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EFFECTS OF SALT STRESS ON *ORIGANUM MAJORANA* AND IMPROVEMENT VIA ASSOCIATION WITH HALOPHYTES PLANTS: *SPERGULARIA SALINA* AND *APTENIA CORDIFOLIA*

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Abstract

This study explores the effect of salinity on the growth of oregano (*Origanum majorana*) and the potential mitigating effects of co-cultivation with the halophytic plants *Spergularia salina* and *Aptenia cordifolia*. Morphological parameters such as biomass and length of aerial part (LPA) were measured, along with physiological parameters such as leaf water content, chlorophyll content, proline and sugar levels. Under saline conditions, the biomass of co-cultured oregano increased by 15% compared to that grown alone, while LPA increased by 10%. In addition, co-culture resulted in a 20% increase in leaf water content and a 15% rise in chlorophyll levels compared to oregano grown alone. A 10% reduction in proline and a 25% increase in sugar concentration were also observed in co-cultured oregano compared to that grown alone. These results highlight the potential of halophyte plants to improve the salinity tolerance of glycophyte plants, offering a promising strategy for sustainable agriculture in areas affected by salinity.

Keywords: Salinity, *Origanum majorana*, salt tolerance, *Spergularia salina*, *Aptenia cordifolia*

INTRODUCTION

One of the most harmful abiotic stressors that plants can experience is salt stress (Van Zelm *et al.*, 2020), it has become a major obstacle to agricultural production (Dong *et al.*, 2024). The FAO reports that the global area affected by salinity comprises 424 million hectares of arable land (0 to 30 cm) and 833 million hectares of subsoil (30 to 100 cm), representing 73% of all mappable land (FAO, 2021). Soil salinity is characterized by increased concentrations of soluble salts, mainly NaCl, resulting from excessive evaporation in relation to precipitation (Zhou *et al.*, 2024). While salinization may be due to natural processes, it is also exacerbated by human actions such as irrigation with salt water, seawater intrusion and the intensive use of fertilizers (Hopmans *et al.*, 2021). Climate change, with its prolonged droughts and rising sea levels, is set to exacerbate this scourge (Negacz *et al.*, 2022).

The majority of cultivated species are glycophytes, whose growth and development are greatly inhibited by salinity (Munns and Tester, 2008), and we have other species, the halophytes, which are highly resistant to salinity due to their highly efficient antioxidant enzyme system, cellular salt transport and sequestration processes and osmotic control (Hamed *et al.,* 2013; Lutts and Lefèvre, 2015; Zhang *et al.,* 2023). It is difficult to increase glycophyte crops' salinity tolerance. Environmental and genetic variables can impact the polygenic characteristic of salinity tolerance (Assaha *et al.,* 2017; Zsögön *et al.,* 2017). Because of the possibility of losing polygenic features during backcrossing, conventional breeding through the introgression of desirable traits is challenging (Frank, 2003). Faced with these challenges, it is essential to explore innovative solutions to mitigate the effects of salt stress on crops. Halophytes, plants adapted to saline environments, are proving to be a promising biological technique for the phytoremediation of saline soils (Zhang *et al.,* 2023).

The need for aromatic and medicinal plants has grown in recent years in a number of industries, including agro-alimentary, fragrances, pharmaceuticals, and natural cosmetics. However, environmental limitations like salinity can have an impact on the development and productivity of aromatic and medicinal plants, just like they can on most other cultivated plants. *Origanum majorana* L., a native of the Mediterranean area belongs to the Lamiaceae family, is a plant of economic and culinary importance, widely used for its aromatic and medicinal properties (Novak *et al.,* 2000; Jafari Khorsand *et al.,* 2022; Taha *et al.,* 2023). However, halophytes like *Aptenia cordifolia* and *Spergularia salina* are well known for their resilience to extreme environmental circumstances (Karakas *et al.,* 2020; Pungin *et al.,* 2023).

In this study, we aim to assess how salt stress affects *Origanum majorana* and to study the possible benefits of combining *Spergularia salina* and *Aptenia cordifolia*. We will examine the morphological, physiological and biochemical responses of oregano to saline conditions, using NaCl concentrations of 0, 34, 86, and 172 mM NaCl, and compare the performance of oregano grown alone and in association with these halophyte plants. The results of this research could provide crucial information for the development of more resilient and sustainable agricultural practices in saline environments.

MATERIALS AND METHODS

Plant Material

The study used three plants, *Origanum majorana* (glycophyte plant), and two halophyte plants, *Spergularia salina* and *Aptenia cordifolia*. Oregano plants were obtained by cuttings, with the cuttings prepared 30 days before the start of the experiment. Similarly, Atriplex was obtained by cuttings from mother plants grown in the experimental greenhouse at the Faculty of Science, University Ibn Tofail. Salina plants were harvested in the Oued Malah region (El Khadir *et al.,* 2024a) and obtained by germination.

Culture Conditions and Experimental Design

The plants studied were grown in 2L pots containing a mixture of maamoura soil, peat and compost in a 2 : 1 : 1 ratio. The experiments were carried out in an experimental greenhouse at the Faculty of Science, University Ibn Tofail. For the experimental set-up, oregano was grown alone, as well as in combination with *Spergularia salina* and *Aptenia cordifolia*.

Salt Treatment

Salt stress was applied by watering the plants with NaCl solutions of different concentrations: 0, 34, 86, and 172 mM. Watering was carried out every other day over a 4-week period.

Parameters Studied

To evaluate the effects of salt stress, several morphological, physiological and biochemical parameters were measured. Total plant biomass (g) was determined using a precision balance. The length of the aerial part (cm) and the length of the roots (cm) were measured using a millimeter ruler. Root volume (ml) was estimated by water displacement using a graduated cylinder. Leaf water content (%) was calculated by determining the difference in weight between fresh and dry leaves. Chlorophyll concentration (mg/g MF) was measured by extraction with acetone and spectrophotometric determination using the method described by Arnon (1949). Proline content was determined using the method described by Bates *et al.* (1973), while sugars were quantified using the method of Dubois *et al.* (1956).

Statistique

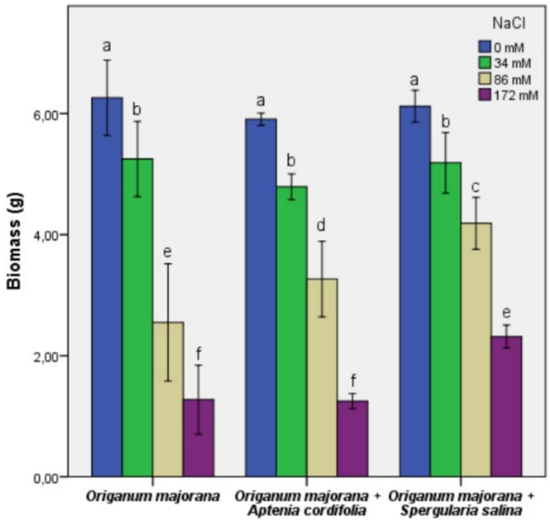
Results are expressed as means ± standard deviation. Statistical analysis was performed by two-factor analysis of variance (ANOVA 2) followed by Tukey's significant difference test, using a significance level of 5% ($P < 0.05$). In addition, these data were subjected to Pearson correlation analysis and principal component analysis (PCA). Statistical analyses were performed using IBM SPSS Statistics version 23.

RESULTS

Morphological Parameters

Biomass

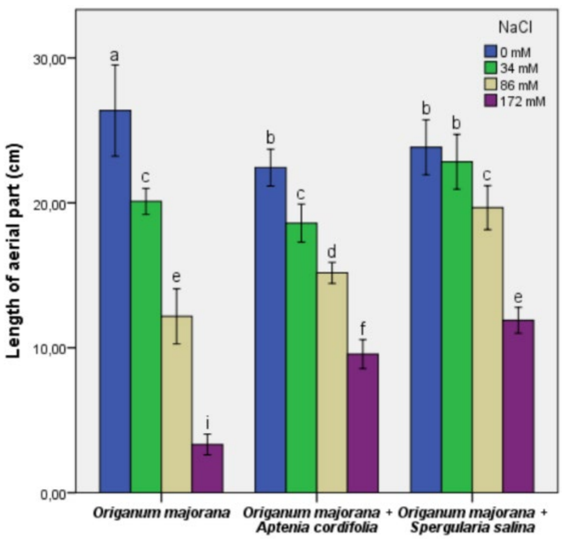
The results show a decrease in the biomass of oregano plants with increasing NaCl concentrations. At 172 mM NaCl, the biomass of oregano alone decreased significantly, with a 79.66% reduction compared with conditions without salt. In comparison, plants associated with *Aptenia cordifolia* showed a slightly less pronounced reduction, with a difference of 66.78% at the same salt concentration. However, the association with *Spergularia salina* stood out with a reduction of only 62.41%, suggesting a better ability to maintain biomass in the presence of salt stress.



1: *Variation in oregano biomass in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

Length of Aerial Part

The length of the aerial part of oregano plants decreased with increasing NaCl concentrations. At 172 mM NaCl, the length of the aerial part of oregano alone decreased markedly, showing a reduction of 87.36% compared with conditions without salt. In contrast, plants combined with *Aptenia cordifolia* showed a less pronounced reduction, with a difference of 71.47% at the same

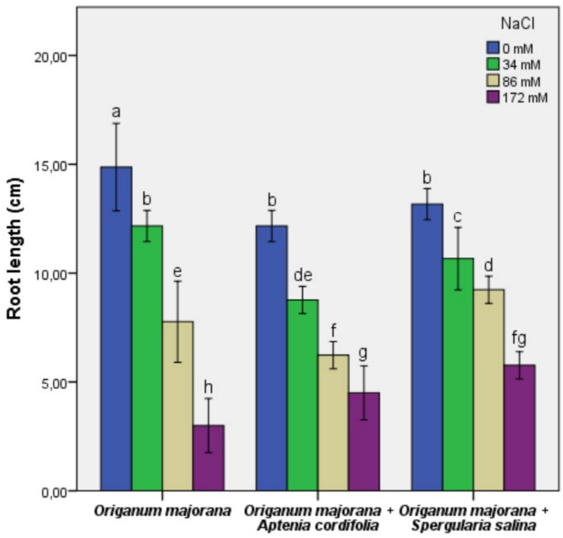


2: *Variation in oregano length of aerial part in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

salt concentration. However, the association with *Spergularia salina* stood out with a decrease of only 47.66%, suggesting a better ability to maintain the length of the aerial part in the presence of salt stress. These percentage variations underline the differentiated effectiveness of plant associations in preserving the length of the aerial part in response to salt stress.

Root Length

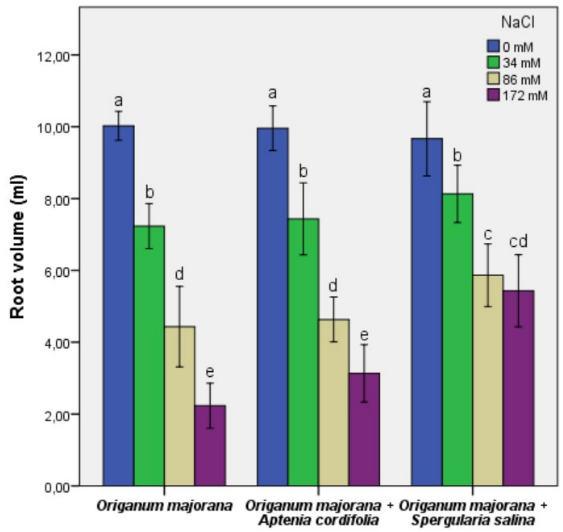
The results show a reduction in the root length of oregano plants with increasing NaCl concentrations. At 172 mM NaCl, the length of the root part of oregano alone decreased significantly, with a reduction of 80.56% compared with conditions without salt. In comparison, plants combined with *Aptenia cordifolia* showed a less pronounced reduction, with a difference of 65.85% at the same salt concentration. However, the association with *Spergularia salina* stood out with a decrease of only 33.08%, suggesting a better ability to maintain root length in the presence of salt stress. These percentage variations underline the differentiated effectiveness of plant associations in preserving root length in response to salt stress.



3: *Variation in oregano root length in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

Root Volume

Les données montrent une réduction du volume racinaire des plants d'origan avec l'augmentation des concentrations de NaCl. À 172 mM de NaCl, le volume racinaire de l'origan seul est de 2,23 ml, tandis qu'en association avec *Aptenia cordifolia* et *Spergularia salina*, il atteint respectivement 3,13 ml et 5,43 ml. Ainsi, l'association avec *Spergularia salina* semble favoriser une meilleure préservation du volume racinaire de l'origan par rapport à l'association avec *Aptenia cordifolia*.

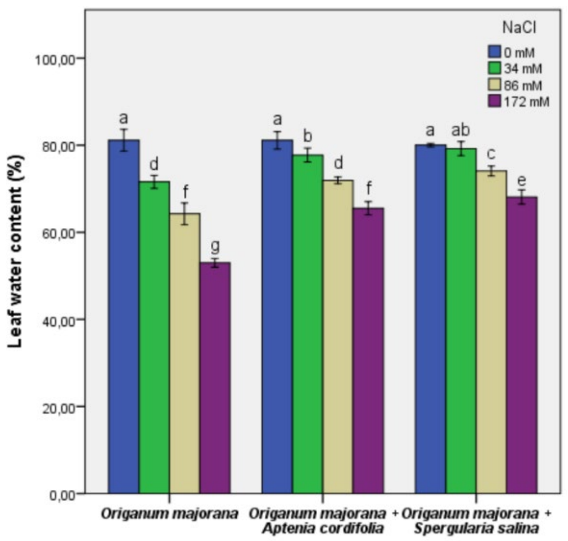


4: *Variation in oregano root volume in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

Physiological Parameters

Water Content

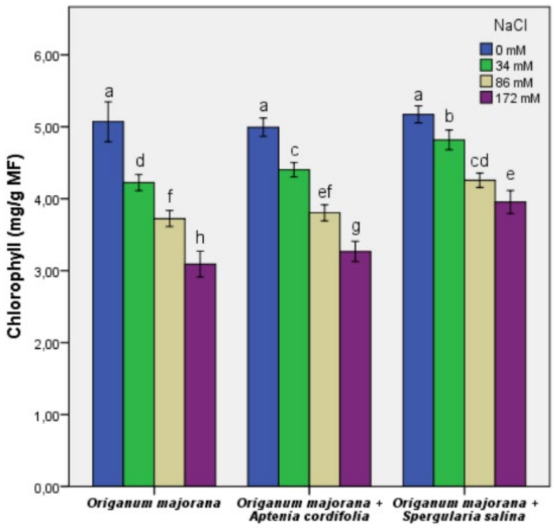
The water content of oregano plant leaves showed a progressive reduction with increasing NaCl concentrations. At 172 mM NaCl, the water content of oregano leaves alone decreased significantly, showing a 28.13% drop compared with conditions without salt. In comparison, plants combined with *Aptenia cordifolia* showed a slightly smaller reduction, with a difference of only 15.60% at the same salt concentration. However, the association with *Spergularia salina* stood out with a reduction of just 7.67%, suggesting a better ability to maintain leaf hydration in the face of salt stress.



5: *Variation in oregano water content in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

Chlorophyll Content

The chlorophyll content of oregano plants showed a progressive decrease with increasing NaCl concentrations. At 172 mM NaCl, the chlorophyll content of oregano alone decreased significantly, with a drop of 39.20% compared with conditions without salt. In comparison, plants combined with *Aptenia cordifolia* showed a slightly smaller reduction, with a difference of only 34.49% at the same salt concentration. However, the association with *Spergularia salina* stood out with a reduction of only 23.64%, suggesting a better ability to preserve chlorophyll content in the face of salt stress.



6: *Variation in oregano chlorophyll content in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

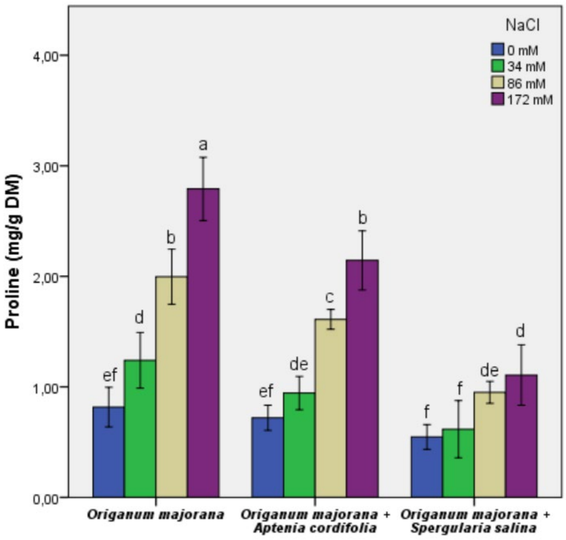
Effect of Salt Stress on Biochemical Parameters

Proline Content

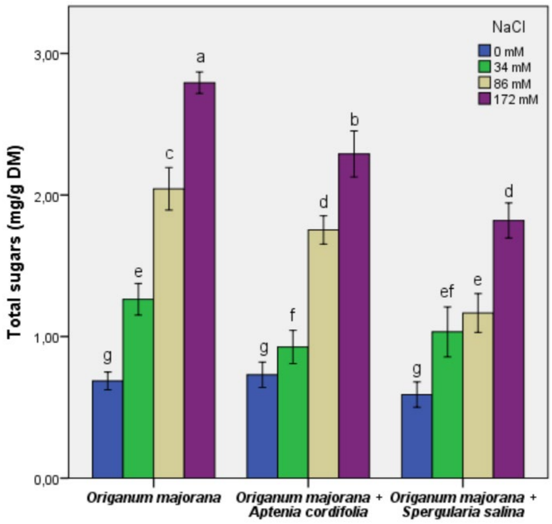
Analysis of proline secretion revealed a progressive increase with increasing NaCl concentrations, indicating an adaptive response to salt stress in oregano plants. At 172 mM NaCl, the proline concentration in oregano alone was significantly higher, with an average of 2.79 mg/g DM, an increase of 241.28% compared with conditions without salt. This increase was also observed in plants combined with *Aptenia cordifolia* and *Spergularia salina*, although to a lesser extent. In addition, the association with *Spergularia salina* seemed to induce a slightly less pronounced proline response than the associations with *Aptenia cordifolia* and oregano alone, which could indicate a difference in the stress response between the different plant associations.

Total Sugar Content

Analysis of total sugars revealed a progressive increase with increasing NaCl concentrations, suggesting an adaptive metabolic response in



7: *Variation in oregano proline content in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*



8: *Variation in oregano total sugar content in different salt stress treatments (Values with different letters in the column have statistical significance at a 5% level)*

oregano plants exposed to salt stress. At 172 mM NaCl, the concentration of total sugars in oregano alone was significantly higher, with an average of 2.79 mg/g DM, an increase of 307.74% compared with conditions without salt. This increase is also observed, albeit to a lesser extent, in the case in association with *Aptenia cordifolia* and *Spergularia salina*. Furthermore, the association with *Spergularia salina* seems to induce a slightly less pronounced response in total sugars compared to associations with *Aptenia cordifolia* and oregano alone, which could indicate a difference in stress response between the different plant associations.

Analysis of Variance

Salt stress (NaCl) has a significant effect for all variables, indicating that increasing salt concentration has a significant impact on biomass, above-ground and root growth, as well as on plant physiology, such as leaf water content, chlorophyll, proline and total sugars. When growing *Origanum majorana* alone or in association with *Aptenia cordifolia* and *Spergularia salina*, there was a significant difference for most parameters, meaning that the presence of *Origanum majorana* alone results in different metabolic and physiological responses compared to its associations with halophytes. The interaction between salt stress and cultivation in association with *Aptenia cordifolia* and *Spergularia salina* was also significant for all the parameters studied, underlining that *Origanum majorana*'s response to different salt concentrations depends on its cultivation in association with halophytes.

Correlation Analysis

Correlation analysis revealed several significant associations between the parameters studied. It showed a highly significant correlation ($P < 0.05$) between biomass and length of aerial part ($r = 0.957$), root length ($r = 0.950$), root volume ($r = 0.954$), water content ($r = 0.893$) and chlorophyll content ($r = 0.949$). Proline content showed a significant negative correlation ($P < 0.05$) with chlorophyll content ($r = -0.923$), water content ($r = -0.936$), root volume ($r = -0.891$), root length ($r = -0.793$), biomass ($r = -0.857$) and height of aerial part ($r = -0.906$). Similarly, proline content showed a strong positive correlation with sugar content ($r = 0.943$).

I: *Analysis of variance results for different parameters measured in the study*

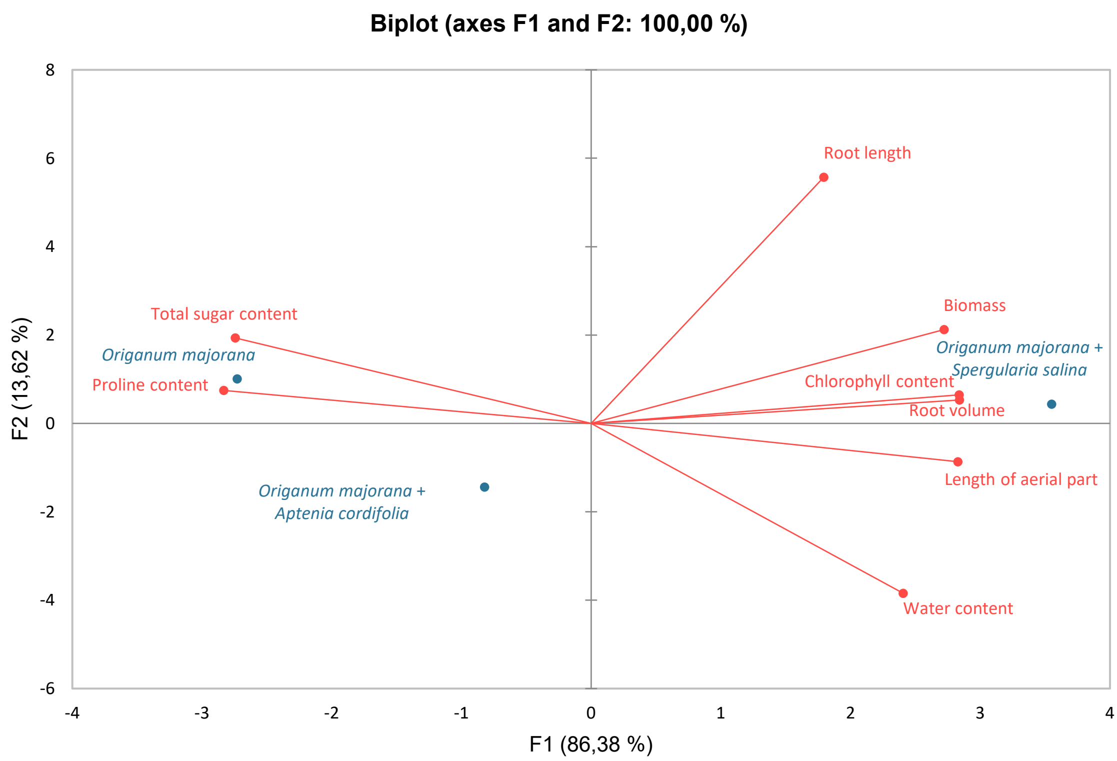
Source of variance	Biomass	Length of aerial part	Root length	Root volume	Water content	Chlorophyll content	Proline content	Total sugar content
Salt stress (A)	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***
Cultivation in association (B)	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***
A*B	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***

(* $P \leq 0.05$; ** $P \leq 0.05$; *** $P \leq 0.01$)

II: *Pearson correlation between studied parameters*

	Biomass	Length of aerial part	Root length	Root volume	Water content	Chlorophyll content	Proline content	Total sugar content
Biomass	1							
Length of aerial part	0,957**	1						
Root length	0,950**	0,942**	1					
Root volume	0,954**	0,931**	,929**	1				
Water content	0,893**	0,950**	0,833**	0,909**	1			
Chlorophyll content	0,949**	0,947**	0,916**	0,978**	0,927**	1		
Proline content	-0,857**	-0,906**	-0,793**	-0,891**	-0,936**	-0,923**	1	
Total sugar content	-0,956**	-0,965**	-0,903**	-0,953**	-0,961**	-0,964**	0,943**	1

(ns: not significant; * P ≤ 0.05; ** P ≤ 0.05; *** P ≤ 0.01)



9: *Principal component analysis of the parameters studied*

Principal Component Analysis

Principal component analysis (PCA) showed that the first two factorial axes F1 (86.38%) and F2 (13.62%) showed variance in responses to salt stress in *Origanum majorana* grown alone and in association with the two halophytic plants *Spergularia salina* and *Aptenia cordifolia*. Interpretation of the PCA biplot highlights the relationships between different parameters and cultivation alone and in association with the two halophytic plants under salt stress conditions. Under saline stress conditions *Origanum majorana* grown alone shows a high secretion of proline and sugars. On the other hand, the combination of oregano with *Spergularia salina* shows the best growth parameters, with a high water content and the highest chlorophyll level. The combination of oregano with *Aptenia cordifolia* is at an intermediate level in terms of performance.

DISCUSSION

The results obtained showed that exposure of oregano plants to salt stress adversely affected their growth. Plants subjected to saline conditions showed a reduction in all the growth parameters studied. This reduction is due to osmotic stress, specific ion toxicity and metabolic disturbances, which reduce photosynthetic efficiency, meristematic activity and plant cell elongation (Toubali *et al*., 2023).

Morphological and physiological parameters of oregano grown on its own show a marked deterioration with increasing salinity. Biomass decreases significantly as salt concentration increases, indicating that oregano is particularly sensitive to salt stress. Moreover, the length of the aerial and root parts of oregano also shrinks with increasing salinity, underlining the plant's difficulty in maintaining growth under saline conditions. At the same time, the root volume of oregano decreases considerably, which can be attributed to the toxicity of Na^+ and Cl^- ions present in saline soil. Leaf water content also decreases, which is a direct indicator of plant dehydration under salt stress. Chlorophyll content, essential for photosynthesis, decreases with increasing salinity, further affecting the plant's ability to produce biomass. In response to salt stress, oregano increases its secretion of proline and soluble sugars, which are osmoprotectants helping the plant to maintain osmotic balance and protect cellular structures.

However, the association of oregano with the halophytic plants *Spergularia salina* and *Aptenia cordifolia* has shown promising results in mitigating the negative effects of salinity on the morphological and physiological parameters of oregano. Unlike oregano grown alone, where biomass, root length, root volume, water content, chlorophyll content and secretion of proline and sugars are all negatively affected by increasing salinity, cultural association with *Spergularia salina* and *Aptenia cordifolia* reduced these adverse effects.

The results show that the biomass of oregano grown in association decreases less pronounced with increasing salinity, which can be attributed to the ability of halophytic plants to clean salts from the soil, as indicated by Hasanuzzaman *et al.* (2014). Halophytic plants, such as *Spergularia salina*, possess a soil desalination mechanism, making the soil more compatible with the cultivation of salinity-sensitive plants. This observation is reinforced by the work of Mezni *et al.* (2012), who showed that the roots of halophytic plants accumulate less Na^+, with higher concentrations in stems and leaves.

With regard to root length, although increasing salinity results in root shrinkage in oregano grown alone, this shrinkage is less marked in the presence of *Spergularia salina* and *Aptenia cordifolia*. This highlights the role of halophytic plants in preparing the soil, making it more suitable for salinity-sensitive crops, similar to the observations of Karakas *et al.* (2021) regarding the reduction of chloride accumulation in tomato roots in association with halophytes. Furthermore, the root volume of oregano increases up to 6 cm in the presence of *Spergularia salina*, despite the increase in salinity, which is a significant result compared to the sharp decrease observed in the crop alone.

The water content of the leaves of oregano grown in association is also better maintained than in the case of the crop alone, indicating better resistance to dehydration under salt stress. Chlorophyll content, essential for photosynthesis, decreased less markedly in associated crops, which is consistent with studies by Ghaffarian *et al.* (2020) and Karakas *et al.* (2021), showing improved chlorophyll a and b contents in intercrops. These results suggest that halophytic plants can improve the photosynthetic metabolism of salinity-sensitive plants.

Furthermore, the secretion of proline and soluble sugars, although significantly increased in oregano grown alone under salt stress, was less pronounced in crops associated with *Spergularia salina* and *Aptenia cordifolia*. This indicates that the crop association helps oregano to better regulate its osmosis and manage salinity-induced water stress. This observation is in line with the work of El-Khadir *et al.* (2024b), who demonstrated an innovative approach to soil salinity management using a strategy based on the association of sage (*Salvia officinalis*) with halophytic plants.

These results are in line with those found by El Khadir *et al.* (2024c), who reported that a cultural association between Lavender and *Atriplex prostrata* had a significant effect on its growth in a saline environment. This improvement could be attributed to the fact that these halophytic plants possess a specific, highly efficient osmotic regulation mechanism and antioxidant enzyme system, enabling them to cope with various abiotic stresses and resist metals. They also use cellular mechanisms for the transfer and sequestration of salt and metal cations (Lutts and Lefèvre, 2015).

In addition, desalination of contaminated soils, particularly in salinity-affected landscapes, through the use of plants, has become a cost-effective and ecologically acceptable method (Dickinson *et al.,* 2009). This approach highlights the importance of combined cropping with halophytic plants as an effective strategy not only for improving crop tolerance to salt stress, but also for restoring soil quality.

To our knowledge, this research represents the first demonstration of improved tolerance of oregano plants to salt stress through the use of halophytic plants. Despite certain limitations, the many advantages of this practice are making it increasingly popular.

CONCLUSION

The effects of climate change are increasing soil salinity, posing a major challenge for the cultivation of medicinal plants, including oregano, which is increasingly in demand for its health benefits. This increased demand is driving the domestication of oregano in soils with high electrical conductivity (EC). Our results show that by combining oregano with the halophytic plants *Spergularia salina* and *Aptenia cordifolia*, the salinity tolerance of oregano is improved, reducing negative effects on various morphological and physiological parameters. For example, association with *Spergularia salina* resulted in a 20% increase in oregano biomass and a 15% reduction in cell damage. This strategy of cultivation in association with halophytes could offer an effective method of growing salinity-sensitive plants in saline environments, contributing to more sustainable and resilient agriculture. The results are very promising because they pave the way for potential applications for crops under semi-operational and operational conditions, particularly in farming systems located in saline or arid regions. However, larger-scale trials would be needed to validate its economic and environmental effectiveness in improving agricultural yields while meeting the challenges of climate change.

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