

EFFECTS OF NaCl STRESS ON GROWTH, ION HOMEOSTASIS AND SECONDARY METABOLITE ACCUMULATION IN GARDEN CRESS (*Lepidium sativum* L.) AND PURSLANE (*Portulaca oleracea* L.)

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ABSTRACT

NaCl represents a major source of salinity stress in agricultural lands, particularly in coastal regions where irrigation is practiced. Plant species differ considerably in their tolerance to salinity stress and this variation influences growth performance and plant physiology. In this study, garden cress (*Lepidium sativum* L.), known for its high antioxidant capacity and purslane (*Portulaca oleracea* L.), a halotolerant vegetable species, were cultivated under four irrigation water salinity levels (0, 50, 100 and 200 mM NaCl). Growth parameters (plant fresh weight and plant height), physiological traits (total chlorophyll content, tissue electrical conductivity), biochemical attributes (ascorbic acid and selected flavonoids, namely apigenin and catechin) and mineral nutrient contents (Mg, Na and K) were evaluated. Salinity significantly affected all measured parameters and induced pronounced species-specific responses. The NaCl concentration associated with the highest flavonoid accumulation differed between the two species; for purslane, the maximum flavonoid content was obtained in catechin under 200 mM NaCl treatment (37.806 mg kg⁻¹), whereas for cress, the maximum flavonoid content was obtained in apigenin under 100 mM NaCl treatment (39.074 mg kg⁻¹). Compared with the control treatment, increasing salinity resulted in consistent reductions in plant fresh weight and plant height, whereas tissue electrical conductivity and Na accumulation increased. Changes in K and Mg contents reflected ion imbalance induced by NaCl stress. The results indicate that two species exhibit distinct physiological and biochemical adaptive strategies in response to NaCl stress.

Keywords: *Portulaca oleracea* L., *Lepidium sativum* L., salinity stress, flavonoids, apigenin, catechin

INTRODUCTION

Today, salinity is considered one of the most important abiotic stress factors limiting agricultural production. Particularly in agricultural areas close to coastal regions, irrigation waters used may contain high salt concentrations, or salinity levels may increase over time. An increase in irrigation water salinity reduces soil water potential, thereby limiting water uptake by plants and leading to adverse effects on growth, yield, and quality parameters.

Although sodium chloride is the most abundant salt, it is also present in rainwater at concentrations of 6–50 mg/kg. High salinity can be toxic to plants and also adversely affects water uptake. Cell growth is affected by soil salinity more rapidly than plant functions. In plants, the response to the increase in external osmotic pressure resulting from elevated salt levels around the roots is faster than the response to Na⁺ accumulation in the leaves. Plants can adapt to salinity by tolerating osmotic stress, excluding Na⁺, and exhibiting tolerance to Na⁺, while also differing in their degree of salinity tolerance [Munns and Tester 2008].

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In the study by [Negrão et al. 2017], it was reported that the leaves of some plants were more successful than those of other plants in maintaining their photosynthetic functions as a result of adverse effects, primarily including yellowing, caused by Na accumulation at toxic levels. At the same time, it was recommended that the effects of salinity on plants should be evaluated at the level of components related to salinity tolerance. One of the key strategies to mitigate salinity stress is the characterization of agricultural species that exhibit relatively high salinity tolerance. In addition, understanding how yield, quality traits, and adaptive responses of these species change under different salinity levels is of considerable importance. In the study by Alam et al. [2021], 27 tomato cultivars were grown under high salinity conditions and evaluated based on growth parameters, relative leaf water content, percent yield reduction, membrane stability index, measurement of stress tolerance indices, photosynthetic pigment measurement, mineral analysis, leaf proline content, total phenols and flavonoids, free radical scavenging capacity, and enzyme measurements. The study reported significant findings regarding the salt tolerance levels of certain tomato cultivars and stated that these data could be utilized in tomato improvement and grafting studies.

Some plant species are utilized for human consumption, not only through agricultural production but also by being collected from their natural habitats. The ability of some of these plants to grow without requiring care under conditions in which cultivated plants need maintenance is considered an indication of their tolerance to environmental stress factors such as diseases, pests, drought, and salinity. Polat et al. [2015] reported that 55 wild plants from the Espiye-Giresun region of Türkiye were used for medicinal purposes, including plant parts such as leaves, capitula, flowers, roots and whole plant biomass. It has been stated that some of these plants are used in folk medicine against ailments such as flu, high cholesterol, diabetes disease and the common cold.

Within this framework, purslane (*Portulaca oleracea* L.) emerges as a prominent vegetable due to its resilience. Although it is cultivated to a limited extent in Türkiye, purslane is widely consumed by being collected from the wild, and it has gained significant attention due to its high antioxidant, mineral, and vitamin content. Previous studies have shown that purslane is more tolerant to salinity compared to many other vegetable species [Shannon and Grieve 1999, Alam et al. 2014]. Indeed, studies conducted on different genotypes have reported that purslane exhibits responses ranging from tolerant to sensitive under salinity stress, and that this tolerance varies depending on the genotype [Alam et al. 2014]. Another study has described purslane (*Portulaca oleracea* L.) as a highly salt-tolerant plant, i.e. a halophyte [Yazdani-Biouki et al. 2023].

Garden cress (*Lepidium sativum* L.) is a leafy vegetable with high antioxidant and anti-inflammatory properties, largely due to its high flavonoid content [Vazifeh et al. 2022]. At the same time, in a study [Sat et al. 2013] conducted on two different garden cress cultivars (*Lepidium sativum* cv. Dadas, İzmir), it was reported that cress is a good source of ascorbic acid and mineral elements.

Among the mechanisms of salt stress tolerance in plants are the maintenance of ion homeostasis, regulation of ion transport, osmotic adjustment, and enhancement of antioxidant metabolism. However, information regarding ion transporters involved in salt uptake, transport, and compartmentation remains limited for many agricultural crops [Balasubramaniam et al. 2023].

Flavonoids are important secondary metabolites that are widely present in plants and play a protective role against biotic and abiotic stresses. Apigenin and catechin are flavonoid compounds that stand out for important antioxidant and defensive roles in plants as well as for their health benefits in humans such as antioxidant, anti-inflammatory, and anticancer properties [Patel et al. 2007, Ganeshpurkar and Saluja 2020]. Various stress conditions have been reported to increase flavonoid accumulation, and this effect varies depending on the type and intensity of the stress [Plazas et al. 2019, Zarinkamar et al. 2021].

Ascorbic acid (vitamin C) is also an important antioxidant in plants and exhibits species-dependent responses under salinity stress [Neocleous et al. 2014]. In addition, salinity is known to alter the uptake and distribution of mineral elements such as Na, K, and Mg in plants, and ion imbalance is recognized as one of the primary effects of salt stress [Ghassemi Golezani and Nikpour-Rashidabad 2017, Hannachi and Labeke 2018].

The aim of this study is to comparatively examine the responses of garden cress (*L. sativum* L.) and purslane (*P. oleracea* L.) to different NaCl levels in terms of growth, physiological, biochemical, and mineral nutrition parameters.

MATERIALS AND METHODS

Experimental site and plant material

The experiment was conducted in a greenhouse at the Dardanos Campus of Çanakkale Onsekiz Mart University (ÇOMÜ). Purslane (*P. oleracea* L. cv. Tunç) and garden cress (*L. sativum* L. cv. Bahar) were used as the plant materi-

als. The plants were subjected to four salinity levels using NaCl supplied through irrigation water. Treatments were: 0 (control), 50, 100, and 200 mM NaCl.

Growth conditions and experimental design

Plastic pots (36 cm length × 27 cm width × 7 cm height) with drainage holes and a total surface area of 972 cm² were used in the experiment. Twelve sowing points were established at equal intervals in each pot, providing an allocated surface area of 81 cm² per sowing point and the study consisted of twelve pots for each plant and each pot had 12 sowing points. Ten seeds were sown at the center of each point. Following seedling emergence, thinning was performed to minimize plant competition, leaving four uniform plants per sowing point. The 4 plants located at the center of the 81 cm² area. As a result, each plant had a surface area of 20.25 cm² available for growth.

Growing medium

Field soil sourced from the Dardanos Research and Application Farm of the Faculty of Agriculture at Çanakkale Onsekiz Mart University was used as the growing medium. Prior to sowing, the soil was sieved to remove debris, homogenized, and distributed equally into the pots. The basic physical and chemical properties of the growing medium are presented in Table 1.

Table 1. Physical and chemical properties of the growing medium used in the experiment

Parameter	Unit	Analysis result	Lower limit	Upper limit	Low	Sufficient	High
pH (su)	pH	7.9	6.0	7.2	–	–	*
Organic matter	%	2.5	2.9	6.2	*	–	–
Phosphorus (M3)	mg kg ⁻¹	low	20	40	*	–	–
Total nitrogen	g/kg	sufficient	1	2	–	*	–
Potassium (available)	mmol(+) kg ⁻¹	high	1.5	3	–	–	*
Calcium (available)	mmol(+) kg ⁻¹	high	15	25	–	–	*
Magnesium (available)	mmol(+) kg ⁻¹	high	4.5	10	–	–	*
Organic carbon	g kg ⁻¹	14.2	17	50	*	–	
Potential mineralized nitrogen	mg N kg ⁻¹	high	22	32	–	–	*
Cation exchange capacity	mmol(+) kg ⁻¹	438	75	200	–	–	*
Total aluminum	g kg ⁻¹	low	94	115	*	–	–
Total iron	g kg ⁻¹	high	5	8	–	–	*
Clay	%	40	20	40	–	–	*
Soil moisture	%	6.4	10	30	*	–	–

* Indicates the levels (low, sufficient, or high) of the physical and chemical properties.

Growing conditions and salt stress treatments

Seeds of purslane and garden cress were sown at a depth of approximately 2 mm in the soil. The soil surface was covered with 1 cm of peat, both to prevent seed exposure by surface erosion during irrigation and to provide a more permeable surface for easier seedling emergence compared to field soil. The plants were irrigated every evening with irrigation water used for agricultural purposes in the existing greenhouses (EC: 470 µS cm⁻¹) using a strainer-equipped bucket, until water was observed exiting from the drainage holes at the bottom of the pots.

The newly emerged plants were initially grown under slightly windier external conditions to promote root development and were cultivated in the greenhouse 18 days after sowing (the first week of September). During the experiment, the greenhouse ventilations and doors were kept continuously open. To allow the plants to reach a certain developmental stage before initiating salt stress, they were irrigated only with water in the greenhouse for 14 days. After this period, salt stress treatments were applied exposing the plants to NaCl stress for 17 days. Plants that reached harvest maturity were harvested simultaneously in all treatments. Samples that were not analyzed immediately were stored in a deep freezer (–20 °C) until the time of analysis.

Experimental design

The experiment was established according to a Randomized Complete Block Design, and each treatment was conducted with three replications, with each replication (plot) being consisted of one pot as described above. Accordingly, from the total of 48 plants (12 hills/sowing points × 4 plants) in each replication, 12 morphologically uniform and healthy plants were selected, and all morphological measurements and chemical analyses were carried out on these plants.

Measurements and analyses

Chlorophyll measurements were conducted directly on the leaves, while for all other chemical analyses, the edible parts of purslane and garden cress, including leaves and tender stems, were used.

Plant fresh weight (g)

The harvested plants were cut at the root-shoot junction, and the fresh weights of the plants were determined using a precision balance.

Plant height (cm)

Plant height was measured and recorded from the root collar to the tip of the plant.

Ascorbic acid (vitamin C) content (mg 100 g⁻¹)

Ascorbic acid analysis was performed according to the method of [Pearson and Churchill 1970]. For this purpose, 25 g of fresh sample was weighed and treated with 175 mL of 0.04% oxalic acid. The mixture was filtered through filter paper, and 1 mL of the filtrate was diluted with 9 mL of distilled water. Similarly, 1 mL of the sample was mixed with 9 mL of 2,6-dichlorophenol indophenol. The transmittance values of the reference and sample solutions were measured at a wavelength of 520 nm using a UV–Vis spectrophotometer (Shimadzu UV-1800), and the ascorbic acid contents were calculated.

Apigenin and catechin content (mg kg⁻¹)

For sample extraction, 10 mL of 96% ethanol was added to 2 g of plant material, mixed in a homogenizer for 2 minutes, and incubated overnight in a water bath at 45 °C. The samples were then centrifuged at 4000 rpm for 5 minutes, and the supernatant was completely evaporated using a rotary evaporator. The resulting extracts were dissolved in 1 mL of methanol [Kiselev et al. 2007]. The amounts of apigenin and catechin were determined using high-performance liquid chromatography (HPLC). Analyses were performed with a Shimadzu Prominence HPLC system (DAD detector, SPD-M20A). The mobile phase consisted of A: 3% formic acid and B: methanol, and the method was modified from [Gomes et al. 1999].

Total chlorophyll content (SPAD)

Total chlorophyll content was determined using a portable chlorophyll meter (SPAD). SPAD measurements were taken in the early morning from the upper surface of leaves that were neither too young nor too old.

Tissue membrane permeability

Tissue electrical conductivity was determined according to the method of [Fan and Sokorai 2005]. Five grams of leaf sample were incubated in 50–70 mL of distilled water at 23 °C on a shaker (100 rpm). Tissue electrical conductivity values were measured at the 1st (C₁) and 60th (C₆₀) minutes. The samples were then autoclaved at 121 °C for 25 minutes, cooled, and the total conductivity (C_t) was measured. Membrane permeability was calculated using the following equation:

$$E = (C_{60} - C_1) / C_t \times 100$$

Analysis of Na⁺, K²⁺, and Mg⁺

For elemental analyses, the samples were digested in a microwave oven. For this purpose, 1 g of dry sample was placed in Teflon vessels, and 10 mL of 65% concentrated HNO₃ was added. The dissolution was carried out in a closed system in a CEM MARS 6 microwave oven for a total of 30 minutes, with the temperature raised up to 200 °C. Elemental analyses were performed using an atomic absorption spectrophotometer (A Analyst 800, Perkin

Elmer). Calibration curves were prepared with single-element standards, and the results were calculated in mg L⁻¹. Each sample was read three times to ensure the reliability of the measurements [Jones et al. 1991, Müftüoğlu et al. 2014, Kacar 2016].

Statistical analysis

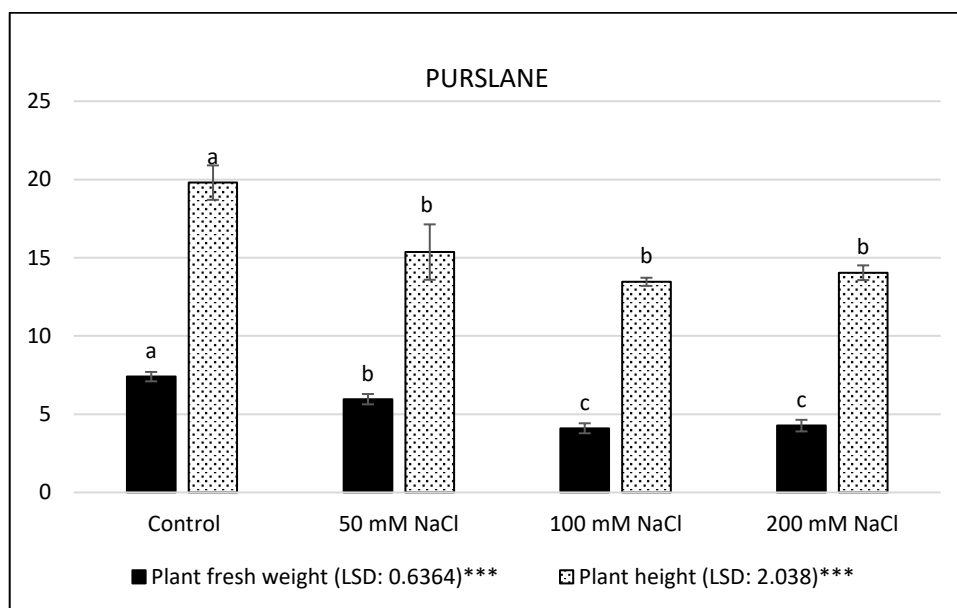
The obtained data were subjected to analysis of variance (ANOVA) using the JMP® ver. 14 statistical packages (SAS Institute, Cary, NC, USA). For factors found to be statistically significant in the ANOVA, the least significant difference (LSD) multiple comparison test was applied to determine differences among treatment means. In all statistical evaluations, the significance level was accepted as $P \leq 0.05$. The data are introduced as mean $\pm$ standard deviation ($n = 3$).

RESULTS

Growth responses of purslane and garden cress to NaCl stress

NaCl treatments significantly affected plant fresh weight and plant height in both purslane and garden cress (Figures 1, 2 and 3). Growth declined progressively with increasing salinity in both species; however, the magnitude of growth inhibition differed markedly.

Figure 1. Effects of salt stress on plant fresh weight (g) and plant height (cm) in purslane. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. *** indicates significant differences between means at $p < 0.001$, according to the least significant difference (LSD) test



In purslane, fresh weight decreased from 7.40 g in the control to 5.96, 4.10 and 4.27 g under 50, 100 and 200 mM NaCl, corresponding to reductions of 19.5%, 44.5% and 42.3%, respectively. Plant height similarly declined by 22.4–32.0%, although no significant differences were detected between the two highest salinity treatments, indicating that growth inhibition reached a plateau under severe stress.

Garden cress exhibited substantially greater sensitivity to salinity. Fresh weight declined from 5.21 g in the control to 3.42, 2.50 and 1.93 g under 50, 100 and 200 mM NaCl, representing reductions of 34.3%, 52.0% and 62.9%, respectively. Plant height decreased progressively with increasing NaCl concentration, reaching a 58.8% reduction at 200 mM, with all salinity treatments differing significantly from one another.

Figure 2. Effect of salt stress on plant fresh weight (g) and plant height (cm) in garden cress. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. ** and *** indicate significant differences between means at $p < 0.01$ and $p < 0.001$, respectively, according to the least significant difference (LSD) test

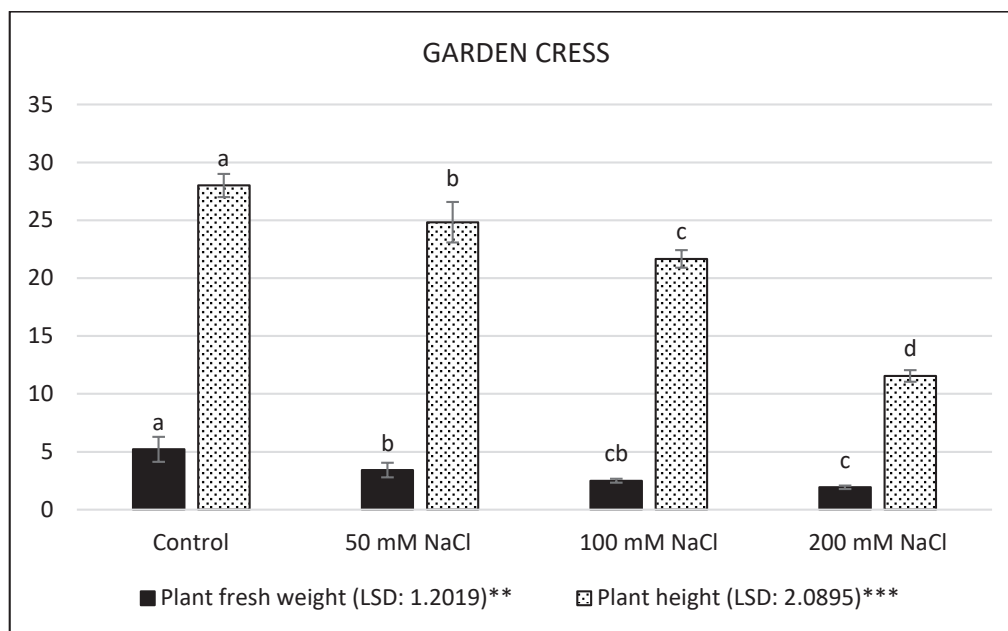
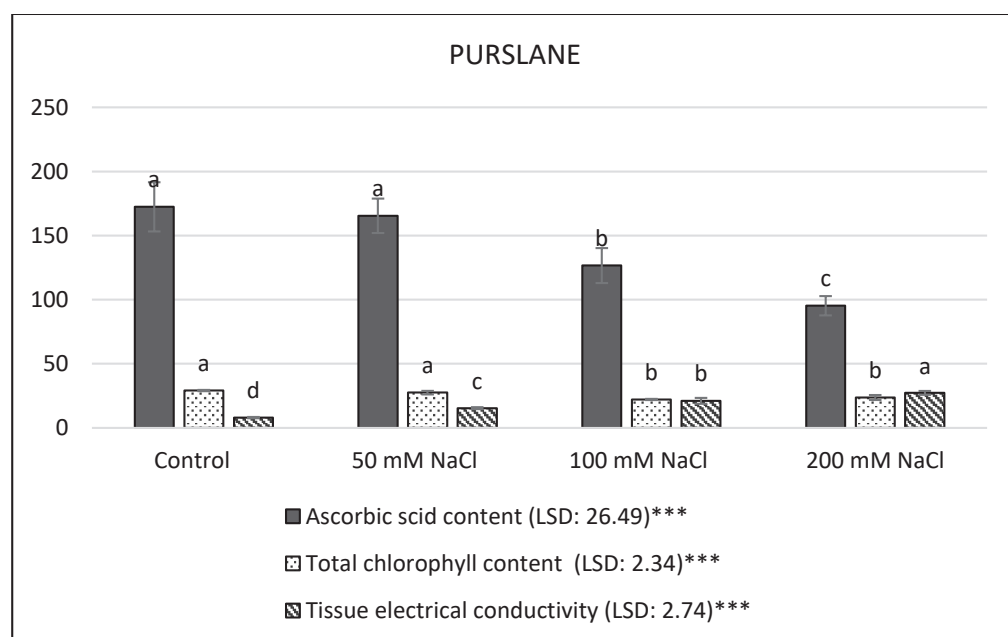


Figure 3. The effect of salt stress on ascorbic acid ($\text{mg } 100 \text{ g}^{-1}$), total chlorophyll (SPAD), and tissue electrical conductivity (%) in purslane. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. *** indicates significant differences between means at $p < 0.001$, according to the least significant difference (LSD) test



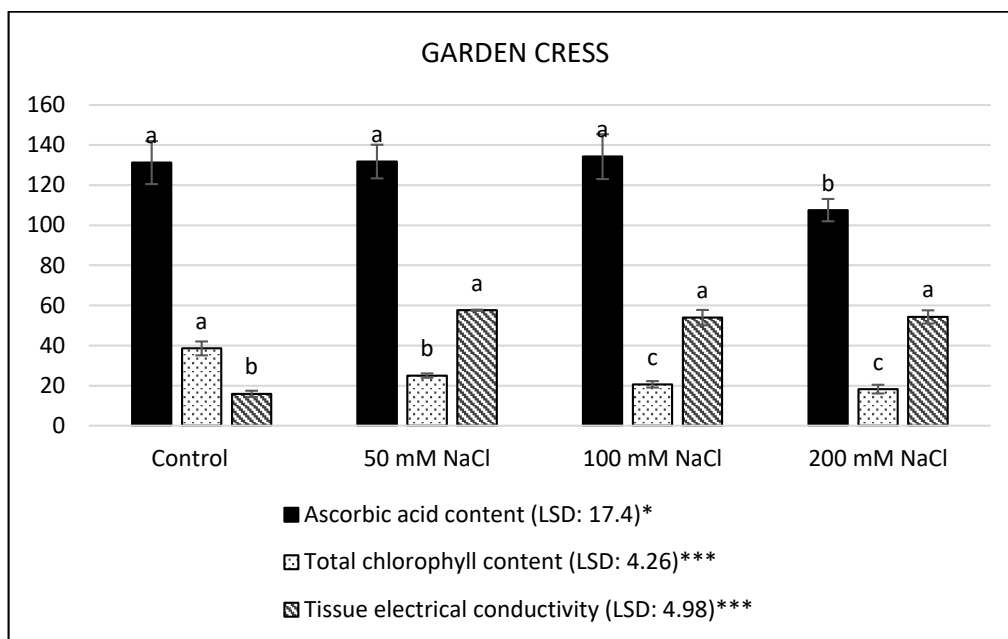
Overall, although salinity reduced vegetative growth in both species, purslane maintained considerably greater biomass and shoot growth than garden cress throughout the salinity gradient, indicating superior morphological tolerance.

Effects of NaCl stress on ascorbic acid, chlorophyll content and tissue electrical conductivity

Salinity significantly influenced ascorbic acid concentration, total chlorophyll content and tissue electrical conductivity in both species (Figures 4 and 5). In purslane, ascorbic acid declined gradually with increasing salinity, with significant reductions becoming evident at 100 and 200 mM NaCl. Total chlorophyll remained relatively stable under mild stress but decreased significantly under moderate and severe salinity. In contrast, tissue electrical conductivity increased continuously with increasing NaCl concentration, indicating progressive membrane damage.

Garden cress displayed a different physiological response. Ascorbic acid remained statistically unchanged up to 100 mM NaCl and declined only under severe salinity. However, chlorophyll content decreased sharply even at 50 mM NaCl and reached a plateau under higher salinity. Tissue electrical conductivity increased dramatically under all NaCl treatments and remained consistently higher than in purslane, suggesting that membrane integrity was disrupted even under relatively mild salt stress.

Figure 4. The effect of salt stress on ascorbic acid (mg 100 g⁻¹), total chlorophyll (SPAD), and tissue electrical conductivity (%) in garden cress. Data are presented as the mean of three replicates ± standard deviation. Means within the same column followed by the same letter are not significantly different. * and *** indicate significant differences between means at $p < 0.05$ and $p < 0.001$, respectively, according to the least significant difference (LSD) test



Collectively, these results indicate that although both species experienced physiological impairment under saline conditions, garden cress exhibited earlier chlorophyll degradation and more severe membrane damage, whereas purslane maintained greater physiological stability.

Effects of NaCl stress on catechin and apigenin accumulation

Salt stress significantly affected catechin and apigenin concentrations in both species (Figures 6 and 7). In purslane, both flavonoids exhibited a progressive increase with increasing salinity. Although slight reductions were observed under 50 mM NaCl, catechin and apigenin increased markedly under moderate and severe salinity, reaching their highest concentrations at 200 mM NaCl.

Figure 5. Effect of salt stress on catechin and apigenin content (mg kg^{-1}) in purslane. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. *** indicates significant differences between means at $p < 0.001$, according to the least significant difference (LSD) test

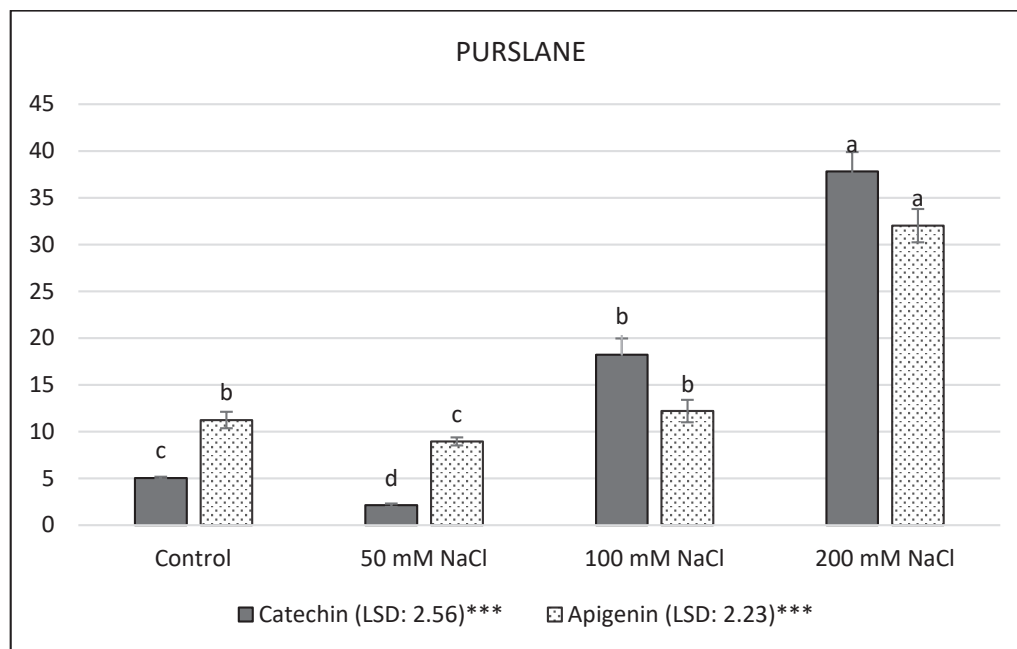


Figure 6. Effects of salt stress on catechin and apigenin contents (mg kg^{-1}) in garden cress. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. *** indicates significant differences between means at $p < 0.001$, according to the least significant difference (LSD) test

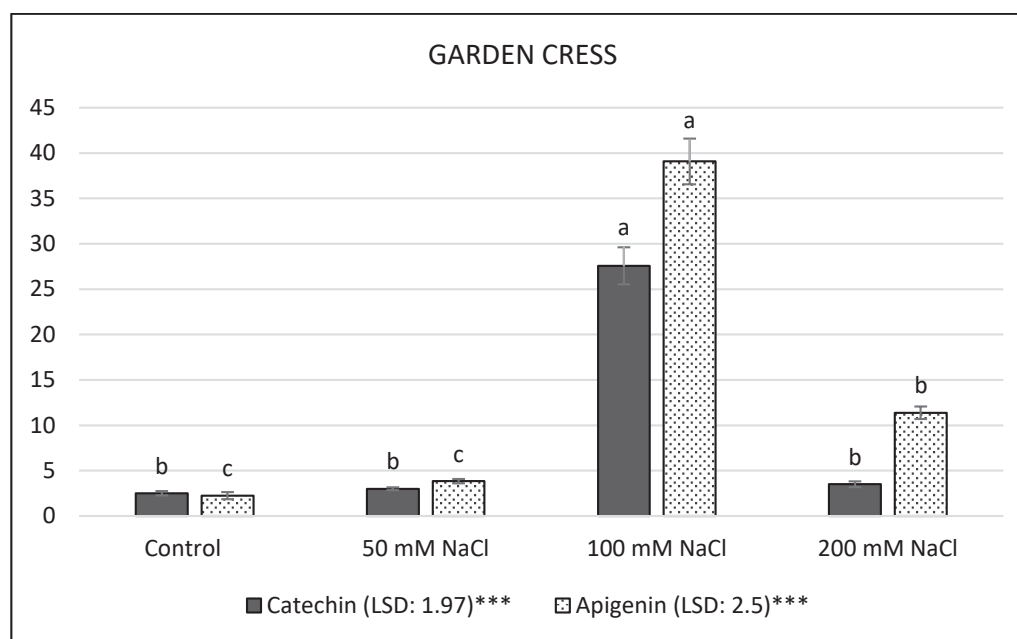
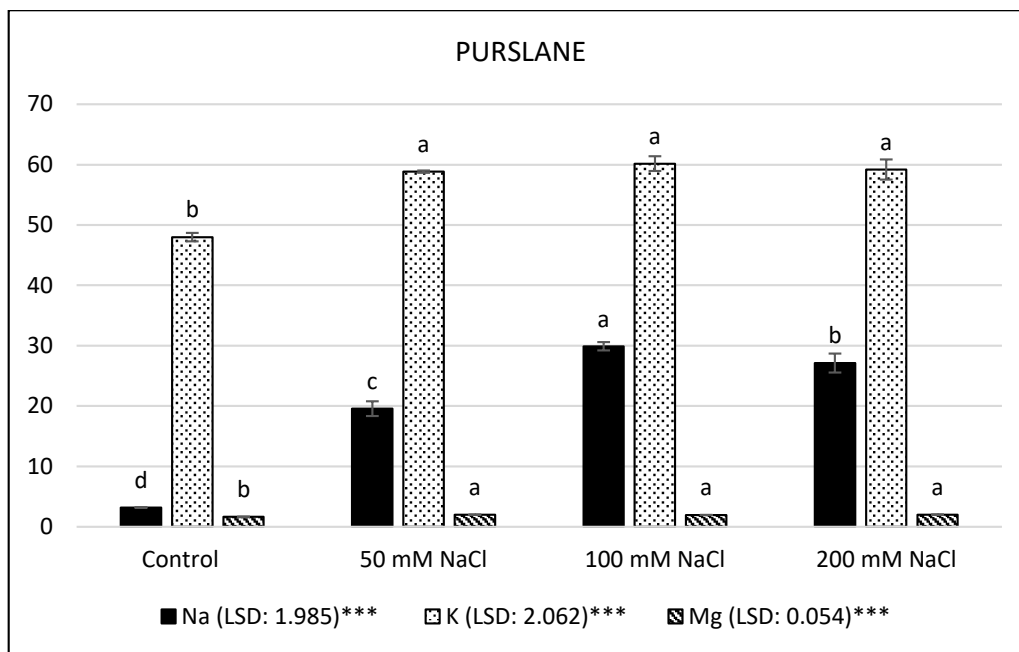


Figure 7. Effects of salt stress on elemental (Na^+ , K^+ , and Mg^{2+}) contents (g kg^{-1}) in purslane. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. *** indicates significant differences between means at $p < 0.001$, according to the least significant difference (LSD) test



Garden cress exhibited a biphasic response. Catechin and apigenin increased substantially under moderate salinity and reached maximum levels at 100 mM NaCl, but both compounds declined sharply under 200 mM NaCl. Despite remaining above or close to control values, their concentrations were considerably lower than those observed at 100 mM NaCl.

These contrasting patterns indicate that purslane maintained flavonoid biosynthesis under severe salinity, whereas the antioxidant response of garden cress weakened once salt stress exceeded a critical threshold.

Effects of NaCl stress on mineral composition

NaCl treatments significantly affected Na^+ , K^+ and Mg^{2+} concentrations in both species (Figure 8). Sodium accumulation increased markedly with increasing salinity in both species. However, the accumulation pattern differed considerably. Purslane accumulated Na^+ while maintaining relatively stable or even increased K^+ concentrations and only minor changes in Mg^{2+} , indicating effective ionic regulation despite increasing external salinity.

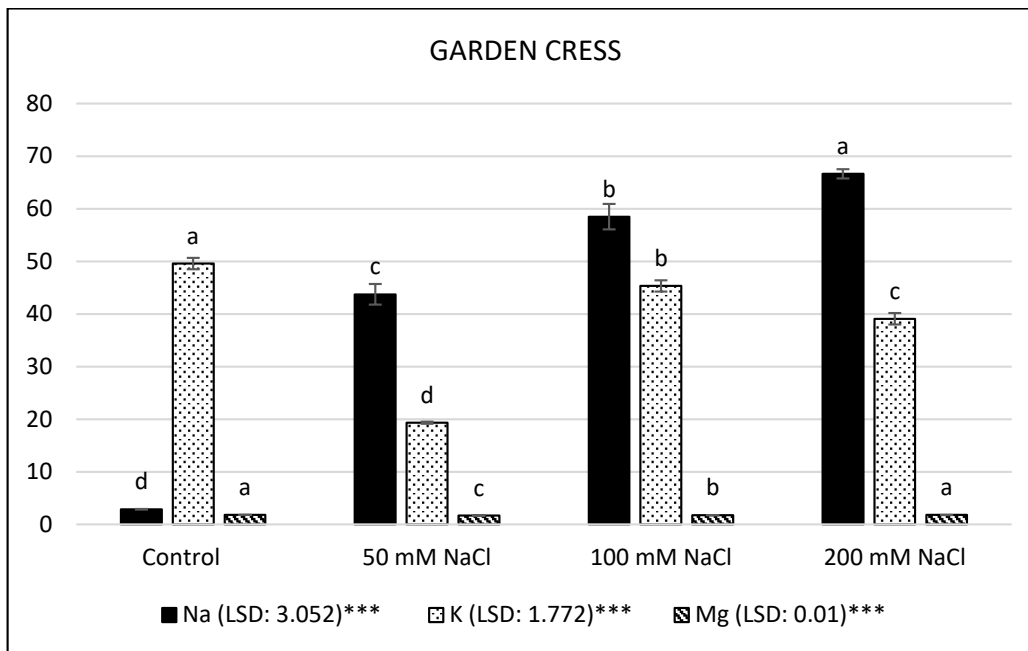
In contrast, garden cress exhibited continuous Na^+ accumulation accompanied by a pronounced reduction in K^+ concentration, particularly under low and moderate salinity. Magnesium content declined under 50 and 100 mM NaCl before partially recovering at 200 mM. Consequently, purslane maintained a substantially more favorable ionic balance than garden cress, particularly through its ability to preserve K^+ homeostasis despite elevated Na^+ accumulation.

Overall comparison between purslane and garden cress

Although salinity adversely affected both species, the severity of the responses differed considerably. Purslane exhibited smaller reductions in growth, greater preservation of chlorophyll content, lower electrolyte leakage, sustained flavonoid accumulation under severe salinity, and a superior capacity to maintain ionic homeostasis. In contrast, garden cress experienced greater growth inhibition, earlier physiological deterioration, reduced antioxidant metabolite accumulation under severe stress, and substantial disruption of mineral balance.

Taken together, the integrated morphological, physiological, biochemical and ionic responses consistently demonstrate that purslane possesses considerably greater tolerance to NaCl stress than garden cress.

Figure 8. Effects of salt stress on elemental (Na^+ , K^+ and Mg^{2+}) contents (g kg^{-1}) in garden cress. Data are presented as the mean of three replicates $\pm$ standard deviation. Means within the same column followed by the same letter are not significantly different. *** indicates significant differences between means at $p < 0.001$, according to the least significant difference (LSD) test



DISCUSSION

Salinity is among the most important abiotic stresses limiting vegetable production worldwide because it simultaneously imposes osmotic stress, ion toxicity, oxidative damage, and nutritional imbalance. Consequently, plant tolerance to salinity depends on the coordinated regulation of multiple physiological and biochemical processes rather than on a single adaptive trait. The present study clearly demonstrates that although both purslane (*Portulaca oleracea* L.) and garden cress (*Lepidium sativum* L.) were adversely affected by increasing NaCl concentrations, the magnitude and nature of their responses differed substantially. The integrated evaluation of growth, physiological characteristics, antioxidant metabolism, flavonoid accumulation, and mineral nutrition consistently identified purslane as considerably more salt tolerant than garden cress.

The reduction in plant fresh weight and plant height observed in both species agrees with the widely documented inhibitory effects of salinity on plant growth. Salt stress initially decreases soil water potential, thereby restricting water uptake and cell expansion, while prolonged exposure results in excessive Na^+ accumulation, nutrient imbalance, and reduced photosynthetic carbon assimilation, ultimately suppressing biomass production. Similar reductions in vegetative growth have been reported for purslane under saline conditions by Xing et al. [2019], and Guevara-Olivar et al. [2024], whereas Kiremit et al. [2023] described comparable responses in garden cress. However, an important distinction emerged between the two species. Growth inhibition in garden cress increased almost proportionally with salinity and became particularly severe at 200 mM NaCl, whereas purslane exhibited moderate reductions and a tendency toward stabilization under severe stress. This response is characteristic of facultative halophytes, which possess efficient mechanisms for osmotic adjustment and ion compartmentation that enable continued growth under saline environments. The contrasting growth patterns therefore indicate that purslane maintains cellular function more effectively once a critical salinity threshold has been reached, whereas the adaptive capacity of garden cress becomes progressively overwhelmed.

The physiological measurements further reinforce this interpretation. Chlorophyll degradation, electrolyte leakage, and changes in ascorbic acid collectively provide insight into the balance between oxidative damage and antioxidant protection during salt stress. Chlorophyll loss is a common consequence of reactive oxygen species (ROS)

accumulation, which accelerates pigment degradation while inhibiting chlorophyll biosynthesis. In the present study, chlorophyll remained relatively stable in purslane under mild salinity and declined only under moderate and severe stress, whereas garden cress exhibited substantial chlorophyll loss even at the lowest NaCl concentration. Similar reductions have been reported in tomato [Krupa-Mańkiewicz et al. 2015], lettuce [Kiran 2019], and garden cress [Kiremit et al. 2023]. The delayed chlorophyll degradation observed in purslane suggests a greater ability to preserve the photosynthetic apparatus and maintain carbon assimilation during salinity.

Membrane stability exhibited an equally contrasting pattern. Electrolyte leakage increased gradually with increasing NaCl concentration in purslane, whereas garden cress showed a sharp increase even under mild salinity, with little additional increase thereafter. Because electrolyte leakage reflects membrane lipid peroxidation caused by ROS, these findings indicate that membrane integrity deteriorated much earlier in garden cress than in purslane. Similar increases in membrane permeability under salt stress have been reported in purslane genotypes by Zaman et al. [2020]. The ability of purslane to delay membrane disruption likely contributes directly to its superior maintenance of growth and photosynthetic performance under saline conditions.

Interestingly, the responses of ascorbic acid differed from those of chlorophyll and membrane stability. Garden cress maintained relatively stable ascorbic acid concentrations up to moderate salinity before declining under severe stress, whereas purslane exhibited a gradual decrease throughout the salinity gradient. At first glance, this pattern could suggest greater antioxidant protection in garden cress. However, the simultaneous occurrence of severe chlorophyll degradation and high membrane leakage indicates that maintenance of ascorbic acid alone was insufficient to prevent oxidative damage. Instead, the lower ascorbic acid concentration in purslane likely reflects its utilization during ROS detoxification, while additional antioxidant mechanisms compensated for its depletion. This observation emphasizes that salt tolerance should not be inferred from a single antioxidant metabolite but rather from the overall effectiveness of the antioxidant network.

The flavonoid responses strongly support this interpretation. Flavonoids such as catechin and apigenin function as important non-enzymatic antioxidants that scavenge ROS, stabilize cellular membranes, contribute to osmotic adjustment, and regulate stress-responsive signaling pathways [Shomali et al. 2022, Wu et al. 2023]. In purslane, both compounds accumulated progressively with increasing salinity and reached their highest concentrations under 200 mM NaCl, indicating sustained activation of secondary metabolism even under severe stress. Similar protective roles of flavonoids have been emphasized by Patil et al. [2024], who identified flavonoid accumulation as an important determinant of salinity tolerance.

Garden cress exhibited a distinctly different pattern. Catechin and apigenin increased markedly under moderate salinity but declined substantially under severe stress. Comparable biphasic responses have been reported for garden cress sprouts exposed to NaCl [Farhat et al. 2023] and for plants subjected to heat stress [Alhaithloul et al. 2021]. Such responses suggest that moderate stress activates flavonoid biosynthesis, whereas prolonged or intense stress exceeds the metabolic capacity required to sustain secondary metabolite production. Consequently, the inability of garden cress to maintain flavonoid accumulation under severe salinity likely contributed to the extensive chlorophyll degradation and membrane damage observed at high NaCl concentrations. In contrast, the sustained induction of catechin and apigenin in purslane appears to compensate for the gradual depletion of ascorbic acid, thereby maintaining antioxidant protection during prolonged salt exposure.

Among all measured parameters, ion homeostasis provides perhaps the clearest mechanistic explanation for the contrasting salinity tolerance of the two species. Excessive Na⁺ accumulation disrupts enzyme activity, osmotic regulation, and nutrient acquisition, particularly through competition with K⁺ for membrane transport systems. Consequently, maintenance of a high cytosolic K⁺/Na⁺ ratio is widely recognized as one of the principal determinants of salt tolerance [Li and Si 2019, Malakar and Chattopadhyay 2021]. Both species accumulated substantial amounts of Na⁺ under saline conditions; however, their ability to regulate accompanying mineral nutrients differed markedly.

Purslane maintained or even increased K⁺ concentrations despite increasing Na⁺ accumulation while also preserving Mg²⁺ levels. Potassium is essential for enzyme activation, stomatal regulation, protein synthesis, and osmotic adjustment, whereas magnesium is indispensable for chlorophyll biosynthesis and numerous enzymatic reactions. The maintenance of these essential cations despite elevated Na⁺ strongly suggests efficient selective ion transport, intracellular Na⁺ sequestration, and effective ionic compartmentation. Similar responses have been reported in purslane by Uddin et al. [2012] and Samet and Çikili [2019], supporting its characterization as a facultative halophyte.

In contrast, garden cress accumulated considerably greater quantities of Na⁺ while simultaneously exhibiting pronounced reductions in K⁺ concentration and transient decreases in Mg²⁺. Such disruption of ionic balance is characteristic of salt-sensitive and has been associated with reduced photosynthesis [Sardar et al. 2023], impaired enzyme

activity [Zhang et al. 2022], and growth inhibition [Breš et al. 2022]. Although Mg^{2+} partially recovered under severe salinity, this adjustment appeared insufficient to compensate for the substantial loss of potassium homeostasis. Therefore, the superior performance of purslane is best explained not by reduced Na^+ uptake itself but by its greater capacity to maintain ionic balance despite elevated sodium accumulation.

Taken together, the present findings demonstrate that salinity tolerance results from the integration of multiple complementary mechanisms rather than from any individual physiological trait. Purslane maintained relatively stable growth, delayed chlorophyll degradation, preserved membrane integrity, sustained flavonoid biosynthesis, and effectively regulated K^+ and Mg^{2+} homeostasis under increasing NaCl concentrations. These coordinated responses collectively limited oxidative damage and maintained cellular function under severe salinity. In contrast, garden cress exhibited progressive growth inhibition, early impairment of photosynthesis, rapid membrane disruption, transient antioxidant activation, and pronounced ionic imbalance, indicating that its protective mechanisms become insufficient as salinity intensifies.

From an agronomic perspective, these contrasting adaptive strategies suggest that purslane is a promising leafy vegetable for cultivation in saline soils or under saline irrigation, where conventional vegetable crops often suffer severe yield reductions. Moreover, the marked accumulation of catechin and apigenin under high salinity indicates that moderate salt stress may further enhance the functional and nutritional value of purslane. Conversely, successful cultivation of garden cress appears to require low-salinity environments or management practices designed to reduce salt accumulation and improve ionic balance, including potassium fertilization, organic amendments, or exogenous biostimulant and antioxidant applications. Future research should investigate the molecular basis of the contrasting responses identified here, particularly genes involved in Na^+ transport, K^+ retention, antioxidant metabolism, and flavonoid biosynthesis, to facilitate the development of leafy vegetable cultivars with improved salinity tolerance.

CONCLUSIONS

The present study demonstrates that salinity significantly affects the growth, physiology, antioxidant metabolism, and mineral nutrition of both purslane (*Portulaca oleracea* L.) and garden cress (*Lepidium sativum* L.), although the magnitude of these responses differs markedly between the two species. The integrated evaluation of morphological, physiological, biochemical, and ionic traits consistently showed that purslane possesses substantially greater tolerance to NaCl stress than garden cress.

Compared with garden cress, purslane maintained higher biomass, delayed chlorophyll degradation, lower membrane damage, sustained accumulation of catechin and apigenin under severe salinity, and a greater capacity to preserve K^+ and Mg^{2+} homeostasis despite increased Na^+ accumulation. In contrast, garden cress exhibited greater growth inhibition, early physiological deterioration, reduced flavonoid accumulation under severe stress, and pronounced disruption of ionic balance, indicating a comparatively limited capacity to adapt to prolonged salinity.

These findings demonstrate that salinity tolerance results from the coordinated regulation of multiple adaptive mechanisms rather than from a single physiological trait. The superior performance of purslane reflects the integration of efficient ion homeostasis, maintenance of photosynthetic integrity, and sustained antioxidant defense, enabling better adaptation to saline conditions.

From an agronomic perspective, purslane appears to be a promising leafy vegetable for cultivation in saline environments while also offering enhanced nutritional value through increased flavonoid accumulation. Conversely, successful cultivation of garden cress is likely to require low-salinity conditions or appropriate stress-mitigation practices. Future studies should focus on the molecular mechanisms underlying these adaptive responses and evaluate the long-term agronomic and nutritional performance of both species under field conditions.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

DECLARATION OF THE USE OF GENERATIVE AI TOOLS

In the preparation of this manuscript, artificial intelligence (AI) tools were used solely for language editing, translation, and grammatical refinement to improve clarity and consistency. These tools were not used to generate the scientific content of the manuscript. The authors checked the output for errors and take full responsibility for the final text.

AUTHOR CONTRIBUTION

Conceptualization: T.S., N.Ö. Methodology: T.S., N.Ö. Software: T.S., N.Ö. Validation: T.S., N.Ö. Formal analysis: T.S., N.Ö. Investigation: T.S., N.Ö. Resources: T.S., N.Ö. Data curation: T.S., N.Ö. Writing, original draft: T.S., N.Ö. Writing, review and editing: T.S., N.Ö. Visualization: T.S., N.Ö. Supervision: T.S., N.Ö. Project administration: T.S., N.Ö. The authors declare that they have contributed equally to the article. All authors read and approved the final manuscript.

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