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RESEARCH ARTICLE

A comparative study of morpho-physiological responses of wild and cultivated *Solanum* species to water stress: the case of *S. sisymbriifolium* and *S. macrocarpon*

Ahuéfa Mauricel Kégbé · Kolawolé Valère Salako · Bruno Enagnon Lokonon · Sylvanus Mensah · Kandioura Noba · Achille Ephrem Assogbadjo

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Abstract Crop wild relatives are closely related taxa of cultivated crops and are well adapted to a wide range of environmental conditions. With the current global warming and challenges in agriculture and food production, increasing attention must be given to these crop wild species as they can provide genetic resources that may be helpful to address some of the current challenges in agriculture (e.g., adaptation to drought). In this study, we compared the morpho-physiological performances of *Solanum macrocarpon* and its wild relative *Solanum sisymbriifolium* under different watering conditions in Benin. Seedlings were grown in plastic pots under shade-house and subjected to low, moderate, and high-water supply (i.e., 25%, 50% and 75%, respectively of the pot holding capacity). Parameters related to seedlings growth, biomass allocation and stomatal density were investigated. Descriptive statistics and linear mixed effect models were used for data analysis. Results revealed highly significant differences of morpho-physiological parameters between wild and cultivated *Solanum* species along the watering gradient. First, seedlings from the wild relative demonstrated higher morphological growth parameters than seedlings of the cultivated species irrespective of the watering level. Second, the wild relative also showed better performances in terms of biomass allocation and number of stomata, regardless of leaves faces and watering level than the cultivated species. Water stress reduced values of morpho-physiological parameters for both wild and cultivated species. Contrary to our expectations, the wild relative instead of being resistant, was

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A. M. Kégbé (✉) · A. E. Assogbadjo
Laboratoire d'Ecologie Appliquée, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, 01 BP 526 Cotonou, Benin
e-mail: kegbem@gmail.com

A. E. Assogbadjo
e-mail: assogbadjo@gmail.com

K. V. Salako · B. Enagnon Lokonon · S. Mensah · A. E. Assogbadjo
Laboratoire de Biomathématiques et d'Estimations Forestières, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, 04 BP 1525 Cotonou, Bénin
e-mail: salakovalere@gmail.com

B. Enagnon Lokonon
e-mail: brunolokonon@gmail.com

S. Mensah
e-mail: sylvanus.m89@gmail.com

S. Mensah
Chair of Forest Growth and Dendroecology, Albert-Ludwigs-University Freiburg, Tennenbacher Str. 4, 79106 Freiburg im Breisgau, Germany

K. Noba
Laboratory of Botany-Biodiversity, Department of Plant Biology, Faculty of Sciences and Techniques, Cheikh Anta Diop University, P.O Box 5005, Dakar, Fann, Senegal
e-mail: kandioura.noba@gmail.com

found to also be sensitive to water stress. However, it was found to be more tolerant to drought than the cultivated species, and therefore could be considered when selecting rootstocks for crop improvement.

Keywords Morpho-physiology · Biomass allocation · Water stress · Stomatal density · Wild relative of *Solanum*

Introduction

Climate change reflects the long-term variations in climatic variables (e.g., precipitation, temperature) and events, and has adverse impacts on food production especially in Sub-Saharan Africa where agriculture is heavily dependent on precipitation (FAO 2016; Nelson et al. 2009). Among these climatic events, drought most severely affects nutrition and food security especially in Africa where people largely rely on natural resources (FAO 2016; Shiferaw et al. 2014). Agriculture provides the major part of food and feed resources, and represents the main source of income in the region (Block 2014). Reports indicated that economic losses induced by drought represent approximatively 70% of the total production in Sub-Saharan Africa (Bhavani et al. 2008). Furthermore, the low capacity to predict climate fluctuations expose vulnerable African people's livelihoods to climatic shocks, especially those in arid and semi-arid areas. To mitigate the impacts of drought, smallholder farmers refer to techniques like irrigation, which require high material, financial and time investment (Ouko and Kenduiwa 2005). Moreover, the efficiency of the practice is henceforth questionable, first because of the increasing conflicts between population, farmers and breeders for water (Pimentel et al. 2004), and second because many of water sources are rain-dependent (McCarthy et al. 2001; Shiferaw et al. 2014). Nevertheless, over the years, farmers have developed local practices to enhance their resilience and avoid/reduce drought effects on crops. These well-established strategies range from the selection of drought-tolerant and fast-growing cultivars requiring low external inputs, to the smart use of land and water saving strategies (Mercer and Perales 2010; Shiferaw et al. 2014).

Recently, crop wild relatives received increasing attention from different stakeholders, including scientists and farming communities. These species reportedly offer a wide range of opportunities for enhancing food security and alleviating poverty (Maxted et al. 2012). They can also provide a wide range of benefits (Maxted et al. 2006). For instance, crop wild relatives have the potential to thrive in harsh environmental conditions. Recent research revealed that wild relative species have important resistance genes, which help them cope with biotic and abiotic factors especially in the context of climate change (Zhang and Batley 2020; Zhang et al. 2017). Their importance in breeding programs has been widely explored, and evidence of improvement of cultivated species based on their wild relative has also been documented (Hajjar and Hodgkin 2008; Zhang et al. 2017). However, several other cultivated species are yet to be explored to better understand the performance of cultivated crops and their wild relative. This is the case for *Solanum* species.

Research showed that wild *Solanum* species possess some stress-responses genes or families of genes (for instance ABA/water stress/ripening induced) that allow them to survive and develop in difficult environmental conditions such as drought. For instance, dehydrin genes (pLC30-15) are present in *Solanum chilense* and *Solanum peruvianum*, two wild relatives of tomato (Arms et al. 2015; Fischer et al. 2013). Indeed, dehydrin genes encode for a number of proteins which are associated with crucial protective functions, and play important role in plant adaptability to abiotic stress (Hassan et al. 2015). Plants can respond to water deficit by avoiding water loss, during transpiration process through the control of stomata closure (Haworth et al. 2015; Seemann and Critchley 1985). Immediate responses such as leaf rolling or folding can also be noted under a short period of water deficits, providing insights into how plants minimize leaf surface area to reduce water loss. Over a long period, plants escape water deficit by regulating the development of stomata (Dunn et al. 2019; Shirvani et al. 2024). These changes depend on several biochemical and molecular regulators resulting from enzymatic activities (Blum 2017; Bohnert and Jensen 1996; Joshi et al. 2016; Vurukonda et al. 2016). For instance, radical and non-radical agents play a key role during biotic and abiotic stresses and authors reported that Reactive Oxygen Species induced in stressed plants is controlled by a series of enzymatic reactions such as nicotinamide adenine dinucleotide phosphate (NADPH) oxidase, xanthine oxidoreductase (XOR), and myeloperoxidase (MPO) (Mhamdi and Van Breusegem 2018; Shirvani et al. 2024).

One of the most important constraints for optimal crop production in Sub-Saharan Africa is water availability. Water shortage negatively influences the yield of leafy vegetables and consequently affects local farmers in various ways. Numerous research investigated the use of wild *Solanum* species to improve crops such as tomato (Deb et al. 2019; Fenstemaker et al. 2022; Fenstemaker 2021; Tejada-Alvarado et al. 2023), potato (Ibañez et al. 2021; Kud et al. 2022; Nicolao et al. 2023; Obidiegwu et al. 2015) and eggplant (Haliński et al. 2017; Kouassi et al. 2021; Plazas et al. 2022), but little is still known about leafy vegetables, although they are at the forefront in food security and nutrition programs. Hajjar and Hodgkin (2008) reported that six and ten wild relative species have successfully contributed to the improvement of potato and tomato traits, respectively. However, to the best of our knowledge, morphological and physiological parameters of both wild relative and cultivated leafy vegetables of *Solanum* species in response to abiotic stress have not been investigated. Therefore, information on agro-morphological performances of these species is required. Given the predicted climatic changes and their potential impacts on crop productivity (Gnanglè et al. 2011), it is important to evaluate the responses of wild relative species under water deficit to generate empirical evidence that inform the development of resistant cultivars, and contribute to enhanced food security in West Africa.

Solanum sisymbriifolium is a wild and weedy species belonging to the cosmopolite family of *Solanaceae* (Samuels 2009, 2015). The species was demonstrated to have a high potential in biological control (Cortés and López-Hernández 2021; Hajihassani et al. 2020; Yin et al. 2022) and possesses several medicinal (Figueiredo et al. 2021) and nutritional properties as well (Biswas et al. 2023). Unfortunately, it is threatened by several factors such as agricultural expansion, environmental and climate changes (Sintayehu 2018) as many crop wild relatives worldwide.

In this study, we focused on the adaptive responses of *Solanum macrocarpon* L. and *Solanum sisymbriifolium* Lam. to water stress (Fig. 1C–E). Specifically, we aimed at (1) quantifying effects of watering regimes on agro-morphological performances of *S. sisymbriifolium* Lam. and *S. macrocarpon* L. and, (2) comparing the physiological responses of both species under water stress. We hypothesized that (H1) *Solanum* species would respond differently to the water stress since plants growth and water availability are closely dependent, and that (H2) the wild species *S. sisymbriifolium* would better adapt to water shortage conditions than the cultivated species.

Material and methods

Experimental site

The experimentation was carried out at the research station of the Laboratory of Biomathematics and Forest Estimations of the Faculty of Agronomic Sciences. The station is in the subdistrict of Sekou (06° 37′ 32.2″ North latitude and 02° 14′ 10.9″ East longitude) near Allada and is characterized by a subequatorial climate with two rainy seasons (from March to July and September to November) and two dry seasons (from December to February and July to August). The average annual temperature is 28 °C for an average annual rainfall of 1000 mm (Adomou et al. 2006). The experiment took place in April 2020 and ended in July 2020.

Material collection for the experiment

Prior to the experiment, fruits of *S. sisymbriifolium* and *S. macrocarpon* were collected from the field during exploration in the district of Ketou, located in the Guineo-Congolean zone. Then, seeds were carefully extracted from fruits, carefully sun-dried and stored in bottles to avoid insects' attacks and moisture. A nursery was installed and monitored for 6 weeks. Healthy seedlings at four full leaves stage were used for the experiment and transplanted in the prepared plastic pots. Special attention was given to the vigorous and healthy seedlings of six leaves and that did not differ in size for transplantation.

Experimental design and monitoring

The experimental design was a split-plot with three blocks. Plastic pots of 11 L capacity were used to avoid seepage. A set of 10 plastic pots was used as experimental unit. The main factor was watering regimes (in plots) while the secondary factor was

Fig. 1 *Solanum* species grown under water stress. First line, left to right: *Solanum macrocarpon* and *S. sisymbriifolium* **A**; *S. macrocarpon* and *S. sisymbriifolium* flowering **B**; second line, left to right: *S. sisymbriifolium* **C**, **D** and *S. macrocarpon* fruiting **E**

species (in sub-plots). A total of 180 plastic pots (2 species × 10 seedlings (one seedling per plastic pot) × 3 watering regimes × 3 replicates) were used for the experiment. Pots were filled with dry topsoil (80%) mixed with poultry manure (20%) and installed under a shade-house (Fig. 1A, B). A water drop test was done to determinate the water holding capacity of the pots. Five pots containing substrate (soil + poultry manure) were randomly selected and saturated with water using a graduate container until no more than three drops of water came out (Brischke and Wegener 2019; Marshall et al. 2019). The watering regimes (25%, 50%, 75%) were then determined from the total quantity of water added. Thereafter, all the pots were watered for a week before seedlings transplantation.

After transplantation, seedlings were watered twice a day for 1 week before the start of the stress treatments. Effects of two factors were evaluated: species (with two levels: wild and cultivated) and watering regimes (with three levels: watered at 25%, watered at 50% and watered at 75% of the water holding capacity of the pot). No pretreatment was applied in contrary to what is mostly recommended for the *Solanum* species because of their poor germination potential (Commander et al. 2008; Spicer and Dionne 1961). Watering was done with 5 days interval and weeds were removed daily to avoid competition effects and pest attacks.

Data collection

Seedling total height and leaf number were measured at the start of the watering regime. During the stress experiment, data collection started 1 week after transplantation and was performed every 3 days. The experiment was performed for 3 months. Total height, stem collar diameter, number of leaves and the stomatal density were assessed from each seedling. The total height was measured using a tape and the stem diameter using an electronic caliper. The total number of leaves was counted. Stomatal density was determined using a microscope. For this estimation, one fully developed leaf was considered when counting from the top for each seedling. Nail impressions were directly realized on the field. A very thin film of clear nail polish was applied on a small area of both sides of the leaf and allowed to dry (10–15 min). The dried nail polish coat was gently removed with a transparent tape, fixed on the microscopic slide and labelled as described in Kardel et al. (2010). The samples were taken to the lab for microscopic observation. The region enclosed by the objective of the microscope was considered as unit area for the determination of the number of stomata. This process was performed in three randomly selected areas on the leaves and on the two faces (adaxial and abaxial).

Fresh and dried weight (leaves, stems and roots) of seedlings were also collected. Every 2 weeks, two individuals were randomly harvested per species for each watering regime and block, making a total of 2 (individuals) × 2 (species) × 3 (watering regimes) × 3 (blocks) = 36 individuals for monitoring the biomass production. Above and below-ground parts of seedlings were carefully separated and weighed. Shortly after, fresh leaves, stems and roots were cut into small pieces and packed separately. The oven drying was done at 70 °C for leaves and 105 °C for roots and stems (Afful et al. 2019; Tejada-Alvarado et al. 2023). Dry weight check began 12 h later and was performed repeatedly at a 6-h frequency to constant weight. The constant weight was recorded for each sample using an electronic scale with a sensitivity of 0.01 g.

Data analysis

All data collected were first submitted to descriptive statistics (means and standard errors) per species and watering regimes. Then, inferential analyses were applied to evaluate the effect of water stress on both species. For longitudinal data on morphometric traits and biomass, a linear mixed effects model on longitudinal data was applied (height, stem collar diameter, and number of leaves collected every 3 days, and biomass collected every 2 weeks) to assess the effect of watering regimes (25%, 50% and 75%) on seedling morphometric traits and biomass across time. In this model, watering regimes (treatment), species and date were considered as fixed factors while block was considered as random. The variation across times of the morphometric traits and biomass following watering regimes were plotted and analyzed for each species. Moreover, the difference between the species at every measurement time was assessed using a t-test.

For cross-sectional data (data collected on morphometric traits and biomass, biomass allocation, and stomatal density) a linear mixed model was used to evaluate the influence of watering regimes (25%, 50% and 75%) and species on their variation. Watering regimes and species were considered as fixed, and blocks were considered as random. The total biomass was obtained by adding the biomass of leaves, stem, and roots of seedlings. The ratio or mass fraction was computed for the seedlings' parts, by dividing the mass of each part by the total plant mass. Furthermore, an analysis of variance followed by a Student–Newman–Keuls post-hoc test was then performed to evaluate the effect of watering regimes on dried biomass of the seedlings for each species. For the stomatal density, one additional factor, i.e., leaf face (internal and external) was considered as fixed factor. All statistical analyses were implemented in R software version 4.2 with 0.05 significance level. The R package nlme (Pinheiro et al. 2018) was used to fit the mixed-effects models.

Results

Effect of water stress on seedling morphometric of the cultivated species and its wild relative

The interaction of time (sacrifice) and species, and that of time and watering regimes was significant ($p < 0.05$) for height, and number of leaves but not for collar diameter, indicating that the patterns of variation of height, and number of leaves across times differed between both species and among the watering regimes; this was not the case for collar diameter. The three-way interaction of time, species, and watering regimes was also significant for total height, and number of leaves. The variance due to blocks was largely lower than the variance of residuals, showing negligible block effect (Table 1).

Table 1 Effects of species, watering regimes and dates on height, diameter, and number of leaves

Source of variation	Degrees of freedom	Height		Diameter		Number of leaves	
		F	*p*	F	*p*	F	*p*
Time	1	322.47	< 0.0001	2.18	0.1401	4102.18	< 0.0001
Water regime	2	10.08	< 0.0001	1.46	0.2335	57.8	< 0.0001
Species	1	30.58	< 0.0001	0.93	0.3343	0.24	0.624
Time: watering regimes	2	5.31	0.0051	0.47	0.6233	49.49	< 0.0001
Time: Species	1	18.14	< 0.0001	0.32	0.5731	56.25	< 0.0001
Watering regimes: Species	2	1.21	0.2983	1.76	0.1722	16.9	< 0.0001
Time: watering regimes: Species	2	4.38	0.0127	0.26	0.7697	24.57	< 0.0001
Block variance		0.35		0.65		0.9	
Residual variance		604.55		1287.65		77.16	

Figure 2 illustrates the temporal variation of height and number of leaves for the watering regimes and species. Overall, there is an increasing trend in total height, diameter, and number of leaves with time. However, as time increased, *S. sisymbriifolium* showed the highest values for the total height compared to *S. macrocarpon* (Fig. 2A) while both species showed the lowest values of diameter for severe watering regime 25% (Fig. 2B). *S. sisymbriifolium* produced a lower number of leaves under limited water availability (25%) when compared to *S. macrocarpon* (Fig. 2C). The differences between species and among watering regimes become marked with increasing time.

Effect of water stress on biomass and resources allocation between the cultivated species and its wild relative

Table 2 shows the effects of species, watering regimes across time (sacrifice) on fresh and dried weights of stems, leaves, roots and number of secondary roots. Species, watering regimes and time, and their interactions had significant effects ($p < 0.05$) on biomass parameters, except the effect of watering regimes on the number of secondary roots. The variance of blocks was largely lower than the variance of residuals suggesting that there is no block effect (Table 2). The comparison between the two species for each watering regime and biomass is presented below.

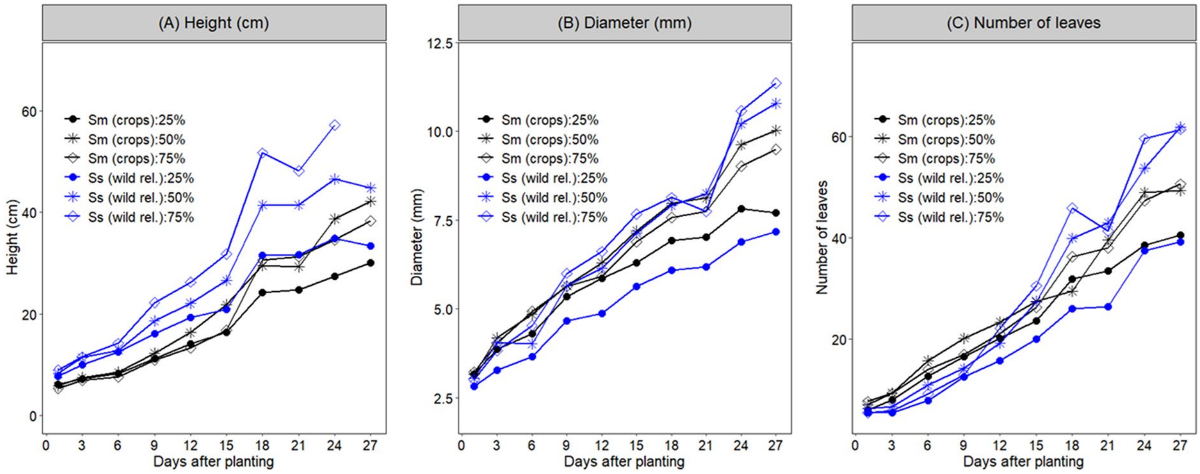

Fig. 2 Temporal variation of height **A**, diameter **B** and number of leaves **C** for different watering regimes and species: Ss = *Solanum sisymbriifolium*; Sm = *Solanum macrocarpon*; Watering regimes = 25%, 50% and 75%; wild rel = wild relative

Table 2 Effects of species, watering regimes and time on fresh and dried weight of stems, fresh and dried weight of leaves, fresh and dried weight of roots, and number of secondary roots. df = degrees of freedom

Source of variation	df	Fresh weight of leaves		Dry weight of leaves		Fresh weight of stems		Dry weight of stems		Number of secondary roots		Fresh weight of roots		Dry weight of roots	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Species	1	35.79	< 0.0001	66.03	< 0.0001	108.69	< 0.0001	116.81	< 0.0001	17.75	0.0001	97.36	< 0.0001	63.48	< 0.0001
Watering regime	2	13.16	< 0.0001	8.28	0.0005	17.96	< 0.0001	23.55	< 0.0001	2.35	0.1006	24.18	< 0.0001	19.36	< 0.0001
Time	1	31.47	< 0.0001	19.57	< 0.0001	99.68	< 0.0001	130.47	< 0.0001	7.11	0.0089	76.16	< 0.0001	54.43	< 0.0001
Time: Watering regime	2	7.45	0.0009	4.42	0.0143	9.25	0.0002	15.46	< 0.0001	1.84	0.164	7.92	0.0006	4.69	0.0112
Time: Species	1	8.18	0.0051	3.71	0.0569	47.7	< 0.0001	78.26	< 0.0001	7.7	0.0065	37.1	< 0.0001	22.7	< 0.0001
Watering regime: Species	2	5.51	0.0053	5.58	0.005	15.8	< 0.0001	19.29	< 0.0001	0.8	0.4542	17.23	< 0.0001	13.86	< 0.0001
Time: Watering regime: Species	2	4.74	0.0107	4.29	0.0162	14.17	< 0.0001	23.3	< 0.0001	0.89	0.4122	8.82	0.0003	4.64	0.0116
Variance block		0.003		1.57		0.004		0.0004		1.04		0.0007		0.0002	
Variance residual		45.74		8.07		42.78		6.24		5.34		10.2		4.06	

Overall, *S. sisymbriifolium* showed the highest values for fresh and dried weight of stems when compared with those of *S. macrocarpon* (Fig. 3). However, the positive response of *S. sisymbriifolium* to water stress became larger with 50% and 75% watering regime, when compared to *S. macrocarpon*. Similar patterns were observed for fresh and dried weight of leaves (Fig. 4) and roots (Fig. 5).

Figure 6 shows the mean relative biomass allocation (%) to roots, stems and leaves of *S. sisymbriifolium* and *S. macrocarpon* plants grown at different watering regimes (25%, 50% and 75%). Overall, significant differences were observed between roots, stems and leaves following the development stage and the watering regime. At younger stages (S1, S2), both species allocated more biomass to leaves than other parts (Fig. 6). However, at the same stage, biomass allocation to leaves was significantly higher in *S. sisymbriifolium* than *S. macrocarpon*, especially in limited water conditions (25% and 50%). As plants grew older (S3, S4), more biomass was allocated to the stems. But *S. sisymbriifolium* invested more in stems biomass than *S. macrocarpon* under the three watering regimes, at the developing stages S3 and S4 (Fig. 6).

Effect of water stress on stomatal density between the cultivated species and its wild relative

The number of stomata was not influenced by the watering regimes ($p = 0.658$; Table 3). However, it was significantly different between the species ($p = 0.001$) and leaves faces (internal and external) ($p < 0.01$). We found no significant interaction effects between these factors (Table 3).

The mean number of stomata was greater (14.16) with *S. sisymbriifolium* when compared to *S. macrocarpon* (10.46) (Fig. 7A). The evaluation of the stomatal density of leaves showed a high mean number of stomata for the internal face (14.23) whereas a significant lower number was observed for the external face (9.47) (Fig. 7-).

Discussion

We found that *S. macrocarpon* and its wild ancestor *S. sisymbriifolium* responded differently to water stress. As expected, watering regimes and date, both

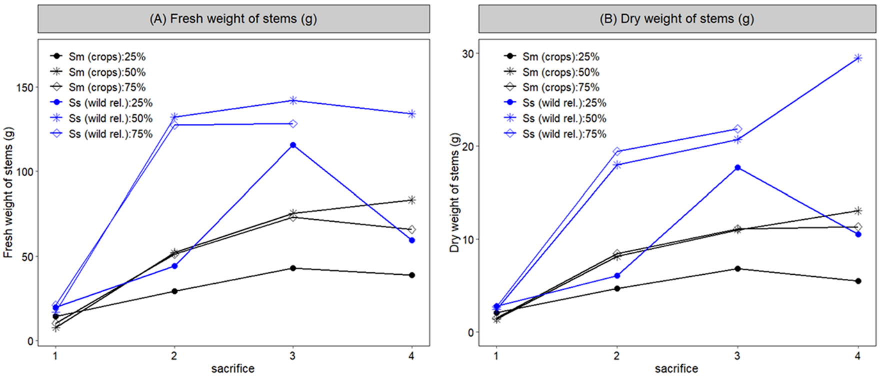

Fig. 3 Trend of mean values for fresh weight of stems (A) and dried weight of stems (B) in function of time (sacrifice) regarding watering regimes and species. Ss = *Solanum sisymbriifolium*; Sm = *Solanum macrocarpon;* Watering regimes = 25%, 50% and 75%; wild rel = wild relative. The interrupted line was generated by the death of the individuals for that specific treatment

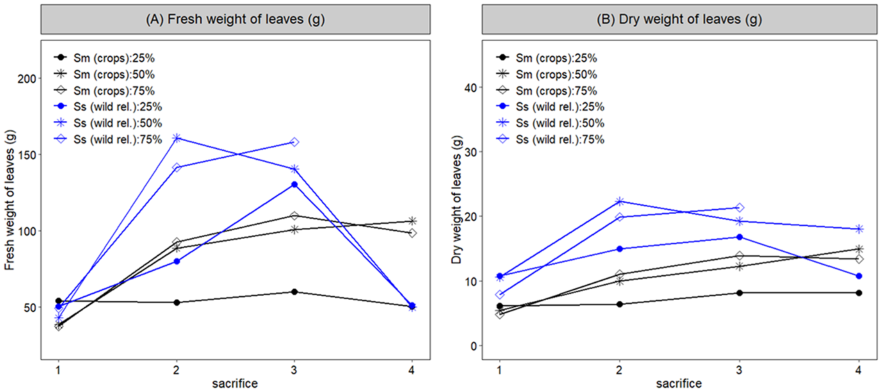

Fig. 4 Trend of mean values for fresh weight of leaves **A** and dried weight of leaves **B** with respect to time (sacrifice) regarding watering regimes and species. Ss = *Solanum sisymbriifolium* (in blue); Sm = *Solanum macrocarpon* (in black)*;* Watering regimes = 25%, 50% and 75%; wild rel = wild relative

individually or combined significantly affected seedlings' total height and their number of leaves. Water stress limited the growth rate in both species, but the effect was more pronounced with the cultivated species *S. macrocarpon*. However, no significant difference was observed for the stem collar diameter. The decline in plant growth with increased water stress has widely been reported in many crops in arid and semi-arid regions, where agriculture is mainly rain-dependent (Sharma et al. 2019). Limited resources would induce functional adjustments at the whole plant level, much consistently with its ability to acquire the limiting resource (Freschet et al. 2018). Indeed, *S. sisymbriifolium* as many *Solanum* species is native to Central and South America (Jagatheeswari 2014), where it has therefore regularly been exposed to harsh environmental conditions. The observed performances of the species could be explained by its inbuilt tolerance capacity to the harsh environmental conditions (for instance high thermal temperature, extreme drought due to low precipitations) (Kouassi et al. 2021) that occur in its center of origin (Jaeger 1986). Like many *Solanum* species, *S. sisymbriifolium* is a perennial shrub, with hairy leaves and stems (Sahu et al. 2017) which potentially offer some characteristics that would play a substantial role in lowering water losses and heat stress. Changes at morphological, physiological, and even molecular occurring in stressed plants have been studied repeatedly (Blanchard-Gros et al. 2021; Marco et al. 2015; Sharma et al. 2019). Drought as an abiotic stress can adversely affect growth in plants, their development and even chances of survival (Dresselhaus and Hückelhoven 2018; Mibei et al. 2017; Zayova et al. 2017).

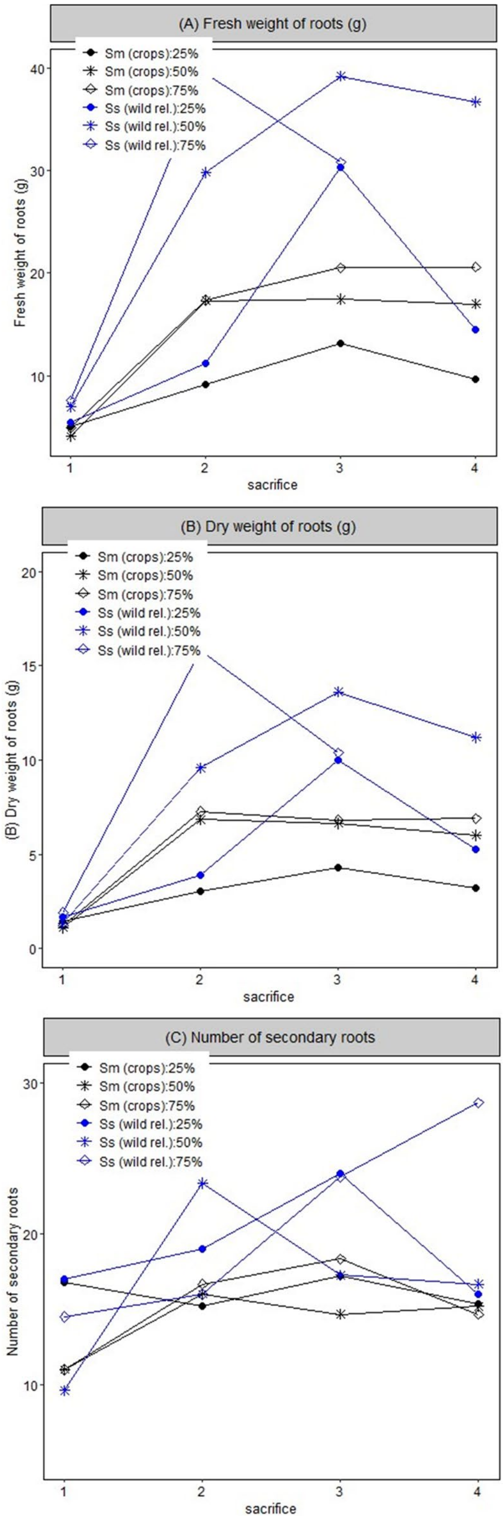

Fig. 5 Trend of mean values for fresh weight of roots **A**, dried weight of roots **B** and number of secondary roots **C** in function of time (sacrifice) regarding watering regimes and species. Ss = *Solanum sisymbriifolium*; Sm = *Solanum macrocarpon*; Watering regimes = 25%, 50% and 75%; wild rel = wild relative

Several authors also reported that plastic adjustment would be under the control of a set of genes that play a key role in activating plants defense strategies (Egea et al. 2018; Kapazoglou et al. 2023; Wu et al. 2019). Our result is in accordance with previous research that gave a comprehensive overview on the likely response of *Solanum* species to drought stress. For instance, Sseremba et al. (2018) evaluated the stability of the cultivated *Solanum aethiopicum* Shum under varied water deficit stress levels, and found a negative response in the species growth. Similarly, Coleman (2008) demonstrated that the wild species *Solanum gandarillasii* is much tolerant to drought stress compared to the cultivars. In addition, Plazas et al. (2022) assessed the tolerance to water stress in eight wild relatives of eggplant and found a large diversity in the species response to drought. Blanchard-Gros et al. (2021) also reported varied responses between *S. chilense* and the cultivated *S. lycopersicum*, with the lowest yield reduction recorded in the wild *S. chilense* species. Our finding therefore supports our first assumption, and our suggestion that wild and cultivated *Solanum* species respond differently to water stress.

Artificially induced drought increases biomass to leaves of both *S. sisymbriifolium* and *S. macrocarpon* at younger stages (S1, S2). The tendency changed with a shift of biomass in favour of stems, compared to the other plants' parts as seedlings grow larger (S3, S4). However, this observation was more pronounced in the wild species *S. sisymbriifolium* than its cultivar *S. macrocarpon*. *S. sisymbriifolium* therefore, demonstrated better performances regardless of water supply, supporting the second hypothesis that wild *Solanum* species adapt better to water shortage. These findings are consistent with previous works which provided a large variation in biomass allocation patterns among plants in response to drought (Bhatt et al. 2014; Cella Pizarro and Bisigato 2010; Poorter et al. 2015, 2012). According to Poorter et al. (2012), there is evident difference between fast-growing species and slow-growing species, indicating that species

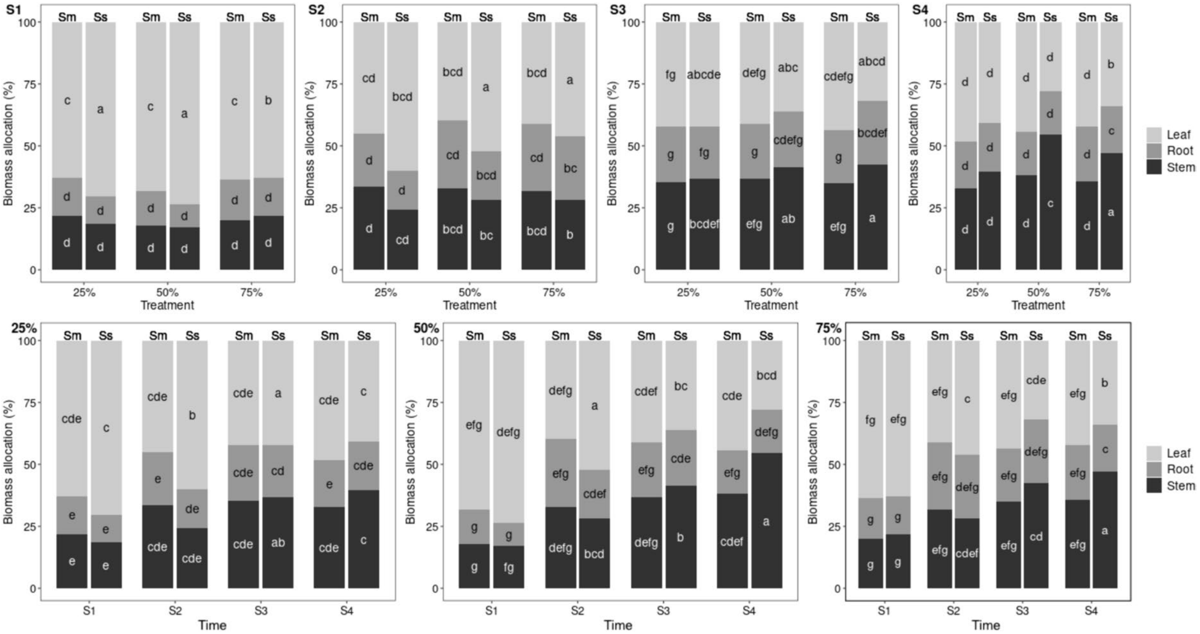

Fig. 6 Mean relative biomass allocation (%) to roots, stems and leaves of *Solanum sisymbriifolium* (Ss) *and S. macrocarpon* (Sm) plants grown at three watering regimes 25%, 50% and 75%. Different letters show significant differences in biomass allocation across plant parts and watering regimes for each time (sacrifice) (post-hoc comparisons among plant parts × water × species). S1 = time 1; S2 = time 2; S3 = time 3; S4 = time 4

Table 3 Results from the linear mixed effects model showing the effects of watering regimes, species and leaves faces on mean number of stomata

Source of variation	Degrees of freedom	Mean number of stomata	
		F	*p*
Species	1	10.94	0.0014
Water regime	2	0.42	0.6583
Face	1	23.35	< 0.001
Species: water regime	2	0.47	0.6294
Species: face	1	0.01	0.9191
Water regime: face	2	0.33	0.7201
Species: water regime: face	2	0.35	0.7082
Block variance		2.49	
Residual variance		22.63	

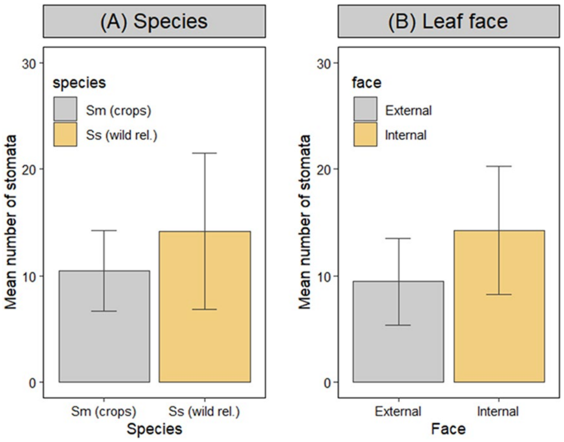

Fig. 7 Mean number of stomata in function of species **A**, leaves face **B**. *Ss* = *Solanum sisymbriifolium*; *Sm* = *Solanum macrocarpon*; *Int* = internal face; *Ext* = external face: wild rel = wild relative

identity (life history) might also highly affect physiological modifications such as allocation of biomass (Chen et al. 2019; Tilman 1988). Indeed, fast growing species invest at younger stages, either more biomass to leaves when the limiting resource is located above the ground, for an improvement of light capture, and thus the optimization of photosynthetic activities (carbon assimilation), or more biomass to roots when the limited resource is located below the ground. Lower water availability would reduce water uptake per unit roots mass, and consequently, decreases plant transpiration. In other words, the tolerance to water stress in plant species strongly depends on the roots' efficiency in accessing the limiting resource, and their ability to avoid water losses especially in the leaves through the reduction of respiration process. Surprisingly, no significant change was found in the root biomass of our *Solanum* species grown under limited-water conditions (25% and 50%), demonstrating that the species biomass partitioning did not follow the optimal partitioning theory which posits that plants should allocate more biomass to the parts that have limited access to resources (Poorter and Nagel 2000). Henceforth, we suspect that either the applied watering regime was most probably not enough to induce strong stress in plants, or root development has been hindered due to the plastic pots capacity. Generally, herbaceous species possess a likely freedom to modify their biomass distribution (functional equilibrium theory), contrarily to tree species that have widely been reported to maintain the relationship between the above and the below-ground parts (Poorter et al. 2015). Indeed, according to this theory, plants change the physiological activity of leaves, stems and roots regarding the available above and below ground resources such as light, CO2, water and nutrients. Besides, authors also highlighted that plants invest more biomass to a mechanical support and less in photosynthetic tissues with age/size (Müller et al. 2000; Poorter et al. 2015), supporting our finding that *S. sisymbriifolium* seedlings allocated more resource to the stems as they grew older, regardless of watering regimes probably for a need of a strong mechanical stability. Our findings are therefore, in line with those of Blanchard-Gros et al. (2021) who found that resistance to drought in *Solanum* species is associated with an ensemble of morphological, physiological and genetic traits instead of a single trait.

Water deficit affects the stomatal development in plants. For instance, research by Boguszewska-Mańkowska et al. (2018) and Pieczynski et al. (2013) on cultivated potato found that the higher the number of stomata, the more tolerant the genotypes. The evaluation of the stomatal density revealed a substantial difference between wild and cultivated species and, a great number of stomata was found in the internal face compared with the external face of leaves. Under the same watering regime, the wild species *S. sisymbriifolium* had the greatest number of stomata per unit of leaf area. Actually, plant leaf area relates with incident light capture, respiration and photosynthesis activities (Lehnebach et al. 2018). Furthermore, stomatal control is strongly related to their ability in managing stomatal conductance, photosynthetic and transpiration mechanisms (McAdam and Brodribb 2012). We thereby assume that *S. sisymbriifolium* as a wild species, possesses a high number of stomata per unit leaf area and better controls stomatal conductance under water stress while withstanding the water shortage, compared to *S. macrocarpon*. In a comparative study of three genotypes of the wild potato *S. kurtzianum*, Ibañez et al. (2021) found a pronounced decrease in the stomatal conductance of the most tolerant genotype in response to water stress, which the authors suggested may be associated with the high stomatal density and decreased stomatal size. Tanaka et al. (2013) also reported a high number of stomata in plants, enhancing the rate of photosynthesis, and concluded that a stomatal density could be a specific characteristic of an improved photosynthetic capacity. Our results are in line with our assumption and demonstrate that *S. sisymbriifolium* has a better control of transpiration and photosynthesis under limited water conditions than *S. macrocarpon*. These authors also deepened our understanding about the relationship between water availability and plants photosynthetic features. They demonstrated that drought induces the decrease of photosynthetic pigments in plants, resulting from the degradation of thylakoid membranes with several impacts on photosynthesis activity. In other words, the thylakoid membranes play an important role by serving as a basis for absorption, translocation as well as transformation of light in chloroplasts during photosynthesis process (Prasad et al. 2008). Since our study did not look at the effects of water stress on stomata size, further experimental analysis is needed to evaluate the likely existing relationship between stomata size and the responses of studied *Solanum* species under water stress.

Conclusion

Our study demonstrated that water stress substantially limited plant growth and led to significant variations of biomass allocation. *S. sisymbriifolium* showed better performances compared to its cultivated *S. macrocarpon*. In addition, we observed changes at seedlings level following the development stage (plant size), with a shift in biomass allocation, probably to withstand the adverse conditions. Altogether, the wild *S. sisymbriifolium* is more drought-tolerant than *S. macrocarpon*. It is therefore possible to introduce the species as an interesting candidate into future breeding programs, and improvement of the adaptability capabilities of the cultivated species. However, this study is a pilot one and we recommend further research with the others CWRs to confirm the behaviour of species.

Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by Ahuéfa Mauricel Kégbé. Data analysis was performed by Bruno Enagnon Lokonon, Kolawolé Valère Salako and Ahuéfa Mauricel Kégbé. The first draft of the manuscript was written by Ahuéfa Mauricel Kégbé All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the present study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that are relevant to the content of this article.

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