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Article

Effect of Salinity on Photosynthetic Performance in Cup Plant (*Silphium Perfoliatum* L.).

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Abstract

Soil salinity is recognized as a critical abiotic stress that limits plant growth on marginal lands. The cup plant (*Silphium perfoliatum* L.), a perennial bioenergy species with high biomass potential, has been proposed for cultivation on saline-degraded soils; however, its responses to salt stress remain insufficiently characterized. In the present study, the physiological responses of cup plant to neutral (NaCl) and alkaline (NaHCO₃) salt stress at concentrations of 100, 200, and 300 mM were evaluated in a pot experiment conducted under controlled conditions. The assessed indicators included relative chlorophyll content (CCI), chlorophyll a fluorescence parameters (Fv/Fm, Fv/Fo, PI), and gas exchange characteristics, namely net photosynthetic rate (Pn), stomatal conductance (gs), transpiration rate (E), and intercellular CO₂ concentration (Ci). Dose-dependent decreases in all measured physiological parameters were induced by salinity. A more pronounced negative effect was observed under alkaline salt stress than under neutral salt stress. For instance, at 300 mM NaHCO₃, chlorophyll content and photosynthetic rate were substantially reduced compared with those recorded under the corresponding NaCl treatment. Even at the moderate salinity level of 100 mM, reductions in photosynthetic performance were detected relative to the control. Overall, photosynthetic efficiency and gas exchange in cup plant were markedly impaired by salinity, particularly under conditions of high bicarbonate concentration. These findings provide new insight into the physiological limitations of *S. perfoliatum* under acute salt stress and demonstrate that alkaline salinity, associated with elevated pH due to HCO₃⁻, exacerbates stress effects beyond the osmotic and ionic impacts of neutral salinity.

Keywords: *Silphium perfoliatum* L.; soil salinity; relative chlorophyll content; chlorophyll fluorescence; gas exchange

1. Introduction

In response to the growing challenges of climate change, soil degradation, and the need to reduce greenhouse gas emissions, the transformation of global energy systems has become a strategic priority for many countries and international organizations [1,2]. Achieving climate neutrality targets requires diversification of energy sources and a shift away from fossil fuels toward low-emission renewable technologies. In this context, biomass plays a particularly important role, as it can be locally sourced, integrated with agricultural systems, and relatively easily converted into heat, electricity, and biofuels [3,4,5]. Among biomass feedstocks, energy crops are gaining increasing interest because their cultivation allows for stable and predictable raw material production in areas with limited agricultural suitability [6,7].

A particularly promising species in this group is cup plant (*Silphium perfoliatum* L.), a perennial herb with high biomass productivity, well adapted to variable environmental conditions, and relatively low agronomic requirements. Previous studies have demonstrated its high yield potential on marginal soils [8,9]. *S. perfoliatum* exhibits considerable habitat flexibility and a strong ability to

adapt to less fertile or marginal soils. Field trials conducted on heavy soil under Central European climatic conditions have shown that this species can produce substantial yields of both green and dry biomass even under limited soil resources and variable water availability [9]. Thus, cup plants represent a promising alternative to traditional energy crops such as giant miscanthus or willow, particularly in areas unsuitable for intensive agriculture. The species can also be integrated into agro energy systems, contributing to soil quality improvement and carbon sequestration [8,10]. Research has shown that perennial cultivation of *S. perfoliatum* increases water retention, reduces erosion, and supports soil organism development (Auerswald et al., 2025). Moreover, its extended flowering period benefits pollinator populations, aligning with biodiversity conservation efforts in agricultural landscapes. Therefore, integrating cup plant into agricultural practices can contribute both to renewable energy production and environmental enhancement [11]. Additionally, *S. perfoliatum* biomass can be utilized in various conversion technologies, including agricultural biogas plants, combustion, or as a component in solid fuels, increasing its market potential [12].

Excessive soil salinity is one of the most severe stress factors limiting plant growth and development [13,14]. Soil salinity induces osmotic stress, preventing water uptake from the substrate, leading to cellular dehydration, reduced turgor, and inhibited shoot elongation. Simultaneously, ionic stress arises from excessive sodium (Na^+) and chloride (Cl^-), potentially causing ion toxicity, nutrient imbalances, and deficiencies in essential elements such as potassium (K^+) and calcium (Ca^{2+}) [15,16]. At the physiological level, salt stress significantly affects plant water relations, including reduced hydraulic conductivity and limited root water uptake (dos Santos et al., 2022). Photosynthesis is also impaired due to decreased chlorophyll content, reduced photosystem activity, and lower CO_2 assimilation rates. Salt stress additionally influences metabolic enzyme activity and the production of reactive oxygen species (ROS), which may damage cell membranes, chloroplasts, and mitochondria [17,18]. Another adaptive mechanism involves modulation of plant hormone levels. Elevated abscisic acid (ABA) promotes stomatal closure and reduces transpiration, while changes in cytokinin and auxin concentrations regulate growth and cell division [19,20]. Prolonged salinity can also modify osmolyte composition, including accumulation of proline and soluble sugars, which protect cells under osmotic stress conditions [21,22].

Despite the cup plant's broad environmental adaptability, detailed information on its tolerance to soil salinity particularly under different types of salt stress remains limited. Most research on plant salinity stress has focused on neutral salts (primarily NaCl), whereas many salt-affected soils also contain alkaline salts (such as NaHCO_3) that raise soil pH. How *S. perfoliatum* copes with alkaline versus neutral salinity is an open question and represents a clear research gap. Therefore, the aim of this study was to evaluate the physiological responses of cup plant to salt stress induced by two distinct salt types (neutral NaCl and alkaline NaHCO_3) applied at equal concentrations. We formulated a specific hypothesis that salt type would significantly influence the severity of plant stress responses. In particular, we hypothesized that alkaline salinity (NaHCO_3) would exert more deleterious effects on cup plant physiology than an equivalent concentration of neutral salinity (NaCl), due to the additional high-pH (bicarbonate) stress. Furthermore, a proportional, concentration-dependent decline in plant performance was expected under both salt types, with higher salt levels causing more pronounced reductions in chlorophyll content, photosynthetic efficiency, and gas exchange rates.

2. Materials and Methods

2.1. Pot Experiment

The pot experiment was conducted at the University of Rzeszów, Poland. Seeds of *Silphium perfoliatum* L. were obtained from the Institute of Plant Breeding and Acclimatization – National Research Institute, Bydgoszcz, Poland. The experiment was conducted in a growth chamber (model GC-300/1000, JEIO Tech Co., Ltd., South Korea) under the following conditions: temperature 22 ± 2 °C, relative humidity $60 \pm 3\%$, photoperiod 16/8 h (day/night), and maximum light intensity of

approximately $300 \mu\text{E m}^{-2} \text{s}^{-1}$. Seeds were sown in seed trays, and after germination, the seedlings were transplanted into 15×15 cm plastic pots, three per pot. The pots were filled with a slightly acidic substrate (pH: KCl 6.35; H_2O 6.52) with a sandy-loam consistency. Substrate moisture was maintained at 60% of field water capacity. One month after transplanting (plant height 8-12 cm), salt stress was induced by watering the soil with neutral (NaCl) or alkaline (NaHCO_3) salt solutions. Salt solutions were applied at concentrations of 100, 200, and 300 mM, at 100 ml per pot. Control plants were watered with the same volume of deionized water.

The salt concentrations of 100, 200, and 300 mM were selected to encompass a range from moderate to severe salinity stress in a short-term pot study. These levels ensured that both threshold effects (at the lower end) and extreme stress responses (at the higher end) could be observed. It is noted that 300 mM represents an unusually high salinity that would rarely occur homogeneously in field soils; however, such a concentration serves as a model stress condition to probe the upper limits of the plant's physiological tolerance in controlled settings. Using NaCl and NaHCO_3 as salt sources allowed us to simulate two distinct types of saline soils: neutral salinity (dominated by chloride, with minimal direct effect on soil pH) versus alkaline salinity (dominated by bicarbonate, causing elevated soil pH). By applying equal molar concentrations of Na^+ in these two chemical forms, we could directly compare plant responses to neutral vs. alkaline salt stress under equivalent ionic strength.

The experiment was conducted with four biological replicates per treatment; each replicate consisted of three plants grown in a separate pot. All measurements were performed on each replicate pot (or its soil) with an appropriate technical replicate.

2.2. Physiological Measurements

Physiological measurements of the plants were taken four times on the first or second fully developed leaves at intervals of 7, 14, 21, and 28 days after the application of the salt solution to the soil. For physiological traits, repeated measurements within a pot were treated as technical replicates (subsamples), while pots were treated as biological replicates. Specifically, relative chlorophyll content and chlorophyll fluorescence parameters were recorded five times for each pot during each sampling period. Gas exchange parameters were recorded three times for each pot during each sampling period. Physiological parameters were assessed using methods previously described by Jańczak-Pieniążek et al. [23].

2.2.1. Relative Chlorophyll Content

Relative chlorophyll content was measured using a CCM-200 plus chlorophyll content meter (Opti-Sciences, Hudson, NH, USA). Measurements were performed five times per pot (on fully developed leaves), and the mean value was calculated for each pot and sampling term.

2.2.2. Chlorophyll Fluorescence

Chlorophyll fluorescence was measured using a Pocket PEA fluorimeter (Hansatech Instruments, King's Lynn, Norfolk, UK) equipped with dark-adaptation clips. Before measurement leaves were dark-adapted for 30 minutes using these clips, which were attached to the upper part of the leaf blade while avoiding the main vein [24]. Fluorescence was recorded under red actinic light with a peak wavelength of 627 nm, applied for 1 s at a maximum intensity of $3500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. The following parameters were evaluated: maximum efficiency of water-splitting on the donor side of PSII (F_v/F_o), maximum photochemical efficiency of PSII (F_v/F_m), and the performance index (PI). Measurements were performed five times per pot (on fully developed leaves), and the mean value was calculated for each pot and sampling term.

2.2.3. Gas Exchange

Gas exchange parameters were measured using an LCpro-SD photosynthesis system (ADC Bioscientific Ltd., Herts, UK). The following parameters were recorded: net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i). During measurements, PAR intensity was set to $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ and chamber temperature was maintained at 23°C . Measurements were taken three times per pot (on fully developed leaves), and the mean value was calculated for each pot and sampling term.

2.3. Soil Analysis

Soil samples were air-dried, homogenized, and sieved through a 2 mm mesh. Representative subsamples were collected for the determination of soil pH and electrical conductivity (EC). Soil pH was measured potentiometrically in distilled water and in 1 M KCl solution, representing active and exchangeable acidity, respectively [25]. Soil suspensions were prepared at a 1:5 (w/w) ratio (soil:solution). Briefly, 5 g of soil were placed in 100 cm^3 beakers and mixed with 25 cm^3 of distilled water or 1 M KCl. The suspensions were stirred thoroughly and left to equilibrate for 24 h. After re-mixing, pH was measured using a pH meter (HI 4221, Hanna Instruments) at 20°C . EC was measured in soil-water suspensions using a conductivity meter (HI 2316, Hanna Instruments). EC values, expressed in mS, were used as an indicator of soil salinity [26]. For each pot, soil pH was measured three times both in distilled water ($\text{pH}_{\text{H}_2\text{O}}$) and in 1 M KCl (pH_{KCl}). Soil electrical conductivity (EC) was also measured three times per pot, and mean values were used for further analyses.

2.4. Statistical Analysis

Statistical analysis was performed using TIBCO Statistica 13.3.0 software (TIBCO Software Inc., Palo Alto, California, USA). Normality of distribution was assessed using the Shapiro-Wilk test ($\alpha=0.05$), and homogeneity of variance was confirmed using Levene's test ($\alpha=0.05$). A two-way analysis of variance (ANOVA) with repeated measures (including time as a factor) was performed. Salinity relationships were also assessed using one-way analysis of variance (ANOVA). Significant differences between means were identified using Tukey's post hoc test at $\alpha \leq 0.05$.

3. Results

3.1. Relative Chlorophyll Content

Chlorophyll content decreased under salt stress (Figure 1). Irrigation with 100 mM NaCl caused a significant reduction in chlorophyll content only in Term III. On the other terms, this concentration did not significantly affect the parameter compared to the control. Higher NaCl concentrations (200 and 300 mM) led to a significant decrease in chlorophyll content at all terms. Differences between these two concentrations were observed only in Terms II and IV. Application of NaHCO_3 also reduced chlorophyll content relative to the control, but the effect was less pronounced than that of NaCl. The lowest chlorophyll values were recorded at 200 and 300 mM NaHCO_3 . At 100 mM NaHCO_3 , chlorophyll content was similar to that observed at 300 mM NaCl. In Term I, all treatments except the control showed the lowest chlorophyll content. This value increased in Term II, but statistically significant differences were detected only for 200 mM NaHCO_3 . In Term III, chlorophyll content decreased compared to Term IV; however, the difference was not statistically significant.

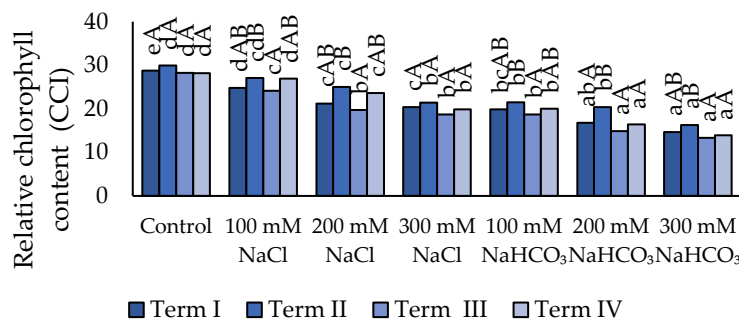


Figure 1. Impact of NaCl and NaHCO₃ salt stress and sampling time on relative chlorophyll content. Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey’s HSD test ($p \leq 0.05$).

3.2. Chlorophyll Fluorescence

3.2.1. Maximum Efficiency of Water-splitting on the Donor Side of PSII (Fv/Fo)

Under salt stress, a decrease in the F_v/F_0 parameter was observed (Figure 2). Irrigation with neutral salt (NaCl) caused a significant reduction in F_v/F_0 only at concentrations of 200 and 300 mM, which was observed across all terms. Alkaline salt induced a stronger decline in F_v/F_0 compared to neutral salt. No significant differences in F_v/F_0 were detected at 300 mM NaCl or 100 mM NaHCO₃. The greatest decrease in F_v/F_0 was observed at 200 and 300 mM for both salts; however, statistically significant differences compared to 100 mM were only found for 300 mM. In Term III, the lowest F_v/F_0 values were recorded across all salinity treatments, but statistical significance was observed only for 100 mM NaCl compared to the other terms. The highest F_v/F_0 values were recorded in Term II, yet significant differences were found only for 200 mM NaHCO₃ relative to the other terms.

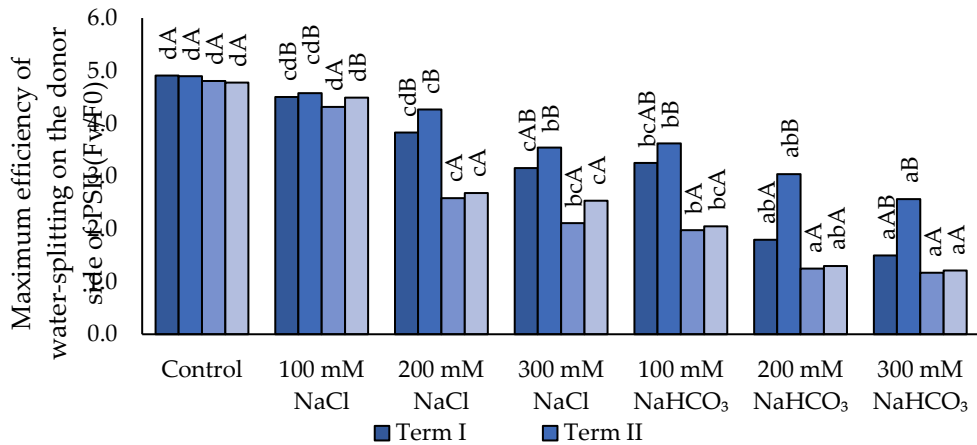


Figure 2. Impact of NaCl and NaHCO₃ salt stress and sampling time on maximum efficiency of water-splitting on the donor side of PSII (F_v/F_0). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey’s HSD test ($p \leq 0.05$).

3.2.2. Maximum Photochemical Efficiency of PSII (Fv/Fm)

Salt stress resulted in a reduction of the F_v/F_m parameter (Figure 3). Irrigation with neutral salt (NaCl) at 100 and 200 mM did not cause statistically significant differences compared to the control. Only the application of 300 mM NaCl led to a significant decrease in F_v/F_m across all terms. Alkaline salt further reduced F_v/F_m values. Irrigation with 100 and 200 mM NaHCO₃ did not differ from 300 mM NaCl. A significant reduction in F_v/F_m was observed only after the application of 300 mM

NaHCO₃, specifically in Terms I, III, and IV. In Term II, the highest Fv/Fm values were recorded; however, statistically significant differences were detected only for 200 and 300 mM NaHCO₃ compared to the other terms.

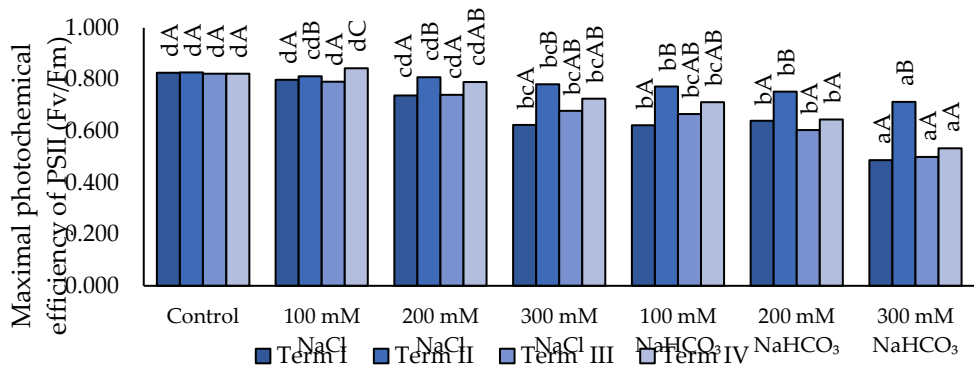


Figure 3. Impact of NaCl and NaHCO₃ salt stress and sampling time on maximum photochemical efficiency of PSII (Fv/Fm). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey’s HSD test ($p \leq 0.05$).

3.2.3. Performance Index (PI)

As a result of applying salt stress, a decrease in the PI parameter value was observed relative to the control (Figure 4), except for the 100 mM and 200 mM concentrations of NaCl (Term II). A significant decrease was recorded when using the 300 mM concentration of neutral salt compared to the 100 mM concentration. A further reduction in the PI parameter value was found following the application of NaHCO₃, however, differences compared with the 200 mM neutral salt concentration were observed only at 300 mM. In Term II, a significantly highest PI value was recorded compared to the remaining Terms in all variants, except for the control, in which the value of this parameter did not differ between the Terms.

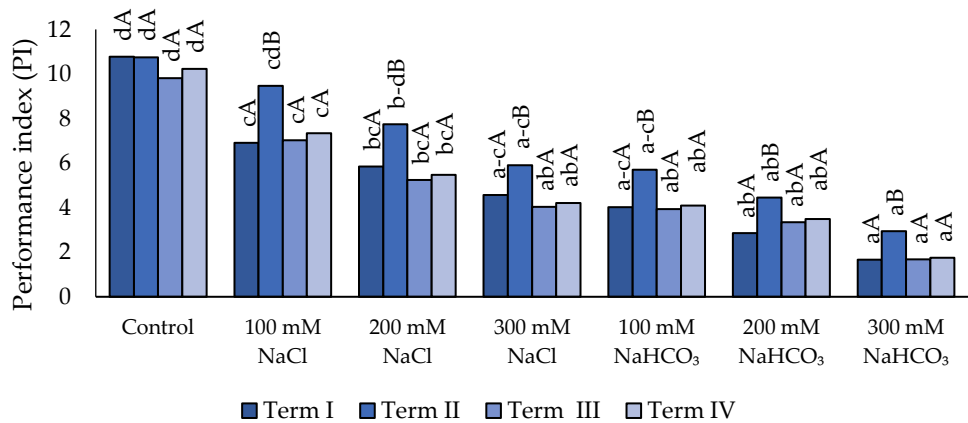


Figure 4. Impact of NaCl and NaHCO₃ salt stress and sampling time on performance index (PI). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey’s HSD test ($p \leq 0.05$).

3.3. Gas Exchange

3.3.1. Net Photosynthetic Rate (Pn)

Soil salinity resulted in a reduction of the gas-exchange parameter Pn (Figure 5) compared to plants not subjected to this stress (control), except for the use of NaCl at a concentration of 100 mM

(Term I and Term II). The application of NaHCO₃ caused a further decrease in Pn values. However, no statistically significant differences were found between the use of 300 mM neutral salt and the concentrations of 100 mM and 200 mM alkaline salt. The application of 300 mM alkaline salt resulted in a significantly lowest Pn value compared to the remaining salinity variants, except for the alkaline-salt concentrations of 100 mM (Term I) and 200 mM (Term I and Term III). In Term II, the highest value of the analyzed parameter was observed only in the variants with 100 mM and 200 mM alkaline salt.

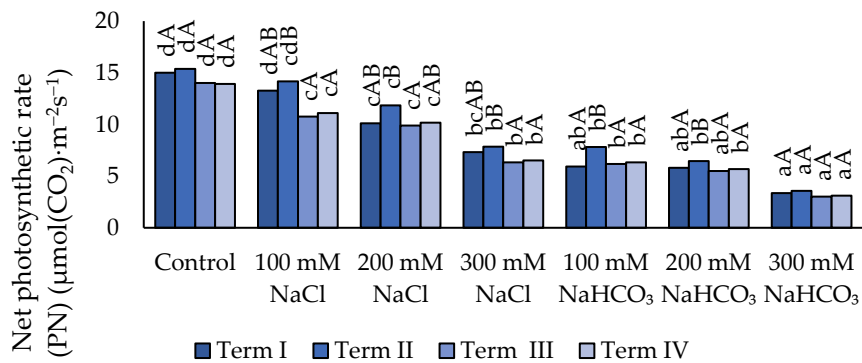


Figure 5. Impact of NaCl and NaHCO₃ salt stress and sampling time on *net* photosynthetic rate (Pn). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey's HSD test ($p \leq 0.05$).

3.3.2. Stomatal Conductance (gs)

Under salt stress, a decrease in the gs parameter value (Figure 6) was recorded relative to the control. However, when 100 mM NaCl was applied, no significant effect of salinity on the value of the parameter analyzed was observed. The use of 200 mM and 300 mM concentrations caused a significant decrease in gs compared to the control (except for 200 mM in Term III and Term IV). The application of NaHCO₃ led to a further reduction in gs values. The 300 mM neutral salt and 100 mM alkaline salt concentrations did not differ from each other. The lowest value of the analyzed parameter was recorded under the 300 mM alkaline salt concentration, compared to all other salt treatments except for the alkaline-salt concentrations of 200 mM and 100 mM (Term II). The highest gs value was observed in Term II, although it did not differ significantly from the values recorded in the remaining Terms in any of the experimental variants.

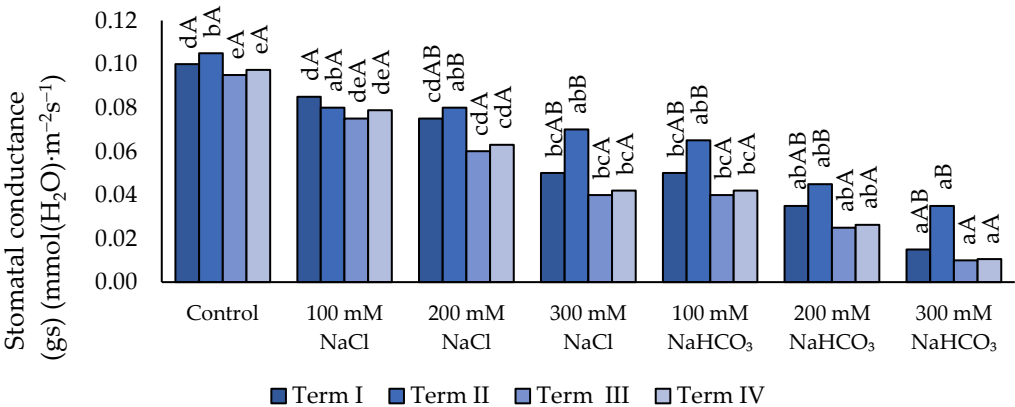


Figure 6. Impact of NaCl and NaHCO₃ salt stress and sampling time on stomatal conductance (gs). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey's HSD test ($p \leq 0.05$).

3.3.3. Transpiration Rate (E)

Soil salinity caused a decrease in the value of the E parameter (Figure 7) compared with the control, except for the variant with 100 mM NaCl (Term I and Term II). Higher concentrations of this salt (200 mM and 300 mM) led to a further decline in E relative to the control; however, no significant differences were found between these concentrations. No significant effect on the value of the analyzed parameter was observed between 300 mM neutral salt and 100 mM or 200 mM NaHCO₃. A significantly lowest E value was observed only under the 300 mM concentration, which was lower than the 100 mM concentration (except in Term II). In Term II, the lowest E value was recorded compared with the remaining Terms in all salinity variants, except for the 200 mM neutral salt concentration.

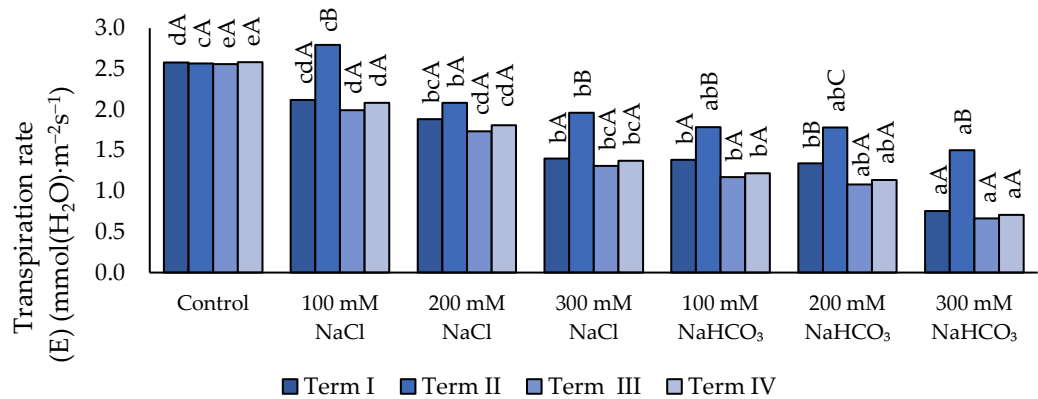


Figure 7. Impact of NaCl and NaHCO₃ salt stress and sampling time on transpiration rate (E). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey's HSD test ($p \leq 0.05$).

3.3.4. Intercellular CO₂ Concentration (Ci)

Under soil salinity, an increase in the Ci parameter value (Figure 8) was observed compared with the control, except for the variant in which 100 mM NaCl was applied (Term II). The application of 300 mM neutral salt caused a significant increase in Ci compared with the 200 mM concentration, but only in Term I and Term III. The use of 300 mM neutral salt did not result in changes compared with 100 mM NaHCO₃. The higher alkaline-salt concentration caused an increase in the value of the analyzed parameter compared with the lower concentrations. Under the 300 mM concentration, a significant increase in Ci was recorded compared with the 100 mM concentration, except in Term II. In Term III, the highest Ci value was observed across all salinity treatments; however, this was statistically confirmed only for the variants with 200 mM and 300 mM neutral salt and 100 mM alkaline salt.

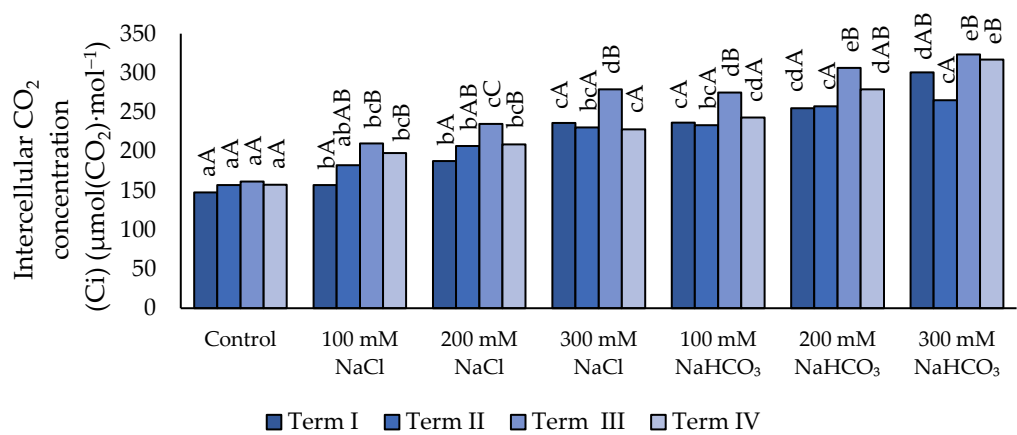


Figure 8. Impact of NaCl and NaHCO₃ salt stress and sampling time on intercellular CO₂ concentration (Ci). Different uppercase letters indicate significant differences among sampling terms within each treatment, while different lowercase letters indicate significant differences among treatments within the same sampling term, based on ANOVA followed by Tukey’s HSD test ($p \leq 0.05$).

3.4. Soil Analysis

3.4.1. Soil pH

Soil pH and salinity levels changed in response to the salt treatments, with clear differences between neutral and alkaline salt addition (Figure 10, Figure 11). NaHCO₃ tended to increase soil pH (measured in H₂O), whereas NaCl had little effect on pH. In fact, only the highest NaHCO₃ treatment (300 mM) caused a statistically significant rise in pH_{H₂O} compared to the control (no-salt) soil, while 100 mM and 200 mM NaHCO₃ produced slight, non-significant pH increases. All NaCl-treated soils had pH_{H₂O} values similar to the control. Soil pH measured in KCl (pH_{KCl}) was consistently lower than pH_{H₂O} and showed smaller absolute changes. Addition of NaCl caused no significant pH_{KCl} change versus control, and NaHCO₃ caused only a modest increase. A significant elevation in pH_{KCl} was observed only at 200 mM and 300 mM NaHCO₃, by approximately +4.8% and +6.7% relative to control, respectively.

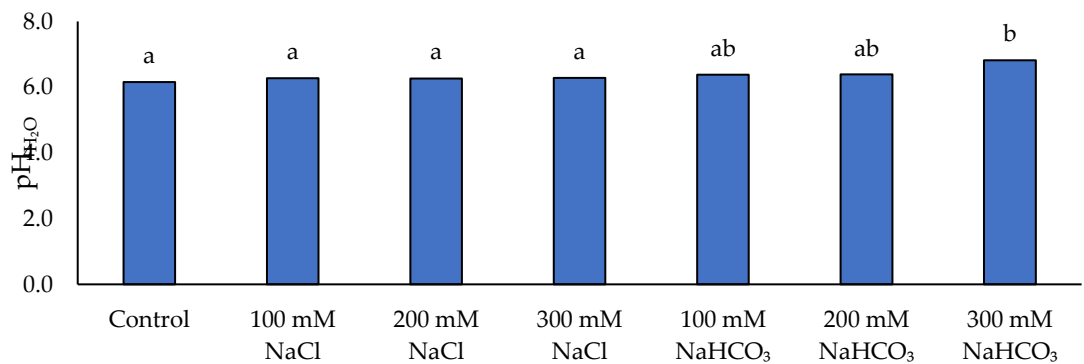


Figure 9. Soil pH in H₂O on the applied NaCl and NaHCO₃ salt solutions. Different lowercase letters indicate significant differences among treatments, based on ANOVA followed by Tukey’s HSD test ($p \leq 0.05$).

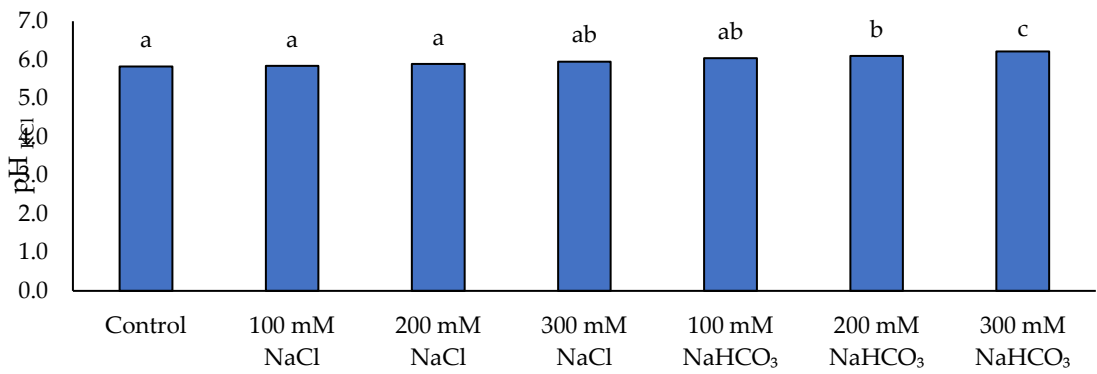


Figure 10. Soil pH in KCl on the applied NaCl and NaHCO₃ salt solutions. Different lowercase letters indicate significant differences among treatments, based on ANOVA followed by Tukey’s HSD test ($p\leq0.05$).

3.4.2. Soil Electrical Conductivity (EC)

Soil electrical conductivity increased as a result of soil salinization (Figure 11). EC increased with increasing salt concentration for both salt types, reflecting higher soluble salt content. However, a statistically significant jump in EC (compared to control) was detected only at the highest concentration (300 mM). At 300 mM NaCl, the soil EC was about 92.8% above the control value, whereas 300 mM NaHCO₃ led to an EC increase of approximately 117.4% over control. These results indicate that substantial salinization of the soil occurred only under the most severe treatment, with NaHCO₃ contributing slightly more to EC rise than NaCl at the same molarity.

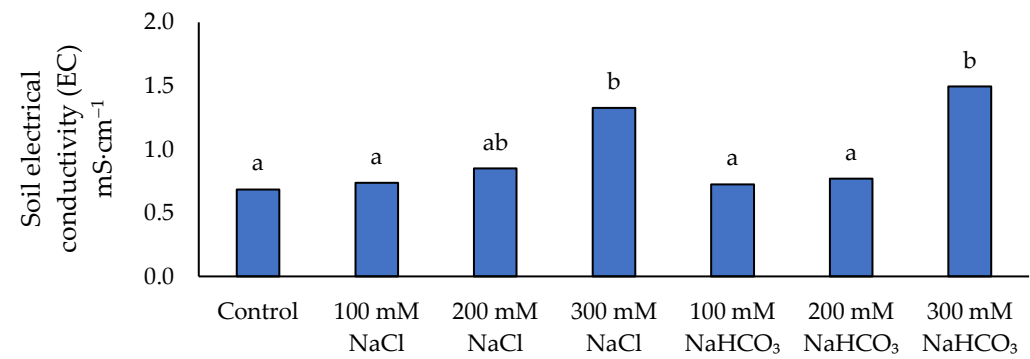


Figure 11. Soil electrical conductivity depending on the applied NaCl and NaHCO₃ salt solutions. Different lowercase letters indicate significant differences among treatments, based on ANOVA followed by Tukey’s HSD test ($p\leq0.05$).

4. Discussion

In the conducted study, the effects of salt stress induced by neutral and alkaline salts at concentrations of 100, 200, and 300 mM on the physiological responses of *Silphium perfoliatum* L. were evaluated. This species, due to its high biomass productivity and perennial growth habit, is considered a crop with strong potential for bioenergy systems [10]. Therefore, assessing its response to soil salinity is important in the context of future cultivation on degraded, marginal, and salinizing lands [27]. The results demonstrated that salt stress induced by both NaCl and NaHCO₃ significantly reduced the physiological parameters analyzed. Soil salinity, as a typical abiotic stressor, disrupts key physiological and biochemical processes in plants. Excessive accumulation of Na⁺ ions lead to ionic imbalance, a decrease in soil water potential, and difficulties in water uptake, as confirmed by previous studies [28,29]. High salt concentrations also adversely affect photosynthesis. Components

necessary for the functioning of the photosynthetic apparatus, such as chlorophylls, photosystems, and carbon metabolism enzymes, undergo degradation under salt stress [30].

In the present study, reductions in chlorophyll content and fluorescence parameters were observed, indicating impaired photosystem II efficiency and disturbances in photochemical processes. At the same time, salinity decreased gas exchange parameters—net photosynthesis (Pn), stomatal conductance (gs), and transpiration (E)—confirming constraints on CO₂ uptake and plant water regulation [31,32]. These effects intensified with increasing salt concentrations, particularly under NaHCO₃ treatment, consistent with previous findings that alkaline salts are more toxic than neutral [33,34]. The negative impact of salinity on photosynthesis is multilevel, encompassing osmotic, ionic, and biochemical stress [21,29,35]. Osmotic stress limits water availability and induces stomatal closure, leading to reduced gs and Pn [19,21,22]. Ionic stress, caused by excess Na⁺ and Cl⁻, disrupts the transport of ions essential for chlorophyll biosynthesis, destabilizes cell membranes, and damages thylakoids, thereby reducing the efficiency of light energy conversion [37,38]. Similar damage to the photosynthetic apparatus under high salinity has been reported in seedlings of *Robinia pseudoacacia* [39]. Alkaline salts such as NaHCO₃ are more toxic than neutral salts because they induce both ionic stress and substrate alkalization. Elevated soil pH reduces the availability of key ions (Mg²⁺, Fe²⁺, Mn²⁺) necessary for chlorophyll biosynthesis and photosystem functioning. Consequently, chlorophyll content, chlorophyll fluorescence, and CO₂ assimilation decrease, as confirmed by other studies [32,33]. Additionally, the HCO₃⁻ ion can destabilize cellular and thylakoid membranes, contributing to pigment degradation and reduced photosystem efficiency [32]. Under alkaline stress, increased production of ROS leads to lipid peroxidation, chlorophyll degradation, and damage to Calvin cycle enzymes, including RuBisCO [18,39]. These further decreases photosynthetic parameters (Pn, gs, E). Stomatal closure, a protective response, additionally limits CO₂ uptake, intensifying the decline in photosynthetic performance [33,38].

At later measurement dates, a partial improvement in physiological parameters was observed, indicating the activation of multilayered adaptive mechanisms that enable plant functioning under prolonged salt stress. In the adaptive phase, plants enhance the activity of enzymatic components of the antioxidant system, such as superoxide dismutase (SOD) and catalase (CAT). These enzymes effectively neutralize excess ROS, which accumulate rapidly during the initial phase of stress and cause damage to membrane lipids, proteins, and photosynthetic structures [40]. Earlier studies by Rohman et al. [41] and Rohman et al. [42] also reported increased SOD activity under salt stress, confirming the activation of protective mechanisms aimed at reducing oxidative damage. Simultaneously, plants intensify the synthesis of osmolytes proline, glycine betaine, soluble sugars, and osmoregulatory proteins. These compounds decrease the osmotic potential of the cytoplasm, allowing the maintenance of turgor and continuation of metabolic processes despite limited water availability [43,44]. During later measurement periods, a partial recovery of physiological parameters was again observed, suggesting further activation of adaptive mechanisms enabling plant functioning under prolonged salt exposure. A similar trend was reported by Jańczak-Pieniążek et al. [45] in wheat seedlings, where improved physiological parameters at later stages were attributed to repair processes. Together, these mechanisms indicate that plants not only respond defensively to salt stress but also undergo physiological and biochemical adaptation that enables relatively stable functioning despite persistent environmental stressors [46].

In all treatments, soil pH measured in KCl was lower than pH in H₂O. This is a well-known effect of using a saline extract, which displaces exchangeable H⁺ from soil colloids and thus produces a lower pH reading. Notably, adding NaHCO₃ significantly increased soil pH in H₂O, while causing only a small increase in pH_{KCl}. This indicates that much of the added alkalinity was buffered by exchangeable soil acidity (H⁺ ions at cation exchange sites), so the net increase in exchangeable pH was limited. Electrical conductivity (EC) values reflected the degree of salinity: only the 300 mM treatments caused a sharp increase in EC, confirming that these soils had become highly saline. Such a high EC corresponds to a very low soil water potential, effectively inducing osmotic drought for plants [47]. This means that at a concentration of 300 mM, in addition to specific ionic effects, plants

likely experienced severe limitations in water uptake due to the high salt concentration in the soil solution. Besides osmotic stress, the type of salt imposed qualitatively different stresses on plants. Neutral salt (NaCl) supplies an excess of Na^+ and Cl^- ions, which can lead to ion-specific toxicity and nutrient imbalances (e.g., Na^+ competes with K^+ uptake, Cl^- antagonizes NO_3^- uptake) [48,49], along with the osmotic effects of elevated solute concentrations. Alkaline salt (NaHCO_3) also introduces Na^+ but also drastically raises the pH of the soil solution. High environmental pH can cause precipitation or reduced availability of essential nutrients such as iron, calcium, and magnesium. For example, Fe^{2+} can precipitate as $\text{Fe}(\text{OH})_3$ under alkaline conditions [50]. This induced nutrient deficiency (often manifested by iron chlorosis and other symptoms) adds an additional layer of stress to the plant. Consequently, NaHCO_3 treatments were more detrimental to the plant than NaCl treatments at equivalent salt levels. In our results, chlorophyll content and photosynthetic efficiency decreased more under NaHCO_3 treatment, consistent with the combination of stresses (salinity and alkalinity) in these treatments. In summary, the presence of bicarbonate and the resulting high soil pH intensified the negative effects of salinity, making alkaline salt stress significantly more detrimental to *S. perfoliatum* than neutral salt stress under the conditions of this experiment.

The limitations of this study should also be noted. This study was conducted in a growth-chamber pot environment, which, while allowing tight control of variables, does not fully replicate field conditions. The controlled setting (uniform soil medium, constant climate) lacks the complexity of natural habitats. Factors such as rainfall variability, soil heterogeneity, and microbial interactions were not represented. The salt levels used (100-300 mM NaCl or NaHCO_3) were relatively high and imposed acutely; these concentrations effectively induced stress responses, but such extreme salinity might seldom occur homogeneously in open-field soils. The experiment also focused on short-term physiological responses and did not assess longer-term adaptation, growth, or reproductive effects under salinity. Additionally, we measured primarily physiological and growth indicators; other parameters like tissue ion accumulation, osmolyte levels, or antioxidant enzyme activities were not examined and could be topics for future research to elucidate the plant's internal tolerance mechanisms. These limitations should be kept in mind when extrapolating our findings. Nonetheless, the controlled approach and replicated design provided clear, comparative insights into how neutral vs. alkaline salinity affect cup plant physiology. The results serve as a valuable baseline for understanding *S. perfoliatum* responses to salt stress and will inform subsequent studies under more complex or long-term conditions.

5. Conclusions

This experiment demonstrated that soil salinity whether caused by NaCl or NaHCO_3 markedly impairs the photosynthetic performance and physiological status of cup plant (*Silphium perfoliatum*). All measured indicators of plant function (chlorophyll content, chlorophyll fluorescence parameters, gas exchange rates, etc.) showed significant declines with increasing soil salt concentration, confirming that salinity stress directly limits the species' photosynthetic efficiency and overall vigor in a controlled setting. Importantly, the type of salinity influenced the severity of the response: alkaline salt (NaHCO_3) consistently caused more pronounced physiological disruptions than an equivalent concentration of neutral salt (NaCl). In other words, high bicarbonate levels (alkaline pH) exacerbated the detrimental effects of salinity beyond the osmotic and ionic stress imposed by NaCl alone. Overall, *S. perfoliatum* exhibited substantial sensitivity to elevated salinity, especially under alkaline conditions, as evidenced by sharp reductions in chlorophyll content, photosynthetic gas exchange, and photochemical efficiency at high salt levels. These conclusions delineate the short-term physiological limits of cup plant under saline conditions. Future studies should build on this work by examining longer-term and field-scale responses to salinity in *S. perfoliatum*, in order to fully assess its capacity to maintain growth and productivity on salt-affected soils.

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Abbreviations

The following abbreviations are used in this manuscript:

Fv/Fm	maximum photochemical efficiency of PSII
Fv/Fo	maximum efficiency of water-splitting on the donor side of PSII
PI	PSII performance index
PN	net photosynthetic rate
Fv/Fm	maximum photochemical efficiency of PSII
gs	stomatal conductance
Ci	intercellular CO ₂ concentration
gs	stomatal conductance

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