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Salvia officinalis photosynthetic parameters capability to stand different salt stress levels

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ABSTRACT

Salvia officinalis, commonly known as sage, is a medicinal plant valued for its therapeutic properties. This study investigates the effects of salt stress on *S. officinalis* L., focusing on its vegetative growth, and photosynthetic performance under varying salinity levels (5, 25, 50, 100, 150, and 200 mM) and the duration of exposure. Salt stress significantly reduced shoot length, leaf relative water content (RWC), and overall plant growth, primarily due to decreased soil water potential, ion toxicity, and disrupted nutrient balance. Prolonged exposure to high salinity further impaired cell division and elongation, exacerbating growth inhibition. Photosynthetic efficiency (P_N) declined under salt stress, with short-term exposure causing rapid but temporary reductions, while long-term exposure led to sustained decreases driven by stomatal limitations (reduced stomatal conductance, Gs, and transpiration rate, *E*) and non-stomatal factors such as toxic ion accumulation and reduced enzymatic activity. The study highlights the role of water-use efficiency (WUE) in mitigating salt stress, as sage seedlings accumulated compatible solutes to maintain osmotic balance and sustain photosynthesis. This adaptive mechanism enabled plants to reduce water loss and cope with ion toxicity, enhancing resilience to salinity. However, physiological responses were strongly influenced by both the intensity and duration of salt exposure, with higher concentrations and prolonged stress amplifying negative effects. These findings underscore the complex interplay of osmotic, ionic, and photosynthetic adjustments in *S. officinalis* under salt stress, providing insights into its adaptive strategies and limitations in saline environments. To deepen our understanding of how plants tolerate salt stress and to develop strategies for enhancing crop resilience, it is essential to conduct further research that quantifies the accumulation of compatible solutes – such as proline, sugars, and organic acids – in leaves subjected to saline conditions. These solutes play a crucial role in mitigating the adverse effects of salt stress.

Keywords: *Salvia officinalis*, photosynthetic performance, salt stress, responses.

INTRODUCTION

Salt stress poses a significant challenge that interferes with crop growth, decreases yields, and adversely affects plant health. Its detrimental effects are evident in various forms, including morphological changes like stunted growth, chlorosis, and poor seed germination (Hasanuzzaman and Fujita, 2022; Alsharafa, 2023b; Balasubramaniam et al., 2023). Physiologically, it leads to reduced photosynthesis and nutrient imbalances (Atta et al., 2023; Balasubramaniam et al., 2023), while biochemically, it causes oxidative stress, electrolyte leakage, and destabilization of cell membranes (Kumar et al., 2021; Zhao et al., 2021). The effects of salinity can be divided into two primary phases: the first phase involves osmotic stress, which occurs early as increased salt uptake lowers water potential around the roots, restricting water flow into plant cells and hindering growth (Hasanuzzaman and Fujita, 2022; Alsharafa, 2023b; Balasubramaniam et al., 2023). Prolonged exposure to salt leads to the accumulation of toxic ions over time, further disrupting nutrient absorption and causing significant damage to plant cells and tissues (Kumar et al., 2021;

Zhao et al., 2021). *Salvia officinalis* L., commonly known as sage, is a perennial herb belonging to the Lamiaceae (mint) family. It has been widely utilized in traditional medicine and culinary practices for centuries (Abu-Darwish et al., 2013; Jedidi et al., 2019; Salević et al., 2022). Extensive research has been conducted to investigate the biological properties and traditional applications of *S. officinalis* (Ghorbani and Esmaeilizadeh, 2017). The aerial parts of the plant are rich in a variety of phytochemicals, such as phenolic compounds, flavonoids, fatty acids, terpenes, terpene derivatives, and primary metabolites (Ghorbani and Esmaeilizadeh, 2017; Es-sbihi et al., 2021). However, the concentration and composition of these metabolites are significantly influenced by environmental factors (Russo et al., 2013). Among these, drought and salinity are the most critical stressors affecting the phytochemical profile of *S. officinalis* (Nowak et al., 2010; Es-sbihi et al., 2021; Mohammadi-Cheraghabadi et al., 2021).

Salinity stress negatively impacts plant growth, development, and primary carbon metabolism, primarily due to ion toxicity. It induces oxidative stress, physiological water deficits, and nutrient imbalances in plants. The accumulation of sodium (Na^+) and chloride (Cl^-) ions in the soil increases osmotic potential, disrupts nutrient uptake, and causes toxicity, all of which hinder plant growth and development. These effects are influenced by the intensity and duration of salinity exposure (Biswas et al., 2011; Rehman et al., 2019).

Salvia officinalis exhibits moderate salinity (75 mM NaCl) tolerance (Taarit et al., 2010). Other species in the Lamiaceae family, such as *Rosmarinus officinalis* (rosemary), demonstrate moderate salinity tolerance (Tounekti et al., 2008). In contrast, *Mentha spp.* (mint) and *Ocimum basilicum* (basil) are more sensitive to salinity, with high salt levels causing stunted growth, reduced essential oil yield, and leaf yellowing (Aziz et al., 2008; Ciriello et al., 2024). *Thymus vulgaris* (thyme) and *Origanum spp.* (oregano) show moderate salinity tolerance, employing strategies like ion exclusion and osmotic adjustment to cope with salt stress (Bistgani et al., 2019; Azimzadeh et al., 2024). Overall, while some Lamiaceae species like rosemary and thyme are relatively salt-tolerant, others like sage and basil require careful management in saline environments.

In *S. officinalis*, salinity stress has been shown to reduce plant height, chlorophyll content, and essential oil production. These changes impair photosynthetic efficiency and may accelerate leaf senescence (Kulak et al., 2020; Chele et al., 2021; Es-sbihi et al., 2021). This study aimed to evaluate the effects of varying salt stress levels and exposure durations on the growth parameters and photosynthetic performance of *S. officinalis*. The findings provide valuable insights into the plants adaptive mechanisms and limitations under saline conditions.

MATERIAL AND METHODS

Plant growth condition.

The *S. officinalis* seedlings are cultivated under controlled conditions, receiving 14 hours of light at approximately 80 μmol m^{-2} s^{-1} at 21 °C, followed by 10 hours of darkness at 20 °C, with a relative humidity of 55–60%. Afterward, they are transplanted into a soil mix of peat moss, perlite, and vermiculite in a 2:1:1 ratio. Following six weeks of growth, the plants undergo salinity treatments for varying durations.

Salinity stress treatment.

To induce salinity stress, 6-week-old growing seedlings are used in salinity treatments as designed previously (Al-Sammarraie *et al*., 2020). 6-weeks-old plants irrigated with a 5 (Control samples irrigated with tap water), 25, 50, 100, 150, or 200 mM NaCl solution three times per week for up to 8 days. Leaves samples were collected at 2, 4, 6, and 8 days of treatment.

Analysis of growth parameters

The root and shoot length of seedlings will be measured on 2, 4, 6 and 8 days of salinity stress (Bandurska *et al*., 2012).

Assessment of leaf relative water content

The relative water content (RWC) of the shoot was determined using fully expanded leaves from four plants per treatment. The shoots were cut and immediately weighed to record the fresh weight (FW). They were then submerged in deionized water in a petri dish and incubated for 48 h to achieve full turgidity, after which the turgid weight (TW) was measured. Subsequently, the shoots were oven-dried at 65

°C for 96 h and weighed again to obtain the dry weight (DW). The RWC was calculated using the formula: [(FW- DW) × (TW—DW)] × 100 as described by Turner (1986) and Bandurska *et al*., (2012).

Photosynthesis measurements

To assess certain aspects of photosynthesis, including the net photosynthetic rate (P_N), stomatal conductance (Gs), intercellular CO_2 concentration (Ci), photosynthetic water use efficiency (WUE), and transpiration rate (E), a portable photosynthesis device named CIRAS-3, developed by PP Systems in Amesbury, MA, USA, will be utilized. The CIRAS-3 will automatically collect data at 5-second intervals. Additionally, the device incorporates an automatic control mechanism to maintain specific environmental conditions during measurements. These conditions include a constant CO_2 concentration of 380 µmol mol^{-1}, a relative humidity of 60%, and a leaf temperature of 28 °C. The experiments will be conducted under a photon flux density of 80 µmol m^{-2} s^{-1}, as described by Alsharafa (2023c).

Statistical analysis

For all experiments, samples were analyzed and all the assays were carried out in triplicate. Results are expressed as mean ± SD. ANOVA and Tukey's test performed the comparison between means and the *P* value of ≤ 0.05 was considered significant.

RESULTS

S. officinalis growth parameters changes

Different salt stress levels influenced the growth parameters of *S. officinalis* plants. The shoot length shows significantly lower changes than the control (Fig. 1), indicating a negative effect of salt stress levels on shoot growth. However, the root length did not significantly change compared to the control, indicating no adverse effect of salt stress levels on root growth (Fig. 2).

Long-term exposure to salt stress elevation (100, 150, and 200 mM) reflects the deleterious imposition of salinity on shoot length. In this point; 100 mM NaCl reduced shoot growth by 6 and 15% of shoot growth after 6 and 8 days of exposure respectively. Shoot growth reduction of 150 mM NaCl application reached 10, 22, and 31% of shoot growth after 4, 6, and 8 days of exposure respectively. Moreover, 200 mM NaCl application caused growth reduction reached 6, 15, and 38% after 4, 6 and 8 days of exposure respectively.

Relative water content *S. officinalis* leaves

To assess salt stress elevation and duration of exposure impact on plant growth, we measured the relative water content as presented in Figure 3. The relative water content estimation indicated long-term exposure to salt stress elevation (150 and 200 mM) reduced RWC. 150 Mm NaCl reduced leaves RWC by 18%, 13%, and 7% after 4, 6, and 8 days of exposure, respectively, compared with the control. While 200 Mm NaCl reduced

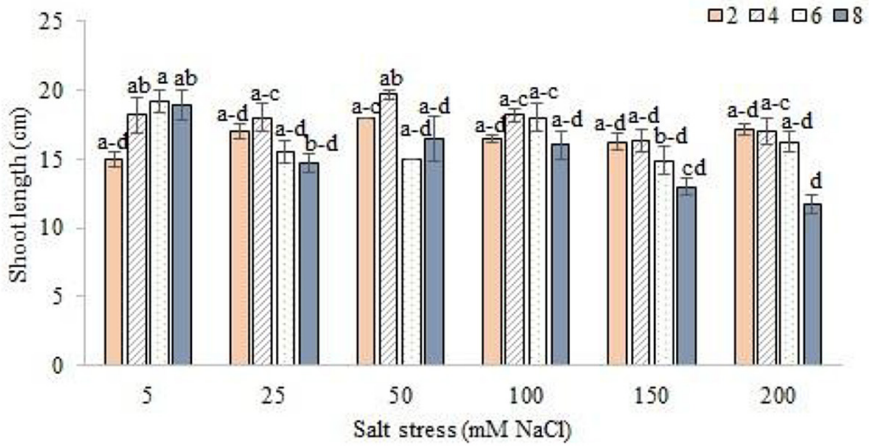

Figure 1. Effects of salt stress on the shoot length of *S. officinalis*. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 3. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$)

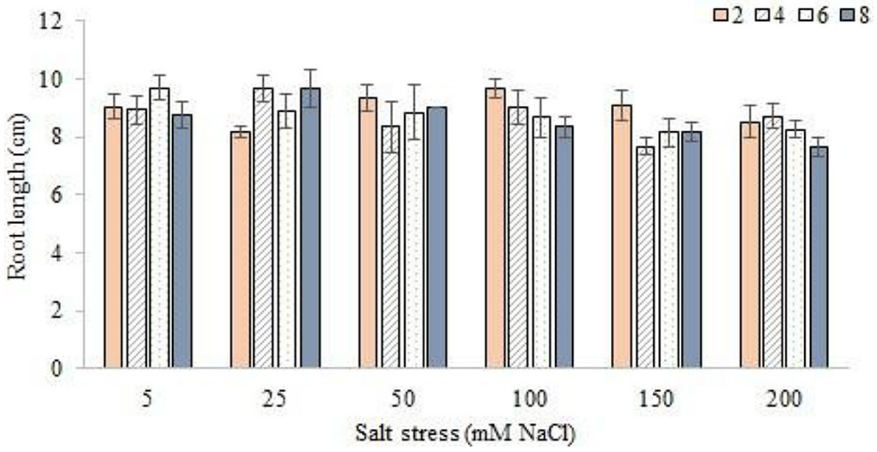

Figure 2. Effects of salt stress on the root length of in *S. officinalis*. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 3. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$)

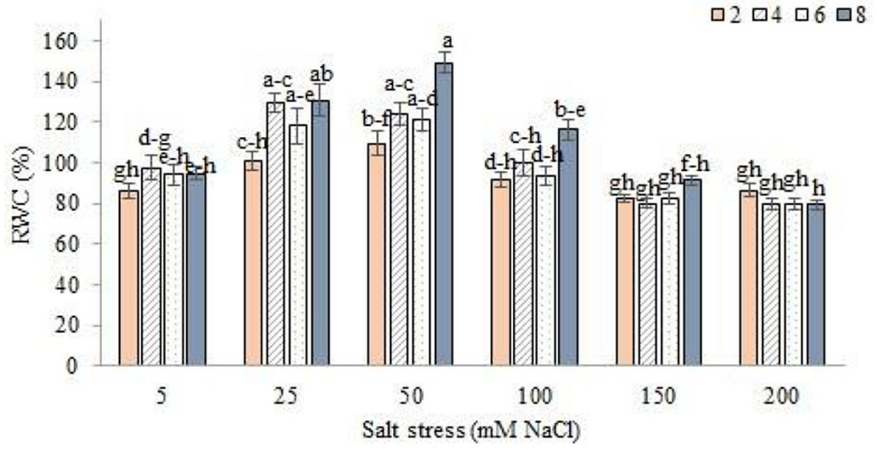

Figure 3. RWC of *S. officinalis* leaves subjected to salinity stress. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 18. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$)

leaves RWC by 18%, 16%, and 17% after 4, 6, and 8 days of exposure respectively, compared with the control.

Photosynthesis data

The net photosynthetic rate (P_N; µmol CO_2 m^2 s^{-1})

The net photosynthetic rate of *S. officinalis* leaves was affected in different manners by the duration of salt stress exposure and salt stress elevation that resulted from the application experienced in this study (Fig. 4). 25 mM NaCl salt stress level exhibited a significant reduction of leaves P_N reaching 33 and 22% after 2 and 4 days of exposure, respectively, compared with the control. While 50, and 100 mM salt stress levels reduced P_N reached 61 and 72% after 2 days of exposure, respectively, then recovered this reduction to reach 10 and 17% after 4 days of exposure, respectively, compared with the control. 150 mM NaCl salt stress level exhibited a significant reduction of leaves P_N reaching 20 and 18% after 2 and 4 days of exposure, respectively, compared with the control. At these durations of exposure, 200 mM salt stress level, significantly reduced leaves P_N to 35 and 50%, respectively, compared with the control. The severe effect of salt stress appeared after long-term exposure (6 and 8 days) for all salt stress elevations (25, 50, 100, 150, and 200 mM) that significantly reduced to 90, 91, 92, 90, and 92% after 6 days of exposure, respectively, compared with the control. Moreover, the significant reduction reached 82, 82, 85, 88, and

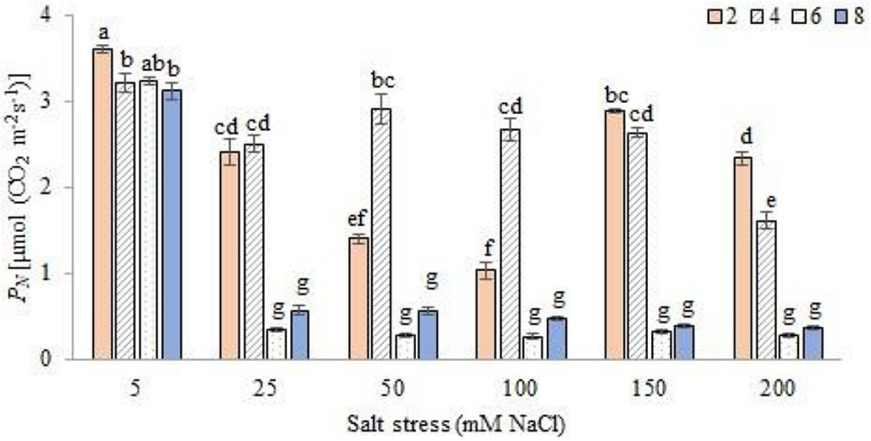

Figure 4. Net photosynthetic rate (P_N) of *S. officinalis* leaves subjected to salt stress. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 7. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$). Bars bearing different letters indicate significant differences

89% after 8 days of exposure, respectively, compared with the control.

Photosynthetic water use efficiency (WUE; mmol CO_2 mol^{-1} H_2O)

Photosynthetic water use efficiency of *S. officinalis* leaves evaluation during various salt stress levels presented in Fig. 5. WUE was significantly reduced in sage leaves grown in 25 mM NaCl salt stress level as the duration of salt stress increased (4, 6, and 8 days) by 33, 68 and 64% respectively, compared with control. Sage plants grown in 50 mM NaCl salt stress level showed significantly reduced WUE of about 8, 43, and 41% after 2, 4, and 6 days of exposure respectively, compared with the control. 100 mM NaCl treatment reduced WUE significantly by about 5, 4, and 11% after 4, 6, and 8 days of exposure respectively, compared with the control. This response of WUE was similar after treatment with 150 mM NaCl which caused a 10, 12, and 6% reduction after 4, 6, and 8 days of exposure respectively, compared with the control. Early reduction of WUE appeared after 200 mM NaCl treatment that showed 3, 25, 22, and 10 % significantly decreased WUE levels after 2, 4, 6, and 8 days of exposure respectively, compared with the control.

Transpiration rate (E; mmol H_2O m^2 s^{-1})

Salt stress reduces *E* significantly, with more pronounced effects observed at higher salinity levels and exposure time (Fig. 6). Low NaCl dose

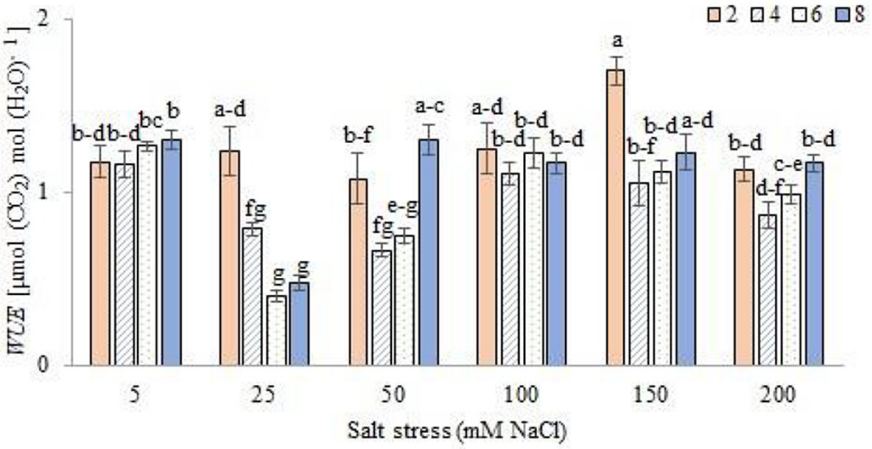

Figure 5. Water use efficiency (WUE) of *S. officinalis* leaves subjected to salt stress. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 7. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$). Bars bearing different letters indicate significant differences

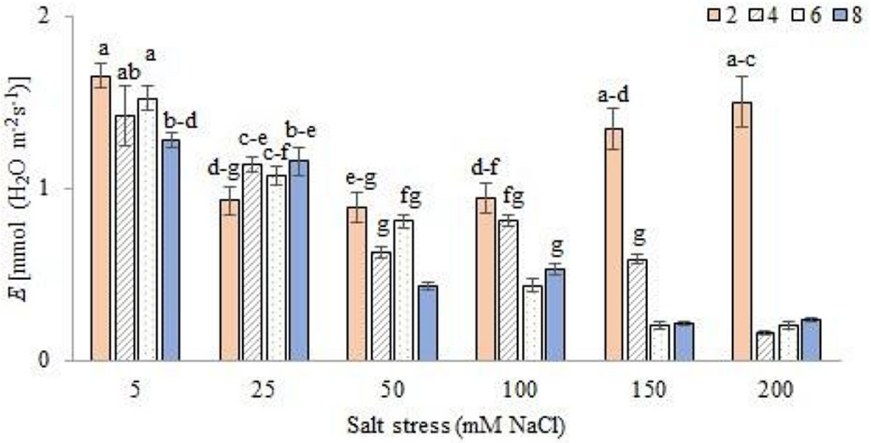

Figure 6. Transpiration Rate (*E*) of *S. officinalis* leaves subjected to salt stress. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 8. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$). Bars bearing different letters indicate significant differences

treatment (25, and 50 mM) showed 44, 43, 72 and 59% significant *E* reduction of sage leaves after 2, 4, 6, and 8 days of 25 mM NaCl treatment respectively, compared with the control. While sage leaves response to 50 mM NaCl treatment exhibited 47, 56, 47, and 66% significant *E* reduction after 2, 4, 6, and 8 days respectively, compared with the control. 100 mM NaCl treatment left sage leaves close to reduction levels of 50 mM NaCl treatment which showed 43, 43, 72, and 59% significant *E* reduction after 2, 4, 6, and 8 days respectively, compared with the control. High NaCl dose treatment (150 and 200 mM) had a severe impact on sage leaves *E* which significantly decreased after 2, 4, 6, and 8 days of 150 mM exposure reaching 17, 59, 87, and 82% respectively, compared with the control. In contrast, 200 mM exposure significantly decreased *E* to 9, 89, 87, and 82% after 2, 4, 6, and 8 days respectively, compared with the control.

Stomatal conductance (Gs; mol $CO_2 m^2 s^{-1}$)

Figure 7 shows that different exposure times and salt levels affected the *Gs* of *S. officinalis* leaves by significant reduction from the control. The *Gs* of *S. officinalis* leaves reduced significantly to 25 mM NaCl treatment, reaching 71, 53, 67, and 55% lower than the control after 2, 4, 6, and 8 days, respectively. At 50 mM NaCl treatment, *Gs* of *S. officinalis* leaves response was 66, 64, 74, and 86% lower than the control after 2, 4, 6, and 8 days, respectively. Rising NaCl dose treatment to 100

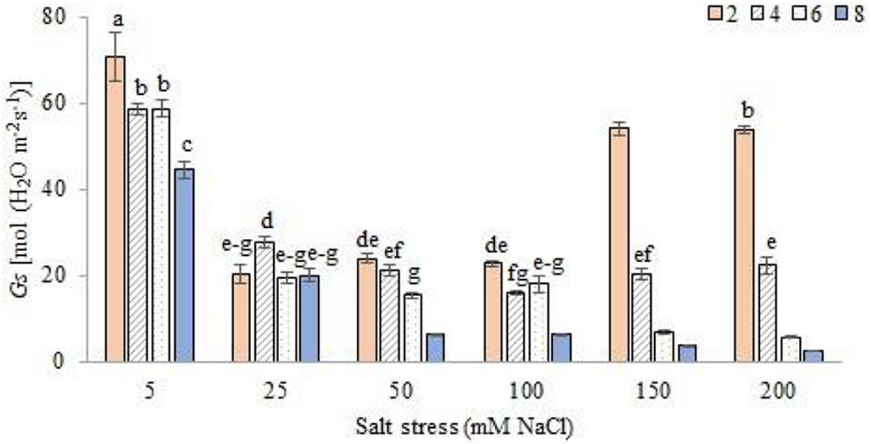

Figure 7. Stomatal conductance (*Gs*) of *S. officinalis* leaves subjected to salt stress. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 8. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$). Bars bearing different letters indicate significant differences

mM nearly kept a similar response to that 50 mM treatment that reached 68, 73, 69, and 86% lower than the control after 2, 4, 6, and 8 days, respectively. High NaCl dose treatment (150, and 200 mM) showed a similar response and became stronger and reached 24, 65, 85, and 92% significant *Gs* reduction of sage leaves after 2, 4, 6, and 8 days of 150 mM NaCl treatment, respectively, compared with the control. While sage leaves response to 200 mM NaCl treatment exhibited 24, 62, 90, and 94% significant *Gs* reduction after 2, 4, 6, and 8 days respectively, compared with the control.

Internal CO_2 concentration (C_i; µmol mol^{-1})

The level of salt stress and duration of salt exposure had significant effects on C_i when compared to non-salt-stressed sage leaves (Fig. 8). Salt stress levels (25, 50, and 100 mM) exhibited early significant reduction of C_i from the control after 2, 4, 6, and 8 days, respectively reached 36, 4, and 8% of 25 mM, 26, 8, 12, 18% of 50 mM, and 25, 21, 14, and 6% of 100 mM. In contrast, high salt stress levels (150, and 200 mM) had a low reduction impact which reached 24, 17, and 9% after 4, 6, and 8 days, respectively of 150 mM compared to the control. C_i reduction from the control of sage plants to 200 mM exposure reached 11 and 14% after 4, and 6 days, respectively compared to the control.

DISCUSSION

The current findings indicate that salt stress affects the vegetative parameters of *S. officinalis* L. Previous studies have also reported the adverse effects of salt stress on the growth of *S. officinalis* L. (Aslani and Razmjoo, 2018; Essbihi et al., 2021). Extended exposure to salt stress at increasingly high concentrations (100, 150, and 200 mM) underscores the severe consequences of salinity on shoot length. The observed decline in growth parameters under salinity stress can be explained by the decreased soil water potential, which reduces cell water content, thereby impairing plant growth and heightening ion toxicity (Kadıoğlu, 2021; Alsharafa, 2023b; El-Khadir et al., 2024). Moreover, as salt stress increases, the accumulation of ions disrupts the balance of essential nutrient ratios and concentrations, ultimately impeding optimal plant growth (Kulak et al., 2020). Additionally, salinity stress negatively affects cell division and elongation, leading to a decrease in overall plant growth (Kamran et al., 2020; Bayat et al., 2022; Alsharafa, 2023b).

The relative water content (RWC) of leaves is a reliable indicator of plant water status during periods of stress, reflecting a plants ability to maintain water balance and resist water loss under adverse conditions (Parida and Das, 2005). This study found that irrigating *S. officinalis* with saline water significantly decreased the RWC of its leaves, dependent on both the intensity of salt stress and the duration of exposure, especially at higher salt concentrations (150 and 200 mM). This decline in RWC was similarly observed in the reduction of shoot length. The decline in plant growth under salinity stress may result from a

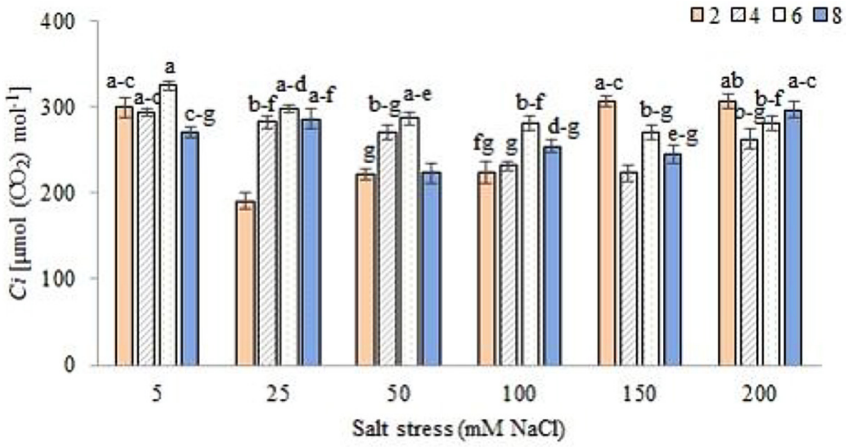

Figure 8. Internal CO_2 concentration (C_i) of *S. officinalis* leaves subjected to salt stress. The impact of different salinity stress and time points compared to the control. Data represent mean values ± SD, n = 10. Different letters denote statistically different means (Tukey's test; $P \leq 0.05$). Bars bearing different letters indicate significant differences

decrease in photosynthesis and energy reserves. In saline environments, the closure of leaf stomata typically leads to reduced gas exchange, which in turn lowers the rate of photosynthesis (Chaves et al., 2009; Chele et al., 2021).

Photosynthetic analysis reveals that plants exhibit varied responses to abiotic stress, including rapid and long-term adaptations, which are influenced by the type, duration, and severity of the stress, ultimately affecting their photosynthetic performance and sensitivity (Oelze et al., 2012; Alsharafa et al., 2014; Alkhsabah et al., 2018; Kalaji et al., 2018; Alsharafa, 2023c). Changes in P_N can reflect the plants ability to adapt to stressors such as drought and salinity. In addition, it helps in understanding how plants respond to different stress conditions (Chaves et al., 2009; Muhammad et al., 2021; Alsharafa, 2023c). Stomatal closure induced by salt stress exacerbates the decline in P_N by limiting CO_2 availability. Additionally, the accumulation of toxic ions and reduction in enzymatic activity further contribute to decreased P_N, as the efficiency of carbon fixation declines (Chaves et al., 2009; Yang et al., 2020). Our study changes in P_N in *S. officinalis* leaves were attributed to short-term exposure (2 and 4 days) and low slat level or long-term (6 and 8 days) exposure to various salt stress levels. Short-term exposure to salt stress (over periods of 2 and 4 days) can cause a quick yet temporary decline in photosynthetic efficiency as an initial physiological response. It may take plants longer to adapt their metabolic and physiological processes to manage salinity effectively which mainly occurs by non-stomatal limitation. The decrease in P_N in *S. officinalis* under prolonged salinity stress is primarily attributed to stomatal limitations (Li et al., 2020), driven by reductions in *Gs* and *E*. These declines become more significant at higher salinity levels, suggesting a strong correlation between the physiological response and both the intensity of salt concentration and the duration of exposure. Consequently, salt stress triggers osmotic stress, which reduces water availability to plants and, in turn, negatively impacts P_N by lowering *Gs* and *E*. Furthermore, these parameter changes occur parallel with variations in the RWC of sage leaves, supporting this observation. WUE is a valuable indicator of a plants ability to cope with environmental stressors, including salt stress (Omamt et al., 2006; Khataar et al., 2018). Plants with enhanced WUE are typically more resilient to saline conditions, as they sustain photosynthesis while reducing water loss. In this study, the observed increase in WUE under salt stress, reaching levels comparable to the control, is attributed not to higher transpiration rates but to the accumulation of compatible solutes—such as proline, sugars, organic acids, and polyamines—in salt-stressed sage seedlings (Sun et al., 2019; Singh et al., 2022; Alsharafa, 2023a). Nevertheless, *Ci* enhances or has a low reduction impact at higher salinity levels and the duration of exposure suggests non-stomatal factors become more influential (Ran et al., 2021).

In conclusion, the findings of this study demonstrate that salt stress significantly impacts the vegetative growth and physiological processes of *S. officinalis* L. High salinity levels (100, 150, and 200 mM) reduce shoot length, RWC, and overall plant growth, primarily due to decreased soil water potential, ion toxicity, and disrupted nutrient balance. Additionally, salt stress impairs cell division and elongation, further hindering growth. P_N declines under salinity, with short-term exposure causing rapid but temporary reductions in efficiency, while long-term exposure leads to sustained decreases driven by stomatal limitations (reduced *Gs* and *E*) and non-stomatal factors such as toxic ion accumulation and reduced enzymatic activity.

The study highlights the role of *WUE* in enhancing salt stress resilience, as sage seedlings accumulate compatible solutes (e.g., proline, sugars, organic acids, and polyamines) to maintain osmotic balance and sustain photosynthesis. These adaptive mechanisms help mitigate water loss and ion toxicity, enabling plants to cope with salinity stress. However, the severity of physiological responses depends on both the intensity and duration of salt exposure, with higher concentrations and prolonged stress exacerbating negative effects. Overall, the results underscore the complex interplay of osmotic, ionic, and photosynthetic adjustments in *S. officinalis* under salt stress, providing insights into its adaptive strategies and limitations in saline environments.

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