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ORIGINAL ARICLE

Integrative impacts of salicylic acid and water deficit stress on physiological processes of medicinal herb *Bacopa monnieri* (L.)

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Abstract

Rapid environmental fluctuations, particularly water deficit stress, significantly hinder a plant's growth by constraining primary metabolic processes. Salicylic acid (SA), a recognized plant hormone, exhibits a noteworthy role in alleviating water stress impacts on leaf gas exchange. This study investigates the interaction between SA and water deficit (WD) stress in *Bacopa monnieri* (L.). Different SA doses (50, 75, 100, and 125 mg/l) were foliar-sprayed, with water deficit imposed by reduced irrigation (well-watered, water deficit 1, and water deficit 2). Pooled data from 2 years indicated increased electrolyte leakage and decreased photosynthetic pigments, photosynthesis rate, and protein content in WD2-stressed plants. Moderate SA concentrations with WD1 and WD2 stress positively impacted photosynthesis-related traits and enhanced defense mechanisms, reflected in increased total protein, leaf water potential, and chlorophyll stability index. Positive correlations between photosynthesis rate and antioxidants suggests SA's role in fortifying plant defense mechanisms against stress. Overall, this research underscores SA's resilient role in mitigating water deficit stress effects by regulating various physiological and metabolic processes, ultimately supporting plant growth.

Keywords *Bacopa monnieri* · Salicylic acid · Water deficit · Photosynthetic efficiency · Leaf water potential

Introduction

Plants incessantly endured stress from hostile atmospheric conditions like water deficit, salinity, heavy metals, high and low temperatures. Out of this water deficit is more inimical for plants and accelerates pervasively by inadequate rainfall and elevated temperature while excessive soil evaporation also leads to moisture deficiency in soil (Atkinson & Urwin, 2012). Water stress is more atrocious for the cultivation of highly irrigated crops and several other plants that thrive in wet and marshy places (Knapp et al., 2015). *Bacopa monnieri* (L.), an important medicinal herb belongs to Scrophulariaceae family, grown naturally in wet places and cultivated during the rainy season in India. It contains numerous secondary metabolites such as bacoside-A, brahmin, saponins, and antioxidants that could potentially cure neurodegenerative disorders and are important for memory boosting. Pharmaceutical drug manufacturing relies heavily on agricultural practices for acquiring raw materials owing to the limited availability of its wild resources. Even though Indian farmers prefer the rainy season for their cultivation because frequent irrigation is indispensable for growing crops. However, current climatic modifications, for instance, irregular rainfall patterns, rain shifting, and high temperatures, lead to water deficit stress and cause obstacles during its cultivation (Bukhari et al., 2021; Tiwari et al., 2010). Water limitation notably retarded plant growth by impairing the photosynthesis process and leaf water potential due to impeding the stomata activity. Stomatal closure is undoubtedly necessary to maintain a steady level of accessible moisture during a water deficit situation, and it also abolishes CO_2 absorption (Naeem et al., 2018). Concurrently, the photosynthetic electron chain is overly reduced because of the restriction of CO_2 uptake due to closed stomata during water stress in plants. Due to the interruption of carbon assimilation, excessive light energy is not dissipated by chloroplasts, which inevitably stimulates the formation of reactive oxygen species

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(ROS) in plants (Feng et al., 2016). Moreover, these ROS are attacked on the thylakoid membrane, PSII-associated protein (D1), and photosynthetic pigments (Batra et al., 2014; Hazrati et al., 2016). ROS-induced membrane injury enhanced the electrolyte leakage and also disturbed the plant's water status (Ahir et al., 2014; Dogan, 2020).

The responses of plants are exposed to stressful circumstances associated with certain signaling pathways that activate the stress alleviation perception with rectifying the metabolism (Jahan & Rautela, 2022; Verma et al., 2016). Meanwhile, molecular response of plants to adopt tolerance accelerated with combination of stress that influences hormonal and metabolic balance (Priya et al., 2023). In fact plant hormones act as a crucial integrator in signal cascading of resilient mechanism that responds to stress (Gupta et al., 2017; Ramegowda & Senthil-Kumar, 2015). A hormonal signaling network that mediates immunity, growth, and response to abiotic stressors is created when hormonal interactions come together (Pandey et al., 2021; Shaukat et al., 2022). In this context, salicylic acids (SA) emerge naturally in plants and pretend to be a signaling molecule, eliciting the defense response during stress and ensuring the growth (Wani et al., 2016). Meanwhile, foliar application of SA can elevate the plant's potential to withstand the water deficit stress with enhancement in photosynthetic attributes, leaf water status, and cease the electrolyte leakage (Pandey et al., 2017; Wang et al., 2020). The main objective of this study is to assess how salicylic acid interacts with water deficit stress and improving the physiological and biochemical aspects that affect plant growth and its secondary metabolites. These aspects, including leaf water potential, electrolyte leakage, pigment content, total soluble protein, photosynthetic rate, gas exchange, transpiration rate, and stomatal conductance, play a pivotal role in mitigating the stress repercussions on plants' growth.

Methods and materials

A pot experiment was carried out on *B. monnieri* (L.) at G.B Pant University of Agriculture and Technology, Pantnagar, Uttarakhand (India) during the year 2021 and same experiment was repeated in 2022 also. Three propagules of uniform thickness (10 ± 2 cm) with 3 nodes were planted in each pot (having area 0.456 m^2 with 20 kg soil capacity) with equal spacing from center. Water deficit was subjected to 1 month old plants through decreased irrigation level. Pots were divided into three levels: (i) regular irrigation (WW), (ii) 2 time irrigation within a week (WD 1) and 1 time irrigation within a week (WD 2). Freshly prepared solution of salicylic acid (SA) was applied two times as foliar spray with varied concentrations (50, 75, 100, 125 mg/l) upon all levels plants except their respective controls. Each treatment consisted of three replications, first spray was applied after one week from the water deficit treatment and 1 month later applied second spray. For physio-biochemical estimation samples were collected on the seventh day from the second spray.

Physio-biochemical estimation

Electrolyte leakage (%)

The total inorganic ions leaked out from the leaves were estimated by the method of Dionisio-Sese and Tobita (1998). After washing fresh leaves were taken in a test tube containing 10 ml of distilled water placed in a water bath at 32 °C for 10 min, and filtrate was used to measure electrical conductivity (EC1) with an electrical conductivity meter. The sample was once again placed in a water bath at 121 °C for 30 min in order to properly release the electrolytes from the tissues. The filtrate was then measured further to determine EC2. The electrolyte leakage was calculated by using the formula:

$$\text{Electrolyte leakage }(\%) = \text{EC1}/\text{EC2} \times 100$$

Chlorophyll stability index (%)

The chlorophyll stability index (CSI) was estimated using the method of Murphy (1962). One set of test tubes containing fresh leaves (1 g) was put in 20 ml of distilled water and heated in a water bath for 30 min at 65 °C. Another set was kept at room temperature. Normal and heated leaf samples were homogenized in 80% acetone, and 652 nm wavelengths were used to estimate the sample reading. The chlorophyll stability index (CSI) was calculated using the formula given below:

$$\text{CSI\%} = 1 - \frac{\text{Total chlorophyll of heated samples}}{\text{Total chlorophyll of unheated samples}} \times 100$$

Estimation of chlorophyll and carotenoid content

Chlorophyll and carotenoid content were estimated using DMSO, a method given by Hiscox and Israelstam (1979). 50 mg of fresh leaf were taken in test tubes, and 10 ml of dimethyl sulfoxide (DMSO) was added. The test tubes were incubated in a hot air oven for three hours at 65 °C. Using a multiple wavelength spectrophotometer, the absorbance of DMSO containing chlorophyll, and carotenoid content was measured after three hours of incubation at 480, 645, and 663 nm. As a blank, pure DMSO was used. The formula described by Wellburn (1994) was used to calculate the levels of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid.

Photosynthetic attributes and maximum efficiency of PSII (Fv/Fm)

Net photosynthesis rate (An), stomatal conductance (gs), transpiration (E), and intercellular carbon dioxide concentration (Ci) were determined by using a portable infrared gas analyzer (LICOR, Lincoln-6200, USA). During leaf gas exchange measurements, photosynthesisally active radiation (PAR) was set at 1250 µmol m^{-2} s^{-1} and leaf temperature at 35 °C. The maximum efficiency of PSII (Fv/Fm) in leaf samples was measured after achieving the adaptation in the dark for 10 min with the help of Handy PEA (Hansatech, UK). Observations were recorded between 9 and 11 AM to prevent photoinhibition.

Leaf water potential

The water potential (Ψw) was measured on a completely expanded middle leaf that was exposed to light, corresponding to the midday potential. A water potential apparatus (psychrometer, model PSYPRO) had been used to assess leaf water potential. A one cm leaf disc was cut and placed into the sample chamber (thermocouple). This system determined the water potential by measuring the relative humidity in equilibrium with the sample.

Total protein content

The total protein content was estimated using the method given by Bradford (1976). The leaf sample was homogenized with extraction buffer. The homogenized mixture was centrifuged for 20 min at 12,000 rpm at 4 °C. 80 µl of supernatant was taken from extracted protein samples in test tubes, and 2 ml of extraction buffer and 6 ml of dye solution were mixed together. The test tubes were incubated in the dark until the blue color developed, and the optical density at 595 nm was measured with a spectrophotometer. The protein amount in samples was calculated from the BSA standard curve.

Statistical analysis

The data was statistically analyzed using ANOVA (analysis of variance) for assessment of different attributes for each treatment. DMRT (Duncan's Multiple Range Test) was applied to determine the statistical significant level at $p < 0.05$ by using SPSS (ver. 22) statistical program. Three replications of each treatment were taken for analysis during investigation.

Results

An excessive increase in the leakage of electrolytes from cells indicates the deterioration of lipid membranes as a consequence of ROS attack, which emerges from unpleasant conditions, particularly water deficits. The water deficit exposed plants noticed upsurge of electrolyte ions leakage by 117.5%, and 90.0% in WD2 and WD1 respectively over control. However, SA (at 75 mg/l conc.) interaction with water deficit stress treatment unveiled the decline occurrence of electrolyte leakage out in both WD2 and WD1 by 7.52% and 6.26%, respectively over control. Despite the possibility that highest doses of SA (above 75 mg/l) showed the toxic interaction with water deficit treatments by upsurge in electrolyte leakage than well watered grown plants (Table 1). Meanwhile, similar SA dose without stress interaction also depicted the slight increment in amount of electrolyte ions up to 2.56% in comparison to control. Our results also indicates the significant positive correlation between oxidative indicator (H_2O_2) and electrolyte leakage ($r = 0.822^{**}$) (Table 2).

The current findings revealed the considerable constraints of water deficit stress on photosynthesis linked traits like photosynthetic pigments, chlorophyll stability index, CO_2 assimilation rate, somatal conductance, transpiration rate and intercellular CO_2 concentration. Photosynthetic pigments such as chlorophyll a, b and total chlorophyll are declined by 18.19%, 21.54% and 21.29% respectively in WD 2 in comparison to well watered control plants. Consequently, abolished level of photosynthetic pigments also impacted the chlorophyll stability index (CSI) and decline up to 20.15%, 12.12% in WD2 and WD1 significantly. The results indicate the plausible insights of SA and WD stress interaction on CSI improvement in terms of improving the amount of photosynthetic pigments. Indeed, SA (75 mg/l conc.) and WD1 stress interaction significantly upturn the chlorophyll a and chlorophyll b by 24.78%, and 19.39% including 23.07% rise in total chlorophyll amount over control. Similar insights of stress interaction with SA was recorded in terms of CSI improvement by 36.18%) in comparison to control (Table 1). Moreover, carotenoid content was also hiked in all treatments over control, but integrative treatment of water deficit stress with SA exhibited significant upsurge of carotenoid than without SA. Highest amount of carotenoid was obtained from combined treatment of WD1 and WD2 stress and SA (75 mg/l conc.) by 32.3%, and 25.7% significantly in comparison to control. The study results clearly shown that moderate conc. of SA were more significantly than high concentrations to promote the photosynthetic pigments with water deficit stress interaction. In addition, well-watered group plants were also impacted

Table 1 Integrative effects of water deficit stress and salicylic acid on physio-biochemical attributes of *B. monnieri* L.

Water level	SA (mg/l)	Chl a (mg g^{-1} FW)	Chl b (mg g^{-1} FW)	Total Chl (mg g^{-1} FW)	Caro (mg g^{-1} FW)	CSI (%)	EC (%)	LWP (MPa)
Well watered (WW)	0	0.964c	0.524a–c	1.614c	0.253a	31.23b	20.45a	− 0.270a
	50	1.146ef	0.628c	1.923fg	0.339e	36.77cd	21.86bc	− 0.360ab
	75	1.252g	0.660c	2.076h	0.391f	41.9e	20.97ab	− 0.310ab
	100	1.14ef	0.621c	1.910e–g	0.342e	37.94cd	23.98d	− 0.330ab
	125	1.121e	0.608bc	1.875ef	0.325c–e	37.24cd	24.7de	− 0.320ab
Water deficit 1 (WD1)	0	0.889b	0.468ab	1.400b	0.287a–c	27.44a	38.87c	− 0.980h
	50	1.136ef	0.577bc	1.863ef	0.328de	36.56cd	22.41h	− 0.470cd
	75	1.203fg	0.626c	1.986gh	0.335e	42.53e	21.73bc	− 0.400bc
	100	1.118e	0.603bc	1.867ef	0.332e	36.11cd	24.48de	− 0.500d
	125	1.101de	0.572bc	1.818d–f	0.311b–e	35.14c	26.1f	− 0.690f
Water deficit 2 (WD2)	0	0.789a	0.411a	1.270a	0.277ab	24.94a	44.50i	− 1.250i
	50	1.101de	0.563bc	1.808de	0.317c–e	36.36cd	25.02e	− 0.590e
	75	1.156ef	0.613bc	1.921fg	0.318c–e	39.67de	21.99c	− 0.660ef
	100	1.083de	0.599bc	1.824d–f	0.314b–e	37.92cd	26.07f	− 0.820g
	125	1.031d	0.568bc	1.732d	0.289a–d	35.15c	27.88 g	− 0.890g

Different letter(s) indicate statistically significant differences in treatment means determined by Duncan's multiple range test at $p < 0.05$ (n = 3) with all treatments compared to the normally irrigated, unsprayed group

Table 2 Correlation coefficient (r value) between H_2O_2, hydrogen peroxide; MDA, malondialdehyde; EC, electrolyte leakage; TC, total chlorophyll; CARO, carotenoid; Pn, photosynthesis rate; TSP, total soluble protein; SOD, superoxide dismutase APOX, ascorbate peroxidase; PRO, proline; and TPC, total phenolics content in 2021–2022

	H_2O_2	MDA	EC	TC	CARO	Pn	TSP	SOD	APOX	PRO	TPC
H_2O_2	1	0.891^{**}	0.822^{**}	-0.717^{**}	-0.51	-0.736^{**}	-0.663^{**}	-0.545^{*}	-0.396	-0.488	-0.396
MDA	0.891^{**}	1	0.969^{**}	-0.850^{**}	-0.507	-0.837^{**}	-0.842^{**}	-0.598^{*}	-0.401	-0.525^{*}	-0.542^{*}
EC	0.822^{**}	0.969^{**}	1	-0.878^{**}	-0.485	-0.838^{**}	-0.898^{**}	-0.566^{*}	-0.439	-0.547^{*}	-0.580^{*}
TC	-0.717^{**}	-0.850^{**}	-0.878^{**}	1	0.804^{**}	0.955^{**}	0.977^{**}	0.835^{**}	0.730^{**}	0.798^{**}	0.867^{**}
CARO	-0.51	-0.507	-0.485	0.804^{**}	1	0.803^{**}	0.717^{**}	0.861^{**}	0.870^{**}	0.800^{**}	0.809^{**}
Pn	-0.736^{**}	-0.837^{**}	-0.838^{**}	0.955^{**}	0.803^{**}	1	0.926^{**}	0.875^{**}	0.785^{**}	0.825^{**}	0.870^{**}
TSP	-0.663^{**}	-0.842^{**}	-0.898^{**}	0.977^{**}	0.717^{**}	0.926^{**}	1	0.785^{**}	0.686^{**}	0.733^{**}	0.846^{**}
SOD	-0.545^{*}	-0.598^{*}	-0.566^{*}	0.835^{**}	0.861^{**}	0.875^{**}	0.785^{**}	1	0.733^{**}	0.841^{**}	0.912^{**}
APOX	-0.396	-0.401	-0.439	0.730^{**}	0.870^{**}	0.785^{**}	0.686^{**}	0.733^{**}	1	0.819^{**}	0.812^{**}
PRO	-0.488	-0.525^{*}	-0.547^{*}	0.798^{**}	0.800^{**}	0.825^{**}	0.733^{**}	0.841^{**}	0.819^{**}	1	0.864^{**}
TPC	-0.396	-0.542^{*}	-0.580^{*}	0.867^{**}	0.809^{**}	0.870^{**}	0.846^{**}	0.912^{**}	0.812^{**}	0.864^{**}	1

**Correlation is significant at $p < 0.01$ *Correlation is significant at $p < 0.05$

a similar manner when SA was applied without stress integration.

During current investigation, we measured gas exchange attributes such as stomatal conductance, intercellular CO_2, and transpiration rate to determine the photosynthesis rate in *B. monnieri* (L.) plants subjected to combined water deficit stress and SA treatment. The study found that the plants exposed to WD2 experienced a 26.55% decline in their photosynthesis rate compared to control. Additionally, a similar pattern of depreciation was observed in intercellular CO_2 concentration, stomatal conductance, and transpiration rate, with an 8.80%, 58.20%, and 38.28% decrease, respectively, in the WD2 stress plants as compared to control. We also analyzed the negative correlation between oxidative indicators and Photosynthesis traits [total chlorophyll ($r = -0.717^{**}$) and photosynthesis rate ($r = -0.736^{**}$)] that depicted in Table 2. Our research displayed that, in contrast with the control, the stress interaction with 75 mg/l of SA raised the photosynthetic rate by 25.32% and 29.14% in WD2 and WD1 sequentially. Apart that similar dose of SA also applicable in relation to increase photosynthesis rate by 36.09% in non-stressed plants over control. The study suggested that SA may play a role in regulating the function of stomata, which are the tiny pores on plant leaves that control gas exchange. The experiment showed that a dose of 75 mg/l of SA combined with WD1 resulted in a slight increase of 3.03% in stomatal conductance and a 6.53% increase in transpiration rate. Meanwhile, the same SA concentration also promoted the increment in intercellular CO_2 (Ci) by 18.4% in WD2 compared to the control (Fig. 1). Current results was also showed significant positive correlation between photosynthesis rate and SOD ($r = 0.875^{**}$), APOX ($r = 0.785^{**}$) (Table 2). The study outcomes also depicted that WD2 condition negatively influence the value of maximum efficiency of PSII photochemistry (Fv/Fm) significantly by 5.88 decline over control without SA. Meanwhile, WD1 stress shown insignificant changes in Fv/Fm value without SA. Although, those water deficit plants treated with SA foliar application (75 mg/l) found higher Fv/Fm by 9.18% (WD1), 6.73% (WD2) in comparison to control (Fig. 2).

Water potential is useful variable to evaluate the physiological water status of plants. In comparison to control plants (− 0.27 MPa), the WD2 plants significant decline the water potential by − 1.25 MPa. However, the plants sprayed with SA able to revive the leaf water status than non-treated ones over water limited situations (Fig. 3). Out of all the doses of SA, it was found that the moderate dose had the most efficient impact on the leaf water potential along with water deficit stress. Plants treated with 75 mg/l of SA had the highest leaf water potential when combined with water deficit stress, e.g., WD1 (− 0.40 MPa), while 50 mg/l of SA was more suitable for WD2 (− 0.59 MPa) (Table 1). Water deficit stress suppressed the growth and development of plant accompanied by ROS induction which prominently strikes the bio-molecules such as protein. The current investigation also exhibited the decline in total protein amount in *B. monnieri* (L.) by 33.17% at WD2 and 27.94% at WD1 in comparison to control. It was found that total protein content was elevated in Bacopa plants with integrative treatment of water deficit stress (WD1 and WD2) and SA (75 mg/l) foliar application, showing an upsurge 26.58% and 21.22% than control. Furthermore, mild SA conc. also showed positive insights in relation to total protein (30.43%) enhancement in non stressed plants over control (Fig. 2b).

Discussion

The ability of cell membranes to hold on to water and minerals that is indispensable for the proper functioning of the cell. Reactive oxygen species (ROS) were produced in excess during the drought or water deficit condition, which stimulates the deterioration of membrane integrity and permits ion leakage (Gill & Tuteja, 2010; Sedaghat et al., 2017). Current investigation affirmed the overabundance of electrolyte ions leakage in plants when exposed to water deficit-induced stress. In line with current outcomes prior study also favored the interaction of water stress and excess electrolyte leakage in *Curcuma alismatifolia* (Jungklang et al., 2017), and *Ocimum basilicum* (Zulfiqar et al., 2021). Nonetheless, earlier investigations agreed about salicylic acid efficiency to abate the water deficit induced electrolyte leakage in many plants like *Impatiens walleriana* (Safari et al., 2021), *Gardenia jasminoides* (Yao et al., 2016), and *Stevia rebaudiana* (Janah et al., 2021). According to the current investigation, the SA foliar application resolved the water deficit-induced toxicity in *B. monnieri* in terms of electrolyte leakage. Our findings are consistent with *Solanum lycopersicum* in relation to elevated growth and yield including decline electrolytes leakage under combined treatment of salicylic acid and drought (Chakma et al., 2021). Similarly, SA plays a potential role to curtail the electrolyte leakage in *Pistacia vera* (L.) when exposed to osmotic stress (Bastam et al., 2013).

A longer duration of water restriction leads to impairment in photosynthetic pigments, which is responsible for light interception and electron transfer excitation processes (Doupis et al., 2013). Their degradation decreased the photochemical activity of PSII (Fv/Fm) which leads to increased excitation energy, resulting in excessive energy, ROS production, and lipid peroxidation thus inhibiting NADPH oxidation and electron transfer to the reaction centers (Wang et al, 2021; Zhao et al., 2021). The present investigation depicted that water deficit exposed plants significantly decline the photosynthetic pigments and maximum efficiency of PSII photochemistry (Fv/Fm) than well watered. In agreement with our findings, reduced soil moisture hinders the photosynthesis process through impaired the chlorophyll in *Thymus daenensis* (Bahreininejad, 2013). Moreover, similar repercussions of water deficit stress leads to growth retardation due to decline content of chlorophyll in *Valeriana officinalis* (Mustafavi et al., 2016). Even that the SA able to mitigates thylakoidal depletion and lumen deformation, preserving the structural integrity of chloroplasts under drought stress by detoxifying ROS (Lobato et al., 2021; Mubarik et al., 2021). Apart from that SA helps to delay the D1 protein degradation and functional damage to PSII including improved the adenosine triphosphate (ATP) production (Shemi et al., 2021). SA was also found to be more effective in enhancing the photosynthetic pigments level in *Allium hirtifolium* (Yousefv et al., 2022), and *Ocimum basilicum* (Damalas, 2019) over water deficit induced stress. Plants that have a higher level of chlorophyll, which is indicated by a high chlorophyll stability index (CSI), are able to withstand stress and produce more dry matter. Conversely, water deficit stress diminishes the production of chlorophyll and accelerates its breakdown, which leads to a decrease in the CSI values (Mohan et al., 2000). Present results displayed

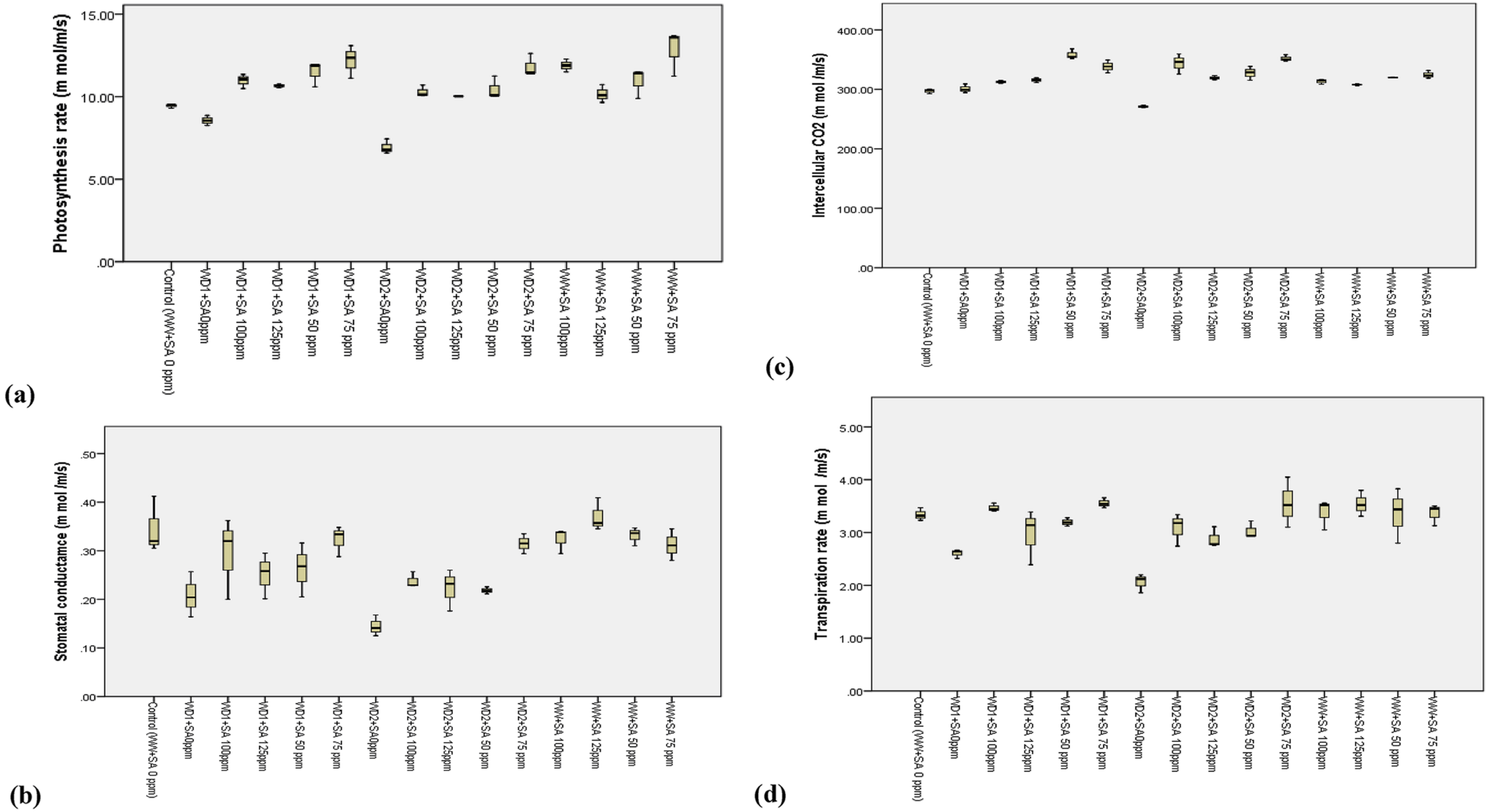

Fig. 1 Boxplot depicting the dispersion of 15 different treatments (water deficit stress with or without SA and control) on photosynthetic attributes **a** photosynthesis rate, **b** stomatal conductance, **c** intercellular CO_2, and **d** transpiration rate of *B. monnieri* (L.). Experiment was repeated twice (2021 and 2022), and pool data of each treatments estimated by t-test (n = 3). Inside the Whisker boxplot, the bold line represents the median; box edges represent upper and lower quartiles and excluding outliers for error. (WW, well watered; WD1, water deficit 1; WD2, water deficit 2; SA, salicylic acid)

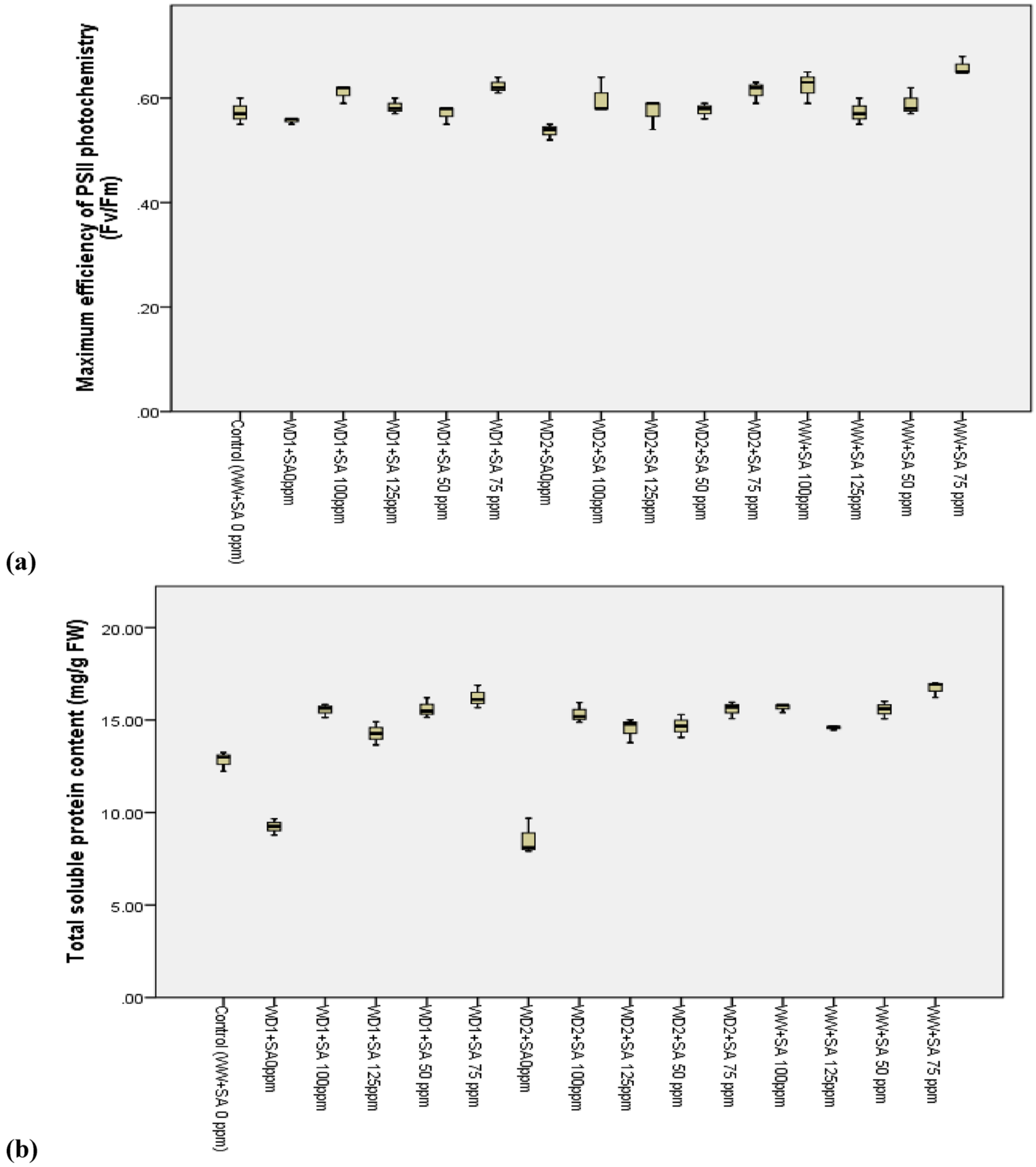

Fig. 2 Boxplot depicting the dispersion of 15 different treatments (water deficit stress with or without SA and control) on **a** maximum efficiency of PSII photochemistry (Fv/Fm) and **b** total soluble protein content in *B. monnieri* (L.). Experiment was repeated twice (2021 and 2022), and pool data of each treatments estimated by t-test (n = 3). Inside the Whisker boxplot, the bold line represents the median; box edges represent upper and lower quartiles and excluding outliers for error. (WW, well watered; WD1, water deficit 1; WD2, water deficit 2; SA, salicylic acid)

the detrimental consequence of water deficit stress on CSI of Bacopa plants. The previous study favored our results about the impact of water stress on CSI and showed its association with chlorophyll pigment impairment due to oxidative stress in wheat (Ravichandran et al., 2018). Furthermore, several reports claimed that SA significantly recover the photosynthetic pigments stability during water deficit stress treatment in *Brassica juncea* (Godara et al., 2016), and *Mangifera indica* (Hmmam et al., 2022). Carotenoid serves as protective pigment and disperses the excess excitation energy due to photoxidation in plants (Tattini et al., 2004). Reports support the SA role as protective molecule which linked with carotenoid enhancing, which help to detoxify the drought stress in *Mentha arvensis* (Elhakem, 2019). In agreement of present results, prior study also showed SA relation in carotenoid enhancement in *T. vulgaris* and *M. piperita* over drought (Jahani et al., 2021; Khalil et al., 2018). Due to water deficit situation within root zone, water uptake consistency hindered and plants instantly close their stomata and maintain water status but that response impacted the gas

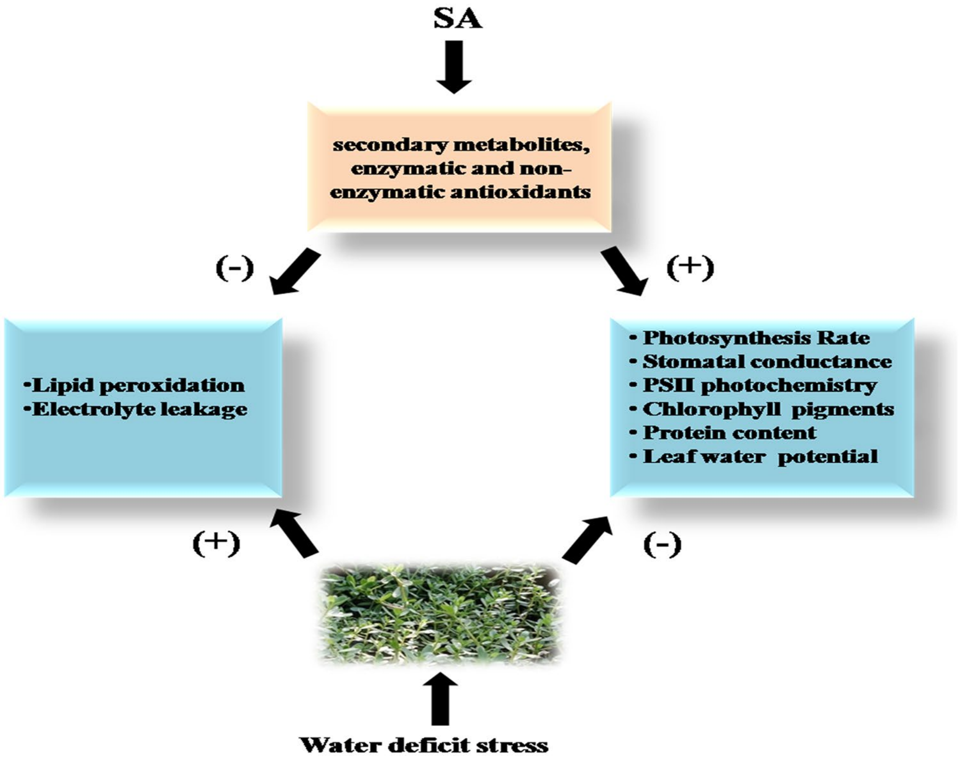

Fig. 3 Diagrammatic representation depicting the physiological response of *B. monnieri* (L.) towards the integrative treatment of salicylic acid (SA) and water deficit stress Physiological processes trending upward are indicated by a positive (+) sign, while a negative (−) sign represents a declining trend

exchange attributes also (Bacelar et al., 2007). In mild water deficit, stomatal closure causes a decrease in photosynthetic rate. This decline can be attributed to a reduction in ATP synthase due to decreased stomatal conductance in plants, leading to low ATP content (Santos et al., 2009). The current finding also indicates the water deficit induced oxidative stress influenced the gas exchange attributes like stomatal conductance, internal CO_2, and transpiration rate consequently strike the photosynthetic rate of *B. monnieri* (L.). Even that SA administration regulates the stomata function by triggering the anti-oxidative mechanisms including ethylene and ABA action in plants under Water stress (Iqbal et al., 2022). It has been observed that SA enhances photosynthetic rate by controlling stomatal closure in soybean plants exposed to PEG-induced water stress (Tang et al., 2017). Our recent study also indicates the SA's role in provoking plant tolerance in terms of accelerated antioxidants and secondary metabolite (bacoside-A) amount with water deficit stress interaction in *B. monnieri* (Jahan et al., 2023). Research findings clear the SA association with drought tolerance in olive plants with enhanced SA concentration endogenously during water deficit treatment (Abboud et al., 2021). Besides that, current findings displayed the ameliorative efficiency of SA concerning photosynthesis-associated attributes in stressed Bacopa. A recent report also favored our findings about SA application for substantially improving the photosynthetic efficiency of *Aristotelia chilensis* by prompting the antioxidants under drought stress (González-Villagra et al., 2022). SA regulates the uptake and fixation of carbon in the chloroplasts by inducing high activity of RUBISCO that stimulates CO_2 assimilation and promotes plant growth (Khalvandi et al., 2021). Furthermore, drought and SA interaction with Rubisco activation were affirmed by transcription analysis of the Rubisco large subunit (RbcL) in *Zea mays,* which assisted CO_2 assimilation (Shao et al., 2018).

Leaf water potential is a crucial physiological indicator for gauging plant water stress responses reliably (Chowdhury et al., 2017). The study revealed a noteworthy decrease in water potential due to drought, shifting from − 0.88 MPa in unstressed leaves to − 1.18 MPa in stressed soybean plants (Makbul et al., 2011). The current investigation affirmed the decline in leaf water potential under water deficit stress, but the application of salicylic acid (SA) spray ameliorated this, improving leaf water potential amid water stress. Previous research has established SA's beneficial role in mitigating water stress impacts on *Eucalyptus globule* by enhancing antioxidants and osmolytes, thereby sustaining water potential (Jesus et al., 2015). Similarly, in *Vigna radiate*, osmotic stress induced a water potential decrease, whereas SA administration resulted in an increase (Syeed et al., 2021). Water deficit-induced free radicals can damage proteins and expedite degradation, impacting biomass accumulation in plants, as corroborated by Jahan et al. (2022). Consistency with prior research is found in the mannitol-induced osmotic stress effect on *B. monnieri*'s regenerative shoot growth, attributed to reduced protein content akin to water stress (Debnath, 2008). This aligns with another study demonstrating increased protein content in *Verbascum sinuatum* sprayed with SA under PEG-induced drought conditions (Karamian et al., 2020).

Conclusions

The present study interpreted the intimate interaction between water deficit stress and SA as improving the physiological response of *B. monnieri*. Stress interactions with SA significantly promoted photosynthesis-related traits and protein synthesis, which ultimately play a crucial role in biomass formation. Besides that, amended stomata activity and osmolyte synthesis help to sustain leaf water status in SA-WD stress exposed plants. It seems that integrative SA-WD stress treated plants accomplish this by up-regulating defense mechanisms like the synthesis of secondary metabolites and antioxidants. Despite this, the relationship between stress and SA on plant signaling, as well as the feedback these signals have on the systems regulating endogenous SA levels, must be explored through molecular research. In future, an integrated study combining genomics, computational biology, and molecular biology may yield more accurate information on the plant defense response and physiological modulation mediated by SA-WD stress. Overall, the current outcomes substantiate that stress and SA interaction are more beneficial to cultivating high-quality medicinal plants. And that perception could also help cultivation practices in drought-prone areas by curtailing excess irrigation demand.

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Declarations

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