

¹Mediterranean Agronomic Institute of Chania, Chania, Greece

²Faculty of Agricultural Technology, T.E.I. of Epirus, Arta, Greece

Responses of lettuce (*Lactuca sativa* L. var. *longifolia*) grown in a closed hydroponic system to NaCl- or CaCl₂-salinity

Gokce Tas¹, Nicolas Papadandonakis¹, Dimitrios Savvas²

(Received April 6, 2005)

Summary

Lettuce plants (*Lactuca sativa* L. var. *longifolia*) grown in a closed hydroponic system using perlite as substrate were exposed to similar levels of NaCl- and CaCl₂-salinity in an attempt to distinguish between osmotic and salt-specific effects on plant growth and quality. A standard nutrient solution for lettuce (control) was compared with two salinity levels and each salinity level was imposed by adding either NaCl or CaCl₂ to the standard nutrient solution. The mean electrical conductivity in the root zone, as indicated by the values measured in the drainage solution, was 2.5, 3.7, 3.5, 5.6 and 5.4 dS m⁻¹ in the control, the low NaCl-, the low CaCl₂-, the high NaCl- and the high CaCl₂-salinity treatment, respectively. The increase of NaCl-salinity in the root zone restricted the shoot growth of lettuce. In contrast, the CaCl₂-salinity had no significant effect on the above-ground growth of the plants. The root growth was not affected by any salinity treatment. The leaf Cl concentration was increased in all salinity treatments but the NaCl-salinity resulted in significantly higher Cl levels in leaf compared to CaCl₂-salinity at similar Cl concentrations in the root zone. The leaf Mg concentration was decreased in all salinity treatments but the most marked suppression was observed at the highest CaCl₂- level. The leaf K was restricted by salinity without significant differences between salinity levels and source. The leaf chlorophyll and ascorbic acid concentrations were not affected by either of the salinity treatments. It was concluded that the effects of salinity on lettuce are primarily Na-specific.

Introduction

The expansion of modern agricultural technology has enormously increased crop productivity, but in most cases this was accompanied by a corresponding increase of water consumption in agriculture. However, the irrigation water resources of good quality, characterized by low salt content, are limited. As a consequence, water with relatively high salt concentration is increasingly used to irrigate crop plants. In most cases, the dominating salt cation is Na, but Ca and Mg may be also in excess in the irrigation water, especially in semi-arid regions with high solar irradiation (SONNEVELD, 2000; URRESTARAZU and GARCÍA, 2000; SAVVAS et al., 2003). The accompanying anions are commonly Cl⁻, SO₄²⁻ and HCO₃⁻ (GRATTAN and GRIEVE, 1999). Many studies were concerned with the effects of salinity on horticultural crops and the mechanisms implicated in growth suppression caused by salinity (reviewed by GRATTAN and GRIEVE, 1999; SHANNON and GRIEVE, 1999; SONNEVELD, 2000; MUNNS, 2002). A major question raised in many of the studies concerned with salinity was the discrimination between osmotic and ion specific salt effects (LEVITT, 1980; SHANNON and GRIEVE, 1999). Osmotic effects are due to changes caused in the osmotic potential of the external solution in the root zone, and depend on the total equivalent salt concentration, regardless of salt species. In contrast, salt specific growth suppression is caused by one or more of the particular ions being in excess in the external solution. Osmotic effects are frequently confounded with specific effects, because in most cases high total salt concentrations

in the rooting medium are accompanied by unbalanced nutrient ratios (LAGERWERFF and EAGLE, 1961).

Lettuce is one of the most important vegetable plants worldwide, which is considered moderately sensitive to salinity (MAAS and HOFFMAN, 1977; SHANNON et al., 1983). However, the results reported by various investigators regarding the responses of lettuce to salinity are in some cases contradictory. Thus, SHANNON et al. (1983) reported a reduction of fresh weight at a rate of 4.5% for each unit of electrical conductivity (EC) increase above 4.6 dS m⁻¹, whilst TARAKCIOGLU and INAL (2002) found no significant effect of salinity increase up to 7 dS m⁻¹ on lettuce grown in solution culture. In field grown lettuce, AYERS et al. (1951) found a salinity threshold EC in the saturation extract of 1.3 dS m⁻¹ and a slope of 13% in yield decrease above that level, while PASTERNAK et al. (1986) reported that yield and quality of iceberg lettuce was not affected by sprinkling with irrigation water having an EC of 4.4 dS m⁻¹. The above disagreements may originate from differences in both the salts involved in the total salt concentration and the cultivated varieties tested. Indeed, SHANNON et al. (1983) have shown that lettuce cultivars exhibit considerable differences in inherent salt tolerance.

In view of the above background, the present investigation was designed to study the responses of Romaine-type lettuce, which occupies a considerable growing area in some Mediterranean countries, to low and moderate salinity levels, and to assess whether possible growth suppressions are due to specific Na toxicity or due to other toxicity or osmotic stress. To attain this goal, lettuce plants were grown in isosmotic salinity levels achieved by adding either NaCl or CaCl₂ to a basic nutrient solution used as control treatment.

Materials and methods

The experiment was conducted in a glasshouse at the Mediterranean Agronomic Institute of Chania, Greece. Seedlings of Romaine type lettuce (*Lactuca sativa* L. var. *longifolia*) at the 3-leaf stage were planted on 11 June 2004 in opaque, polyethylene bags containing perlite. Excess heating was prevented using automatic shade screens on the top of the greenhouse.

Nutrient solution was automatically prepared by means of a computer controlled installation and supplied to the plants via a drip irrigation system. Five separate fertigation ducts were connected to the controlling system, which enabled automated preparation and supply of five different nutrient solutions to the plants (experimental treatments). Four replications per treatment were established in a completely randomized experimental design. Each experimental plot included 12 lettuce plants. Spacing between plants within a row was 30 cm.

A standard nutrient solution for lettuce with an electrical conductivity of 2.2 dS m⁻¹, corresponding to a control treatment, was compared with 4 salinity treatments. The latter were obtained by adding either NaCl or CaCl₂ at equal doses (on chemical equivalent basis) to the standard nutrient solution up to two target EC levels (3.2 and 4.8 dS m⁻¹). All EC values were measured at 25 °C. Ten days after planting, recycling of the drainage solution was initiated according to the

method of reference nutrient solution proposed by SAVVAS and MANOS (1999) and SAVVAS (2002). This method is based on replenishment of nutrient uptake in the recycling nutrient solution at constant nutrient ratios but varying absolute doses depending on the on-line measured volume and EC of the recycled drainage solution. The nutrient ratios in both the standard nutrient solution and the reference nutrient solution used after recycling initiation to replenish plant uptake were as suggested by DE KREIJL et al. (1999) for closed systems. The pH of the solution supplied to the plants was set at 5.6. After initiation of recycling, the pH and the EC of the drainage solution were daily monitored throughout the cropping period, while the macro- and micronutrient concentrations in both the drainage water and the nutrient solution supplied to the crop were measured at fortnight intervals after planting to prevent nutritional imbalances.

Harvesting of the commercially ripe plants took place on 19 July 2004. To assess the influence of the treatments on plant growth, both the above-ground plant part (shoot) and the root of all plants from each plot were separately weighed. Furthermore, the shoot of 2 randomly selected plants from each plot was dried at 105 °C to constant weight and then weighed to determine the dry to fresh weight ratio.

To determine the effects of NaCl- and CaCl₂-salinity on nutrient uptake, all leaves of a randomly selected plant per plot were dried at 65 °C for 48 h and then ground to pass a 40 mesh sieve. Subsequently, 0.5 g of the ground material was used to determine the Na, Ca, Mg, K, and P concentrations by employing inductively-coupled plasma atomic emission spectroscopy (ICP-AES, Leeman Labs Inc, PS 1000 AT) after dry ashing at 600 °C for 4 hours and extraction by means of 2 N HCl. Chloride was extracted from 0.25 g of ground plant material using water at 85 °C and measured by titration with 0.1 N AgNO₃ in the presence of K₂CrO₄ (EATON et al., 1995). Moreover, the concentration of organically-bound N in leaf was determined by Kjeldahl digestion (MILLS and JONES, 1996). The ICP-AES instrument was also used to measure at fortnight intervals the macro- and micronutrient concentrations in the nutrient solutions (except NO₃⁻ which was measured by ion selective electrode and Cl⁻ which was measured as described above).

To determine the influence of the salinity treatments on the leaf chlorophyll content, an external leaf was sampled from a randomly selected plant per experimental unit and then a leaflet of 0.5 g was obtained from a comparable position of each leaf. Subsequently, the extract obtained after grinding the leaflet in a mortar in the presence of 30 ml of acetone 80% and 0.1 g of CaCO₃ was used to determine chlorophyll a and b by a spectrophotometer (Hewlett Packard 8452A) at 663 and 646 nm, respectively. The concentration of vitamin C in lettuce leaf was determined as follows: a leaflet of 5 g was homogenized and vitamin C was extracted using 25 ml oxalic acid 1%. Subsequently, the extract was filtered and titrated by a dye solution, which was prepared by dissolving 84 mg of NaHCO₃ and 100 mg of 2,6-dichlorindophenol-indophenol sodium in 80 ml of distilled hot water (AOAC Method 967.21).

The data were subjected to one way analysis of variance and when a significant F test was obtained, all possible comparisons between the five treatment means were carried out by employing Duncan's Multiple Range Test ($P = 0.05$).

Results

The actual electrical conductivity in the nutrient solution supplied to the plants, which was prepared by recycling the entire amount of drainage water, was fluctuating close to the target values (Fig. 1a). In particular, the mean EC values were 2.2, 3.2, 3.1, 5.0, and 4.7 dS m⁻¹ in the control, the low NaCl-, the low CaCl₂-, the high NaCl- and the high CaCl₂-salinity treatments, respectively. The EC in the drainage solution of the salinity treatments was initially increasing but 20 days after planting a leveling out was observed (Fig. 1b). The mean EC

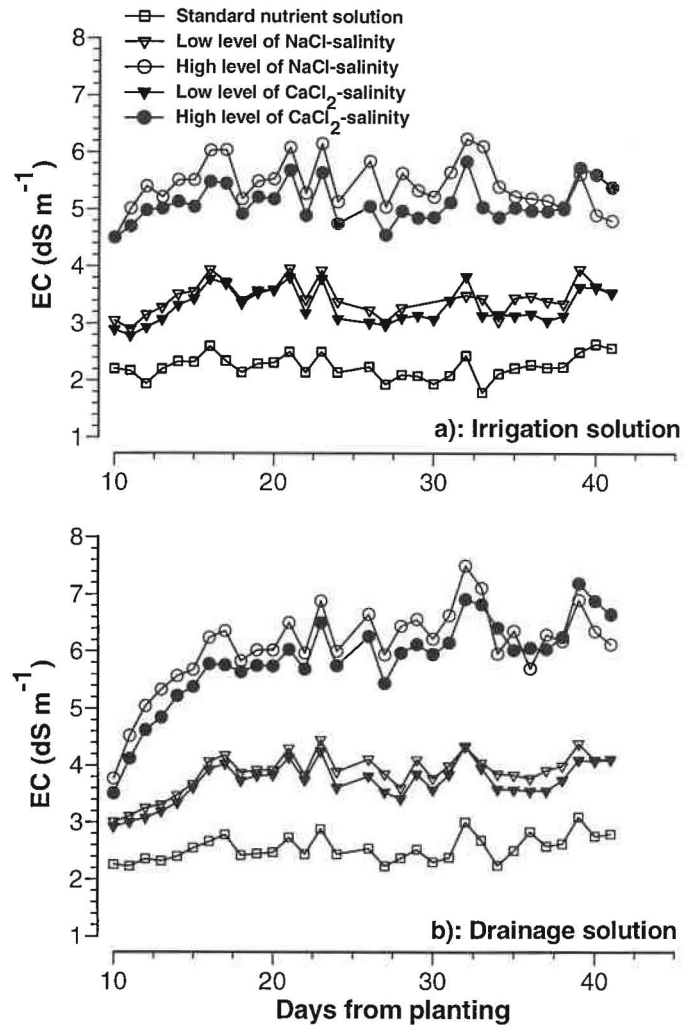


Fig. 1: Course of electrical conductivity (EC) a) in the irrigation nutrient solution and b) in the drainage solution originating from a lettuce crop grown in closed hydroponics as influenced by different salinity treatments.

values in the drainage water were 2.5, 3.7, 3.5, 5.6, and 5.4 dS m⁻¹ in the control, the low NaCl-, the low CaCl₂-, the high NaCl- and the high CaCl₂-salinity treatments, respectively.

Increasing the NaCl-salinity in the root zone restricted the shoot fresh weight of lettuce (Tab. 1). In contrast, the CaCl₂-salinity had no significant effect on lettuce growth. The shoot dry weight was

Tab. 1: Effect of salinity level and source (NaCl and CaCl₂) on growth of lettuce plants cultivated in a closed hydroponic system. Values are means of four measurements. In each column, values followed by the same letter do not differ significantly at $P = 0.05$.

Treatment	Shoot fresh wt. (g per plant)	Shoot dry/fresh wt.	Root dry wt. (g per plant)
Standard N.S.*	430.7 a	0.045 a	17.96 a
Low NaCl-salinity	325.6 b	0.046 a	16.56 a
High NaCl-salinity	265.4 c	0.052 ab	16.87 a
Low CaCl ₂ -salinity	402.5 a	0.051 ab	18.54 a
High CaCl ₂ -salinity	400.6 a	0.061 b	15.79 a

* N.S.: Nutrient solution

less severely affected by NaCl-salinity, as indicated by the shoot dry to fresh weight ratio. However, a significant increase of the shoot dry/fresh weight ratio with reference to the control treatment was observed only at the highest CaCl₂-salinity treatment. The root dry weight was not affected by any salinity treatment. To quantify the depressing effect of NaCl-salinity on lettuce growth, the linear model of MAAS and HOFFMAN (1977) was applied, which revealed a decrease in the shoot growth at a rate of 12.9% per unit of EC increase above 2.51 dS m⁻¹ (Fig. 2).

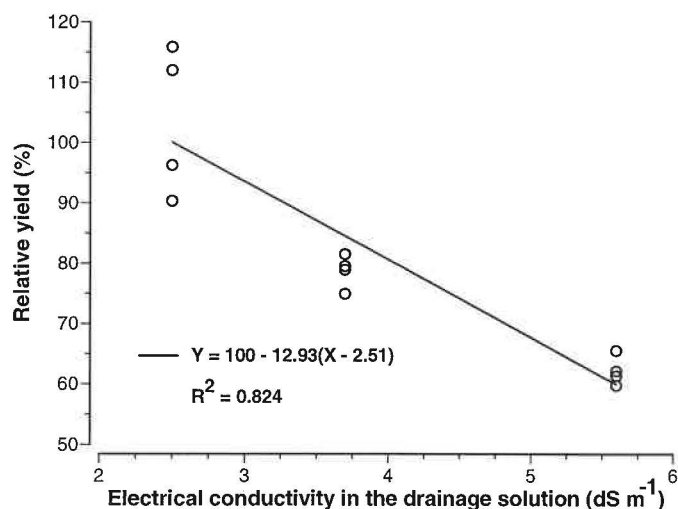


Fig. 2: Response of relative yield to increased electrical conductivity (EC) in the drainage solution due to accumulation of NaCl in the root zone of a lettuce crop grown in a closed hydroponic system. Relative yield was calculated from the fresh weight of lettuce plants grown with a standard nutrient solution.

The Na concentration in the shoot tissue was raised as the external NaCl-concentration increased (Tab. 2). The shoot Ca concentration was slightly increased by the CaCl₂-salinity, but the increase was significant only at the highest salinity level, while the NaCl-salinity suppressed the translocation of Ca to the shoot. The Cl concentration in the leaf of lettuce was increased by NaCl-salinity, while the CaCl₂-salinity enhanced significantly the leaf Cl only at the highest CaCl₂-concentration level in the root zone. The shoot Mg concentration was diminished by all salinity treatments but the most marked suppression was observed at the highest CaCl₂-level. The K concentration in the shoot tissue was restricted by salinity without significant differences between salinity levels and source. The shoot P concentration was also decreased by salinity without consistent differences between the two salinity sources, although at the low

Tab. 2: Effect of salinity level and source (NaCl and CaCl₂) on macronutrient concentrations (mmol g⁻¹ dry wt.) in leaf of lettuce plants cultivated in a closed hydroponic system. Values are means of four measurements. In each column, values followed by the same letter do not differ significantly at P = 0.05.

Treatment	Na	Cl	Ca	Mg	K	P	Organic-N
Standard N.S.*	0.16 a	1.66 a	2.01 a	0.86 a	5.08 a	1.03 a	4.26 a
Low NaCl-salinity	0.48 b	2.65 b	1.54 b	0.73 b	4.27 b	0.88 bc	4.25 a
High NaCl-salinity	1.10 c	3.54 c	1.34 b	0.75 b	4.05 b	0.91 bc	4.05 ab
Low CaCl ₂ -salinity	0.13 a	1.70 a	2.08 a	0.77 b	4.48 b	0.97 ab	4.24 a
High CaCl ₂ -salinity	0.13 a	3.15 d	2.52 c	0.59 c	4.13 b	0.81 c	3.79 b

*: N.S.: Nutrient solution

CaCl₂-salinity level the difference to the control and the NaCl-salinity treatments was not significant. The organic-N in the shoot tissues was decreased significantly only by the highest CaCl₂-salinity level. As shown in Tab. 3, salinity had no effect on the concentrations of ascorbic acid and chlorophyll a and b in lettuce leaf, within the EC range tested in this experiment, irrespective of salinity source.

Tab. 3: Effects of salinity level and source (NaCl and CaCl₂) on leaf chlorophyll and ascorbic acid content (mg g⁻¹ fresh wt.) in a lettuce crop cultivated in a closed hydroponic system. Values are means of four measurements. In each column, values followed by the same letter do not differ significantly at P = 0.05.

Treatment	Ascorbic acid	Chlorophyll a	Chlorophyll b	Total chlorophyll
Standard N.S.*	11.28 a	1.61 a	0.54 a	2.14 a
Low NaCl-salinity	11.81 a	2.07 a	0.94 a	3.02 a
High NaCl-salinity	11.96 a	1.55 a	0.76 a	2.31 a
Low CaCl ₂ -salinity	8.66 a	1.95 a	0.68 a	2.63 a
High CaCl ₂ -salinity	10.19 a	2.04 a	0.88 a	2.91 a

*: N.S.: Nutrient solution

Discussion

The results regarding the impact of equally high external NaCl and CaCl₂ concentrations on lettuce growth clearly indicate that the response of lettuce to moderate salinity depends mainly on the source of salinity rather than the level of the osmotic potential in the external solution. On the other hand, Cl does not seem to be involved in the growth suppression. It is well known, that the EC is linearly related to the equivalent salt concentration of a solution, and differences in this relationship due to salt speciation are negligible, when considering the range that can significantly alter plant growth rates (SAVVAS and ADAMIDIS, 1999; SONNEVELD et al., 1999). Hence, an equal increase of the EC in a nutrient solution by adding either NaCl or CaCl₂ results in similar Cl concentrations in the solution. Indeed, the Cl concentrations in the two salinity levels tested in our experiment were similar, irrespective of using NaCl or CaCl₂ to induce salinity (data not shown). However, growth suppression was observed only when salinity was caused by adding NaCl to the standard solution. These results point out a sodium-specific restriction of lettuce growth.

Sodium may affect plant growth either at intracellular level by impairing the activity of salt sensitive enzymes related to photosynthesis (GREENWAY and OSMOND, 1972; DOWNTON et al., 1985; BALL and ANDERSON, 1986; SEEMANN and SHARKEY, 1986) or at intercellular

level by reducing cell turgor in mesophyll due to Na buildup in the cell walls (MUNNS and PASSIOURA, 1984; MUNNS, 2002), or due to competitive suppression of nutrient cation uptake (GRATTAN and GRIEVE, 1999). Competitive suppression of nutrient uptake by Na may have occurred at least for Ca and probably also for K and Mg. However, a causal relationship between the restricted K and Mg uptake and the reduced growth in the NaCl salinity treatments seems unlikely, since K and Mg were reduced also by CaCl₂-salinity. However, the leaf Ca concentration in the NaCl-salinity treatments was below the critical sufficiency range (2-2.8% in dry wt. as suggested by MILLS and JONES, 1996). Hence, a relationship between the depressing effect of Na on Ca uptake and the growth of lettuce is likely. It is well known that Ca plays a key part in maintenance of membrane integrity and selectivity, thereby restricting the uptake of harmful ions such as Na⁺ (GREENWAY and MUNNS, 1980). Presumably, the declined Ca translocation to the shoot enhanced sodium influx. Lettuce is a rosette-forming plant during vegetative growth and thus the plant has a limited capability to retain sodium in stems and leaf petioles, which is a common adaptation mechanism of nonhalophytes to NaCl-salinity (GREENWAY and MUNNS, 1980; MUNNS, 2002). Hence, a higher translocation of Na to the photosynthetically active leaves of lettuce with increasing external NaCl levels, and thus a higher specific sensitivity to Na during vegetative development is reasonable.

Inhibition of photosynthesis at biochemical level by the increased leaf Na concentration is likely but the lack of any effect of the tested salinity range on the leaf chlorophyll content does not support this consideration. A more likely explanation is an accumulation of sodium in the cell walls of leaves (FLOWERS et al., 1991), which affects the water relations of the individual cells but not the transpiration flow via the xylem. This consideration is consistent with the finding that, the CaCl₂-salinity treatments neither suppressed plant growth nor imposed a substantial buildup of Ca in the shoot that might imply excessive Ca accumulation in the cell walls of leaf. Further evidence supporting the hypothesis of Na-buildup in the cell walls of leaf is provided by the good agreement of the data regarding the relative yield reduction due to increasing NaCl-salinity with the linear model of MAAS and HOFFMAN (1977). A linear relationship is characteristic for osmotic salinity effects (SONNEVELD et al., 2004). However, if the hypothesis involving Na-specific effects on lettuce growth due to accumulation of Na in the cell walls of leaf is true, the mechanism of growth reduction is principally an osmotic one.

The salinity threshold value (STV) of 2.51 dS m⁻¹ in the nutrient solution is similar to that calculated by SONNEVELD et al. (2004) using the linear model of MAAS and HOFFMAN (1977). However it is double as high as that calculated by AYERS et al. (1951) in field-grown lettuce using the saturation extract to assess the soil salinity. This is reasonable, since the salts in a soil saturation extract are diluted to roughly half of their concentration at field capacity (SHANNON and GRIEVE, 1999), while the salt concentration in the latter is still lower than that in the actual soil solution (U.S. SALINITY LABORATORY STAFF, 1954). On the other hand, the STV found in the present study is half as high as that calculated by SHANNON et al. (1983) in solution culture. This discrepancy may be partly ascribed to genotypic differences between cultivars, which according to SHANNON et al. (1983) may be appreciable. However, SHANNON et al. (1983) used a mix of NaCl and CaCl₂ at an 1:1 equivalent ratio to increase salinity. Hence, assuming that the salinity effects are due only to NaCl as suggested by our results, the values found by SHANNON et al. (1983) are in agreement with those found in the present study. The slope of relative yield decrease found in our experiment (12.9%) with increasing NaCl-salinity is similar to that reported by AYERS et al. (1951) for soil salinity but much higher than that found by SHANNON et al. (1983). The alleviating effects of Ca on NaCl-salinity are well known (GREENWAY and MUNNS, 1980). Hence, the different rates of salinity

yield decrease between our study and that of SHANNON et al. (1983) may be ascribed to the increasing Na:Ca ratio with rising salinity in the former, while in the latter this ratio was maintained constant.

Our results (Tab. 2) suggest that, with increasing external Cl concentrations, the translocation of Cl to the shoot is much more intensive if the accompanying cation is Na in comparison to Ca. High Ca concentrations suppress the transport of Cl from the roots to the leaves (XU et al., 2000). However, the restriction of Cl uptake by Ca was obviously not the main reason for the different response of lettuce to isosmotic salinity induced by NaCl or CaCl₂, since the shoot Cl concentration at the high CaCl₂-salinity was higher than that measured with low NaCl-salinity, but growth was restricted only by the latter. The decrease of shoot P concentration in all salinity treatments is not likely to originate from competition of H₂PO₄⁻ by Cl⁻ in uptake (GRATTAN and GRIEVE, 1999). It seems that the well known depressing effect of Cl⁻ on nitrate uptake (PEREZ-ALFOCEA et al., 1993) stimulates an increase in rhizosphere pH, which results in an increased concentration of HPO₄²⁻ and thus in a decreased P uptake (XU et al., 2000). Nevertheless, a competitive suppression of NO₃⁻ uptake by Cl⁻ was not reflected in the concentration of organic-N in lettuce shoot, presumably because the plants utilized in metabolism as much nitrate as they needed and stored the excess NO₃⁻ in vacuoles.

In conclusion, the Romaine type of lettuce is specifically sensitive to Na. This may be attributed to increased translocation of Na to the shoot and accumulation in the cell walls, since at the vegetative stage lettuce lacks stems that could retain Na in xylem parenchyma. The CaCl₂-salinity is not harmful to lettuce at EC levels up to 5.5 dS m⁻¹. The uptake of Cl is reduced by Ca at isosmotic external concentrations of NaCl and CaCl₂ but this is not the main reason for the different response of lettuce to NaCl- and CaCl₂-salinity. To further clarify the mechanisms implicated in the suppression of lettuce growth by Na, the effects of NaCl-salinity should be compared to those of Na₂SO₄-salinity at constant and increasing Na:Ca ratios in the external solution. Gas exchange, leaf water and osmotic potential measurements might be helpful to interpret the results from such a study.

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Address of the authors:

Miss Gokce Tas and Mr. Nicolas Papadandonakis, Mediterranean Agronomic Institute of Chania, P.O. Box 85, Chania 73100, Greece.
 Prof. Dimitrios Savvas*, Faculty of Agricultural Technology, T.E.I. of Epirus, P.O. Box 110, Arta 47100, Greece.

* Author for correspondence (e-mail: savvas@teiep.gr).