

Salt response of *Crithmum maritimum*, an oleagineous halophyte

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Abstract: *Crithmum maritimum* is a perennial Apiaceae growing naturally in rocky coasts. The oil extracted from its seeds seems to be convenient for human consumption. Physiological aspects of its salt response were studied in a laboratory with NaCl concentration ranging from 0 to 300 mM. The results show that *C. maritimum* is a facultative halophyte, since it does not require salt for maximal growth. Fifty percent reduction in shoot DW, leaf surface area and leaf number were observed at 150 mM NaCl, indicating that *C. maritimum* is moderately tolerant to NaCl. Culture in the presence of NaCl led to large accumulation of Na⁺ and Cl⁻ in leaf tissues, without significant change in leaf water content. Thus, *C. maritimum* seemed to be able to sequester salt in leaf cells for osmotic adjustment. Indeed, the mean salt concentration in leaf tissue water was always higher than medium osmolarity. Growth was limited mainly by salt-induced decrease in the number of leaves. Biomass production per unit of leaf surface area was diminished only at highest salt concentrations. The presence of NaCl in the medium imposed a strong restriction in nutrient (K⁺ and Ca²⁺) acquisition, which was due to inhibition of both root intrinsic performance for ion transport and root growth. In summary, salinity restricts *C. maritimum* growth through limitation of mineral nutrient acquisition, rather than osmotic and ionic deleterious effects.

Resumen: *Crithmum maritimum* es una Apiaceae perenne que crece en costas rocosas. El aceite extraído de sus semillas parece ser adecuado para el consumo humano. Se estudiaron aspectos fisiológicos de su respuesta a la sal en el laboratorio, usando concentraciones de NaCl que fluctuaron entre 0 y 300 mM. Los resultados muestran que *C. maritimum* es una halófito facultativa, ya que no requiere sal para alcanzar su máximo crecimiento. Se observó una reducción de 50% en el peso seco de la parte aérea, en el área foliar y en el número de hojas a una concentración de 150 mM NaCl, lo cual indica que *C. maritimum* es moderadamente tolerante al NaCl. El cultivo en presencia de NaCl produjo una fuerte acumulación de Na⁺ y Cl⁻ en tejidos foliares, sin cambios significativos en el contenido de agua en la hoja. Por lo tanto, *C. maritimum* pareció ser capaz de secuestrar sal en células foliares para el ajuste osmótico. De hecho, la concentración media de sal en el tejido foliar fue siempre superior que la osmolaridad promedio. El crecimiento estuvo limitado principalmente por un decremento en el número de hojas inducido por la sal. La producción de biomasa por unidad de área foliar se vio reducida solamente con las concentraciones salinas más elevadas. La presencia de NaCl en el medio impone fuertes restricciones en la adquisición de nutrientes (K⁺ y Ca²⁺), lo cual se debió a la inhibición tanto del desempeño intrínseco de la raíz para el transporte de iones, como del crecimiento radicular. En resumen, la salinidad restringe el crecimiento de *C. maritimum* a través de la limitar la adquisición de nutrientes minerales, más que por efectos deletéreos osmóticos e iónicos.

Resumo: A *Crithmum maritimum* é uma Apiaceae perene vegetando naturalmente nas costas rochosas. O óleo extraído das suas sementes parece ser conveniente para o consumo humano. Os aspectos fisiológicos da sua resposta ao sal foram estudados em laboratório sob concentrações de NaCl variando entre 0 a 300 mM. Os resultados mostram que a *C. maritimum* é

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uma halófita facultativa, já que não requer sal para o crescimento máximo. Verificou-se uma redução de cinquenta por cento no lançamento DW, na superfície das folhas e no número de folhas a 150 mM de NaCl, indicando que a *C. maritimum* é moderadamente tolerante ao NaCl. A cultura, na presença de NaCl, conduziu a uma grande acumulação de Na⁺ e Cl⁻ nos tecidos foliares, sem mudanças significativas no teor de água na folha. Assim, a *C. maritimum* parece ser capaz de sequestrar sal nas células das folhas por ajustamento osmótico. Assim, a concentração média de sal na água dos tecidos das folhas foi sempre maior que as osmolaridade média. O crescimento foi limitado principalmente pelo decréscimo induzido pelo sal no número de folhas. A produção de biomassa, por unidade de área superficial da folha, só diminuiu às maiores concentrações de sal. A presença de NaCl no meio impôs uma forte restrição na absorção de nutrientes (K⁺ e Ca²⁺), a qual foi devida à inibição, quer da performance intrínseca da raiz para o transporte de iões, quer do crescimento da raiz. Em síntese, a salinidade restringe o crescimento da *C. maritimum* através da limitação da absorção de nutrientes e não pelos efeitos iônicos e osmóticos nocivos.

Key words: *Crithmum maritimum*, halophyte, ion content, leaf surface area, NaCl, net assimilation ratio, relative growth rate, salt tolerance.

Introduction

Salinity is a widespread problem leading to decreased yields in irrigated agriculture, which counteracts the purpose of irrigation (Scheumann 1997). Moreover, because management of agricultural salinization involves periodic leaching of salts, this creates poor-quality drainage water, which enters natural water reservoirs of fresh water. The standard approach to this issue would be to increase salt tolerance of crop species, but its current success remains limited. An alternative approach is to make use of those plants that have high tolerance for salinity *i.e.* halophytes. In halophytes, the complex of characteristics required for salt tolerance is already present, and all that is needed is to make an optimal use of these species. Increasing attention is paid to halophytes. A list of more than 2 600 halophytic species was recently published by Menzel & Lieth (1999). Several authors proposed large scale use of non-diluted seawater for irrigation (Koyro & Huchzermeyer 1999; Sleimi *et al.* 1999). However, halophytic species differ in their degree of salt tolerance. It is, therefore, important to select promising plants with adequate yield and tolerance characteristics (Koyro 1997). One aim of current studies dealing with salt tolerance is to determine the level of salinity tolerance of a number of halophytic species and to study the mechanism by which the plants survive high salinity.

Crithmum maritimum L. ('sea fennel' or 'samphire') is a spontaneous plant of the family Apiaceae, the geographical distribution of which extends along the European Atlantic coasts, Azores, Madeira and Canary islands, Mediterranean and Black Sea coasts, NW Africa and W Asia. It grows in rocky sea-cliffs under the influence of salt-rich sprays. It is rarely found on sand or gravel (Pateira *et al.* 1999). The flowering period of this taxon ranges from May to October. Several uses of *C. maritimum* are known for culinary purposes and its leaves have been used for aromatic and medicinal purposes as a tonic and diuretic (Ruberto *et al.* 2000). We have shown that oil extracted from *Crithmum* seeds is of good nutritional quality, and could be used for human consumption (Zarrouk *et al.* 2003).

The experiments reported here assessed NaCl tolerance of *C. maritimum*. Growth parameters, water content, tissue ion contents (Na⁺, Cl⁻, K⁺ and Ca²⁺) were determined for plants cultivated on sand in greenhouse, and irrigated with nutritive solution containing NaCl (0 - 300mM).

Materials and methods

Plant material and treatment

C. maritimum seeds were collected in September from their native salty ecosystem, close to the Mediterranean sea coast (Korbous, 40 km S-E of

Tunis). They were sown in pots (two seeds per pot) filled with sand, and irrigated with distilled water until germination. At the early developmental stages, seedlings were watered once per day with a nutrient solution (Hamza 1977). Iron was supplied as an EDTA complex at $3 \mu\text{g Fe ml}^{-1}$. Two months-old seedlings were divided in 6 lots of 10 plants each, and NaCl was introduced in the irrigation medium at different concentrations (0, 50, 100, 150, 200, and 300 mM). To avoid osmotic shock, the change to salinity treatment was gradual, with 50 mM NaCl daily increments.

Experiments were performed in a greenhouse under controlled conditions ($25 \pm 5^\circ\text{C}$ and $60 \pm 10\%$ relative humidity). Plants were harvested at the beginning of the salt treatment and after 5 weeks of exposure to salinity. Leaves, stems and roots were harvested separately.

Growth measurements

Growth parameters were organ fresh weights (FW) and dry weights (DW, measured after 96 h at 80°C), and leaf surface area (LiCor areameter). Mean relative growth rate (RGR) and net assimilation ratio (NAR) (Abdelly *et al.* 1995, 1996; Hunt 1990) were estimated as follows:

$$\text{RGR} = (\ln(DW_2) - \ln(DW_1)) / \Delta t$$

where, DW_1 and DW_2 correspond to initial and final harvests, respectively, and Δt is the treatment duration.

$$\text{NAR} = (DW_2 - DW_1) / LA \Delta t$$

where, LA stands for the logarithmic mean leaf area calculated over the treatment period:

$$LA = (LA_2 - LA_1) / (\ln A_2 - \ln A_1)$$

LA_1 and LA_2 corresponding to initial and final leaf surface areas, respectively.

Nutrient (K^+ and Ca^{2+}) uptake and use efficiencies were calculated from K^+ and Ca^{2+} amounts in whole plant K^+ and Ca^{2+} (WPA):

$$\text{Ion uptake efficiency} = \text{WPA} / \text{Root DW}$$

$$\text{Ion use efficiency} = \text{Plant DW} / \text{WPA}$$

where, DW stands for the logarithmic mean $DW = (DW_2 - DW_1) / (\ln DW_2 - \ln DW_1)$.

Ion content determination

Ions were extracted in 0.5% (v/v) HNO_3 . After filtration, Na and K were assayed by flame emission photometry (FES) (Corning, UK). Ca was assayed by flame atomic absorption spectrophotometry (AAS) at 427 nm (Instrumental laboratory,

USA). Cl^- was determined by coulometry with a Haake Büchler Chloridometer.

Results and discussion

Growth

Final biomass declined regularly from *ca.* 13 to *ca.* 1 g DW per plant when NaCl concentration was increased from 0 to 300 mM (Fig. 1A). This growth response was approximately the same for both root and shoot, as illustrated by the relative stability of shoot to root ratio. Both total leaf surface area and leaf number paralleled whole plant biomass (Fig. 1B). Salt treatment did not result in strong reduction of mean surface area of individual leaves, except at 300 mM NaCl, which treatment severely limited leaf expansion (Fig. 1B). However, at this salt concentration, plants did not exhibit any

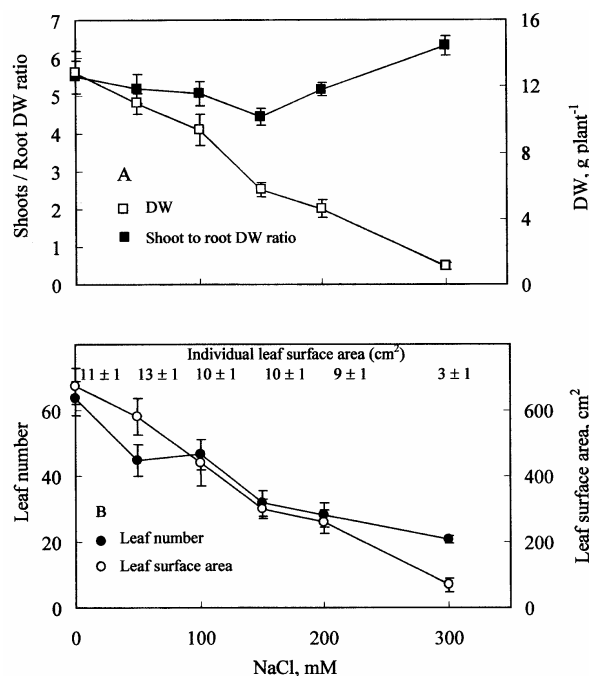


Fig. 1. Effect of NaCl on plant growth. A: whole plant dry weight and shoot to root DW ratio were determined at the final harvest, after two months of culture in the presence of the indicated NaCl concentrations. Means of 10 replicates and confidence limits for $p = 0.05$. B: leaf number and total leaf surface area per plant. Values of individual leaf surface area at the top of the panel are expressed as cm^2 per leaf (means of 10 replicates and confidence limits for $p = 0.05$).



Fig. 2. *Crithmum maritimum* plants at the final harvest. From left to right, the NaCl concentrations in the culture medium are : 0, 50, 100, 150, 200, and 300 mM.

symptom of toxicity such as chlorosis or leaf necrosis (Fig. 2).

From these results, *C. maritimum* should be considered a facultative halophyte with growth decreasing in response to rising NaCl levels in the medium. The presence of thriving populations of *C. maritimum* in the vicinity of the sea may be explained by the characteristics of the microhabitat of this species. It is always found in cracks of rocks or cliffs, a situation which probably limits rhizosphere salinization by authorizing the leaching of salt. Of course, one cannot discard the possibility that other differences between *C. maritimum* natural habitat and our study conditions, such as light intensity or root aeration, should be responsible for the sensitivity to NaCl observed in greenhouse.

Accumulation of dry matter during the salt treatment period depends on both the initial size of plants and the growth activity (Hunt 1990). Mean relative growth rate (RGR), is a convenient mean to isolate the effect of salt on the growth activity. RGR depends on leaf area and its intrinsic capacity of carbon assimilation (Cramer *et al.* 1990). The latter, commonly named net assimilation ratio (NAR), corresponds to the rate of biomass production per unit of leaf surface area (Abdelly *et al.* 1995). In the lower range (0 - 100 mM) of NaCl concentrations, RGR was positively correlated with leaf surface area (Fig. 3A) and independent from NAR (Fig. 3B). At higher NaCl concentrations (150 - 300 mM), RGR was positively correlated with both leaf surface area and NAR. Thus, at lower NaCl concentrations, growth rate was limited by the development of the photosynthetic organs, but not by their specific photosynthetic capacity. At higher concentrations, RGR depended simultaneously on leaf expansion and assimilation capacity.

Reduction of NAR at higher salinity levels could result from a decrease in photosynthesis and/or an

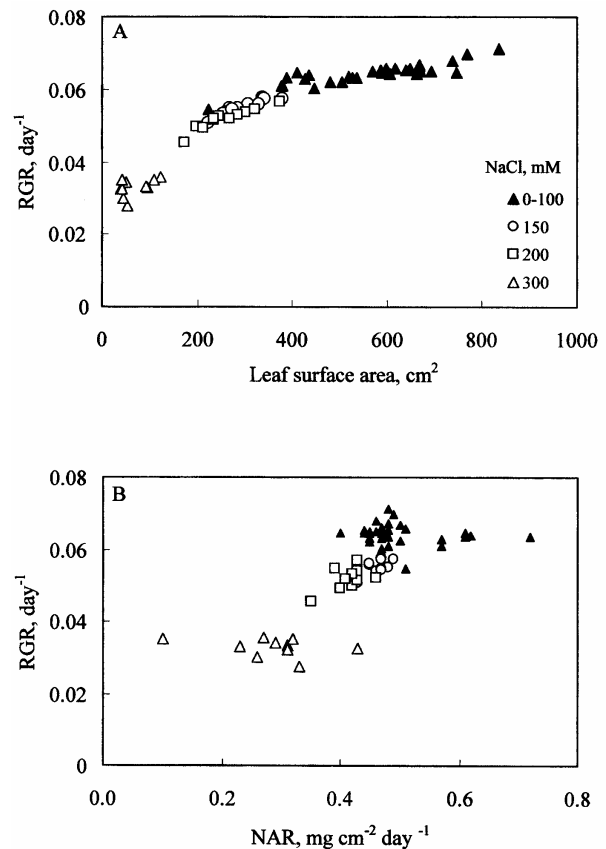


Fig. 3. Relationship between whole plant growth rate and leaf development. RGR is the whole plant relative growth rate. Inserts: symbol keys to NaCl concentrations in the medium. A: Leaf surface area is the total leaf surface area per plant. B : NAR is the net assimilation ratio, i.e. the rate of increase in whole plant biomass per unit of leaf surface area during the salt treatment.

increase in maintenance respiration. These changes could be the consequences of the build-up of Na^+ and Cl^- at high concentrations in leaves (see below).

Our results are in agreement with several other data. Comparing the physiological responses to salt of 4 halophytes (*Aster tripolium*, *Spartina anglica*, *Puccinellia maritima* and *Elymus pycnanthus*), Rozema & Van Diggelen (1991) observed that the decrease of net photosynthesis per unit of leaf surface area was not the main factor responsible of the growth reduction. The same result was observed in *Spartina alterniflora* (Sleimi 2002) and in some spontaneous *Medicago* species (Abdelly *et al.* 1995). Ball (1988) found that the growth reduction of a salt-stressed mangrove species could be attributed entirely to a decrease in leaf area ratio. Only at very high salinity level was NAR inhibited.

Na⁺ and Cl⁻ accumulation and water relations

Na^+ and Cl^- contents increased in both shoots and roots as NaCl concentration in the medium

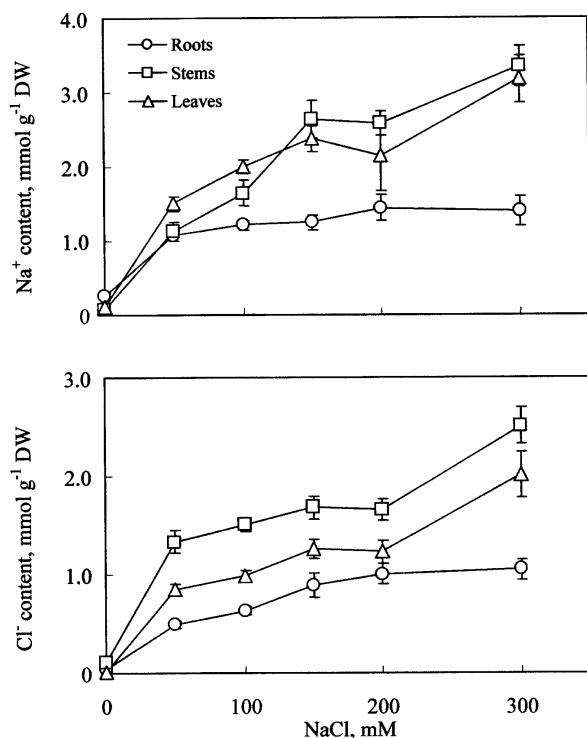


Fig. 4. Effect of salinity on sodium and chloride accumulation. The contents were measured at the end of the salt treatment. Means of 10 replicates and confidence limits for $p = 0.05$.

was changed from 0 to 300 mM NaCl (Fig. 4). For all treatments, contents in Na^+ and Cl^- were significantly higher in shoots than in roots. For Na^+ , values higher than 3 mmol g^{-1} DW were reached in leaves at 300 mM NaCl. Furthermore, Na^+ content systematically exceeded Cl^- content.

Hydric status and ion accumulation

The leaf water status was poorly sensitive to the treatments. Even at the highest NaCl concentrations in the medium, the water content of leaves was maintained at value close to that of control (range of variation: 6.0 to 6.5 ml g^{-1} DW). When the NaCl concentration in medium was increased from 0 to 300 mM, the leaf Na^+ content augmented from 0.15 to 3.2 mmol g^{-1} DW (Fig. 4A). One may estimate the mean Na^+ concentrations in leaf tissues by dividing these values by the corresponding water contents. At 300 mM NaCl, the mean Na^+ concentration in leaves amounted to 460 mM. The maintenance of leaf hydration in spite of such a high Na^+ accumulation (Fig. 5) indicates that much of Na^+ in leaves was osmotically active. Thus, it was probably accumulated inside cells. The same conclusion applies for Cl^- (not shown).

Because enzymes from halophytes display the same sensitivity to high NaCl concentration as those of glycophytes, when assayed *in vitro*, it has been accepted that most of the accumulated Na^+ is excluded from the cytoplasm (Flowers *et al.* 1977). This has led to the concept of Na^+ compartmentalization within vacuoles, as an essential feature of

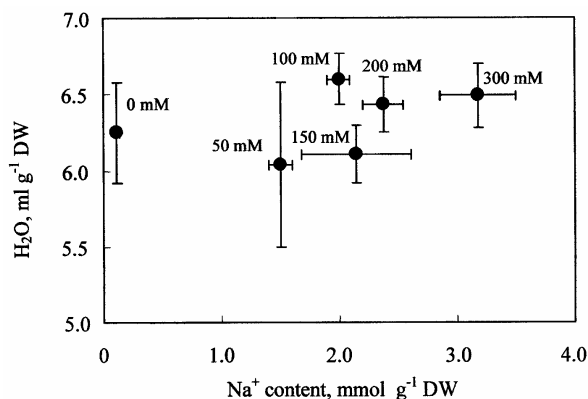


Fig. 5. Relationship between water content and Na^+ content in leaves. The contents were measured at the end of the salt treatment. Means of 10 replicates and confidence limits for $p = 0.05$. The numbers are the NaCl concentrations in the medium (mM).

halophytic plants (Serrano *et al.* 1999). As discussed above, the large Na^+ accumulation in *C. maritimum* leaves seemed to be intracellular. Thus it may be hypothesized that it was largely restricted to vacuoles.

On the presumption that K^+ , Na^+ , and Cl^- ions were accumulated as diffusible, osmotically active solutes, we approximated their contribution to osmotic adjustment by summing their calculated mean concentrations in leaf tissues (Fig. 6). Unknown anions supposed to be univalent (A⁻) were introduced to equilibrate the electrostatic net charge of ($\text{K}^+ + \text{Na}^+$) accumulated in excess over Cl^- . Although crude, this calculation evidences the role of Na^+ and Cl^- as main contributors to the osmotic adjustment at all NaCl concentrations. This is a classical halophytic trait.

Nutrient accumulation

In response to NaCl treatments, K^+ and Ca^{2+} contents were lowered in all parts of the plants (Fig. 7). The amounts of these ions absorbed by roots during the treatment period were estimated from changes in whole plant K^+ and Ca^{2+} between the initial and the final harvests.

In the presence of NaCl, the growth inhibition was associated with a decrease in K^+ and Ca^{2+} uptake (Table 1). This effect could result from two factors, namely (i) inhibition of root growth, and/or (ii) decreased intrinsic capacity of root for ion uptake (uptake efficiency). Uptake efficiency was es-

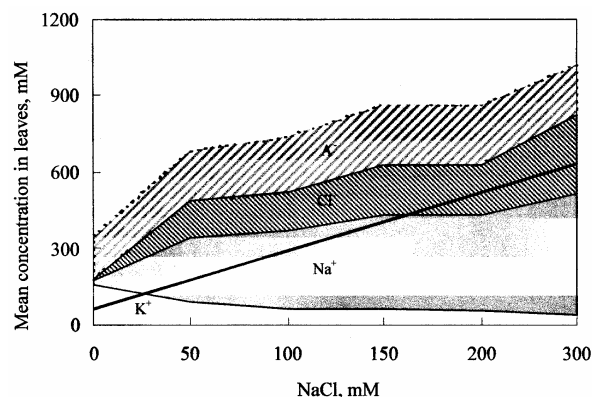


Fig. 6. Apparent mean ion concentration in leaves. The concentrations were estimated by dividing ion contents by water contents (data from Figs. 4 and 5). A⁻ stands for unknown anion, supposed univalent, needed to equilibrate the cation excess over Cl^- . The dark line is the osmolarity of the medium.

timated as the change in ion content of whole plant during the treatment period divided by the mean root DW calculated over this period (Table 1). The uptake could be expressed as $M = R \cdot E$, where R is the mean root DW and E is the uptake efficiency. Thus, any salt-induced change in M could be expressed as

$$\Delta M \approx R \Delta E + E \Delta R$$

where, Δ stands for difference of the corresponding quantity between two salt treatments. This analysis indicates that for both K^+ and Ca^{2+} , addition of 50 to 150 mM NaCl to the medium inhibited ion uptake mainly through uptake efficiency decrease. At higher NaCl concentrations, the restriction of root growth was the main factor responsible for uptake limitation. Fig. 8 illustrates these results for K^+ .

The causes of the sensitivity to NaCl of K^+ and Ca^{2+} uptake efficiency are not identified. One of them could be a direct competition between Na^+ and the other cations for root transporters. Spe-

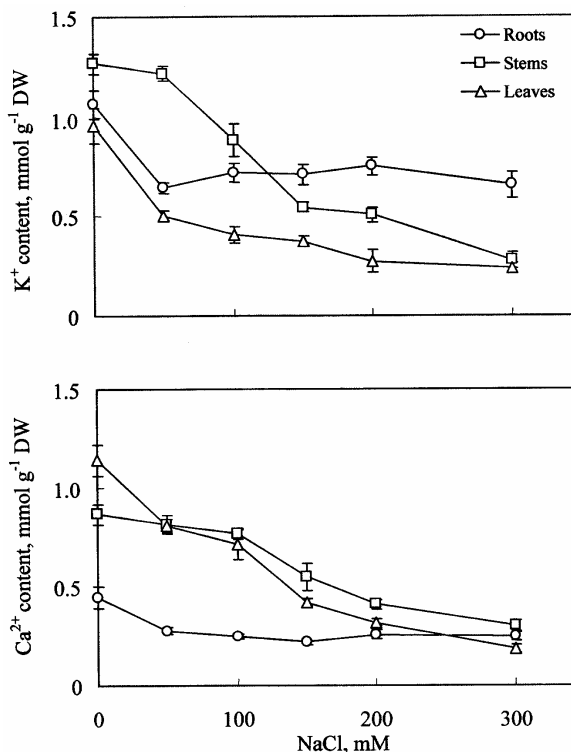


Fig. 7. Effect of salinity on potassium and calcium accumulation. The contents were measured at the end of the salt treatment. Means of 10 replicates and confidence limits for $p = 0.05$.

Table 1. Effect of salinity on K⁺ and Ca²⁺ nutrition. Uptake efficiency: change in the ion amount in whole plant over the treatment period rationed to the mean root DW. Use efficiency: whole plant biomass deposited per mmol of ion utilised. Means of 10 replicates and confidence limits (p= 0.05).

	NaCl, mM					
	0	50	100	150	200	300
	Whole plant DW (g plant ⁻¹)					
	12.9 ± 1.3	11.0 ± 0.6	9.4 ± 0.9	5.7 ± 0.4	4.61 ± 0.5	1.10 ± 0.2
	Mean root DW (g plant ⁻¹)					
	0.38	0.34	0.31	0.22	0.17	0.06
	Whole plant content (mmol plant ⁻¹)					
K ⁺	14.0 ± 1.0	8.5 ± 0.5	5.5 ± 0.6	2.6 ± 0.2	1.8 ± 0.2	0.3 ± 0.04
Ca ²⁺	11.8 ± 1.4	7.9 ± 0.4	6.0 ± 0.6	2.4 ± 0.2	1.5 ± 0.2	0.2 ± 0.04
	Uptake efficiency (mmol g ⁻¹ root DW)					
K ⁺	36.6	24.8	17.5	11.4	10.1	3.6
Ca ²⁺	30.8	23.0	19.1	10.5	8.3	2.0
	Use efficiency (g DW mmol ⁻¹)					
K ⁺	2.81 ± 0.1	4.37 ± 0.1	5.12 ± 0.2	5.92 ± 0.2	6.67 ± 0.2	9.41 ± 0.7
Ca ²⁺	4.36 ± 0.3	6.11 ± 0.2	6.8 ± 0.3	8.90 ± 0.2	9.54 ± 0.4	13.1 ± 1.3

cially for Ca²⁺, this effect is considered as an important factor of salt sensitivity (Davenport *et al.* 1997; Greenways & Munns 1980). Indeed, it is well known that enrichment of the medium in Ca²⁺ improve plant tolerance to salinity (Alberico & Cramer 1993; Cachorro *et al.* 1994). Furthermore,

the maintenance of K⁺/Na⁺ selectivity of root transport is under the control of Ca²⁺ (Lüttge & Laties 1967; Torii & Laties 1966) and Ca²⁺ must be present in the environment of the root cell membranes to ensure their correct functioning (Cramer *et al.* 1985, 1987). Thus, Na⁺ could limit K⁺ transport both by direct competition and through displacement of Ca²⁺.

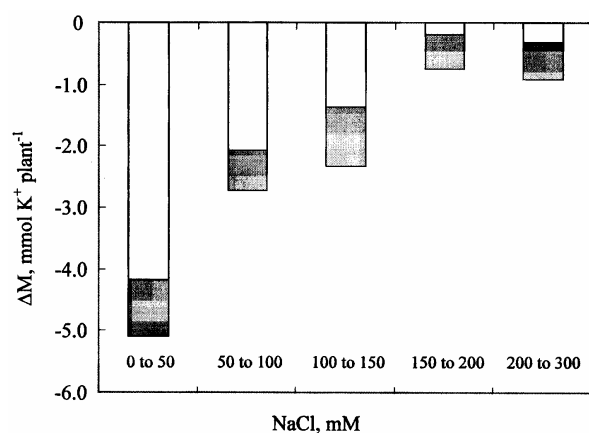


Fig. 8. Effect of salinity on K⁺ uptake. ΔM is the change in whole plant K⁺ due to salt treatment (difference between the control without NaCl and the treatment with the indicated NaCl concentration). ΔM results from (i) modification of root efficiency to transport K⁺, (white bars), and (ii) modification of root biomass (grey bars).

Conclusions

C. maritimum appears to be a facultative halophyte, since its maximum growth rate was obtained in the absence of NaCl. It displays a moderate tolerance to NaCl since the salt concentration leading to 50 % reduction in shoot DW, leaf surface area and leaf number was 150 mM NaCl. Salinity could have at least three different adverse effects, osmotic imbalance, ion toxicity and limitation of mineral nutrient acquisition (Niu *et al.* 1995). Osmotic imbalance is clearly not involved in *C. maritimum* growth reduction in the presence of salt. Indeed, no leaf dehydration accompanied salt accumulation. We observed no sign of toxicity, such as necrotic or chlorotic lesions in leaves, even at the highest levels of salt accumulation in these organs. Furthermore, growth seemed to be more limited by reduction in leaf surface area than by

inhibition of photosynthesis, since biomass production per unit of leaf surface area was diminished only at highest salt concentrations. Finally, the presence of NaCl in the medium imposed a strong restriction in nutrient (K^+ and Ca^{2+}) acquisition, which was due to inhibition of both root intrinsic performance for ion transport and root growth.

In summary, our results show that salinity restricts *C. maritimum* growth through limitation of mineral nutrient acquisition, rather than osmotic and ionic deleterious effects.

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