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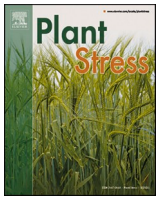

Citrullus colocynthis regulates photosynthetic and biochemical processes to develop stress resilience and sustain growth under sub-optimal temperatures

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ABSTRACT

Sub-optimal temperatures posed significant challenges to leaf photosynthesis and plant growth. This study examined the eco-physiological adaptations of a desert vine (*Citrullus colocynthis*) to unfavorable temperatures (15/25 °C, 25/35 °C, and 35/45 °C) over 35 days. Plants grown in moderate temperatures increased shoot number and leaf canopy (55 %), chlorophyll a (2.5 folds), and carotenoid accumulation compared to other treatments. Conversely, high-temperature stress resulted in longer shoot development with fewer primary branches, while low temperatures constrained both shoot and leaf growth. Plants treated with high heat exposure produced more oxidative stress markers (MDA and H_2O_2, by two folds), causing greater cellular damage while attaining lesser growth. During the high-temperature episode, plants increased their antioxidant enzyme activities and proline (2.5-fold) levels to protect the tissues from oxidative damage. Plants treated with either moderate or higher heat stress increased the potential quantum yield of photosystem II (Fv/Fm) and maximum quantum yield ΦPSII in the young leaves, which indicated the constitutive plant adaptation to unfavorable temperatures. Additionally, photosynthetic efficiency differed with leaf age and temperature; mature leaves performed better physiologically at low temperatures, whereas young leaves adapted better at high temperatures stress. The results suggested that *C. colocynthis* plants were highly adaptable to unfavorable temperatures by regulating the plants' thermal homeostatic ability through their photosynthetic and biochemical processes. This study provided deeper insights into species-specific eco-physiological responses to sub-optimal temperatures and contributed to our broader understanding of plant resilience and ecological adaptability in the era of global climate change.

1. Introduction

Plant growth is influenced by environmental factors such as temperature, light, humidity, water, and nutrition. Temperature variations have become a major constraint to plant growth, productivity, and distribution worldwide due to recent climate changes (Suzuki et al., 2014; Challinor et al. 2014; Raza et al. 2021). Photosynthesis, transpiration, respiration, and germination are all affected by temperature (Battisti and Naylor 2009; Hatfield and Prueger 2015; Janda et al. 2019; Gull et al. 2019). Temperature effects on plants vary widely and is

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Table 1
Results of one-way ANOVA showing the effects of temperature (15/25, 25/35, and 35/45°C) on some growth parameters and biochemical attributes in *Citrullus colocynthis*. ns: non-significant at P ≥0.05, significant values *: P≤0.05, **: P≤0.01 and ***: P≤0.001.

Growth parameters	df	Mean Squares	F-Ratio	P-Value
Shoot length	2	1.013	95.90	<0.001
Number of lateral shoots	2	0.320	8.67	<0.01
Number of green leaves	2	0.003	0.731	ns
Number of dry leaves	1	6.435	62.92	<0.001
Average leaf size	2	0.245	16.68	<0.01
Chl *a*	2	0.222	98.51	<0.001
Chl *b*	2	0.016	94.21	<0.001
Carotenoids	2	0.014	132.18	<0.001
H_2O_2	2	0.157	118.49	<0.001
MDA	2	0.404	15.86	<0.01
Proline	2	0.949	50.23	<0.001
APX	2	0.812	7.93	<0.05
GPX	2	0.177	98.08	<0.001
CAT	2	1.215	29.59	<0.001
SOD	2	0.896	1,208	<0.001

species-specific; some plants do much better at low temperatures, but others prefer high temperatures (Ferrante and Mariani 2018). High-temperature-adapted plants are also affected by sunlight, moisture drainage, elevation, and day-night temperature differences. Both lower and higher temperatures can cause unfavorable conditions that affect several metabolic processes, such as protein folding, membrane stability, phytohormonal pathways, cytoskeletal organization, transport, and enzymatic reactions, leading to the production of reactive oxygen species (ROS) that cause oxidative stress (Wahid et al. 2007; Wang et al. 2009; Hasanuzzaman et al. 2013; Song et al., 2022). High-temperature stress usually causes ROS accumulation in both mitochondria and chloroplasts, which can cause DNA damage and cell membrane lipid peroxidation (Bowler et al. 1992; Kukavica and Jovanovic 2004). High temperatures would affect the activity of photosynthesis and respiration by altering the internal structure of the chloroplasts, inactivation of Rubisco enzyme, decreasing photosynthetic pigments, disrupting the photosystem II, and changing membranes' fluidity (Los and Murata 2004), and changing electron transport mechanisms and gas exchange parameters (Zhu 2016; Li et al. 2018; Gull et al. 2019; Sharma et al. 2020).

Exposure to low temperatures ranging from 0 °C to 15 °C can significantly affect plant growth, development, and crop yield (Song et al. 2020; Bhattacharya 2022). The severity and duration of cold exposure determine the extent of this impact. Cold temperatures can cause physical injuries to plants, including surface lesions, dehydration, desiccation, internal discoloration, and accelerated senescence, leading to tissue damage (Bhattacharya 2022). Additionally, these conditions can trigger physiological changes within plant cells, which may result in reversible or irreversible harm due to damage to the plasma membrane and metabolic machinery (Liang et al. 2020). When exposed to low temperatures, plants undergo various physiological and biochemical adjustments such as the production of protective proteins like cold shock proteins, synthesis of compatible solutes such as glycine betaine and proline, changes in metabolic composition, suppression of photosynthesis, and detoxification of reactive oxygen species (ROS) through enzymatic and non-enzymatic antioxidants (Hassan et al. 2021). In addition, low temperatures can impede the activity of enzymes involved in photosynthesis, resulting in diminished chlorophyll production and a consequent decrease in photosynthetic efficiency. Furthermore, cold stress compromises the fluidity and functionality of chloroplast membranes—critical sites for photosynthesis—by causing physical constriction of the plant cell membranes (Bhattacharya et al. 2022; Aslam et al. 2022.

It has been reported that most metabolic processes increase when temperatures rise to a point that varies from one plant species to another. The main biological processes become unbalanced during extreme temperatures, reducing plant growth or even leading to death (Yang et al. 2006; Gomathi et al. 2013). High temperatures cause severe water loss (desiccation) when transpiration exceeds water absorption by the roots. The rate of photosynthesis declines rapidly after a critical temperature is reached. However, plants' respiration is less sensitive to high temperatures; if extreme heat continues for weeks, respiration continues day and night, depleting the plant's food reservoir and eventually causing its death (Atkin et al. 2005; Źróbek-Sokolnik 2012; Smith and Dukes 2013).

Plants are capable of sensing and responding to temperature changes by undergoing a range of morphological, physiological, and biochemical adjustments to maintain viability and function (Raza et al. 2019; Palit et al. 2020; Hayes et al. 2021). Plants can survive harsh environmental conditions by balancing growth, development, and stress tolerance (Raza et al. 2020). Temperature changes act as networked thermostats, altering cellular equilibrium (Raza et al. 2020; Ruelland and Zachowski 2010). The electron chemistry of the PSII complex is particularly susceptible to damage at high temperatures (Allakhverdiev et al. 2008). However, the plant has evolved several mechanisms to protect and maintain PSII through an efficient repair system. Photoinhibition occurs when damage exceeds the PSII repair rate, reducing photosynthetic efficiency and crop production (Ahmad et al. 2020; Ma et al., 2021). Besides, high temperatures alter membrane fluidity and the activity and stability of enzymes like Rubisco and Rubisco activase (Sage and Kubien

Fig. 1. Phenotypic variations in *Citrullus colocynthis* plants exposed to different temperatures (15/25, 25/35, and 35/45 °C).

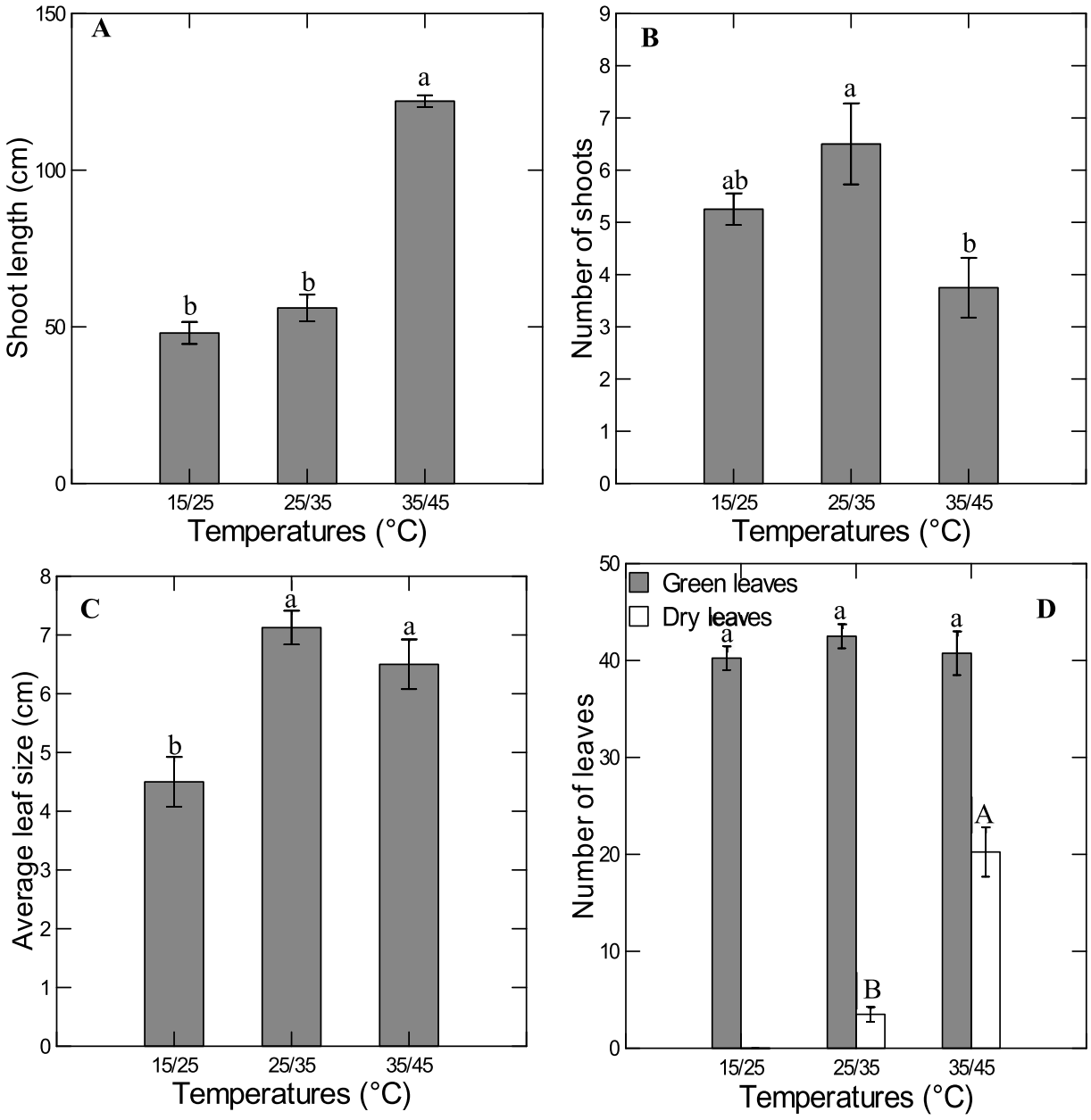

Fig. 2. Effects of different temperatures (15/25, 25/35, and 35/45 °C) on growth parameters (means ± SE) such as A: shoot length, B: number of shoots, C: average leaf size, and D: number of leaves in *Citrullus colocynthis*. Means with different letters within a certain trait are significantly different at $P \leq 0.05$, according to Duncan's multiple-range tests.

2007; Yamori et al. 2014). In most studies on photosynthetic acclimation in tropical plants, net photosynthesis measurements are used, which produce conflicting results. For example, net photosynthesis levels decreased in response to high temperatures in plants grown in an *in-situ* experiment (Doughty 2011) and in potted plants (Cheesman and Winter 2013). However, Li et al. (2020) reported that the net photosynthesis of four subtropical montane trees was increased in response to elevated temperatures. Those authors indicated that the light-saturated photosynthetic rate and stomatal conductance were increased in three of these tree species at higher temperatures.

When plants are exposed to unfavourable temperatures, they must undergo physiological, biochemical, and molecular changes that alter signaling and transcriptional pathways, resulting in the production of ion transporters, osmoregulators, proteins, and antioxidants (Fitter and Hay 2002; Hasanuzzaman et al. 2013;). It has been demonstrated that the thermotolerance of plants increases ROS-scavenging enzymes such as catalase, ascorbate peroxidase, guaiacol peroxidase, and superoxide dismutase (Bowler et al. 1992; Shi et al. 2001; Wang et al. 2014). Such enzymes scavenge ROS, such as superoxide radicals ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH), which are generated as byproducts of various cellular processes and can accumulate under heat stress (Suzuki and Mittler 2006). As a result, plants' tolerance to environmental stresses is highly correlated with their ability to scavenge and detoxify ROS (Foyer et al. 1994). Due to climate change, the Arabian desert will likely become drier and hotter. Therefore, studying how desert plants can tolerate temperature changes is crucial to studying their physiological and biochemical attributes.

Defining one critical high/low temperature for different terrestrial plants is difficult. In extreme temperatures, some plants wilt while others thrive. In most plants, the temperature threshold controlling life processes' constancy is genetically determined. It varies from some degrees over zero to about 35 °C (Singh et al. 2015). Around 10-15 °C over

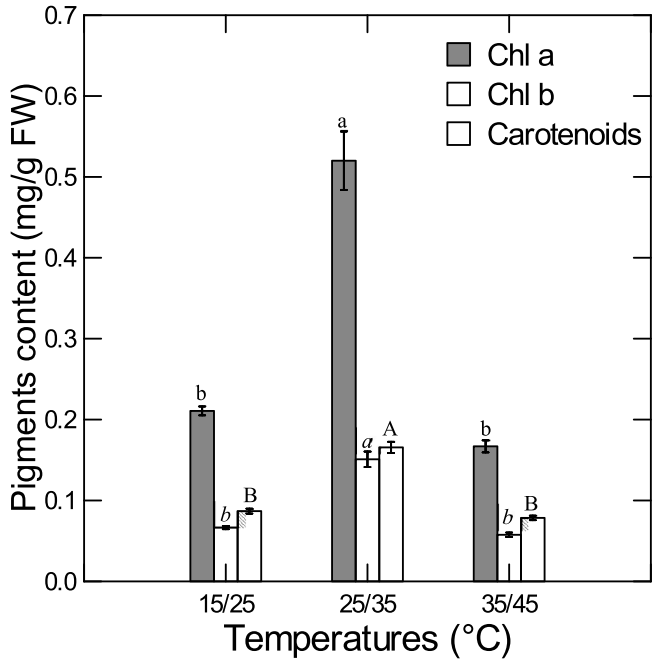

Fig. 3. Effects of different temperatures (15/25, 25/35, and 35/45 °C) on the photosynthetic pigments (means ± SE) in *Citrullus colocynthis*. Means with different letters within a certain pigment are significantly different at P ≤ 0.05, according to Duncan's multiple-range tests.

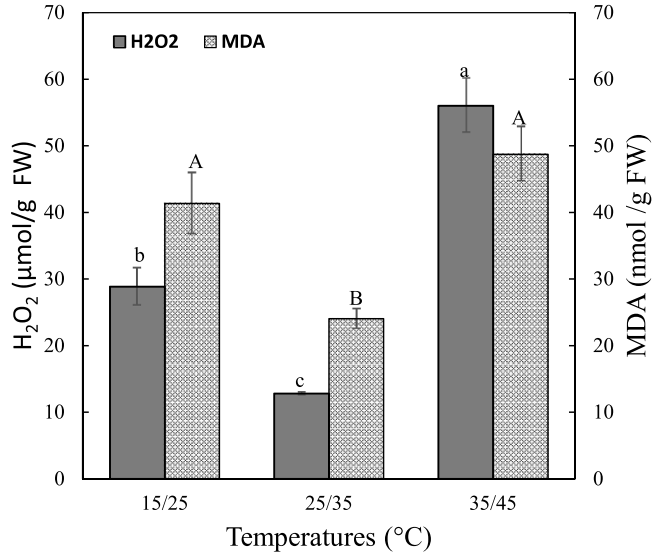

Fig. 4. Effects of different temperatures (15/25, 25/35, and 35/45 °C) on the concentrations (means ± SE) of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) in *Citrullus colocynthis*. Means with different letters in a certain metabolite are significantly different at P ≤ 0.05, according to Duncan's multiple-range tests.

the optimum temperature causes heat stress (Larkindale et al. 2005; Źróbek-Sokolnik 2012). A plant that prefers sunny, dry locations is considered relatively heat resistant (Stushnoff et al. 1984; Źróbek-Sokolnik 2012). According to Źróbek-Sokolnik (2012), the thermal death point for aquatic plants and plants growing in shaded habitats is 38–42 °C following several hours of exposure. For temperate plants with hydrated and metabolically active organs, the thermal death point could be 45–55 °C following several hours of exposure. Still, it can reach 60–65 °C when plants are exposed for a few hours daily for desert plants (Źróbek-Sokolnik 2012; Zhanassova et al. 2021).

Citrullus colocynthis (L.) Schrad (bitter apple, Cucurbitaceae) is a common perennial plant of the UAE desert and widely distributed in the Arabian Peninsula, India, Africa, and other tropical regions of the world (El-Keblawy et al. 2017; Kiran et al. 2020). *C. colocynthis* was reported to grow in European countries such as islands of the Spain and the Grecian archipelago (Bhasin et al. 2020). As an inhabitant of sand dunes in hot, arid regions, *C. colocynthis* can withstand drought, nutrient deficiency, strong winds, high temperatures, and sandblasting (Dane et al. 2007). Besides, there is potential for its use as a therapeutic activity, feedstock for edible oil and biodiesel, and animal feed, making it a potential cash crop (Abushamleh et al. 2022). As a creeping vine, this species has interesting growth strategy and is able to reduce erosion and preventing desertification. However, such creeping nature exposes the plants to very high temperatures on sandy soils of the hot, arid climate of the UAE. In a trial experiment, a thermal camera measured the ambient and internal temperatures of *Citrullus colocynthis* during summer on a sand dune in the UAE. When the ambient temperature was 44-48 °C, the maximum temperatures measured inside and on the dune were 58 °C and 73 °C, respectively. Besides, the internal temperature of *C. colocynthis* was above 50 °C for 4-5 hours per day (Ali El-Keblawy, unpublished data). The appearance and disappearance of *C. colocynthus* in different geographical regions, such as Egypt and the Kingdom of Saudi Arabia, were dependent on both abiotic (soil water content, soil texture, and temperature) and biotic factors (El-Absy 2022). Several studies investigated the effect of different temperatures on seed germination of *C. colocynthis*, such as El-Keblawy et al. (2019), who reported that the germination of *C. colocynthis* seeds was significantly higher at moderate and higher temperatures (20/30 and 25/35 °C) than that at lower temperatures (15/25 °C). However, there were limited studies on the effect of temperature on growth, such as Onwueme and Lawanson (1973), who studied the effect of heat stress on subsequent chlorophyll accumulation in seedlings of *C. colocynthis*. To the best of our knowledge, there was no investigation about the responses of *C. colocynthis* to sub-optimal temperatures, particularly in terms of growth, photosynthesis, and phytochemical reactions, under controlled experimental conditions.

The present study aimed to assess the morphological, physiological, and biochemical responses of *C. colocynthis* to temperature stress under controlled experiment conditions. The study assesses the impact of temperatures (low, 15/25 °C; moderate, 25/35 °C; and high, 35/45 °C) on chlorophyll content, photosynthesis efficiency, proline, and other enzymatic antioxidants and ROS. We used genetically identical plants produced from cuts of a specific individual plant. This helped eliminate the impact of genetic variations, especially since several genetic accessions were defined within the same population (Al-Nablsi et al. 2021). As it is a perennial evergreen of the hot deserts, we hypothesize that *C. colocynthis* performs optimally at moderate rather than low and high temperatures and can survive and grow at low and high temperatures by activating different physiological and biochemical tolerance mechanisms to maintain plant growth and development.

2. Material and methods

2.1. Vegetative propagation by plant cutting

A fully mature *C. colocynthis* individual grown in the botanical garden of the University of Sharjah was selected to be the source of stolon segments used for producing genetically identical individuals (clones). The chosen individual occupied a ground area of around 12 m, with several main primary shoots and several secondary and tertiary shoots that could be used in the plant propagation experiment. Parts of the plant's main stems were covered with moist soil to stimulate aerial rooting. Each shoot with newly developed adventitious roots was segmented into stolons with a sterilized scalpel (Xu and Zhou 2017; Hongpakdee et al. 2018). Stolons, with a minimum of one node with

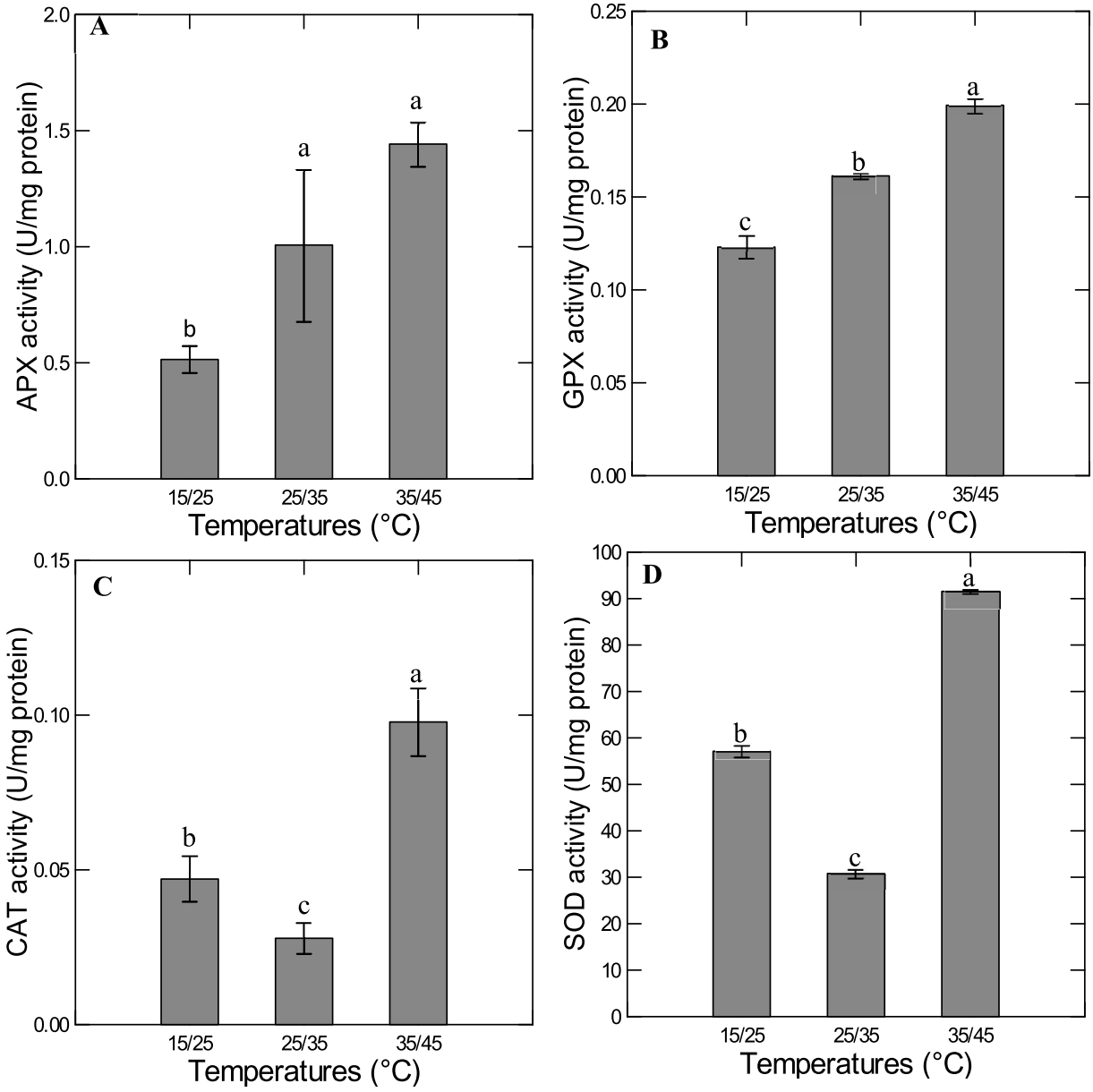

Fig. 5. Effects of different temperatures (15/25, 25/35, and 35/45 °C)) on the activities of some antioxidant enzymes (means ± SE), A: ascorbate peroxidase (APX), B: guaiacol peroxidase (GPX), C: catalase (CAT) and D: superoxide dismutase (SOD) in *Citrullus colocynthis*. Means with different letters are significantly different at $P \leq 0.05$, according to Duncan's multiple-range tests.

new adventitious roots, perennating buds, and an apex, were buried in a plastic pot (18 cm height and 20 cm diameter) filled with a mixture of sand and peat moss in a ratio of 1:2. The pots were moved to a growth chamber adjusted at 20/30 °C and adequately watered. A transparent plastic sheet covered the prepared 50 pots to maintain proper humidity and temperature conditions. The leaves emerged after one week, and well-developed roots were observed after two weeks. The plastic sheet was removed when the plants had four well-developed leaves.

2.2. Temperature treatment

Citrullus colocynthis plants of the same accession were moved after two months to three CONVIRON plant growth chambers (model E-15) adjusted to low (15/25 °C), moderate (25/35 °C), and high (35/45 °C) temperatures each with two light regimes (the low temperatures coincided with 12 hrs dark and the high temperatures with 12 hrs light). The plants intended for high temperatures were acclimated at 30/40 °C for two weeks before being raised gradually to 35/45 °C. Six plants were used for each temperature treatment. Soil moisture was monitored using a tensiometer. The irrigation frequency varied based on the plants' size and the growth chamber temperature. Plants were watered when the moisture level reached 50 % of the soil field capacity. The plants were irrigated once a week with 10 % of Hoagland nutrient solution.

2.3. Growth and morphological parameters

The plants were grown at the different temperatures for 35 days. The following growth and morphological attributes were measured for six plants in each temperature treatment: the number of shoots/plant, the total number of leaves/plant, the number of yellow leaves/plant (i.e., leaf shedding as an indication of stress), the longest shoot length (cm), and the average size of leaves (widest diameter + narrowest diameter/2). Measurements incorporated all branches and their leaves, with averages computed per plant to serve as replicates. After 35 days of

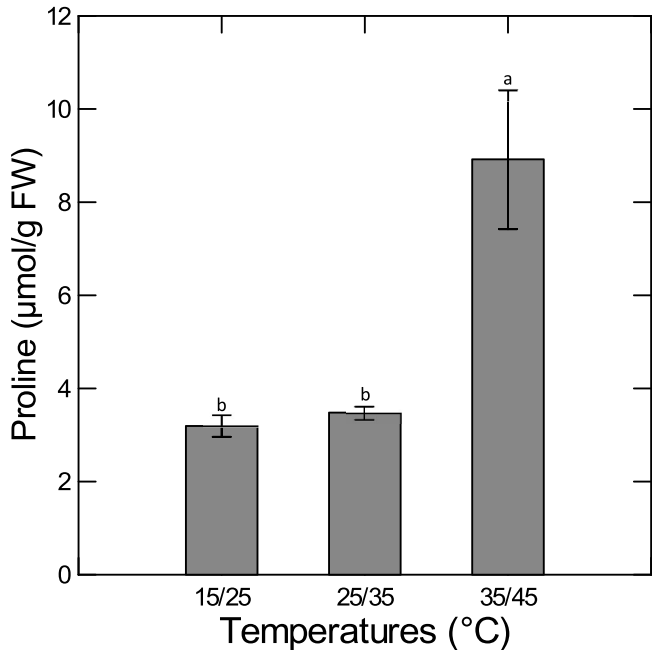

Fig. 6. Effects of different temperatures (15/25, 25/35, and 35/45 °C) on the proline concentration (means ± SE) in *Citrullus colocynthis*. Means with different letters are significantly different at P ≤ 0.05, according to Duncan's multiple range tests.

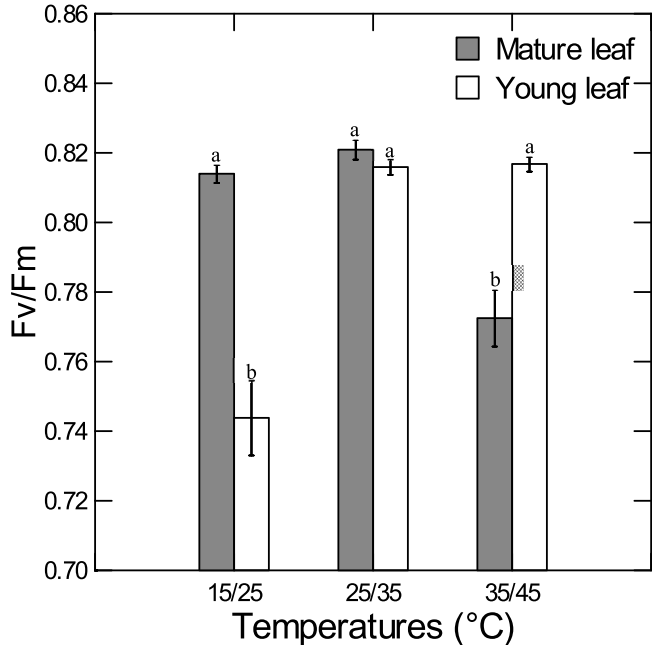

Fig. 7. Effects of temperature (15/25, 25/35, and 35/45 °C) and leaf age on the efficiency of photosystem II (Fv/Fm) in *Citrullus colocynthis*. Bars with different lowercase letters within a certain temperature indicate significant differences at P ≤0.05, according to Duncan's multiple range tests.

temperature treatment, the plants were harvested, and the leaves were separated and thoroughly cleaned with running tap water and then distilled water. The leaves were then frozen in liquid nitrogen, ground, and stored at -80 °C freezer until used for the biochemical analyses.

2.4. Determination of pigments' content

The ground leaf tissues were mixed with 4 mL of cooled methanol and incubated at 4 °C for 30 min in the dark. After centrifugation for 5 min at 21,000 g, 200 µL of supernatant was used to measure 470, 653, and 666 nm absorbances using a microplate reader (Bio Tek Instruments, EPOCH2C, USA). In this study, chlorophyll a, b, and carotenoid concentrations were calculated using the specific absorption coefficient of methanol (Lichtenthaler and Wellburn 1983; Warren 2008; Prodhan et al. 2017).

2.5. Determination of reactive oxygen species

2.5.1. Hydrogen peroxide

Hydrogen peroxide (H_2O_2) content was measured using (Velikova et al. 2000) methodology. In an ice bath, 0.1 g of cryogenically ground leaf tissues were homogenized with 1 mL of 0.1 % (w/v) trichloroacetic acid (TCA). After centrifuging at 10,000 g for 15 min, 0.5 mL of the supernatant was mixed with 0.5 mL of 10 mM potassium phosphate buffer (pH 7.0) and 1 mL of 1 M potassium iodide. A Bio Tek Instruments EPOCH2C microplate reader measured the supernatant absorbance at 390 nm. Calculation of H_2O_2 content was performed using standard curves prepared using different concentrations of H_2O_2.

2.5.2. Malondialdehyde

The lipid peroxidation is measured by malondialdehyde (MDA) produced by 2-thiobarbituric acid (TBA) (Zhou and Leul 1998). We homogenized cryogenically ground leaves samples (0.1 g) in 3 mL of 0.1 % (w/v) trichloroacetic acid (TCA) in 0.1 % (w/v) water. The homogenate was centrifuged at 10,000 g for 15 min. Then, we added 2 mL of TCA containing 0.5 % (w/v) TBA to the supernatant aliquot containing 0.8 mL. The mixture was heated to 95 °C for 30 min and cooled on ice quickly. The contents were centrifuged at 12,000 g at 4 °C for 15 min to pellet any TBA precipitate. Microplate readers (Bio Tek Instruments, EPOCH2C, USA) were used to measure the absorbance of supernatants (200 µL) at 532 nm and 600 nm. Using an extinction coefficient of 155 mM^{-1} cm^{-1}, MDA was represented as nmol/g FW.

2.6. Determination of antioxidant enzyme activities

2.6.1. Preparation of enzyme extract

Cryogenically ground fresh leaves were weighed and mixed with 1 mL potassium phosphate buffer (pH 7.0), 1 mM EDTA, 2 % (w/v) polyvinyl pyrrolidone (PVP), and 0.05 % (w/v) Triton X-100 (Gossett et al. 1994). A microplate reader (Bio Tek Instruments, EPOCH2C, USA) was used to determine catalase, ascorbate peroxidase, and guaiacol peroxidase activities from the homogenate centrifuged for 10 min at 4 °C at 10,000 g. The Bradford method was used to determine the protein concentration in all samples. In this method, A 96-well plate was incubated for 5 min at room temperature with 10 µl of enzyme extract mixed with 190 µL of Bradford reagent. The blank was 190 µL of Bradford reagent and 10 µL of enzyme extraction buffer, and the absorbance was measured at 595 nm. Bovine Serum Albumin (BSA) was used as a standard curve to calculate the protein concentration in each enzyme extract.

2.6.2. Estimation of the antioxidant enzyme activities

Catalase (CAT) activity was measured by observing the disappearance of H_2O_2 at 240 nm, taking extinction coefficient (Δε) 2.8 $mM^{-1}cm^{-1}$ at 240 nm as 43.6 $mM^{-1}cm^{-1}$ (Patterson et al. 1984). To determine CAT activity, enzyme extract (190 µL) and reaction mixture (190 µL) containing 100 mM potassium phosphate (pH 7.0) and 10.5 mM H_2O_2 were treated at 25 °C for 2 min using the initial linear rate of decrease in absorbance at 240 nm (Miyagawa et al. 2000).

We measured ascorbate peroxidase (APX) at 25 °C using enzyme extract (10 µL) and a reaction mixture (190 µL) containing 50 mM

Table 2
Results of two-way ANOVAs (F-values) showing the effects of growth temperatures (15/25, 25/35, and 35/45 °C) and leaf age (young and mature) on some chlorophyll fluorescence attributes in *Citrullus colocynthis*. *: P≤0.05, **: P≤0.01 and ***: P≤0.001.

Source of variation	df	Fv/ Fm	ΦPSII	qP	NPQ	ETR	Photon energy dissipation [(1 − qP)/NPQ]
Temperature (T)	2	28.96*	14.01*	12.26*	0.11^{ns}	14.00*	5.13*
Leaf Type (L)	1	4.85*	4.34*	2.82^{ns}	0.14^{ns}	4.34*	0.92^{ns}
T X L	2	50*	11*	7.8*	0.87^{ns}	10.6*	0.05^{ns}
Error	28						

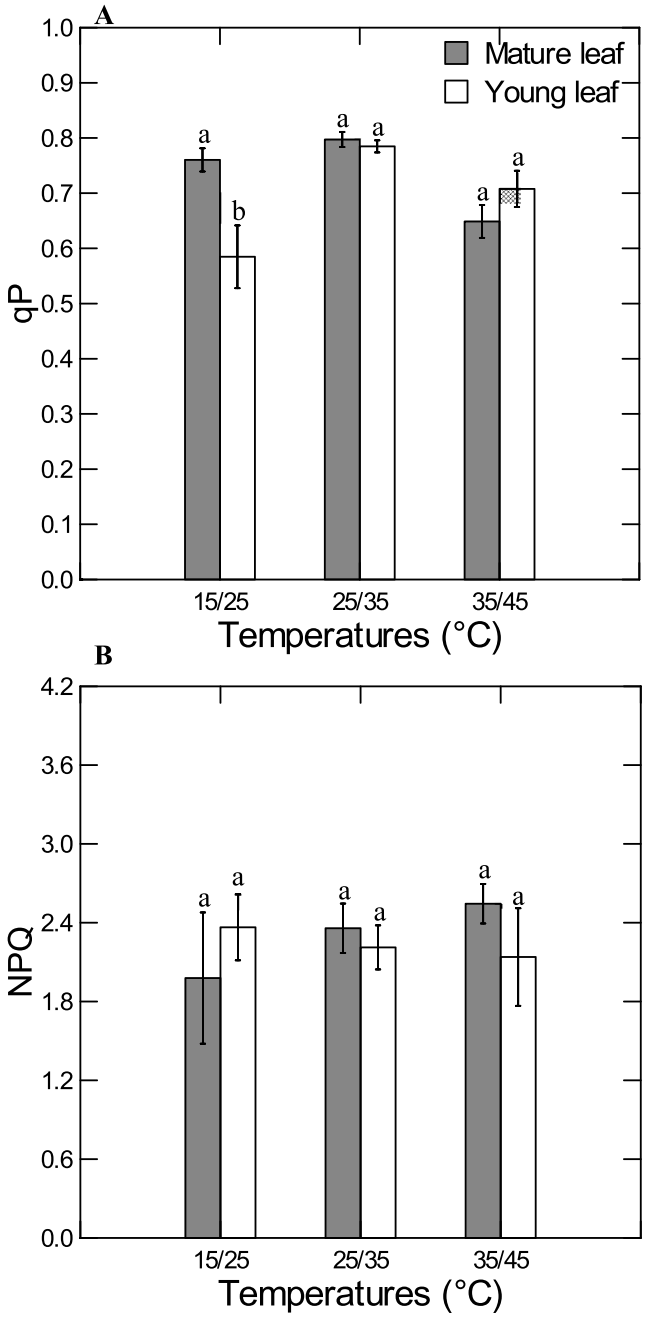

Fig. 8. Effects of temperature (15/25, 25/35, and 35/45 °C) and leaf age photosynthetic attributes: (A) photochemical fluorescence quenching (qP), and (B) non-photochemical fluorescence quenching (NPQ) in *Citrullus colocynthis*. Bars with different lowercase letters within a certain temperature indicate significant differences at P ≤0.05, according to Duncan's multiple range tests.

potassium phosphate (pH 7.0), 0.2 mM EDTA, 0.5 mM ascorbic acid, and 0.25 mM H_2O_2. A decrease in absorbance at 290 nm for 1 min was measured, and an extinction coefficient of (Δε) 2.8 $mM^{-1}cm^{-1}$ was used to determine how much ascorbate was oxidized.

Guaiacol peroxidase (GPX) activity was assessed in 96 well plates using enzyme extract (10 µL) and a reaction mixture (190 µL) containing 50 mM potassium phosphate (pH 7.0), 2 mM H_2O_2, and 2.7 mM guaiacol. As tetraguaiacol forms, the absorbance at 470 nm increases for 3 min (Δε = 26.6 $mM^{-1}cm^{-1}$).

A modified protocol from McCord and Fridovich (1969) and Fimognari et al. (2020) was used to measure superoxide dismutase activity. The following reagents are required: KH_2PO_4/K_2HPO_4 buffer (50 mM) at pH 7.8, xanthine oxidase (25 mg in 500 mL phosphate buffer, 0.5 mM Xanthine), Na_2-EDTA (1.0 mM) and cytochrome C (0.1 mM). Cytochrome C, xanthine, and Na_2-EDTA were mixed equally to form a SOD master mixture. In a 96-well plate, 5 µL of plant enzyme extract was mixed with 135 µL of phosphate buffer, 60 µL of SOD Master Mix, and 5 µL of xanthine oxidase. An absorbance measurement was performed using a microplate reader at 550 nm, 25 °C for 2-3 min, and SOD activity was measured in U/mg protein in the blank wells. An inhibition reaction was used to measure SOD. The superoxide radicals will reduce cytochrome C in the blank.

2.7. Determination of proline content

We analyzed proline in *C. colocynthis* leaves from three different temperatures according to the methods of (Bates et al. 1973). The cryogenically ground samples (0.1 g) were homogenized in 500 µL of 3 % aqueous sulfosalicylic acid before being centrifuged for 5 min at 14, 000 g to separate the homogenate from the sulfosalicylic acid. A homogenate of 100 µL was mixed with 200 µL of glacial acetic acid and 200 µL of acid-ninhydrin. One mL of toluene was added, and the mixture vortexed for 15-20 seconds after being incubated for 1 hour at 96 °C. Toluene-containing chromophore was transferred into a fresh tube, and 200 L from the chromophore phase was measured at 520 nm; 200 µL toluene as a reference (blank). An electronic microplate reader (BioTek Instruments, EPOCH2C, USA) was used to measure the amount of proline using the absorbance at 520 nm of the organic toluene phase. The proline content was determined for each sample using a standard curve derived from Sigma-Aldrich's pure proline and calculated on a fresh weight basis (Abraham et al. 2010).

2.8. Pulse-modulated chlorophyll fluorescence measurements

Chlorophyll fluorescence measurements were conducted between 09:00 a.m. - 4:00 p.m. using a Pulse-modulated fluorescence monitoring system (FMS-2, Hansatech Instruments Ltd., Norfolk, UK) according to the method (Genty et al. 1989; Maxwell and Johnson 2000; Hussain and Reigosa 2011, 2017). Three fully expanded young and mature leaves were selected from each temperature regime and dark-adapted using Walz leaf clips for 20 min. After dark adaptation, leaves were successively illuminated at an intensity of 0.5 µmol m^{-2} s^{-1} for measuring F_0 (the minimum fluorescence of dark-adapted leaves), with a saturating pulse of 1800 µmol m^{-2} s^{-1} to obtain Fm (the maximum fluorescence of dark-adapted leaves), followed by calculation of Fv=Fm −F_0 and Fv/ Fm (the maximum quantum efficiency of dark-adapted PSII). Other

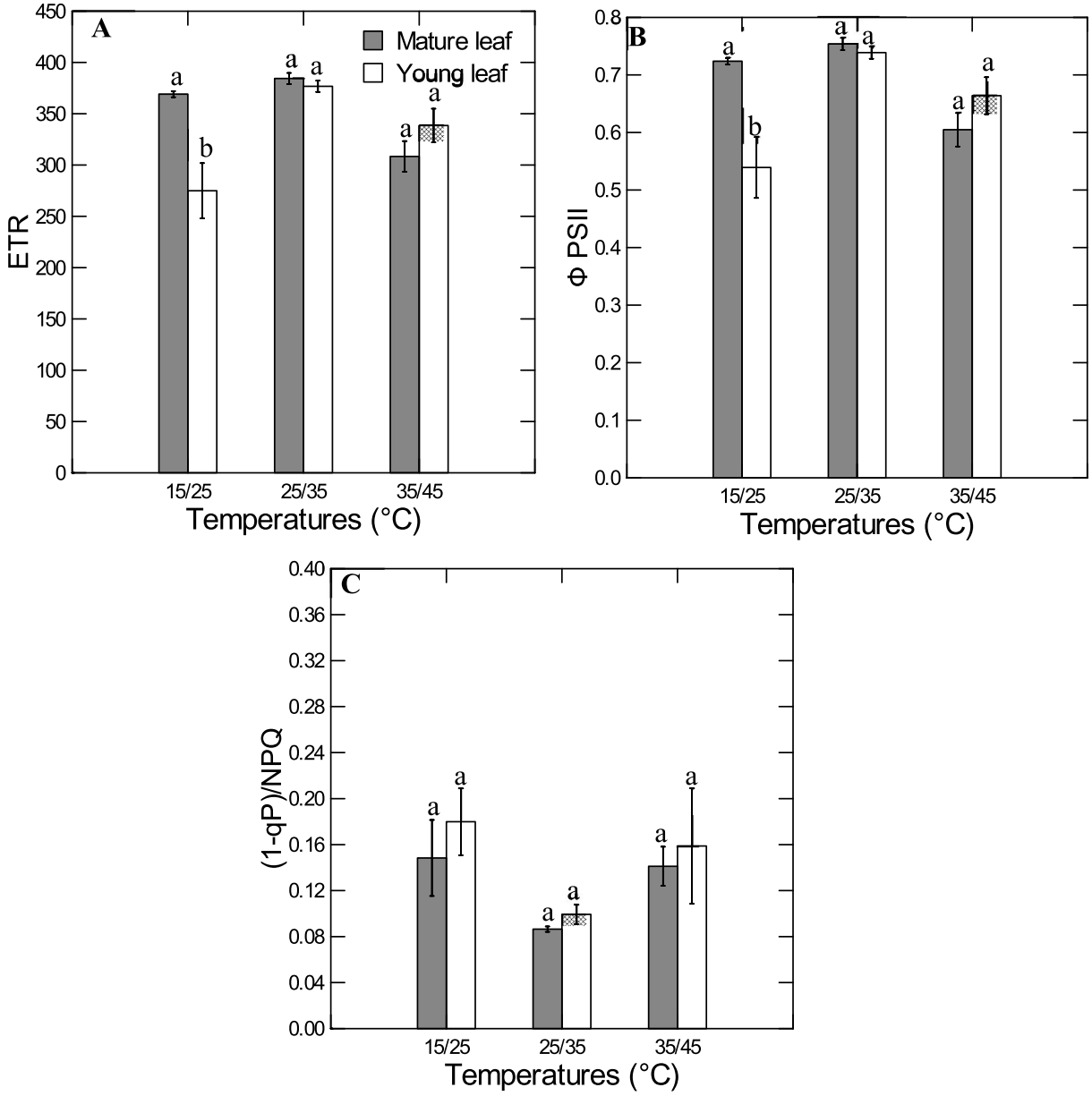

Fig. 9. Effects of the different temperatures (15/25, 25/35, and 35/45 °C) and leaf age on photosynthetic attributes A: ETR (Electron Transport rate), B: ΦPSII (quantum yield) and C: (1-qP)/NPQ (heat energy dissipation) of *Citrullus colocynthis*. Bars with different lowercase letters within a certain temperature indicate significant differences at P ≤0.05, according to Duncan's multiple range tests.

chlorophyll fluorescence parameters, including the efficiency of photosystem II photochemistry (Fv/Fm), quantum yield (ΦPSII), quenching (qP), and non-photochemical fluorescence quenching (NPQ), were measured using the fluorescence monitoring system (Genty et al. 1989; Maxwell and Johnson 2000).

2.9. Statistical analyses

One-way ANOVAs were used to assess the impact of temperature on all morphological and biochemical attributes of *C. colocynthis* grown at different temperatures. In addition, two-way ANOVAs were used to assess the effects of temperature and leaf age on photosynthetic attributes, including F_0, Fm, Fv/Fm, Fv, qP, NPQ, ETR, (1-qP)/NPQ (heat energy dissipation), ΦPSII, and Fs of *Citrullus colocynthis*. Furthermore, Pearson's correlations were calculated to assess the relationships between the different growth and biochemical traits of *C. colocynthis* grown under different temperatures. Duncan's test assessed the significant differences between the means of different treatments. All statistical analyses were performed using SYSTAT, version 13.

3. Results

3.1. Growth parameters

Temperature had a significant impact on all growth attributes ($P < 0.001$, Table 1), except for the number of green leaves ($P > 0.05$). Shoot length was significantly longer at warmer temperatures (122 cm) than at moderate (56 cm) and cooler (48 cm) temperatures (Fig. 1, and Fig. 2A). The number of primary branches (shoots) was substantially fewer at higher temperatures (3.75 shoots) than at intermediate temperatures (6.5 shoots), but not at lower temperatures (5.25 shoots). However, there was no significant difference between the number of branches of plants at low and high temperatures ($P > 0.05$) (Table 1, Fig. 2B). Additionally, the leaf size was significantly larger in plants grown at

Table 3
Pearson's correlations among some growth parameters and biochemical traits of *Citrullus colocynthis* grown under different temperatures (15/25, 25/35, and 35/45°C). *: P≤0.05, **: P≤0.01 and ***: P≤0.001.

	Shoot length	Number of shoots	Number of green leaves	Number of dry leaves	Average leaf size	Chl a	Chl b	Carotenoids	H_2O_2	MDA	Proline	APX	GPX	CAT
Shoot length	1.000													
Number of shoots	-0.635*	1.000												
Number of green leaves	-0.015	0.361	1.000											
Number of dry leaves	0.955***	-0.687	-0.226	1.000										
Average leaf size	0.343	0.210	0.244	-0.412	1.000									
Chl a	-0.545	0.730**	0.383	-0.918***	-0.026	1.000								
Chl b	-0.524	0.723**	0.351	-0.929***	0.241	0.904***	1.000							
Carotenoids	-0.488	0.671*	0.418	-0.935***	0.234	0.900***	0.948***	1.000						
H_2O_2	0.853**	-0.751*	0.106	0.937**	-0.132	-0.839**	-0.837**	-0.809**	1.000					
MDA	0.564	-0.775*	-0.043	0.887*	-0.487	-0.860*	-0.89***	-0.845**	0.904***	1.000				
Proline	0.941***	-0.578	0.339	0.951**	0.242	-0.550	-0.559	-0.505	0.895***	0.676*	1.000			
APX	0.741*	-0.518	0.206	0.638	0.535	-0.109	-0.126	-0.054	0.539	0.298	0.769*	1.000		
GPX	0.892***	-0.327	0.391	0.964**	0.625	-0.160	-0.146	-0.104	0.626	0.315	0.858**	0.890***	1.000	
CAT	0.886***	-0.737*	0.163	0.953**	-0.054	-0.767*	-0.783*	-0.729*	0.984***	0.863**	0.941***	0.648	0.701*	1.000
SOD	0.839**	-0.749*	-0.017	0.942**	-0.147	-0.90***	-0.89***	-0.878**	0.976***	0.862**	0.830**	0.476	0.559	0.948***

moderate and higher temperatures than those grown at lower temperatures. The leaf size was significantly larger in plants exposed to moderate temperatures than in those exposed to the lowest temperatures by 58.3 %, but only by 9.6 % in those grown at the warmer temperatures (Figs. 1, and 2C). Furthermore, there was no significant difference in green leaves between plants at the three temperatures. However, the total number of produced leaves (green and dry) was substantially greater at higher temperatures than at the lower two temperatures; 20.2 and 3.5 dry leaves/plants were collected from the warmer and moderate temperatures, respectively, but none from the lower temperatures (Fig. 2D).

3.2. Pigment contents

To quantify the level of leaf senescence, chlorophyll a and b contents were measured. The results showed that growth temperatures significantly affected different types of pigments ($P < 0.001$, Table 1). Chlorophyll a, b, and carotenoids concentrations attained significantly greater values at moderate temperatures than at cooler temperatures by 145 %, 127 %, and 90.6 %, respectively. Similarly, they were also higher at moderate temperatures compared to warmer temperatures by 211.5 %, 161.7 %, and 111.2 %, respectively (Fig. 3).

3.3. Oxidative damage (H_2O_2 and MDA)

Oxidative damage due to unfavorable growth conditions was assessed by measuring hydrogen peroxide (H_2O_2) and Malondialdehyde (MDA) production. MDA is a measure of lipid peroxidation and damage to plant membranes and can be used as a marker of oxidative stress in plants under biotic and abiotic stresses. Interestingly, the MDA and H_2O_2 levels increased significantly at low and high temperatures compared to moderate temperatures. However, the increase was pronounced for MDA at lower temperatures and H_2O_2 at higher temperatures. MDA and H_2O_2 levels were significantly higher at warmer than moderate temperatures by 337 % and 102.8 %, respectively, and at lower than moderate temperatures by 125 % and 72.0 %, respectively (Fig. 4).

3.4. Antioxidant enzyme activities

Plants develop antioxidant enzymes such as APX, GPX, CAT, and SOD to prevent oxidative damage caused by ROS. The ANOVA results indicated significant effects of temperature on the four assessed antioxidants ($P < 0.05$, Table 1). The activities of the four enzymatic antioxidants were significantly greater at warmer than cooler and moderate temperatures. The exception was the insignificant APX difference between mild and high temperatures ($P > 0.05$). APX, GPX, CAT, and SOD activities were significantly higher at higher temperatures than at moderate temperatures by 43.2 %, 23.6 %, 250.6 %, and 197.2 %, respectively, and at low temperatures by 180.5 %, 62.0 %, 108 %, and 60.3 %, respectively (Fig. 5). Besides, APX and GPX activities were much lower at low temperatures (0.51 and 0.12 U/mg protein, respectively) than at moderate temperatures (1.01 and 0.16 U/mg protein, respectively). However, CAT and SOD activity was significantly greater at the lower (0.05 and 57.1 U/mg protein) than at moderate temperatures (0.03 and 30.8 U/mg protein) (Fig. 5). Such findings indicate that the accumulation of antioxidants is temperature dependent.

3.5. Effects of different temperatures on proline level

Plants produce osmolytes such as proline to stabilize cell membranes, maintain water balance, and protect the cells from damage caused by thermal stress. Temperature had a significant effect on the proline content. Proline was significantly more abundant at higher temperatures (8.9 μmol/g fresh weight) than at moderate and lower temperatures (3.5 and 3.2 μmol/g fresh weight, respectively) (Fig. 6).

3.6. Chlorophyll fluorescence measurements

The photosystem II efficiency (Fv/Fm), a ratio that represents the maximum potential quantum efficiency of Photosystem II, showed that old leaves were more efficient in photosynthesis at low temperatures than young leaves. However, at high temperatures, young leaves were more efficient (Fig. 7).

Leaf age and plant growth temperatures and their interactions had no significant effect on NPQ ($P > 0.05$). Interesting, growth temperatures and the interaction between growth temperatures and leaf age, significantly affected qP ($P < 0.01$, Table 2). Young leaves' qP value was lower than mature leaves at lower temperatures but higher at warmer temperatures. The difference was significant at lower temperatures but not at higher temperatures. The qP in young leaves at low temperatures was less than that of mature leaves by 22.4 % (Fig. 8).

The ANOVA test showed significant effects for temperature, leaf age, and their interaction on ETR and ΦPSII ($P < 0.05$, Table 2). The highest values of these traits occurred at moderate temperatures and in mature leaves. In both traits, the mature leaves attained higher values than young leaves at low temperatures; the opposite was true at higher temperatures; the values were higher in young than mature leaves. However, the difference was significant only for ETR at the low temperature. The ΦPSII and ETR values were higher in mature leaves than in young leaves at low temperatures, with a difference of 25.3 % and 25 %, respectively (Fig. 9).

The impact of temperature on heat energy dissipation, [(1 - qP)/NPQ], was significant, whereas leaf age and the interaction between leaf age and temperature had no significant effect (Table 2). The impact of temperature on heat energy dissipation, [(1 - qP)/NPQ], is significant, whereas leaf age and the interaction between leaf age and temperature have no significant effect (Table 2). Heat energy dissipation was significantly higher at moderate and high temperatures than at low temperatures. Besides, heat dissipation was significantly lower at moderate temperatures compared to low and high temperatures (Fig. 9).

3.7. Pearson correlation matrix

Pearson correlation coefficient showed a significant positive relationship between shoot length and number of dry leaves ($r = 0.955$, $P < 0.001$), H_2O_2 ($r = 0.853$ $P < 0.001$), proline ($r = 0.941$), APX ($r = 0.741$, $P < 0.05$), GPX ($r = 0.892$, $P < 0.001$), CAT ($r = 0.886$, $P < 0.001$) and SOD ($r = 0.839$, $P < 0.01$). However, a significant negative relationship existed between shoot length and number of shoots ($r = -0.635$, $P \leq 0.05$, Table 3). Besides, there were positive relationships between oxidative markers (H_2O_2 and MDA), proline, and antioxidant enzymes. For example, between H_2O_2 and proline ($r = 0.895$, $P < 0.001$), CAT ($r = 0.984$, $P < 0.001$) and SOD ($r = 0.976$, $P < 0.001$), while between MDA and proline ($r = 0.676$, $P < 0.05$), CAT ($r = 0.863$, $P < 0.01$) and SOD ($r = 0.862$, $P < 0.01$).

4. Discussion

Different plant species have their preferred range of growth temperatures and will grow well under these optimal temperatures. Growth and development is generally reduced when sub-optimal thermal conditions are encountered (Berry and Björkman 1980; Suzuki et al., 2014; Bhattacharya, 2022). High temperatures can, directly and indirectly, affect plant growth and productivity through various biological processes. It is difficult to ascertain specific plant adaptation to high temperatures in the field due to large daily and seasonal temperature fluctuations (Allakhverdiev et al., 2008; Źróbek-Sokolnik 2012; Hayes et al. 2021). Our study showed that *C. colocynthis* survived 35 days at 45 °C for 12 hours per day, indicating that it is among the most heat-tolerant desert plants (Hatfield and Prueger 2015). The results showed a positive relationship between the temperature and shoot length; the highest temperatures significantly increased the elongation of the creeping shoot more than the moderate and lower temperatures (Fig. 2A). Besides, we reported the development of several tendrils, especially at the tips of the lateral and epical shoots, at 35/45 °C than the other lower temperatures. Furthermore, around 20 leaves per plant died at the lower parts of the main branches in plants that grew at high temperatures, compared to only five and zero in plants at moderate and lower temperatures, respectively (Fig. 2). Such results indicated that the accelerated growth of the creeping shoots, together with the development of tendrils and death of the lower basal leaves, might be an adaptation for the plants in the field to avoid the hot soil surface. A similar result was reported for the creeping melon (*C. lanatus*); temperatures above 25 °C and up to 40 °C significantly increased the main shoots and prolific lateral growth (Buttrose and Sedgley 1978). Furthermore, Rosolem et al. (2013) reported that higher temperatures (39/29 °C) significantly increased plant height and reproductive branches but decreased leaf area and chlorophyll in cotton plants compared to lower temperatures (25/15 °C and 32/22 °C, day/night temperatures).

Both high and low temperatures can significantly affect the foliar chlorophyll content and photosynthetic activity, reducing growth and reproduction. Our study showed that chlorophyll content and chlorophyll fluorescence parameters in *C. colocynthis* were negatively impacted by both high and low-temperature stresses compared to moderate temperatures. Similarly, in the watermelon, high and low-temperature stresses negatively affected chlorophyll fluorescence parameters (such as Fv/Fm, ΦPSII, qP, and ETR) compared to moderate temperatures (Hou et al. 2016). Researchers reported that temperature stress reduces chlorophyll biosynthesis in addition to plant impairment and degradation (Efeoğlu and Terzioğlu 2009; Abdou et al. 2013). The impact of unfavourable temperatures on foliar chlorophyll is particularly important as it is the most important component of the photosynthetic apparatus; it absorbs light energy from the sun and converts it into chemical energy. Our results showed significant reductions in chlorophyll a, b, and carotenoid concentrations at low and high temperatures compared with moderate temperatures, indicating that both low and high temperatures are not favorable for the growth of *C. colocynthis*. Similarly, photosynthetic pigments decreased at low (4 °C) and high (42 °C) temperatures in two lentil cultivars (Al-Quraan et al. 2014). Besides, watermelon cultivars showed reduced chlorophyll content under high- (42/40 °C) and low-temperature (12/10 °C) stresses compared to moderate temperatures (28/20 °C) (Hou et al. 2016). When a cell is exposed to thermal stress, the photosynthetic apparatus is the first site to be disrupted (Berry and Björkman 1980; Mathur et al. 2014). Researchers have reported that low temperatures can limit enzyme activities in photosynthesis, leading to reduced chlorophyll synthesis and an overall decline in photosynthetic rates. Cold stress also causes a physical constriction of plant cell membranes, affecting the fluidity and function of chloroplasts where photosynthesis occurs (Bhattacharya et al. 2022; Aslam et al. 2022). Furthermore, high temperatures decrease the activity of the RUBISCO enzyme, harming photosynthesis (Jajoo and Allakhverdiev 2017; Sharma et al. 2020). High-temperature stress can also disrupt the structure and function of the photosynthetic apparatus, including the thylakoid membranes and photosystems I and II, further diminishing photosynthetic activity (Mathur et al. 2014; Jajoo and Allakhverdiev 2017).

The photochemical efficiency of photosystem II (PSII) is susceptible to environmental conditions such as temperature, salinity, and allelochemical stress (Ferrante and Maggiore 2007; Hussain and Reigosa 2011; Hussain et al. 2020; Panuccio et al. 2022). The maximum quantum yield of PSII, Fv/Fm, is an indicator of plant health and photosynthesis of plants after temperature treatment. Our results indicated that Fv/Fm attained a greater value in young than in old leaves of *C. colocynthis* at higher temperatures, but the opposite was true at lower temperatures (Fig. 7). Such a result indicates that *C. colocynthis* young leaves suffered less PSII damage at the higher temperature (35/45 °C). However, plants under high temperatures showed greater mature leaf

mortality at the main branches' base. Still, there was an insignificant difference in the number of green leaves between the plants at the three temperatures. Similarly, in *Acer saccharum* trees, extensive shedding of partially expanded leaves occurred immediately after exposure to high temperatures but was followed by a second flush of newly formed leaves (Filewod and Thomas 2014). During heat stress, plants reallocate resources from old to young leaves, shedding older leaves (Poorter et al. 2012). When leaves are lost due to extreme heat, long-term carbon deficits and possibly reduced plant growth are likely to occur (Aparecido et al. 2020). Therefore, leaf-shedding, resource reallocation from older to younger leaves, high efficiency of photosystem II (PSII), and dissipation of excess photon energy as heat further support a hypothesis that C. colocynthis adopts several strategies to survive the high temperature in dry arid deserts.

The lower photochemical efficiency and function of PSII (i.e., lower Fv/Fm ratio) in young leaves of C. colocynthis at lower temperatures revealed that the lower temperatures might be unfavorable for young leaves. Specifically, the relative electron transport rate (ETR) was reduced by 25 % in young C. colocynthis leaves than in mature leaves under 15/25 °C. ETR is the product of PSII's effective photochemical yield and photosynthetic photon flux density (Kromkamp et al. 1998). The reduction in ETR indicated a possible relative increase in photorespiration (Wingler et al. 1999) that reduces oxidative stress when the photosynthetic CO_2 assimilation rate is restricted (Voss et al. 2013). The result implied that the young leaves might be under stress at lower temperatures. The result was further supported by the significantly smaller branches and leaf size at lower temperatures. The overall results indicated that the lower temperatures are unfavorable for the growth and development of this species. Besides, seeds developed and matured under the lower temperature conditions attained deep dormancy, but those produced at higher temperatures fully germinated under wide ranges of light and temperatures (El-Keblawy et al. 2017; Abushamleh et al. 2022). Although C. colocynthis is a perennial evergreen species under the environmental conditions of the UAE, we observed consistently that the growth of this species was significantly reduced in the winter but increased during the summer. Under natural conditions, the temperatures could be above 45-50 °C for a few hours. However, it was evident that exposing the plants for 12 hours at 45 °C could have a deleterious impact on the overall eco-physiological performance.

Several environmental factors, including temperature stresses, can exacerbate plant oxidative damage. ROS accumulation may be enhanced by oxidative damage. In the present study, the two ROS, hydrogen peroxide H_2O_2, and Malondialdehyde (MDA) were detected in higher levels in plants grown under sub-optimal conditions (low and high temperatures) than in plants grown under moderate and favourable temperatures (Fig. 4). ROS, such as superoxide anion, hydrogen peroxide, and singlet oxygen, are extremely reactive and interact with cell compartments. One of the negative effects of ROS is lipid peroxidation, which degrades lipid-based membranes, ultimately damaging structures and cells (Suzuki and Mittler 2006). MDA is a common biomarker of lipid peroxidation and the result of lipid peroxidation in plants can be assessed accurately. In adverse environmental conditions, an increase in free radicals leads the plant to overproduce MDA, a well-known marker of oxidative stress (Gill and Tuteja 2010). MDA accumulation can damage plant cells, leading to cell death, reduced photosynthesis, and leading to lesser growth. Therefore, plants would normally adapt biologically to manage their ROS levels in order to survive (Mansoor et al. 2022).

Plants have evolved an antioxidative defense machinery to prevent oxidative damage caused by ROS (Hussain et al. 2019). It has been reported that plants with higher levels of antioxidant enzymes were more tolerant of oxidative stress. The high levels of H_2O_2 and MDA in *C. colocynthis* were associated with significant increases in the activity of superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and guaiacol peroxidase (GPX) activity at the higher than moderate and low temperatures. APX plays a major role in catalyzing the conversion of H_2O_2 into H_2O. This enzyme is the electron donor in the ascorbate-glutathione cycle that facilitates the breakdown of H_2O_2 molecules, directly protecting plant cells against adverse environmental conditions (Caverzan et al. 2012). Similarly, GPX is among the proteins detoxifying H_2O_2, primarily breaking down aromatic electron donors such as guaiacol (Sharma et al. 2012). GPX is considered a general indicator of oxidative stress and is involved in many vital biosynthetic processes and defense against abiotic stress (Mazorra et al. 2002; Sharma et al. 2012; Erofeeva 2015). When compared to the moderate temperature exposure in our study, high temperatures significantly increased the levels of APX and GPX; but low temperatures significantly reduced them. These observations indicated that these enzymes were induced in response to higher temperatures, but not during exposures to lower temperatures. Some earlier studies similarly indicated an increase in APX activity after exposure to high temperatures (Park et al. 2004; Balfagon et al. 2018). Conversely, others showed a reduction in its activity under lower temperatures (Zhang et al. 1997; Kawakami et al. 2002; Song et al. 2005). In addition, other studies showed inconsistent effects of temperatures on GPX activity. For example, similar to our study, GPX activity increased under high temperatures but decreased under low temperatures in watermelon (Rivero et al. 2001) and *Eupatorium odoratum* (Lu et al. 2008). However, in tomato plants, the GPX activity decreased at both low and high temperatures compared to moderate temperatures (Rivero et al. 2001).

Our study showed that the enzymatic antioxidants SOD and CAT activity significantly increased at both low and high compared to moderate temperatures. However, these enzymes attained significantly greater levels at high than low temperatures. The antioxidant CAT decomposes H_2O_2 into oxygen and water molecules (Mhamdi et al. 2012; Zhanassova et al. 2021). Similarly, SOD converts superoxide anion to oxygen and hydrogen peroxide as a defense against ROS (Jaleel et al. 2009). The increase in the activity of CAT and SOD at higher temperatures was proposed as an enhancement of heat-shock proteins (Prasad et al. 1994). Our results are consistent with other studies conducted on wheat and barley found the enhanced activity of CAT enzyme under high-temperature stress (Almeselmani et al. 2006; Zhanassova et al. 2021). Besides, Zhanassova et al. (2021) showed an increase in SOD activity in the roots of barley plants in response to high-temperature stress. In the present study, at low temperatures H_2O_2 and MDA increased while APX and GPX activity decreased. Accordingly, APX and GPX are not involved in detoxification and are sensitive to lower temperatures. It appears that the activity of these enzymes is species-specific in terms of their response to temperature. However, CAT and SOD activities increased; such results indicate that ROS detoxification in *C. colocynthis* plants under low temperatures might be dependent on CAT and SOD increment.

Plants may experience dehydration and reduced turgor pressure due to heat stress (Hare et al. 1998). One way of maintaining cellular hydration and turgor is by adjusting the osmotic potential. It involves the accumulation of compatible solutes, such as proline and sugars, which help stabilize the cell membranes, maintain the water balance within the cell, and protect the cells from damage caused by heat (Alhaithloul 2019). Our results indicated that the proline level was significantly increased under higher temperatures. Similarly, Alhaithloul (2019) indicated that proline and other osmotic solutes, such as mannitol, inositol, and sorbitol, were increased in response to both high temperatures and drought stress in the desert *Artemisia sieberi alba*. Besides, proline was increased in response to high temperatures in several species, including watermelons (Shin et al. 2021) and paprika seedlings (Bhandari et al. 2018). Generally, small amounts of proline occur in plants under normal conditions to maintain membrane integrity by sustaining turgor pressure (Trovato et al. 2008; Gupta and Huang 2014). However, the proline level is increased in response to environmental stress to improve plants' tolerance. It regulates mitochondrial and photosynthetic functions, prevents enzyme destruction, scavenges free radicals, maintains protein structures, and buffers cellular redox

potential (Kishor et al. 2005; Farooq et al. 2008; Hayat et al. 2012).

5. Conclusion

Citrullus colocynthis can withstand low and high temperatures by adjusting its morphological, biochemical, and physiological functions. The enhanced activities of antioxidant enzymes and higher content of proline in plants grown at high temperatures compared to those at lower and moderate temperatures indicated that *C. colocynthis* was able to adapt to thermal changes and to maintain its growth and development in the hot desert conditions. Interestingly, the ROS, antioxidant enzymes, and proline changes were not equal at the different temperature treatments, suggesting that *C. colocynthis* might plausibly harnessed differential mechanisms in response to different temperatures' scenarios. Among the other survival strategies of *C. colocynthis* for heat stress in dry, arid deserts are leaf-shedding, resource reallocation from older to younger leaves, and the high efficiency of photosystem II (PSII). Besides, the significantly lower photochemical yield and photosynthetic efficiency (with smaller leaves and branches) at lower than higher temperatures; indicated that the lower temperatures are unfavorable for the growth and development of this species. To further understand this species' adaptations to heat tolerance and its reversibility, more in-depth studies are needed to determine the molecular mechanisms that underpin the growth and resilience of this remarkable viney desert plant.

Intuitional Review Board Statement

Not applicable.

Informed Consent Form

Not applicable.

CRediT authorship contribution statement

Attiat Elnaggar: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **François Mitterand Tsombou:** Methodology, Formal analysis, Data curation. **M. Iftikhar Hussain:** Writing – original draft, Resources, Methodology, Formal analysis, Data curation. **Ahmed M. Almehdi:** Writing – original draft, Validation, Resources, Formal analysis. **Zainul Abideen:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Jean Wan Hong Yong:** Writing – review & editing, Writing – original draft, Validation, Supervision, Funding acquisition. **Ali El-Keblawy:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

On the behalf of all the authors I acknowledge these two above points.

Data availability

Data will be made available on request.

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Supplementary materials

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