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Salinity Stress and Olive: An Overview

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ABSTRACT

Olive (*Olea europaea* L.) is a schleropyllous evergreen tree which is an important tree crop with a large distribution in the Mediterranean and Middle East regions. The environmental adaptability of the olive tree and its tolerance to drought and salinity has made it possible for most of these new plantations to be established in arid and marginal areas. In many such areas the only water available for irrigation is saline. Recent research indicates that certain olive cultivars are able to tolerate salinity of 5800 mg l^{-1} (EC ≈8 dS m^{-1}) producing new growth at a leaf Na concentration of 4-6 mg g^{-1} Dwt. Salt tolerance in olives significantly depends on the cultivar and is most likely due to control of salt translocation to the shoots. Many studies show that the mechanism of salt tolerance is placed in the roots preventing the translocation of toxic ions, rather than absorption. The exchange of K^+-Na^+ at the plasmalemma membrane seems to promote the modulation of Na^+ transport to the shoot. A high level of NaCl salinity significantly reduces the concentration of N, NO_3, K and nitrate reductase in the leaves, leading to an alteration in nutritional status. In salt tolerant cultivars, either a low or moderate salinity have a negligible effect on the growth of olive. However, in salt sensitive cultivars it reduces olive growth, which is associated with the reduction of CO_2 assimilation rate, stomatal and mesophyll conductance. Salinity tends to reduce fruit size, oil content and the ratio of unsaturated/saturated fatty acids but it has no effect on total phenol content. Salt tolerance in olive cultivars is associated with effective mechanisms of ion exclusion and retention of Na^+ and Cl^- in the roots. It should be possible to establish new cultivation in arid and saline lands by understanding the physiology of tolerance to salinity, screening salt tolerant cultivars and utilizing advanced agro-techniques in saline conditions.

Keywords: olive, photosynthesis, salinity, tolerance mechanism, yield and quality

Abbreviations: ECe, electrical conductivity of soil saturation extract; **EC_w**, electrical conductivity of irrigation water; **Pn**, net photosynthesis; **NR**, nitrate reductase; **ROS**, reactive oxygen species; **TDS**, total dissolved salts.

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INTRODUCTION

Salinization of lands has received more attention because of its progressive increase throughout the world (Munns 1993; Szablocs 1994; Kozlowski 1997). It is estimated that approximately a third of the world's irrigated lands and half the lands in semiarid and costal regions are affected by salinization (Epstin *et al*. 1980). The problem is serious so that 1000 Mha of land is affected by soil salinization (Szablocs 1994; Tester and Davenport 2003). Of the 1.5 Bha that is cultivated, about 5% (77 Mha) is affected by salt (Munns *et al*. 1999). Increased salinization of arable land is expected to have devastating global effects, resulting in 30% land loss within next 25 years and up to 50% by the middle of 21st century (Wang *et al*. 2003). Hence, it should be found an effective way to use saline lands by the cultivation of tolerant cultivars or other agro-techniques. The significance of salinity for the agronomical and physiological aspects of plants is enormous. All salts can affect plant growth, but not all inhibit growth. Among the most common effects of salinity is growth inhibition by NaCl. For some plants, particularly fruit trees such as citrus and grapevines, accumulation of both Na and Cl^- in the roots and aerial parts is most damaging to the plants often by inhibiting photosynthesis (Flower and Yeo 1988; Munns 1993; White and Broadley 2001). In other cases, Na is the primary cause of ion-specific damage (such as reduction in K activity). There was a reduction in photosynthesis in salinity treated plants reported by many researchers (Dowton 1977; Ball and Farguhar 1984; Behboudian *et al*. 1986).

Over 9 million hectares of the world's surface is planted with olives, 98% of which are grown in the Mediterranean basin alone. In terms of olive oil, the world's production is around 2.2 million tons, and the European Union produces 75% of it. Within the EU, Spain is the first producer with 50% of the total, followed by Italy (24%) and Greece (22%) (Aragüés *et al*. 2004). The Middle East and North Africa (mainly Morocco and Tunisia) produce approximately 14% and 4%, respectively. The rest is produced by other countries. These figures indicate the importance of olive produc-

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tion in the Mediterranean and Middle East regions. In the last decade, irrigated olive orchards have steadily increased in olive producing countries. In general, the cultivation of olives, one of the most economically valuable trees, is highly encouraged because of its limited water requirement in areas which are subjected to prolonged summer drought (Aragüés *et al.* 2004). Critically, the problem of salinization is increasing, often due to mismanagement of agriculture practice. Therefore, studies in olive should be devoted to understand the physiology of tolerance to salinity in olive, and increasing salt tolerance by either tradition breeding or genetic modification technologies.

The olive originated in the eastern Mediterranean area, and has been cultivated by man since ancient times. Trees are extremely long-lived (up to 1000 yr) and tolerance of drought, salinity and almost total neglect, and so have been reliable producers of food and oil for thousands of years. Earliest references of olive oil use and international trade date to 2000-3000 BC. The olive was spread throughout the Mediterranean, Europe and North Africa very early, due to its ease of vegetative propagation and cultivation in dry climates. The Romans built on earlier work on olive culture by Greeks, Arabs, and Egyptians, and refined olive oil extraction and improved cultivars used for oil (Kiritsakis *et al.* 1998). Today, the industry remains largely confined to Mediterranean countries of Europe, the Middle East, and North Africa, where it began thousands of years ago. The California industry began in the late 1800s as settlers planted orchards from cuttings taken from the original trees planted at Spanish missions.

There are studies that suggest that olive is moderately tolerant to salinity however, there is a considerable variation among salt tolerant cultivars (such as Mission, Manzanillo and Kalamata) so that several examples of successful use of saline water for irrigation can be found (Rhoades *et al.* 1992). In addition, little evidence exists in relation to the exact mechanism of salt tolerance of olive. In this paper the literature that pertains to salinity and the deleterious effect of salinity on the physiological aspects is reviewed. In the first part of each section, some general aspects of salinity and then specific research on olive are discussed.

PLANT GROWTH

In general, salinity stress results in an obvious stunting of plant (Greenway and Munns 1980). The rapid response of salt stress is the reduction in the rate of leaf expansion that results the inhibition of expansion as salt concentration increases (Xu *et al.* 2000; Tabatabaei 2006). Salt stress also causes a considerable reduction in the fresh and dry weights of leaves, stems and root (Hernnandez *et al.* 1995). The accumulation of salt in the root zone induces the development of osmotic stress (reduction in osmotic potential) and impairs cell ion homeostasis by prevention of the uptake of nutrients and increases the concentrations of Na^+ and Cl^- to potential toxic levels within the cells (Marschner 1995). These primary stresses induce the generation of reactive oxygen species, or ROS (Melloni *et al.* 2003), cause hormonal changes (Munns 2002), alteration of carbohydrate metabolism (Gao *et al.* 1998), reduce the activity of certain enzymes (Tabatabaei 2006) and impair photosynthesis (Chartzoulakis *et al.* 2002). As the result of these metabolic modifications, both cell division and elongation decline and may be completely inhibited, while cell death is accelerated (Munns 2002).

The available data in relation to salinity effects on olive reveals that olive growth in terms of leaf area, shoot length, both fresh and dry weight is reduced by imposing either moderate or high salinity (Bortolini *et al.* 1991; Tattine *et al.* 1992; Marin *et al.* 1995; Chartzoulakis *et al.* 2002; Tabatabaei 2006). The extent of reduction in olive growth varies significantly according to the duration of salt exposure and the cultivar (Chartzoulakis 2005).

The decline in leaf growth is an early response of the plants to salinity (Munns and Termaat 1986) and appears to be more sensitive compared to total dry weight. Chartzoulakis *et al.* (2002) reported that six Greek olive cultivars varied in their salinity tolerance, and the effect of salt stress at 200 mM NaCl on total leaf area was greater than that on the total dry weight. Tabatabaei (2006) found that the leaf area in three olive cultivars, Mission, Manzanillo and Zard, at 150 mM NaCl was significantly reduced compared to total dry weight. However, Wiesman *et al.* (2004) found that long-term irrigation with intermediate saline water (EC = 4.2 dS m^{-1}) had no effect on the vegetative growth of Barnea olive. Furthermore, Leaf abscission at high salinity (150 mM) occurred in cvs. Manzanillo and Zard led to a further reduction in leaf area. This may be caused by ion accumulation in the leaves, particularly old leaves (Greenway and Munns 1980). The reduction in plant growth was due to the reduced leaf growth, which Cramer (2002) reported.

Beside the reduction in vegetative growth of olive in response to salinity, it reduces the number of perfect flowers per inflorescence, the viability and germinability of the pollen and fruit set in olives (Therios and Misopolinos 1988; Cresti *et al.* 1994). The reduction in shoot/root ratio of olive trees grown in saline conditions (Chartzoulakis *et al.* 2002) causes the alteration of dry matter partitioning between root and shoot (**Fig. 1**).

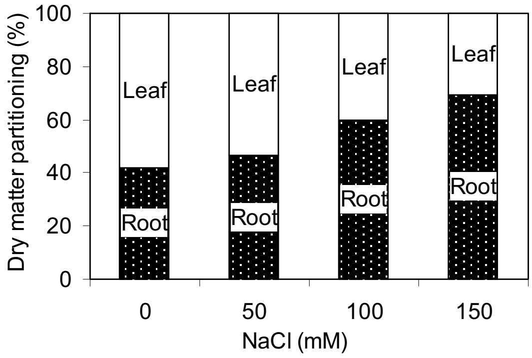

Fig. 1 Effect of salinity on the partitioning of dry matter in the root and shoot in Mission cultivar.

PHOTOSYNTHESIS AND STOMATAL CONDUCTANCE

Plant growth is the result of certain integrated and regulated physiological processes. An important physiological process is photosynthesis in which growth as biomass production is a measure of net photosynthesis (Pn) and therefore, environmental stress affecting growth also affects photosynthesis. The reduction of photosynthetic rat is due to several factors: (1) dehydration of cell membranes which reduce their permeability to CO_2 (2) salt toxicity, (3) reduction of CO_2 supply because of hydroactive closure of stomata, (4) enhanced senescence induced by salinity, (5) changes of enzyme activity induced by changes in cytoplasmic structure, and (6) negative feedback by reduced sink activity (Reddy *et al.* 1992; Parida *et al.* 2004). Two aspects of salinization, total dissolved salt (TDS) and their ionic composition, i.e. NaCl or other salts like $CaCl_2$, $MgCl_2$, affect photosynthetic activity. High salt concentration in soil and water yield high osmotic potential, which reduces the uptake of water by plants. The reduced water potential causes osmotic stress, which reversibly inactivates photosynthetic electron transport via shrinkage of intercellular space due to the efflux of water through water channels in the plasma membrane (Allakhveriev *et al.* 2000). Moreover, under high salt conditions Na ions leak into the cytosol and inactivate both photosynthetic and respiratory electron transport (Allakhveriev *et al.* 2000). The concentration of K is reduced under saline conditions leading to a reduction in quantum yield of oxygen evolution due to malfunctioning of photosystem II (Banus and Primo-Millo 1992).

Salinity also reduces photosynthetic rate due to a reduction in stomatal conductance resulting in restricted availability of CO_2 for the carboxylation reaction (Brugnoli and Bjorkman 1992). Stomatal closure minimizes the loss of water by transpiration and this affects chloroplast light harvesting and energy conversion systems thus leading to altered chloroplast activity (Reddy *et al.* 1991). The extent to which stomatal closure affects photosynthetic capacity depends on the magnitude of partial pressure of CO_2 inside the leaf.

In olive, both rates of net photosynthesis (Pn) and stomatal conductance were distinctly affected by NaCl salinity, although the effect varied with species and salt concentration (**Fig. 2**). Salinity increases the thickness of olive leaves (Bongi and Lorato 1989) leading to reduced mesophyll conductance by extending and creating a tortuous CO_2 pathway toward the chloroplast (Evans *et al.* 1994).

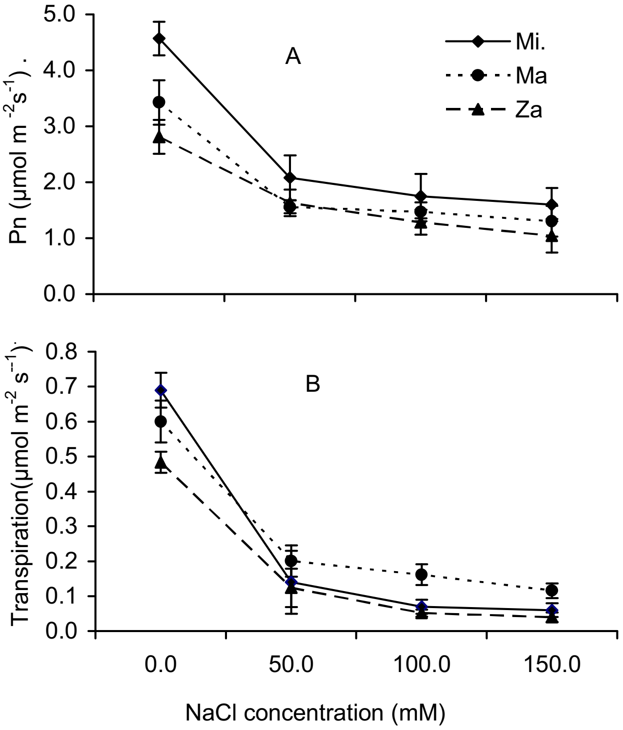

Fig. 2 The effect of salinity on the Pn (A) and transpiration rate (B) in three cultivars of olive (Mi, Mission; Ma, Manzanillo; Za, Zard).

Chartzoulakis *et al.* (2002) reported that one-year-old plants of six olive cultivars exposed to 200 mM NaCl for five months exhibited a significant decrease in assimilation rate at the end of the experiment ranging from 20% for salt tolerant Klamata to 62% for moderately sensitive Amphissis in young leaves. Tattine *et al.* (1995) found a marked reduction in photosynthesis in olive plants grown at 100 and 200 mM NaCl. The relationship between CO_2 assimilation and Na^+ or Cl^- content in cv. 'Frantoio' leaves is poor and changes drastically between salinity and stress relief period. They also reported a full recovery of photosynthesis in 50 and 100 mM salt stressed plants during the relief period for salt tolerant, accompanied by an increase in stomatal conductance and transpiration. Lorato *et al.* (2002) indicated that the low chloroplast CO_2 concentration set by both low stomatal and mesophyll conductance is the main limitation of photosynthesis in moderately salt stressed olive. Upon mild and moderate osmotic potential caused by either water or salinity stress, photosynthesis reduces in olive mainly due to stomatal closure (Angelopoulos *et al.* 1996). However, as the stress progress, biochemical constraints may limit the photosynthetic CO_2 fixation more directly. The limitation of CO_2 assimilation in salinity stressed plants causes the over reduction of the photosynthetic electron chain leading to the production of ROS. The other deleterious effect of salinity on olive is that the performance may be adversely affected by salinity by inducing nutritional disorders. These disorders may result from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant (Tabatabaei *et al.* 2004)

The reduced growth in three olive cultivars, Mission, Manzanillo and Zard, at high salinity (150 mM NaCl) and N concentration is associated with a remarkable inhibition of Pn (Tabatabaei 2006). The lowest inhibition was observed in Mission, which had a lower Na concentration in the leaves. The positive relationship between K/Na and Pn (**Fig. 3**) suggests that the Pn rate is associated with salt content, which is in disagreement with Tattini *et al.* (1995) who reported that the Pn rate is independent from salt content. The dependence of salinity and Pn rate varies according to the cultivar as reported by Chartzoulakis *et al.* (2002). The reduction of Pn in olive would be partly due to lower water availability in saline conditions. Loreto *et al.* (2002) demonstrated that the limitation of Pn in saline conditions in olive cultivars was a rustle of the low chloroplast CO_2 concentration, caused by the reduction in both stomatal and mesophyll conductance.

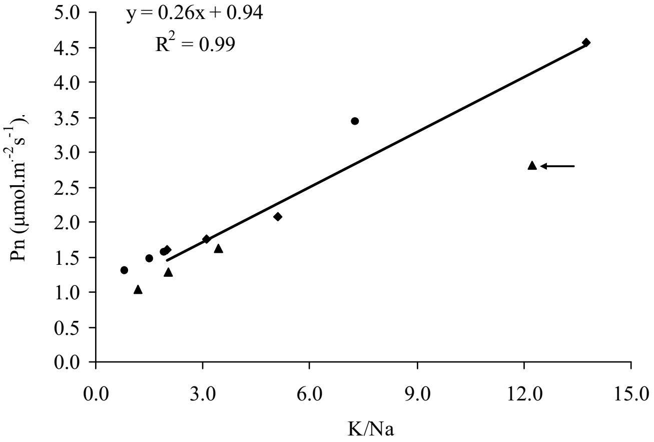

Fig. 3 Relationship between Pn and K/Na ratio of young leaves of olive trees (the labeled data has not been considered).

MINERAL NUTRIENTS

The cultivated plants are mainly glycophytes (Greenway and Munns 1980) and have evolved in low salinity conditions. The mechanisms they have developed for absorbing, transporting and utilizing mineral nutrients from saline substrates may not operate as efficiently or under saline as non-saline conditions. The concentration of Na^+ and Cl^- often exceed that of most macronutrients by one or two orders of magnitude, and by even more in the case of micronutrients. Hence, a high concentration of Na^+ and Cl^- in the root zone is most likely to depress nutrient ion availability and produce an extreme ratio of Na/Ca, Na/K, Ca/Mg, and Cl/NO_3. As result, the plant becomes susceptible to osmotic and specific ion injury as well as to nutritional disorders that may reduce its yield or quality.

In saline conditions nutrient imbalances can result through various ways: from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant or may be caused by physiological inactivation of a given nutrient (like K) resulting in an increase in the plant's internal requirement for that essential element (Grattan and Grieve 1994; Malakouti *et al.* 2003). It is reasonable to believe that two or more of these processes may be occurring at the same time, but whether they ultimately affect crop yield or quality depends upon the salinity level, composition of salts, the crop species, the nutrient in question and a number of environmental factors.

The availability and uptake of nutrients by plants in saline conditions are affected by many factors in the soil-plant environment. The solid phase of the soil and the concentration and composition of solutes in the soil solution controls the activity of the nutrient ion. Soil solution pH will influence the speciation and thus availability of certain nutrients. The concentration and ratios of accompanying elements can influence the uptake and transport of a particular nutrient and indirectly may affect the uptake and translocation of others. These interactions are complicated further by numerous environmental factors such as aeration, temperature, and both biotic and abiotic stresses.

The relationship between salinity and mineral nutrition of olive seems to be complex and studies of their interaction were mainly conducted in the greenhouse or in young plants. According to the literature that pertains to salinity and mineral nutrition of olive, the interaction between salinity and N, K, Ca has been demonstrated. The effect of salt stress on the concentrations of N, P, K, Ca, Mg, and Na in the young and mature leaves, shoots, and roots of six major Greek olive cvs. 'Koroneiki', 'Mastoidis', 'Kalamon', 'Amphissis', 'Kothreiki', and 'Megaritiki' were investtigated on self-rooted one-year-old plants (Loupassaki *et al.* 2002). In the no-NaCl controls, significant differences in the concentration of mineral elements in the tissues of the tested cultivars were found. The higher concentrations of mineral nutrients occurred in the roots and the lower ones in stems, with the only exception of N and in part of K ('Koro-neiki' and 'Amphissis'), where the lower values were found in the roots. Between cultivars, the differences in the concentration of mineral elements were clearer in the stems and to a lesser degree in the roots than in young or mature leaves. In salinized plants, over all cultivars and treatments, Na in young leaves, mature leaves, shoot, and roots increased 14, 18, 11, and 6 times, respectively. In all cultivars, the higher Na concentration was recorded in the roots followed by shoots, mature, and young leaves with the exception of the salt-sensitive 'Amphissis', which had the higher Na concentration (0.758% ± 0.03) in mature leaves. The concentration of K dropped in all organs as a result of the saline treatments.

Olive plants grown at various levels of salinity were affected differently by the rise in N in the nutrient solutions (Tabatabaei 2006). Interaction between salinity and N affects growth and metabolism of plants in order to cope with the changes taking place in their environment (Papadopoulus and Rendig 1983; Shenker *et al.* 2003). An apparent increase in salt tolerance has been noted when N levels supplied under saline conditions exceeded those that were optimum under non-saline conditions (Papadopoulus and Rendig 1983), implying that increased fertilization, especially N, may ameliorate the deleterious effects of salinity (Ravikovitch and Porath 1967). However, factors involved in salinity-N interaction are not well documented. Reports on the effects of salinity on N metabolism have focused on nitrate reductase (NR) activity.

As NR is a substrate inducible enzyme (Marschner 1995) and its decreased activity under salinization has been attributed by some researchers to decreased NO_3 uptake by plants under salt stress (Lacuesta *et al.* 1990; Abdelbaki *et al.* 2000). The decrease of NO_3 is accompanied by a high Cl^- uptake (Parida *et al.* 2004) and a low rate of xylem exudation in high osmotic conditions either by NaCl or other nutrients (Tabatabaei *et al.* 2004). Either the reduced NO_3 uptake or translocation leads to a lower NO_3 concentration in the leaves, consequently reducing NR activity of leaves under salinity conditions. Tabatabaei (2006) found that the NR activity was reduced with increasing NaCl salinity from 0 mM to 150 mM in three olive cultivars. This finding agreed with Cramer and Lips (1995), who indicated that salinity may control NR activity through NO_3 uptake since NR activity is largely determined by NO_3 flux into the metabolic pool, rather than by tissue NO_3 content itself. Most researchers have focused on the inhibitory role of Cl^- on NR activity, however the effect of Na on NR activity is still not known.

A clear relationship between Na concentration of leaves and NR reduction was proved by Parida *et al.* (2004) and Tabatabaei (2006) suggesting that Na may have an indirect effect on NR activity. It is most likely that at a low level of NaCl treatments the increased concentration of N and K in the leaves may be responsible for favorable growth of the plants. In general, high salinity causes a depression in NR activity, nitrate and N concentration and the K/Na ratio in salt-sensitive olive cultivars and the adverse effects of Salinity becomes more pronounced at both high and low levels of N concentration in the solution. Increasing N from 100 to 200 mg l^{-1} in the solution increases NO_3 concentration in the olive leaves, however it was ineffective at 300 mg l^{-1} in restoring the decrease in leaf NO_3 caused by the increased salinity. This indicates that the effect of salinity could be an independent factor according to cultivar from that of N if that N is not the limiting factor. Under salinity conditions, increasing N fertilization in salt-sensitive cultivars is ineffective in counteracting the adverse effects of salinity, which may build up during the growth period or high salinity conditions. However, in salt-tolerant cultivars increasing N fertilization can be an effective tool to restore decreased growth caused by high salinity.

Reduction in both K and K/Na at high salinity is another opposing effect of salinity, which impairs the function of K in the salinized olive. A reduction in K concentration and K/Na ratio in saline conditions was reported by Rush and Epstein (1978), Devitt *et al.* (1981) and Jackson and Volk (1997). The increased saline concentration in roots with increasing salinity in the root zone implies an exclusion mechanism. This mechanism is most likely to act in low or moderate salinity as reported by Chartzoulakis *et al.* (2002). Remarkable genotypic differences exist on Na transport to leaves so that Na concentration of leaves in cv. 'Mission' remained at a low level at a higher salinity concentration (Tabatabaei 2006). It could be that salt tolerance in olive trees is associated with the ability to reduce uptake and/or transport of saline ions.

Taking into account all available information on the interaction between salinity and nutrients, there is a genotypic difference among olive cultivars in their ability to accumulate Na, K or NO_3 ions in the shoot, when salinity is applied in the root zone. At high salinity in most cultivars, Na is transported and accumulated to the aerial parts, resulting in toxicity symptoms. Tatini (1994) reported that the resistance mechanism of salt tolerant olive cultivars is probably related to the ability to maintain an appropriate K/Na ratio in an actively growing tissue. The decline of K concentration under salinity conditions has been demonstrated (Greenway and Munns 1980; Devitt *et al.* 1981). This was also the case for olive trees, particularly in salt-sensitive cultivars. Hence, to maintain of relatively either high K concentration or K/Na ratio in the leaves plays an important role in regulation of monovalent cationic osmoticum and physiological function of K in either Pn or N assimilation.

YIELD AND QUALITY

Existing data on the effect of salinity on yield of olive trees are few and in some cases are contradictory. Generally, it is accepted that high salinity levels reduce olive tree yield (Gucci and Tattini 1997). Bouaziz (1990) did not find any adverse effect of irrigation with brackish water on yield, oil percentage of the fruit and alternate bearing. Klein *et al.* (1994) reported either an increase of 12% or a decrease of 18% in the yield of Manzanillo trees, irrigated with 4.2 dS m^{-1} under field conditions, depending on planting density. When the EC of the irrigation water was 7.5 dS m^{-1}, oil yield and fresh-fruit yield declined to 74 to 89% and 68 to 83% of the control, respectively. Wiesman *et al.* (2004) reported that young Barnea olive trees irrigated with 4.2 dS m^{-1} water produced 20% higher yield than those irrigated with 7.5 dS m^{-1}.

The decline in both leaf growth and leaf abscission in high salinity (150 mM) is an early response of the plants to salinity (Munns and Termaat 1986). Since the leaves are considered as photosynthetic sources of the plant, this causes a significant reduction in the supplement of photo-

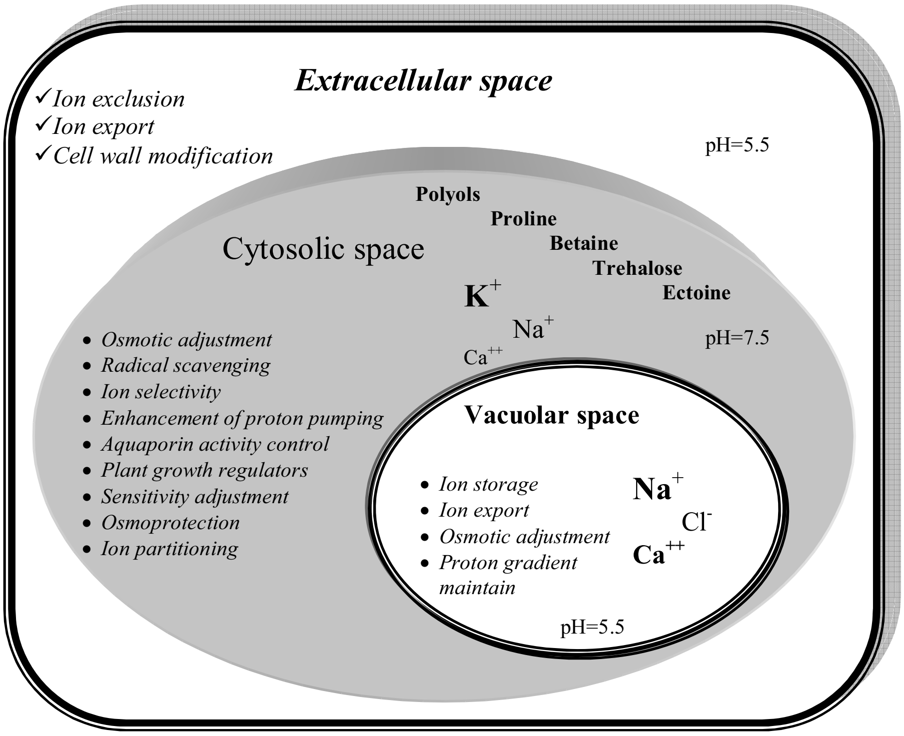

Fig. 4 Biochemical process of plants in tolerance to salt stress (see text for details).

assimilates to the sinks (such as fruits and merstimatic points). It is well known that high salinity decreases fruit weight and the moisture content of fruits (Stefanoudaki 2004; Klein *et al.* 1994). Salinity does not affect (Klein *et al.* 1994) or reduce the oil content of the fruit, although the extent of this reduction changes with cultivar (Stefanoudaki 2004; Wiesman *et al.* 2004). Chartzoulakis *et al.* (2004) reported that irrigation of Koroneiki olives with saline water increased Na^+ and $Cl^−$ concentration in olive fruit, like in other plant tissues. However, fruit K^+ concentration were higher than that in leaves, while the concentration of Na fruit was lower than that of leaves. The additional supply of potassium reduced to some extent the adverse effects of salinity by reducing the transport and accumulation of toxic ions in both leaves and fruits (Chartzoulakis 2005). On the other hand a potassium supplement caused a sharp increase of K^+ concentration in the fruits, resulting in an earlier change of fruit color from green to dark and finally fruit maturation (Chartzoulakis *et al*. 2004).

A few studies have been carried out on the effect of salinity on olive oil quality. Short-term results showed that total phenol concentration increased in the olive oil produced with high NaCl levels of irrigation water (Stefanoudaki 2004; Wiesman *et al.* 2004), as has been also reported for water stress (Cresti *et al.* 1994). Separation of the phenolic compounds by HPLC analysis of the Koroneiki oil extract showed an increasing tendency for the second fraction of the secoiridoid derivatives with salinity levels (Stefanoudaki 2004). Fatty acid composition of olive oil is also affected by salinity (Zarrouk *et al.* 1996). Palmitic acid, the major saturated fatty acid as well as the total saturated fatty acids increase with increasing salt concentration in the irrigation water. The ratio of unsaturated/saturated fatty acids is higher in the control and decreases significantly at moderate and high salinity levels (Zarrouk *et al.* 1996; Stefanoudaki 2004; Wiesman *et al.* 2004; Grattan *et al*. 2006). In addition, the oleic/linoleic acid ratio decreases by increaseing the salinity of water used for olive irrigation (Cresti *et al.* 1994 and Stefanoudaki 2004). These changes may account for the accelerated fruit ripening (Marzouk *et al.* 1990). In contrast to the above reports, no changes in the fatty acid composition of the oil were found when trees were irrigated with brackish water for 12 years (Bouaziz 1990).

SALT TOLERANCE

One of the most effective ways to overcome salinity problems is the introducing of salt tolerant cultivars. It is well know that differences in tolerance to salinity exist not only among different species, but also within certain species (Flowers *et al*. 1985; Plaut and Heuer 1985). In addition, the sensitivity or tolerance to salinity might vary according to the growing medium, the type of salinity in terms of composition and concentration, and the plant growth stage. Imposing NaCl salinity to plant affects water and ion transport processes, which could change the nutritional status and ion balance (Lauchli and Epstein 1990) as well as many physiological processes (Seeman and Critchley 1985; Munns and Termaat 1986). Plants develop a plethora of biochemical and molecular mechanisms to cope with salt stress. Biochemical pathways leading to products and processes that improve salt tolerance are likely to act additively and probably synergistically (Reddy *et al.* 1991). Biochemical strategies include (1) selective accumulation or exclusion of ions, (2) control of ion uptake by roots and transport into leaves, (3) compartmentalization of ions at the cellular and whole-plant levels, (4) synthesis of compatible solutes, (5) change in photosynthetic pathway, (6) alteration in membrane structure, (7) induction of antioxidative enzymes, and (8) induction of plant hormones (**Fig. 4**).

Olive is considered as a moderately salt tolerant plant (Rugini and Fedeli 1990) and is mainly cultivar dependent. In comparison with other Mediterranean-grown tree crops, olive is more tolerant than citrus but less tolerant than date palm (Ayers and Westcot 1976). According to Bernstein (1965) olive growth is reduced only by 10% when the electrical conductivity of the soil saturation extract (ECe) is 4–6 dS m^{-1}. This value can be as high as 6–8 dS m^{-1} in soils with a high calcium status. As other glycophytic species of medium tolerance to salinity, osmotic adjustment in olive was mainly achieved by accumulation of inorganic ions. Differences in osmotic adjustment between two cultivars reflected the respective exclusion capacity for Na^+ and Cl^- (Gucci *et al.* 1997). Recent studies suggest that olive trees can be irrigated with water containing 5800 mg l^{-1} (EC ≈8 dS m^{-1}), producing new growth at leaf Na levels of 4 to 5 mg g^{-1} (Al-Saket and Aesheh 1987; Tattini *et al.* 1992). Therios and Misopolinos (1988) reported that three-year old olive trees did not suffer salt stress at NaCl concentrations lower than 80 mM (ECw of 8.0 dS m^{-1}) during a 90-day culture period. Irrigation water with 137 mM NaCl (EC$_w$ of 13.7 dS m^{-1}) has been found to be the tolerance limit for olive trees (Rugini and Fedeli 1990). However, olive trees can tolerate even higher EC values, when NaCl represents a small portion of the soluble salts. The type of salts contained in the irrigation water is also related to the degree of plant damage. Bartolini *et al.* (1991) irrigating one-year old olive plants, cv. 'Maurino', containing either NaCl or Na_2SO_4 reported that Na_2SO_4 was more deleterious to the general growth than NaCl. Therois and Misoplinos (1988) studied the relative tolerance to NaCl of the olive cultivars 'Amphissis', 'Chondrolia', 'Chalkidikis', 'Koroneiki' and 'Megaritiki'. On the basis of toxicity symptoms and other measured parameters of growth, 'Chrondrolia' and 'Chalkidikis' seem to be more sensitive to NaCl than the other 3 cultivars. Salinity up to 80 mM NaCl increased the percentage of perfect flowers in 'Chondrolia' and 'Chalkidikis' and decreased it in 'Megaritiki'. Salinity also significantly reduced water absorption. Tabatabaei (2006) reported that cv. 'Mission' is able to tolerate 150 mM salinity. He also found that cvs. 'Zard' and 'Manzanillo' were moderately tolerant to salinity.

Taking into account all published information on the effects of salinity on growth and production of olive, a guideline for the quality of irrigation water for olives can be recommend. According to Chartzoulakis (2005), an optimum EC$_w$ value of used irrigation waters for olives is below 2.5 dS m^{-1}. The use of saline waters holding EC$_w$ >5 dS m^{-1} can cause a major problem for olives growth. In addition, the concentration of Na$^+$ and Cl$^-$ should be below 300 and 400 mg L^{-1}, respectively. A potential and cost effective source for irrigation water in olive-growing areas is the reuse of reclaimed wastewater, which contains essential nutrients for plants, such as nitrogen, phosphorus and K. In the island of Crete, Greece the use of such water would increase the irrigated area by 5.3% (Tsagarakis *et al*. 2001).

Tolerance to salinity appears to be cultivar dependent. Genotypic responses of olive to NaCl salinity have been extensively investigated with several works already conducted (Robinson 1987; Therios and Misopolinos 1988; Benlloch *et al.* 1991; Tattini *et al.* 1992; Benlloch *et al.* 1994; Tattini *et al.* 1994; El-Sayed Emtithal *et al.* 1996; Chartzoulakis *et al.* 2002a; Al-Absi *et al.* 2003; Tabatabaei 2003). The growth of all cultivars tested so far is reduced under salt stress to varying degrees. The available data shows that salinity tolerance of young olive cultivars, 'Pajarero', 'Lechino', 'Chetoui' and 'Chalkidikis' are considered as moderately sensitive, 'Cordal Manzanillo', 'Frantoio', 'Koroneiki', 'Chemlali', 'Zard' and 'Hotjiblanca' as moderately tolerant, while 'Mission', 'Kalamata', 'Picual', 'Lechin de Sevilla' and 'Megaritiki' as tolerant (Therios and Misopolinos 1988; Benlloch *et al.* 1991; Tattini *et al.* 1992; Benlloch *et al.* 1994; Chartzoulakis *et al.* 2002b; Tabatabaei 2006). A list of olive cultivars tested for salinity tolerance is given in **Table 1**. However, the tolerance of adult plants grown under field conditions may be different of that obtained with young plants grown in pots.

Salt tolerance in olive cultivars is associated with effective mechanisms of ion exclusion and retention of Na$^+$ and Cl$^-$ in the root (Tattini *et al.* 1994; Chartzoulakis *et al.* 2002b). It is more likely that K–Na exchange at the plasmalemma is involved in regulating the transport of Na$^+$ to the shoot by preventing apoplastic transport into the xylem (Gorham *et al.* 1985; Storey and Walker 1999). Specific proteins crossing the plasma membrane mainly regulate the entry of salts into root. K$^+$ channels and other non-selective cation channels are considered responsible for Na$^+$ uptake, while its efflux is mediated by Na$^+$/H$^+$ antiporters (Blumwald *et al.* 2000). In terms of Cl$^-$, various non-selective anion channels and Cl$^-$/nH$^+$ symporters appear to regulate Cl$^-$ accumulation into root cells (Tyerman and Skerrett 1999; White and Broadley 2001). Although such transporters have not been identified yet in olive we can, however, infer that differences among genotypes in the uptake and accumulation of salts probably reflect differences in the expression, the abundance or the properties of these carriers. Furthermore, the salt tolerance mechanism may be related to the capacity of olive to accumulate salt in the leaf vacuoles (Loreto and Bongi 1987). Sodium compartmentation into the vacuole appears to constitute the most effective way for cells to handle efficiently high concentrations of salts and prevent their toxic effects on the cytoplasm. Na$^+$ compartmentation is regulated by Na$^+$/H$^+$ antiporters (Hasegawa *et al.* 2000), the activity of which increases with Na$^+$ concentration within plant cells (Ballesteros *et al.* 1997).

CONCLUSION

Salinity tolerance in olive (*Olea europaea* L.) is a cultivar-dependent characteristic. Understanding the mechanisms involved in salt-tolerance of olive trees is crucial to select salt tolerant genotypes or to engineer salt-sensitive genotypes with genetic traits inducing salt tolerance. The characterization of genes that contribute to salt tolerance and the underlying physiological processes could lead to the identification of specific physiological and biochemical markers for salt tolerance in olives.

Although olive tree cultivation is expanding to many parts of the world during the last decades, its main production is concentrated in the Mediterranean and the Middle East regions, where 97% of the world's olive oil is produced (COI 2003). Irrigation of olives with saline water will inevitably increase in the future in the Mediterranean due to

Table 1 The tolerance of olive cultivars to salinity.

Resistance	Cultivar	Country	Reference
Tolerant	Megaritiki, Lianolia Kerkiras, Kalamata, Kothreiki, Mission	Greece	Therios and Misopolinos 1988; Chartzoulakis *et al.* 2002a, 2002b; Tabatabaei 2006
	Frantoio	Italy	Tattini *et al.* 1992, 1994
	Arbequiña, Picual, Jabaluna Nevadillo, Lechin de Sevilla, Cañivano, Esscarabajuelo	Spain	Benlloch *et al.* 1994; Marin *et al.* 1995
	Hamed	Egypt	El-Sayed Emtithal *et al.* 1996
	Chemlali	Tunisia	Bouaziz 1990
Moderately tolerant	Amphissis, Koroneiki, Mastoidis, Valanolia, Adramitini	Greece	Therios and Misopolinos 1988; Chartzoulakis *et al.* 2002a, 2002b
	Zard, Manzanillo	Iran	Tabatabaei 2006
	Maurino, Coratina, Carolca, Maraiolo	Italy	Bartolini *et al.* 1991; Briccoli Bati *et al.* 1994; Tattini *et al.* 1994
	Aggezi, Toffahi	Egypt	El-Sayed Emtithal *et al.* 1996
	Nabali Muhassan	Jordan	Al-Absi *et al.* 2003
Sensitive	Chalkidikis, Throubolia, Aguromanaki	Greece	Therios and Misopolinos 1988; Chartzoulakis *et al.* 2002a, 2002b
	Leccino	Italy	Tattini *et al.* 1994
	Bouteillan, Nabal	Egypt	El-Sayed Emtithal *et al.* 1996
	Pajarero, Chetoui, Calego, Cobrancosa, Meski	Spain	Benlloch *et al.* 1994; Marin *et al.* 1995

negative effects of population growth and climate change on the availability and quality of existing fresh water supplies. As a consequence, the risk of land salinization will exacerbate threaten agricultural production particularly in countries with a semi-arid or arid climate.

The salt tolerance in olive tree, like most other plants, is associated with the restriction of Na^+ and/or Cl^- transport from the root to the shoot. This inclusion/exclusion trait for both Na^+ and Cl^- is heritable (Sykes 1992), suggesting that breeding and selection for Na^+ and Cl^- excluding genotypes will continue to be a potentially rewarding area of research. Furthermore, attention should be given to the intracellular distribution of Na^+ and Cl^- (levels in the apoplast versus cytoplasm, vacuole), the possibility of ion recirculation as a factor in olive resistance (Na^+ removal from the xylem and possible recirculation to the phloem) and the improved understanding of membrane transporter systems for Na^+ and Cl^-.

Moreover, management of nutrients in saline conditions plays an important role in improving the growth of olive. An increase in N concentration at increased salinity concentration in salt-sensitive cultivars (such as cvs. 'Manzanillo' and 'Zard') is unlikely to improve growth and nutrition; however, in salt-tolerant cultivars N concentration in the root zone should be increased in order to improve plant growth. At a high salinity concentration, both high and low N concentrations in the root zone have opposing effects on olive tree growth. Therefore, the use of nutrients at saline conditions for both salt-sensitive and tolerant cultivars should be carefully managed. Recently, in the central part of Iran where land is affected by NaCl salinity, canal fertilization is used for establishing olive orchards. In this technique, young olive trees are planted into the canals filled with a mixture of manure and orchard debris. It helps to improve aeration, maintain moisture, supply nutrients and prevent root distribution into saline areas. A precise investigation needs to be conducted to evaluate the advantages of this technique in saline conditions.

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