Morpho-Physiological Responses and Salinity Tolerance Mechanisms of Anabasis articulata (Forssk.) Seedlings under NaCl Stress Gradient

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Research Article

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Abstract

Anabasis articulata (Forssk.) Moq. is a perennial halophyte widely distributed in the arid regions of North Africa, particularly in the Algerian Sahara, and in the Middle East. It plays an essential ecological role in combating desertification and stabilising dunes. This study explores its salt tolerance mechanisms through a rigorous experimental approach including seed collection, sandy substrate preparation, transplantation, and the application of a water regime inducing progressive salt stress (0 to 300 mM NaCl). Biometric and hydric analyses, subjected to statistical treatments, highlight exceptional resilience. Stress decreases leaf expansion ($m = -0.03 \pm 0.01 cm^2$) and branch elongation ($m = -1.32 \pm 0.33 cm$), but the species compensates with architectural restructuring, tripling the number of branches at 150mM. *A. articulata* simultaneously maintains stable water homeostasis up to 300 mM, with a leaf water content (55.27 ± 0.71%) significantly higher than that of the roots and stems ($P < 0.0001$). This result confirms that the aquifer parenchyma plays the role of a water reservoir. By combining root growth stimulation ($Y = 0.03168 X$) with an adaptive succulence strategy, the plant demonstrates a remarkable ability to exploit sodium as an osmotic driver. These plasticity mechanisms make this taxon a crucial strategic element for the restoration of saline arid ecosystems in Algeria and worldwide.

Introduction

In semi-arid and arid ecosystems, soil salinity represents a major abiotic factor that limits plant productivity (Flowers and Colmer 2008). According to Ungar (1991), this ambient factor decisively influences the presence, geographical distribution, and zonation of plants. Halophytes have a biological ability to thrive optimally in environments enriched with sodium chloride, unlike glycophytes whose metabolism is hindered by the presence of salts (Munns and Tester 2008; Flowers et al. 2010). These organisms use specific tolerance strategies to withstand osmotic and ionic stress due to high salinity, notably osmotic adjustment through the accumulation of Na^+ and Cl^- ions, vacuolar compartmentalisation, and preference for K^+ (Munns and Tester 2008).

In Algeria, this issue is taking a worrying turn, as more than 3.2 million hectares of land are affected by salinisation, a phenomenon particularly widespread in the Low Sahara regions and the vast steppe plains. The potential evapotranspiration, which is significantly higher than precipitation, characterises the arid climate and promotes the capillary rise of salts that accumulate on the surface, particularly in the regions of Chotts and Sabkhas, this soil degradation imposes severe selection on the local vegetation, making Algerian saline ecosystems exceptional natural laboratories for observing extreme adaptations (El Hafed, 2019).

The response of plants to salt stress is a complex function that depends on genotypic specificity, the saline concentration of the environment, and the phenological development stage of the plant (Wang et al. 2003). The study of these adaptive responses relies on multidisciplinary approaches, including anatomical, ecological, physiological, and molecular methods (Wang et al.2003). Halophytes consider sodium (Na^+) as an indispensable component of their metabolism; it plays an active role in photosynthesis, osmotic adjustment, and the maintenance of the water potential gradient (Joshi et al. 2015). Moreover, although both Na^+ and Cl^- ions are involved in osmotic adjustment in response to salinity, Na^+ ions play a more effective role than Cl^- ions in regulating cellular water potential (Ramos et al. 2004).

In hypersaline biotopes, halophytes naturally evolve, expressing heterogeneous degrees of tolerance according to the taxa (Belkhodja and Bidai, 2004). Unlike glycophytes that are sensitive to salt, halophytes know how to optimise their vegetative growth on salt-enriched soils thanks to particular physiological adaptations such as ion accumulation and osmotic adjustment (Niu et al. 1995). These species do not merely tolerate high salinity concentrations dominated by sodium and chlorine; the presence of these ions in the rhizosphere proves indispensable for the completion of their biological cycle (Hasegawa et al. 2000).

The family Amaranthaceae, redefined according to phylogenetic classifications (APG IV 2016), is one of the most resilient plant groups in arid and hypersaline environments, with more than 2,000 species whose morphological diversity is particularly pronounced (Kadereit et al. 2014). In the northern Algerian Sahara, this family is widespread in hostile ecosystems, such as gypsiferous plains and salt basins, thanks to emblematic species like *Anabasis articulata*. The species survives thanks to a dual

adaptive strategy: a bimodal root architecture, which maximises the exploitation of rainwater and deep aquifers while avoiding wind erosion, and a strict metabolic adjustment through the accumulation of compatible solutes to cope with water stress and intense evapotranspiration (Voznesenskaya and al. 2007; Sage 2004). In addition to its ecophysiological performance, *Anabasis articulata* constitutes a major socio-economic base as an essential pastoral resource and a source of bioactive molecules for biodiscovery (Al-Joufi et al. 2022). However, with the increase in anthropogenic and climatic pressures, the sustainable valorisation of this strategic potential now requires rigorous scientific governance to preserve the balance of these fragile ecosystems.

In this context of valorisation and preservation, the present work aims to decipher the adaptive strategy of *Anabasis articulata* in response to salinity. The main objective is to analyse the trade-off between maintaining structural integrity and the plasticity of growth parameters under increasing NaCl gradients. This work, by studying the resilience mechanisms of this spontaneous halophyte from the northern Algerian Sahara, sheds new light on the survival capabilities of Saharan taxa in the face of increasing osmotic and ionic constraints.

Material and Methods

Studied specie

Anabasis articulata (Amaranthaceae), locally named "Adjrem" or "Baguel," is a spontaneous perennial halophyte characteristic of Saharan ecosystems (Ozenda 1991; Chehma 2006). Morphologically (Fig. 1. A1 and A2), it appears as a low bush (up to 2 m) with a thick and twisted trunk, displaying a bluish-green colouration. Its articulated branches, almost leafless, exhibit a marked xerophytic adaptation: they are deciduous during periods of extreme drought (Ozenda 1983).

The species blooms between November and December (Quezel and Santa 1962). The flowers, a rosy white, are solitary in the axils of the opposite leaves. The fruit is distinguished by the presence of three wings resulting from the expansion of the sepals (Fig. 1. B1 and B2). Widely distributed in Saharan stony soils, it is particularly abundant on the plateaus of Oued Righ (Kherraze et al. 2010).

Seed Collection and Substrate Preparation

The collection of *Anabasis articulata* seeds was carried out on January 15, 2021, at the Goug station (Oued Righ Region; 32.812410 N; 5.872965 E) from healthy individuals that had reached their physiological maturity (Fig. 2). Simultaneously, a substrate based on sand collected in situ from the rhizosphere of the species was prepared according to a rigorous protocol: sieving at 2 mm, successive leachings with filtered water to eliminate salts, physicochemical characterisation (pH and EC), and stabilisation by drying in a greenhouse for 72 hours.

Cultivation and Transplantation Setup

The sowing was carried out on January 28, 2021, in trays, under a distilled water irrigation regime every 48 hours. After 15 days of growth, the most vigorous seedlings (3–4 leaf stage) were transplanted into plastic pots containing 3.3 kg of a sand-soil mixture (2 :1 v/v), topped with a 2 cm layer of washed gravel for drainage to prevent root hypoxia. The experiment, conducted until May 15, 2021, at the Biophysical Station of Touggourt (C.R.S.T.R.), followed

Water Regime and Induction of Salt Stress

The management of irrigation was based on a gravimetric approach aimed at maintaining the substrate at 100% of its retention capacity (RC). The latter was previously determined according to the Aubert (1978) method using the formula: CR (%) = (P(wet) - P(dry)) / P(dry) * 100

The monitoring of the water status was ensured by systematic weighings every 48 hours, allowing for precise compensation of losses due to evapotranspiration. An initial establishment phase of one month, under exclusive irrigation with distilled water, was observed to stabilise the plant material. At the end of this vegetative growth phase, salt stress was induced for the six treatment modalities by the addition of sodium chloride (NaCl) solutions, prepared by mass dissolution (m/v) in distilled water. In contrast, the control batches (P0-S and P0-T) continued to receive irrigation with distilled water only (condition C0) (Table I), serving as a non-saline reference for the experiment. The thermal conditions in the greenhouse, oscillating between 15°C and 35°C with peaks at 45°C, faithfully reproduced the characteristic amplitudes of the species' natural habitat.

Biometric and Hydric Analyses

At the end of the 32-day experimental phase under salt stress, various growth and water status indicators were quantified. Leaf morphometry was characterised by counting the leaves and measuring their linear dimensions (length L and width l). The leaf area (S) was estimated by applying the correction coefficient of Bonhomme et al. (1982): S = (L * l) * 0.75. At the same time, vegetative development was assessed by measuring the elongation of the stems, branches, and root system, complemented by counting the secondary branches. At harvest, the aerial (epigeal) and root (hypogeal) parts were separated at the collar after a thorough cleaning of the root system. The fresh biomass (FB) was immediately weighed, then the samples were dehydrated in an oven (105°C for 24 hours) until a constant dry weight (DW) was obtained. These measurements made it possible to determine the dry matter content (DM, %) and the water content (WC, %) according to Coulibaly's (2014) equations: DM = (BM / FM) * 100 and MC = 100 - DM.

Data analysis

The data related to morphological parameters were subjected to a paired t-test (dependent samples t-test) to determine if their mean difference was significantly different from zero ($p < 0.05$), with the notable exception of root length, which was analysed using simple linear regression to model the underlying functional relationships. Concurrently, the water data (dry matter and water content) were analysed using a one-way analysis of variance (One-Way ANOVA) to identify significant effects of the studied factor; in the case of significant differences ($p < 0.05$), a Tukey's post-hoc multiple comparison test (HSD) was applied to discriminate homogeneous groups and quantify inter-means differences. All these analyses were performed using GraphPad Prism version 10.4.2 software.

Results

Morphological Parameters

Number of leaves (LN) and Leaf area (LA):

The analysis of the number of leaves (LN) under saline conditions showed no statistically significant difference between the control plants and those exposed to NaCl ($t = 2.131$; $P = 0.0706$), although a slight increasing trend was observed at 50 mM (Fig. 3A1). In contrast, leaf area (LA) was significantly affected by salt stress ($t = 5.701$; $P < 0.0007$). The control plants reached a maximum leaf area at 150 mM, while the application of NaCl induced an immediate and significant reduction in leaf area (m -0.03 ± 0.01 cm²) compared to the controls (Fig. 3A2).

Branching and elongation:

The number of branches showed a biphasic response ($t = 3.589$; $P < 0.0089$). The proliferation peaked at 150 mM NaCl (26.19 ± 7.30 branches) compared to the control (10.25 ± 2.25). Beyond 200 mM, branching decreased but remained higher than the control up to 300 mM (Fig. 3B1). Conversely, branch elongation was significantly inhibited ($t = 3.990$; $P < 0.0053$), with an average decrease of 1.32 ± 0.33 cm compared to the baseline control length (5.23 cm) (Fig. 3B2).

Stem and root length:

The stem length remained relatively stable despite a moderate overall reduction ($t = 9.636$; $P < 0.0001$), maintaining an average of 3.42 ± 0.22 cm under stress (Fig. 3C). The root length showed a positive linear correlation with salinity ($F_{1,7} = 10.45$; $P < 0.0144$), with an average increase of 0.03168 cm per mM of added NaCl (Fig. 3D).

3.2. Biomass Allocation and Water Status

Distribution of dry matter:

A significant heterogeneity was observed in the distribution of biomass ($F = 21.85$; $P < 0.0001$). The allocation was prioritised to the roots (48.03 ± 0.03%) and stems (48.07 ± 0.03%), while the chlorophyllous branches showed significantly lower dry matter (44.73 ± 0.71%; $P < 0.0001$) (Fig. 4A1).

Water homeostasis:

The water content was significantly higher in the branches (55.27 ± 0.71%) compared to the roots (51.97%) and the stems (51.93%) ($F = 21.85$; $P < 0.0001$). This water status remained stable across the entire salinity gradient up to 300 mM of NaCl (Fig. 4B2).

Discussion

Architectural plasticity and energy trade-offs under salt stress

The stability of the number of leaves (LN) observed in *Anabasis articulata* indicates the maintenance of continuous foliar meristematic activity, ensuring a functional capacity for organ production. This result is consistent with the work of Debez et al. (2003, 2006), which established that certain halophyte species continue to produce aerial biomass at NaCl concentrations between 100 and 300mM. However, the significant reduction in leaf area (LA) from the onset of stress suggests that salinity influences cell expansion earlier than the initial phase of organ initiation (Munns and Tester 2008). Physiologically, this retraction constitutes a priority adaptive response to the water deficit induced by the osmotic component of salt. The decrease in turgor pressure mechanically limits wall elongation, a common phenomenon in halophytes to reduce the surface exposed to evapotranspiration (Parida and Das 2005; Munns and Gilliham 2015). This "miniaturisation" could also reflect a preventive compartmentalisation strategy: by limiting the size of the leaves, the plant restricts the transpiration flow and, by extension, the massive import of toxic Na^+ and Cl^- ions into the mesophyll (Flowers and Colmer 2008). This adaptation allows for the maintenance of minimal photosynthetic activity while preserving water integrity (Slama et al. 2015).

The analysis of branching reveals a biphasic and plastic response. The proliferation of secondary axes, peaking at 150 mM NaCl, suggests a release of apical dominance and a redistribution of cytokinins that compensate for the reduction in leaf area by densifying the canopy (Thomas and Bohnert 1993). This compensatory strategy, characteristic of resilient halophytes like *Atriplex halimus* (Boughalleb et al. 2009), optimises light capture while diluting toxic ions in the new tissues. Although an inhibition of branch elongation is observed beyond 200 mM due to the increase in the osmotic pressure of the medium (Benamar et al. 2009), the persistence of branching up to 300 mM attests to the architectural robustness of this Chenopodiaceae (Khan et al. 2010). This response is regulated by a complex hormonal balance, potentially involving an accumulation of abscisic acid (ABA) or a reduction in cytokinins (Itai 1999), as well as an energy trade-off where resources are diverted from elongation to homeostasis mechanisms (Binzel et al.1985; Zhu 2001).

Root elongation and structural robustness

Contrary to the results of Ansli (2019) and Benrebiha et al. (1987), which reported a severe decrease in stem growth proportional to NaCl, our results show a relative structural stability. This maintenance of integrity relies on a rigorous management of ionic homeostasis, where sodium is actively sequestered in the vacuoles of cortical cells, thus preserving the activity of apical meristems (Flowers and Colmer 2008). At the same time, the stimulation of root elongation observed up to 300 mM indicates a strategy of active exploration of the edaphic volume. This maintenance of turgor necessary for cell extension, even under low external water potential, is comparable to the performance of other desert halophytes such as *Suaeda fruticosa* or *Atriplex*

centralasiatica (Wang et al. 2004; Hameed et al. 2012). This resilience is likely mediated by hormonal regulation involving auxin and ABA (Hasegawa et al. 2000), allowing the avoidance of inhibition of root enzymatic pathways despite hypersalinity.

Biomass Allocation and Water Homeostasis

The integrated analysis reveals a preferential allocation towards the roots (RDM) and stems (SDM). The low dry matter content of chlorophyllous branches (BDM) compared to other organs confirms an adaptive succulence strategy. As Grigore (2012) points out, the development of aquifer parenchyma allows for an effective dilution of accumulated toxic ions. This dynamic fundamentally distinguishes *A. articulata* from models such as *Hordeum maritimum* (root exclusion) or *Limoniastrum guyonianum* (glandular excretion) (Munns & Tester 2008; Rouari et al. 2024). The stability of dry matter up to 300 mM exceeds that of *Atriplex halimus* (Walker et al. 1987) and is closer to that of *Traganum nudatum* (El Hafed 2019). It relie on strict vacuolar compartmentalisation that preserves organic biosynthesis (Flowers & Colmer, 2015). This optimised management results in a branch water content (BWC) higher than that of the roots, confirming their role as a water reservoir. This water homeostasis, comparable to that of *Sesuvium portulacastrum* (Slama et al. 2007) or *Atriplex griffithii* (Khan et al. 2000), results from an effective osmotic adjustment through parenchyma expansion (Karimi et al. 2005; Ogburn and Edwards 2010; Grigore et al. 2014). Na^+ is used as an osmotic driver to maintain turgor (El Hafed 2019; Flowers and Colmer 2015). Coupled with xeromorphic traits that limit transpiration losses, this hydraulic resilience allows *A. articulata* to preserve its functional integrity in the face of physiological drought, where less specialised taxa would suffer irreversible wilting (Shabala 2013).

Conclusions

The results of this study demonstrate the remarkable morpho-physiological plasticity of *Anabasis articulata* in response to salt stress, confirming its ability to preserve its functional integrity under severe ionic constraints. The species exhibits a contrasting adaptive response: while the increase in salinity induces a reduction in leaf area and longitudinal elongation, it simultaneously triggers a compensatory structural stabilisation. This architectural reorganisation primarily occurs within the chlorophyllous ramial system, whose proliferation compensates for the expansion deficit to maintain optimal photosynthetic capacity.

On a physiological level, the observed weight and water stability, particularly between 100 and 200 mM NaCl, demonstrates effective homeostasis. The ramial system establishes itself as the nerve center of hydraulic resilience, acting as a strategic reservoir. Through the expansion of the aquifer parenchyma, the species performs a "stem dilution" of the accumulated toxic ions. This mechanism, coupled with a rigorous vacuolar compartmentalisation of sodium used as an osmotic driver, ensures the maintenance of cellular turgor and prevents irreversible wilting.

From an ecological perspective, this research positions *A. articulata* as a major biological model for studying salinity tolerance in Saharan environments. Its strategy, based on a compromise between limiting exposure surfaces and maintaining a privileged water state in the succulent branches, highlights its strategic potential for the restoration of degraded arid ecosystems. This synergy of adaptive traits makes this taxon a fundamental pillar for understanding the survival mechanisms of fleshy halophytes in the face of extreme environmental stresses.

Declarations

Conflict of Interest:

The authors declare that they have no conflict of interest.

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Author Contribution

KHERRAZE Mohammed Elhafed and TRABELSI Hafida conceived the study, developed the methodology, and provided overall supervision of the work. BELAOUDMOU Chaima, LAKEHAL Soumia, and KHERRAZE Mohammed Elhafed carried out the experiments, collected the data, and performed the analyses. KHERRAZE Mohammed Elhafed and TRABELSI Hafida contributed to the interpretation of the results, the scientific discussion, and the validation of the conclusions. KHERRAZE Mohammed Elhafed drafted the initial manuscript. TRABELSI Hafida, BELAOUDMOU Chaima, and LAKEHAL Soumia participated in the critical revision of the scientific content. All authors read, corrected, and approved the final version of the manuscript and jointly assume responsibility for its content.

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Tables

Table

Code Traitement	**C_0**	**C_1**	**C_2**	**C_3**	**C_4**	**C_5**	**C_6**
Concentration (mM)	0	50	100	150	200	250	300
Concentration (g/L)	0	3	6	9	12	15	18

Figures

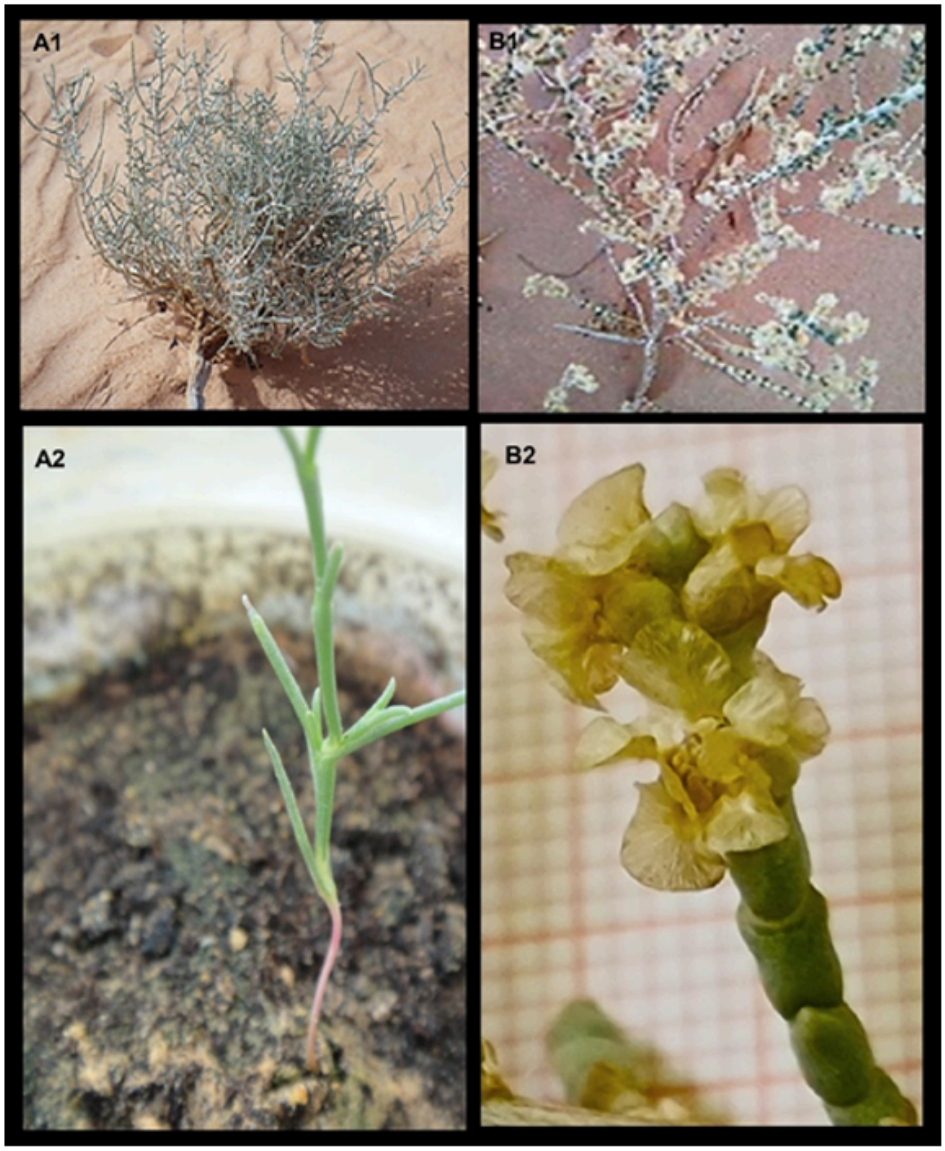

Fig.1.

Figure 1

Phenology and developmental stages of *Anabasis articulata* (Forssk.) Moq. A1: Habit of the adult plant. A2: Seedling stage. B1: Fruit-bearing stage. B2: Detail of flowering (Anthesis)

Fig.2.

Figure 2

Morphology of seeds and germination of *Anabasis articulata* (Forssk.) Moq.

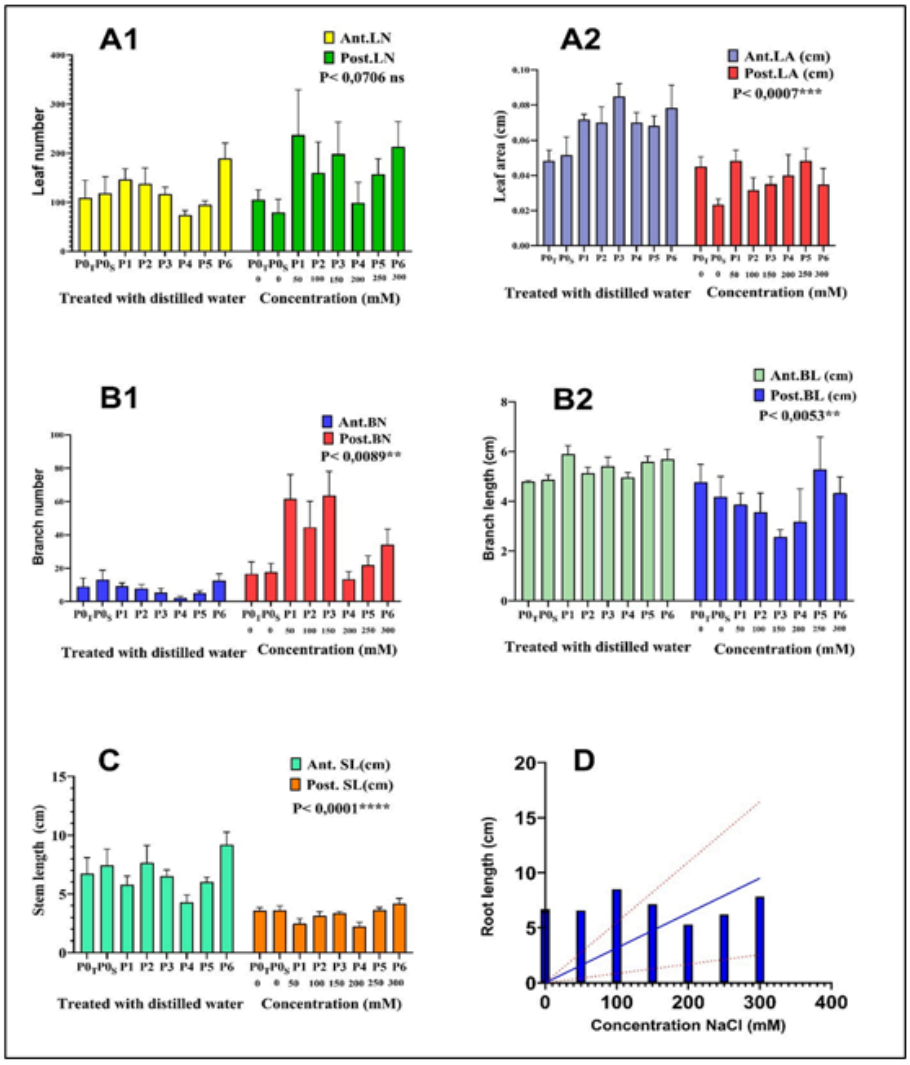

Fig.3.

Figure 3

Impact of salt stress on the aerial and underground growth parameters of *Anabasis articulata*: (A1-A2) Leaf dynamics, (B1-B2) Architecture of branching, (C) Stem elongation, and (D) Root growth kinetics. (Ant." (Anterior): the initial state before treatment and "Post." (Posterior): the final state after 21 days of stress. The data represent the means ± standard error (SE). In (D), the linear regression line (Y = 0.03168X) is accompanied by its 95% confidence interval (red dashed lines). LN (Leaf Number): Total number of leaves per individual. LA (Leaf Area): Average leaf area (cm²). BN (Branch Number): Number of secondary branches. BL (Branch Length): Average length of secondary branches (cm). SL (Stem Length): Length of the main axis or the stem (cm).

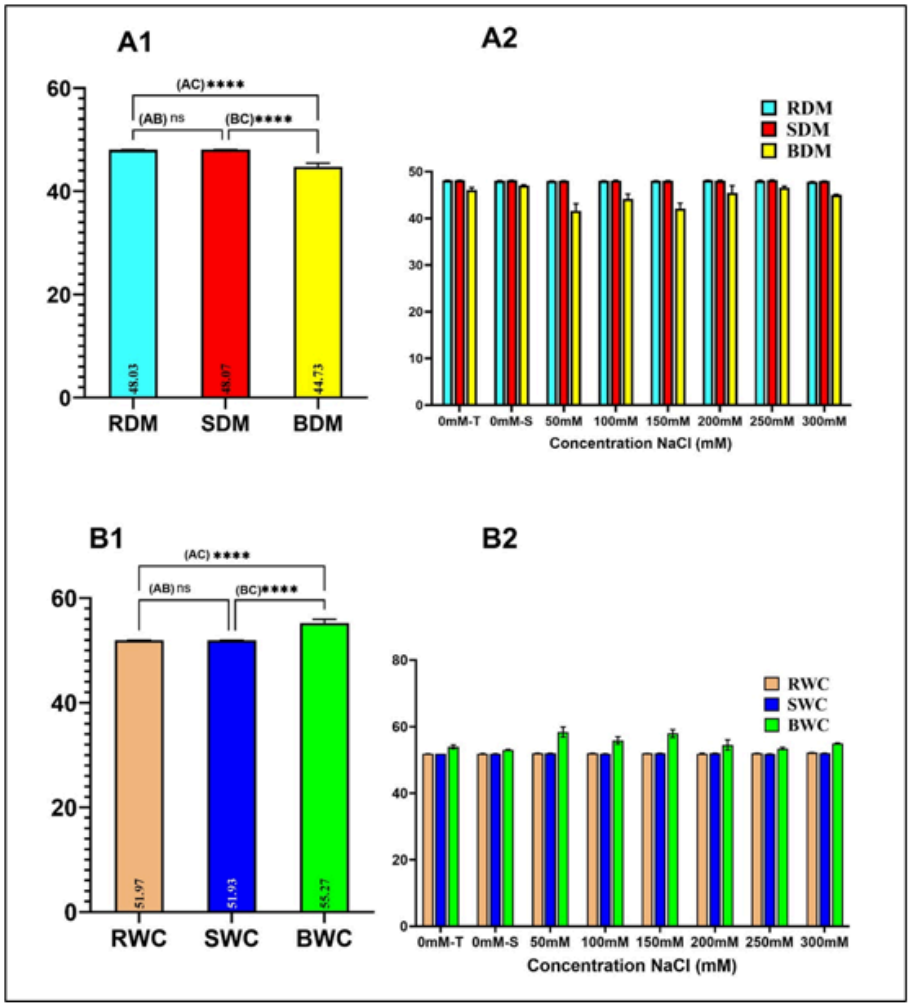

Fig.4.

Figure 4

Impact of salt stress on the partitioning of dry matter (DM) (A1, A2) and water content (WC) (B1, B2) at the level of roots (R), stems (S), and branches (B). The error bars represent standard error (± SE) and the asterisks indicate the levels of statistical significance (****P < 0.0001).