W. J. (2016). Genotype× environment interaction and selection for drought adaptation in sweetpotato (*Ipomoea batatas* (L.) Lam) in Mozambique. *Euphytica*, *209*(1), 261–280. https://doi.org/10.1007/s10681-016-1684-4

Beest, M., Le Roux, J. J., Richardson, D. M., Brysting, A. K., Suda, J., Kubešová, M., & Pyšek, P. (2012). The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany*, *109*(1), 19–45. https://doi.org/10.1093/aob/mcr277

Bouslama, M., & Schapaugh, W. T. (1984). Stress tolerance in soybeans. I. Evaluation of three screening techniques for heat and drought tolerance. *Crop Science*, *24*(5), 933–937. https://doi.org/10.2135/cropsci1984.0011183X002400050026x

Brasileiro, A. C., Morgante, C. V., Araujo, A. C., Leal-Bertioli, S. C., Silva, A. K., Martins, A. C., & Saraiva, M. A. (2015). Transcriptome profiling of wild Arachis from water-limited environments uncovers drought tolerance candidate genes. *Plant Molecular Biology Reporter*, *33*(6), 1876–1892. https://doi.org/10.1007/s11105-015-0882-x

Chen, Y., Chen, P., & de los Reyes, B. G. (2006). Differential responses of the cultivated and wild species of soybean to dehydration stress. *Crop Science*, *46*(5), 2041–2046. https://doi.org/10.2135/cropsci2005.12.0466

Comai, L. (2005). The advantages and disadvantages of being polyploid. *Nature Reviews Genetics*, *6*(11), 836–846. https://doi.org/10.1038/nrg1711

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*(1), 52–58. https://doi.org/10.1038/nclimate1633

Du Plooy, C. P., Van den Berg, A. A., Hammes, P. S., & Holtzhausen, L. C. (1992). Storage root formation at individual nodes of the sweet potato (*Ipomoea batatas* (L.) Lam). *South African Journal of Plant and Soil*, *9*(3), 136–138. https://doi.org/10.1080/02571862.1992.10634616

Farquhar, G. D., & Sharkey, T. D. (1982). Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, *33*(1), 317–345. https://doi.org/10.1146/annurev.pp.33.060182.001533

Farrant, J. M., Brandt, W., & Lindsey, G. G. (2007). An overview of mechanisms of desiccation tolerance in selected angiosperm resurrection plants. *Plant Stress*, *1*(1), 72–84.

Gajanayake, B., Reddy, K. R., Shankle, M. W., & Arancibia, R. A. (2013). Early-season soil moisture deficit reduces sweetpotato storage root initiation and development. *HortScience*, *48*(12), 1457–1462. https://doi.org/10.21273/HORTSCI.48.12.1457

Gajanayake, B., Reddy, K. R., Shankle, M. W., & Arancibia, R. A. (2014a). Growth, developmental, and physiological responses of two sweetpotato (*Ipomoea batatas* (L.) Lam) cultivars to early season soil moisture deficit. *Scientia Horticulturae*, *168*, 218–228. https://doi.org/10.1016/j.scienta.2014.01.018

Gajanayake, B., Reddy, K. R., Shankle, M. W., Arancibia, R. A., & Villordon, A. O. (2014b). Quantifying storage root initiation, growth, and developmental responses of sweetpotato to early season temperature. *Agronomy Journal*, *106*(5), 1795–1804. https://doi.org/10.2134/agronj14.0067

GRIN Germplasm Resources Information Network (2018). Retrieved from https://npgsweb.ars-grin.gov/gringlobal/search.aspx (accessed March 2018).

Grüneberg, W. J., Manrique, K., Zhang, D., & Hermann, M. (2005). Genotype × environment interactions for a diverse set of sweetpotato clones evaluated across varying ecogeographic conditions in Peru. *Crop Science*, *45*(6), 2160–2171. https://doi.org/10.2135/cropsci2003.0533

Grüneberg, W. J., Ma, D., Mwanga, R. O. M., Carey, E. E., Huamani, K., Diaz, F., … Yencho, G. C. (2015). Advances in sweetpotato breeding from 1992 to 2012. In J. Low, M. Nyongesa, S. Quinn, & M. Parker (Eds.), *Potato and sweetpotato in Africa: Transforming the value chains for food and nutrition security* (pp. 3–68). Oxfordshire: CAB International.

Hahn, S. K., Alvim, P. D. T., & Kozlowski, T. T. (1977). *Ecophysiology of tropical crops* (pp. 237–247). New York: Acadademic Press.

Havaux, M., Ernez, M., & Lannoye, R. (1988). Correlation between heat tolerance and drought tolerance in cereals demonstrated by rapid chlorophyll fluorescence tests. *Journal of Plant Physiology*, *133*(5), 555–560. https://doi.org/10.1016/S0176-1617(88)80007-5

Honsdorf, N., March, T. J., Berger, B., Tester, M., & Pillen, K. (2014). High-throughput phenotyping to detect drought tolerance QTL in wild

barley introgression lines. *PLoS One*, *9*(5). https://doi.org/10.1371/journal.pone.0097047

Hotz, C., Loechl, C., de Brauw, A., Eozenou, P., Gilligan, D., Moursi, M., & Meenakshi, J. V. (2012). A large-scale intervention to introduce orange sweet potato in rural Mozambique increases vitamin A intakes among children and women. *British Journal of Nutrition*, *108*(1), 163–176. https://doi.org/10.1017/S0007114511005174

Huber, S. C. (2000). Chapter 12. Starch-sucrose metabolism and assimilate partitioning. In A. S. Raghavendra (Ed.), *Photosynthesis: A comprehensive treatise* (pp. 163–174). Cambridge: Cambridge University Press.

Kapinga, R. S., Tumwegamire, S., Ndunguru, J., Andrade, M. I., Agili, S., & Mwanga, R. O. M. (2010). Catalogue of orange-fleshed sweetpotato varieties for Sub-Saharan Africa. International Potato Center. Retrieved from https://cipotato.org/wp-content/uploads/2014/08/005374.pdf (accessed February 2019).

Kays, S. J., & Bouwkamp, J. C. (1985). The physiology of yield in sweet potato. *Sweet Potato Products: A Natural Resource of the Tropics*, *1985*, 79–133.

Khoury, C. K., Heider, B., Castañeda-Álvarez, N. P., Achicanoy, H. A., Sosa, C. C., Miller, R., … Struik, P. C. (2015). Distributions, ex situ conservation priorities, and genetic resource potential of crop wild relatives of sweetpotato [*Ipomoea batatas* (L.) Lam., I. series Batatas]. *Frontiers in Plant Science*, *6*, 251. https://doi.org/10.3389/fpls.2015.00251

Kitahara, K., Nakamura, Y., Otani, M., Hamada, T., Nakayachi, O., & Takahata, Y. (2017). Carbohydrate components in sweetpotato storage roots: Their diversities and genetic improvement. *Breeding Science*, *2017*, 16135.

Kivuva, B. M., Githiri, S. M., Yencho, G. C., & Sibiya, J. (2015). Screening sweetpotato genotypes for tolerance to drought stress. *Field Crops Research*, *171*, 11–22. https://doi.org/10.1016/j.fcr.2014.10.018

Kramer, P. J. (1983). Water relations of plants – Chapters 12 and 13. New York: Academic Press.

Kusumi, K., Hirotsuka, S., Kumamaru, T., & Iba, K. (2012). Increased leaf photosynthesis caused by elevated stomatal conductance in a rice mutant deficient in SLAC1, a guard cell anion channel protein. *Journal of Experimental Botany*, *63*(15), 5635–5644. https://doi.org/10.1093/jxb/ers216

Laurie, R. N., Laurie, S. M., Du Plooy, C. P., Finnie, J. F., & Van Staden, J. (2015). Yield of drought-stressed sweet potato in relation to canopy cover, stem length and stomatal conductance. *Journal of Agricultural Science*, *7*(1), 201.

Lewthwaite, S. L., & Triggs, C. M. (2012). Sweet potato cultivar response to prolonged drought. *Agronomy New Zealand*, *42*, 1–10.

Low, J. W., Ortiz, R., Vandamme, E., Andrade, M., Biazin, B., & Grüneberg, W. J. (2020). Nutrient-dense orange-fleshed sweetpotato: Advances in drought-tolerance breeding and understanding of management practices for sustainable next-generation cropping systems in sub-Saharan Africa. *Frontiers in Sustainable Food Systems*, *4*, 50. https://doi.org/10.3389/fsufs.2020.00050

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Medrano, H., Escalona, J. M., Bota, J., Gulías, J., & Flexas, J. (2002). Regulation of photosynthesis of C3 plants in response to progressive drought: Stomatal conductance as a reference parameter. *Annals of Botany*, *89*(7), 895–905. https://doi.org/10.1093/aob/mcf079

Meyers, S. L., Arancibia, R. A., Shankle, M. W., Main, J., Bandara, K. G. M. C. P., & Reddy, K. R. (2017). Sweet potato storage root initiation. Mississippi State University Extension Service. Retrieved from http://extension.msstate.edu/publications/sweetpotato-storage-root-initiation (accessed October 2018).

Minot, N. (2010). Staple food prices in Malawi. Food Security Collaborative Working Papers 58558. East Lansing, MI: Michigan State University, Department of Agricultural, Food, and Resource Economics.

Mohanraj, R., & Sivasankar, S. (2014). Sweet potato (*Ipomoea batatas* [L.] Lam) - A valuable medicinal food: A review. *Journal of Medicinal Food*, *17*(7), 733–741. https://doi.org/10.1089/jmf.2013.2818

Mwanga, R. M., Odongo, B., Ocitti, Obwoya, C., Gibson, R. W., & Smit, N. M. (2001). Release of five sweetpotato cultivars in Uganda. *HortScience*, *36*(2), 385–386. https://doi.org/10.21273/HORTSCI.36.2.385

Mwanga, R. O., Andrade, M. I., Carey, E. E., Low, J. W., Yencho, G. C., & Grüneberg, W. J. (2017). Sweetpotato (*Ipomoea batatas* L.). In H. Campos, & P. D. Caligari (Eds.), *Genetic improvement of tropical crops* (pp. 181–218). Cham: Springer.

Oloka, B. M. (2019). Genetic linkage map construction and QTL analysis of important pest and agronomic traits in two bi-parental sweetpotato SNP mapping populations. PhD Dissertation. Raleigh, NC: North Carolina State University.

Padmaja, G. (2009). Uses and nutritional data of sweetpotato. In G. Loebenstein & G. Thottappilly (Eds.), *The sweetpotato* (pp. 189–234). Dordrecht: Springer.

Placido, D. F., Campbell, M. T., Folsom, J. J., Cui, X., Kruger, G. R., Baenziger, P. S., & Walia, H. (2013). Introgression of novel traits from a wild wheat relative improves drought adaptation in wheat. *Plant Physiology*, *161*(4), 1806–1819. https://doi.org/10.1104/pp.113.214262

Pochapski, M. T., Fosquiera, E. C., Esmerino, L. A., dos Santos, E. B., Farago, P. V., Santos, F. A., & Groppo, F. C. (2011). Phytochemical screening, antioxidant, and antimicrobial activities of the crude leaves' extract from Ipomoea batatas (L.) Lam. *Pharmacognosy Magazine*, *7*(26), 165. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3113358/?tool=pmcentrez&report=abstract (accessed February 2020).

Porch, T. G., Beaver, J. S., Debouck, D. G., Jackson, S. A., Kelly, J. D., & Dempewolf, H. (2013). Use of wild relatives and closely related species to adapt common bean to climate change. *Agronomy*, *3*(2), 433–461. https://doi.org/10.3390/agronomy3020433

Ravi, V., Naskar, S., Makeshkumar, T., Babu, B., & Krishnan, B. P. (2009). Molecular physiology of storage root formation and development in sweet potato (*Ipomoea batatas* (L.) Lam.). *Journal of Root Crops*, *35*(1), 1–27.

Rolston, L. H., Clark, C. A., Cannon, J. M., Randle, W. M., Rilery, E. G., Wilson, P. W., & Robbins, M. L. (1987). 'Beauregard' sweetpotato. *HortScience*, *22*, 1338–1339.

Sattler, M. C., Carvalho, C. R., & Clarindo, W. R. (2016). The polyploidy and its key role in plant breeding. *Planta*, *243*(2), 281–296. https://doi.org/10.1007/s00425-015-2450-x

Schlaepfer, D. R., Bradford, J. B., Lauenroth, W. K., Munson, S. M., Tietjen, B., Hall, S. A., & Lkhagva, A. (2017). Climate change reduces extent of temperate drylands and intensifies drought in deep

soils. *Nature Communications*, *8*(1), 1–9. https://doi.org/10.1038/ncomms14196

Solis, J., Villordon, A., Baisakh, N., LaBonte, D., & Firon, N. (2014). Effect of drought on storage root development and gene expression profile of sweetpotato under greenhouse and field conditions. *Journal of the American Society for Horticultural Science*, *139*(3), 317–324. https://doi.org/10.21273/JASHS.139.3.317

Suprunova, T., Krugman, T., Fahima, T., Chen, G., Shams, I., Korol, A., & Nevo, E. (2004). Differential expression of dehydrin genes in wild barley, *Hordeum spontaneum*, associated with resistance to water deficit. *Plant, Cell & Environment*, *27*(10), 1297–1308.

Taduri, S., Lone, A., Meyers, S. L., Shankle, M. W., & Reddy, K. R. (2017). *Sweetpotato cultivar responses to interactive effects of temperature, drought, and carbon dioxide*. Poster session presented at the Managing Global Resources for a Secure Future Meeting, Tampa, FL. Retrieved from https://scisoc.confex.com/crops/2017am/webprogram/Paper107834.html (accessed February 2019).

Taiz, L., & Zeiger, E. (2006). Plant physiology (4th edition). Sunderland: Sinauer Associates.

Trenberth, K. E., Dai, A., Van Der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, *4*(1), 17–22. https://doi.org/10.1038/nclimate2067

Van Heerden, P. D. R., & Laurie, R. (2008). Effects of prolonged restriction in water supply on photosynthesis, shoot development and storage root yield in sweet potato. *Physiologia Plantarum*, *134*(1), 99–109. https://doi.org/10.1111/j.1399-3054.2008.01111.x

Villordon, A., LaBonte, D., & Firon, N. (2009). Development of a simple thermal time method for describing the onset of morpho-anatomical features related to sweetpotato storage root formation. *Scientia Horticulturae*, *121*(3), 374–377. https://doi.org/10.1016/j.scienta.2009.02.013

Wong, S. C., Cowan, I. R., & Farquhar, G. D. (1979). Stomatal conductance correlates with photosynthetic capacity. *Nature*, *282*(5737), 424–426. https://doi.org/10.1038/282424a0

Yang, P. M., Huang, Q. C., Qin, G. Y., Zhao, S. P., & Zhou, J. G. (2014). Different drought-stress responses in photosynthesis and reactive oxygen metabolism between autotetraploid and diploid rice. *Photosynthetica*, *52*(2), 193–202. https://doi.org/10.1007/s11099-014-0020-2

Yencho, G. C., & Pecota, K. V. (2009). Progress Report to North Carolina Sweet Potato Commission. Retrieved from https://potatoes.ncsu.edu/pdf/NCSPCBRDRPT08.pdf (accessed February 2019).

Zaharieva, M., Gaulin, E., Havaux, M., Acevedo, E., & Monneveux, P. (2001). Drought and heat responses in the wild wheat relative *Aegilops geniculata* Roth. *Crop Science*, *41*(4), 1321–1329. https://doi.org/10.2135/cropsci2001.4141321x

Zhang, F., Xue, H., Lu, X., Zhang, B., Wang, F., Ma, Y., & Zhang, Z. (2015). Autotetraploidization enhances drought stress tolerance in two apple cultivars. *Trees*, *29*(6), 1773–1780. https://doi.org/10.1007/s00468-015-1258-4

How to cite this article: Nhanala SEC, Yencho GC. Assessment of the potential of wild *Ipomoea* spp. for the improvement of drought tolerance in cultivated sweetpotato *Ipomoea batatas* (L.) Lam. *Crop Science*. 2021;61:234–249. https://doi.org/10.1002/csc2.20363