Comparative Response of Two Olive (*Olea europaea* L.) Cultivars to Salinity*

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Abstract: Two olive (*Olea europaea* L.) cultivars, Leccino and Barnea, were exposed to increasing concentrations of NaCl (control, 2560, 5120 and 7680 mg l^{-1} of NaCl, which is equal to 4.0 dS m^{-1}, 8.0 dS m^{-1} and 12.0 dS m^{-1} salinity) in a sand culture. Plants were harvested and separated into different organs. Thin root, thick root, shoot and leaves were analysed for Na^+, Cl^-, K^+, Ca^{+2} and Mg^{+2} contents. Dry weights of the plants were determined. Shoot elongation was also measured. Increasing NaCl inhibited growth of the plants. However, this effect was only statistically significant in Barnea. The growth of Leccino was not statistically affected by the salinity. Cultivars took up similar amounts of NaCl by thin roots but translocated to leaves in different quantities. Salinity negatively affected the K^+, Ca^{+2} and Mg^{+2} contents of plant tissues. On the whole, the major effect of the NaCl treatment was observed in the K^+ content, followed by Ca^{+2} and Mg^{+2}. The Na^+/K^+ ratio of the plants increased with increasing salt treatments. The results clearly show that *Olea europaea* L. cultivars may possess an effective salt exclusion mechanism operating in the root system.

Key Words: Dry matter, Ion uptake and translocation, Salinity, Na^+/K^+ ratio, *Olea europaea* L.

İki Zeytin (*Olea europaea* L.) Çeşidinin Tuzluluğa Göreceli Tepkisi

Özet: Çalışmada kum kültüründe yetiştirilen iki zeytin (*Olea europaea* L.) çeşidine, Leccino ve Barnea, artan NaCl dozları (kontrol, 2560, 5120 ve 7680 mg l^{-1} NaCl; sırasıyla 4, 8 ve 12 dS m^{-1} tuzluluk yaratacak şekilde) uygulanmıştır. Daha sonra bitkiler hasat edilmiş ve ince kök, kalın kök, gövde ve yapraklarına ayrılmıştır. Bitki dokularında Na^+, Cl^-, K^+, Ca^{+2} ve Mg^{+2} analizleri yapılmıştır. Bitkilerin kuru madde ağırlıkları belirlenmiştir. Aynı zamanda sürgün uzunlukları alınmıştır. Tuzluluk bitki gelişimini sınırlandırmıştır. Bununla beraber, bu etki sadece Barnea'da istatistiksel açıdan önemli bulunmuştur. Leccino çeşidinin sürgün uzunluğu ise tuzluluktan istatistik olarak önemli derecede etkilenmemiştir. Çeşitler, ince kökleriyle benzer miktarlarda NaCl almış ancak yapraklara farklı seviyelerde iletmişlerdir. Tuzluluk bitki dokularının K^+, Ca^{+2} ve Mg^{+2} içeriklerini azaltmıştır. Genel olarak, artan tuzluluktan en fazla K^+ içeriği etkilenmiş, bu elementi Ca^{+2} ve Mg^{+2} izlemiştir. Bitki dokularının Na^+/K^+ oranı tuzluluk ile artış göstermiştir. Sonuçlar, *Olea europaea* L. çeşitlerinin kök sistemlerinde etkin olarak çalışan ve alınan tuzu dışlayan bir denetim mekanizmasının var olabileceğini ortaya koymuştur.

Anahtar Sözcükler: Kuru madde, İyon alımı ve iletimi, Tuzluluk, Na^+/K^+ oranı, *Olea europaea* L.

Introduction

Most of the salt stresses in nature are due to Na^+ salts, particularly NaCl. The term halophyte means "salt tolerant plant", but is used specifically for plants that can grow in the presence of high concentrations of Na^+ salts. Plants that cannot grow in the presence of high concentrations of Na^+ salts are called glycophytes ("sweet" plants). The olive is considered as moderately salt tolerant (Therios and Misopolinos, 1988; Rugini and Fedeli, 1990) and is generally cultivated in areas in which water is the main limiting factor in agricultural production (Tattini et al., 1994). Cultivar specificity, however, is extremely variable in the olive (Tattini et al., 1992). For instance, Leccino is evaluated as "relatively low salt tolerant" (Tattini, 1994). The salt tolerance of many woody species seems to be associated with the exclusion of Cl^- and/or Na^+ from their shoots and leaves. Salt-exclusion is one of the most important factors determining the ability to withstand salinity in glycophytes (Lewitt, 1980). Na^+ and Cl^- accumulate

basically in the shoots of less tolerant genotypes such as Leccino, suggesting that the exclusion mechanism probably occurs at the root level (Tattini et al., 1992). However, K^+ and Na^+ fluxes under saline conditions have not been estimated for olive species and there is no information concerning the influence of K^+-Na^+ selectivity on salt-resistance. According to Flowers et al. (1977), halophytes accumulate large quantities of ions in their tissues, whereas mesophytes are generally known to limit the uptake of ions (Greenway and Munns, 1980). The efficiency of the salt-exclusion mechanism is probably strictly related to the ability of plants to maintain an adequate K^+ transport rate and high external Na^+ concentrations (Yeo and Flowers, 1984). On the other hand, there is an inverse relationship between NaCl and the K^+, Ca^{+2} and Mg^{+2} contents of plants (Zidan et al., 1991; Ashraf, 2002).

The aims of the study were to determine the comparative response of 2 *Olea europaea* L. cultivars differing in resistance to salinity and to estimate the selectivity of Na^+, Cl^-, K^+, Ca^{+2} and Mg^{+2} fluxes.

Materials and Methods

Plant Materials

Two olive cultivars, Barnea and Leccino, were used as test plants in the experiment. At the beginning of the experiment, homogeneous seedlings taken from a commercial nursery were removed, cut at about 15 cm in length and planted in 3 l containers with coarse sand of 0.6-0.8 mm particle size. Coarse sand was chosen as a growing medium to facilitate the maintenance of a steady salt concentration by a high leaching rate, without developing oxygen stress within the root system. The use of coarse sand allowed complete drainage from the bottom of the container, without the need to apply a vacuum at the bottom of the container, since the hydrostatic water pressure required for drainage in coarse sand is close to zero. In addition, the use of coarse sand facilitated the eventual quantitative recovery of the root system.

Salt Treatments

The experiment was set up according to a completely randomised block design with 6 replicates and 1 plant per pot, making a total of 6 plants per replicate. Seedlings were grown for 2 months using half-strength Hoagland's solution (Hoagland and Arnon, 1950) until they reached about 30 cm. After 2 months, the control and 3 different NaCl doses (2560, 5120 and 7680 mg l^{-1} of NaCl, which is equal to 4 dS m^{-1}, 8 dS m^{-1} and 12 dS m^{-1}, respectively) and half-strength Hoagland's solution were applied in buckets together twice a day. The conductivity of irrigation water was nearly 1 dS m^{-1} (640 mg l^{-1} of NaCl).

Chemical and Physiological Analyses

Plant heights were measured weekly. Shoot elongation was expressed as a percentage, in relation to initial length, in order to eliminate differences in the initial size and vigour of the cultivars. Dry weight accumulation was determined as grams per plant. Salinisation continued without symptoms of damage for 95 days, and then plants were gently removed from the substrate, the roots were washed with deionised water and the plants were divided into thin root, thick root, shoot and leaves. Thin roots were selected mechanically by hand from the growing media. For nutrient analyses, plant organs were placed in paper bags and dried in a forced-air oven at 70 ^{o}C for 72 h. The samples were then ground in a stainless steel Wiley mill to 0.5 mm particles (Kacar, 1972). The ground samples were wet digested in a mixture of nitric acid:perchloric acid (HNO_3:$HClO_4$) (4:1) and then Na^+, K^+ and Ca^{+2} contents in the digest were determined using flame photometry (Jenway PFP7), and Mg^{+2} was determined using atomic absorbtion spectrophotometry (Varian SpectrAA 220FS). The Cl^- contents of the samples were determined using a chloridemeter (Jenway PCLM 3) (Kacar, 1972).

Statistical Analyses

Analysis of variance was performed for obtained data according to the method described to Little and Hills (1978). Mean separation was performed using least significant difference (LSD) at $P \leq 0.05$.

Results and Discussion

Growth was evaluated on the basis of 2 important parameters, shoot elongation (SE) and dry weight (DW). Cultivars differed in terms of average SE (Figure 1). However, growth was not linear for the cultivars and the difference was only statistically significant in Barnea. On the whole the lowest SE was measured in the highest salinity level, 12 dS m^{-1}. Barnea was more vigorous than Leccino. All salts can affect plant growth, but not all
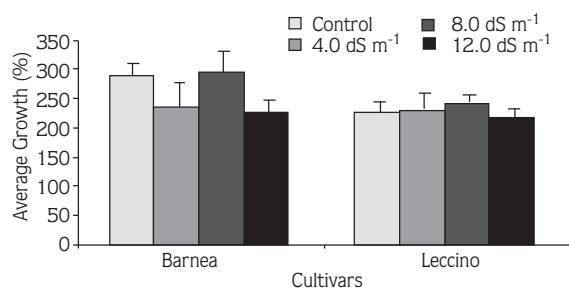
Figure 1. Average growth of Barnea and Leccino olive plants as affected by salinity. (LSD value at 5% level is 59.08 for Barnea and nonsignificant for Leccino).
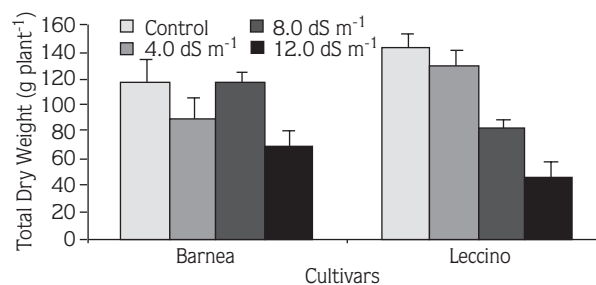

Figure 2. Total dry weight of Barnea and Leccino olive plants as affected by salinity. (LSD value at 5% level is 38.41 for Barnea and 30.20 for Leccino).

inhibit growth (Tester and Davenport, 2003). Various researchers have stated that olive cultivars to vary in the degree of their response to high salinity (Therios and Misopolinos, 1988; Benlloch et al., 1991; Chartzoulakis et al., 2002). Growth reduction by salt treatment was significantly higher in Leccino than in Frontoio under saline conditions (Tattini, 1994) and growth reduction following salt treatment in olive is generally attributed to excessive salt accumulation in growing tissues (Lewitt, 1980). According to Tattini et al. (1992), growth reduction of olive plants is related to leaf Na^+ and Cl^- accumulation. As reported by Jeschke and Wolf (1988), the growth rate of castor beans at different salinity levels was not related to the Cl^- content of the leaves but rather to Na^+ content.

Salinity significantly reduced the total dry weight of the cultivars (Figure 2). The greatest reduction in DW accumulation in Barnea in determined in the highest salt treatment, 12 dS m^{-1}. However, the reduction in DW accumulation in Leccino was linear and higher than in Barnea. Presumably, SE and DW are inversely affected by each other (Tattini et al., 1994). Barnea was more vigorous but a low DW accumulator. Leccino accumulated fairly high DW but was not as vigorous as Barnea. There is no correlation between the extent of Cl^- retranslocation and growth depression caused by salinity in several species. With regard to Na^+, however, there were significant correlations between decrease in dry matter production and Na^+ retranslocation from leaves, and in particular, the efflux of Na^+ from the roots (Staples and Toenniessen, 1984). Several hypotheses have been proposed to explain the adverse effects of salinity on plant growth, such as a salt exclusion mechanism, reduced root permeability and water availability enhancement of stomatal resistance,

reduced translocation of assimilates to roots, the amount of cytokinins reaching the tops, lower protein synthesis and decreased activity of enzymes, such as PEP and RuBp carboxylase. Salinity also affects the organelle ultrastructure and mitochondria, and causes distortion of the tonoplast (Therios and Misopolinos, 1988).

The exact mechanism of the differential response to NaCl of the 2 cultivars tested is not known and this might be a subject for further research.

The effects of salinity on tissue Na^+ and Cl^- contents of Barnea and Leccino are given in Figures 3 and 5 and in Figures 4 and 6, respectively. Cultivars differed in uptake and translocation of Na^+ and Cl^-, and the differences were statistically significant. The cultivars took up the ions proportionally to the applied concentrations (Chartzoulakis et al., 2002). Except for the highest salinity level, 12 dS m^{-1}, the Na^+ content of thin roots was higher in Leccino, but lower in leaves, than in other plant organs. However, at the highest salinity level, 12 dS m^{-1}, Leccino accumulated a higher amount of NaCl in leaves than in other plant organs. In Barnea, the thin root Na^+ content was highest. This cultivar clearly retained the ions in thin roots (Chartzoulakis et al., 2002). A similar difference was also observed in respect of the Cl^- the content of the cultivars. Presumably, the cultivars tried to accumulate the ions in thin roots and prevent translocation to thick roots, shoot and leaves. Barnea was clearly more successful at operating this mechanism. According to Tattini et al. (1994), the mechanisms of salt resistance in *Olea europaea* are probably due to the control of net salt import to the shoot. The mechanism is located within the root system, and prevents salt translocation, rather than salt absorption. As reported by various researchers, halophytes accumulate large
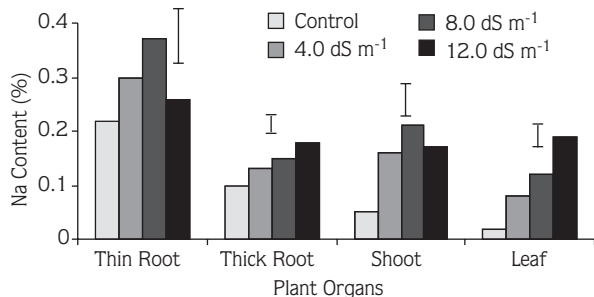
Figure 3. Effect of salinity on tissue Na content of Barnea. The bars represent LSD at 5% level.
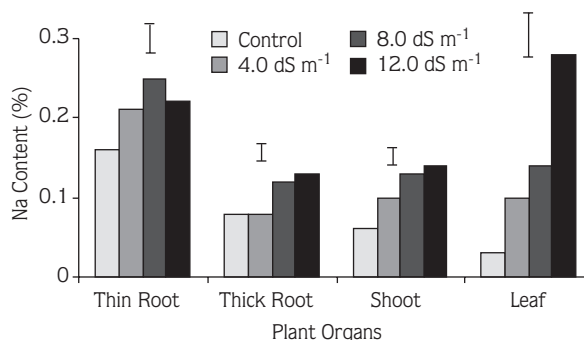

Figure 4. Effect of salinity on tissue Na content of Leccino. The bars represent LSD at 5% level.
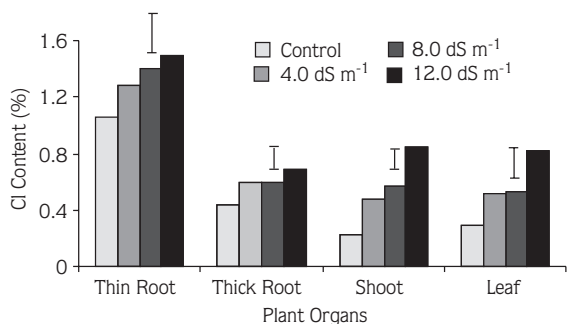

Figure 5. Effect of salinity on tissue Cl content of Barnea. The bars represent LSD at 5% level.
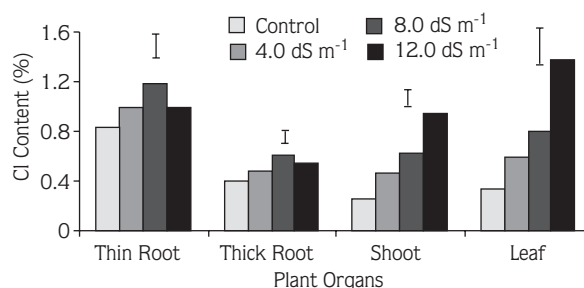

Figure 6. Effect of salinity on tissue Cl content of Leccino. The bars represent LSD at 5% level.
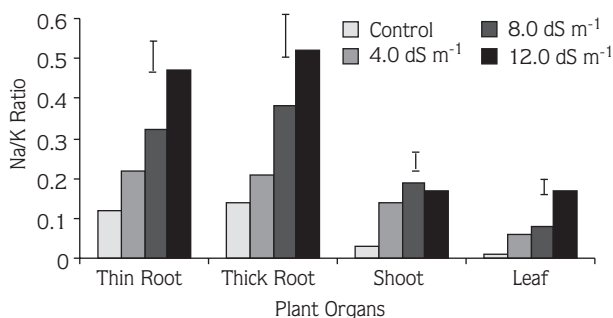

Figure 7. Effect of salinity on the tissue Na/K ratio of Barnea. The bars represent LSD at 5% level.
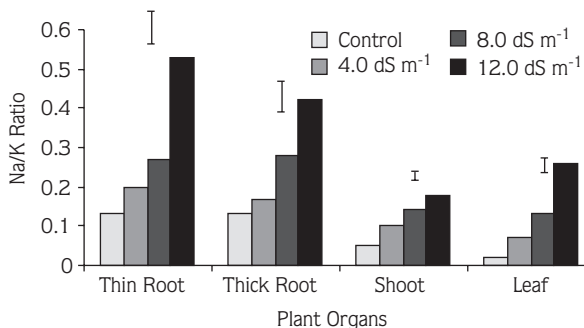

Figure 8. Effect of salinity on the tissue Na/K content of Leccino. The bars represent LSD at 5% level.

quantities of ions (Na^+ and Cl^-) in their tissues in order to adapt to a saline environment (Flowers et al., 1977), whereas mesophytes are generally known to limit the uptake of these ions (Greenway and Munns, 1980; Wyn Jones, 1981). Preferential accumulation of Na^+ and/or Cl^- is known to account for salt-tolerance in crop species, and specific injury is due to the accumulation of these ions rather than osmotic stress, which was suggested as the major factor in salt sensitivity (Gratten and Grieve, 1999; Jacoby, 1999).

Higher thin root concentrations in olive cultivars might result from low translocation potential (i.e. low mobile elements) or from a feedback control, from demand by vegetative growth which regulated the uptake and translocation from root to canopy. Translocation of "low mobile" elements such as Na^+ could be governed by fixation on the cell walls of the plant. The higher concentration of other readily mobile elements such as Cl^- in the thin roots compared to concentrations in the canopy can only be explained by a feedback control

mechanism. It is well known that high sink demand enhances uptake and translocation, particularly of readily mobile elements (Hale and Orcutt, 1987). According to Jacoby (1979), ions accumulate in the root or in the basal part of the shoot, from where they are returned to the root system and excreted back into the medium.

Greenway and Munns (1980) compared Na^+ and Cl^- contents in the leaves of 7 salt-tolerant and salt-sensitive varieties or subspecies. In 4 of these plants, tolerance was related to lower contents of Na^+ as well as of Cl^-. In 2 cases, there was little difference in the concentrations of either ion, or else there was some increase in the concentrations of both ions in the tolerant plants. Na^+ and Cl^- were excluded from the leaves of the tolerant varieties and species, but exclusion was much more efficient for Na^+ than it was for Cl^-. According to Jacoby (1999), salt toxicity is avoided by employing compatible osmotic cytoplasm adjustment and by confining salt, in particular Na^+, to the vacuoles. Some plants excrete Na^+ from the cytoplasm by active Na^+/H^+ antiport in the vacuole, and also to the apoplast. Other plants that apparently lack the Na^+/H^+ antiporter accumulate organic solutes and K^+ salts, and they prevent Na^+ influx to the roots and its translocation to the more sensitive shoots. The latter is accomplished by selective Na^+ absorption from the ascending xylem sap and its recirculation to the roots via the phloem.

Barnea accumulated a greater amount of Na^+ and Cl^- than did Leccino in plant tissues. Most probably, the salt tolerance of a plant depends on the regulation of ion transport, and the ion translocation process is not related to initial uptake levels in thin roots. Although the thin root ion content of Leccino was lower, this cultivar translocated more Na^+ and Cl^- to leaves. Especially in the highest treatment, 12 dS m^{-1}, Leccino could not prevent the translocation of NaCl. According to Ashraf (2002), NIAB-78, the most salt-tolerant cotton cultivar, retained more Na^+ concentration in the roots than did the moderately tolerant MNH-93 and Ravi, this being evidence of the retention of high Na^+ in the roots being one of the important salt-tolerance mechanisms in some plant species to restrict the uptake of ions into the shoots. As reported by Tattini (1994), different olive cultivars differ in uptake and translocation of NaCl, and in this respect Leccino might be regarded as a relatively low salt-tolerant olive cultivar. In terms of salinity resistance higher plants may be classified into 2 groups, salt excluders and salt includers. Salt excluders possess mechanisms that ensure that salt reaches the shoot only in very small amounts. This might be due to a very efficient selectivity toward K^+ during absorption. Another possibility is that Na^+ is absorbed in significant amounts but is reabsorbed from xylem sap in proximal parts of the root, or in the shoot, and is then either stored or retranslocated to the soil. In contrast, salt includers absorb salt and store it at high amounts in stem and leaves (Staples and Toenniessen, 1984) and Na^+ recirculation contributes to salt resistance in many plants (Wieneke and Lauchli, 1980; Winter, 1982; Walker, 1986; Jeschke and Wolf, 1988; Matsushita and Matoh, 1991). It is evident that, whatever the strategy by which a plant is able to adapt to salinity, transport phenomena plays a significant role.

The effects of salinity on K^+, Ca^{+2} and Mg^{+2} contents of different plant organs are given in Table 1. Relationships between NaCl treatments and macronutrients are statistically significant. Salinity negatively affected the K^+, Ca^{+2} and Mg^{+2} contents of plant tissues. On the whole, the major effect was observed in K^+ content followed by Ca^{+2} and Mg^{+2}. In contrast to Na^+ and Cl^-, the cultivars took and translocated a large quantity of K^+ to the canopy. Initial ion uptake levels were greater in Barnea than in Leccino. It is clear that the K^+ uptake level is inversely related to Na^+ and Cl^- contents in plant tissues (Chartzoulakis et al., 2002). The highest salinity level, 12 dS m^{-1}, reduced the K^+ content of leaves, shoots, thick roots and thin roots of Leccino to 29.5%, 31.7%, 47.6% and 60.4% of the levels in the control plants, respectively. The percentages of K^+ reduction in Barnea were 24.9%, 38.2%, 48% and 70.8% in leaves, shoots, thick roots and thin roots, respectively (Table 1). However, the same response was not observed for tissue Ca^{+2} and Mg^{+2} contents, and the decrease in Ca^{+2} and Mg^{+2} contents of the plant tissues was not as strong as that in K^+.

Probably, the presence of Ca^{+2} and K^+ enhances Na^+ exclusion by controlling channel selectivity. A high K^+ concentration in the growing medium also ensures an adequate supply for the plant in the presence of excess Na^+ (Jacoby, 1999). As reported by Ashraf (2002) there is an inverse relationship between NaCl and K^+, Ca^{+2} and Mg^{+2} contents of cotton leaves. Low accumulations of Na^+ and K^+ were found in the shoots of cotton subjected to saline conditions. Na^+ exclusion was found to be

Table 1. Effect of salt treatments on calcium, magnesium and potassium content (%/g DW) in different tissues of olive plants.

Treatment NaCl (dS m^{-1})	Leccino					Barnea			
	Thin Root	Thick Root	Shoot	Leaf		Thin Root	Thick Root	Shoot	Leaf
				Calcium					
Control	1.24a*	0.83a	0.43a	0.70a		1.33a	0.84a	0.53ab	0.78a
4.0	1.15a	0.70b	0.45a	0.65ab		1.36b	0.80a	0.55a	0.66ab
8.0	0.88b	0.69b	0.45a	0.51c		1.05b	0.72b	0.45c	0.59b
12.0	0.81b	0.66b	0.37b	0.54c		0.60c	0.69b	0.50bc	0.58b
				Magnesium					
Control	0.48a	0.25a	0.12ab	0.20a		0.52a	0.24a	0.18a	0.19ns
4.0	0.47ab	0.20b	0.13a	0.18a		0.50a	0.23ab	0.18a	0.17ns
8.0	0.44b	0.20b	0.13a	0.14b		0.47a	0.20b	0.17ab	0.15ns
12.0	0.40c	0.18b	0.11b	0.15b		0.33b	0.21ab	0.15b	0.15ns
				Potassium					
Control	1.19a	0.61a	1.17a	1.53a		1.98a	0.73a	1.65a	1.53a
4.0	1.05ab	0.50b	1.00b	1.44a		1.26b	0.62a	1.27b	1.54a
8.0	0.94b	0.44b	0.97b	1.04b		1.14b	0.41b	1.09c	1.50ab
12.0	0.47c	0.32c	0.80c	1.08b		0.58c	0.38b	1.02c	1.15b

* Values are means of 6 replications. Means separations by "Least Significant Difference" (LSD) at P ≤ 0.05.

associated with salt tolerance in 4 Indian cotton varieties. The salt-tolerant variety of *G. barbadense*, Giza-45, had less Na$^+$ and more K$^+$ in its leaves compared with the sensitive variety, Dandana.

Various researchers have stated that presence of K$^+$, and in particular Ca^{+2}, ions has been shown to reduce Na$^+$ influx to plant cells (Zidan et al., 1991) and consequently to reduce Na$^+$ damage (Lahaye and Epstein, 1971) and yield reduction (Ben-Hayin et al., 1987).

According to Ashraf and Ahmad (2000), salt-tolerant and salt-sensitive cultivars of *G. hirsutum* did not differ in terms of leaf or root Na$^+$ concentrations. The salt-sensitive cultivars accumulated more Cl$^-$ in the leaves than did all the 3 salt-tolerant lines at the highest salt level. The salt-tolerant cultivars had higher concentrations of K$^+$, Ca^{+2} and K$^+$/Na$^+$ ratios in the leaves than the salt-sensitive lines at the highest NaCl concentration. As reported by Tattini et al. (1992) K$^+$, Ca^{+2} and Mg^{+2} tissue contents were always decreased to a greater extent in salt-sensitive Leccino than in salt-tolerant Frontoio, indicating a reduced salt tolerance of the most vigorous variety. It has been observed that NaCl decreased K$^+$ content is associated with plants showing the most relevant growth reduction (Wyn Jones et al., 1979). The

major effect observed on K$^+$ content, above all in roots, seems to be a result of a specific antagonism towards uptake (Storey and Wyn Jones, 1977). However, K$^+$ content never reached levels of incipient deficiency. On the whole, Mg^{+2} resulted in a less affected cation, but leaves of Leccino plants supplied with 100 mM NaCl showed Mg^{+2} contents near deficiency level (Hartmann et al., 1966).

The Na$^+$/K$^+$ ratio of the plants increased with increasing salinity in the growing medium (Figures 7, 8). The Na$^+$/K$^+$ ratio of Leccino was higher than that of Barnea in thin roots. The balance between Na$^+$ and K$^+$ in plant tissues is one of the distinctive phenomena of the salt-tolerance mechanism. This happens due to selective distribution of Na$^+$, Cl$^-$ and K$^+$, with partial exclusion of Na$^+$ from growing tissues and transport of K$^+$ in meristematic cells and leaf mesophyll cells (Ashraf, 2002). As reported by Tattini (1994), salt tolerance in *Olea europaea* is mainly achieved by the efficiency of a salt-exclusion/retention mechanism operating at the root level that prevents Na$^+$ accumulation into actively growing shoots, while maintaning appreciable K$^+$ transport rates. Na$^+$ transport outward across the plasmalemma is carried out by a Na$^+$/H$^+$-antiporter and the activity of this proton

pump is higher in salt-resistant than in salt-sensitive species (Niu et al., 1993).

According to Tattini et al. (1992), the Na^+/K^+ ratio was always higher in salt-sensitive Leccino than in salt-tolerant Frontoio leaves, indicating a reduced selectivity of Leccino for K^+ ions. In this regard, plant tolerance to salinity was related to the Na^+/K^+ ratio in the leaf more than to the absolute Na^+ content (Samra, 1985). On the other hand, a low Na^+/K^+ ratio is recommended as a sensible criterion of salt tolerance in higher plants (Jeschke, 1984; Gorham, 1990) and the Na^+/K^+ ratio for non-halophytes should be <1 for optimal efficiency (Wyn Jones et al., 1979).

Conclusions

The results clearly show that *Olea europaea* L. cultivars may possess an effective salt-exclusion mechanism operating in the root system. However, the cultivars differed in respect of ability to use this mechanism. The cultivars tested took up similar amounts of Na^+ and Cl^- by thin roots but translocated them to leaves to different extents. Most probably, the control mechanism operating in thin roots prevents salt translocation rather than salt absorption. Salinity negatively affected the K^+, Ca^{+2} and Mg^{+2} contents of plant tissues. On the whole, the major effect was observed in K^+ content followed by Ca^{+2} and Mg^{+2}. The effect of salinity on plant growth was only statistically significant in Barnea. However, salinity reduced the total dry weight of the cultivars significantly. The results suggest that the translocation rate of the ions and the Na^+/K^+ ratio might be evaluated as reliable criteria giving clues to salt-tolerance levels of *O. europaea* cultivars. In this respect, Leccino may be defined as more sensitive to salinity than Barnea.

References

Ashraf, M. 2002. Salt tolerance of cotton: Some new advances. Critical Review in Plant Sciences, 21: 1-30.

Ashraf, M. and S. Ahmad. 2000. Influence of sodium chloride on ion accumulation, yield components, and fiber characteristics in salt-tolerant and salt-sensitive lines of cotton (*Gossypium hirsutum* L.). Field Crops Res. 66: 115-127.

Ben-Hayin, G., U. Kafkafi. and R. Ganmore-Neumann. 1987. Role of internal potassium in maintaining growth of cultured citrus cells on increasing NaCl and $CaCl_2$ concentration. Plant Physiol. 85: 434.

Benlloch, M., F. Arboleda, D. Barranco and R. Fernandez-Escobar. 1991. Response of young olive trees to sodium and boron excess in irrigation water. Hort Science. 26: 867-870.

Chartzoulakis, K., M. Loupassaki, M. Bertaki and I. Androulakis. 2002. Effects of NaCl salinity on growth, ion content and CO_2 assimilation rate of six olive cultivars. Scientia Horticulturae. 96: 235-247.

Flowers, T.J., P.F. Troke and A.R. Yeo. 1977. The mechanism of salt tolerance in halophytes. Annu. Rev. Plant Physiol. 28: 89-121.

Gorham, L. 1990. Salt tolerance in the triticale: Ion discrimination in rye and triticale. J. Exp. Botany 4: 601-614.

Gratten, S.R. and C.M. Grieve. 1999. Mineral nutrient acquisition and response by plants grown in saline environments. In: Handbook of Plant and Crop Stress. 2nd edition. (Ed. M. Pessarakli). Marcel Dekker Inc., New York, pp. 203-229

Greenway, H. and R. Munns. 1980. Mechanism of salt tolerance in non-halophytes. Annu. Rev. Plant Physiol. 31: 149-190.

Hale, M.G. and D.M. Orcutt. 1987. The Physiology of Plants under Stress. John Wiley and Sons Inc. NY, USA.

Hartmann, H.T., K. Uriu and O. Lillehand. 1966. Olive Nutrition. (Ed. N.F. Childers). Temperate to Tropical Fruit Nutrition. Hort. Publications, Rutgers State University. pp. 252-261

Hoagland, D.R. and D.I. Arnon. 1950. The Water Culture Method for Growing Plants Without Soil. Circular 347, College of Agriculture, University of California, Berkeley.

Jacoby, B. 1979. Sodium recirculation and loss from *Phaseolus vulgaris* L. Ann. Bot. 43: 741-744.

Jacoby, B. 1999. Mechanisms involved in salt tolerance of plants. In: Handbook of Plant and Crop Stress. 2nd Edition. (Ed. M. Pessarakli). Marcel Dekker Inc., New York. pp. 97-123

Jeschke, W.D. 1984. K^+-Na^+ exchange at cellular membranes, intracellular compartmentation of cations, and salt tolerance. In: Salinity Tolerance in Plants: Strategies for Crop Improvement. (Eds. R.C. Staples and G.H. Toenniessen). John Wiley and Sons Inc., New York. pp:37-66.

Jeschke, W.D. and O. Wolf. 1988. Effect of NaCl salinity on growth, development, ion distribution, and ion translocation in Castor bean (*Ricinus communis* L.). J. Plant Physiol. 132: 45.

Kacar, B. 1972. Bitki ve Toprağın Kimyasal Analizleri, II. Bitki analizleri. Ankara Üniversitesi Ziraat Fakültesi Yayınları, No. 453, Ankara, Turkey.

Lahaye, P.A. and E. Epstein. 1971. Calcium and salt toleration by bean plants. Physiol. Plant 25: 213.

Lewitt, J. 1980. Responses of Plants to Environmental Stresses. Vol. II. Water, radiation, salt, and other stresses. Academic Press Inc., New York.

Little, T.M. and F.J. Hills. 1978. Agricultural Experimentation: design and analysis. John Wiley and Sons Inc., NY, USA.

Matsushita, N. and T. Matoh. 1991. Characterization of Na^+ exclusion mechanism of salt-tolerant reed plants in comparison with salt-sensitive rice plants. Physiol Plant. 83: 170.

Niu, X., M.L. Narasimhan, R.A. Salzman, R.A. Bressan and P.M. Hasegawa. 1993. NaCl regulation of plasma membrane H^+-ATPase gene expression in a glycophyte and a halophyte. Plant Physiol. 103: 713-718.

Rugini, E. and E. Fedeli. 1990. Olive as an oilseed crop. In: Biotechnology in Agriculture and Forestry. Legumes and Oilseed Crops (Ed. Y.P.S. Bajaj). Springer-Verlag, Berlin, Germany. 593-641.

Samra, J.S. 1985. Sodicity tolerance of grapes with reference to the uptake of nutrients. Indian J. Hortic. 43: 60-65.

Staples, R.C. and G.A. Toenniessen. 1984. Salinity Tolerance in Plants. Strategies for Crop Improvement. John Wiley and Sons Inc. NY, USA.

Storey, R. and G.R. Wyn Jones. 1977. Quaternary ammonium compounds in plants in relation to salt resistance. Phyto chemistry 16: 447-453.

Tattini, M. 1994. Ionic relations of aeroponically-grown olive genotypes, during salt stress. Plant and Soil 161: 251-256.

Tattini, M., P. Bertoni and S. Caselli. 1992. Genotypic responses of olive plants to sodium chloride. J. Plant Nutr. 15: 1467-1485.

Tattini, M., C. Ponzio, M.A. Coradeschi, R. Tafani and M.L. Traversi. 1994. Mechanism of salt tolerance in olive plants. Acta Hort. 356: 181-184.

Tester, M. and R. Davenport. 2003. Na^+ tolerance and Na^+ transport in higher plants. Annals of Botany 91: 503-527.

Therios, I.N. and N.D. Misopolinos. 1988. Genotypic response to sodium chloride salinity of four major olive cultivars (*Olea europea.* L.). Plant and Soil 106: 105-111.

Walker, R.R. 1986. Sodium exclusion and potassium-sodium selectivity in salt-treated trifoliate orange (*Poncirus trifoliata*) and Cleopatra mandarin (*Citrus reticulata*) plants. Aust. J. Plant Physiol. 13: 293.

Wieneke, J. and A. Lauchli. 1980. Effects of salt stress on distribution of Na^+ and some other cations in two soybean varieties differing in salt tolerance. Z. Pflanzenernahr Bodenk. 143: 55.

Winter, E. 1982. Salt tolerance of *Trifolium alexandrinum* L. II. Ion balance in relation to its salt tolerance. Aust. J. Plant Physiol. 9: 221.

Wyn Jones, R.G. 1981. Salt tolerance. In: Physiological Processes Limiting Plant Productivity. (Ed. C.B. Johnson). Butterworths, London. pp. 271-292

Wyn Jones, R.G., G.J. Brady and J. Speirs. 1979. Ionic and osmotic relations in plant cells. (Eds. D.L. Laidman and R.G. Wyn Jones). Recent Advances in the Biochemistry of Cereals. Academic Press, Inc., New York, pp. 63-104.

Yeo, A.R. and T.J. Flowers. 1984. Mechanisms of salinity resistance in rice and their role as physiological criteria in plant breeding. In: Salinity Tolerance in Plants: Strategies for Crop Improvement. (Eds. R.C. Staples and G.H. Toeniessen). John Wiley and Sons Inc, New York. pp. 151-170.

Zidan, I., B. Jacoby, I. Ravina and P.M. Neumann. 1991. Sodium does not compete with calcium in saturating plasma membrane sites regulating ^{22}Na influx in salinized maize roots. Plant Physiol. 96: 331.