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The Relative Salt Tolerance of 'Rangpur' Seedlings and 'Arbequina' Olive Cuttings

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The salinity tolerance of citrus rootstocks varies but grafted citrus trees are generally considered to be more sensitive to salinity stress than olive trees that are usually grown from cuttings. We compared the salt tolerance of 6-month-old seedlings of the relatively salt tolerant citrus rootstock Rangpur (*Citrus limonia* Osbeck) with similar sized rooted cuttings of olive (*Olea europaea* L. cv. Arbequina). Well-fertilized plants were grown in native Candler sand in a greenhouse and watered with either no salt (0 mM NaCl) or 50 mM NaCl for citrus, or with 0 or 100 mM NaCl for olive. Salinity increased Cl^- and Na^+ concentration in leaves and roots of both species and reduced total plant growth, leaf photosynthetic rate and stomatal conductance. High concentrations of Cl^- and Na^+ caused a decrease in leaf chlorophyll *a* in citrus but not in olive even at the higher salinity level. Decreased growth and gas exchange were apparently due to toxic effects of Cl^- and/or Na^+ and not due to osmotic stress since both species were able to osmotically adjust to salinity and maintained higher leaf turgor than the non-salinized control plants. The lower osmotic potential values in salinized olive (100 mM NaCl) than in citrus (50 mM NaCl) implied that osmoregulation was more efficient in olive than in citrus.

Soil salinity is a common worldwide problem associated with arid or semi-arid regions and near coastal areas. Citrus trees in Florida can be affected by salinity in irrigation water, especially where there is poor soil drainage (Syvertsen et al., 1989). Olive trees grown in arid regions around the Mediterranean basin are often affected by saline soils due to the poor quality of irrigation water during the dry season (Chartzoulakis et al., 2002b; Tattini et al., 1995).

The salinity tolerance of crops varies widely, but citrus trees are considered salt sensitive whereas olive trees are moderately tolerant to salinity (Maas and Hoffman, 1977). Since all commercial citrus trees are grafted onto rootstocks, the salt tolerance of citrus trees has been associated with the ability of the root system to restrict the uptake and/or transport of salt ions to shoots (Levy and Syvertsen, 2004). The accumulation of Cl^- in citrus leaves and, thus, relative salt tolerance, has been linked to tree growth (Castle and Krezdorn, 1975) and to tree water use (Moya et al., 1999, 2003; Syvertsen et al., 1989). Species with high growth and water use rates tend to accumulate relatively high levels of Cl^- in their leaves. In addition, high concentrations of Cl^- and/or Na^+ in the leaves of citrus trees have been frequently related to nutrient imbalances and reductions in gas exchange and water relations (Walker et al., 1993; Zekri and Parsons, 1992). Rangpur is one of the most salt-tolerant citrus rootstocks since trees on Rangpur accumulate Cl^- at a relatively slower rate than trees on other rootstocks (Zekri and Parsons, 1992).

Rootstocks are not commonly used for olive as commercial trees are propagated by rooted cuttings. The analysis of rootstock-scion relations in olive trees has been rarely studied and there is little published information about its grafting characteristics (Caballero and Del Río, 2004). Salinity tolerance in olive trees, usually characterized by Na^+ accumulation in leaves, is a cultivar-dependent characteristic (Marín et al., 1995; Tattini, 1994) that has been related to a mechanism of salt ion exclusion by roots thereby preventing Na^+ translocation rather than Na^+ absorption (Benlloch et al., 1991; Tattini, 1994). The salt sensitivity of photosynthesis in olive trees, however, tends to be more dependent on concentrations of leaf Cl^- than on leaf Na^+ (Gucci and Tattini, 1997). Olive has been described as a moderately salt tolerant species that can be cultivated in saline soils where other fruit trees can not grow (El-Gazzar et al., 1979). 'Arbequina' is a relatively salt-tolerant olive cultivar based on shoot growth, leaf Na^+ and K^+ contents and K^+/Na^+ ratio under salinity stress (Marín et al., 1995). Relationship between olive tree water use and salinity tolerance, either to Na^+ or Cl^-, has not been described but the relatively salt tolerant olive grows very rapidly (Marín et al., 1995) so probably has relatively high water use rates.

To gain insights about mechanisms of salt tolerance in citrus and olive, we analyzed growth parameters, leaf gas exchange, chlorophyll fluorescence, water relations and mineral nutrition in both leaves and roots of these two species grown under salinity stress. This work is part of a larger comparative study of physiological responses to salinity stress in citrus and olive (Melgar et al., 2007). In addition, we wanted to compare the relative transpiration of these species to test the validity of Moya's (1999) hypothesis about the inverse relationship between salinity tolerance and water use.

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Materials and Methods

Plant material and growing conditions. The study was conduced at the University of Florida's Citrus Research and Education Center (Lake Alfred, FL, 28.09N, 81.73W). Rooted cuttings of *Olea europaea* L. 'Arbequina' (olive) and seedlings of Rangpur lime (Rl, *Citrus limonia* Osbeck) were grown in 1.5-L containers filled with autoclaved Candler fine sand soil. All plants were about 6 months old, growing vigorously and were watered three times per week with 100 mL of half-strength Hoagland's solution, which was at sufficient volume to leach from the bottom of all pots. Plants were grown in a greenhouse with maximum photosynthetically active radiation (*PAR*) (LI-170; LICOR, Inc., Lincoln, NE) at plant level of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with natural photoperiods. Average day/night temperature was 36/21°C and relative humidity varied from 40% to 100%.

To avoid osmotic shock, salt treatments were applied in increasing daily increments of 10 mm NaCl for citrus and of 20 mm NaCl for olive trees along with half-strength Hoagland's solution until final concentrations of 50 mm NaCl for citrus and 100 mm NaCl for olive trees were achieved. In citrus, we used 50 mm NaCl in the irrigation water since this concentration can cause a 50% growth reduction in about 2 months (Zekri and Parsons, 1992). In olive, we used 100 mm NaCl because this concentration is considered a critical threshold for reductions in growth (Chartzoulakis et al., 2002b; Loreto and Bongi, 1987).

Salt treatments were maintained for 12 weeks. The experimental design was a 2 × 2 factorial of two species (Olive and Rl) × two salt treatments (0 mm NaCl and 50 mm NaCl for Rl, or 0 mm NaCl and 100 mm NaCl for olive) with six replicate plants in each treatment.

Gas exchange parameters. Net gas exchange measurements were made 2, 4, 6, and 8 weeks after initiating the salinity treatments using a single mature leaf chosen from the middle of the shoot of each plant. Net CO_2 assimilation rate (A_{CO2}), stomatal conductance (g_s), leaf transpiration (E_{lf}) and leaf water use efficiency (WUE = A_{CO2}/E_{lf}) were determined with a LICOR portable photosynthesis system (LI-6200; LI-COR Inc.) using a 250-cm^3 gas exchange cuvette. The LICOR-6200 was equipped with constant light source (Model QB1205LI-670, Quantum Devices Inc., Barneveld, WI) to maintain *PAR* photon flux above 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which exceeds saturating *PAR* for citrus (Syvertsen, 1984). All gas exchange measurements were made in the morning (08:00–10:00 hr) to avoid high afternoon temperatures and low humidity. During all measurements, leaf temperature was 32 ± 2 °C, leaf to air vapor pressure difference was 2.4 ± 0.4 kPa, and ambient CO_2 concentration was 360 ± 20 $\mu mol \cdot mol^{-1}$ within the cuvette.

Chlorophyll analysis. Eight weeks after salinity treatment began, two leaf discs (0.45 cm^2 each) were removed from the same leaf used for gas exchange measurements (avoiding major veins). Chlorophyll was extracted from the discs for at least 72 h in the dark using *N,N*-dimethylformamide. Absorbances at 647 and 664 nm were determined with a UV-VIS spectrophotometer (Model UV2401PC, Shimadzu, Columbia, MD). Chlorophyll *a*, chlorophyll *b* and total chlorophyll were calculated using equations of Inskeep and Bloom (1985).

Water relations. On two selected clear days during week 11, pots were covered with plastic bags sealed around the base of the stem to stop evaporation from the soil. Whole plant transpiration was measured by weight loss from each pot during 6 to 7 daylight hours and averaged over the 2 d. After harvesting 1 week later, total leaf area per plant was measured (LI-3000; LI-COR Inc.) and used to express whole plant transpiration rate (E_{wp}) in units of mg H_2O $cm^{-2} \cdot h^{-1}$.

Water relation measurements were made during week 12. Predawn (06:00–08:00 hr) leaf water potential (Ψ_W) was measured using a Scholander-type pressure chamber (PMS instrument, Corvallis, OR) equipped with a hand lens to observe end points (Scholander et al., 1965). Leaves were immediately wrapped in aluminium foil, frozen by immersing in liquid nitrogen and subsequently stored at –18 °C until needed. Leaf osmotic potential (Ψ_Π) was measured after thawing and equilibrating to 25 ± 1 °C with an osmometer (Digital Osmometer, Wescor, Logan, UT). The measurements were carried out according to the manufacturer's instructions. Leaf pressure potential (Ψ_P) was calculated as the difference between leaf water potential and osmotic potential.

Growth and ion concentration. At the end of the experiment, plants were separated into leaves, stems, and roots. Leaves were briefly rinsed with deionized water and roots were gently washed free of sand. Tissues were oven-dried at 60 °C for at least 48 h and dry weights were measured. Dried leaves and roots were ground to a powder and tissue chloride concentration was measured in tissue sub-samples using a silver ion titration chlorodimeter (HBI Chlorodimeter; Haake Buchler, Sandle Brook, NJ) after the tissue had been extracted in a solution of 0.1 n nitric acid plus 10% acetic acid (García-Sánchez et al., 2006). Root Na^+ concentration was determined with an inductively coupled plasma atomic emission spectrometer (ICPES) after the tissue had been dry-ashed overnight at 500 °C and suspended in 1 m HCl.

Statistical analysis. Gas exchange data were subjected to a repeated measures analysis of variance to determine whether treatments differed over time. The other data were subjected to a factorial analysis with two species × two salinity level and six replicate plants per treatment. Means were separated by Duncan's multiple range test at $P \leq 0.05$ using SPSS statistical package (SPSS, Chicago).

Results

Gas exchange parameters. Salt reduced net gas exchange parameters beginning in the fourth to sixth week of the experiment in salinized Rl (Fig. 1). Six weeks after the beginning of the salinity treatments, reductions in the gas exchange parameters were greater for olive than for Rl. This may have been related to the higher NaCl treatment in olive than in Rl because by the end of the experiment, salinity-induced decreases of net gas exchange were similar for both species except for WUE, which was more reduced by salinity in Rl than in olive. A_{CO2}, g_s and WUE of both species were reduced from 27% to 45% by salinity compared with the control treatment. When gas exchange characteristics of non-salinized leaves of olive and Rl were averaged over 8 weeks, A_{CO2} was 17.9 and 14.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and stomatal conductance (g_s) was 1.1 and 0.6 $mol \cdot m^{-2} \cdot s^{-1}$ for olive and Rl, respectively. Average leaf WUE, however, was 1.63 for olive and 2.37 $mmol \cdot mol^{-1}$ for Rl.

Water relations. Whole plant transpiration (E_{wp}) was higher in olive than in Rl and the salt treatment decreased E_{wp} more in Rl than in olive (Fig. 2). Responses of leaf water relation parameters (Ψ_W, Ψ_Π, and Ψ_P) to salt treatment differed between the species (species x salt interaction $P \leq 0.001$) (Table 1). Salinity decreased Ψ_W in Rl but not in olive. Although Ψ_Π was decreased sufficiently by the salinity treatments in both olive and Rl to increase Ψ_P, the

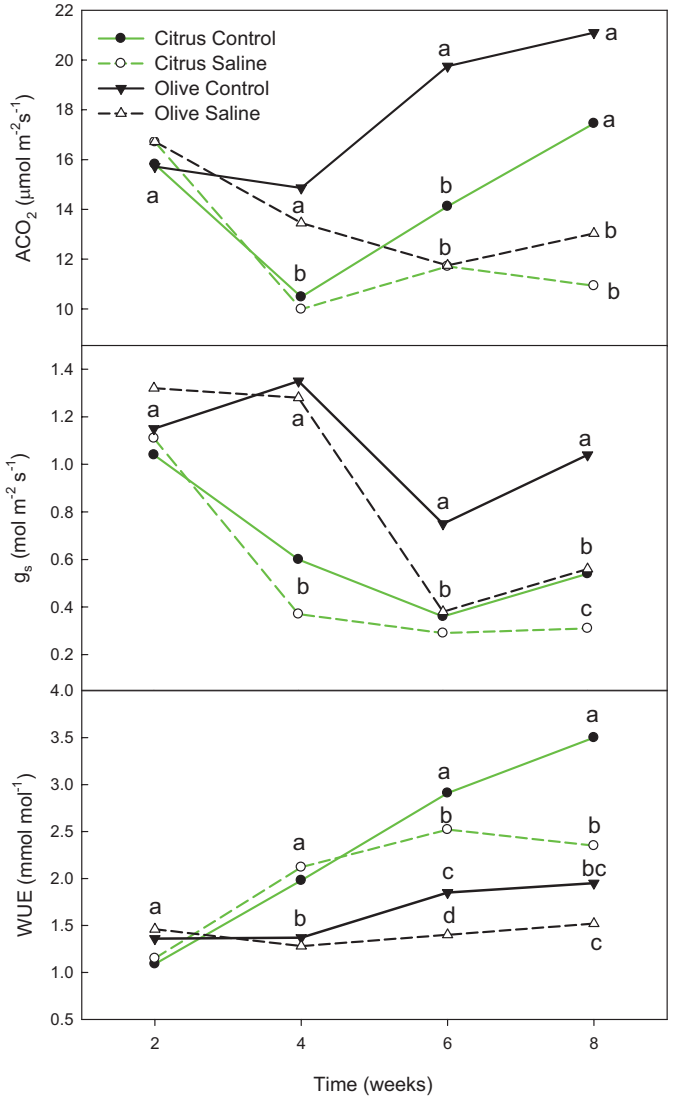

Fig.1. Effect of salinity (S, 50 mM NaCl in citrus or 100 mM in olive) on CO_2 assimilation rate (A_{CO2}), stomatal conductance (g_s) and water use efficiency (WUE) in leaves of 'Rangpur' (Rl) citrus and 'Arbequina' (A) olive trees relative to 0 NaCl control (C) trees. Each value is the mean of six plants (±SE). Means with different letters in the same week are significantly different at $P \leq 0.05$ according to the Duncan's test (n=6); NSNonsignificant.

magnitude of the decrease in Ψ_Π and increase in Ψ_P was greater in olive than in Rl.

Leaf chlorophyll concentration. Total leaf chlorophyll as well as chlorophylls *a* and *b* were significantly greater in olive than Rl in both control and saline treatments (Table 2). In olive, salt treatment did not affect leaf chlorophyll concentration but in Rl, salt treatment decreased leaf chlorophyll *a* and total leaf chlorophyll and increased the chlorophyll *a/b* ratio. Leaf chlorophyll *b* was not affected by the salt treatment in either species.

Growth parameters. In the non-salinized control treatment, the similarly aged olive and Rl plants had similar total plant dry weight (TPDW) (Table 3). However, Rl had a higher root dry weight and lower shoot to root ratio (S/R) than olive. In addition, Rl had thinner or less dense leaves since leaf dry weight to area ratio (LDW/area) was lower for Rl than for olive leaves. Salinity decreased TPDW in both olive and citrus. Salt treatment decreased leaf and stem dry weight but not root dry weight. There

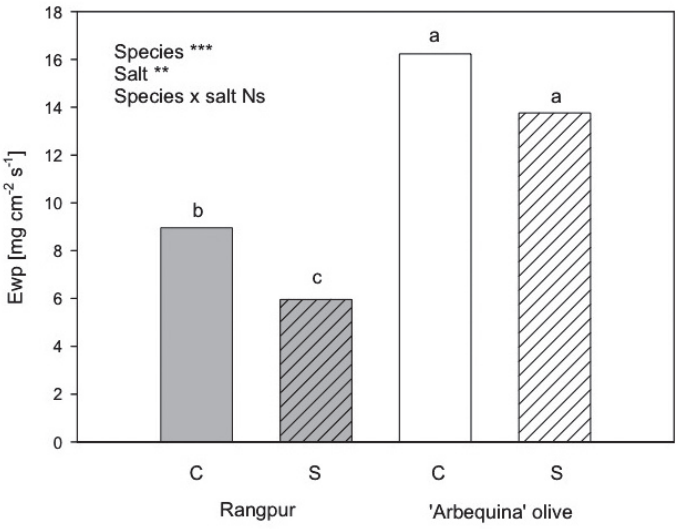

Fig. 2. Effects of salinity (S, 50 mM NaCl in citrus or 100 mM in olive) on mean (n=6) whole plant transpiration (E_{wp}) of 'Rangpur' and 'Arbequina' olive trees at the end of the experiment. 0S = non-salinized control treatment. Different letters at the top of each bar indicate significant differences at $P \leq 0.05$ (Duncan's test). NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 1. Effects of salinity on mean (n=6) water potential (Ψ_W), osmotic potential (Ψ_Π) and turgor potential (Ψ_P) of 'Rangpur' citrus and 'Arbequina' olive leaves.

Species	Salt	Ψ_W (MPa)	Ψ_Π (MPa)	Ψ_P (MPa)
Rangpur	Control	–0.31 a[z]	–1.85 a	1.54 c
	Salt	–0.59 b	–2.52 b	1.93 b
Arbequina	Control	–0.54 b	–2.05 a	1.52 c
	Salt	–0.61 b	–3.29 c	2.68 a
		Analysis of variance		
Species		***	***	**
Salt		***	***	***
Species × salt		**	**	***

[z]Means within a column followed by different letters are significantly different at $P \leq 0.05$ according to the Duncan test.
**, ***Significant at $P \leq 0.01$ or 0.001, respectively.

Table 2. Effects of salinity on mean (n=6) concentrations of chlorophyll (Chl) *a*, *b* and total (mg·dm^{-2}) and chlorophyll *a/b* ratio of 'Rangpur' citrus and 'Arbequina' olive plants at the end of the experiment.

Species	Salt	Chl a	Chl b	Total Chl	Chl a/b
Rangpur	Control	0.033 b[z]	0.011	0.044 b	3.37 b
	Salt	0.023 c	0.005	0.028 c	4.39 a
Arbequina	Control	0.044 a	0.025	0.069 a	1.86 c
	Salt	0.045 a	0.028	0.073 a	1.69 c
		Analysis of variance			
Species		***	***	***	***
Salt		NS	NS	NS	NS
Salt × species		*	NS	*	*

[z]Means within a column followed by different letters significantly different at $P \leq 0.05$ according to the Duncan test.
NS, *, ***Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Table 3. Effects of salinity on mean (n=6) leaf DW, leaf area, root DW, stem DW, total plant DW, leaf DW to leaf area ratio and shoot/root (dimensionless) of 'Rangpur' citrus and 'Arbequina' olive plants.

Species	Salt	Leaf DW (g)	Leaf area (cm^{-2})	Stem DW (g)	Root DW (g)	TPDW (g)	LDW/area ($g \cdot m^{-2}$)	S/R
Rangpur	Control	4.29	613	5.08	3.59	12.97	70 c[z]	2.45 b
	Salt	2.71	404	3.20	2.45	8.35	67 c	2.29 b
Arbequina	Control	3.83	306	4.95	1.39	10.17	125 b	5.91 a
	Salt	0.79	41	2.48	1.24	4.52	191 a	2.63 b
				Analysis of the variance				
Species		NS	**	NS	***	NS	***	***
Salt		**	*	*	NS	*	***	***
Salt × species		NS	NS	NS	NS	NS	***	***

[z]Means within the same column followed by different letters are significantly different at $P \leq 0.05$ according to the Duncan test.

NS, *, **, ***Nonsignificant or significant differences at $P \leq 0.05$, 0.01 or 0.001, respectively.

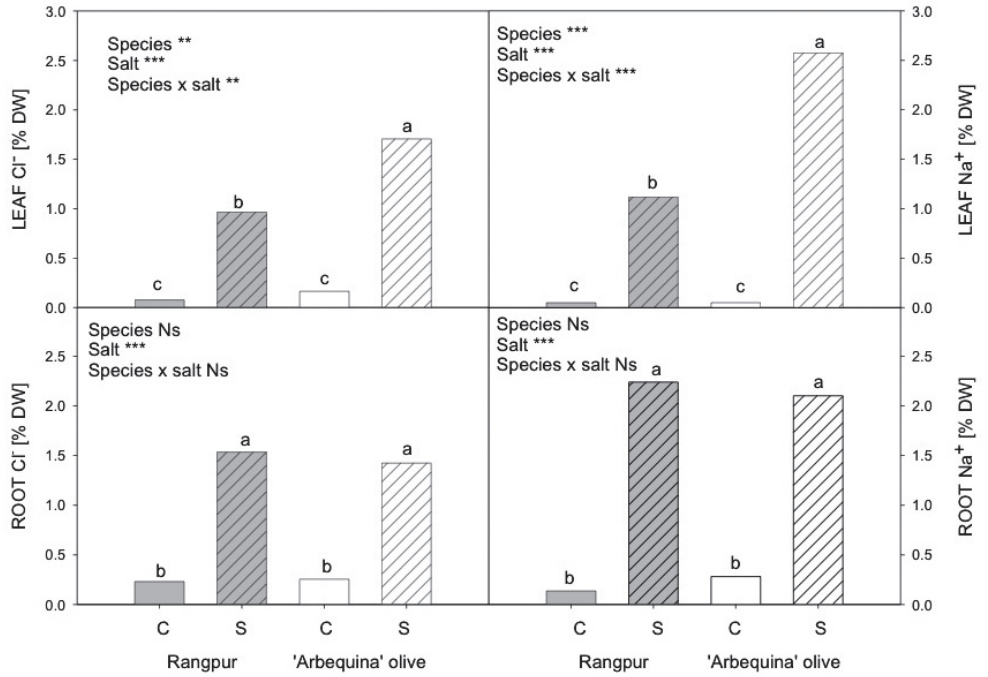

Fig. 3. Effects of salinity (S, 50 mM NaCl in citrus or 100 mM in olive) on mean (n=6) Cl^- and Na^+ concentration ($mg \cdot g^{-1}$ dry weight) in leaf and root tissue of 'Rangpur' citrus and 'Arbequina' olive at the end of the experiment. 0S= non-salinized control treatment. Different letters at the top of each bar indicate significant differences at $P \leq 0.05$ (Duncan's test). NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

was a significant interaction of salt × species in LDW/area and S/R. Salinized olive plants had higher LDW/area and a lower S/R than non-salinized plants. The decrease in S/R ratio in salinized olive was due to the decrease in total leaf area. In Rl, however, growth allocation was not affected by salinity as LDW/area and S/R were not affected.

Leaf and root Na^+ and Cl^- concentration. There were significant species × salt interactions for the leaf Cl^- and Na^+ concentrations (Fig. 3). Although the salt treatments increased leaf Cl^- and Na^+ concentrations in both species, olive leaves had higher values of both salt ions than Rl. Root Cl^- and Na^+ concentrations were also increased by salinity and were similar for both species. Concentrations of both Cl^- and Na^+ in roots of salinized Rl exceeded those in leaves. Concentrations of both salt ions in salinized olive were similar in leaves and roots.

Leaf mineral nutrition. Leaf N, expressed on a leaf dry weight basis, was relatively high in Rl compared to olive, but was not significantly affected by salinity (Table 4). Leaf N concentration was increased by the salt treatment in olive. Leaf Ca^{2+} concentration was decreased by salinity in Rl but was unaffected in olive. Leaf K^+ concentration was increased, and K^+/Na^+ ratio was decreased by salt treatment in both olive and Rl.

Discussion

Although net CO_2 assimilation rate was reduced by salt treatment in both species, changes in leaf turgor potential were not responsible for this decline in A_{CO2} since turgor potential was increased by salinity. Both A_{CO2} and g_s were reduced similarly but g_s was not responsible for the reduction of A_{CO2} because there were no reductions in C_i (Melgar et al, 2007). A decrease in C_i would have occurred with the decrease in A_{CO2} if stomatal limita-

Table 4. Effects of salinity on mean (n=6) total-N, Ca^{2+}, K^+ concentration (% dry weight) and K^+/Na^+ in leaves of 'Rangpur' citrus and 'Arbequina' olive.

Species	Salt	Total-N	Ca^{2+}	K^+	K^+/Na^+
Rangpur	Control	3.95 a[z]	1.87 a	0.19	16.07
	Salt	3.60 a	1.09 b	0.24	0.23
Arbequina	Control	2.75 b	0.54 c	0.16	13.94
	Salt	3.58 a	0.54 c	0.24	0.09
Analysis of the variance					
Species		**	***	NS	NS
Salt		NS	***	**	***
Salt × species		**	***	NS	NS

[z]Means within a column followed by different letters are significantly different at $P \leq 0.05$ according to the Duncan test.

NS, *, **, ***Nonsignificant or significant differences at $P \leq 0.05$, 0.01 or 0.001, respectively.

tions to CO_2 diffusion were a dominant limitation (Farquhar and Sharkey, 1982). Taken together, these responses imply that salt induced decreases in photosynthesis were not related to osmotic effects on leaf water relations but rather to direct effects of toxic salt ions on A_{CO2}.

There is a controversy about the relative importance of Cl^- or Na^+ toxicity because these ions often accumulate together (Storey and Walker, 1999; García-Sánchez et al., 2002b). Based on reductions in growth, Na^+ accumulation is an important determinant of salt tolerance (Benlloch et al. 1991) but the salt sensitivity of photosynthesis in olive trees tends to be more dependent on concentrations of leaf Cl^- than on leaf Na^+ (Gucci and Tattini, 1997). Although Na^+ accumulation can reduce leaf water potential, no clear association between water deficit and photosynthesis reduction was found here or in previous studies (Loreto et al., 2003). Bongi and Loreto (1989) considered a Cl^- concentration of 80 mM on a tissue water basis as the threshold for photosynthesis reduction in olive leaves. At concentrations greater than this threshold, photosynthetic impairments were associated with morphological changes in leaves along with reductions in growth, stomatal conductance and water potential.

A decrease in leaf chlorophyll concentration has been described in citrus rootstocks irrigated with high NaCl concentration (Zekri, 1991; García-Sánchez et al., 2002b). In our experiment, high concentration of Cl^- and Na^+ in Rl leaves caused a decrease in leaf chlorophyll *a* and thus, an increase in the chlorophyll *a*/*b* ratio. Despite the two fold greater salt concentration in olive, leaf chlorophyll concentration was greater in olive than in RL and was not reduced by the salt treatment (Table 2). Thus, there was no evidence that reductions in olive A_{CO2} were linked with reductions of leaf chlorophyll.

Olive leaves grown under salt stress were thicker or denser (higher LDW/area) than the control leaves. This higher LDW/area was not the result of a salt-induced increase in leaf succulence as has been observed in other species (Gebauer et al., 2004; Sobrado, 2005) since olive leaves from salt and control treatment had similar leaf water content (data not shown). The increase in LDW/area was due to the fact that leaf area expansion of olive was reduced by 86% whereas leaf dry weight was only reduced 79% in the salt treatment (Table 3; Chartzoulakis et al., 2002b). Increases in leaf thickness alone can reduce rates of photosynthesis (Syvertsen et al., 1995).

Salinity decreased growth (TPDW) in both citrus and olive. However, the pattern of growth distribution (S/R ratio) responded in different ways in the two species. Due to the reduction in shoot growth but not root growth, S/R was significantly decreased by salinity in olive. Similar decreases in olive S/R by salinity have been observed in previous experiments (Tattini et al., 1992; Klein et al., 1994; Chartzoulakis et al., 2002a) suggesting that olive roots are less sensitive to salt stress than shoots. In Rl, however, salinity did not affect S/R. Similarly, García-Sánchez and Syvertsen (2006) did not observe significant differences in S/R between control and salt treated trees for either salt sensitive or tolerant rootstocks. However, Zekri (1991) found that S/R in sour orange and Cleopatra mandarin decreased with increasing NaCl concentration in the irrigation water.

In both olive (Tattini et al., 1992) and citrus (García-Sánchez et al., 2002a), salt tolerance has been associated with the ability to prevent the uptake and/or translocation of salt ions from the root to shoot. 'Rangpur' is considered to be a good salt excluder (Maas, 1993). Our observation that Cl^- and Na^+ concentration was higher in roots than leaves of Rl (Fig. 3) suggest that the salt exclusion mechanism involves the low transport of Na^+ and Cl^- from roots to shoots as opposed to uptake avoidance by the roots . In olive, however, Na^+ and Cl^- concentrations in leaves and roots were similar so there was no apparent inhibition of Na^+ and/or Cl^- transport from roots to shoots. Some salt exclusion mechanism in olives apparently works effectively at low and moderate levels of salinity (Chartzoulakis et al., 2002b, Tattini et al., 1995) but at 100 mM NaCl, any exclusion ability may have been overwhelmed as salt ions accumulated in both roots and leaves.

The salinity effect on increasing leaf K^+ concentration along with decreasing the K^+/Na^+ ratio due to the increase of Na^+ concentration occurred similarly in both species. Plants with the ability to maintain a high K^+/Na^+ ratio under saline condition have relatively high salt tolerance (Benlloch et al., 1991). Root selectivity for K^+ instead of Na^+ could play an important role in salt tolerance because a high K^+/Na^+ ratio is much more important than a low Na^+ concentration in many species (Maathuis and Amtmann, 1999). In addition, high leaf K^+ concentration can facilitate osmotic adjustment with relatively less energy expenditure than the accumulation of other compatible solutes like mannitol and glucose in olive trees (Tattini et al., 1995), or proline and prolinebetaine in citrus trees (Storey and Walker, 1999). Both salinized olive and Rl lowered Ψ_Π sufficiently to increase turgor. Higher Na^+ and K^+ concentrations observed in salt treated trees compared with control trees may have contributed to this adjustment. The lower Ψ_Π values at higher NaCl treatment values in olive than in Rl, imply that osmoregulation was more efficient in olive than in Rl. Thus, olive trees under 100 mm salt stress had similar Ψ_W values as non-salinized control trees. Osmoregulation is an important mechanism of salt tolerance especially in relatively poor salt excluding cultivars or under severe saline stress (Gucci and Tattini, 1997).

Since olive was exposed to twice the salinity concentrations as Rl, it was not possible to directly compare their relative Na^+ and Cl^- uptake. It is interesting to note, however, that olive had higher leaf transpiration and whole plant water use than Rl and olive accumulated higher levels of both Na^+ and Cl^-. This would tend to support the idea of Moya et al. (1999, 2003) that water use and Cl^- ion accumulation are related.

Competition between Cl^- and NO_3^- uptake can occur in plants grown under salinity stress (Grattan and Grieve, 1992). Reductions in leaf N under salinity have been observed in some citrus species (Zekri and Parsons, 1992) and can be related to reduced water use

and growth (Lea-Cox and Syvertsen, 1993). In our experiment, leaf N concentration in salinized Rl plants was similar to those of the control treatment even though leaf Cl^- was increased and whole plant water use was decreased by salinity (Fig. 2). Leaf N concentration was increased by salt treatment in olive, which probably was a consequence of a concentration effect when LDW/area was increased and leaf growth was limited by salt stress.

In conclusion, the salinity treatments reduced total plant dry weight in both species, and increased LDW/area and decreased S/R in olive but not in Rl, which was exposed with a lower salinity concentration. Toxicity of Cl^- and Na^+ could have had different injury effects in olive and citrus plants. High Cl^- and/or Na^+ concentration in leaves reduced chlorophyll *a* and increased chlorophyll *a*/*b* ratio in citrus leaves but not in olive. Future work should investigate if olive can enhance the salt tolerance of other olive cultivars when used as a rootstock.

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