How Salinity Affects Co$_2$ Fixation by Horticultural Crops

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Abstract. **It has been recognized widely that sequestration of atmospheric CO$_2$ by terrestrial ecosystems can contribute significantly to the stabilization of atmospheric CO$_2$. The carbon sequestration potential of crop lands should be considered as a modest but non-negligible contribution to climate change mitigation. Salinity is one of the most important environmental factors limiting crop production of marginal agricultural soils in many parts of the world. In our research, several physiological analyses were performed in atmospheric CO$_2$, in daylight, both in normal conditions and with salinity (40 mM NaCl). Crops like melon or pepper showed significantly lower photosynthetic rates when they were grown in saline conditions. Also, the total chlorophyll content and carbon percentage were lower in the salinity-treated plants of these species. For lettuce, treated plants showed a significant decrease in photosynthetic rates and chlorophyll content, but there were no differences in carbon content. On the other hand, there were no significant differences in the values of total chlorophyll content, photosynthetic rate, or carbon content for tomato and watermelon plants when control and NaCl-treated plants were compared. The mineral composition data showed greater increases of sodium in both roots and leaves of melon and pepper when plants were treated with NaCl compared with the rest of the species. In conclusion, tomato and watermelon seem to be more efficient in CO$_2$ fixation than the other crops of this experiment and this seems to be related to their greater salinity tolerance.**

Understanding and quantifying carbon sources and sinks is one of the main challenges for the scientific community to quantify global climate change parameters. The main objective is to assess the carbon balance in crops for identifying the agricultural practices that result in lower emissions. Currently, crop lands represent approximately one-third of Europe's land area (Smith et al., 2005). In this direction, Hutchinson et al. (2007) concluded that the CO$_2$ fixation potential of crop lands should be considered. However, from an agricultural perspective, there are some results that suggest that there could be a positive carbon balance in agricultural crops (Mota-Cadenas et al., 2010) with respect to increased CO$_2$ fixation (Adams et al., 1990; Long, 1991; Reddy and Hodges, 2000; Reilly et al., 2003).

Salinity is one of the most important environmental factors limiting the crop production of marginal agricultural soils in many parts of the world (Bernstein, 1975). This abiotic stress is becoming even more prevalent as the intensity of agriculture increases (Zhu, 2002). Salinity limits global agricultural productivity, rendering an estimated one-third of the world's irrigated land unsuitable for crop production (Frommer et al., 1999). Because of this, knowledge about the behavior of NaCl-tolerant and sensitive plants in these conditions is gaining importance (Grieve, 2000). Salinity effects on plants include ion toxicity, osmotic stress, mineral deficiencies, physiological and biochemical perturbations, and combinations of these stresses (Hasegawa et al., 2000; Munns, 1993, 2002; Neumann, 1997; Yeo, 1998).

Osmotic stress resulting from the low water potential of saline soils forces the plants to minimize water loss because growth depends on the ability to preserve a high net photosynthetic rate and a low transpiration simultaneously (Koyro, 2006). In this context, plant growth is related to energy use and gas exchange. Furthermore, salt uptake, accumulation, and transport within the plant have to be tightly controlled and coordinated to avoid the problem of ion stress (Carvajal et al., 1999).

Increases in ambient salt concentrations lead to the toxic accumulation of Na$^+$ ions in the cytosol. High concentrations of Na$^+$ in the cellular and extracellular compartments negatively affect the acquisition and homeostasis of essential nutrients such as K$^+$ and Ca^{2+} (Maas et al., 1982; Maathuis, 2006). Calcium is an essential element for plants. The ability of Ca^{2+} to form intermolecular linkages is important for maintaining the integrity and structure of membranes and cell walls (Cramer,

2002; Munns, 2002). Other specific symptoms of salt toxicity include a low K:Na ratio. In the cytosol, the presence of K$^+$ is essential for the activation of many enzymes (Maathuis, 2006). The role of K$^+$ is vital for protein synthesis, maintaining cell turgor, and stimulating photosynthesis (Peoples and Koch, 1979). As a result of physicochemical similarities between Na$^+$ and K$^+$, excess Na$^+$ tends to substitute for K$^+$ at binding sites and hence impairs cellular biochemistry (Maas and Grieve, 1987).

Another effect of salt stress is the alteration of water relations (Martínez-Ballesta et al., 2006). Therefore, to conserve water, plants close their stomata. This simultaneously restricts the entry of CO$_2$ into the leaf, reducing photosynthesis. At higher concentrations, NaCl may also directly inhibit photosynthesis (Stepien and Johnson, 2009).

The process of photosynthesis is a primary target of many forms of environmental stress, including salinity (García-Sánchez et al., 2002; Liska et al., 2004; Stepien and Klobus, 2006). So, it is important to know how plant CO$_2$ fixation varies with salinity for different crops of major commercial importance.

One of the current solutions to these problems is to increase the salt tolerance of conventional crops and plants of agronomic interest, but the gain in yield is, generally, low (Tester and Davenport, 2003). To be able to complete our knowledge of the physiological processes related to plant salinity stress in such crops, measurements of gas exchange and ionic relations are needed. In this research, we performed a comparative study of carbon fixation by different plant species under conditions of salinity. For this, the net photosynthetic rate, g_S, and transpiration rate were measured at atmospheric CO$_2$ during the daytime, and they were related to the total chlorophyll, carbon, and mineral contents of these species. All these parameters were measured under controlled greenhouse conditions and with 40 mM NaCl in the nutrient solution.

Materials and Methods

Plant material and growth conditions. The experiment was carried out with seedlings obtained from a commercial nursery for horticultural plants in Murcia, Spain. All the species used are commercially important in Murcia agriculture. The species were tomato (*Lycopersicon esculentum*, var. Royesta), lettuce (*Lactuca sativa*, var. Iceberg), pepper (*Capsicum annuum*, var. Lamuyo), melon (*Cucumis melo* var. Piel de sapo), and watermelon (*Citrullus lanatus*, var. Susanita). All of them were F1 commercial hybrids. The experiment was conducted during the Winter–Spring period of 2009 in a greenhouse of the CEBAS-CSIC "La Matanza" Experimental Farm (Santomera, Murcia, Southeast Spain) under a semiarid Mediterranean climate.

The experiments were carried out in an aluminum-framed greenhouse with polyethylene covers and mechanical ceiling windows for passive venting. The greenhouse was vented when the temperatures exceeded the norm. Daily mean temperature and relative humidity

were calculated from measurements taken every 10 min using data loggers (AFORA SA; Barloworld Scientific, Murcia, Spain). A total of 50 plants, 10 of each species, were placed in a randomized design using five plants per treatment and cultivar with each plant being grown in a perlite-filled, 20-L container (40 cm diameter).

All plants were grown under the same conditions and irrigated with Hoagland nutrient solution [$\approx$2 dS·m^{-1} electrical conductivity (EC)] twice a day under natural light conditions. After 10 d of transplanting, the application of 40 mM NaCl in the nutrient solution started ($\approx$6 dS·m^{-1} EC). The untreated controls and remaining plants did not show any symptoms of deficiency or toxicity.

The plants were harvested 90 d after transplanting the seedlings. The fruits were separated from the rest of the plant, which was divided into leaves, stems, and roots.

Leaf gas exchange parameters. Net assimilation of CO_2 (ACO_2) and g_S were measured using a portable photosynthesis system (Model LCA-4; ADC Bioscientific Ltd., Hoddesdon, U.K.) and a PLC-4N leaf chamber (11.35 cm^2) configured to an open system. The abaxial g_S was measured on the most recent fully expanded leaves. The measurements were made every 2 h from 0900 HR to 1200 HR to avoid the high temperatures and low humidity of the afternoon and only on clear days to minimize the impact of variations in light intensity.

Measurement of chlorophylls. Leaf samples (10 mg fresh weight) were kept in Eppendorf tubes with 1 mL of 80% acetone, at 4 °C in the dark, for 24 h. After this, the supernatant was transferred to an assay tube until the green color of the pellet disappeared. The absorption of the extracts was measured with a spectrophotometer at 663 and 645 nm. The concentrations of the chlorophylls in the extracts (mg·L^{-1}) were determined using the Arnon equation (Arnon, 1949).

Mineral elements. The concentrations of calcium, magnesium, potassium, and sodium were analyzed on samples of plant material that had been ground finely in a mill grinder after drying at 65 °C to constant weight. The samples were digested in a microwave (CEM Mars Xpress, Matthews, NC), reaching 200 °C in 20 min and holding at this temperature for 2 h, using 5 mL of concentrated HNO$_3$, 17 mL of H$_2$O, and 3 mL of H$_2$O$_2$. The concentrations of the elements were measured by inductively coupled plasma spectrometry (Iris Intrepid II; Thermo Electron Corporation, Franklin, MA).

Carbon analysis. The plants were dried in an oven at 65 °C until constant weight to determine the dry weight and to dry the samples of the different plant parts before grinding them in a laboratory analytical mill (IKA A10 model; IKA werke Gmbh & Co. KG, Staufen, Germany).

The total carbon contents were analyzed in leaves, stems, fruits, and roots using a CN analyzer (Thermo-Finnigan 1112 EA elemental analyzer; Thermo-Finnigan, Milan, Italy). These data were used for calculating grams of CO_2 fixed per plant. For calculation of grams of CO_2 fixed per square meter of each crop, planting distance (PD) was taken into account (PD $_{lettuce}$ = 6.5 plants/m^2, PD $_{pepper}$ = 2.2 plants/m^2, PD $_{tomato}$ = 2 plants/m^2, PD $_{melon}$ = 1 plant/m^2, and PD $_{watermelon}$ = 0.4 plants/m^2).

Statistical analysis. An analysis of variance was made to determine the effects of the treatment on the several determined parameters. Mean comparisons were performed using the Tukey honestly significant difference test. All analyses were performed with SPSS Inc. statistical software package (SPSS Inc., Chicago, IL).

Results

In this experiment, the salt tolerance and its relationship with plant CO_2 fixation were analyzed for five different crop species. In

Figure 1, all the results for net assimilation of CO_2 and g_S at two different times of the morning are shown. In general, only slight differences between the two times of measurement were observed for ACO_2 for any of the plants studied. The highest values were obtained in tomato and melon. Watermelon plants exposed to salinity only showed a significant decrease at 0900 HR. However, pepper and melon only showed a significant decrease at 1200 HR but not at 0900 HR, whereas lettuce showed differences at both times. The g_s only differed significantly between NaCl-treated and control plants at 0900 HR in lettuce and pepper; the highest value at this time was in tomato plants and the lowest was in pepper. The same behavior was observed at 1200 HR; a significant decrease only occurred in salt-treated lettuce and pepper compared with control plants. The rest of the species maintained similar values at 0900 HR and at 1200 HR.

The results obtained for total chlorophylls content are shown in Figure. 2. Significant decreases of this pigment content were found in lettuce, pepper, and melon plants grown under saline conditions compared with plants grown in control solution. Comparing all the crops, the highest values were obtained in watermelon and melon and the lowest in pepper.

In Table 1, the results of the mineral analyses are summarized. In tomato and watermelon, no significant differences between control and NaCl-exposed plants were observed for any of the elements analyzed in leaves. However, for lettuce, pepper, and melon leaves, greater differences were found when control plants were compared with plants grown under salinity. In lettuce, potassium (K) was decreased significantly in the roots of NaCl-treated plants, but calcium (Ca) and magnesium (Mg) only showed a decrease in the leaves. In pepper, decreases in K and Ca were observed in both leaves and roots of NaCl-treated plants, but no differences were
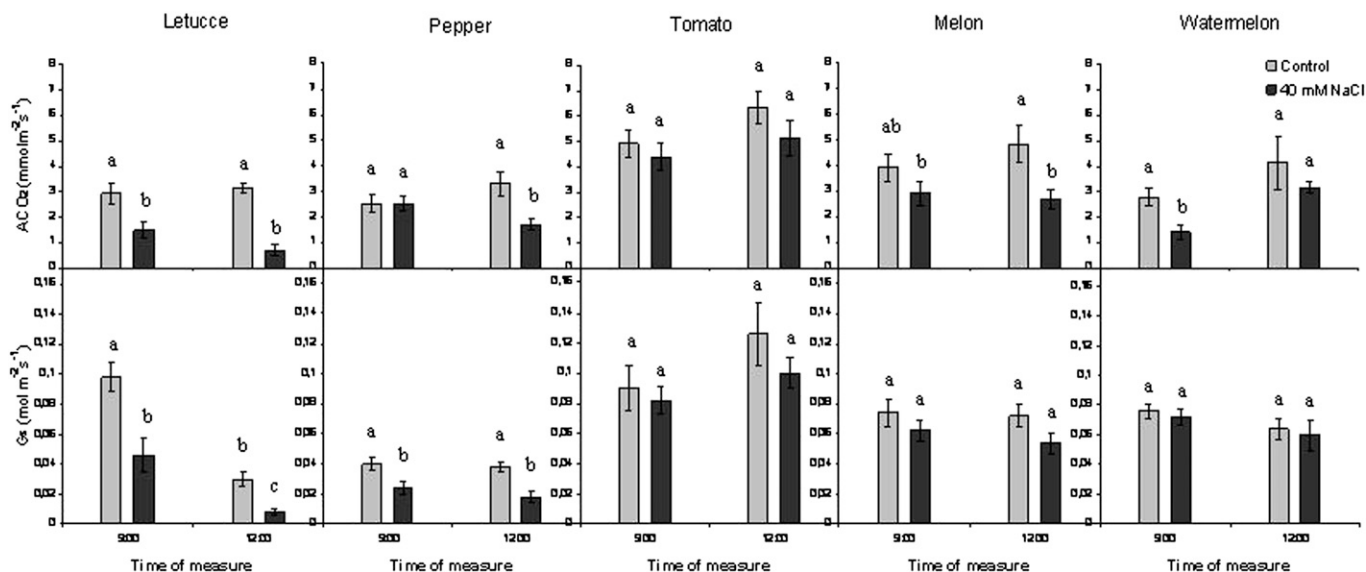

Fig. 1. Net assimilation of CO_2 (ACO_2) and stomatal conductance (g_s) in leaves of lettuce, pepper, tomato, melon, and watermelon plants grown in control and salinity conditions (40 mM NaCl). Data are means of five plants ± SE. Different letters for each bar of different plants indicate significant differences according to Tukey test ($P < 0.05$).
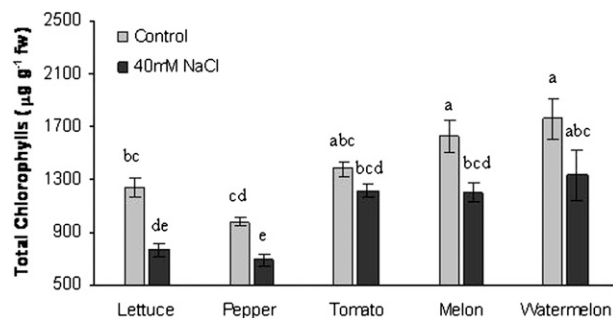
Fig. 2. Total chlorophyll content in leaves of lettuce, pepper, tomato, melon, and watermelon plants grown in control and salinity conditions (40 mM NaCl). Data are means of five plants ± SE. Different letters for each bar of different plants indicate significant differences according to Tukey test ($P < 0.05$).

Table 1. Effect of NaCl on the mineral composition of different parts of the control and treated with 40 mM NaCl plants.

Treatment			Potassium (mmol·g^{-1} dw)	Calcium (mmol·g^{-1} dw)	Sodium (mmol·g^{-1} dw)	Magnesium (mmol·g^{-1} dw)
Lettuce	Leaf	Control	1.92 ± 0.10 a	0.58 ± 0.04 a	0.25 ± 0.04 c	0.65 ± 0.05 a
		NaCl 40 mM	1.76 ± 0.07 a	0.41 ± 0.03 b	0.75 ± 0.04 b	0.49 ± 0.04 b
	Root	Control	1.36 ± 0.10 b	0.25 ± 0.02 c	0.42 ± 0.05 c	0.64 ± 0.05 a
		NaCl 40 mM	0.98 ± 0.04 c	0.26 ± 0.02 c	0.96 ± 0.06 a	0.53 ± 0.05 a
Pepper	Leaf	Control	0.89 ± 0.02 a	0.73 ± 0.03 a	0.09 ± 0.01 c	0.55 ± 0.02 a
		NaCl 40 mM	0.48 ± 0.08 b	0.62 ± 0.02 b	1.24 ± 0.10 a	0.52 ± 0.02 a
	Root	Control	0.99 ± 0.04 a	0.48 ± 0.04 c	0.52 ± 0.03 b	0.31 ± 0.03 b
		NaCl 40 mM	0.49 ± 0.04 b	0.32 ± 0.02 d	1.49 ± 0.12 a	0.27 ± 0.03 b
Tomato	Leaf	Control	0.35 ± 0.06 b	1.17 ± 0.14 a	0.03 ± 0.003 c	0.63 ± 0.08 a
		NaCl 40 mM	0.35 ± 0.05 b	1.23 ± 0.06 a	0.10 ± 0.01 c	0.82 ± 0.10 a
	Root	Control	0.67 ± 0.05 a	0.47 ± 0.03 b	0.54 ± 0.02 b	0.33 ± 0.02 b
		NaCl 40 mM	0.50 ± 0.07 a	0.37 ± 0.02 b	1.42 ± 0.05 a	0.26 ± 0.01 b
Melon	Leaf	Control	0.83 ± 0.08 a	1.50 ± 0.14 a	0.20 ± 0.02 c	0.99 ± 0.11 a
		NaCl 40 mM	0.50 ± 0.05 c	1.18 ± 0.09 a	1.22 ± 0.13 a	0.75 ± 0.10 a
	Root	Control	0.64 ± 0.07 b	0.25 ± 0.03 b	0.61 ± 0.06 b	0.37 ± 0.10 b
		NaCl 40 mM	0.49 ± 0.04 c	0.20 ± 0.03 b	1.53 ± 0.19 a	0.31 ± 0.04 b
Watermelon	Leaf	Control	0.33 ± 0.04 a	1.25 ± 0.15 a	0.07 ± 0.01 b	0.69 ± 0.04 a
		NaCl 40 mM	0.38 ± 0.09 a	1.62 ± 0.20 a	0.18 ± 0.01 b	0.83 ± 0.12 a
	Root	Control	0.36 ± 0.03 a	0.34 ± 0.05 b	0.39 ± 0.14 b	0.22 ± 0.02 b
		NaCl 40 mM	0.36 ± 0.01 a	0.22 ± 0.02 b	2.05 ± 0.21 a	0.24 ± 0.03 b

Data are means of five replicates ± SE. Different letters in each column for each species indicate a significant difference according Tukey test at $P < 0.05$.
dw = dry weight.

observed for Mg. In melon plants, K values were lower in leaves and roots of plants treated with NaCl. Regarding sodium (Na), as expected, the concentrations were higher in plants treated with NaCl. However, the values were higher in the roots than in leaves of all the species studied. The highest concentrations were observed in roots of watermelon plants. For the Na/K ratio, a very high increase can be observed (Fig. 3) in leaves of melon and pepper plants exposed to NaCl. However, there were smaller increases in lettuce, watermelon, and tomato leaves. In roots, there were also increases for all plants treated with NaCl, these being greater in pepper, tomato, melon, and watermelon but lower in lettuce.

Finally, Figure 4 shows the results for percent of carbon and calculation of CO_2 fixation. In Figure 4, it can be seen that the percentage of carbon fixed showed significant decreases in the salinity treatment with respect to control plants for pepper and melon, but not in the remaining species. Similar results were obtained when CO_2 per plant and per square meter of crop were determined. Thus, the absolute values of CO_2 fixation per

plant (Fig. 4) showed significant reductions in pepper and melon plants resulting from salinity. Tomato and watermelon plants had higher values of CO_2 fixation than the other species, particularly lettuce. The results were similar when comparing the different crops under salinity, although pepper and melon plants showed significant decreases under these conditions when compared with control plants.

Discussion

One of the ecological benefits of sustainable agriculture is the fact that every plant population can sequester CO_2 and thus counteract the greenhouse effect (Geissler et al., 2009). However, environmental stress would affect the CO_2 sequestration as a result of its interaction with the physiology of the plant. Under saline conditions, plants have to control different mechanisms that could affect their

growth rate and morphology, resistance to water stress (reduction of the water potential), avoidance of ion toxicity and nutrient imbalance, and regulation of CO_2 and H_2O exchange through the stomata (Koyro, 2003; Marschner, 1995; Munns, 1993, 2002; Rengasamy et al., 2003; Volkmar et al., 1998).

The rate of photosynthetic CO_2 assimilation is generally reduced by salinity (Brugnoli and Lauteri, 1990). The results obtained in our plants showed significant decreases for ACO_2 and g_s in lettuce and pepper under salinity, whereas melon only showed a significant decrease in the photosynthetic rate (measurements at 1200 HR). Salinity has been shown to reduce photosynthesis primarily by a decrease in g_s (Burman et al., 2003) or in CO_2 diffusion to the chloroplasts (Wilson et al., 2006; Yang and Lu, 2005). In this sense, the reduction observed in ACO_2 has been reported to be attributable partly to a reduced g_s and the consequent restriction of the availability of CO_2 for carboxylation (Downton et al., 1985; Farquhar et al., 1982; Seemann and Critchley, 1985). The fact that in lettuce, there was no consistent relationship between ACO_2 and g_s could be related to the stomatal closure produced in salt-stressed plants by which the decreases in partial CO_2 pressure in the plant forced the assimilation of more CO_2, thereby making the carbon signatures of the newly formed plant tissue less negative (Van Groenigen and Van Kessel, 2002). No significant differences in these parameters were found in tomato and watermelon plants measured at 1200 HR. In other research, non-stomatal inhibition of photosynthesis has been observed for several species. This could be caused by the effect of NaCl on photosynthetic mechanisms unrelated to stomatal closure (Flexas et al., 2008). According to Kao et al. (2006) and Moradi and Ismail (2007), species with relatively higher salt tolerance would have less affected gas exchange parameters.

Salinity can affect chlorophyll contents through inhibition of chlorophyll synthesis or an acceleration of its degradation (Reddy and Vora, 1986). In our experiment, the chlorophyll content results for all the species supported those obtained for the rate of photosynthesis, there being significant decreases of this parameter in NaCl-treated lettuce, melon, and pepper plants. The chlorophyll content has been related to salinity resistance in alfalfa (Winicov and Seemann, 1990), sunflower (El-Hendawy et al., 2005), and soybean (Lu et al., 2009).

The effects of salinity at the cellular level are the result of osmotic and ionic imbalance (Hasegawa et al., 2000; Hayashi and Murata, 1998; Joset et al., 1996; Muranaka et al., 2002a, 2002b; Murphy and Durako, 2003; Ranjbarfordoei et al., 2002). The increase of Na^+ reduces the absorption and translocation of K^+, Ca^{2+}, and Mg^{2+} (Ball et al., 1987; Hasegawa et al., 2000). Our results showed that the Ca content in leaves only decreased in lettuce and pepper plants cultivated in the presence of NaCl. It is known that salinity reduces plant Ca^{2+} uptake and translocation (Halperin et al., 1997). Electrostatically bound
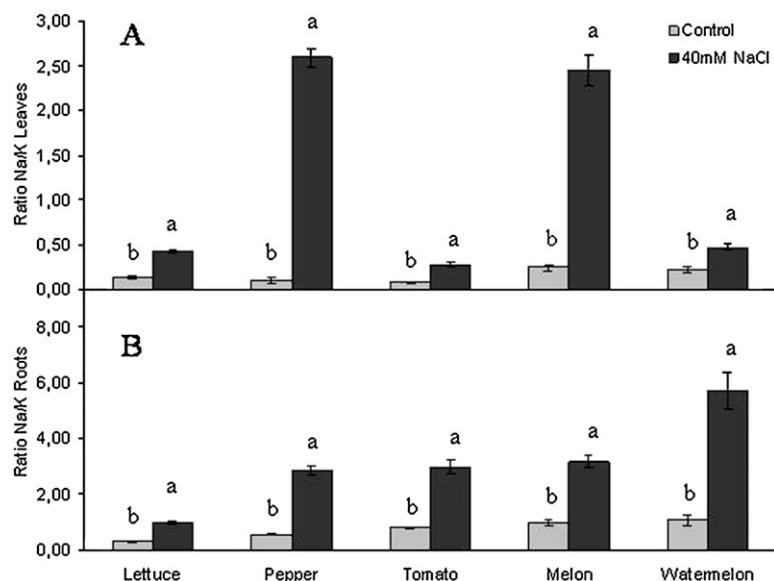
Fig. 3. Effect of salinity on ratio of Na/K in leaves (**A**) and roots (**B**) of lettuce, pepper, tomato, melon, and watermelon plants grown in control and salinity conditions (40 mM NaCl). Data are means of five plants ± SE. Different letters for each bar of different plants indicate significant differences according to Tukey test ($P < 0.05$).

Fig. 4. Carbon percentage, CO_2 fixation per plant and CO_2 fixation per square meter of culture of lettuce, pepper, tomato, melon, and watermelon plants grown in control and salinity conditions (40 mM NaCl). Data are means of five plants ± SE. Different letters for each bar of different plants indicate significant differences according to Tukey test ($P < 0.05$).
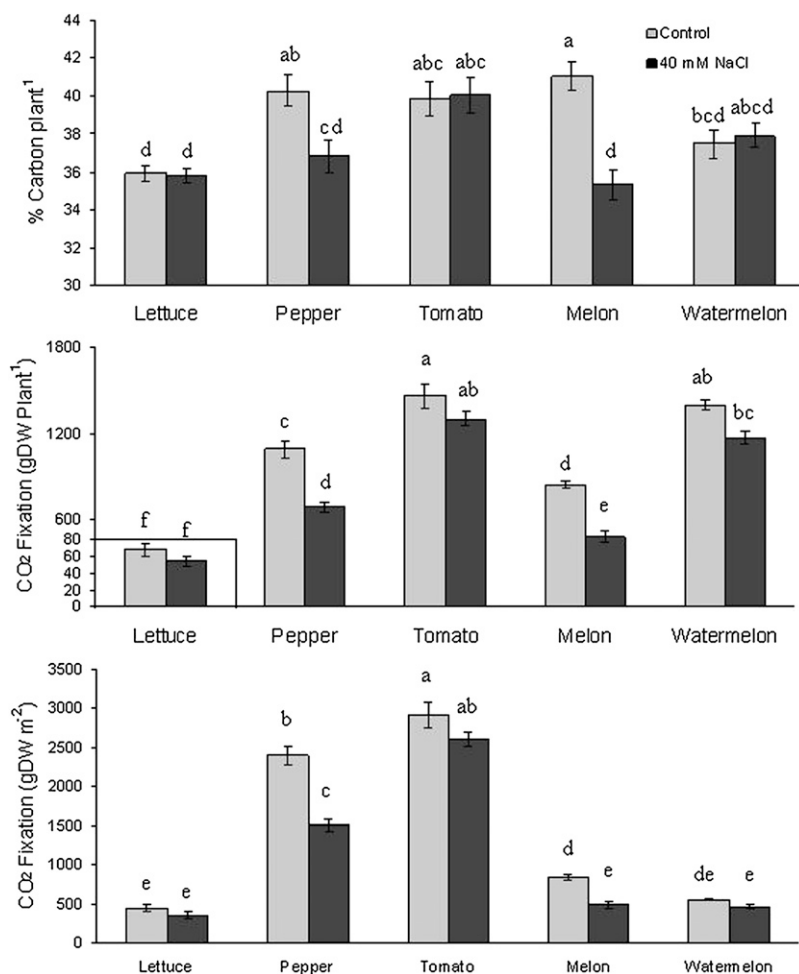
Ca^{2+} is essential to preserve the structure and function of cell walls and plasma membranes and its displacement by Na^+ affects membrane transport; this is one of the primary toxic effects of salinity (Cramer et al., 1985; Lynch et al., 1987; Rengel, 1992). Because of this, higher accumulation of Ca^{2+} in plants might be a factor involved in conferring salt tolerance (Yetişir and Uygur, 2009). Therefore, the decreased tissue levels of Ca in lettuce and pepper plants may be related to their NaCl sensitivity. On the other hand, in our experiment, significantly lower leaf Mg concentrations were obtained in lettuce grown in saline conditions compared with control plants, but this did not occur in the rest of the species. The results indicate that, in general, these species are moderately adapted to salt stress depending on the NaCl concentration used (40 mM NaCl is not a very high concentration for such cultivated plants).

In saline conditions, all the species showed a significant increase of leaf Na, but in tomato and watermelon, the Na values in saline conditions were very low. Salinity not only caused high Na accumulation in plants, but also influenced the uptake of essential nutrients such as K and Ca through effects on ion selectivity. High Na^+ contents inhibit K^+ uptake and accumulation (Zhao et al., 2007). K^+ plays a role in a wide range of metabolic functions in plants, including photosynthesis, enzyme activation, osmotic potential, stomatal behavior, osmoregulation, cell expansion, and other physiological processes (Elumalai et al., 2002; Maathuis and Sanders, 1996; Marschner, 1995). In our experiment, the leaf K content in pepper and melon was reduced significantly by salinity. These results are in accordance with those of Lycoskoufis et al. (2005) and Kaya et al. (2007) for pepper and melon, respectively.

Accumulation of Na^+ and impairment of K^+ nutrition is typically among the major effects in salt-stressed plants, and for this reason, the Na^+/K^+ ratio is considered a useful parameter for assessment of the salt tolerance of plant species (Cuin et al., 2003). Thus, high levels of Na^+ or high Na^+/K^+ ratios can disrupt various enzymatic reactions in the cytoplasm (Blaha et al., 2000). With high concentrations of Na^+ in the leaf apoplast and/or vacuole, plant cells have difficulty in maintaining low cytosolic Na^+ and, perhaps as importantly, low Na^+/K^+ ratios (Gorham et al., 1990; Maathuis and Amtmann, 1999). Figure 3 shows that for all the species, there were significant increases of the Na/K ratio in treated plants compared with the controls. However, melon and pepper showed much higher increases than lettuce, watermelon, or tomato, indicating that the latter species could be more salinity-tolerant. However, other criteria like marketable production or leaf and fruit quality should be taken into account. Low Na^+/K^+ ratios are also related closely to salt resistance in artichoke (Graifenberg et al., 1995), tomato (López and Satti, 1996), chickpea (Ozcan et al., 2000), and *Brassica napus* (Qasim and Ashraf, 2006).

The percentage carbon content of pepper and melon plants showed a significant reduction under salinity (Fig. 4). These results are in accordance with those obtained for the other parameters analyzed in this study, indicating that lettuce, pepper, and melon plants are less tolerant to salinity than the other species studied in this work. Almost all of the results obtained showed that lettuce, pepper, and melon are species less adapted to saline conditions and that these crops seem to be less efficient in CO_2 fixation and, therefore, these plants have less capacity for carbon accumulation. Obviously, when plant CO_2 fixation (determined per plant) was studied, there was a strong reduction in lettuce plants compared with the other species as a result of the lower biomass. A significant decrease in NaCl-treated plants with respect to control plants was observed only in pepper and melon. In all cases, the species moderately tolerant to salinity (tomato and watermelon) seem to be more efficient in CO_2 fixation than the sensitive ones (lettuce, melon, and pepper). However, regarding CO_2 fixation per square meter of culture, watermelon (PD = 0.4 plants/m^2) had a lower efficiency compared with tomato (PD = 2 plants/m^2), whereas lettuce (PD = 6.5 plants/m^2), pepper (PD = 2.2 plants/m^2), and melon (PD = 1 plants/m^2) exhibited significant decreases of CO_2 fixation under salinity compared with control plants.

We conclude that the species more tolerant of saline conditions (tomato and watermelon) showed a higher capacity for fixation of atmospheric CO_2 than the sensitive species (lettuce, melon, and pepper). These results seem to be related to the capacity of each species to maintain the photosynthetic processes and g_S in stressing situations. Thus, tomato and watermelon showed no significant differences in almost all of the parameters measured, especially those related to photosynthesis, under salinity compared with control conditions, these being the species that showed more efficient carbon fixation under stressing conditions. However, planting distance should be taken into account when total carbon fixation is analyzed, because the efficiency of plant growth in absolute values of carbon sequestration will depend on this factor.

Literature Cited

Adams, R.M., C. Rosenzweig, R.M. Peart, J.T. Ritchie, B.A. McCarl, J.D. Glyer, R.B. Curry, J.W. Jones, K.J. Boote, and L.H. Allen. 1990. Global climate change and US agriculture. Nature 345:219–224.

Arnon, D. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiol. 24:1–15.

Ball, M.C., W.S. Chow, and J.M. Anderson. 1987. Salinity-induced potassium deficiency causes loss of functional photosystem II in leaves of the grey mangrove, *Avicennia marina*, through depletion of the atrazine-binding polypeptide. Aust. J. Plant Physiol. 14:351–361.

Bernstein, L. 1975. Effects of salinity and sodicity on plant growth. Annu. Rev. Phytopathol. 13: 295–312.

Blaha, G., U. Stelzl, C.M.T. Spahn, R.K. Agrawal, J. Frank, and K.H. Nierhaus. 2000. Preparation of functional ribosomal complexes and effect of buffer conditions on tRNA positions observed by cryoelectron microscopy. Methods Enzymol. 317:292–309.

Brugnoli, E. and M. Lauteri. 1990. An evaluation of the effect of salinity on photosynthesis, p. 741–744. In: Baltscheffsky, M. (ed.). Current research in photosynthesis. Vol. IV. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Burman, U., B.K. Garg, and S. Kathju. 2003. Water relations, photo-synthesis and nitrogen metabolism of Indian mustard (*Brassica juncea* Czern. & Coss.) grown under salt and water stress. J. Plant Biol. 30:55–60.

Carvajal, M., V. Martínez, and C.F. Alcaraz. 1999. Physiological function of water-channels, as affected by salinity in roots of paprika pepper. Physiol. Plant. 105:95–101.

Cramer, G.R. 2002. Sodium-calcium interactions under salinity stress, p. 205–227. In: Lauchli, A. and U. Luttge (eds.). Salinity. Environment–plants–molecules. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Cramer, G.R., A. Lauchli, and V.S. Polito. 1985. Displacement of Ca^{2+} by Na$^+$ from the plasmalemma of root cells. Primary response to salt stress? Plant Physiol. 79:207–211.

Cuin, T.A., A.J. Miller, S.A. Laurie, and R. Leigh. 2003. Potassium activities in cell compartments of salt-grown barley leaves. J. Expt. Bot. 54:657–661.

Downton, W.J.S., W.J.R. Grant, and S.P. Robinson. 1985. Photosynthetic and stomatal responses of spinach leaves to salt stress. Plant Physiol. 77:85–88.

El-Hendawy, S.E., Y. Hu, and U. Schmidhalter. 2005. Growth, ion content, gas exchange, and water relations of wheat genotypes differing in salt tolerances. Aust. J. Agr. Res. 56:123–134.

Elumalai, R.P., P. Nagpal, and J.W. Reed. 2002. A mutation in the Arabidopsis KT2/KUP2 potassium transporter gene affects shoot cell expansion. Plant Cell 14:119–131.

Farquhar, G.D., M.C. Ball, S. Von Caemmerer, and Z. Roksandic. 1982. Effect of salinity and humidity on 13C value of halophytes. Evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia 52:121–124.

Flexas, J., M. Ribás-Carbo, A. Díaz-Espejo, J. Galmes, and H. Medrano. 2008. Mesophyll conductance to CO_2: Current knowledge and future prospects. Plant Cell Environ. 31:602–621.

Frommer, W.B., U. Ludewig, and D. Rentsch. 1999. Taking transgenic plants with a pinch of salt. Science 285:1222–1223.

García-Sánchez, F., J.L. Jifón, M. Carvajal, and J.P. Syvertsen. 2002. Gas exchange, chlorophyll and nutrient contents in relation to Na$^+$ and C$_{12}$ accumulation in 'Sunburst' Mandarin grafted on different rootstocks. Plant Sci. 162:705–712.

Geissler, N., S. Hussin, and H.W. Koyro. 2009. Interactive effects of NaCl salinity and elevated atmospheric CO_2 concentration on growth, photosynthesis, water relations and chemical composition of the potential cash crop halophyte *Aster tripolium* L. Environ. Exp. Bot. 65:220–231.

Gorham, J., A. Bristol, E.M. Young, R.G.W. Jones, and G. Kashour. 1990. Salt tolerance in the triticeae—K/Na discrimination in barley. J. Expt. Bot. 41:1095–1101.

Graifenberg, A., L. Giustiniani, O. Temperini, and M. Lipucci di Paola. 1995. Allocation of Na, Cl, K and Ca within plant tissues in globe artichoke (*Cynara scolimus* L.) under saline-sodic conditions. Sci. Hort. 63:1–10.

Grieve, C.M. 2000. Salt tolerance of vegetables. Irrig. J. 50:28–30.

Halperin, S.J., L.V. Kochian, and J.P. Lynch. 1997. Salinity stress inhibits calcium loading into the xylem of excised barley (*Hordeum vulgare*) roots. New Phytol. 13:419–427.

Hasegawa, P.M., R.A. Bressan, J.K. Zhu, and H.J. Bohnert. 2000. Plant cellular and molecular responses to high salinity. Annu. Rev. Plant Physiol. Mol. Biol. 51:463–499.

Hayashi, H. and N. Murata. 1998. Genetically engineered enhancement of salt tolerance in higher plants, p. 133–148. In: Satoh, K. and N. Murata (eds.). Stress responses of photosynthetic organisms: Molecular mechanisms and molecular regulation. Elsevier, Amsterdam, Lausanne, New York, Oxford, Shannon, Singapore, Tokyo.

Hutchinson, J.J., C.A. Campbell, and R.L. Desjardins. 2007. Some perspectives on carbon sequestration in agriculture. Agr. For. Meteorol. 142:288–302.

Joset, F., R. Jeanjean, and M. Hagemann. 1996. Dynamics of the response of cyanobacteria to salt stress: Deciphering the molecular events. Physiol. Plant. 96:738–744.

Kao, W.Y., T.T. Tsai, H.C. Tsai, and C.N. Shih. 2006. Response of three Glycine species to salt stress. Environ. Exp. Bot. 56:120–125.

Kaya, C., A.L. Tuna, M. Ashraf, and H. Altunlu. 2007. Improved salt tolerance of melon (*Cucumis melo* L.) by the addition of proline and potassium nitrate. Environ. Exp. Bot. 60:397–403.

Koyro, H.W. 2003. Study of potential cash crop halophytes in a quick check system task. Veg. Sci. 38:5–17.

Koyro, H.W. 2006. Effect of salinity on growth, photosynthesis, water relations and solute composition of the potential cash crop halophyte *Plantago coronopus* (L.). Environ. Exp. Bot. 56:136–146.

Liska, A.J., A. Shevchenko, U. Pick, and A. Katz. 2004. Enhanced photosynthesis and redox energy production contribute to salinity tolerance in Dunaliella as revealed by homology-based proteomics. Plant Physiol. 136:2806–2817.

Long, S.P. 1991. Modifications of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? Plant Cell Environ. 14:729–739.

López, M.V. and S.M.E. Satti. 1996. Calcium and potassium enhanced growth and yield of tomato under sodium chloride stress. Plant Sci. 114:19–27.

Lu, K.X., B.H. Cao, X.P. Feng, Y. He, and D.A. Jiang. 2009. Photosynthetic response of salt-tolerant and sensitive soybean varieties. Photosynthetica 47:381–387.

Lycoskoufis, I.H., D. Savvas, and G. Mavrogianopoulos. 2005. Growth, gas exchange, and nutrient status in pepper (Capsicum annum L.) grown in recirculating nutrient solution as affected by salinity imposed to half of the root system. Sci. Hort. 106:147–161.

Lynch, J., G.R. Cramer, and A. Lauchli. 1987. Salinity reduces membrane-associated calcium in corn root protoplasts. Plant Physiol. 83:390–394.

Maas, E.V., R.A. Clark, and L.E. Francois. 1982. Sprinling-induced foliar injury to pepper plants:

Effects of irrigation frequency, duration and water composition. Irrig. Sci. 3:101–109.

Maas, E.V. and C.M. Grieve. 1987. Sodium-induced calcium deficiency in salt-stressed corn. Plant Cell Environ. 10:559–564.

Maathuis, F.J.M. 2006. The role of monovalent cation transporters in plant responses to salinity. J. Expt. Bot. 57:1137–1147.

Maathuis, F.J.M. and A. Amtmann. 1999. K^+ nutrition and Na^+ toxicity: The basis of cellular K^+/Na^+ ratios. Ann. Bot. (Lond.) 84:123–133.

Maathuis, F.J.M. and D. Sanders. 1996. Mechanisms of potassium absorption by higher plant roots. Physiol. Plant. 96:158–168.

Marschner, H. 1995. Mineral nutrition of higher plants. 2nd Ed. Academia Press, London, UK.

Martínez-Ballesta, M.C., C. Silva, C. López-Berenguer, F.J. Cabañero, and M. Carvajal. 2006. Plant aquaporins: New perspectives on water and nutrient uptake in saline environment. Plant Biol. 8:535–546.

Moradi, F. and A.M. Ismail. 2007. Responses of photosynthesis, chlorophyll fluorescence and ROS-scavenging systems to salt stress during seedling and reproductive stages in rice. Ann. Bot. (Lond.) 99:1161–1173.

Mota-Cadenas, C., C. Alcaraz-López, M. Iglesias, M.C. Martínez-Ballesta, and M. Carvajal. 2010. Investigation into CO_2 absorption of the most representative agricultural crops of the region of Murcia. 5 Feb. 2010. <http://www.lessco2.es/pdfs/noticias/ponencia_cisc_ingles.pdf>.

Munns, R. 1993. Physiological processes limiting plant growth in saline soils. Some dogmas and hypotheses. Plant Cell Environ. 16:15–24.

Munns, R. 2002. Comparative physiology of salt and water stress. Plant Cell Environ. 25:239–250.

Muranaka, S., K. Shimizu, and M. Kato. 2002a. A salt-tolerant cultivar of wheat maintains photosynthetic activity by suppressing sodium uptake. Photosynthetica 40:509–515.

Muranaka, S., K. Shimizu, and M. Kato. 2002b. Ionic and osmotic effects of salinity on single-leaf photosynthesis in two wheat cultivars with different drought tolerance. Photosynthetica 40:201–207.

Murphy, K.S.T. and M.J. Durako. 2003. Physiological effects of short term salinity changes on *Ruppia maritima*. Aquat. Bot. 75:293–309.

Neumann, P. 1997. Salinity resistance and plant growth revisited. Plant Cell Environ. 20:1193–1198.

Ozcan, H., M.A. Turan, O. Koc, Y. Cikili, and S. Taban. 2000. Growth and variations in proline, sodium, chloride, phosphorus and potassium concentrations of chickpea (*Cicer arietinum* L. cvs.) varieties under salinity stress. Turk. J. Agric. For. 24:649–654.

Peoples, T.R. and D.W. Koch. 1979. Role of potassium in carbon dioxide assimilation in *Medicago sativa* L. Plant Physiol. 63:878–881.

Qasim, M. and M. Ashraf. 2006. Time course of ion accumulation and its relationship with the salt tolerance of two genetically diverse lines of canola (*Brassica napus* L.). Pak. J. Bot. 38:663–672.

Ranjbarfordoei, A., R. Samson, R. Lemeur, and P. van Damme. 2002. Effects of osmotic drought stress induced by combination of NaCl and polyethylene glycol on leaf water status, photosynthetic gas exchange, and water use efficiency of *Pistacia khinjuk* and *P. mutica*. Photosynthetica 40:165–169.

Reddy, M.P. and A.B. Vora. 1986. Changes in pigment composition. Hill reaction activity and saccharides metabolism in bajra (Penisetum typhoides S & H) leaves under NaCl salinity. Photosynthetica 20:50–55.

Reddy, R. and H.F. Hodges. 2000. Climate change and global crop productivity: An overview. Climate change and global crop productivity. CAB International, Wallingford, UK. p. 512.

Reilly, J., F. Tubiello, B. McCarl, D. Abler, R. Darwin, K. Fuglie, S. Hollinger, C. Izaurralde, S. Jagtap, J. Jones, L. Mearns, D. Ojima, E. Paul, K. Paustian, S. Riha, N. Rosenberg, and C. Rosenzweig. 2003. US agriculture and climate change: New results. Clim. Change 57:43–69.

Rengasamy, P., D. Chittleborough, and K. Helyar. 2003. Root-zone salinity and plant-based solutions for dry land salinity. Plant Soil 257:249–260.

Rengel, Z. 1992. The role of calcium in salt toxicity. Plant Cell Environ. 15:625–632.

Seemann, J.R. and C. Critchley. 1985. Effects of salt stress on the growth, ion content, stomatal behaviour and photosynthetic capacity of a salt sensitive species, *Phaseolus vulgaris* L. Planta 164:151–162.

Smith, P., O. Andren, T. Karlsson, P. Perala, K. Regina, M. Rounsevell, and B. van Wesemael. 2005. Carbon sequestration potential in European croplands has been overestimated. Glob. Change Biol. 11:2153–2163.

Stepien, P. and G.N. Johnson. 2009. Contrasting responses of photosynthesis to salt stress in the glycophyte Arabidopsis and the halophyte Thellungiella: Role of the plastid terminal oxidase as an alternative electron sink. Plant Physiol. 149:1154–1165.

Stepien, P. and G. Klobus. 2006. Water relations and photosynthesis in *Cucumis sativus* L. leaves under salt stress. Biol. Plant. 50:610–616.

Tester, M. and R. Davenport. 2003. Na^+ tolerance and Na^+ transport in higher plants. Ann. Bot. (Lond.) 91:503–537.

Van Groenigen, J.W. and C. Van Kessel. 2002. Salinity-induced patterns of natural abundance carbon-13 and nitrogen-15 in plant and soil. Soil Sci. Soc. Amer. J. 66:489–498.

Volkmar, K.M., Y. Hu, and H. Steppuhn. 1998. Physiological responses of plants to salinity: A review. Can. J. Plant Sci. 78:19–27.

Wilson, C., X. Liu, S.M. Lesch, and D.L. Suarez. 2006. Growth response of major USA cowpea cultivars II. Effect of salinity on leaf gas exchange. Plant Sci. 170:1095–1101.

Winicov, I. and J.R. Seemann. 1990. Expression of genes for photosynthesis and the relationship to salt tolerance of alfalfa (*Medicago sativa*) cells. Plant Cell Physiol. 31:1155–1161.

Yang, X.H. and C.M. Lu. 2005. Photosynthesis is improved by exogenous glycinebetaine in salt-stressed maize plants. Physiol. Plant. 124:343–352.

Yeo, A.R. 1998. Molecular biology of salt tolerance in the context of whole-plant physiology. J. Expt. Bot. 49:915–929.

Yetişir, H. and V. Uygur. 2009. Plant growth and mineral element content of different gourd species and watermelon under salinity stress. Turk. J. Agric. For. 33:65–77.

Zhao, Q., B.L. Ma, and C.Z. Ren. 2007. Growth, gas exchange, chlorophyll fluorescence, and ion content of naked oat in response to salinity. Crop Sci. 47:123–131.

Zhu, J.K. 2002. Salt and drought stress signal transduction in plants. Annu. Rev. Plant Biol. 53:247–273.