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ARTICLE

Germination and Photosynthetic Responses to Salinity and Alkalinity in *Avicenna marina* Propagules

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ABSTRACT

Avicenna marina (Forssk.) Vierh is a halophytic mangrove. The reproductive unit is green and has photosynthetic propagules. Mangroves are naturally exposed to fluctuations in some abiotic factors at the soil surface, including salinity and alkalinity. The objective of this study was to determine the effects of two salts including NaCl and $NaHCO_3$ on germination processes and discuss the relationships between cotyledon photosynthesis and embryo axis growth in *A. marina* propagules. These propagules came from Al Birk, located on the shoreline of the Saudi Red Sea. The results showed that the studied salts did not affect neither the final germination percentage nor the embryo axis growth. However, rooting and root growth were delayed by both salts at 300 mM and were strongly inhibited by 600 mM $NaHCO_3$. Both NaCl and $NaHCO_3$ reduced the photosynthetic activity. These two salts did not affect the other photosynthetic parameters, including stomatal conductance, net transpiration, and intercellular CO_2. Thereafter, the reduction in net photosynthesis was not related to any limitation of stomatal conductance. The early germination phase was independent of cotyledon photosynthesis, whereas rooting and root growth may be limited by reduced photosynthesis under NaCl and $NaHCO_3$.

KEYWORDS

Avicenna marina propagules; cotyledons; embryo growth; germination; photosynthesis; alkalinity; salinity

1 Introduction

Mangroves are halophytic trees and shrubs that grow in the intertidal zone, constituting a specific ecosystem on tropical and subtropical coastlines [1]. They thus play an important role in coastal protection against soil erosion, high wave energy, tidal flooding, and tropical cyclones [2]. The mangrove ecosystem is well known for its biodiversity and provides a habitat for wildlife [3]. Mangroves have several economic and medicinal uses, including fodder for animals such as camels and cattle, and firewood in coastal areas [1]. Secondary compounds from mangrove species have been reported to have antimicrobial, antioxidant, and other beneficial effects on human health [1]. However, scientists suggest that about 33%–44% of mangrove ecosystems may be lost in the future due to an increase in sea level and human impacts [4]. Thus, these areas need urgent protection.

Avicenna marina is the most common species along the Red Sea coast of Saudi Arabia [5] and can be used for mangrove ecosystem restoration [6]. An understanding of the responses of mangrove species to abiotic stress is required to ensure the conservation and management of mangrove ecosystems [7]. In *A. marina*, salt tolerance during the vegetative stages is assured by several mechanisms, including salt accumulation in leaf cells, stimulation of antioxidative activity, salt exclusion by roots, and salt excretion via salt glands [2,5]. However, the effects of different salts during its germination and early stages of growth are largely unknown.

The propagation of *A. marina* occurs via propagules (i.e., the fruits). The latter is an oval, heart-shaped, two-valved capsule that is 20–25 mm in diameter, sometimes with an apex that has a short beak. The capsule is well-developed and exendospermous, and the embryo is enveloped by a thin pericarp [8]. The embryo axes and the cotyledons are green and photosynthetic. The propagules of mangroves are naturally exposed to saline seawater. Thus, salinity is the main factor that influences germination and establishment on this species [5,8]. The main ions that compose seawater include the cations Na^+, K^+, Ca^{2+}, and Mg^{2+} and the anions Cl^-, SO_4^{2-}, CO_3^{2-}, and HCO_3^- [9]. The two latter ions increase pH and cause alkaline stress. One study [5] showed that toxic ions (Na^+ and Cl^-) mainly accumulate in the pericarp away from the embryo axes and cotyledons. The same authors suggest that the early development of the embryonic axis inside the propagule before dispersal from the mother plant might help in overcoming high salinity during the germination stage and seedling establishment. However, the salt tolerance mechanisms during germination and early seedling growth in *A. marina* (Forssk.) Vierh. remain unclear.

In *A. marina*, the cotyledons are photosynthetic and may contribute to embryo axis growth and early seedling growth. Their role under stress conditions is essential for the success of seedling establishment [10]. We hypothesized that photosynthesis activity may influence germination. However, information on the relationships between photosynthesis, germination, and embryonic axis growth is scarce. Thus, the main goals of this investigation were to (i) determine the effects of two salts, namely NaCl and $NaHCO_3$, on germination and embryo axis growth, (ii) determine the effects of these salts on cotyledon photosynthesis, and (iii) investigate the extent of photosynthetic inhibition by these two salts and its subsequent effects on germination and early seedling growth.

2 Materials and Methods

2.1 Propagule Collection

Propagules were collected in April 2018 from Al Birk (18°11′36″N, 41°32′50″E) on the Saudi Arabian Red Sea shoreline. They were transported in plastic bags to the laboratory at King Khalid University (Abha, Saudi Arabia). Healthy propagules were carefully selected and stored under laboratory conditions for 1 day.

2.2 Germination and Growth Experiment

The propagules of *A. marina* are crypto-viviparous, whereby the embryo grows but does not rupture the pericarp. Thus, for this experiment, “germination” refers to propagule growth initiation, i.e., radicle elongation. To study propagule germination and embryo growth, an experiment was conducted in a glasshouse with a 14/10 h photoperiod, 27/18°C temperature, and 60/75% relative humidity day/night regime. Surface sterilization of the propagules was achieved by incubation in 2% (v/v) NaOCl for 1 min, followed by rinsing three times for 2 min with distilled water.

For the experiment, 15 propagules were sown in 20-cm-diameter plastic trays (plates) filled with a 3-cm-thick layer of peat-moss/vermiculate (3:1) moistened with 1 L distilled water or a suitable solution containing 300 or 600 mM of NaCl or $NaHCO_3$. To maintain the salinity concentration, the plates were enveloped with transparent plastic films to limit any evaporation.

2.3 Pericarp Rupture Percentage

Pericarp rupture was scored over time, and mean values ± SE were calculated from triplicate plates (N = 3 × 15). The numbers of propagules with ruptured pericarps were counted and recorded after 1, 3, 6, 8, 10, 13, and 15 days.

2.4 Germination Percentage

Germination was scored over time as visible radicle protrusion. Mean values ± SE were calculated from triplicate plates (N = 3 × 15). Germinated propagules were counted and recorded after 1, 3, 6, 8, 10, 13, and 15 days, following which the germination percentage was calculated.

2.5 Rooting and Seedling Growth

Rooting or root initiation refers to the date when the first root appeared following pericarp rupture and radicle emergence. Mean values ± SE were calculated from triplicate plates (N = 3 × 15). Rooting percentage was calculated after 1, 3, 6, 8, 10, 13, and 15 days.

At 15 days of the salinity treatment, after root initiation, the seedlings were harvested. Cotyledons, embryo axes, and roots were separated, and their fresh weights were determined using an electronic balance. Samples were then oven-dried at 70°C for 7 days and re-weighed to determine their constant dry weights.

2.6 Relative Water Content (RWC) Determination

Relative water content was determined as follows: RWC = (fresh weight – dry weight)/(dry weight) [11].

2.7 Gas Exchange Analysis

Photosynthetic parameters (photosynthetic rate, *A*; stomatal conductance, *gs*; transpiration, *E*; internal CO_2 concentration, *Ci*) were measured using a Licor-6400 (Licor, Lincoln, NB, USA) photosynthesis apparatus with a 6400-05 Conifer Chamber. The measurements were performed on the cotyledons under a photosynthetic photon flux density of 350–400 $\mu mol/(m^2\ s)$.

To estimate the intrinsic water use efficiency, we used the following ratio: iWUE = A/gs [12].

2.8 Statistical Analyses

A one-way analysis of variance (ANOVA) was used to assess the significant effects of salinity and alkalinity. Homogeneity of variances was achieved with the Levene's test. Tukey's test ($P < 0.05$) was used to compare the mean values. Statistical analysis was performed with the statistical package SPSS (version 17.00) for Windows (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 Pericarp Rupture Percentage

Pericarp rupture began one day after sowing and reached 55.6% under the distilled water treatment. Under 300 and 600 mM NaCl, the pericarp rupture percentage was 38%. Under 300 and 600 mM $NaHCO_3$, the pericarp rupture percentages were 24.44% and 46.7%, respectively. After 15 days, the pericarp percentage reached 98.8 under the distilled water and 300 mM treatments, but reached 88.89% under 600 mM NaCl. Under 300 and 600 mM $NaHCO_3$, the pericarp rupture percentages were 95.56% and 93.3%, respectively. Tukey's test ($P < 0.05$) showed no significant effect of NaCl and $NaHCO_3$ (Figs. 1A and 1B).

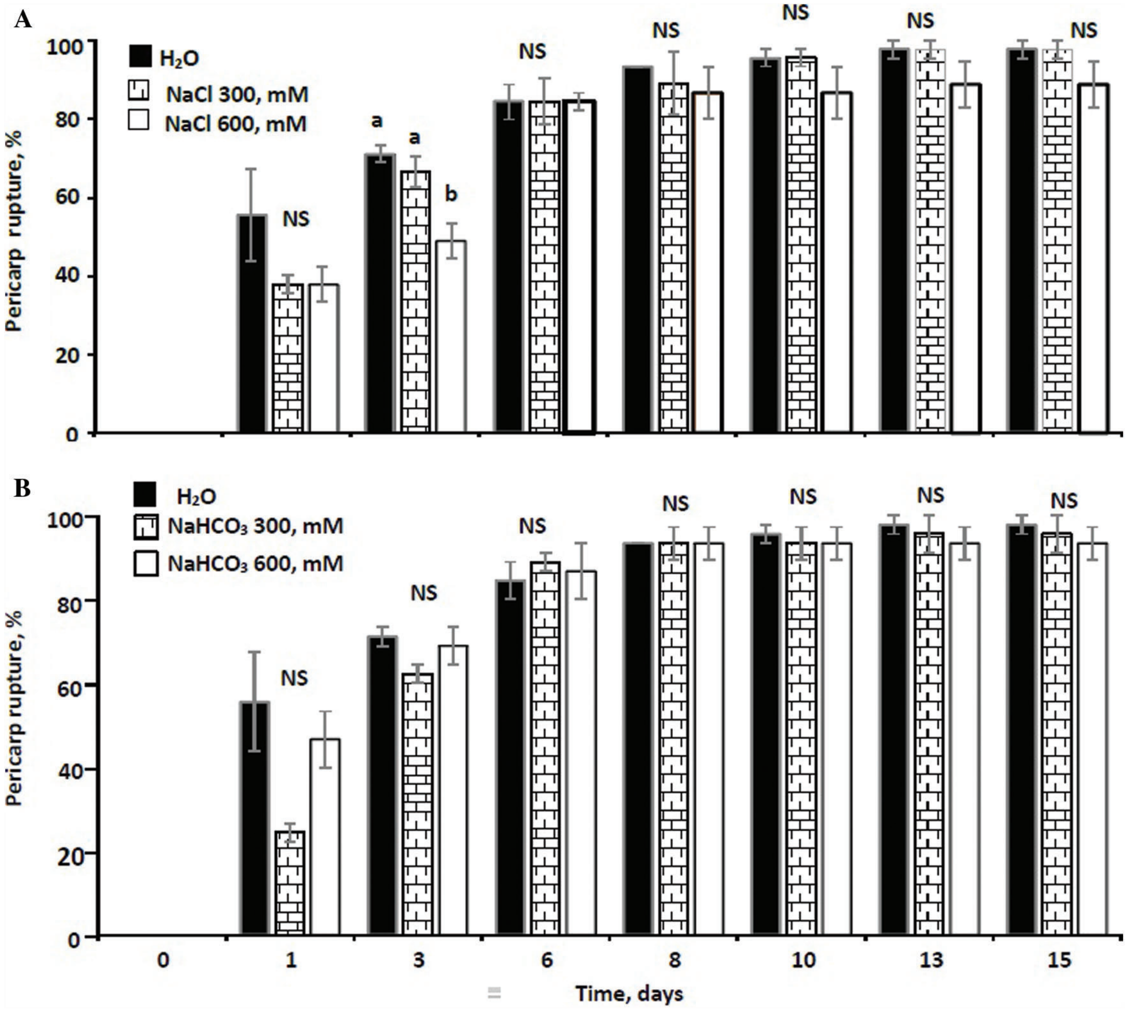

Figure 1: Pericarp rupture percentage over time in *A. marina* propagules under (A) saline and (B) alkaline stress. (means of 3 replicates ± SE). Means with different letters are significantly different at $P < 0.05$

3.2 Germination Percentage

Germination began by radicle emergence at 3 days after sowing either under distilled water or salt and alkaline stress. The salt and alkaline stress delayed germination but did not affect the final germination percentage. For instance, after 6 days, the germination percentages were 71.1%, 44.4%, and 42.2% under H_2O, 300, and 600 mM NaCl, respectively. Tukey's test ($P < 0.05$) indicated a significant effect of NaCl (Fig. 2A). Under 300 and 600 mM $NaHCO_3$, the germination percentages were 40% and 48.9%, respectively. Tukey's test ($P < 0.05$) showed no significant effect of $NaHCO_3$ (Fig. 2B). After 15 days, the germination percentage reached 95.6% under distilled water, but was 88.9% and 84.4% under 300 and 600 mM NaCl, respectively (Fig. 2A). Under alkaline stress, the germination percentage reached 93.3% under either 300 or 600 mM $NaHCO_3$ (Fig. 2B). Tukey's test ($P < 0.05$) showed no significant effects either under NaCl or $NaHCO_3$ (Figs. 2A, 2B).

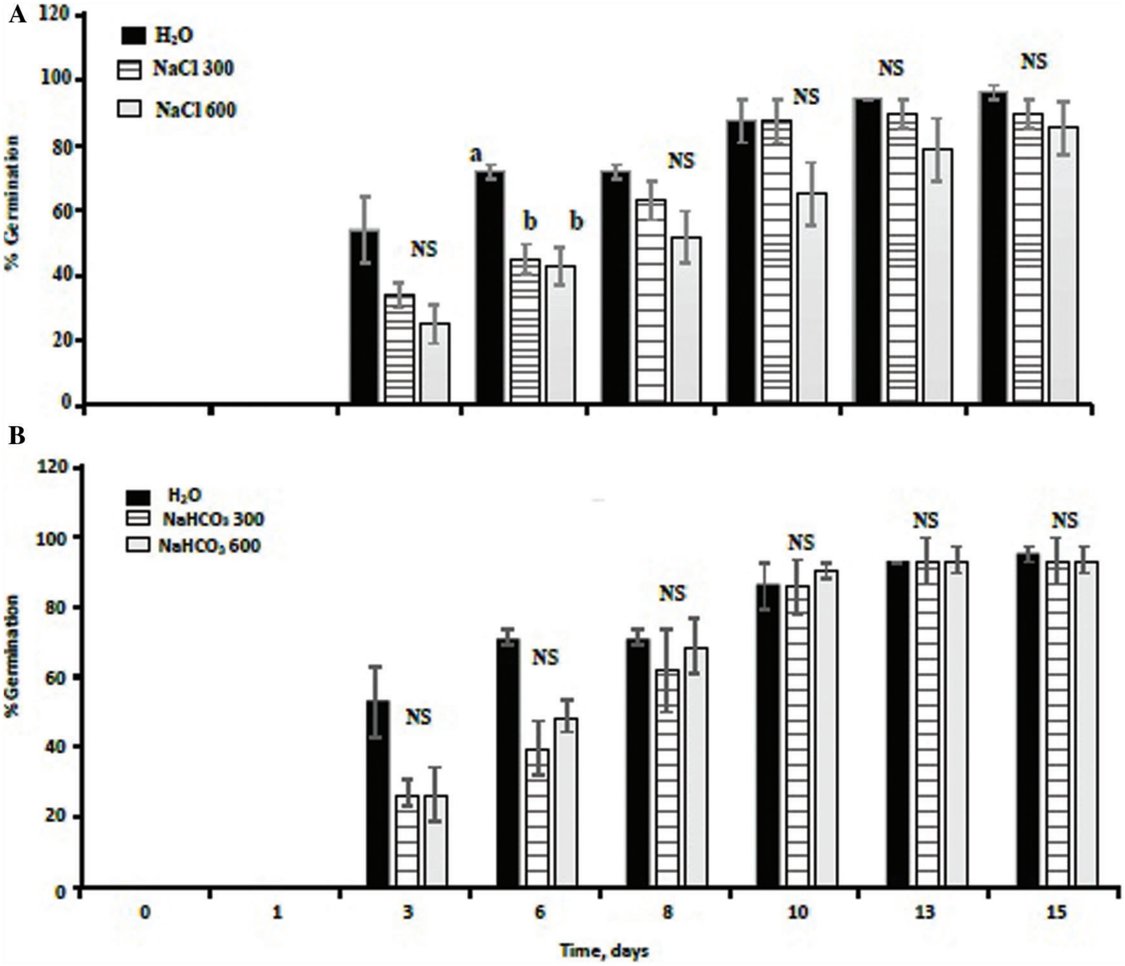

Figure 2: Germination percentage over time in *A. marina* propagules under (A) saline and (B) alkaline stress. (means of 3 replicates ± SE). At each time point, means with different letters are significantly different at $P < 0.05$

3.3 Rooting

Rooting began 6 days after sowing under distilled water, and the rooting percentage reached 24.4%. Salt and alkaline stress delayed the rooting process. For instance, under 600 mM NaCl, the rooting percentage reached only 8.9% at 6 days after sowing and 0% under alkaline conditions. The rooting percentage reached 17.8% and 13.3% under 300 and 600 mM $NaHCO_3$, respectively.

After 15 days, the rooting percentage was 71.1% under distilled water and reached 62% under both 300 and 600 mM NaCl concentrations. Under 300 mM $NaHCO_3$, the rooting percentage was 53.3%, and no rooting occurred under 600 mM $NaHCO_3$. Tukey's test ($P < 0.05$) indicated significant effects of both salts (NaCl and $NaHCO_3$) on this parameter (Figs. 3A and 3B).

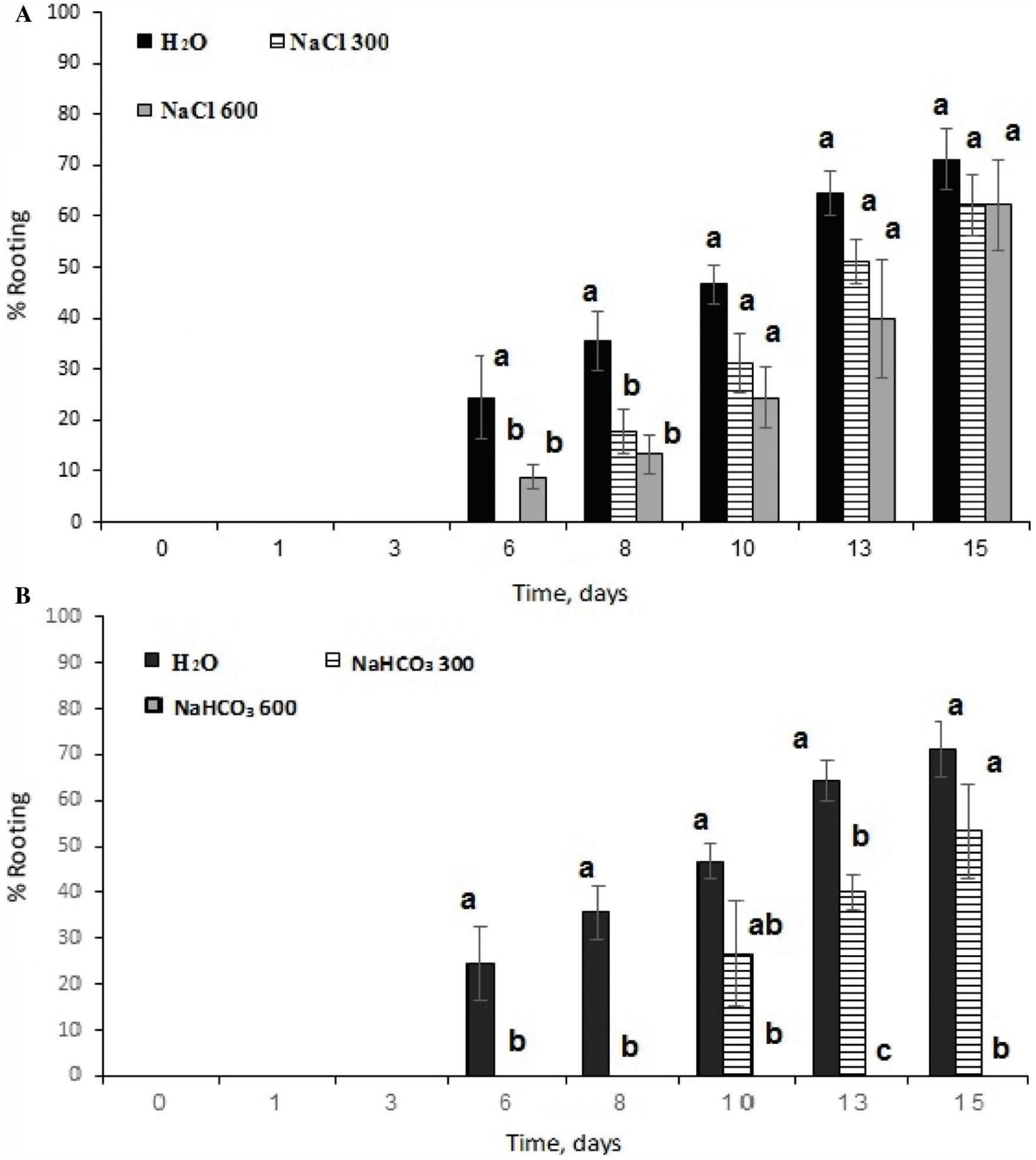

Figure 3: Rooting percentage over time in *A. marina* propagules under (A) saline and (B) alkaline stress. (means of 3 replicates ± SE). Means with different letters are significantly different at $P < 0.05$

3.4 Seedling Growth

No significant effects of 300 and 600 mM NaCl or $NaHCO_3$ on cotyledon growth were found (Table 1). Embryo axis growth was not significantly affected by these salts according to Tukey's test ($P < 0.05$) (Table 1). Root growth was not affected by NaCl concentration but was significantly reduced under 300 mM $NaHCO_3$ ($P < 0.05$).

Table 1: Effect of two salts: NaCl and $NaHCO_3$ on relative water content (RWC) and Growth of cotyledons, embryonic axe and root of *A. marina*. Dry mass: g. $plant^{-1}$

Salt concentration	RWC, g			Growth, g		
	Cotyledons	Axe	Root	Cotyledons	Axe	Root
0	2.30 ± 0.13 a	2.39 ± 0.63 a	3.05 ± 1 b	1.79 ± 0.28 a	0.17 ± 0.01 a	0.06 ± 0.01 a
300 mM NaCl	1.94 ± 0.07 b	2.85 ± 017 a	5.92 ± 0.19 a	2.49 ± 0.62 a	0.13 ± 0.03 a	0.05 ± 0.01 a
600 mM NaCl	1.85 ± 0.04 b	2.60 ± 0.12 a	5.56 ± 0.28 a	1.66 ± 0.11 a	0.11 ± 0.03 a	0.04 ± 0.01 a
300 mM $NaHCO_3$	2.08 ± 0.37 ab	2.83 ± 0.06 a	4.14 ± 0.40 a	2.13 ± 0.37 a	0.11 ± 0.01 a	0.01 ± 0 b
600 mM $NaHCO_3$	1.9 ± 0.14 b	2.57 ± 0.09 a	-	1.78 ± 0.14 a	0.11 ± 0.01 a	-

3.5 Relative Water Content

Both NaCl and $NaHCO_3$ salts decreased the water content in the cotyledon tissues. Tukey's test ($P < 0.05$) showed significant effects of the two salts on this parameter (Table 1). However, no significant effects of the two salts on water content in the embryo axis were noted according to Tukey's test ($P < 0.05$) (Table 1). Relative water content significantly increased under 300 and 600 mM NaCl and 300 mM $NaHCO_3$ according to Tukey's test ($P < 0.05$) (Table 1).

3.6 Cotyledon Gas Exchange

One-way ANOVA showed that salinity had a significant effect on photosynthetic activity (A). (F = 5.141; $P = 0.02$). One-way ANOVA also indicated that alkalinity had a significant effect on A (F = 7.854; $P = 0.005$) (Fig. 4A). gs was not significantly affected by 300 and 600 mM NaCl compared to the control (Fig. 4B). Under the $NaHCO_3$ treatments, only 600 mM resulted in significantly higher gs as compared to the control (Fig. 4B) (F = 1.567; $P = 0.241$).

The transpiration (E) measurement showed no significant effect of NaCl (F = 3.095; $P = 0.075$) or $NaHCO_3$ (F = 3.217; $P = 0.069$) (Fig. 4C). Internal CO_2 (Ci) measurement showed no significant effect of both concentrations of NaCl (F = 1.211; $P = 0.325$) or $NaHCO_3$ (F = 2.740; $P = 0.097$) (Fig. 4D).

The intrinsic water use efficiency was not significantly reduced by either NaCl concentrations compared to the control (F = 3.076; $P = 0.076$) (Fig. 4E). For $NaHCO_3$, a significant reduction was recorded under 600 mM compared to the control (Fig. 4E) (F = 5.063; $P = 0.021$), as also determined by Tukey's test ($P < 0.05$) (Fig. 4E).

4 Discussion

This work aimed to determine the effects of salt and alkaline stress on propagule germination and photosynthetic activity in the cotyledons of *A. marina*. In this species, the reproductive unit is green and possesses photosynthetic propagules. This mangrove is a salt-tolerant species during the vegetative stages, though salt and alkaline stress can affect early seedling growth. We were therefore interested in whether photosynthesis reduction under NaCl and $NaHCO_3$ in *A. marina* cotyledons affects propagule germination and early seedling growth.

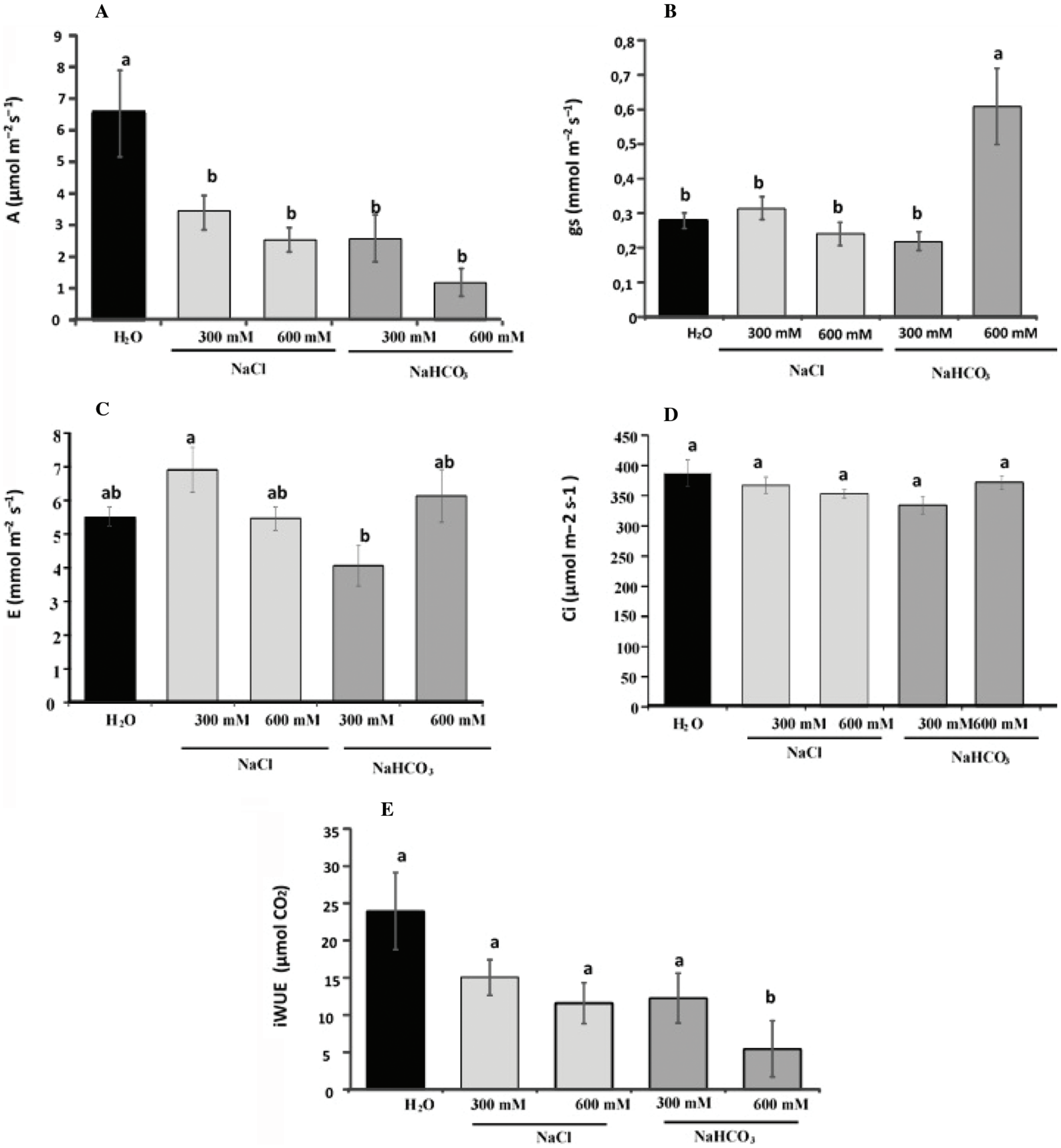

Figure 4: Effect of saline and alkaline stress on photosynthetic parameters in *A. marina* cotyledons under (A, net photosynthetic rate; gs, stomatal conductance; E, transpiration; Ci, internal CO_2 concentration; iWUE, intrinsic water use efficiency) (means of 5 replicates ± SE). Means with different letters are significantly different at $P < 0.05$

4.1 Effect of Salt and Alkaline Stress on Germination and Seedling Growth

The optimum germination of *A. marina* propagules (95.56%) was obtained under distilled water (Figs. 1A and 1B). However, alkaline and saline conditions did not significantly reduce germination. This suggests that *A. marina,* which grows along coastlines, has developed special mechanisms to tolerate high alkaline and saline conditions during the germination process. In halophytic plants, including mangroves, rapid germination leads to fast seedling establishment [13]. Both rapid propagule germination and mangrove growth are important. The propagules of *A. marina* are viviparous and therefore lose their viability rapidly [14]. However, the germination capacity of other mangrove species was found to decrease under high salt concentrations, as reported for *Avicennia officinalis* (L.) [2]. In the two physiographic types of *Avicennia schaueriana* Stapf and Leechm. ex Moldenke, the germination percentages were 45.1%, and 76.4% under low salinity, and germination was inhibited under higher salinity [15]. The same result was obtained for *Laguncularia racemosa* (L.) [14]. Thus, we suggest that the high germination capacity of *A. marina* under high salt and alkaline stress may explain why it is considered a dominant mangrove species along several coastlines throughout the world.

NaCl delayed rooting and root development, whereas a higher concentration of $NaHCO_3$ completely inhibited root development. In plants, the rapid elongation of the roots is primarily the result of the massive expansion of young cells produced by ongoing division in the meristem tissues. Excessive salinity has been reported to inhibit both root cell production and cell expansion [16]. Alkaline treatment has serious adverse impacts on root growth and is accompanied by marked ROS accumulation in the roots [17]. Excess ROS accumulation under various stressors is a major cause of cellular damage. In rice, the exogenous application of procyanidins, which are antioxidants, significantly alleviated alkalinity-induced cellular damage and improved alkalinity-induced reductions in seedling growth [17]. Thus, we can speculate that in *A. marina*, alkaline stress causes ROS accumulation and inhibits rooting and root growth by altering hormone growth metabolism. For instance, in Brassica rapa, salt induced a high level of ROS accumulation, which resulted in perturbations to auxin metabolism by modifying both the biosynthesis of IAA and its catabolism, thereby causing root growth inhibition [18].

4.2 Effect of Salt and Alkaline Stress on Photosynthesis

The propagules of *A. marina* have a high total sugar concentration in comparison with the seeds of other halophytes [5]. Some authors suggest that the high sugar content in the propagules prevents water loss and increases viability. Soluble sugar accumulation is a sign of adaptation to salinity in plants [19,20]. Plants accumulate sugar via photosynthesis. In viviparous propagules, the germination process occurs in the mother plant before dissemination. Since the embryo cotyledons are photosynthetic, they act as the source of photo-assimilates for the early growth phase of seedlings. In the current experiment, the photosynthetic activity in the *A. marina* cotyledons was significantly reduced by saline and alkaline stresses compared to the control (Fig. 4A). This was accompanied by rooting inhibition and root growth reduction under $NaHCO_3$, but embryo axis growth was not affected. By contrast, the water content in the cotyledons and the growth of the embryo axis were not affected by the two salt treatments. Instead, we detected a significant increase in the water content of the roots. Thus, the root growth inhibition caused by alkaline stress resulted from the accumulation of toxic ions and not from the water status alteration. In the propagules of *A. marina,* toxic ions, including Cl^- and Na^+, accumulated in the coat, while K^+ accumulation was observed in the cotyledons and embryonic axis, which maintained a high K^+/Na^+ ratio [5]. Thus, we suppose that the low toxic ion accumulation and the high sugar accumulation in the *A. marina* cotyledons allowed this species to maintain normal embryo axis growth even under high saline and alkaline stresses. It is suggested that the large reserved mass in the folded cotyledons of *A. marina* propagules sustains embryo growth and seedling establishment under salinity [5]. Such high reserve accumulation is noteworthy when compared to some other halophyte seeds. For instance, sugar accumulation in the propagules of *A. marina* was about 3-fold higher than in the seeds of *Halophyrum mucronatum* (L.) Stapf [21] and 75-fold higher than in the seeds of *Kochia indica* Wight [22]. The high sugar content in the *A. marina* propagules is considered as an avoidance mechanism that reduces water loss from the propagules by the high ambient osmotic pressure [5]. However, we suggest that sugar accumulation not only prevents water loss but also allows embryo axis growth under seawater when the photosynthetic activity is reduced under alkaline and saline stresses.

Stomatal conductance was not affected by the two NaCl concentrations and 300 mM $NaHCO_3$, but it was stimulated by 600 mM $NaHCO_3$. Thus, the reduction in photosynthesis activity was not related to the limitation of stomatal conductance. The impairment of photosynthetic enzyme activities and reduction in chlorophyll and carotenoid contents and/or chloroplast ultrastructure alteration could explain the reduced photosynthetic activity by salt and alkaline stresses [5,23]. A decline in photosynthetic activity was also observed in *A. marina* [8] and two other mangrove species, including *Kandelia candel* (L.) Druce and *Bruguiera gymnorhiza* (L.) Lam. [24]. The same feature was also observed in some other halophytes, such as *Aeluropus littoralis* (Gouan) Parl. [25]. By contrast, in other halophytes, such as *Cakile maritima* Scop. [26], *Sesuvium portulacastrum* (L.), *Tecticornia indica* (Willd.) K.A.Sheph. & Paul G.Wilson [23], and *Limoniastrum guyonianum* [27], salinity stimulated photosynthetic activity. On the contrary, it is well-known that photosynthesis diminution is accompanied by conductance and internal CO_2 concentration (Ci) reductions. This was not the case in the present study. By contrast, in *Chenopodium quinoa* cultivated under saline conditions, photosynthetic activity was not affected, although stomatal conductance was severely reduced [28].

The Ci is used to determine the assimilation ability of mesophyll cells for CO_2 [29]. In this study, although the two tested salts decreased photosynthesis, there was no effect on Ci. The same result was found in 14 barley genotypes [28] and in *Polygonum arenastrum* [30]. To explain these results, it has been suggested that Ci remains steady or increases at very low gs values (<5 mmol H_2Om^{-2} s^{-1}), whereas Ci generally decreases under full to intermediate conductance conditions [31]. This behavior has been observed in rice under salinity [32] and barley under water stress [33]. This result confirmed that salt did not affect stomatal conductance, and thus the reduction in photosynthesis rate could be explained by the decrease in the activity of certain enzymes. Intrinsic water use efficiency (iWUE) exhibited similar trends as photosynthesis rate. Its reduction under high saline and alkaline stresses was because of a decline in the net photosynthetic rate rather than stomatal conductance since the latter remained constant under stress conditions [25]. The persistence of stomatal conductance led to constant transpiration since the latter occurs via stomatal conductance.

5 Conclusion

In conclusion, a reduction in photosynthesis did not alter the early germination phases under saline and alkaline stresses, whereas alkaline stress caused rooting inhibition, root growth reduction, and altered seedling establishment.

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Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

References

1. Glasenapp, Y. I., Korth, X., Nguyen, V., Papenbrock, J. (2019). Sustainable use of mangroves as sources of valuable medicinal compounds: Species identification, propagation and secondary metabolite composition. *South African Journal of Botany, 121,* 317–28. DOI 10.1016/j.sajb.2018.11.020.
2. Alam, M. R., Mahmood, H., Rayhan, K. M. L., Rahman, M. M. (2018). Adaptive phenotypic plasticity of *Avicennia officinalis* L. across the salinity gradient in the sundarbans of Bangladesh. *Hydrobiologia, 808,* 163–174. DOI 10.1007/s10750-017-3420-z.

3. Onyena, A. P., Sam, K. (2020). A review of the threat of oil exploitation to mangrove ecosystem: Insights from Niger delta, Nigeria. *Global Ecology and Conservation, 22,* e00961. DOI 10.1016/j.gecco.2020.e00961.
4. McFadden, L., Spencer, T., Nicholls, R. J. (2007). Broad-scale modeling of coastal wetlands: What is required? *Hydrobiologia, 577,* 5–15. DOI 10.1007/s10750-006-0413-8.
5. Barhoumi, Z., Ahmed, A. H., Kamel, A. S. (2018). Traits allowing *Avicennia marina* propagules to overcome seawater salinity. *Flora, 242,* 16–21. DOI 10.1016/j.flora.2018.03.003.
6. Khan, M. A., Aziz, I. (2001). Salinity tolerance in some mangrove species from Pakistan. *Wetlands Ecology and Management, 9,* 229–233. DOI 10.1023/A:1011112908069.
7. Hoppe-Speer, S. C. L., Adams, J. B., Rajkaran, A., Bailey, D. (2011). The response of the red mangrove *Rhizophora mucronata* Lam. to salinity and inundation in *South Africa*. *Aquatic Botany, 95(2),* 71–76. DOI 10.1016/j.aquabot.2011.03.006.
8. Barhoumi, Z., Hussain, A. A., Atia, A. (2021). Physiological response of *Avicennia marina* to salinity and recovery. *Russian Journal of Plant Physiology, 68,* 696–707. DOI 10.1134/S1021443721040026.
9. Saleh, M. Y., Sarhan, M. S., Mourad, E. F., Hamza, M. A., Abbas, M. T. et al. (2017). A novel plant-based-sea water culture media for *in vitro* cultivation and in situ recovery of the halophyte microbiome. *Journal of Advanced Research, 8(6),* 577–590. DOI 10.1016/j.jare.2017.06.007.
10. Lim, H., Li, Z., Shen, Z., Luo, M., Liu, Y. et al. (2020). Physiological and proteomic responses of mangrove plant *Avicennia marina* seedlings to simulated periodical inundation. *Plant Soil, 450,* 231–254. DOI 10.1007/s11104-020-04474-8.
11. Anjum, S. A., Tanveer, M., Hussain, S., Ullah, E., Wang, L. et al. (2016). Morpho-physiological growth and yield responses of two contrasting maize cultivars to cadmium exposure. *CLEAN–Soil, Air, Water, 44(1),* 29–36. DOI 10.1002/clen.201400905.
12. Ehleringer, J. R., Hall, A. E., Farquhar, G. D. (1993). *Stable isotopes and plant carbon water relations*. NY, New York: Academic Press.
13. Liu, R., Wang, L., Tanveer, M., Song, J. (2018). Seed heteromorphism: An important adaptation of halophytes for habitat heterogeneity. *Frontiers in Plant Science, 9,* 1515. DOI 10.3389/fpls.2018.01515.
14. Siddiqi, N. A. (2001). *Mangrove forestry in Bangladesh.* Institute of Forestry and Environmental Sciences, University of Chittagong, Chittagong.
15. Cavalcanti, V. F., Andrade, A. C. S., Soares, M. L. G. (2007). Germination of *Avicennia schaueriana* and *Laguncularia racemosa* from two physiographic types of mangrove forest. *Aquatic Botany, 86(3),* 285–290. DOI 10.1016/j.aquabot.2006.10.008.
16. Zidan, I., Azaizeh, H., Neumann, P. M. (1990). Does salinity reduce growth in maize root epidermal cells by inhibiting their capacity for cell wall acidification? *Plant Physiology, 93(1),* 7–11. DOI 10.1104/pp.93.1.7.
17. Zhang, H., Liu, X. L., Zhang, R. X., Yuan, H. Y., Wang, M. M. et al. (2017). Root damage under alkaline stress is associated with reactive oxygen species accumulation in rice (*Oryza sativa* L.). *Frontiers in Plant Sciences, 8,* 1580. DOI 10.3389/fpls.2017.01580.
18. Pavlović, I., Pěnčík, A., Novák, O. V., Sandra, V., Brkanac, R. et al. (2018). Short-term salt stress in brassica rapa seedlings causes alterations in auxin metabolism. *Plant Physiology et Biochemistry, 125,* 74–84. DOI 10.1016/j.plaphy.2018.01.026.
19. Slama, I., Abdelly, C., Bouchereau, A., Flowers, T., Savouré, A. (2015). Diversity, distribution, and roles of osmoprotective compounds accumulated in halophytes under abiotic stress. *Annals of Botany, 115(3),* 433–447. DOI 10.1093/aob/mcu239.
20. Hussain, S., Khaliq, A., Tanveer, M., Matloob, A., Hussain, H. A. (2015). Aspirin priming circumvents the salinity-induced effects on wheat emergence and seedling growth by regulating starch metabolism and antioxidant enzyme activities. *Acta Physiologiae Plantarum, 40,* 1–12. DOI 10.1007/s11738-018-2644-5.
21. Siddiqui, S. Z., Khan, M. A. (2011). The role of enzyme amylase in two germinating seed morphs of *Halopyrum mucronatum* (L.) stapf. in saline and non-saline environment. *Acta Physiologiae Plantarum, 33,* 1185–1197. DOI 10.1007/s11738-010-0646-z.

22. Zahran, M. A., Abdel Wahid, A. A. (1982). Halophytes and human welfare. In: Sen, D. N., Rajpurohit, K. S. (Eds.), *Contributions to the ecology of halophytes*, pp. 235–257, Dr. W. Junk Publishers, The Hague, Netherlands.
23. Rabhi, M., Castagna, A., Remorini, D., Scattino, C., Smaoui, A. et al. (2012). Photosynthetic responses to salinity in two obligate halophytes: *Sesuvium portulacastrum* and *Tecticornia indica*. *South African Journal of Botany, 79,* 39–47. DOI 10.1016/j.sajb.2011.11.007.
24. Li, N., Chen, S., Zhou, X., Li, C., Shao, J. et al. (2008). Effect of NaCl on photosynthesis, salt accumulation and ion compartmentation in two mangrove species, *Kandelia candel* and *Bruguiera gymnorhiza*. *Aquatic Botany, 88(4),* 303–310. DOI 10.1016/j.aquabot.2007.12.003.
25. Barhoumi, Z. (2018). Physiological response of the facultative halophyte, *Aeluropus littoralis*, to different salt types and levels. *Plant Biosystems, 153(2),* 298–305. DOI 10.1080/11263504.2018.1478901.
26. Debez, A., Saadaoui, D., Ramani, B., Ouerghi, Z., Koyro, H. W. et al. (2006). Leaf H^+-ATPase activity and photosynthetic capacity of *Cakile maritima* under increasing salinity. *Environmental and Expiremental Botany, 57,* 285–95. DOI 10.1016/j.envexpbot.2005.06.009.
27. Barhoumi, Z., Trabelsi, N., Atia, A., Djebali, W., Chaïbi, W. et al. (2015). Salt stress response in the halophyte *Limoniastrum guyonianum* boiss. *Flora, 217,* 1–9. DOI 10.1016/j.flora.2015.09.003.
28. Turcios, A. E., Papenbrock, J., Tränkner, M. (2021). Potassium, an important element to improve water use efficiency and growth parameters in quinoa (*Chenopodium quinoa*) under saline conditions. *Journal of Agronomy and Crop Science, 207(4),* 618–630. DOI 10.1111/jac.12477.
29. Zhang, M., Hu, C., Sun, X., Zhao, X., Tan, Q. et al. (2014). Molybdenum affects photosynthesis and ionic homeostasis of Chinese cabbage under salinity stress. *Communication in Soil Science and Plant Analysis, 45(20),* 2660–2672. DOI 10.1080/00103624.2014.941855.
30. Geber, M. A., Dawson, T. E. (1997). Genetic variation in stomatal and biochemical limitations to photosynthesis in the annual plant *Polygonum arenastrum*. *Oecologia, 109(4),* 535–546. DOI 10.1007/s004420050114.
31. Roche J, Q., Monaco, T. A., Hole, D. (2006). Stomatal conductance is a key parameter to assess limitations to photosynthesis and growth potential in barley genotypes. *Plant Biology, 8,* 515–521. DOI 10.1055/s-2006-923964.
32. Yeo, A. R., Caporn, S. J. M., Flowers, T. J. (1985). The effect of salinity upon photosynthesis in rice (*Oryza sativa* L.): Gas exchange by individual leaves in relation to their salt content. *Journal of Experimental Botany, 36(8),* 1240–1248. DOI 10.1093/jxb/36.8.1240.
33. Lal, A., Ku, M. S. B., Edwards, G. E. (1996). Analysis of inhibition of photosynthesis due to water stress in the C_3 species *Hordeum vulgare* and *Vicia faba*: Electron transport, CO_2 fixation and carboxylation capacity. *Photosynthesis Research, 49(1),* 57–69. DOI 10.1007/BF00029428.