

Article

Effect of Exogenously Applied Methyl Jasmonate on Yield and Quality of Salt-Stressed Hydroponically Grown Sea Fennel (*Crithmum maritimum* L.)

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Abstract: Salt stress is one of the main limiting factors for plant growth and crop yield. Halophytes have been postulated as a new food source since they are able to grow under saline environments and have suitable minerals and bioactive compounds. See fennel *Crithmum maritimum* L. is a facultative halophyte moderately tolerant to salinity. This study was carried out in order to determine the effect spraying methyl jasmonate (MeJa) on the leaves had on the growth and nutritional quality of NaCl-treated sea fennel plants grown in a hydroponic system. For that, the seedlings were treated with (a) 0.5 mM MeJa, (b) 150 mM NaCl, and (c) 0.5 mM MeJa + 150 mM NaCl. The results showed that NaCl reduced the shoot biomass of baby leaf plants, but the addition of MeJa enabled partial recovery. At the same time, when compared with the plants treated only with NaCl, MeJa favoured the Ca and K uptake and translocation to the leaves of saline-treated plants. However, MeJa did not reduce Na levels. In all treatments, nitrate and nitrite ions were in the range of the acceptable daily intake (ADI) and essential fatty acid content was elevated, although the addition of MeJa to NaCl-treated plants reduced linolenic and linoleic acid contents as compared to the plants treated only with NaCl. Total phenolic compounds were not recovered by MeJa after their decrease by salinity and no differences in antioxidant activity was found between treatments. However, all the plants maintained their antioxidant nutritional properties and increased total flavonoids after MeJa spraying to NaCl-treated plants. These results showed that MeJa spraying alleviated the negative effects of salt stress in *C. maritimum* grown in floating systems, improving the growth of their edible parts and increasing the total flavonoid and mineral content without affecting the total antioxidant capacity of the plant.

Keywords: antioxidant capacity; methyl jasmonate; minerals; salinity

1. Introduction

Fresh fruit and vegetable consumption are recommended by the World Health Organization and the food-based dietary guidelines of countries. This is mainly due to their health promoting components that can prevent chronic diseases as well as several micronutrient deficiencies. However, food-related family lifestyle is one of the factors affecting vegetable consumption [1,2]. Today's urban development, busy lifestyle, and technological societies have contributed to dramatic changes in food demand and consumption [3]. Minimally

processed baby leaf vegetables are one of the innovations in the food sector offering fresh, nutritious, convenient, diversified and ready-to-eat food products [4,5].

Minimally processed baby leaf vegetables are young leaves in different shapes, colours, and taste harvested at various stages of leaf growth, generally ranging 5 to 12 cm depending on the species, nutritional quality, shelf-life and final destination of the product [6]. They are rich in terms of natural antioxidants and antimicrobial substances [7] and, when compared with mature leaves, they do not present any nutritional disadvantage [4] and can even be accepted as superior [8]. Furthermore, baby leafy vegetables are important sources of minerals [9] and vitamins [10].

A floating system is particularly appropriate for baby leaf vegetable production since it allows a precise control of plant nutrition and the maximization of yield and quality of the product [11–13], demonstrating that the floating system could be considered an effective tool to improve quality aspects in artichoke and cardoon, improving the production of secondary metabolites through proper management of the salt concentration in the nutrient solution. Furthermore, the production of halophytes plants could be coupled with other cultivation systems. Thus, an integrated multi-trophic aquaculture system is a sustainable industrial solution when the biomass is produced in a balanced manner, because the waste products from fish culture effluent are used as inputs (nutrients) for plants. In this manner, halophytes can contribute to the removal of nutrients dissolved in the water, improving its quality and making it possible to return it to the fish tanks. Moreover, cultivation of halophytes in a floating system could couple with cascade closed systems, which use drained water and nutrients to irrigate another crop. In these systems, because nutrients tend to reach high concentrations in the leachates, increasing the salinity of this water flow, finding a salt-tolerant crop is key to its optimal running [14].

Basil (*Ocimum basilicum* L.), tatsoi (*Brassica rapa* L.), endive (*Cichorium intibus* L.), red and green lettuce (*Lactuca sativa* L.), rucola (*Eruca vesicaria* (L.) Cav., Syn. *Eruca sativa* Mill.), wild rocket (*Diplotaxis tenuifolia* (L.) DC.), and spinach (*Spinacia oleracea* L.) are the most common baby leaf vegetables grown commercially [11,15], however, each year new ones are added after being characterised as suitable to use as a baby-leaf vegetable [5].

Sea fennel (*Crithmum maritimum* L.), also known as rock samphire, is a perennial halophyte and a native plant of coastal ecosystems. It is naturally grown on maritime cliffs and in sand along seacoasts [16]. It is used fresh or cooked, for flavouring purposes, pickled or as a salad ingredient. Sea fennel is also used as a traditional medicine and is even mentioned in the Hippocratic Corpus [17] due to its content of biologically active compounds and essential oils in cosmetics [18]. It also has potential as an insecticide against pests [19].

Sea fennel has gained more recognition recently due to its phytochemicals, which are well recognized for their health-related effects on human nutrition and well-being. Sea fennel is rich in vitamin C [20], minerals, antioxidant activity (in particular, chlorogenic acid), phenol content [21–25], amino acids, flavonoids and essential oil [18,26]. However, studies on cultivation techniques are limited. There has been research conducted on seed germination [27–31], growing media [32] and response to salinity in *in vitro* conditions [33] or substrate [34] and nutrient solution [35].

Salt tolerance of halophytes differs according to the species. The plant growth and phytochemical pattern of sea fennel is affected by salinity [34], origins of landraces [36,37] and if it is cultivated or wild [16]. For sea fennel, a moderate tolerance to salinity has been reported [34], while high salinity has a negative impact on growth rate and mineral content [35].

Jasmonates (jasmonic acid (JA) and its derivatives) are synthesized from α -linolenic acid of chloroplast membranes and are important signals in plant stress response [38]. Methyl ester of JA (MeJA) stimulates the production of compounds, which affects plant response to stress. However, MeJA has alleviated salinity stress in many horticultural crops such as strawberry [39], broccoli sprouts [40], and tomato [41]. Additionally, MeJA has

increased the bioactive compound composition in broccoli and purple tumorous stem mustard sprouts [42,43].

Sea fennel has the potential for cultivation as a baby-leaf vegetable due to its richness in terms of health-promoting compounds and its suitability for cultivation in drought and saline conditions. However, research into cultivation techniques and treatments that could increase the phytochemicals of the plant, as reported by Renna [16], should be carried out in order to attain more knowledge. The general objective of this study was the cultivation of sea fennel as a baby-leaf vegetable in a floating system under greenhouse conditions. The specific goal of this study was to determine the effect of salinity, added to the nutrient solution as 150 mM NaCl, on plant growth, yield and biochemistry, since this halophyte naturally grows in saline environments and its use in aquaponics systems has not been explored. Additionally, the supply of exogenous MeJA, as an elicitor to cope with salt stress and its effect on nutrient compounds in sea fennel plants, was studied.

2. Material and Methods

2.1. Cultivation and Experiment Design

The experiment was conducted during the fall and spring seasons of 2019 and 2020 at the Technical University of Cartagena, Spain (UPCT; lat. 37°41' N; long. 0°57' W). After one month of sowing, seedlings of sea fennel were transplanted in polystyrene trays and cultivated in a floating system in an unheated 145 m² greenhouse covered with thermal polyethylene. Polystyrene trays containing 54 cells were used, with each cell containing two plants. The plant density was around 400 plants/ha. Aeration was provided using a blow pump connected to a perforated pipe trellis positioned at the bottom of each flotation bed and each level of treatment was carried out in a stainless-steel flotation bed of 1.35 m × 1.25 m × 0.2 m covered with a PVC liner. After one week, the tap water in the beds was replaced with a nutrient solution (pH of 5.8 to 5.6 and EC 2.8 dS/m), containing the following elements in mol/L: NO₃⁻, 7200; NH₄⁺, 4800; H₂PO₄⁻, 2000; K⁺, 6000; Mg²⁺, 1500; and Ca²⁺, 2000. A commercial mixture of microelements at a concentration of 0.02 g L⁻¹ (Nutromix, Biagro S.L., Valencia, Spain) and Fe chelate at a concentration of 0.02 g L⁻¹ (Sequestrene, Syngenta AG, Basel, Switzerland) were added to the solution. The EC and temperature of the nutrient solution were monitored during the growing season using Campbell CS547 sensors (Campbell Scientific Inc., Logan, UT, USA).

Five treatments were considered: control plants (Control1); control plants spraying with Tween 20 (1 mL L⁻¹) in 0.2% EtOH (Control2); an addition of 150 mM NaCl to the nutrient solution (NaCl); spraying with 0.5 mM methyl jasmonate (MeJa); and 150 mM NaCl + 0.5 mM MeJa (NaCl + MeJa). MeJa was diluted in Tween 20 1 mL L⁻¹ in 0.2% EtOH in order to facilitate MeJa leaf penetration. NaCl was added to the nutrient solution after 1 month of transplanting, whereas an amount of 100 mL of MeJa, prepared as described above, was sprayed onto the leaves three times every 10 days. The initial addition was 14 days after the NaCl treatment. The nutrient solution was replaced weekly, and the pH measured every three days and adjusted to 6.5 by adding sulphuric acid. A total of two replicates (trays) per treatment were placed in a random distribution in the greenhouse floating system, and, at harvest, a total of 10 plants per replicate were taken. The shoot and roots were separated for measurements and kept in N₂ liquid for subsequent lyophilisation. The yield and quality analysis, fresh and dry weights of shoots, root growth parameters, chlorophyll and carotenoids, content of fatty acids, total phenolics content, total flavonoids content, and antioxidant capacity were measured.

For determining chlorophylls, total flavonoids, and phenolic content and antioxidant activity, a methanolic extract was obtained with 50 mg of lyophilized sample in 1.5 mL of methanol in a 2 mL Eppendorf tube. It was then vortexed and incubated overnight at 4 °C. After incubation, it was centrifuged at 16,000 × g for 5 min at 4 °C. The supernatant was used as methanolic extract for analysis.

2.2. Fresh, Dry Weights of Shoots and Root Growth Parameters

The fresh weight (FW) of shoots was measured on a scale (Model: RADWAG PS 4500/C2) with an accuracy level of 0.0001 g. The dry weight (DW) of shoots was determined by drying in an oven at 60 °C until constant weight was attained. The shoot hydric content was calculated as the difference between FW and DW referred to DW.

Root length (cm), surface area (cm²), and average diameter (mm) of all primary and secondary roots and root volume (cm³) parameters were measured using a Winrhizo LA 1600 root counter (Regent Inc., Quebec, QC, Canada).

2.3. Mineral Analysis

Anions and cations were extracted from the six samples per treatment and replicate. For that, 0.2 g of *C. maritimum* dry leaf was used and 50 mL of distilled water was added. Then, the tubes were shaken in an orbital shaker (Stuart SSL1, Stone, UK) for 45 min at 110 rpm at 50 °C.

The ion content was quantified by ion chromatography using a Metrosep A SUPP 5 column (Metrohm AG, Zofingen, Switzerland) with a flow rate of 0.7 mL min⁻¹ for anions and a Metrosep C 2–250 column (Metrohm AG, Zofingen, Switzerland) with a flow rate of 1.0 mL min⁻¹ for cations [44].

2.4. Fatty Acids

Fatty acid methyl esters (FAME) were identified following O'Fallon et al.'s [45] methodology, with some modifications. Briefly, 50 mg of freeze-dried samples were placed into a 16 mm × 100 mm screw-cap Pyrex culture tube containing 0.7 mL of 10 N KOH, 1.0 mL of C13:0 internal standard (0.5 mg of C13:0/mL of MeOH), and 5.3 mL of MeOH. The tubes were incubated in a 55 °C water bath for 1.5 h and shaken by hand every 20 min. After cooling in a cold tap water bath, 0.58 mL of 24 N H₂SO₄ were added. The tubes were mixed by inversion and incubated in a 55 °C water bath for 1.5 h with hand-shaking. After cooling below room temperature, 1.5 mL of hexane was added, and the tubes were vortex-mixed for 5 min. Then, the tubes were centrifuged for 5 min at 1500× g and the extracted hexane layer containing the FAMEs was placed in a vial and stored at –20 °C until analysis. A gas chromatography (Agilent 6890 N), coupled to an autosampler system (Gerstel MPS2) and mass spectrometry detector (Agilent 5975), was used for the fatty acid composition of the FAME, using a Supelco SP-2560 (100 m × 0.25 mm × 0.2 μL) capillary column with a flame ionization detector (FID). The gas carrier (20 cm s⁻¹) and a temperature program of 140 °C during 5 min, 140–240 °C at 4 °C min⁻¹, 240 °C during 30 min and finally 140–240 °C at 4 °C min⁻¹. Both the injector and detector temperature were 260 °C. Methyl esters pattern (Sigma-Aldrich 47885-U, Merck KGaA, Darmstadt, Germany) was used for identification.

The double bond index (DBI) was calculated as the unsaturated fatty acid per number of double bonds.

2.5. Chlorophylls and Carotenoids

Methanol extracts (50 μL), obtained as reported in Section 2.1, were used to measure chlorophyll and carotenoids. Spectrophotometric measurements of total carotenoids and chlorophyll content were carried out by measuring the absorbances at 652, 665 and 470 nm, which were measured in a UV-visible spectrophotometer (8453, Hewlett Packard, Columbia, SC, USA). The equations developed by Lichtenthaler and Buschmann [46] were used to determine the individual levels of chlorophyll a, chlorophyll b and total carotenoids. Total chlorophyll and total carotenoids contents were expressed as mg kg⁻¹ DW. Five plants of each replicate were analysed.

2.6. Total Flavonoids Content

Total flavonoid content was determined as described by Meda et al. [47]. Methanolextracts (50 μL), obtained as reported in Section 2.1, MeOH (300 μL) and AlCl₃ (2%) (350 μL)

were mixed and incubated for 20 min at room temperature in darkness and the absorbance was measured at 430 nm. The results were expressed in mg Rutin per kg of FW. Five plants of each replicate were analysed.

2.7. Total Phenolic Content and Antioxidant Capacity

The total phenolic content was determined by the Folin-Ciocalteu colorimetric method, according to Everette et al. [48]. Methanol extracts (50 μ L), obtained as reported in Section 2.1, H₂O distilled (790 μ L) and Folin (50 μ L) were mixed and incubated for 5 min. Then, 150 μ L of a solution of Na₂CO₃ (20%) was added. After 2 h of incubation at room temperature in darkness, the absorbance was measured at 765 nm using a UV-visible spectrophotometer. The results were expressed in mg gallic acid (GA) per kg of FW. Each of the three replicates were analysed in triplicate (instrumental replicate).

The antioxidant capacity was evaluated in terms of their free radical-scavenging potential [49], with the modifications as described by Perez-Tortosa et al. [50]. Methanol extracts (25 μ L) and DPPH (0.1 mM) (600 μ L) were mixed and incubated for 15–20 min at room temperature in darkness and the absorbance was measured at 517 nm. The results were expressed in mg DPPH reduced per kg of FW. Five plants of each replicate were analysed.

2.8. Statistics

The data were analysed statistically by Tukey's test, comparing each cultivar individually, using the SPSS 20.0 software package. Significant differences were determined at $p < 0.05$.

3. Results

3.1. Biomass and Root Growth Parameters

The higher shoot FW was observed in Control1 plants without significant differences regarding Control2 (Figure 1). NaCl treatment reduced the shoot FW of *C. maritimum* plants, while MeJa application in saline condition (NaCl + MeJa) partially recovered the shoot FW when compared with the only NaCl addition, without significant differences regarding Control2. The only MeJa treatment caused a reduction in shoot FW as compared to Control1, but not with respect to Control2. Shoot DW projected a similar pattern to shoot FW. As for total plant DW, NaCl and NaCl + MeJa treatments reached the highest values. Control1 and Control2 values were similar and higher than MeJa treated plants.

Total root length and root surface area were the highest in the NaCl treatment when compared with the rest of treatments, which did not show significant differences for these parameters (Table 1). Root diameter was not modified after any of the treatment applications. Similarly, root volume was significantly higher in the NaCl treatment in relation to Control1 and MeJa.

3.2. Ion Content

Cations (Mg²⁺, Ca²⁺, K⁺, NH₄⁺ and Na⁺) and anions (F⁻, Cl⁻, NO₂⁻, Br⁻, NO₃⁻, PO₄⁻, C₂O₄²⁻) determined in the leaves of *C. maritimum* are shown in Tables 2 and 3. Regarding cations, Mg²⁺ content was higher in NaCl + MeJa treated plants compared to those treated with only NaCl, but no significant differences were found between Control1, Control2, MeJa, and NaCl + MeJa treatments. Ca²⁺ content was similar in all treatments with the exception of the NaCl treatment, where Ca²⁺ content decreased. K⁺ content was similar in Control1, Control2 and MeJa plants and it decreased in NaCl treatment. The two MeJa addition treatments increased the NH₄⁺ content as compared to the Control1 and Control2 treatments. No significant differences appeared among them. Finally, Na⁺ was higher in NaCl and NaCl + MeJa treatments compared with Control1, Control2, and MeJa. The K/Na ratio was higher in Control1, Control2, and MeJa treatments than in both NaCl treatments. However, although the content of K⁺ was higher in NaCl + MeJa treated plants

compared to the NaCl only addition, no significant differences were found in the K/Na ratio between both treatments.

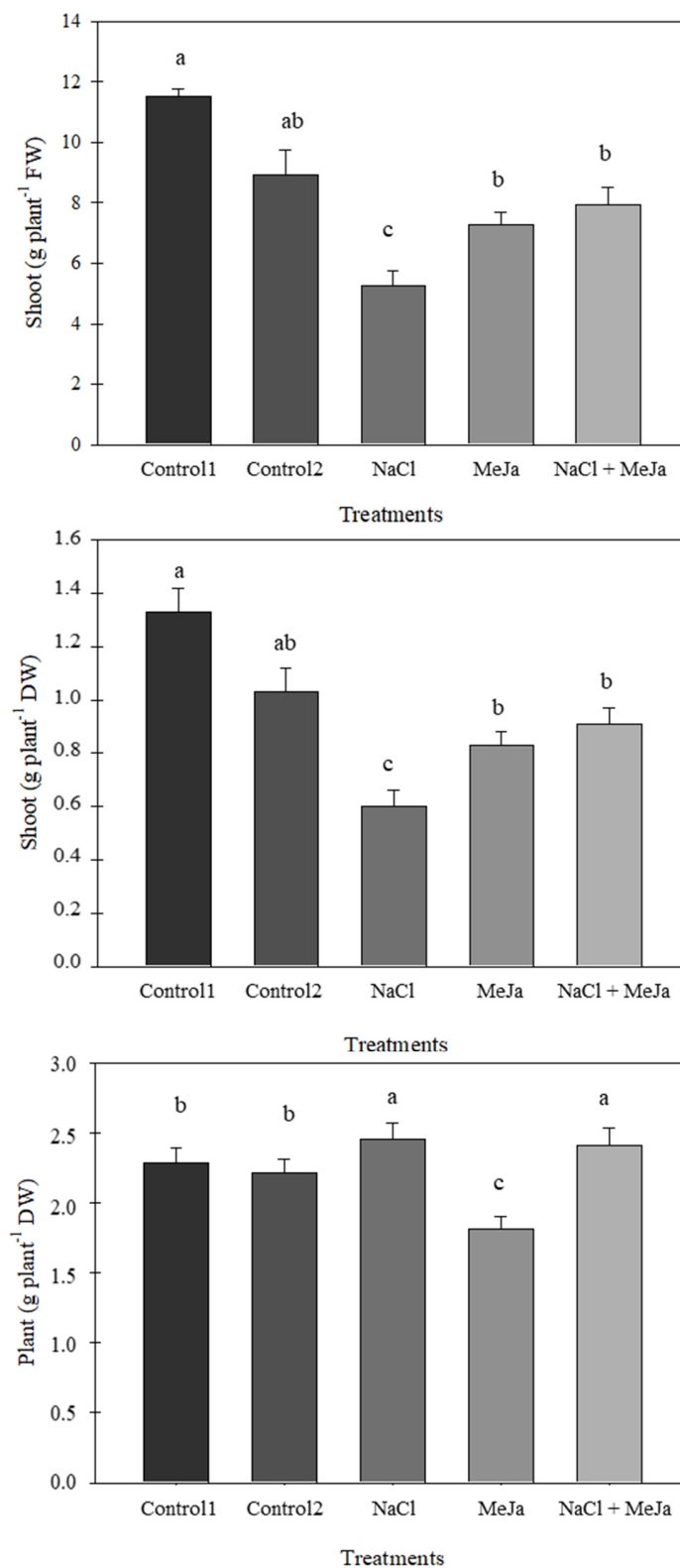


Figure 1. Fresh weight (FW) and dry weight (DW) of the aerial part of *C. maritimum* plants, and DW (gr plant⁻¹) of the whole plant, grown under hydroponic conditions with the following treatments: Control1, Control2, NaCl, MeJa, NaCl + MeJa, ($n = 20$). Different letters (a, b, c) indicate significant differences according to Tukey's test ($p < 0.05$).

Table 1. Root growth parameters (length, surface area, average diameter, and root volume) of *C. maritimum* plants grown under hydroponic conditions with the following treatments: control1, Control2, NaCl, MeJa, NaCl + MeJa, ($n = 20$). Columns with different letters (a, b) for each variable differ significantly according to Tukey's test ($p < 0.05$).

Treatments	Total Length (cm)	Surf Area (cm ²)	Root Dia. (mm)	Root Volume (cm ³)
Control1	222.48 ± 38.19b	35.46 ± 5.66b	0.54 ± 0.04a	0.49 ± 0.08b
Control2	207.84 ± 29.75b	38.99 ± 5.98b	0.60 ± 0.04a	0.62 ± 0.12ab
NaCl	347.57 ± 49.33a	65.05 ± 8.59a	0.63 ± 0.05a	1.01 ± 0.13a
MeJa	207.90 ± 25.61b	33.14 ± 4.64b	0.50 ± 0.03a	0.46 ± 0.086b
NaCl + MeJa	219.14 ± 37.8b	44.25 ± 6.69ab	0.65 ± 0.05a	0.75 ± 0.12ab

Table 2. The content of cations (Mg²⁺, Ca²⁺, K⁺, NH₄⁺, Na⁺ and K/Na ratio) (mg kg⁻¹ FW) in the leaf tissues of *C. maritimum* under the different treatments (Control1, Control2, NaCl, MeJa, NaCl + MeJa), ($n = 10$). Columns with different letters (a, b, c) for each variable differ significantly according to Tukey's test ($p < 0.05$).

Treatment	Mg ²⁺	Ca ²⁺	K ⁺	NH ₄ ⁺	Na ⁺	K/Na
Control1	309.00 ± 6.09ab	997.72 ± 10.036a	2411.01 ± 48.78ab	277.59 ± 23.13a	977.27 ± 70.43b	2.47 ± 0.2a
Control2	299.25 ± 20.21ab	901.05 ± 53.26a	2295.72 ± 125.96ab	251.19 ± 14.84a	1086.10 ± 67.04b	2.11 ± 0.2a
NaCl	255.03 ± 53.10b	692.83 ± 36.78b	1628.10 ± 113.72c	384.90 ± 15.00ab	2698.07 ± 16.54a	0.60 ± 0.1b
MeJa	283.91 ± 12.15ab	926.53 ± 28.21a	2901.40 ± 121.81a	449.18 ± 104.60b	1308.48 ± 51.43b	2.21 ± 0.2a
NaCl + MeJa	342.78 ± 10.98a	1044.16 ± 88.79a	2006.77 ± 134.36b	447.61 ± 48.50b	2703.18 ± 44.96a	0.74 ± 0.1b

Table 3. The content of anions (F⁻, Cl⁻, NO₂⁻, Br⁻, NO₃⁻, PO₄³⁻, C₂O₄²⁻) (mg kg⁻¹ FW) in the leaf tissues of *C. maritimum* under the different treatments (Control1, Control2, NaCl, MeJa, NaCl + MeJa), ($n = 10$). Columns with different letters (a, b, c) for each variable differ significantly according to Tukey's test ($p < 0.05$).

Treatment	F ⁻	Cl ⁻	NO ₂ ⁻	Br ⁻	NO ₃ ⁻	PO ₄ ³⁻	C ₂ O ₄ ²⁻
Control1	20.88 ± 0.97a	2285.63 ± 162.74b	963.25 ± 8.94a	109.62 ± 0.90b	296.95 ± 23.32a	944.38 ± 25.93c	116.46 ± 4.42b
Control2	25.83 ± 4.56a	2515.93 ± 104.79b	845.95 ± 36.81a	105.87 ± 0.86b	229.12 ± 8.13a	911.26 ± 25.64c	108.28 ± 1.11b
NaCl	21.71 ± 0.87a	4385.71 ± 31.93a	453.87 ± 90.22b	109.38 ± 0.67b	255.84 ± 9.10a	940.02 ± 14.36c	134.28 ± 1.89a
MeJa	25.83 ± 1.25a	2840.38 ± 4.00b	970.44 ± 12.22a	120.20 ± 1.40a	276.49 ± 1.66a	1082.62 ± 23.03b	128.90 ± 7.94ab
NaCl + MeJa	24.81 ± 0.75a	4986.10 ± 39.67a	954.57 ± 15.37a	132.47 ± 0.81a	292.59 ± 0.74a	1278.91 ± 20.64a	126.25 ± 6.58ab

A high correlation between shoot Na⁺ and leaf hydric content was observed (Figure 2). Regarding anions, F⁻ and NO₃⁻ content did not show significant differences between treatments in the leaves of *C. maritimum* (Table 3). Cl⁻ content was higher in the NaCl and NaCl + MeJa treated plants compared with the rest of treatments. NO₂⁻ content only decreased in NaCl⁻ treated plants, and Br⁻ content increased in plants treated with both MeJa treatments in comparison to the rest. PO₄³⁻ content was enhanced in MeJa and NaCl + MeJa treated plants, with the increase observed as being higher in plants treated with NaCl + MeJa. Finally, C₂O₄²⁻ content was higher in NaCl treatment and similar in both control treatments.

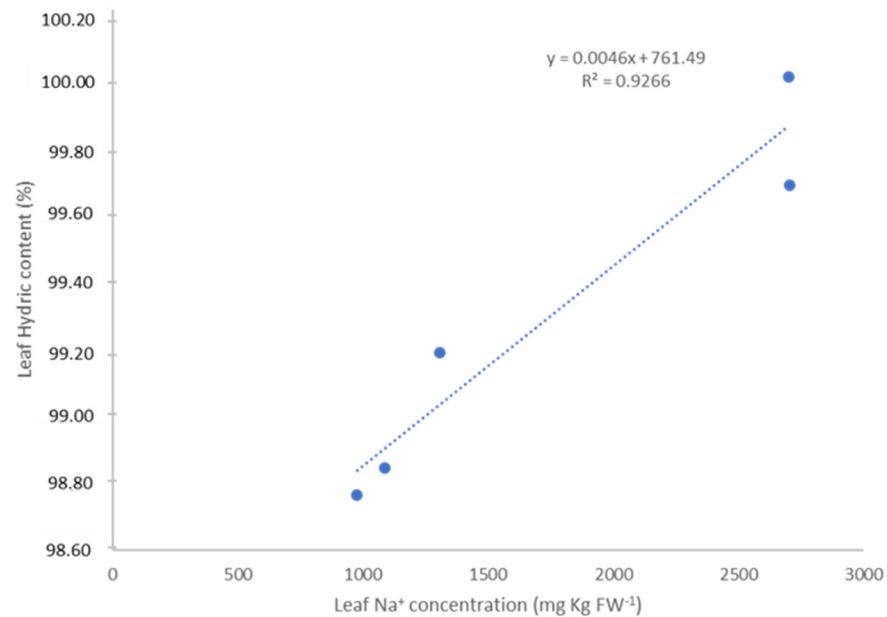


Figure 2. Correlation between leaf hydric content and leaf Na⁺ concentration.

3.3. Fatty Acids

The fatty acids analysis revealed that the *C. maritimum* leaves showed an increase in the unsaturated and saturated fatty acids in the NaCl treatment (Table 4). Among unsaturated acids, the increases were observed in oleic and linoleic acids, whereas NaCl treatment did not affect the content of linolenic acid regarding Control1. This fact produced an increase in the double bond index (DBI). The addition of MeJa to NaCl-treated plants had no significant effect on the content of individual fatty acids regarding Control1, with the exception of the saturated lignocerate acid that was not detected, but the total fatty acids were lower than in the Control2 and NaCl-treated plants. However, considering the percentage of individual fatty acids observed in total (Table 5), the MeJa application in NaCl conditions increased the percentage of oleic and linolenic acids (Omega 3 acids) with regard to the rest of treatments and reduced the linoleic acid content. The MeJa sprayed plants showed similar fatty acid content during the NaCl treatment when compared to Control and MeJa treated plants, but the DBI was lower than that of the Control1 plants.

3.4. Total Phenolic Compounds and Total Flavonoids

Total phenolic compounds determined in the leaves of *C. maritimum* plants are shown in Table 6. The content of total phenolic compounds was similar in Control1, Control2 and MeJa treated plants, but it increased in NaCl and NaCl + MeJa treated plants. Total flavonoids increased in NaCl, MeJa, and NaCl + MeJa treated plants in comparison to both controls. Finally, no significant differences were found in the total antioxidant capacity between treatments.

Table 4. The content of fatty acids (mg gr⁻¹ DW) in the leaf tissues of *C. maritimum* under the different treatments (Control1, Control2, NaCl, MeJa, NaCl + MeJa), (*n* = 10). Rows with different letters (a, b, c) for each variable differ significantly according to Tukey's test (*p* < 0.05), n.s means not significative.

Fatty Acid (mg gr ⁻¹ DW)		Treatment				
		Control1	Control2	MeJa	NaCl	MeJa + NaCl
Saturated fatty acid (SFA)						
Lauric acid	C12:0	-	-	-	0.09 ± 0.00b	-
Myristate acid	C14:0	0.07 ± 0.00a	0.12 ± 0.01a	0.11 ± 0.00a	0.17 ± 0.03b	0.11 ± 0.00a
Palmitate acid	C16:0	1.50 ± 0.02a	1.65 ± 0.01a	1.48 ± 0.02a	2.12 ± 0.31b	1.38 ± 0.00a
Stearate acid	C18:0	0.49 ± 0.04ab	0.43 ± 0.02a	0.47 ± 0.01ab	0.58 ± 0.04b	0.41 ± 0.03a
Arachidate acid	C20:0	0.12 ± 0.01a	0.19 ± 0.02bc	0.15 ± 0.00ab	0.33 ± 0.03d	0.21 ± 0.02c
Behenate acid	C22:0	-	0.29 ± 0.00b	0.17 ± 0.00a	0.30 ± 0.02b	0.23 ± 0.06ab
Lignocerate acid	C24:0	-	0.29 ± 0.00b	0.23 ± 0.00a	0.26 ± 0.00b	-
Monounsaturated fatty acid (MUFA)						
Oleic acid	C18:1 n9	0.41 ± 0.01a	0.39 ± 0.00a	0.31 ± 0.00a	0.69 ± 0.13b	0.42 ± 0.03a
Polyunsaturated fatty acid (PUFA)						
Omega 6 (w6)						
Linoleic acid.	C18:2 n6	8.76 ± 0.12a	10.54 ± 0.40ab	8.90 ± 0.17a	12.44 ± 1.37b	8.70 ± 0.20a
Omega 3 (w3)						
Linolenic acid	C18:3 n3	7.14 ± 0.32a	7.93 ± 0.04ab	6.65 ± 0.35a	10.37 ± 0.223b	6.13 ± 0.00a
DBI (unsaturated fatty acid x number of double bonds)		39.35 ± 2.12b	44.2 ± 3.04ab	56.68 ± 3.56a	38.06 ± 2.16b	36.21 ± 1.98b
w6/w3		1.23 ± 0.07 n.s.	1.33 ± 0.00 n.s.	1.34 ± 0.04 n.s.	1.26 ± 0.15 n.s.	1.42 ± 0.04 n.s.
Total		18.53	21.83	18.48	27.29	17.62

Table 5. Fatty acids content expressed as percentage of the aerial part of *C. maritimum* plants grown under hydroponic conditions with the following treatments: Control1, Control2, NaCl, MeJa, NaCl + MeJa, (*n* = 6).

Fatty Acid (%)		Treatment				
		Control1	Control2	MeJa	NaCl	MeJa + NaCl
Saturated fatty acid (SFA)						
Lauric acid	C12:0	-	-	-	0.003	-
Myristate acid	C14:0	0.38	0.55	0.59	0.62	0.62
Palmitate acid	C16:0	8.11	7.55	8.01	7.77	7.84
Stearate acid	C18:0	2.65	1.96	2.54	2.12	2.33
Arachidate acid	C20:0	0.65	0.87	0.81	1.21	1.19
Behenate acid	C22:0	-	1.32	0.92	1.10	1.30
Lignocerate acid	C24:0	-	1.32	1.24	0.95	-
Monounsaturated fatty acid (MUFA)						
Oleic acid	C18:1 n9	2.21	1.78	1.68	2.53	2.38
Polyunsaturated fatty acid (PUFA)						
Omega 6 (w6)						
Linoleic acid	C18:2 n6	47.37	48.28	48.18	45.04	49.46
Omega 3 (w3)						
Linolenic acid	C18:3 n3	38.61	36.32	36.00	38.04	34.85

Table 6. The content of total phenolic compounds (mg GA kg⁻¹ FW), total flavonoids (mg Rutin kg⁻¹ FW), and antioxidant capacity (mg DPPH reduced kg⁻¹ FW) in the leaf tissues of *C. maritimum* under the different treatments (Control1, Control2, NaCl, MeJa, NaCl + MeJa), (*n* = 10). Columns with different letters (a, b) for each variable differ significantly according to Tukey's test (*p* < 0.05).

Treatments	Total Phenolic compounds (mg GA kg ⁻¹ FW)	Total Flavonoids (mg Rutin kg ⁻¹ FW)	Antioxidant Capacity (mg DPPH _{reduced} kg ⁻¹ FW)
Control1	891.79 ± 15.79a	1965.41 ± 47.17b	113.64 ± 7.17a
Control2	883.09 ± 8.11a	1968.39 ± 6.30b	110.85 ± 5.47a
NaCl	833.53 ± 9.42b	2167.24 ± 22.09a	109.92 ± 5.84a
MeJa	901.50 ± 9.71a	2186.94 ± 597a	108.81 ± 1.77a
MeJa + NaCl	844.40 ± 7.08b	2273.53 ± 0.60a	117.78 ± 1.09a

3.5. Chlorophylls and Carotenoids

Chlorophyll a content was higher in MeJa-treated plants compared to the rest of treatments (Table 7), while a reduction in chlorophyll b was induced by MeJa application in both MeJa and NaCl + MeJa treatments. Finally, carotenoids increased in MeJa treatment, but they remained unmodified in NaCl + MeJa.

Table 7. The content of chlorophyll a (mg kg⁻¹ DW), chlorophyll b (mg kg⁻¹ DW), and carotenoids (C) (mg kg⁻¹ DW) in the leaf tissues of *C. maritimum* under the different treatments (Control1, Control2, NaCl, MeJa, NaCl + MeJa), (*n* = 10). Columns with different letters (a, b, c, d, e) for each variable differ significantly according to Tukey's test (*p* < 0.05).

Treatments	Ch a (mg kg ⁻¹ DW)	Ch b (mg kg ⁻¹ DW)	C (mg kg ⁻¹ DW)	Ch a/Ch b
Control1	12.68 ± 0.05b	7.51 ± 0.40a	2.43 ± 0.09b	1.69 ± 0.00a
Control2	15.41 ± 0.23b	7.92 ± 0.03a	2.62 ± 0.03b	1.94 ± 0.00c
NaCl	16.13 ± 0.45b	8.85 ± 0.29a	2.86 ± 0.21b	1.82 ± 0.00b
MeJa	17.77 ± 0.05a	4.98 ± 0.03b	4.25 ± 0.00a	3.56 ± 0.00e
NaCl + MeJa	14.22 ± 0.01b	4.24 ± 0.08b	3.40 ± 0.01ab	3.35 ± 0.00d

4. Discussion

Salinity is an important problem that affects the growth and development of plants. Halophytes have been suggested as new crops for foodstuffs due to their development of different strategies to cope with salt stress [34,35,51]. In *C. maritimum*, physiological aspects of salt response were determined via salt (NaCl) concentrations ranging from 0 to 300 mM [52]. The results showed almost a 50% reduction in the leaf dry weight at 150 mM NaCl with respect to 0 mM. Moreover, in our work, a 150 mM NaCl treatment reduced leaf biomass of *C. maritimum* plants grown in a hydroponic floating system. However, the studied genotype can be considered as a facultative halophyte since the plants did not need salt to grow and the total plant DW increased under salinity. Leaf plant biomass reduction was in consonance with previous reports, where *C. maritimum* plants irrigated with NaCl, from 100 to 500 mM NaCl, reduced their shoot fresh and dry weights [52], even at moderate (150–170 mM) NaCl concentrations [52,53].

By contrast, root length, root area, and root volume were significantly higher after NaCl treatment in comparison to the rest of treatments. The MeJa only application reduced *C. maritimum* total biomass. It was reported that exogenous application of MeJA decreased photosynthesis [54] and inhibited plant growth [55]. However, MeJa addition contributed to minimize the adverse effect of salinity on shoot biomass (Figure 1). Although it is known that MeJa alleviated the salt stress in glycophyte plants such as rice (*Oryza sativa* L.) [56] and *B. napus* [57], less is known about the addition of MeJa under salinity in halophyte plants. In *Limonium bicolor* (Bunge) Kuntze, exogenous 0.03 mM

jasmonic acid (JA) improved plants biomass after 300 mM NaCl addition, demonstrating that the most relevant physiological parameter involved in plant growth and salt tolerance by MeJa was the net photosynthesis [58], but other mechanisms of MeJa for salt stress alleviation cannot be ruled out in *C. maritimum* plants. Thus, changes in trichome and cuticle composition and thickness, and stomatal density are induced by MeJa [59] and may protect plants from salinity through the observed increase in the leaf hydraulic content as Na concentration increased, but further research is needed. Considering the recent interest in this halophyte as a traditional agri-food product, increasing the edible plant parts by MeJa under salinity has given rise to great interest.

It is well known that salinity may restrict the mineral uptake by the roots [60]. This was the case of several cations as Ca^{2+} and K^+ , demonstrating that limitation in the nutrient uptake may contribute to the general decrease in aerial growth. Ben-Hamed et al. [34] found a gradual reduction of Ca^{2+} and K^+ ions with increasing salinity, the decrease being higher in the leaves and stems when compared to the root. MeJa recovered Ca^{2+} and K^+ ions levels in the leaves of the plants treated with salinity, emphasizing the important role of MeJa on K homeostasis under salt stress [61,62] in *C. maritimum* plants.

It was shown that MeJa may increase root hydraulic conductance in maize [63] and tomato plants [64]. Therefore, a higher water uptake may result in higher Ca^{2+} and K^+ uptake and translocation. This effect of MeJa on ion transport in NaCl + MeJa plants may explain the recovery of Ca^{2+} and K^+ ions and the unmodified K/Na ratio compared to NaCl-treated plants, since it is well established that there are negative effects from salt stress on the coupled water and ion transport [65]. Moreover, these Ca and K increases may add nutritional value to the leaf mineral content of the plants.

In carrot plants, MeJa-induced changes improved mineral balance under salt stress through a reduction in Na^+ and Cl^- accumulation [66]. However, in our experiment, Na^+ and Cl^- content were similar in the leaves of NaCl and MeJa + NaCl treated plants, indicating that the effect of MeJa in saline ions uptake is species-dependent. In addition, a high correlation (0.926) between the leaf hydric content and Na accumulation was found (Figure 2). Osmolyte concentration in the leaves of the sea fennel was significantly raised with increased time periods and NaCl concentrations [40] and, therefore, leaf succulence could also be increased, contributing as a mechanism to cope with salt stress in our plants.

As a facultative halophyte, *C. maritimum* may tolerate Na^+ and Cl^- concentrations that could be compartmentalized in the vacuole [51]. In tomato plants, a higher Cl^- content induced the reduction of nitrate uptake [67]. By contrast, in sea fennel plants the levels of NO_3^- were similar in all treatments, indicating the lack of competence of Cl^- concerning NO_3^- translocation, but NaCl treatment reduced NO_2^- content. MeJa addition restored the level of NO_2^- as well as increased the NH_4^+ levels of Control1 and Control2 plants. This effect of MeJa was described previously for *Vaccinium myrtillus* L. plants, where MeJa up-regulated genes were involved in nitrite transport and metabolism [68]. There is a lack of literature on the effect of MeJa on halophytes, to the best of our knowledge. The existing study reports point to the combined effect of MeJa to salinity on *C. maritimum* plants, but similar gene-regulation in nitrogen metabolism could occur. In any case, from a nutritional point of view, the level of nitrate ions was lower than those of other baby leaf crops such as lettuce (from 700 to 1264 mg kg^{-1} FW), spinach (from 700 to 2013 mg kg^{-1} FW), kale (from 600 to 1181 mg kg^{-1} FW), and chard (from 900 to 1024 mg kg^{-1} FW) [69]. Similarly, low levels of nitrite were detected in lettuce and spinach (up to 197.5 mg kg^{-1}) [70]. The acceptable daily intake (ADI) for nitrate, as determined by the Scientific Committee on Food (SCF), was 0 to 3.7 mg/kg body weight per day. This means that if the average adult consumes approximately 400 g of various vegetables daily, the intake of nitrate is around 222.0 mg/day (FAO/WHO 2013). In this sense, the consumption of 100 gr of *C. maritimum* baby leaf plants do not reach the ADI for nitrate and nitrite.

In studies with halophytes, fatty acid unsaturation is intrinsically high, considering a mechanism of halophytes to high salt stress adaptation [71]. According to this, the higher content of individual fatty acids in this plant was found for linoleic and linolenic acids.

However, in spite of being a halophyte, the *C. maritimum* fatty acids content increased under salinity conditions, indicating a certain lipid metabolism adaptation, although the DBI remained unmodified. Ben Hamed et al. [72] found that in *C. maritimum* plants salinity decreased the percentage of unsaturated fatty acids (C18:3) and increased the percentage of unsaturated fatty acids (C18:2). In another halophyte, *Cakile maritima* Scop., no change in the unsaturation level was observed under salinity as an indication of plant adaptation to salt stress [71]. These differences may reflect the distinct nature of halophytes and their threshold for salt sensibility. In our experiment we observed that *C. maritimum* plants membrane fluidity properties, reflected in the unsaturation degree, seem to be stable under salinity, indicating a genotype adaptation. Moreover, linolenic acid was related to membrane fluidity properties [73], and the reduction of the percentage of this fatty acid from 38 to 34.8% in NaCl-treated plants after MeJa addition may indicate the amelioration of MeJa considering the salt effect on lipid membrane properties. From a nutritional point of view, the analysed treatments characterise these plants as a rich source of essential fatty acids (18:2v6 and 18:3v3), which are involved in human metabolism in consonance with previous results [74], but reductions of omega 3 acids by MeJa spraying to saline plants also have to be considered.

Moreover, a high content of phenolic compounds has been determined in the aerial part of *C. maritimum* plants when compared to other crops. Other vegetables such as caraway (770 GA mg kg⁻¹ FW), chives (567 GA mg kg⁻¹ FW), cowpea (717 GA mg kg⁻¹ FW), pak choi (820 GA mg kg⁻¹ FW), and perilla leaf (687 GA mg kg⁻¹ FW) [75] showed lower levels of total phenolic compounds than the *C. maritimum* plants grown in our experiment. Thus, although both saline treatments, NaCl and NaCl + MeJa, decreased the content of the total phenolic compounds in terms of Control1 and Control2, the plants maintained their antioxidant properties. However, in sweet basil (*Ocimum basilicum* L.) MeJa alleviated the effects of salinity stress on phenolic compounds [59,76]. Moreover, in *Lepidium sativum* L., MeJa acted as a signalling molecule to enhance antioxidant pool and protect plants against injuries caused by Cu toxicity [77]. Del Amor and Cuadra-Crespo [78] observed that after foliar application of MeJa, broccoli plants enhanced salt tolerance effects through growth, photosynthesis, and root respiration increase. These results demonstrated that exogenous JA may be involved in the defence not only during biotic stress, but also during salt stress.

In our plants the total phenolic compounds and antioxidant capacity remained unmodified by the MeJa only addition. Phenolic plant production also depends on the stress intensity and duration. Thus, in our experiment, both 150 mM NaCl and MeJa induced a flavonoid increase rather than total phenolic compounds. A similar result was observed in *Hibiscus sabdariffa* L. seedlings, where flavonoids increased after MeJa application at 50 mM NaCl [79]. The role of JAs in the antioxidant response of halophytic plants to salt stress is still poorly understood and more research is required.

Finally, the effects of salinity stress on chlorophyll a, chlorophyll b and carotenoid were depreciable in comparison with Control1 and Control2. A similar situation was observed in maize (*Zea mays* L.) plants [80]. However, in different *Brassica oleracea* L. varieties, seed priming with distinct MeJa and JA concentrations had an increase or decrease in the Chla/b ratio, indicating the dose and genotypic dependence of MeJa's effect on photosynthesis and PSII protein complex [81]. As the effect of MeJa on the photosynthetic machinery of the halophytes has not yet been studied, new experimentation is required.

5. Conclusions

In summary, MeJa alleviated the adverse effects of salinity on shoot growth, improving edible biomass after NaCl addition in sea fennel plants. This resulted in an increased ratio of the edible parts of this crop. Moreover, MeJa spraying favoured an enhanced Ca²⁺ and K⁺ uptake under salt stress, but it could not prevent Na⁺ translocation to the aerial part. Thus, the beneficial effect of MeJa on plant growth was not related to the Na⁺ toxicity and seemed to be in consonance with the transport of other ions. In fact, the strong relation

between the leaf hydric content and leaf Na levels suggest leaf succulence and osmolyte accumulation as mechanisms to cope with salt stress. From a nutritional point of view, the content of fatty acids was high in *C. maritimum* baby leaf, with linolenic and linoleic acids being the main fatty acids. However, reductions in omega 3 acids by MeJa spraying under salinity conditions must be considered when MeJa was applied to reduce adverse effects of salt stress on aerial growth. All the above results indicate that a hydroponic floating system was a suitable method for growing *C. maritimum* baby leaf, where the addition of MeJa spraying to saline seedlings may alleviate adverse effects of salt stress, does not affect the total phenolic compounds and antioxidant capacity of the plants, but increases total carotenoids and minerals.

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