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BRIEF COMMUNICATION

Leaf gas exchange, water relations, nutrient content and growth in citrus and olive seedlings under salinity

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Abstract

The effects of salinity on growth, leaf nutrient content, water relations, gas exchange parameters and chlorophyll fluorescence were studied in six-month-old seedlings of citrus (*Citrus limonia* Osbeck) and rooted cuttings of olive (*Olea europaea* L. cv. Arbequina). Citrus and olive were grown in a greenhouse and watered with half strength Hoagland's solution plus 0 or 50 mM NaCl for citrus, or plus 0 or 100 mM NaCl for olive. Salinity increased Cl^- and Na^+ content in leaves and roots in both species and reduced total plant dry mass, net photosynthetic rate and stomatal conductance. Decreased growth and gas exchange was apparently due to a toxic effect of Cl^- and/or Na^+ and not due to osmotic stress since both species were able to osmotically adjust to maintain pressure potential higher than in non-salinized leaves. Internal CO_2 concentration in the mesophyll was not reduced in either species. Salinity decreased leaf chlorophyll *a* content only in citrus.

Additional key words: chlorophyll fluorescence, leaf chlorophyll content, NaCl, photosynthesis, rootstock.

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 can be associated with the ability of the root system to restrict the uptake and/or transport to saline ions to shoots (Levy and Syvertsen 2004). 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 (Zekri and Parsons 1992, Walker *et al*. 1993). Rangpur is one of the most salt-tolerant citrus rootstocks since trees grafted onto it accumulate Cl^- at a relatively slower rate than trees on other rootstocks (Zekri and Parsons 1992).

Olive trees are grown from propagated cuttings and their salinity tolerance is a cultivar-dependent characteristic (Marín *et al*. 1995, Tattini 1994) that has been related to a mechanism of salt ion exclusion by roots, preventing salt translocation rather than salt absorption (Benlloch *et al*. 1991, Tattini 1994).

Since considerable variations in salt tolerance exist among citrus and olive trees, we used two different NaCl concentrations in the irrigation water to study their respective salt tolerance. In citrus, we used 50 mM NaCl in the irrigation water since this concentration can cause a

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Abbreviations: Chl - chlorophyll; c_i - internal CO_2 concentration; E - leaf transpiration rate; E_{wp} - whole plant transpiration rate; F_m - maximum fluorescence of dark-acclimated leaves; F_0 - minimum fluorescence of dark-acclimated leaves; F_v/F_m - maximum quantum efficiency of photosystem 2; g_s - stomatal conductance; LDM/area - leaf dry mass to area ratio; P_N - net photosynthetic rate; S/R - shoot to root ratio; TPDM - total plant dry mass; WUE - water use efficiency; Φ - effective quantum yield; Ψ_P - pressure potential; Ψs - osmotic potential; Ψ_W - water potential.

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50 % growth reduction in about two months (Zekri and Parsons 1992). In olive, we used 100 mM NaCl because this concentration is considered a high salinity level (Chartzoulakis *et al.* 2002b) and a critical threshold for reductions in growth (Loreto and Bongi 1987). Olice cv. Arbequina has also been found to be a relatively salt tolerant cultivar based on shoot growth, leaf Na^+ and K^+ contents and K^+/Na^+ ratio (Marín *et al.* 1995). To gain insights into 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.

The study was conduced at the University of Florida, Citrus Research and Education Center (Lake Alfred, 28.09 N, 81.73 W; elevation 51 m). Rooted cuttings of *Olea europaea* L. cv. Arbequina and seedlings of Rangpur (*Citrus limonia* Osbeck) were grown in 1.5-dm^3 containers filled with autoclaved *Candler* fine sand soil. All plants were about six month-old and were watered three times per week with 100 cm^3 of half strength Hoagland's solution which was a sufficient volume to leach from the bottom of all pots. Plants were grown from July to September 2003 in a greenhouse with maximum photosynthetic active radiation (PAR) (measured by *LI-170*; *LI-COR*, Lincoln, NE, USA) at plant level of 1500 $\mu mol\ m^{-2}\ s^{-1}$ 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. Salt treatments were maintained for 12 weeks. The experimental design was a 2 × 2 factorial of two species × two salt treatments (0 mM and 50 or 100 mM NaCl) with six replicate plants in each treatment.

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

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 (Chl) 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 (*UV2401PC*, *Shimadzu*, Columbia, MD, USA). Chl *a*, Chl *b* and total Chl contents were calculated using equations of Inskeep and Bloom (1985).

On two selected clear days during week eleven, 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 the six to seven daylight hours and averaged over the 2 d. After harvesting one week later, total leaf area per plant was measured (*LI-3000*; *LI-COR*) and used to express whole plant transpiration rate (E_{wp}).

Measurements of Chl fluorescence were used to determine changes in the efficiency of energy utilization for electron transport. Chlorophyll fluorescence characteristics were measured during week twelve with a pulse modulated fluorometer (model *OS1-Fl*, *Opti-Sciences*, Hudson, NH, USA). Measurements were taken on one leaf per plant using both light-exposed and dark-acclimated leaves that had been covered with light exclusion clips (*FL-DC*, Opti-Sciences) for at least 15 min prior to fluorescence measurements. Maximum quantum efficiency of photosystem 2 (F_v/F_m) was measured as $F_v/F_m = (F_m-F_0)/F_m$, where F_v was the variable fluorescence, F_m and F_0 were maximum and minimum fluorescence of dark-acclimated leaves, respectively (Maxwell and Johnson 2000). Effective quantum yield (Φ) was calculated as $\Phi = (F'_M-F)/F'_M$, where F'_M and F were maximum and steady-state fluorescence yield in the light-exposed state, respectively (Van Kooten and Snell 1990).

Water relations measurements were made during week twelve. Pre-dawn (06:00 - 08:00 h) leaf water potential (Ψ_W) was measured using a Scholander-type pressure chamber (*PMS Instruments*, Corvallis, OR, USA) 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 ºC until needed. Leaf osmotic potential (Ψs) was measured after thawing and equilibrating to 25 ± 1 ºC with an osmometer (*Digital Osmometer*, *Wescor*, Logan, UT, USA). Pressure potential (Ψ_P) was calculated as the difference between leaf water potential and osmotic potential.

At harvest, plants were separated into leaves, stems and roots. Leaves were briefly rinsed with deionised water and roots were gently washed free of sand. Tissues were oven-dried at 60 °C for at least 48 h and dry masses 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, USA) after the tissue had been extracted in a solution of 0.1 M nitric acid plus 10 % acetic acid. 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.

Data were subjected to a factorial analysis of variance. Means were separated by Duncan's multiple range test at $P \leq 0.05$ using *SPSS* statistical package (*SPSS*, Chicago, IL, USA).

Reductions in gas exchange parameters started in the forth to sixth week of the experiment in salinized citrus (Fig. 1). Six weeks after the beginning of the salinity treatments, reductions in the gas exchange parameters were greater for olive than for citrus. This may have been related to the higher NaCl concentration applied to olive than to citrus. At the end of the experiment, salinity-induced decreases of gas exchange parameters were similar in both species. P_N, g_s and WUE of both species were reduced from 27 to 45 % by salinity compared to the control treatment. At the end of the experiment, non-salinized olive had a higher P_N and g_s but lower WUE than non-salinized citrus. There was no effect of salinity on internal CO_2 concentration (c_i) but olive leaves had higher c_i than citrus. Non-salinized olive had a higher whole plant transpiration (E_{wp}) than citrus (Table 1). Salt treatment decreased E_{wp} in Rangpur. When E_{wp} and single leaf transpiration (E_{lf}) data were compared across treatments, there was a significant positive correlation (data not shown).

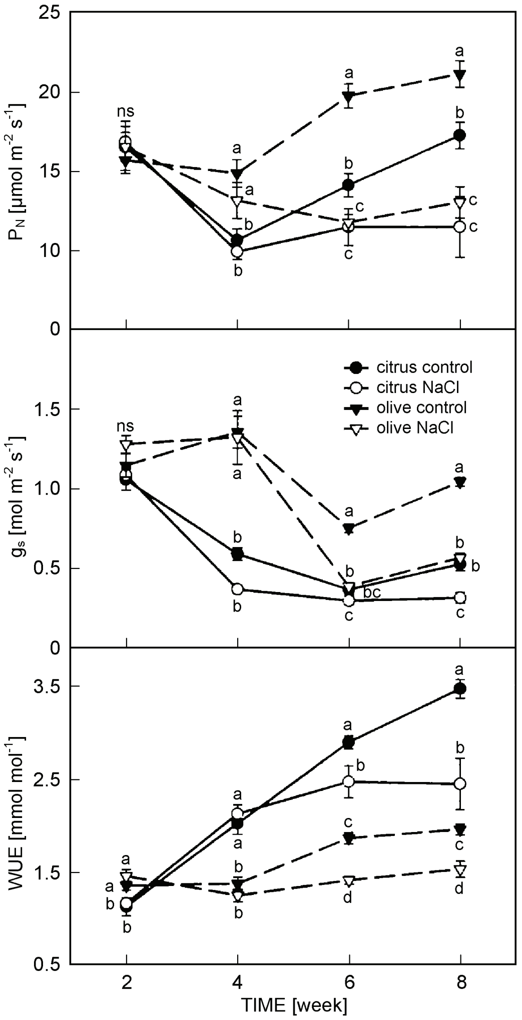

Fig. 1. Effect of salinity (50 mM NaCl in citrus or 100 mM in olive) on net photosynthetic rate (P_N), stomatal conductance (g_s) and water use efficiency (WUE) in leaves of citrus and olive trees. Each value is the mean of six plants ± SE. Means with different letters in the same week are significantly different at $P \leq 0.05$ according to the Duncan's test; ns - non-significant.

Table 1. Leaf water, osmotic and pressure potentials [MPa], transpiration rate of the whole plant, E_{wp} [mg cm^{-2} s^{-1}], internal CO_2 concentration, c_i [µmol mol^{-1}], chlorophyll content [mg dm^{-2}], parameters derived from chlorophyll fluorescence, leaf area [cm^2]. leaf, stem and root d.m. [g plant^{-1}], LDM/area [g dm^{-2}] and Na^+, Cl^-, Ca^{2+}, K^+ [mmol kg^{-1}(d.m.)] and N [mol kg^{-1}(d.m.)] contents in control and 50 or 100 mM NaCl stressed citrus and olive plants. Means (n = 6) within a row followed by different letters are significantly different at $P \leq 0.05$ according to the Duncan's test.

Parameters	Citrus		Olive	
	control	NaCl	control	NaCl
$-\Psi_W$	0.31a	0.59b	0.54b	0.61b
$-\Psi_S$	1.85a	2.52b	2.05a	3.29c
Ψ_P	1.54c	1.93b	1.52c	2.68a
E_{wp}	8.96b	5.96c	16.23a	13.75a
c_i	272.0a	284.0a	305.0a	318.0a
Chl *a*	0.033b	0.023c	0.044a	0.045a
Chl *b*	0.011a	0.005a	0.025a	0.028a
Chl *a*/*b*	3.37b	4.39a	1.86c	1.69c
F_0	77.4ab	89.3a	72.2b	58.3c
F_m	373.0a	367.0a	386.0a	320.0a
F_v/F_m	0.791a	0.753a	0.812a	0.815a
Φ	0.456a	0.452a	0.615a	0.623a
Leaf d.m.	4.29a	2.71a	3.83a	0.79a
Leaf area	612.69a	401.90a	290.02a	39.36a
Stem d.m.	5.08a	3.20a	4.95a	2.48a
Root d.m.	3.59a	2.45a	1.39a	1.24a
LDM/area	0.70a	0.67a	1.25b	1.91c
S/R	2.45a	2.29a	5.91b	2.63a
Leaf Na^+	6.23c	488.0b	5.46c	1123.0a
Root Na^+	59.0b	978.0a	123.0b	918.0a
Leaf Cl^-	22.0c	272.0b	46.0a	481.0a
Root Cl^-	64.0b	433.0a	72.0b	402.0a
Leaf Ca^{2+}	467.0a	272.0b	135.0c	134.0c
Leaf K^+	49.0a	61.0b	41.0a	61.0b
Leaf K^+/Na^+	16.07a	0.23b	13.94a	0.09b
Leaf N	2.818a	2.575a	1.967b	2.556a

Responses of leaf water relations parameters (Ψ_W, Ψ_S and Ψ_P) to salt treatments differed between the species (species × salt interaction at $P \leq 0.001$; Table 1). Salinity decreased Ψ_W in citrus but there were no differences in Ψ_W in olive. Although Ψ_S was decreased sufficiently by the salinity treatments in both olive and citrus to increase Ψ_P, the magnitude of the decrease in the Ψ_S and increase in Ψ_P was greater in olive than in citrus.

Total Chl content as well as Chl *a* and Chl *b* were significantly greater in olive than in citrus leaves for both control and saline treatments (Table 1). In olive, salt treatment did not affect leaf Chl content. In citrus, salt treatment decreased leaf Chl *a* and total Chl content but increased the chlorophyll *a/b* ratio as Chl *b* was not affected by the salt treatment in either species. The Chl fluorescence parameters Φ and F_v/F_m were also higher inr olive than in citrus, regardless of salt treatments. The salt treatment significantly reduced F_m for both species and F_0 for olive, compared to their respective controls. However, Φ and F_v/F_m were not affected by salinity in olive or citrus.

In control treatments, olive and citrus plants had similar total plant dry mass (TPDM), but citrus had a higher root dry mass and lower shoot to root ratio (S/R) than olive (Table 1). In addition, citrus had thinner or less dense leaves since leaf dry mass to area ratio (LDM/area) was higher for olive leaves. Salinity decreased TPDM similarly in olive and citrus. Salt treatment decreased leaf and stem dry mass but not root dry mass. There was a significant interaction of salt × species in LDM/area and S/R. Salinized olive plants had higher LDM/area and a lower S/R than non-salinized plants, but in citrus, LDM/area and S/R were not affected by the salinity treatment.

There were significant species × salt interactions for leaf Cl^- and Na^+ concentrations (Table 1). Although the salt treatments increased leaf Cl^- and Na^+ concentrations in both olive and citrus, olive leaves had higher values than citrus. Root Cl^- and Na^+ concentrations were increased under saline treatments and were similar for both species. Concentrations of both Cl^- and Na^+ in roots of salinized citrus exceeded those in leaves but concentrations of salt ions in salinized olive were similar in leaves and roots.

Leaf N was relatively high in citrus and was not significantly affected by salinity (Table 1). Leaf N concentration was increased by the salt treatment in olive. Leaf Ca^{2+} concentration was decreased by salinity in citrus but was unaffected in olive. Leaf K^+ concentration was increased, but K^+/Na^+ ratio was decreased by salt treatment in both olive and citrus.

Although P_N was reduced by salt treatment in both species, changes in Ψ_P were not responsible for this decline since Ψ_P was increased by salinity. Both P_N and g_s were reduced similarly but g_s was not fully responsible for the reduction in P_N because there were no reductions in c_i. A decrease in c_i would have occurred with the decrease in P_N if stomatal limitations to CO_2 diffusion were a dominant limitation (Farquhar and Sharkey 1982). Taken together, these responses imply that salt induced decreases in photosynthesis were probably not related to osmotic effects on leaf water relations but rather to direct effects of toxic ions. On the other hand, g_s, E and E_{wp} were decreased in salt treated plants of both species. In citrus, E_{wp} is generally reduced by salinity (Walker 1986, Syvertsen and Yelenosky 1988) even though rootstocks with different salt tolerance can have the same rates of transpiration and considerably different water flux through their roots (Storey 1995).

A decrease in leaf Chl content has been described in citrus rootstocks irrigated with high NaCl concentration (García-Sánchez *et al.* 2002b; Almansa et al. 2002). In our experiment, high concentration of Cl^- and Na^+ in citrus leaves caused a decrease only in leaf Chl *a* and thus, an increase in the Chl *a*/*b* ratio. Despite the two fold higher NaCl concentration applied to olive, leaf Chl content was greater in olive than in citrus and was not reduced by the salt treatment (Table 1). Thus, there was no evidence that P_N reductions in olive trees were linked with reductions of leaf Chl. However, P_N reductions in olive trees could have been caused by changes in the leaf anatomy. Olive leaves grown under salt stress were thicker or more dense (higher LDM/area) than the control leaves. This 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). According to Chartzoulakis *et al.* (2002b), the increase in LDM/area is due to the fact that leaf area expansion of olive is more sensitive than leaf dry mass to salt treatment (Table 1) and this salinity induced changes in leaf anatomy could have also altered the CO_2 transfer conductance from the substomatal cavities to the chloroplasts as a consequence of a longer path length over which CO_2 must diffuse (Parkhurst 1994, Syvertsen *et al.* 1995).

Salinity decreased growth (TPDM) in both citrus and olive (Table 1). However, the pattern of growth distribution (S/R) responded in a different way in the two species. Shoot/root was significantly decreased by salinity in olive but not in citrus. This reduction in olive was due to the inhibition effect on shoot growth, since salinity did not have any effect on the root dry mass. Similar decreases in olive S/R by salinity have been observed in previous experiments (Klein *et al.* 1994, Chartzoulakis *et al.* 2002a) and consequently, that olive roots are less sensitive to salt stress than shoots has been suggested. In citrus, however, salinity did not affect S/R. Salinity effects on S/R are not typical in either salt sensitive or tolerant citrus rootstocks (García-Sánchez and Syvertsen 2006).

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 saline ions from the root to shoot. Rangpur is considered to be a good salt excluder (Maas 1993) as we observed a mechanism of decreased transport of Cl^- and Na^+ from citrus to roots since Cl^- and Na^+ concentration was higher in roots than in the leaves (Table 1). In olive, however, Na^+ and Cl^- concentration in leaves and roots were similar so there was no inhibition of Na^+ and/or Cl^- transport roots to shoots and the salt ions were accumulated in both roots and leaves. As several authors suggested (Tattini *et al.* 1995, Chartzoulakis *et al.* 2002b) salt exclusion mechanism in olives works effectively at low and moderate levels of salinity, but at high levels salt ions accumulate in 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 in both species. 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 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). In fact, both salinized olive and citrus lowered osmotic potentials sufficiently to increase Ψ_P; higher Na^+ and K^+ concentrations observed in salt treated trees than in non-salinized control trees may have notably contributed to this adjustment. In this experiment, the lower Ψ_S values in the saline treatment in olive than in citrus, imply that osmorregulation was more efficient in olive than in citrus. Thus, olive trees under 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 stress (Gucci and Tattini 1997, Gadallah 1999). It is thought that the 100 mM NaCl applied to the relatively salt tolerant olive was sufficient to overcome any salt exclusion ability and to elicit increases in Ψ_P through osmoregulation.

Competition between Cl^- and NO_3^- uptake can occur in plants grown under saline stress (Grattan and Grieve 1992). Reductions in leaf N observed in some citrus species under salinity can be also related to reduced water use and growth (Lea-Cox and Syvertsen 1993). In our experiment, leaf N concentration in salinized citrus was similar to those of the control treatment even though leaf Cl^- was increased and whole plant water use was decreased by salinity (Table 1). Leaf N concentration was increased by salt treatment in olive, which may have been a consequence of a concentration effect when leaf growth was limited by salt stress.

In conclusion, the salinity treatments reduced TPDM in both species, increased LDM/area and decreased S/R in olive but the lower salinity treatment in citrus than in olive did not affect these parameters. Toxicity of Cl^- and Na^+ could have had different injury effects in olive and citrus plants.

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