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Authors: Lahbouki, Soufiane, Ech-chatir, Lahoucine, Er-Raki, Salah, Outzourhit, Abdelkader, and Meddich, Abdelilah

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Article

Improving drought tolerance of *Opuntia ficus-indica* under field using subsurface water retention technology: changes in physiological and biochemical parameters

Soufiane Lahbouki[a,b,c], **Lahoucine Ech-chatir**[a,b,d], **Salah Er-Raki**[a,d], **Abdelkader Outzourhit**[c], **and Abdelilah Meddich**[a,b]

[a]Center of Agrobiotechnology and Bioengineering, Research Unit labelled CNRST (Centre AgroBiotech-URL-CNRST-05), "Physiology of abiotic stresses" team, Cadi Ayyad University, Marrakech 40000, Morocco; [b]Laboratory of Agro-Food, Biotechnologies and Valorization of Plant Bioresources (AGROBIOVAL), Department of Biology, Faculty of Science Semlalia, Cadi Ayyad University, Marrakesh, Morocco; [c]Laboratory of Nanomaterials for Energy and Environment, Physics Department, Faculty of Sciences Semlalia, Cadi Ayyad University, P.O. Box 2390, Marrakech 40000, Morocco; [d]Laboratoire des Procédés pour l'Energie Durable et Environnement (ProcEDE), Département de Physique Appliquée, Faculté des Sciences et Techniques Guéliz, Université Cadi Ayyad, B.P. 549, Guéliz Marrakech, Morocco

Corresponding author: **Abdelilah Meddich** (email: a.meddich@uca.ma)

Abstract

The prickly pear (*Opuntia ficus-indica*) is an essential economic and ecological medicinal plant in arid and semi-arid areas, especially in Morocco, where water scarcity affects its survival and growth. Evidence suggests that subsurface water retention technology (SWRT) may enhance crops' drought resistance. A field experiment was conducted to explore SWRT application effects on cactus cladodes' growth and physiological and biochemical performance under drought conditions. Two water regimes were applied (rainfed conditions; irrigated with 4 L of water twice a week) with two treatments (without SWRT; with SWRT). The results showed that cactus cladodes' growth and physiological and biochemical parameters cultivated for 8 months were negatively affected by drought. Drought-exposed cactus cladodes under SWRT application showed an increase in surface area and cladode stomatal densities by 65% and 29%, respectively, compared with no SWRT. This technology reduced drought-induced oxidative stress by mitigating malondialdehyde and hydrogen peroxide excess by 22% and 17%, respectively. Moreover, lower levels of enzymatic and nonenzymatic antioxidant activities were concluded, and soil organic matter and assimilable phosphorus contents were enhanced. In conclusion, our findings highlighted SWRT's positive impacts on the tested parameters, thus presenting it as a promising technology for cactus growth and development improvement under water deficiency.

Key words: cactus, drought stress, subsurface water retention technology, growth, stomatal conductance, biochemical responses

Résumé

La figue de barbarie (*Opuntia ficus-indica*) est une plante médicinale indispensable à l'économie et à l'écologie des régions arides et semi-arides, surtout au Maroc, où le manque d'eau en affecte la survie et la croissance. Apparemment, les techniques de rétention souterraine de l'eau (TRSE) pourraient rendre cette culture plus résistante à la sécheresse. Les auteurs ont procédé à une expérience sur le terrain afin de préciser les effets de telles techniques sur la croissance des cladodes du cactus, ainsi que sur leur performance physiologique et biochimique en période de sécheresse. Dans cette optique, ils ont combiné deux régimes hydriques (culture sèche, irrigation avec quatre litres d'eau deux fois par semaine) à deux traitements (TRSE ou pas). Les résultats de l'expérience indiquent que la sécheresse a une incidence négative sur la croissance ainsi que sur les paramètres physiologiques et biochimiques des cladodes après huit mois de culture. Les cladodes exposés au régime sec avec TRSE présentaient une plus grande surface (65 %) et des stomates plus denses (29 %) que ceux des cactus cultivés sans TRSE. La rétention souterraine d'eau réduit le stress oxydatif causé par la sécheresse en diminuant respectivement l'excédent de malonaldéhyde et de peroxyde d'hydrogène de 22 % et de 17 %. Les auteurs ont aussi relevé une baisse de l'activité des antioxydants, enzymatiques ou pas, parallèlement à une hausse de la quantité de matière organique et de phosphore assimilable présents dans le sol.

Ils en concluent que les TRSE ont un impact positif sur les paramètres examinés et que ces techniques pourraient améliorer la croissance ainsi que le développement du cactus quand il y a pénurie d'eau. [Traduction par la Rédaction]

Mots-clés : cactus, stress de la sécheresse, technique de rétention souterraine de l'eau, croissance, conductance des stomates, réaction biochimique

Introduction

Prickly pear (*Opuntia ficus-indica* (L.)) is a xerophytic and perennial succulent plant of the Cactaceae family that holds an extensive ecological and economic value. Its cladodes and fruits are a source of nutrients for humans and livestock (Barba et al. 2020; Dubeux et al. 2021; Nassrallah et al. 2021). The cactus is considered a multifunctional species with a great adaptation capacity to different uses and extreme growing environments (Apollon et al. 2020; Nassrallah et al. 2021). Notably, it has ability to adapt to semi-arid ecosystems characterized by limited water resources and areas significantly impacted by vegetation depletion, organic matter (OM) loss, and the progressive reduction of soil fertility (Vaezi et al. 2017; Apollon et al. 2020). This adaptation to arid and semi-arid climates makes it an interesting agricultural resource that can also be considered a valuable plant food in these regions (Kumari and Patil 2017; Arba 2020). In Morocco, the total area of cactus has increased from 45 000 ha in 1990 to 88 200 ha in 2019, with a fruit production exceeding 50 000 tons per year (MAFRDWF 2019; Ramdani et al. 2021).

However, cactus production is limited by many various abiotic stresses such as drought (Arba et al. 2018). The negative effects of a long dry period on the yield, growth, and physiological and biochemical parameters of cactus pear have been previously documented (Scalisi et al. 2016; Khodaeiaminjan et al. 2021; Mayer et al. 2021). For instance, many studies showed that after 2 months without irrigation, the size and growth rates of developing cladodes, relative water content, malic acid accumulation, parenchyma thickness, photosynthetic activity, and chlorophyll content were reduced (Scalisi et al. 2016; Campos et al. 2021). Given the constraints, it is important to improve the performance of cactus in semi-arid areas while ensuring that the management of water resources is the primary focus for sustainable agriculture management.

A new technology applied for water conservation in the soil is named subsurface water retention technology (SWRT). This technology uses a polyethylene film installed in a container or U-shape in the root zone of the plants (Guber et al. 2015; Pari et al. 2022). SWRT conserves water and nutrients on top of the membrane and decreases deep drainage (Kavdir et al. 2014; Nkurunziza et al. 2019). The membrane could also improve water availability by helping to retain water near the root zone and thus increasing the efficiency of water use by plants (Guber et al. 2015). Therefore, SWRT improves plant nutrition, morphology, and yield under various abiotic stresses, especially during drought (Guber et al. 2015; Aoda et al. 2021). So far, a few studies have focused on mitigating the negative effects of water stress on plant growth using the SWRT (Kavdir et al. 2014; Miller and Smucker 2015; Aoda et al. 2021). For example, a study conducted by Kavdir et al. (2014) showed that SWRT application mitigated drought, increasing cotton fibers by 50%. On the other hand, Aoda et al. (2021) reported that SWRT application increased the weight of tomato and spicy peppers by 15% and 25%, respectively, as well as water use efficiency and consequently crop yield. However, these earlier studies remain limited to soil parameters, plant growth, and yield. Furthermore, no study has assessed the effects of SWRT application on physiological and biochemical properties of crassulacean acid metabolism (CAM) plants under drought stress in semi-arid regions. Therefore, this study aimed to assess for the first time the effectiveness of SWRT on growth, soil fertility, and plant physiological and biochemical properties of newly developed *O. ficus-indica* cladodes grown under field conditions in semi-arid regions of Morocco.

Materials and methods

Experimental site description

Field experiments were conducted at a private farm localized in the SAADA district (31°37′39.9″N and 08°07′46.7″W), Marrakesh, Morocco, from November 2019 to July 2020. The climate is semi-arid, typically Mediterranean, with an average annual precipitation of about 250 mm. The air temperature is very high in summer (38 °C) and low in winter (5 °C) (Er-Raki et al. 2010). The mean annual value for ET_0, calculated using the FAO-PM equation, is about 1600 mm (Allen et al. 1998). The soil at the experimental site is a silty clay loam (52% of sand, 24% of clay, and 24% of loam) with a bulk density of 1.4 g/cm (Kharrou et al. 2011).

Experimental plan and treatment application

Two-year-old cladodes of *O. ficus-indica* (41.0 ± 0.6 cm in length, 15.1 ± 0.7 cm in width) were utilized in the experiment. The field trial had a randomized plot design with rows of cactus spaced 1 m apart. Each row had 10 plants spaced 1 m apart along the row. Two treatments differentiated by SWRT application and water regimes were performed. Two water regimes were applied throughout the experiment: Unirrigated plants (grown under rainfed conditions) and irrigated plants with 4 L of water twice a week.

To control the volume of irrigation water, a drip irrigation system was used for each row containing drippers of 2 L/h for the irrigated plants. Therefore, the experiment included two treatments for each applied water regime and 10 replicates per treatment:

(1) Control plants without SWRT labeled as (SWRT−)
(2) Plants with SWRT labeled as (SWRT+).

The experimental design showing the distribution of the treatments in the study area is presented in Fig. S1.

Measurements

Cactus growth studies

At harvest, daughter cladodes and roots were separated from the mother cladodes, and growth parameters (cladode area, root length, cladode, and root dry weight) were measured for both roots and newly developed cladodes.

Physiological parameters

The stomatal conductance (gs) was measured before a harvest day at every 2 h intervals from 8 pm to 8 am using a porometer (Leaf porometer, model SC1), due to nocturnal stomatal opening, as described by Scalisi et al. (2016).

The stomatal measurements were evaluated using the epidermal layer removed from young cactus cladodes harvested at 2 am. Thereafter, the state and density of stomata were determined using a scanning electron microscope (Tescan Vega3, Brno, Czech Republic).

Biochemical parameters

The total acid concentration of young cladodes was determined according to the method described by Ojeda-Pérez et al. (2017). From each sample, 10 mg was ground in 20 mL of 60% ethanol, boiled for 5 min, and then titrated with 0.1 N NaOH.

The total sugar content (TSS) was determined based on the Dubois et al. (1956) method using extracts of 0.1 g of fresh young cladodes ground with liquid nitrogen, homogenized with 4 mL of ethanol (80%), and boiled in a water bath at 95 °C for 3 min. Sample aliquots (0.25 mL) were mixed with 0.25 mL of phenol and 1.25 mL of concentrated sulfuric acid. The mixture was allowed to stand for 10 min. Total soluble sugar content was determined by measuring the absorbance at 485 nm.

Proline content was assessed using the Carillo et al. (2008) method. Samples of each fresh young cladode (100 mg) were homogenized in 4 mL of 40% ethanol, after which the homogenate was stored overnight at 4 °C. Afterward, 0.5 mL of solution was put into reaction with 1 mL of a solution containing 60% acetic acid, 1% ninhydrin, and 20% ethanol in a test tube for 20 min at 90 °C, followed by stopping the reaction by immersing the tubes in an ice bath. The absorbance was read at 520 nm.

Malondialdehyde (MDA) content in cactus cladodes was determined according to the method of Rao and Sresty (2000). 0.25 g of frozen cladodes subsamples were homogenized with 10 mL of 0.1% (*w*/*v*) trichloroacetic acid (TCA) and centrifuged at 18 000*g* for 10 min. Two milliliters of supernatant were mixed with 2 mL of 20% TCA containing 0.5% thiobarbituric acid. The mixture was incubated at 100 °C for 30 min and then cooled in ice to stop the reaction. The absorbance was measured at 532 nm. The content of MDA was expressed as nmol MDA g^{-1} of dry weight (DW).

Hydrogen peroxide (H_2O_2) was determined as described by Velikova et al. (2000). From fresh cladode samples, 0.25 g were homogenized in 5 mL of 10% (*w*/*v*) TCA and centrifuged at 15 000*g* for 10 min. 0.5 mL of the supernatant was then mixed with 0.5 mL of potassium phosphate buffer (10 mmol/L, pH 7) and 1 mL of potassium iodide (1 mol/L). Afterward, the mixture was incubated for 1 h in the dark, and absorbance values were taken at 390 nm.

To evaluate the protein content and antioxidant enzyme activity, samples of cladode powder (0.1 g) were homogenized in 5 mL of a solution containing 0.1 mol/L potassium phosphate buffer (pH 7.0), 0.1 g polyvinylpolypyrrolidone, and 0.1 mmol/L ethylenediaminetetraacetic acid (EDTA). The homogenate was then centrifuged at 18 000*g* at 4 °C for 15 min, and the extract was stored at −20 °C (Ait-El-Mokhtar et al. 2019).

The protein content in cactus cladodes was determined using the Bradford (1976) method. The absorbance was taken at 595 nm.

Superoxide dismutase (SOD) was assayed spectrophotometrically by recording the absorbance at 560 nm, according to the method of Beyer and Fridovich (1987), based on the ability to inhibit the photochemical reduction of *p*-nitrobluetetrazolium by SOD enzyme. The activity of SOD was expressed as unit min^{-1} mg protein $^{-1}$.

Catalase activity (CAT) was determined by the method of Aebi (1984), where a reduction in H_2O_2 level was tracked spectrophotometrically at 240 nm for 60 s. Following the protocol, the reaction mixture was composed of 0.1 mol/L potassium phosphate buffer (pH 7.0), 0.1 mmol/L EDTA, 20 mmol/L H_2O_2, and 100 μL of extract in a volume of 100 μL.

Ascorbate peroxidase activity (POX) was measured by following its decrease at 290 nm for 1 min as described by Nakano and Asada (1981). The assay solution contained 100 μL of extract sample, 50 mmol/L potassium phosphate buffer (pH 7.0), 0.5 mmol/L H_2O_2, and 0.1 mmol/L ascorbate.

To evaluate the contents of total phenols (TPC) and total flavonoids (TFC), an extraction of cactus cladodes was performed from finely powdered cladodes samples dried in the oven at 75 °C for 72 h. In 50 mL of methane (80%), 5 g of plant extracts were immersed and shaken with an electric stirrer for 48 h. Thereafter, the obtained mixture was filtered using a Buckner funnel and a Whatman No. 1 filter paper (Santos-Zea et al. 2011).

Total phenol content was determined spectrophotometrically by recording the absorbance at 760 nm using the Folin–Ciocalteu test (Singleton and Rossi 1965). A methanol extract volume of 250 μL was poured into a test tube with 2.5 mL of distilled water, mixed with the Folin–Ciocalteu reagent for 250 μL, and incubated at room temperature for 3 min. A 250 μL of sodium carbonate (Na_2CO_3) was added and kept reacting for 90 min. Total phenol content was expressed as gallic acid equivalent (GAE) per g dry weight (mg GAE g^{-1} DW).

Total flavonoids content was assessed using the aluminum trichloride as described by Tohidi et al. (2017). The methanol extract (50 μL) was combined with 30 μL of a 5% $NaNO_2$ solution and allowed to stabilize for 6 min before adding 60 μL of 10% aluminum chloride ($AlCl_3$) and incubated for 5 min. Afterward, the mixture reaction was stopped by spiking 2 mL of 1 mol/L sodium hydroxide. Then, the final solution was made up to 1000 μL with distilled water. The absorbance of the solutions was then measured at 510 nm, and the results were expressed as mg quercetin equivalents (QE) per g dry weight (mg QE g^{-1} DW).

Table 1. Effect of SWRT on growth parameters of cactus cultivated under unirrigated and irrigated conditions for both treatments: with (SWRT+) and without SWRT (SWRT−).

Treatments		Surface area (cm^2)	Root length (cm)	Number of cladodes	Cladode dry weight (g)	Root dry weight (g)
Unirrigated plants	SWRT−	62.1 ± 4.96^{d}	13.32 ± 2.88^{d}	1.66 ± 0.44^{c}	1.11 ± 0.14^{c}	0.35 ± 0.03^{d}
	SWRT+	102.45 ± 8.65^{c}	17.21 ± 1.11^{c}	2.50 ± 0.71^{b}	2.24 ± 0.52^{b}	0.51 ± 0.07^{c}
Irrigated plants	SWRT−	197.47 ± 15.32^{a}	24.39 ± 1.41^{b}	4 ± 0.74^{a}	3.61 ± 0.74^{a}	1.12 ± 0.09^{a}
	SWRT+	182.62 ± 7.47^{ab}	27.11 ± 1.74^{a}	4 ± 0.89^{a}	3.55 ± 0.30^{a}	0.99 ± 0.03^{ab}

Note: SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data represent the means ± standard error (SE) ($n = 6$). Means in the same column with different letters indicate significant differences at $P \leq 0.05$.

Soil physico-chemical analyses

The soil physico-chemical parameters, such as pH, electrical conductivity (EC), total organic carbon (TOC), OM, and assimilable phosphorus (AP), were determined using soil samples taken near the root system, which were air-dried and sieved (2 mm) for the subsequent analyses. Then, we evaluated pH and EC on a 1/5 (*w*/*v*) diluted soil suspension. TOC and OM were measured according to the procedures described by Aubert (1978). Lastly, AP was determined by the method of Olsen and Sommers (1982).

Statistical analysis

Data were subjected to statistical analysis using factorial ANOVA in SPSS 23.0 for Windows. The variables are based on the mean values of six replicates ± standard error (SE). Comparisons between means were evaluated using Tukey's test separately calculated at $P \leq 0.05$.

Results

Effect of SWRT on cactus growth

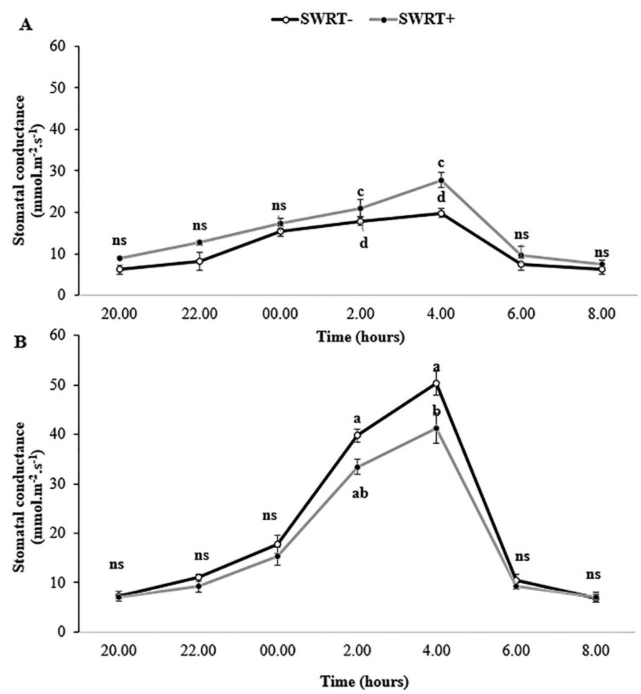
The results of the effect of drought combined with SWRT application on growth parameters are shown in Table 1. The drought had a significant negative effect on plant growth. For example, a 218% decrease was recorded in the cladode area for unirrigated plants compared with irrigated plants. However, the application of SWRT minimized the negative effect of drought. The application of SWRT increased the surface area, number of newly developed cladodes, and dry part of roots and cladodes by 65%, 51%, 102%, and 46%, respectively, compared with the control, resulting in better development of cactus cladodes.

Effect of SWRT on physiological parameters in cactus cladodes

The findings in Fig. 1 suggested that drought negatively affects the values of gs. The application of SWRT significantly affected gs variations in the unirrigated plants starting at 2 am. However, SWRT application significantly alleviated the negative effect of drought at 4 am by 40% compared with control plants. In addition, the large values of gs in all treatments were recorded at 4 am.

Drought stress significantly reduced the level of stomatal densities in cactus cladodes compared with irrigated plants. However, SWRT application in cactus cladodes significantly mitigated the negative impact of drought conditions by 29% compared with the control plants (Fig. 2A). In contrast, the data presented in Fig. 2B show that drought delayed stomatal opening in unirrigated plants until 4 am, whereas SWRT application resulted in a stomatal opening at 2 am, similar to that of irrigated plants.

Fig. 1. Stomatal conductance (gs) of cactus pads grown under (A) unirrigated and (B) irrigated conditions subjected to treatments. SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data presented are means (SD). Means followed by different letters indicate significant differences at $P \leq 0.05$.



Effect of SWRT on biochemical parameters in cactus cladodes

Total soluble sugar in cladodes increased with drought stress compared with that in irrigated cladodes. Additionally, the application of SWRT reduced the TSS in unirrigated plants by 17% compared with control plants (Fig. 3A). On the other hand, the cladode protein content was reduced in the unirrigated plants compared with the irrigated plants. Besides, the application of SWRT under the unirrigated plants showed a positive effect on the cladode protein content in comparison with the control plants (Fig. 3B).

Fig. 2. (A) Stomatal density, (B) scanning electron microscopy of stomata (200×) in cactus pads grown under unirrigated and irrigated conditions submitted to different treatments. SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data presented are means (SD). Means followed by different letters indicate significant differences at $P \leq 0.05$.

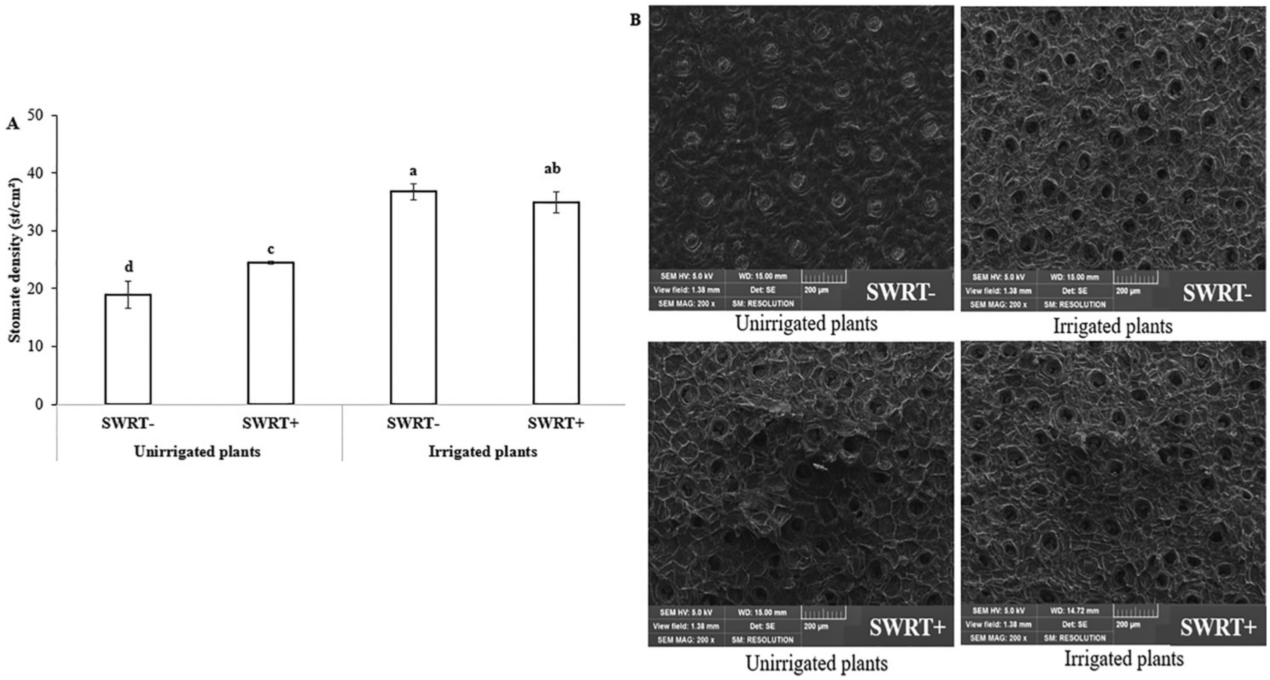


Fig. 3. (A) Total chlorophyll content, (B) protein, (C) proline content, and (D) total acid concentration in cactus pads grown under unirrigated and irrigated conditions submitted to different treatments. SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data presented are means (SD). Means followed by different letters indicate significant differences at $P \leq 0.05$.

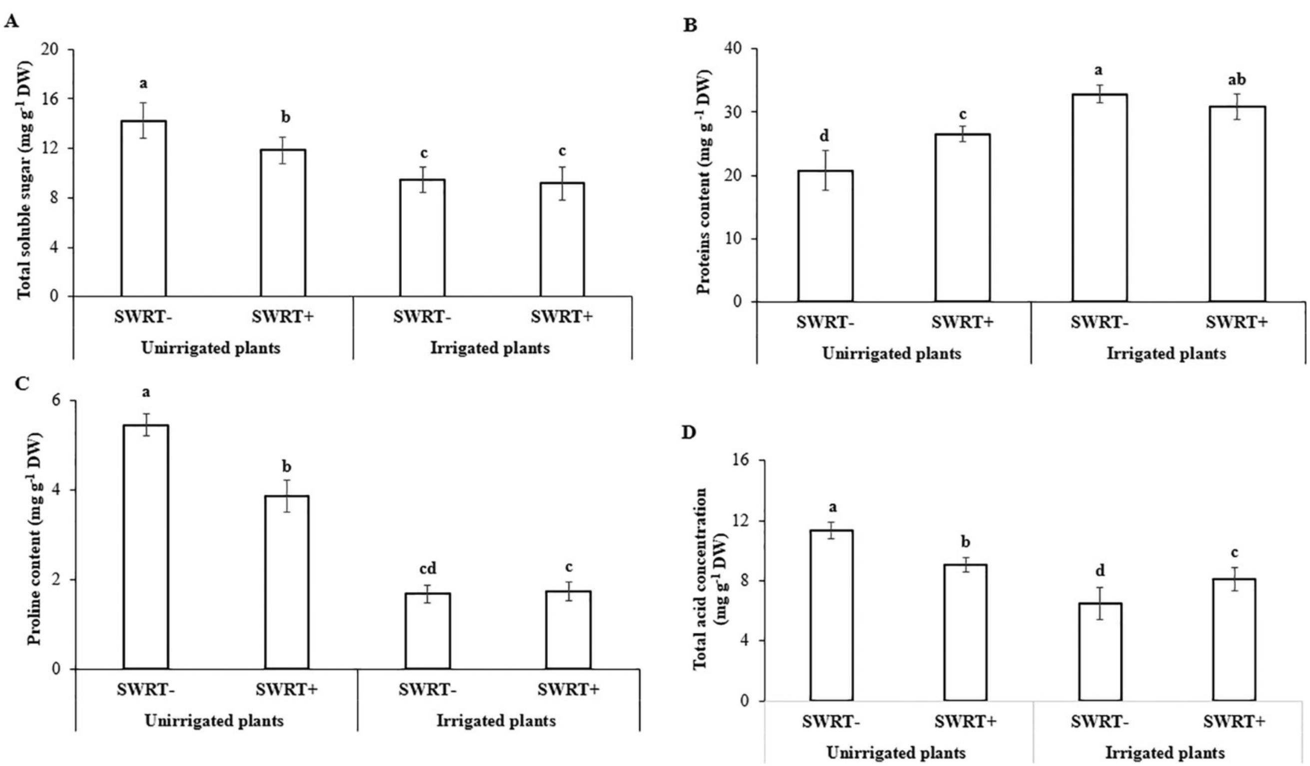


Table 2. Effect of SWRT on MDA and H_2O_2 content of cactus cultivated under unirrigated and irrigated conditions.

Treatments		MDA (nmol g^{-1} DW)	H_2O_2 (nmol g^{-1} DW)
Unirrigated plants	SWRT−	25.36 ± 0.93^{a}	24.38 ± 1.24^{a}
	SWRT+	19.74 ± 1.41^{b}	20.32 ± 1.35^{b}
Irrigated plants	SWRT−	11.15 ± 1.35^{cd}	12.82 ± 0.62^{c}
	SWRT+	12.84 ± 1.70^{c}	12.74 ± 1.65^{c}

Note: SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data represent the means ± standard error (SE) (n = 6). Means in the same column with different letters indicate significant differences at $P \leq 0.05$.

As shown in Figs. 3C and 3D, clear differences were noted in proline content and malic acid concentration between irrigated and unirrigated plants. For unirrigated plants, proline content and malic acid accumulation increased by 69% and 43%, respectively, compared with irrigated plants. However, under drought stress conditions, SWRT application decreased the negative impact of drought by reducing proline content and malic acid accumulation by 29% and 20%, respectively, compared with control plants.

The results showing the oxidative stress marker accumulation in cactus cladodes under both water regimes with/without SWRT application are presented in Table 2. Exposure of cactus plants to drought significantly increased MDA and H_2O_2 by 56% and 47%, respectively, compared with irrigated plants. However, the application of SWRT significantly reduced the accumulation of MDA and H_2O_2 under drought conditions by 22% and 17%, respectively, compared with control plants. Furthermore, there was no difference in the accumulation of MDA and H_2O_2 in cactus cladodes under irrigated treatment in the presence and absence of SWRT.

Drought stress had a significant effect on antioxidant enzyme activities (Fig. 4). Cactus cladodes under drought conditions showed higher SOD, CAT, and POX activities than irrigated plants. However, the application of SWRT, regardless of the water regime, affects the antioxidant enzyme activities. Under irrigated plants conditions, SWRT application significantly increased the antioxidant activities SOD, CAT, and POX compared with the control plants. Conversely, the application of SWRT under unirrigated conditions significantly reduced SOD, CAT, and POX activities by 26%, 16%, and 22%, respectively, compared with control plants.

Drought caused a significant increase in phenolic compounds in cactus cladodes (Fig. 5). Compared with irrigated plants, an increase was recorded in TPC and TFC by 49% and 53%, respectively, under drought conditions. Nevertheless, the SWRT application significantly affected nonenzymatic antioxidants under the same conditions by decreasing TPC and TFC by 32% and 31% in comparison with the absence of SWRT.

Effect of SWRT on soil characteristics

The soil analysis indicated that water stress deteriorated the quality of soil compared with the initial condition (Table 3). In another part, under drought stress, the use of SWRT enhanced the soil quality by inducing a reduction in soil pH and increased the EC and TOC compared with the initial condition. In addition, SWRT improved soil OM and AP by 21% and 26%, respectively, compared with the absence of SWRT.

Discussion

Arid and semi-arid regions are the most vulnerable areas to drought in the world (Zarei 2018). Drought affects the plant's physiological and biochemical processes, resulting in altered growth and development (Ait-El-Mokhtar et al. 2020). Therefore, there is a need to find less expensive techniques that can help plants mitigate the drought stress effects. As far as we know, this is the first study that describes the impact of SWRT application on drought-exposed cactus under field conditions. Moreover, exposure of cactus to drought induces both morphological and physiological changes in the plant. The present investigation revealed that growing cactus plants under drought stress negatively affected growth parameters such as cladode area, root length, and dry biomass.

Furthermore, the reduction in growth is consistent with other studies on cactus exposed to drought (Scalisi et al. 2016; Júnior et al. 2021; Quiroz et al. 2021). Under drought, cactus plants can reduce the size of cladodes, metabolic activities, and suppress the appearance of new cladodes as a strategy to avoid water loss (Zañudo-Hernández et al. 2010; Campos et al. 2021). In addition, cactus plants grown under drought conditions appeared to become healthy with the application of SWRT, and our results showed that growth parameters were significantly increased when SWRT was applied. Indeed, this technology is known for its ability to retain water and prevent its loss by percolation, thereby increasing the availability of water in the soil and then creating a better place for plant establishment (Guber et al. 2015; Almasraf and Hommadi 2018; Roy et al. 2019). The benefits of the SWRT application on plant growth are extensively studied for many plants such as tomato, spicy pepper, and maize (Nkurunziza et al. 2019; Aoda et al. 2021).

Our results also showed that drought reduced physiological parameters such as gs, density, state of stomata, and malic acid accumulation. Furthermore, cactus stomata remained closed in unirrigated plants until 4 am, possibly due to the low temperatures during this period, which decreased transpiration. As it is known, drought causes losses in photochemical activity in cactus plants, which are correlated to a reduction in malic acid consumption and a reduction in stomatal conductance, limiting the flow of CO_2 into the cells (Ojeda-Pérez et al. 2017; Jardim et al. 2021). In addition, water restrictions prevent cactus from absorbing CO_2, by

Fig. 4. (A) Superoxide dismutase (SOD), (B) catalase (CAT), and (C) ascorbate peroxidase (POX) activities in cactus pads grown under unirrigated and irrigated conditions submitted to different treatments. SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data presented are means (SD). Means followed by different letters indicate significant differences at $P \leq 0.05$.

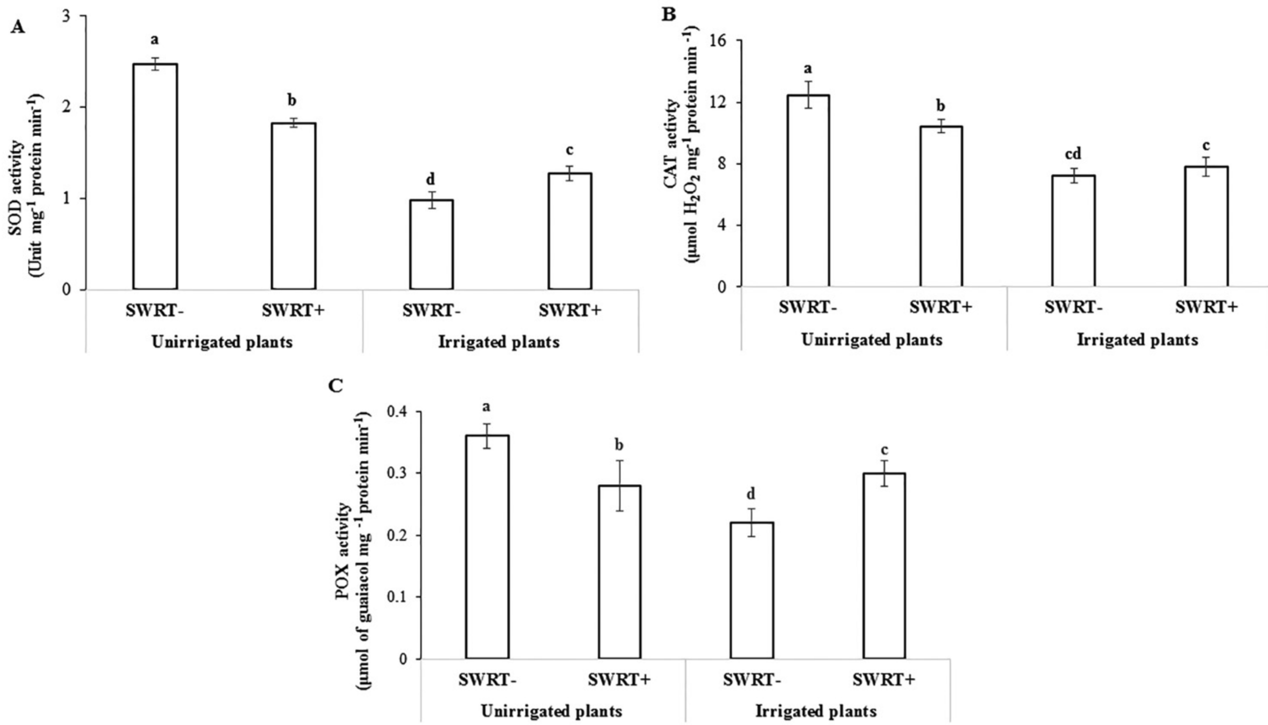
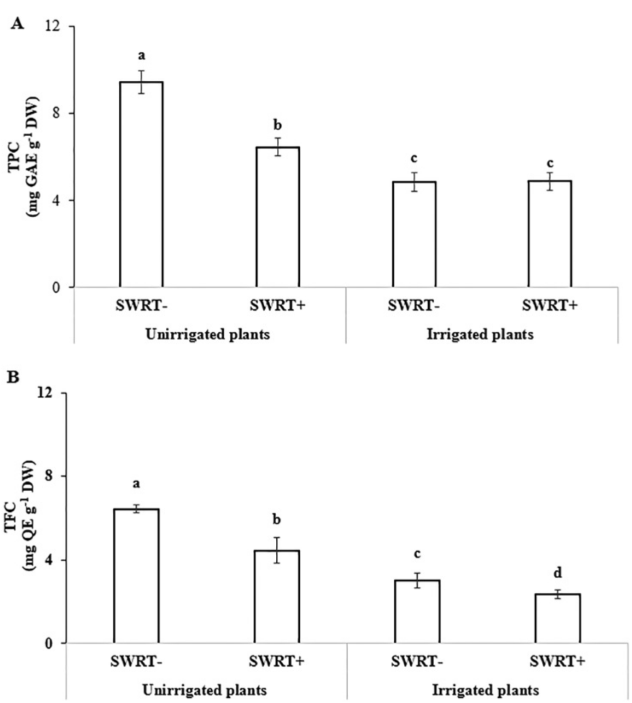


Fig. 5. (A) Total phenolic (TPC) and (B) total flavonoid (TFC) content in cactus pads grown under unirrigated and irrigated conditions submitted to different treatments. SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data presented are means (SD). Means followed by different letters indicate significant differences at $P \leq 0.05$.



closing their stomata (Aragón-Gastélum et al. 2014; Ojeda-Pérez et al. 2017). These results are in agreement with many previous studies that have shown that drought stress affects the water status and physiological parameters of cactus plants (Campos et al. 2021; Navarrete et al. 2021). The application of SWRT increases water holding capacity and also traps more nutrients (Nkurunziza et al. 2019), and both parameters are key factors in improving stomatal aperture and conductance (Bertolino et al. 2019).

Extreme drought in plants generated superoxide (O_2^-) from photosynthetic and respiratory electron leakage in chloroplast and overproduction of reactive oxygen species (ROS) (Qi et al. 2018; Sarker and Oba 2018). The ROS production is usually tracked by MDA and H_2O_2 measurements. These stress markers can cause damage to membrane lipids, proteins, DNA, coupled with a reduction in plant biomass (Liu et al. 2021). In our study, MDA and H_2O_2 contents were generally higher in unwatered plants than in watered plants. Similar findings were reported by Anli et al. (2020) and Khan et al. (2021) in their studies on date palm and rapeseed, respectively. In the present work, the application of SWRT decreased the stress markers under drought. Likewise, our study findings indicated that the application of SWRT reduces oxidative stress. The attenuation of oxidative stress can be attributed to the ability to provide continuous supplies of available water to plants by improving the soil water holding capacity and enhancing soil quality by improving carbon, OM, and AP (Guber et al. 2015; Nkurunziza et al. 2019).

Table 3. Effect of SWRT on field soil physical and chemical characteristics.

Treatments	Before experiment	After experiment			
		Unirrigated plants		Irrigated plants	
		SWRT−	SWRT+	SWRT−	SWRT+
pH	7.90 ± 0.07[a]	7.69 ± 0.04[c]	7.61 ± 0.14[b]	7.49 ± 0.11[d]	7.53 ± 0.09[de]
EC (mS cm^{-1})	1.70 ± 0.22[a]	1.82 ± 0.16[ab]	1.77 ± 0.14[ab]	1.69 ± 0.11[b]	1.72 ± 0.04[ab]
TOC (%)	0.80 ± 0.06[de]	0.82 ± 0.45[d]	1.01 ± 0.23[bc]	1.06 ± 0.11[b]	1.22 ± 0.19[a]
OM (%)	1.30 ± 0.12[e]	1.41 ± 0.23[d]	1.71 ± 0.09[bc]	1.83 ± 0.21[b]	2.09 ± 0.18[a]
AP (%)	31.00 ± 1.22[c]	26.29 ± 2.05[d]	33.25 ± 1.26[b]	33.01 ± 0.24[b]	35.36 ± 0.96[a]

Note: EC, electrical conductivity; TOC, total organic carbon; OM, organic matter; AP, assimilable phosphorus; SWRT−, absence of SWRT; SWRT+, presence of SWRT. Data represent the means ± standard error (SE) ($n = 6$). Means in the same column with different letters indicate significant differences at $P \leq 0.05$.

To avoid cellular damage due to ROS accumulation, plant responses generally follow two trends: (*i*) the production of several compatible solutes and (*ii*) the increase of nonenzymatic and enzymatic antioxidant constituents that are induced to provide secondary protection against oxidative stress (Blum 2017; Lahbouki et al. 2022). Compatible solutes, such as sugars, proteins, and proline, are crucial substances directly involved in plant adaptation to drought stress (Blum 2017). In our study, the sugar, protein, and proline contents were augmented in cactus pads under drought stress conditions. These results are consistent with previous studies on melon and cactus subjected to abiotic stress (Silva-Ortega et al. 2008; Meddich et al. 2021; Lahbouki et al. 2022). However, despite these osmoprotectants, they were insufficient to reduce the oxidative damage caused by the accumulation of H_2O_2 and the consequent increase in lipid peroxidation (Shemi et al. 2021). On the other hand, plants exposed to drought evolve complex antioxidant enzymes to cope with the formed ROS. In the present study, drought-exposed cactus underwent an increase in SOD, CAT, and POX activities in the cladodes. The SOD enzyme plays a primarily defensive role against oxidative damage. SOD catalyzes the dismutation of $O2^-$ and produces H_2O_2. Then, the CAT and POX enzymes intervene to convert H_2O_2 into H_2O and O_2 (Rukmini et al. 2004; Ozkur et al. 2009). These results are also in line with previous studies that reported higher antioxidant enzyme activities in plants exposed to drought (Anli et al. 2020; Denaxa et al. 2020).

The cultivation of cactus plants under drought induces an increase in the accumulation of polyphenol compounds TPC and TFC. The cactus cladodes are rich in phenolic compounds such as phenol and flavonoid (Boutakiout et al. 2018). These compounds play a key role in protecting plants from ROS (Ibrahim et al. 2019). The phenolic compounds defend the plant's proteins and lipid membrane against oxidative stress caused by drought, through their hydrogen or electron donor properties, which neutralize singlet oxygen and scavenge free radicals (Kalogianni et al. 2020). Comparable results were reported in other plants, e.g., white stonecrop and wheat cultivated under drought stress (Koźmińska et al. 2019; Naderi et al. 2020). The findings of this study indicated that SWRT application induces a decrease in the synthesis of antioxidant enzymes and phenolic compounds. This decrease can be attributed to the improvement of both water and nutrient retention efficiency of SWRT application (Kavdir et al. 2014). The availability of water and nutrients in the root zones of plants reduces oxidative stress in plant cells and leads to a decrease in enzymatic and nonenzymatic antioxidant secretion (Chiappero et al. 2019; Nkurunziza et al. 2019). Furthermore, a previous study showed a strong relationship between the enzymatic and nonenzymatic antioxidants in the cactus cladodes (Lahbouki et al. 2021). This is consistent with our study, which shows that decreasing enzymatic antioxidants leads to a decrease in nonenzymatic antioxidants.

Soil analysis findings demonstrated that the application of SWRT improved its physicochemical characteristics after harvest. In the unirrigated condition, the application of SWRT caused a decrease in soil pH. Besides, other elements such as OM and AP increased, compared with the control. Drought stress negatively affects the composition and activity of soil microbial communities, leading to microbial death (Preece et al. 2019). However, the application of SWRT keeps the soil moist. The microbial communities secrete organic acids, which can lead to low soil pH (Dehghanian et al. 2018). In addition, the increase in OM and AP could be explained by the high OM content retained by the applied impermeable membrane, and also the ability of microorganisms to metabolize different compounds produced by plant roots such as carbohydrates and organic acids (Yadav et al. 2021). Therefore, the increase in AP could be due to the pH that plays a key role in the mobility and availability of nutrients in the soil (Ben-Achiba et al. 2009). In addition, the microorganisms could improve soil AP through phosphate solubilization (Etesami and Jeong 2021).

Conclusion

In the present study, drought resulted in decreased growth of cactus cladodes through its obvious effects on physiological and biochemical characteristics. The application of SWRT mitigated the deleterious impact of drought on physiological and biochemical parameters by increasing stomatal density and stomatal conductance. In addition, SWRT mitigated drought-induced changes by improving water and mineral retention in soil.

Our findings imply that using SWRT to mitigate drought-induced negative effects on cactus growth, photosynthesis, antioxidant system, and soil parameters might be a viable alternative for improving plant output in arid and semi-arid environments.

On the other hand, these results remain the first of their kind on the effect of SWRT on physiological and biochemical parameters of plants under water stress. It is interesting to test this methodological approach for another season with other measures such as deep percolation losses and moisture at the bottom of SWRT.

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Author information

Author ORCIDs

Abdelilah Meddich https://orcid.org/0000-0001-9590-4405

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The authors declare no conflict of interest.

Supplementary material

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