

Irrigation Water Quality and Salinity Effects in Citrus Trees*

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I. INTRODUCTION

Most worldwide citrus production at least partially depends on irrigation for economic production (Shalhevet and Levy 1990). Irrigation is inevitably associated with the deterioration of water quality of run-off or ground water, especially due to increases in soluble salts. Poor water quality unavoidably leads to increased soil salinity. Excess salts from irrigation water must be removed from the root zone by leaching from rainfall or irrigation if agriculture is to be sustainable (Shannon 1997).

Citrus trees, and most other fruit trees with the exception of date, pistachio, pomegranate, and perhaps olive trees (Gucci and Tattini 1997), are relatively sensitive to salinity stress. Unlike deciduous fruit trees, world citrus production is limited to a relatively small climatic belt where frosts are not too severe. The best citrus is produced, however, where winter cold is adequate to induce uniform flowering and the development of good fruit color. Human immigration to these mild-climate zones and concomitant urban development competes with citrus for both land and water resources. This trend began in Southern California and is now also evident in the citrus producing areas of Arizona, Texas, Florida, and the Mediterranean coasts.

Increased consumptive use of water also results in the degradation of ground water quality all over the world (Jensen et al. 1990). In many coastal areas, demand for water exceeds the annual renewable supply and this over-exploitation of groundwater can lead to salt water intrusion into aquifers (Bosch et al. 1992). Any future rise in sea level may further threaten coastal ground water quality. However, salinization is caused not only by overuse of ground water, but also from slowing the

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rate of natural drainage to the sea. This process increases salts in ground water, that is already being replenished by increasingly saline irrigation water. Such salinization of the aquifer is not only limited to arid areas but is also evident in higher rainfall humid regions, such as parts of Florida, where salinity of well water increased at a rate of 12 mg L^{-1} per year (Calvert 1982) long before the more recent drought years. Urban requirements for high-quality water will ultimately require citriculture to depend on alternate poorer-quality water sources, including recycled wastewater and brackish water.

The quality of domestic wastewater is also likely to deteriorate. Ironically, as water conservation reduces per capita domestic water use and increases water-use efficiency, effluent is diluted with less fresh water even though the total salt output may not change. The toxic ion content of domestic wastewater can be reduced by replacing the Na^+ with K^+ in water softeners and cleaning agents and also by limiting the use of boron (B) in cleaning agents. The quality of industrial wastewater can be improved by modifying industrial processes to use less-harmful pollutants. The amount of NO_3^- and/or NH_4^+ can be reduced by effluent treatment procedures. Soluble chlorides will continue to be a problem since it is not possible to significantly reduce Cl^- in domestic effluent, nor is there an effective way of removing Cl^- from solution apart from expensive desalination of wastewater.

This review summarizes effects of irrigation water quality and salinity on citrus trees. We have tried to focus on cultural practices that are used to deal with poor-quality irrigation water, especially with respect to salinity, along with physiological responses of rootstocks and scions to salinity stress. Although this review concentrates on information that has become available since the review by Maas (1993), it was often necessary to review older work to develop the appropriate context in which to discuss experimental results. Conclusions about negative and positive aspects of salinity stress and their interaction with other environmental stresses are developed along with contrasting different experimental approaches in the laboratory, greenhouse, and field.

II. MANAGING SALINITY

A. Irrigation and Salinity.

All irrigation water contains salts; moderately saline water containing $200 \text{ mg Cl}^- \text{ L}^{-1}$ will add $1000 \text{ kg Cl}^- \text{ ha}^{-1}$ when applied at 500 mm per annum. If only part of that amount accumulates from year to year, soil

will become non-productive. Even if the overall salt content does not increase from year to year because of adequate leaching, salinity may become high enough to cause damage during rain-free periods, between irrigations, or in portions of the soil that are inadequately leached. Leaching, of course, requires good drainage. In poorly drained soils, fine-textured soils, or when the ground-water table is shallow, leaching requirements may necessitate the construction of an effective drainage system.

The effects of irrigation and salinity on perennial tree crops are cumulative (Hoffman et al. 1989), particularly for citrus (Shalhevet and Levy 1990). In humid areas with high rainfall, injury symptoms on citrus trees from saline irrigation water may be transitory. However, even temporarily affected trees may remain stunted compared with trees not exposed to saline water, especially if young trees are salinity-stressed.

The concentration of salts in a soil is a function of the total salts present and the soil water-content. Soil salinity is related to the electrical conductivity of standard saturated aqueous extract (EC_e). Managing irrigation and fertilization with high-salinity irrigation waters requires routine monitoring of the electrical conductivity of the irrigation water (EC_i) and EC_e . If excess salts accumulate in the soil, it is best to keep the soil near field capacity moisture content so as not to further concentrate the salts. Without adequate rain, it may become necessary to apply irrigations with excess water in order to leach salts from the root zone (leaching fraction). The required frequency of leaching varies with the degree of salinization and evaporative demand. Leaching may be required no less frequently than every other week in some environments and irrigation must be excessive. Areas with compacted soils or poor drainage may need special attention when managing salinity, such as flood leaching or other ways to handle slow percolation and poor aeration.

The method of irrigation and its interactions with the amount of rainfall throughout the season have important effects on responses of citrus trees to salinity. The amount of leaching depends on the amount of rainfall during the wet season and on the volume of soil wet by the irrigation water. Under dry summer conditions in Mediterranean climates, most of the active roots concentrate in the soil volume that is wet by the irrigation water since roots cease to develop at low soil temperatures when the soil is wet by winter rains. In summer-rainfall areas, however, roots grow beyond the irrigated zone.

EC_e measurement standardizes the amount of salts in the soil to conditions when the soil is saturated, but depending on soil moisture content, the actual salinity level in the vicinity of the tree roots may be several times greater than the EC_e . In sandy soils where salts are easily

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leached, using EC_e alone to evaluate soil salinity may not be sufficiently accurate. The EC_e of these soils is only an indication of soil salinity at the time of measurement and can change rapidly following irrigation or rainfall. Without proper water and nutrient management, citrus irrigated with high-salinity water can suffer reduced growth and production. Salt concentrations in the soil solution can be monitored effectively with ceramic suction cups or soil salinity probes after proper calibration to approximate EC_e (Boman 2000). Monitoring of soil solution is important where saline conditions may result from intentional deficit irrigation (Gonzalez-Altozano and Castel 1999) or from water-conserving irrigation scheduling based on soil moisture sensors (Boman et al. 2000) such as tensiometers or capacitance sensors (Fares and Alva 2000). When irrigation amounts do not exceed evapotranspiration, all the dissolved salts in the irrigation water that are not taken up by roots will remain in the root zone. Since the decreasing soil osmotic potential (Ψ_π) reduces water uptake by roots, soil moisture sensors will indicate that the soil water content is high, thereby reducing the amount of water per irrigation. Such a scenario can result in a spiraling increase in soil salinization even with comparatively good-quality water. The soil EC_e , which is linearly correlated to Ψ_π , should be monitored to prevent such problems from developing.

Microirrigation, especially drip irrigation, results in a relatively small soil volume that is routinely wet and leached by irrigation water. In arid climates, this comparatively small soil volume may be surrounded by a saline border and can be underlain by a salinized soil zone. Although drip irrigation can be beneficial for leaching salts away from localized root zones, a light rain may move the salts that accumulated on the surface or at the border of the wetted zone into the root zone. This necessitates the operation of drip irrigation (even during an initial rain event) until adequate rains have occurred to leach out accumulated salts. Salts can also accumulate in the periphery of furrows that are irrigated with saline water.

1. Irrigation Methods

Gravity Irrigation. If adequate water is available, flood or basin irrigation can have an advantage over microirrigation due to the high downward movement of soil water. This leaching depends on soil permeability, drainage, and on the depth to ground water. The interval between irrigations is usually relatively long with these methods, so when the water tables are shallow, ground water salinity can affect soil salinity if the net flow of water is upward for a significant period of time in the absence

of sufficient irrigation or rainfall to maintain downward water flow (Boman 2000). This method usually will depend on skilled labor to maintain uniform irrigation. Thus, basin irrigation is becoming less popular in new large-scale plantings because of the soil grading and skilled labor needed to maintain the system and because it requires a high volume of water. With good drainage, flood irrigation is still an excellent way to leach saline soils before planting. Furrow irrigation with saline water may cause salt buildup in the periphery of the wetted zone as mentioned above. The necessary soil grading, greater need for weed control, and skilled labor to operate such systems make it less feasible than other methods for many locations.

Sprinkler. Overhead irrigation is still practiced in some parts of the world. This method requires comparatively high pressure, high volume, and good-quality water. If used with reclaimed water, there is also the hazard of biological contamination of the fruit. Citrus leaves easily absorb Cl^- and Na^+ from direct contact with water droplets (Eaton and Harding 1959; Ehlig and Bernstein 1959). Salt accumulation is a function of the evaporation rate, which increases the salt concentration of the water film on leaves. Damage can also develop from windblown salt water near the sea.

Severe damage to leaves located in low canopy positions of under-the-canopy sprinkler-irrigated trees or in canopies of overhead-irrigated citrus has been described (Harding et al. 1958; Lundberg 1971; Nakagawa et al. 1980; Spurling 1981; Calvert 1982). Nighttime irrigation was recommended for overhead irrigation with comparatively high salinity (1200 mg L^{-1} TDS; Tucker 1978), since the accumulation of dissolved salts is greater from daytime than nighttime irrigation because of the different evaporative demand. Pulsed irrigation is dangerous, since salt absorption is greater from intermittent than from continuous wetting. The sensitivity of a citrus scion/rootstock combination to injury through direct foliar contact bears no relationship to its general tolerance to soil salinity that will be discussed later. Leaf Cl^- and Na^+ toxicity from direct contact with saline water has different symptoms from toxicity of Cl^- that was absorbed by roots. Contact damage, consisting of burned necrotic, or dry-appearing tips on leaves, is one of the most common visible salt injury symptoms. In some cases, overhead irrigation, particularly at low humidity, will cause ring-shaped lesions on fruit where irrigation water evaporated. There are reports of Cl^- and Na^+ concentrations in leaves from low positions in the canopy that were about four times greater than those of the upper leaves (of grapefruit, 'Valencia' and 'Washington

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Navel' orange). The lowest concentration of either Na⁺ or Cl⁻ generally associated with leaf burn is about 0.25% of leaf dry weight. Young trees (1–2 years) on 'CTRM' (see Table 2.1 for rootstock abbreviations) seem to be more susceptible to saline irrigation water spray and can develop brown "blisters" of dead tissue on their trunks (Boman 1999). Using overhead irrigation with poor-quality water for evaporative cooling (Brewer et al. 1979) during conditions of high evaporative demand can be especially dangerous and can lead to rapid concentration of the remaining salt solution on the leaves.

Under-the-canopy sprinklers, especially microsprinklers, lessen the danger of salt damage to wetted leaves. The use of microsprinklers has become popular in Florida due to water-use restrictions, and because it prevents frost damage better than overhead sprinklers or drip irrigation (Boman and Parsons 1999). Microirrigation systems usually do not wet the entire soil volume. This occurrence is a benefit in arid climates, since more leaching of water usually occurs during irrigation of the limited volume and salts will not accumulate on the soil surface. However, the same increased leaching may also leach nutrients from the soil and increase nitrate concentration in ground water, especially in rainy areas with sandy soils.

Table 2.1. Abbreviations for names of *Citrus* and *Citrus* relatives.

CARZ	Carrizo citrange (<i>C. sinensis</i> [L.] Osbeck. × <i>Poncirus trifoliata</i> L.)
CLEO	Cleopatra mandarin (<i>C. reshnii</i> Hort ex Tan.)
CTRM	Swingle citrumelo (<i>C. paradisi</i> × <i>P. trifoliata</i>)
CTRN	citron (<i>C. medica</i> L.)
FA13	Cleopatra mandarin (<i>C. reshnii</i> × <i>P. trifoliata</i>)
FA5	Cleopatra mandarin (<i>C. reshnii</i> × <i>P. trifoliata</i>)
MACR	Alemow (<i>C. macrophylla</i> Westr.)
RANG	Rangpur lime (<i>C. limonia</i> Osbeck.)
RL	rough lemon (<i>C. jambhiri</i> Lush.)
SB812	Sunki × Beneke (<i>C. sunki</i> × <i>P. trifoliata</i> L.)
RT803	RANG × TROY [<i>C. limonia</i> × (<i>C. sinensis</i> × <i>P. trifoliata</i>)]
GT	Gau Tau (<i>C. aurantium</i> × ?)
SO	sour orange (<i>C. aurantium</i> L.)
SwL	sweet lime (<i>C. aurantifolia</i> L.)
SwO	sweet orange (<i>C. sinensis</i> [L.] Osbeck.)
TRIF	trifoliolate orange (<i>Poncirus trifoliata</i> L.)
TROY	Troyer citrange (<i>C. sinensis</i> × <i>P. trifoliata</i>)
VOLK	Volkameriana (<i>C. volkameriana</i> Chapot)
X639	CLEO × TRIF (<i>C. reshni</i> × <i>P. trifoliata</i>)

Drip. This irrigation method has become common in arid areas and Mediterranean climates. The popularity of drip is not only due to the water savings gained by reducing evaporative losses, but also due to the advantage of this system for irrigation with saline water that was described above. Successful use of a drip system depends on good water filtration and water treatment to prevent bacterial or mineral clogging. The utility of a drip system can be improved by fertigation.

Dripper improvement and chemical prevention of root penetration into the drippers make underground drip systems feasible in citrus orchards. The advantage of this system over regular drip is that the water does not usually reach the surface, so it does not leave salts behind. This system is also advantageous when using reclaimed water that may be contaminated with harmful bacteria. Additionally, underground systems are less prone to damage from orchard operations and from pests like rodents or woodpeckers. Among the disadvantages of subsurface drip systems is the difficulty in monitoring the proper operation of the system. Also, if water does wet the soil surface by capillary action, salts may accumulate there.

2. Fertilizer and Salinity. The frequency of applying fertilizer has a direct effect on the concentration of total salts in the soil solution. A fertilization program that uses frequent applications with relatively low concentrations of salts will normally result in less salinity stress than programs using only two or three applications per year. As described above, light rain can aggravate salinity damage by the leaching of any residual dry fertilizer that was applied in the non-irrigated soil areas between the rows. Relatively expensive controlled-release fertilizers or frequent fertigations are ways to minimize salt stress when using high-salinity irrigation water.

Selecting nutrient sources that do not add potentially harmful ions to already high levels in irrigation water can also avoid compounding salinity problems. The Cl^- in KCl or Na^+ in NaNO_3 materials adds more toxic salts to the soil solution. Repeated fertilizer application with sources like $(\text{NH}_4)_2\text{SO}_4$ can alter soil pH and cause soil nutrient imbalances. Specific ions can also add to potential nutrient imbalances in soil and trees. For example, Na^+ can displace K^+ and lead to K^+ deficiencies. The displacement of Ca^{2+} by Na^+ in the soil cation exchange complex can lead to decreased permeability and destroy soil structure. Such nutrient imbalances can compound drainage problems and aggravate the effects of salinity stress. Salinity problems can be minimized if sufficient soil nutrient concentrations are maintained, especially those of K^+ and Ca^{2+} . Preliminary results suggest that continuous application of nitrates like

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KNO_3 under saline conditions can reduce Cl^- accumulation in scions grafted on susceptible rootstocks, and can increase yield (Bar et al. 1996, 1997; Levy et al. 1999a, 1999c, 2002; Levy and Lifshitz 2000a, 2000b). This effect might be due to competitive exclusion of Cl^- by NO_3^- at the soil-root interface, or, in young trees, a dilution effect due to increased growth.

There are marked differences in the salt index (the salt content per unit nutrient) of particular formulations of fertilizer nutrients. Choosing nutrient sources with a relatively low salt index can reduce salinity problems from fertilizer salts. With high-salinity irrigation water, fertilizer formulations should have low salt index. It may be necessary to increase the frequency of fertilizations, thereby making it possible to reduce the salt content of each application and aid in preventing excess salt accumulation in the root zone. The nutrient storage capacity of citrus trees tends to buffer the different seasonal demands for nutrients associated with specific growth demands. Leaf or fruit analysis should be used to detect excessive Na^+ and Cl^- concentrations, or deficient concentrations of other elements caused by nutrient imbalances from salt stress.

B. Rootstocks and Scions

1. Rootstock Abbreviations. The abbreviations for different rootstocks (Table 2.1) are based on nomenclature of Hodgson (1967).

2. Salt Tolerance. It has been known for many years that citrus rootstocks differ in their ability to absorb the toxic ions, Cl^- , Na^+ , and B, and to translocate ions to the canopy (Oppenheimer 1937; Cooper et al. 1951, 1952; Cooper and Gorton 1952; Cooper 1961; Embleton et al. 1973; Wutscher et al. 1973). Most of these studies were from short-term, comparatively high salinity trials, but results have been corroborated more recently for many rootstocks under field conditions (Levy and Shalhevet 1990, 1991; Garcia Lidon et al. 1998; Levy et al. 1999a,b,c). Because of the relative importance of Cl^- toxicity in citrus (detailed below), salinity tolerance of rootstocks is most often based on the ability of the root system to limit the transport of Cl^- to the leaves. In general, the decreasing order of salinity tolerance (most tolerant to most sensitive) in citrus rootstocks is: 'CLEO', 'RANG', 'SB812', 'X639', 'GT', 'VOLK', 'SO', 'MACR', 'CTRM', 'RL', 'CARZ', and 'TROY', 'C35' citrange, 'CTRN' (see Table 2.2 for details). The above ranking may differ somewhat, however, depending on the specific ions, effects of scion,

Table 2.2. Ranking of rootstock tolerance to Cl⁻ in different studies.

Susceptible	Medium	Tolerant	Scion	Max Cl ⁻ Range	Reference
SwL	SO		SwO	500	Oppenheimer 1937
CTRN>CTRM>RL	SwO>SO	CLEO>RANG	grapefruit	1800	Cooper and Gorton 1952
	SO	CLEO	grapefruit	1200	Cooper et al. 1958
MACR>CARZ>TROY	SwL>SO>CTRM	CLEO>RANG>SUNKI	grapefruit	1200	Peynado and Young 1962
CARZ	CLEO	FA5=FA13	seedlings	4690	Forner et al. 2000
RL>TRIF	CARZ>TROY>SwO	RANG>CLEO>MACR	seedlings	1775	Grieve and Walker 1983
MACR	SO*	CLEO*	lemon	1490	Nieves et al. 1990
RL		SO>CLEO	grapefruit	680	Levy and Shalhevet 1990
SO	VOLK	MACR	lemon	3550	Garcia Legaz et al. 1992
TROY	SO>CITR	CLEO	grapefruit	3400	Boman 1994
CARZ=TROY	RL	VOLK	seedlings	1147	Combrink et al. 1995
SO	CLEO	RANG>VOLK	seedlings	3000	El Hammady et al. 1995
SO	SB812	RT803>GT>CLEO	seedlings	1680	Levy et al. 1999
TROY	SO>SB812>GT	VOLK>RANG>CLEO	grapefruit	880	Levy et al. 2000

*SwO interstock

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conditions of incompatibility, and with disease status (viruses, viroids, root infections, or pests).

Many citrus rootstocks with low growth vigor have good Cl^- exclusion characteristics, whereas some of the vigorous citrus rootstocks exhibit poor Cl^- tolerance (Castle and Krezdorn 1993). Since faster-growing trees always use more water than slower-growing trees, leaves on high-vigor trees would be exposed to relatively more Cl^- in the transpiration stream from saline water than low-vigor trees. Thus, at least part of the mechanism underlying the accumulation of relatively low leaf Cl^- in some citrus rootstocks may be related to their low growth vigor (Moya et al. 1999). However, there are many exceptions to this rule: 'RANG' is a fast-growing rootstock with good salt tolerance and 'VOLK', another fast-growing rootstock, exhibits some salt tolerance, at least as a young tree (Levy and Lifshitz 2000a).

It is important to remember that due to osmotic effects, growth and yield of citrus trees can be reduced by excessive salts regardless of rootstock. The critical salinity level for salt damage varies with the buffering capacity of the soil (soil type, organic matter), climatic conditions, and the soil moisture status. Salinity-induced symptoms such as non-specific chlorosis, smaller leaf size, and impaired shoot growth are often difficult to assess. Cl^- toxicity can be diagnosed by leaf analysis (taking care to sample leaves that were not wet by irrigation water, when only a part of the canopy is wet by irrigation water) and at harvest time by juice analysis (Levy and Shalhevet 1990). Na^+ toxicity symptoms such as tip-burn seldom distinctly appear. Boron toxicity symptoms are usually visible in leaves. Without leaf ion analysis, however, boron toxicity can be confused with other microelement deficiency or herbicide damage symptoms.

Salinity interacts with many horticultural issues when choosing a rootstock. The comparatively high salinity tolerance of 'SO' and its other desirable horticultural characteristics make it a good rootstock to choose to cope with salinity problems. This fact places growers all over the world in a dilemma because trees grafted on 'SO' are susceptible to tristeza. Many tristeza-tolerant rootstocks such as 'RL', 'TRIF', 'CARZ', and 'CTRM' are sensitive to salinity. In addition, recent research indicates that drip-irrigated young trees on 'SO' may be more susceptible to salinity than mature trees (Hamou et al. 1999; Levy et al. 2000). A goal of many plant breeding programs is to develop a substitute rootstock for 'SO' that has similar growth, fruit quality, disease tolerance, and salinity tolerance, but is also tolerant to tristeza.

Poncirus sp. and its hybrids are popular rootstocks in many areas but are susceptible to lime-induced chlorosis in calcareous soils. When

salinity is also a potential problem, the grower is presented with an additional dilemma. Deficit irrigation can prevent lime-induced chlorosis (Levy 1998; Boman et al. 1999), but since these rootstocks are also very susceptible to salinity, it increases the hazard of salinity damage if leaching is reduced with reduced irrigation.

The fact that rootstocks differ in their ability to extract water from saline soil affects the leaching pattern in the soil. For example, salinity stress increased N leaching (Lea-Cox and Syvertsen 1993). Since salinity reduces water use and transpiration differently in different rootstocks, rootstocks can actually affect soil salinity (Levy and Shalhevet 1991).

Most of the breeding work done on citrus rootstocks is aimed at producing dwarfing and disease tolerance (tristeza, phytophthora, and nematode), but not for salinity tolerance (J. R. Furr and J. B. Carpenter, pers. commun. 1975; Hutchison 1985; C. M. Anderson, pers. commun. 2000; G. W. Grosser, pers. commun. 2001). Some new rootstocks have been evaluated for salinity tolerance. Rootstocks released by Forner et al. (2000) include 'F&A13' ('CLEO' × 'TRIF') that accumulated half the amount of Cl⁻ compared with 'CLEO' and only 16% of the amount of Na when irrigated for 7 months with saline water in the greenhouse. The hybrid rootstock 'FA517' (*C. nobilis* Lour × 'TRIF'), was similar to 'CLEO' and much better than 'CARZ' in the same experiment. Two other hybrids, '020324' ('TROY' × 'CLEO') and '030131' ('CLEO' × 'TRIF') were also noted as Cl⁻ and Na⁺ excluders.

'CLEO', which is one of the best Cl⁻ excluding rootstocks, was recognized as a salt-tolerant rootstock even though it was never selected intentionally because of its salt tolerance, but rather as an ornamental (Chapman 1968). Future research should evaluate citrus crosses that were produced in different parts of the world and evaluated for disease tolerance or cold hardiness (Hutchison 1985; Dunaway and Dunaway 1996). There is hope that crosses of 'CLEO' with 'RANG' or 'VOLK' or even 'TRIF' may produce a rootstock that is better than 'CLEO' in terms of salt tolerance, vigor, and yield. Another direction to take may be to try to induce beneficial mutations in 'CLEO'.

3. Ranking of Salinity Tolerance. Table 2.2 summarizes the Cl⁻ tolerance ranking reported in different studies during the last seven decades.

4. Effect of Scion Cultivars. Just as growth and yield responses of citrus scions and rootstocks differ in sensitivity to salinity (Cooper et al. 1951, 1961; Levy 1986, 1997; Levy and Shalhevet 1990, 1991; Levy et al. 1992, 1999a,b; Levy and Lifshitz 2000a), there are scion differences in salt sensitivity of leaf gas exchange physiology that may be attributed to genetic

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differences. Net gas exchange of CO₂ in 'Marsh' grapefruit leaves was more sensitive to salt stress than in 'Navel' or 'Valencia' orange regardless of the rootstock on which they were grafted (Lloyd et al. 1990). This observation was attributed to the higher accumulation of Na⁺ in grapefruit leaves than in orange leaves even though grapefruit leaves also accumulated the most Cl⁻. However, salinity experiments with mature grapefruit and 'Washington Navel' oranges also indicated that grapefruit growth and yield were more susceptible than orange to salinity (Levy and Shalhevet 1991). In this case, salinity effects were manifested by Cl⁻ accumulation in the leaves and yield reduction of grapefruit grafted on salt-sensitive 'RL' (Levy and Shalhevet 1991; Levy et al. 1992).

There are also differences in the susceptibility of different citrus scions to salt damage from overhead irrigation. Similar to the report above, 'Marsh' grapefruit had more leaf damage than 'Temple' or 'Valencia' orange trees when irrigated with water containing 2800 mg L⁻¹ total salts (about 1000 mg Cl⁻ L⁻¹; Calvert and Reitz 1965). This may be related to differences in cuticular permeability to Cl⁻, as well as to the sensitivity of the different cultivars to salinity. Such genetic differences of scion types may also be attributable to different sensitivities to Cl⁻ or to an ability of salt-tolerant types to compartmentalize toxic ions in the vacuoles away from the physiologically active cytoplasm. However, x-ray analysis could not detect such compartmentation in citrus under salinity stress (M. Talon, pers. commun. 2001). It is interesting to note that leaves containing high Cl⁻ levels from saline foliar sprays did not have the same reductions of photosynthetic assimilation of CO₂ that would be expected from similar leaf Cl⁻ levels that accumulated from salinized soil (Romero-Aranda and Syvertsen 1996). Future research should focus on such potential differences (and others) with a goal to achieve an understanding of the underlying mechanisms of salinity tolerance. This understanding may lead to breeding salt-tolerant scions that will continue to yield commercial crops in spite of Cl⁻ or Na⁺ accumulation in their leaves. Breeding of such halophytic-like cultivars, however, seems to be a distant prospect today (Yeo 1998; Barkla et al. 1999).

III. EXPERIMENTAL METHODS IN SALINITY RESEARCH

Reliable data on the yield response of citrus or any other commercial crop to salinity can be obtained only from carefully controlled and well-replicated field experiments conducted across a range of salinity treatments (Shannon 1997). Tests should include mature yielding trees during a long time span (years) in order to evaluate possible cumulative

effects of salinity on tree development and yield. Such experiments are expensive and thus rare (Hoffman et al. 1989). Young seedlings often provide indications as to the anticipated response of the trees to salinity and, as such, seedlings as early indicators may be tools in testing new breeding materials and cultural practices even though in many cases they may fail as rootstocks for mature trees.

A. Leaf Analysis

Leaf analysis was developed as a tool for assessing the nutritional needs of citrus. Some of the standards developed in Riverside, California (Chapman 1968; Embleton and Jones 1964; Embleton et al. 1973) were based on hydroponics along with some actual nutrition field experiments and field observations. The work of Cooper et al. (Cooper et al. 1951, 1955; Cooper and Gorton 1952; Cooper 1961) also contributed to the establishment of tolerances for Cl^- , Na^+ , and B concentrations in citrus leaves.

There are some disadvantages in using leaves for assessment of salt accumulation. Mineral concentrations depend on leaf age, so leaves should be sampled carefully to ensure that they are of the same age (Embleton et al. 1962a). Leaves exposed to saline irrigation water may absorb salt directly through the epidermis (Stolzy et al. 1966) or have non-washable salt residues adsorbed on the leaf surface. Therefore, leaf analysis may not always be indicative of ion uptake by roots. Another serious problem is the tendency of leaves most affected by salinity to abscise before the usual summer/autumn sampling date, resulting in the sampled leaves not being representative.

B. Juice Analysis

Juice analysis can give a better ranking of the susceptibility of citrus rootstocks to salinity (Levy and Shalhevet 1990; Levy et al. 1992, 2000; Levy and Lifshitz 1995, 2000a). Juice analysis has several advantages over leaf analysis. A much more uniform tissue is used and the sample can be much larger. There can be 3 to 6 kg fresh weight of fruit per juice sample vs. about 50 g for leaves. As a rule, in most citrus cultivars (except summer lemon) all the fruits are of a similar calendar age and it is easy to eliminate surface contaminants from the juice. There is no need for extensive preparation of juice samples for analysis since fresh citrus juice can be analyzed directly for Cl^- , Na^+ , and K^+ . Analysis results can be obtained shortly after the juice is extracted (Levy and Shalhevet 1990). The concentration of Cl^- and particularly Na^+ in juice is often lower than that of

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tap water, so care should be exercised to prevent contamination of juice with tap water during juice extraction. Since variability is lower than with leaf analysis, juice analysis can give a better ranking on the uptake of Cl^- and Na^+ by the different rootstocks (Levy and Shalhevet 1990; Levy et al. 1992, 2000; Levy and Lifshitz 1995, 2000a).

C. Seed Mineral Content

Seed tissue of eleven citrus species revealed significant differences in Cl^- concentration calculated on a dry weight basis (Altman and Goell 1970). This result correlated well with the Cl^- concentrations in the leaves of the same plants. However, there was no significant difference in Cl^- concentrations of seeds from 10-year-old 'Clemantine' mandarin grafted on different rootstocks and watered with non-saline water. Increasing the Cl^- concentration of irrigation water from 130 to 1800 mg L^{-1} did not affect the Cl^- concentration of the seeds of 'Shamouti' orange trees grafted on salt susceptible 'Palestine SwL' rootstock. Thus, it does not appear that seed Cl^- concentrations can be a reliable indicator of salinity tolerance, nor is it conveniently sampled tissue.

D. Biochemical Indicators

An intriguing possibility is to identify an indicator of membrane permeability to Cl^- and, thus, an indicator Cl^- tolerance. Treatment with high salinity increased free sterols in the young fibrous roots of salt-tolerant 'RANG', and reduced free sterols in the non-tolerant 'Kharna khatta' rootstock of India (*C. karna* Raf.) (Douglas and Walker 1983). A significant correlation was found between the ratio of the "more planar" cholesterol and campesterol to "less planar" sterols in the free sterol fraction. In the absence of salt stress, this ratio was lowest in 'RANG', intermediate in 'Kharna khatta', and highest in 'Etrog' citron, correlating to their Cl^- exclusion. This finding was interpreted as a potentially useful indicator of membrane permeability of the different genotypes. Another study suggested that the phospholipid to free sterol ratio could be used to assess Cl^- exclusion ability in citrus (Douglas and Sykes 1985). Unfortunately, these studies have not been continued.

E. Seed Germination

Salinity reduces seed germination initially through the osmotic effect of the solution, but there was no evidence that the tolerance to salinity during germination was correlated with the tolerance of the plant to

salinity (Zekri 1993). This finding was confirmed in a recent study (Zekri 2001). 'CARZ', which is a Cl^- accumulator, was the first to germinate at high salinity, 'SO' the last, and 'CLEO', the best Cl^- excluder, was intermediate. The author suggested that stem analysis of seedlings germinated at high salinity could serve as an indicator of Cl^- tolerance.

F. Solution Culture vs. Soil Culture

Much of the early work on the salt tolerance of citrus rootstocks to salinity was based on hydroponics or sand culture. These studies ranked 'RL' and 'SO' as moderately tolerant to salinity (Cooper et al. 1952; Bernstein 1969, 1980). Later, under field conditions, it was found that 'SO' could tolerate salinity (Bielorai et al. 1983, 1985) and that 'RL' was much more sensitive to salinity than 'SO' (Shalhevet and Levy 1990; Levy and Shalhevet 1990, 1991). Thus, ion uptake by roots in solution culture can be different from that by roots growing in soil. Irrigation method can also interact with the response of field-grown rootstocks to salinity (Wutscher et al. 1973).

Roots growing in an aqueous environment encounter entirely different solute gradients than roots in soil. In soil, the mass flow of solution toward the root by transpiration is much greater than the diffusion away from the root unless there is continuous leaching of salts by rainfall or irrigation (Yeo 1998). If a root in soil excludes Na^+ or Cl^- ions, they will not move away from the root. Thus, roots may actually increase soil salinity by salt exclusion. In addition, salinity-tolerant citrus rootstocks can increase the soil salinity because they do not limit water uptake as salinity increases compared with non-selective rootstocks (Levy and Shalhevet 1991). This condition is very different from flowing or stirred hydroponic solutions. In this respect, sand culture may be similar to hydroponics since sand is usually frequently irrigated with an excess of nutrient solution.

Roots also interact with soil microflora such as vesicular arbuscular mycorrhizae (VAM), that are missing in water culture and may be altered or absent in sand culture. Roots develop a different anatomy when grown in solution-culture than when grown in soil. In addition, since nutrient solutions have different aeration and usually a different pH than the soil, salinity responses of solution culture plants are usually different from that of trees in soil. There are examples, however, of short-term, high-salinity hydroponic culture of citrus hybrids where leaf analysis was coupled to plant development and gave a rapid indication of their possible Cl^- tolerance when used as rootstocks under real field situations (Sykes 1985).

G. Seedling Rootstocks vs. Budded Trees

The majority of commercial citrus trees are composed of a rootstock and a scion, which are two different *Citrus* (or *Poncirus*) species or their hybrids. Exceptions may be lime trees (*C. aurantifolia* L.) that are vegetatively propagated from cuttings or 'Emperor' ('Empress') mandarin trees grown as seedlings. The rootstock develops the root system that absorbs water, nutrients, and salts from the soil; the scion develops the branch system and leaves, transpires water, fixes CO₂, flowers, and develops the fruit. It is the scion that suffers most from the stress caused by salinity. Many rootstocks behave differently when scions are budded on them than when grown as unbudded seedlings. For instance, 'MACR' as a rootstock produces a large and prolific tree for virus-free scions in Israel (Levy et al. 1980; Levy and Lifshitz 1995), Arizona (Fallahi and Rodney 1992; Wright 1999), and Spain (A. Garcia Lidon pers. commun. 2001), but on its own roots, 'MACR' will remain a relatively small tree with only a few fruit. To have practical significance, studying physiological processes in un-budded rootstock seedlings should be augmented by studies with grafted scions in order to distinguish between the effect of the rootstock as a root system and the possible effects of shoot anatomy and physiology. Shoot and leaf characteristics of a seedling of a rootstock species have no practical significance once it is grafted. Physiological responses of shoots and leaves (including photosynthetic responses) of rootstock seedlings, however, can yield valuable information about physiological functions of the root system that can have practical significance for understanding underlying mechanisms in the root systems of commercial trees.

The compound genetic system of a citrus tree presents other potential complications that do not occur in seedlings. The specific scion can influence ion uptake by the rootstock (Cooper et al. 1952). The bud-union itself may affect the transfer of nutrients and toxic elements from root to canopy. This is especially true of some specific rootstock/scion combinations that are partially incompatible. In addition, the bud-union is the part of the grafted tree that may be first affected by several virus diseases, further complicating the response of the whole tree to the environment variables.

H. Greenhouse vs. Field Studies

Most of the knowledge about the salinity tolerance of rootstocks comes from water-culture or container experiments. These experiments are usually short-term, and comparatively high salinities are used in order

to measure results quickly. Often the response of mature, grafted trees was different from that of young seedlings in pots (Levy et al. 1992). As with seedlings vs. budded tree studies, pot experiments with confined root systems should be corroborated in long-term orchard experiments before recommendations based on results are adopted in commercial practices. Obviously, long-term field experiments are more difficult and less common than shorter-term pot experiments in fruit trees (Hoffman et al. 1989).

I. Tissue Culture vs. Whole Plant

Much of our physiological knowledge at the molecular level comes from bacterial or animal systems, which are very different from whole plants. Animal cells and respiring plant tissues absorb O_2 and release CO_2 . The O_2 concentration in air is about 21%, while the CO_2 that the green plant tissues combine with water to make sugars is only present at a concentration of about 0.03%. Plant leaves unavoidably transpire a relatively huge volume of water while acquiring CO_2 for photosynthesis. Plant cell suspensions do not transpire and in vitro plants from tissue cultures transpire very little water, so there is relatively little exchange of water and ions with their environment. Toxic ions that are not absorbed by cell or tissue cultures will remain uniformly distributed in the culture media and not accumulate in the media near cells (Yeo 1998). This situation is very different from the accumulation of excluded ions in the rhizosphere of roots growing in soil. Thus, in vitro cultured cells and tissues can tolerate much higher external salinity in the media than a transpiring plant growing in soil.

Variant cell lines selected from cultured somatic cells can exhibit a level of tolerance to salinity (Ben Hayyim and Kochba 1983; Ben-Hayyim and Goffer 1989; Kochba et al. 1982). As stated by Kochba et al. (1982), the salt tolerance of selected cell lines will be of agronomic value only if the tolerance achieved is maintained in all stages of plant development. The major limitation of tissue culture is that the selected salinity tolerance character often cannot be maintained during the regeneration process and tolerance mechanisms that depend on the integrated function of the differentiated tissues cannot readily be identified in cell culture (Shannon 1997; Yeo 1998). Thus, salinity tolerance for terrestrial agriculture is a whole plant function that can best be studied in intact plants in the field.

Induction of natural genetic mutations may offer improvements in salinity tolerance. Flowers and Yeo (1995) state that mutation works best with factors likely to be controlled by a single gene. Tolerance to abiotic stresses is usually a function of a group of complex quantitative genetic

characters and, thus, very few successes have been reported in breeding plants with increased stress tolerance. Garcia-Agustin and Primo-Millo (1992, 1995) treated unfertilized TROY ovules with the mutagen ethyl-methyl-sulphonate, and selected three lines that accumulated little Cl^- and Na^+ along with high concentration of K^+ in leaves when subjected to increasing NaCl in the culture medium. However, two of the selected lines partially lost this characteristic when they were vegetatively propagated from cuttings and grown in the absence of saline selection pressure. Since only a true mutant continues to carry a stable trait in the absence of selection pressure (Garcia-Agustin and Primo-Millo 1992, 1995), these lines apparently were only phenotypically acclimated to salinity and lost this characteristic when propagated.

Cervera et al. (2000) transformed plants of 'CARZ' with the halotolerance gene *HAL2*, which confers Li^+ and Na^+ tolerance in yeast and so was implicated in salt-tolerance mechanisms. The transgenic nature of these plants was confirmed by Southern and Northern analyses, and was the first time that a gene from yeast had been stably integrated and expressed in citrus plants. However, when whole plants were tested in the greenhouse, the transformed 'CARZ' plants did not differ in their susceptibility to salinity from control 'CARZ' plants (L. Peña and M. Talon, pers. commun. 2001). These contrast with results with tomato plants that were transformed with the *HAL1* gene from yeast (Gisbert et al. 2000), which reduced both root and leaf Na^+ and increased K^+ . Cervera et al. (2000) concluded that salt tolerance is a multigenic and quantitative trait, and both improvement and evaluation of this characteristic is difficult. This is especially true for Cl^- toxicity tolerance in citrus, which is not well understood and apparently is not governed by a single gene. Introduction of transgenic genes for salinity tolerance into commercial rootstocks or preferably directly into commercial scion cultivars could result in the production of "halophytic" citrus. This prospect seems remote at the present time due to our lack of basic knowledge about salinity tolerance in citrus. However, progress is rapid in yeast molecular genetics for improvement of salt tolerance in plants (Matsumoto et al. 2002) and a breakthrough is possible.

IV. PHYSIOLOGICAL RESPONSES

A. Amino Acids Accumulation

Non-protein amino acids like proline, often reported as a stress metabolite, increase with drought stress (Levy 1980; Yelenosky 1979) and also with salt stress (Dunn et al. 1998). Proline has been reported to have a

role in stressed plants (Syvertsen 1984; Syvertsen and Smith, Jr. 1984), where it acts as an osmoticum and/or a storage source of N. Arginine concentration in 'VOLK' feeder roots (percent of total amino acids) was doubled by salinity, while phenylalanine ammonia lyase (PAL) was reduced (Dunn et al. 1998). These may reduce the chemical defenses of the plant to nematodes as discussed below. Free proline increased with salinity in the leaves of lemon grafted on the relatively salt-tolerant 'SO', but not when grafted on the more salt-susceptible 'MACR' (Nieves et al. 1991). In another study (Walker et al. 1993), proline increased significantly only in lemon leaves on 'RANG' exposed to Na_2SO_4 but not when irrigated with NaCl. Its increase with salt stress supports its role in stressed plants where it acts as an osmoticum. Betaine levels in leaf tissues of 'CARZ' were also positively related to soil salinity (Duke et al. 1986). These compounds are considered as osmo-protectants, which may be "engineered" into citrus for better total salt (osmotic and drought) tolerance (Nolte et al. 1997) but not for reduction of specific mineral toxicity.

B. Net Gas Exchange of Leaves

There have been several studies comparing stomatal conductance (g_s) and photosynthetic assimilation of CO_2 (A_{CO_2}) in leaves from salinized trees with gas exchange values from non-salinized controls. It is clear that salt stress reduces water use and A_{CO_2} but the underlying mechanisms are still debatable. Much of the controversy surrounding salinity-induced limitations on net gas exchange follows the same argument as the relative importance of osmotic stress vs. toxic ion stress of Na^+ and Cl^- . Osmotic stress from saline soils undoubtedly reduces water use and g_s , but the magnitude of this reduction depends on the rate at which salinity stress develops and the duration over which it exists. Leaf proline concentration (Syvertsen and Yelenosky 1988) and proline-betaine levels (Lloyd et al. 1990; Banuls and Primo-Millo 1992) increased with salinity-induced osmotic stress. Potentially negative osmotic shock effects on plant-water relations usually do not occur if there are ample cations available to gradually allow leaf tissues to lower osmotic potential (Ψ_π) to compensate for losses of turgor. For example, long-term moderate salinity stress lowered leaf Ψ_π such that turgor was maintained and leaves suffered little or no drought stress-like symptoms (Syvertsen et al. 1988). Turgor can be even higher in salt-stressed trees than in non-stressed control trees (Behboudian et al. 1986). This is why controlled salinity studies often gradually build up salt concentrations in the irrigation water to avoid osmotic shock and defoliation.

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Patterns in g_s usually follow patterns in A_{CO_2} , which has caused some researchers to mistakenly link declines in A_{CO_2} to salinity-induced reductions in g_s . This speculation is probably not the case, however, since low g_s probably only directly limits A_{CO_2} at very low leaf water potential (Ψ_w) or at large vapor pressure deficits (Farquhar and Sharkey 1982). In most cases, including moderate salinity stress, changes in A_{CO_2} cause changes in g_s . Lloyd et al. (Lloyd and Howie 1989b; Syvertsen and Lloyd 1994) examined effects of salinity on the relationship between A_{CO_2} and internal CO_2 concentrations and concluded that reductions in A_{CO_2} were due to a direct biochemical inhibition of mesophyll photosynthetic capacity followed by reductions in g_s . Thus, other than osmotic shock responses, most decreases in net gas exchange attributable to salinity are probably caused by ion toxicity responses. Since the most common source of salt stress is NaCl and both ions often accumulate together, it is difficult to determine the relative importance of Na^+ vs. Cl^- ions in reducing A_{CO_2} .

There are many reasons why decreases in the net gas exchange of leaves in response to salinity are complicated by salinity-induced variations in leaf nutrition and by leaf chlorophyll. Increases in leaf Na^+ interact with Ca^{2+} and K^+ , whereas leaf Cl^- interacts with the anions NO_3^- and SO_4^{2-} . Many problems associated with toxic levels of Na^+ are probably due to deficiencies of K^+ and Ca^{2+} . These deficiencies explain why salinity effects can be ameliorated with Ca amendments (Cooper et al. 1958; Banuls et al. 1991; Banuls and Primo-Millo 1992). Ca^{2+} amendments also help remove Na^+ from soil colloids and free Na^+ to be leached. There can also be direct effects of leaf Cl^- on other ions. For example, high Cl^- reduces N uptake (Syvertsen et al. 1993) and decreases NO_3^- N use efficiency (Lea-Cox and Syvertsen 1993).

There are direct effects of salinity on leaf chlorophyll concentrations that are reflected in variations in A_{CO_2} . In the field or in high-light greenhouses, leaf chlorophyll concentration usually decreases with salinity stress in well-watered trees (Syvertsen et al. 1988; Romero-Aranda et al. 1998). Interestingly, surviving leaves from drought-stressed salinized trees did not suffer losses of chlorophyll. In low-light growth chamber studies, however, leaf chlorophyll is affected little by salinity (Lloyd et al. 1987a) and can even be higher in salinized leaves than in non-salinized control leaves (Lloyd et al. 1987b).

Several studies describe decreases in citrus leaf A_{CO_2} in response to elevated leaf Cl^- (Syvertsen and Lloyd 1994; Storey and Walker 1999). Although citrus has been considered to be sensitive to Cl^- toxicity, Syvertsen et al. (1988) found no effect of salinity on gas exchange of remaining leaves on 'Valencia' orange trees on both 'SwO' and 'TRIF' rootstocks despite foliar concentrations (cell sap basis) of Cl^- as high as

400 mol m⁻³ (mM). These trees had already sustained some salinity-induced defoliation such that whole tree-water relations were dramatically affected. Defoliation can actually increase A_{CO_2} of the surviving leaves (Syvertsen 1994; M. Talon, pers. commun. 2001). As leaf canopies became thinner, salinity responses of retained leaves were affected little. The inhibition of citrus leaf photosynthesis by high Cl⁻ concentrations (Walker et al. 1982; Lloyd and Howie 1989a) appears especially prominent when rates of Cl⁻ entry into foliage are rapid. If rapid salinity stress in the field induces leaf abscission, physiological responses to salt stress can only be characterized in the remaining relatively young leaves, that have relatively low concentrations of Cl⁻. This occurrence can lead to a misinterpretation of the relative importance of leaf Cl⁻ relative to leaf Na. Nonetheless, high correlations between net gas exchange and salinity in two orchard sites in Australia (Syvertsen et al. 1988; Lloyd and Howie 1989a) were attributed to a Na⁺ rather than a Cl⁻ effect on citrus leaf gas exchange. Reductions in A_{CO_2} can be attributed to high Na⁺, especially when there are relatively low Ca and K⁺ concentrations in leaves. Although leaf injury can be correlated with Cl⁻ concentrations, studies have shown that reductions in A_{CO_2} depend on the relative sensitivity of the scion type rather than on the absolute concentration of Na⁺ or Cl⁻ (Banuls and Primo-Millo 1995). Salinity caused a progressive loss in variable fluorescence under strong irradiance. Adaxial (upper) surfaces were especially vulnerable to this apparent photoinhibitory damage, which coincides with the apparent bronzing that is typical of Cl toxicity. Predawn increases in maximal fluorescence correlated with leaf Cl⁻ (Lloyd et al. 1986).

Rootstock differences in Cl⁻ exclusion characteristics also are reflected in salinity effects on A_{CO_2} (Lloyd et al. 1987a,b). 'Valencia' orange trees on TRIF rootstock had a less rapid decline in leaf gas exchange when exposed to 1775 mg Cl⁻ L⁻¹ (50 mol m⁻³) NaCl than did equivalent foliage on 'CLEO' despite much higher Cl⁻ concentrations in leaves on scions budded to 'TRIF'. Although this rootstock effect was attributed to higher Na⁺ levels in scion foliage budded on 'CLEO', underlying levels of leaf Cl⁻ were much higher in trees on 'TRIF' than in those on 'CLEO'. In spite of high levels of Na⁺ in NaNO₃ treated leaves, there were no reductions in A_{CO_2} that could be attributed to Na⁺ (Banuls et al. 1997).

C. Salinity Interactions with Physical Environmental Factors

1. High Temperature and Evaporative Demand. There are direct interactions between salinity, leaf water relations, irradiance, leaf temperature, and atmospheric evaporative demand that are impossible to

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separate in the field. Physiological mechanisms underlying environmental interactions with salinity can only be studied in controlled environments. Such studies may provide insights into cultural practices or environmental conditions that can improve production under salinity stress.

Citrus leaves growing in full sun can experience temperatures that exceed air temperature by as much as 10°C (Syvertsen and Albrigo 1980). Leaf temperatures up to 45°C not only exceed optimum temperature for photosynthesis, but also lead to large vapor pressure differences (VPD) between leaves and air. Since citrus stomata are sensitive to evaporative demand, a large VPD can reduce g_s and A_{CO_2} . Transpirational water use is also a function of VPD, and large VPDs can result in very low water use efficiency (WUE). Decreasing VPD by lowering leaf temperature or increasing humidity can increase g_s , A_{CO_2} , and WUE. Mist-ing tree canopies with high-quality water may improve salinity tolerance and decrease accumulation of toxic ions as found in tomatoes (Romero-Aranda et al. 2001). Since salinity stress is greater for sun-exposed than for shaded leaves, additional shade may improve salinity tolerance. Artificial shade screens during the warmest season reduced citrus leaf temperature and improved WUE (Jifon and Syvertsen 2001) and likely would decrease salt stress.

2. Elevated CO₂. Growing plants at elevated CO₂ usually increases growth and A_{CO_2} but at the same time, high CO₂ decreases stomatal conductance. Elevated CO₂ almost always leads to higher WUE, so it can disconnect rapid tree growth from high water use. Thus, elevated CO₂ offers a tool to study mechanisms of salinity tolerance. If salt uptake is coupled with water uptake, then leaves grown at elevated CO₂ should have lower salt concentrations than leaves grown at ambient CO₂ (Ball and Munns 1992). In greenhouse studies using twice ambient elevated CO₂, all citrus rootstock species studied increased growth and WUE in response to CO₂, but 'RANG' and 'CLEO' were less affected by salinity stress than were 'SO' and 'SwO' (Syvertsen and Grosser, unpublished). Generally, the salinity-induced accumulation of Na⁺ in leaves was less when seedlings were grown at elevated CO₂ than at ambient CO₂, implying that the lower Na⁺ accumulation was linked to increased WUE. Na⁺ accumulation, however, was unaffected by elevated CO₂ in 'RANG'. In addition, 'RANG' also had the lowest leaf Cl⁻ concentrations. The accumulation of leaf Cl⁻ in salinized 'SO' was greater at elevated CO₂ than at ambient CO₂. Cl⁻ concentrations were less at elevated CO₂ in 'CLEO', but unaffected by CO₂ in 'RANG'. The decrease in Cl⁻ accumulation at elevated CO₂ in 'CLEO' was related to the increase in WUE, whereas the

increase in leaf Cl^- in 'SO' was not. Thus, relationships between salt ion accumulation and water use differed depending on the specific ions and citrus species.

The growth increases in response to elevated CO_2 in salt-tolerant 'RANG' were less under salt stress than without salt stress and there was little interaction between CO_2 level and salinity for growth responses of 'SO' and 'CLEO'. Seedlings of these three *Citrus* species, therefore, differed from other C_3 non-halophytic species in which the enhancement of growth in response to elevated CO_2 was greater when plants were exposed to salt stress (Ball and Munns 1992). Non-salinized plants were relatively less responsive to elevated CO_2 than salt-stressed plants because non-salinized plants were growing near their maximum growth capacity, whereas salt-stressed plants had a greater potential for growth. This result differed for relatively slow-growing, salt-tolerant 'SO' and 'CLEO', where growth was enhanced by elevated CO_2 similarly at high and low salinity (Syvertsen and Grosser, unpublished). In 'RANG', the adverse effects of salinity on growth were worse at elevated CO_2 . Thus, the salinity tolerance of 'RANG' may be reflected in the near maximum growth response of salinized seedlings at elevated CO_2 , whereas non-salinized seedlings at elevated CO_2 may have a greater potential for growth.

D. Osmotic Stress

Salinity affects citrus in two ways: osmotic stress and toxic ion stress. Dissolved salts exert an osmotic effect that reduces the availability of free (unbound) water through physical processes. This situation is analogous to drought stress and is discussed in detail below. The effect of osmotic stress is different when stress increases gradually and the plant can adjust to it compared with the situation when the Ψ_π of the soil solution decreases abruptly.

1. Gradual Osmotic Stress. The osmotic effect from dissolved salts in the soil solution reduces the availability of free (unbound) water through the physical processes of lowering the energy of the soil solution. More free energy is required to overcome the lower Ψ_π exerted by salts in solution, so there is less water available to roots. The energy required for roots to extract that water is referred to as osmotic stress. Osmotic stress can result in a reduction in root growth followed by a decline of canopy development and yield.

When salinity stress is gradual, salt-tolerant rootstocks, that limit the translocation of the toxic ions Cl^- and Na^+ into the leaves, will acclimate

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to the lower Ψ_{π} in the root zone by closing stomata and reducing transpiration (Syvertsen and Smith, Jr. 1983; Nieves et al. 1991). Ψ_{π} can decrease in the plant by accumulating sugars and other osmoticum such as proline (Banuls and Primo-Millo 1992). Under saline conditions, Ψ_w reached values near -1.8 MPa. This reduction was offset by a decrease in the leaf Ψ_{π} so that turgor was maintained at or above control values. The changes in Ψ_{π} were closely correlated with changes in leaf proline concentration (Syvertsen and Smith, Jr. 1983; Rabe 1990; Eissenstat 1998; Nolte et al. 1997). Under osmotic stress caused by high nutrient concentrations (Syvertsen and Yelenosky 1988), 'CLEO' accumulated more proline than 'SwO' and 'TRIF' seedlings. This response may contribute to the relatively high tolerance of 'CLEO' to salinity. Enhanced accumulation of proline was considered to be a good indicator of superior salinity stress tolerance in breeding programs (Deng et al. 1993; Nolte et al. 1997), especially if the new lines also limit the uptake of Cl^- and Na^+ .

2. Osmotic Shock. Osmotic shock can occur from excessive fertilization and from a drastic increase in water salinity in the soil solution. A rapid shock can occur as a result of light rain leaching accumulated salts into the root zone. The first apparent symptom of such an osmotic shock is abrupt leaf abscission, which may occur within days after the rain event or application of the salt. Typically, the lamina (leaf blade) separates at the abscission zone between the lamina and the petiole. The petiole may remain green and attached to the stem for some time. Leaf analysis of the abscised leaves may not reveal an increase in their Cl^- or Na^+ content. Such leaf drop can be prevented by irrigation during the initial rain period until sufficient rain leaches the previous accumulated salts. Similar leaf abscission is common for situations of sudden drought stress such as that caused by desiccating winds (Schneider 1968). Typically, citrus leaves will not abscise during drought but abscise only when irrigation (or rain) follows a severe drought. Ethylene production may be involved, since elevated ethylene is produced within 2 hours after rehydration (Tudela and Primo Millo 1992).

Osmotic shock, induced either by a sudden salt increase or severe drought stress, increased abscisic acid (ABA) and aminocyclopropane-1-carboxylic acid (ACC) in roots, xylem fluid, and leaves (Gomez-Cadenas et al. 1996, 1998). Under salinity, the pattern of change of ABA, ACC, and proline followed a two-phase response: an initial transient increase (10 to 12 days) overlapping with a gradual and continuous accumulation. This biphasic response appears to be compatible with the proposal that the transitory hormonal (ethylene) rises are first induced

by the osmotic component of salinity and then by Cl^- accumulation (Gomez-Cadenas et al. 1998). Thus, osmotic shock induced ABA, ethylene production, and leaf abscission.

E. Toxic Ions

In addition to osmotic stress, part of the salt sensitivity in citrus is related to the specific toxic effects of accumulation of Cl^- , Na^+ , B, and other ions in leaves (Bernstein 1980). One of the main differences between the effect of salinity on annual plants and trees is the gradual accumulation of toxic elements in the leaves and other plant parts in trees. These elements are transported by the transpiration stream and remain in the plant after transpired water has evaporated.

1. Chloride. Chloride toxicity in woody species is generally more severe and observed in a wider range of species than is Na^+ toxicity (Shannon 1997). Citrus provides a good example. Since Cl^- ion is more toxic to citrus than Na^+ , the concentration of Cl^- in water is an important parameter in deciding the suitability of water for citrus irrigation (Bernstein 1980; Shalhevet and Levy 1990; Levy and Shalhevet 1991; Levy et al. 1992; Maas 1993; Storey and Walker 1999). Cl^- can reduce leaf chlorophyll concentration (Zekri 1991), and cause bleaching or bronzing of sunlit leaves. There is ample evidence that Cl^- can reduce photosynthesis in citrus leaves as discussed previously. Under warm, dry, summer conditions in Australia, a yield decrease of about 20% was calculated for each increase of 35.5 mg L^{-1} (1 mol m^{-3}) of Cl^- concentration in the irrigation water above a threshold concentration of about 152 mg L^{-1} Cl^- (4.3 mol m^{-3}). The yield decrease was attributable to Cl^- toxicity rather than osmotic stress (Cole 1985). A similar negative correlation was found between leaf Cl^- and yield under similar climatic conditions in Israel (Levy et al. 1992).

2. Sodium. Na^+ is a toxic element that is perhaps a greater salinity problem in other plant species than it is in citrus. The significance of Na^+ toxicity in citrus and other fruit trees is often overshadowed by the effect of Cl^- . Na^+ can be harmful through its effect on the absorption of other nutrients, especially K^+ . The amount of Na^+ found in citrus leaves and juice is comparatively low; in lemon juice, it amounts to 0.1 g kg^{-1} fresh weight compared with 10 g kg^{-1} for K^+ and 6 g kg^{-1} for Ca^{++} (Sinclair 1984). The application of NaNO_3 was compared with $\text{Ca}(\text{NO}_3)_2$ for 9 years. The NaNO_3 increased leaf Na^+ concentration from 0.1 to 0.2 g kg^{-1} and reduced the yield of 'Washington Navel' orange by 25%. In the

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same experiment, feeder root Na^+ concentration increased from 0.2 to 0.7 g kg^{-1} . However, it is not clear if all the Na^+ was inside the roots or just adsorbed on the root surface (Jones et al. 1952). In most situations, salinity problems are almost always caused by NaCl . The relatively greater importance of Cl^- than Na^+ is not unique to citrus. In stone fruits, Cl^- was found to be the main damaging ion, whereas Na^+ accumulated in leaves only after membranes had already been damaged by Cl^- (Shannon 1997). This is probably true also for citrus, however, in situations where salinity is caused by non Cl^- salts (mainly sulfates), Na^+ toxicity can appear.

As described for Cl^- , rootstocks can have a significant effect on the amount of Na^+ absorbed from the soil and transported to the leaves. Among the rootstocks, 'CLEO' absorbed more Na^+ than most other rootstocks (Cooper et al. 1958; Taylor and Dimsey 1993; Azab 1998; Levy 1998; Levy et al. 2000). *Poncirus sp.* and its hybrids usually absorb less Na^+ than other rootstocks.

3. Boron. A toxic element of great concern for citriculture is boron. Boron is unique among the toxic elements since the range between deficiency and toxicity is narrow; B deficiency and toxicity can appear in the same orchard. Leaf concentrations of B of 50 to 200 mg kg^{-1} dry weight was considered optimum, and above 200 mg kg^{-1} (Chapman 1968) or 250 mg kg^{-1} (Embleton et al. 1973) was considered to be in the excess range. Toxicity can be caused by high concentrations of available B in the soil, even when the total B concentration is low, such as in some desert sandy soils (Elsewi et al. 1977). Salinity caused an increase in leaf injury of cucumber due to B toxicity (Alpaslan and Gunes 2001). High B soils can be found in some semi-arid regions, including the lower Rio Grande Valley of Texas (Cooper and Gorton 1952), around the Mediterranean, in some fine-textured soils in Victoria, Australia (Penman and McAlphin 1949) and the internal valleys of Israel.

Boron excess can occur in some natural water sources. It is usually higher in reclaimed water (Reboll et al. 2000) and may increase in desalinated water produced by reverse-osmosis of seawater. Natural seawater contains 4 to 5 mg L^{-1} B, but the water that is desalinated by reverse osmosis may still contain more than 1.8 mg L^{-1} B (Nadav 1999) and membranes cannot deliver less than 1 mg L^{-1} B (Taniguchi et al. 2001). Such a level of B may prohibit the utilization of reclaimed water derived from desalinated water for the irrigation of citrus or other B-sensitive plants. A multistage reverse osmosis membrane sea desalination process and a low pressure reverse osmosis process can be recommendable for B management with a reasonable additional cost in drinking water supply (Magara et al. 1998). Scofield and Wilcox (1931)

concluded that irrigation waters containing more than 0.5 mg L⁻¹ of B might injure sensitive crops such as lemons or walnuts. Since irrigation water containing more than 1 mg L⁻¹ may injure other plants, the 1 mg L⁻¹ threshold is probably a safe upper level for B in irrigation water for citrus (Parsons et al. 2001).

Under severe B toxicity, typical symptoms appear in the summer, with leaf abscission in winter leading to completely leafless trees, before they flush in the spring. This can result in branch dieback and sun damage to branches. B toxicity is often accompanied by Cl⁻ toxicity. The orange-yellow mottling of B toxicity is often difficult to distinguish from the bronzing symptoms of Cl⁻ toxicity (Cooper et al. 1955). The nutrition status of the tree has an effect on the appearance of B toxicity symptoms. High rates of N fertilizer, especially Ca (NO₃)₂ (but not (NH₄)₂SO₄), reduced the severity of the B-toxicity symptoms, although the concentration of B in leaves was not reduced (Cooper et al. 1958; Cooper and Peynado 1959). CaSO₄ had no effect on B-toxicity. In high-B soils in Israel, a common practice has been to apply chicken manure to sprinkler-irrigated citrus to counteract B toxicity. The chicken manure may act like a high organic, slow-release fertilizer, thereby improving overall mineral nutrition. The shift from high volume sprinkler to microirrigation along with continuous proportional fertigation also mitigated B toxicity. This effect was probably because of better N and P fertilization and because of increased leaching of the smaller soil volume with water low in B.

Swietlik (1995) described a link between the appearance of B-toxicity symptoms and Zn deficiency. Apparently, Zn-deficient citrus seedlings were more sensitive to B toxicity, as only Zn-deficient seedlings reduced growth in response to high B. The B toxicity symptoms could be reduced with foliar applications of chelated Zn even though the B concentrations in leaves, stems, and roots of the foliar-sprayed seedlings were not reduced. This observation is important since B toxicity and Zn deficiency may occur simultaneously in some soils and Zn deficiency is relatively easy to correct by foliar application.

The susceptibility of different rootstocks to B toxicity and their interaction with scions has a large effect on the development of B toxicity. In grapefruit grafted on different rootstocks, the highest B levels recorded for 'SwL', 'SO' and 'RL' were intermediate, and 'SwO' had the lowest B uptake (Embleton et al. 1962b). In a rootstock trial for 'Nova' mandarin, B was highest in trees on 'Yuma citrange' and *C. taiwanica* and lowest on 'SO' (Georgiou 2000). Outstanding tolerance to B was reported for grapefruit and 'Valencia' orange grafted on *Severinia buxifolia* (Poir)

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Tenore (Cooper et al. 1955). Graft incompatibility may rule out this combination, which also causes abnormal concentrations of other leaf nutrients. 'MACR' was also among the most tolerant rootstocks to high B (Embleton et al. 1962b; Peynado and Young 1962). This may be associated with the fact that scion leaves on this rootstock usually have higher N concentration than other rootstocks (Caro et al. 1977; Levy et al. 1993). 'SO' was much more tolerant to B than 'SwL' and 'RL' in the Negev area of Israel (Levy et al. 1980). Among the scions, lemon was more sensitive than other cultivars, and 'Shamouti' orange was more sensitive than 'Valencia' orange to B toxicity. 'Emperor' mandarin had the lowest B levels regardless of rootstock (Taylor and Dimsey 1993).

4. Lithium. There are some reports that excessive lithium can become toxic in arid areas of California and Arizona (Aldrich et al. 1951; Bradford 1961; Hilgeman et al. 1970). Symptoms included necrotic lesions in grapefruit leaves and defoliation. Injury became evident after the trees were 10 years old and increased in severity as the trees aged. Hilgeman et al. (1970) reported marked differences between citrus species and varieties in either tolerance to Li^+ or their influence on Li^+ uptake. Grapefruit and lemon seem to be more susceptible than orange, and 'Kinnow' mandarin topworked on severely affected grapefruit did not show any symptoms.

Toxicity may be linked to the effect of Li on Ca uptake (Epstein 1960) or to an inhibition of myo-inositol monophosphatase (IMP) that is required for de novo inositol synthesis (Gillaspy et al. 1995). This compound has been related to salinity tolerance in plants (Nelson et al. 1998). The threshold for toxicity was estimated to be 12 mg kg^{-1} in leaf dry weight (Bradford 1961) or between 50 and 90 mg kg^{-1} in leaf dry weight (Embleton et al. 1973). Such a high range may be related to the fact that Li^+ may concentrate at lesions in leaves (Hilgeman et al. 1970). Bradford (1961) noted that Li^+ toxicity symptoms were similar in many respects to B symptoms and soils that have an excess of Li^+ usually are also high in B. There are no recent reports on Li toxicity in citrus.

5. Interaction between Salinity and Nutrient Ions. Salinity can cause nutrient imbalances in various ways. K^+ can be leached from the soil exchange complex if excessive Na^+ is present, and Na^+ may also compete with K^+ at the soil-root interface. This can result in K^+ deficiency under saline conditions. Interestingly, some of the Cl^- -tolerant rootstocks, such as 'CLEO', 'Sunki', and 'Emperor' mandarins, tend to suffer

from K^+ deficiency coupled with an increase in tissue Na^+ content under saline conditions (Behboudian et al. 1986).

One way to observe the interrelations of Cl^- and Na^+ is to use these ions with different anion combinations. Banuls and Primo-Millo (1992) compared the effect of $NaCl$, KCl , and $NaNO_3$ on citrus photosynthesis, and concluded that $NaCl$ and KCl increased Cl^- leaf content and reduced photosynthesis. $NaNO_3$, however, did not affect photosynthesis though it increased leaf Na^+ content. These results were confirmed by Romero-Aranda et al. (1998), who found that decreases in photosynthesis were highly correlated with increases in leaf Cl^- .

F. Vegetative Growth

Growth of all plants is reduced by decreased leaf water potential (Maas 1986). The effect of salinity on plant growth is not always related to the accumulation of toxic elements in citrus leaves if toxic concentrations are not reached. For example, the growth of 'SO' and 'CLEO' was similar even though 'SO' accumulated more Cl^- (Zekri 1991). Salinity also increases the succulence of citrus leaves (Cerdeja et al. 1977) and the thickness of the leaf lamina. Comparative anatomical observations indicated that the mesophyll increased in volume by simultaneous division and expansion of the cells as spongy parenchyma cells became larger and more rounded (Romero-Aranda et al. 1998; Nastou et al. 1999). In a short-term experiment, Sykes (1985) reported that salinity increased leaf water contents acropetally in only some of the rootstocks tested.

G. Fruit Yield and Quality

1. Yield. Many salinity tolerance comparisons have been based on relative reductions in fruit yield. 'Verna' and 'Fino' lemons, on 'SO' and 'MACR' rootstocks, had reduced yields as salinity increased (Nieves et al. 1992). Fruit yields decrease about 13% for each 1.0 dS m^{-1} increase in electrical conductivity of the saturated-soil extract (EC_e) once soil salinity exceeds a threshold EC_e of 1.4 dS m^{-1} (Maas 1993). In Australia (Cole and McCloud 1985), regression analysis during the period 1945–1979 on data from irrigated orchards showed that yield was negatively associated with salinity at the locations with highest salinity.

Fruit yield of 'Washington Navel' orange decreased with increasing salinity due to a reduced number of fruits per tree rather than reduced average fruit weight (Haggag 1997). Increased salinity of ground water caused by seawater intrusion reduced the yield of 'Satsuma' mandarins

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grafted on trifoliolate orange rootstocks in Western Turkey (Aksoy et al. 1996). 'Shamouti' orange on 'SO' did not absorb much Cl^- after 6 years of salinization (up to 0.44% Cl leaf dry weight) with water up to $462 \text{ mg Cl}^- \text{ L}^{-1}$ ($13 \text{ mol m}^{-3} \text{ Cl}^-$). The 14% reduction in yield was mainly due to osmotic stress (Dasberg et al. 1991). However, continued exposure to salinity could have caused accumulation of Cl^- to toxic levels.

2. Internal Quality. Although drought stress can have a profound effect on citrus internal quality, the effect of salinity is usually very subtle. Most salinity studies report a slight increase in juice solids, sometimes accompanied with a similar increase in acidity, which causes the TSS to acid ratio to remain unchanged (Boman 2000; Levy et al. 1978, 1979). This observation implicates a reduced water movement into the fruit due to the osmotic effect of salinity. The production of more solids in fruit may have a significant importance in fruit for processing.

H. Phytochemicals

Citrus fruits contain several phytochemicals and/or nutraceuticals such as carotenoids (lycopene and β -carotene), limonoids, flavonones (naringin and naringin rutoside), folate, and vitamin C that have important medical benefits in human diets. Phenolic compounds have been used to establish taxonomic relationships among fruit cultivars (Berhow et al. 1998) and many phytochemicals vary with rootstocks (Kefford and Chandler 1970). This fact implies that the accumulation of these materials in fruit is subject to variations in water relations, mineral nutrition, and/or plant growth regulators that are attributable to rootstock. There are data indicating that several phytochemicals can be enhanced by preharvest factors such as cultivar and season (Patil 2000). Red and pink grapefruit cultivars have higher lycopene and total carotenoids than white-fleshed ones and concentrations of most phytochemicals change as seasonal maturity progresses. In addition, there are a few studies on effects of soil moisture status, temperature, and freezing on juice constituents (Kefford and Chandler 1970). Flavonones and limonoids increase during post-harvest storage (Patil et al. 2000). Undoubtedly, such responses in fruit are related to dehydration and/or dilution of juice. It is tempting to speculate that just as rootstocks affect salinity tolerance, salinity stress may affect the accumulation of phytochemicals. Controlled salinity stress might enhance the concentration of phytochemicals in juice. We know of no data, however, to support this speculation, but this is an area that may merit future research work.

V. SALINITY AND BIOTIC STRESSES

A. Phytophthora

Multiple stresses can have synergistic effects on plants. Much of the work on interactions between salinity and pathogens has been done using seedlings. In field trees, however, the scion can affect the susceptibility of the rootstock to root rot (Shaked et al. 1984). In greenhouse experiments, irrigation with high-salinity water with a Cl^- concentration of 1670 mg L^{-1} predisposed citrus rootstocks to attack by root pathogens (Combrink et al. 1996). Rootstock seedlings of 'TROY', 'CARZ', 'VOLK', and 'RL' were most affected by the treatment consisting of three root pathogens in combination (*Phytophthora nicotianae*, *Fusarium solani*, and *Tylenchulus semipenetrans*) under saline conditions. Growth of these seedlings subjected to both *Phytophthora* and salinity together was significantly less than that of seedlings subjected to the pathogens either singly or with Cl^- stress alone. *Phytophthora* infection and *Fusarium* root rot were always more severe in combination with Cl^- . 'VOLK' and 'RL' were more severely affected by the three pathogens than 'TROY' and 'CARZ'. In addition, 'TROY' and 'CARZ' citranges, with known tolerance to *P. nicotianae* and *T. semipenetrans*, became more susceptible to these pathogens when irrigated with high-salinity water. Salinity also affected stem infection. Stems of 'SO', 'RL', and 'TROY' were inoculated with a fungus identified as *P. citrophthora*, and regardless of rootstock, NaCl (but not Na_2SO_4) increased stem gummosis (El Guilli 2000), pointing again to the detrimental effect of the Cl^- ion on citrus. Increased disease could have resulted from increased tissue susceptibility in response to salinity stress, inhibition of plant defense (Afek and Szejnberg 1993), and/or decreased root regeneration. *Phytophthora* isolates cultured from diseased citrus growing in the saline soils of the Coachella valley in California tolerated salinity more than a culture isolated from citrus growing in non-saline soil (Blaker and MacDonald 1985). The ability of *Phytophthora* to tolerate high levels of salinity could significantly diminish the resistance of *Phytophthora*-tolerant rootstocks such as 'TROY' under saline conditions (Blaker and MacDonald 1986).

B. Rio Grande Gummosis

Rio Grande gummosis, a disease of unclear etiology, was attributed to irrigation with high-salinity water and to applications of KCl or CaCl_2 but not to K_2SO_4 (Childs 1978). Although the Cl^- levels in the leaves were

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similarly normal in infected and non-infected locations, Cl^- levels in the bark and wood were about 10 times higher than those in the roots and almost four times higher in an orchard infected with Rio Grande gummosis than in the non-infected orchard (Russo et al. 1993). However, analysis of grapefruit trees on different rootstocks in Florida indicated no relationship between rootstock tolerance to salinity and incidence of Rio Grande gummosis (Sonoda and Pelosi 1990). In a long-term salinity experiment at Gilat, Israel (Y. Levy and J. Shalhevet, unpublished results), there was no correlation between the salinity of the irrigation water and appearance of Rio Grande gummosis in 'Marsh' grapefruit. There was adequate disease pressure present, however, as trees at different salinities were infected at random. In Israel, Rio Grande gummosis commonly affects grapefruit trees on 'TROY' or on 'SO' that suffer from lime-induced chlorosis. The problem can be corrected by the application of chelated iron and by modifying the irrigation system from sprinkler to drip. This occurrence leads us to the conclusion that Rio Grande gummosis may be related to soil aeration, to lime-induced chlorosis, or to just general stress that may be caused by different factors and not only salinity.

C. Nematodes

The citrus nematode (*Tylenchulus semipenetrans*) can reduce the salt tolerance of citrus roots and increase Cl^- uptake (Willers and Holmden 1980). Leaf Cl^- levels of severely affected trees varied between 1.75 and 2.00% compared with 0.50–0.90% in less-infected trees under the same conditions; this was true for salinity-tolerant rootstocks and for salinity-sensitive rootstocks, however. At the same experiment, nematodes increased more than three-fold the Cl^- concentration in leaves but decreased the Cl^- concentration in roots (Mashela and Nthangeni 2002). Salinity increased nematode egg production, with the largest number of eggs recovered from 'CLEO' and 'SO' roots, where salinity doubled the number of eggs. Salinity also increased the number of nematode eggs and females on rootstocks with better tolerance to nematodes, such as 'TRIF', 'CTRM', and 'TROY'. However, the nematode number remained small, suggesting that salt-tolerant rootstocks are more susceptible to nematodes and nematode-resistant rootstocks lack salt tolerance (Mashela et al. 1992a). On the other hand, sudden reductions in soil salinity by rain or irrigation offered nematodes a suitable non-osmotic habitat that increased their population densities (Mashela et al. 1992b).

Soil salinity increased the susceptibility of citrus roots to attack by the citrus nematode (Dunn et al. 1998). Thirty days of a high-salinity (0.1 M

NaCl) treatment 6 months after inoculation with nematodes, increased the nematode infection rate by 54%. Phenylalanine ammonia lyase (PAL) activity was inversely correlated with salinity level and with increase in arginine concentration, suggesting that salinity caused a breakdown in root chemical defenses.

D. Mycorrhizae

Citrus trees interact with microorganisms that belong to various groups, including bacteria, fungi, and nematodes. Soil-borne pathogens constitute only a very small fraction of the total population of soil organisms (Katan 1996). These range from true parasites that always harm the roots to microorganisms that may exist in harmony with the plant or even benefit the plant. Citrus is very dependent on vesicular arbuscular mycorrhizae (VAM) colonization, especially under conditions of low soil P concentration or sterilized soils (Kleinshmidt and Gerdemann 1972; Krikun and Levy 1980; Menge et al. 1978).

The ability of VAM to increase tree growth particularly under saline conditions and thus alleviating salinity stress has been reported. However, there have been some reports that VAM can increase Cl^- uptake by plants, just as VAM increases P uptake. VAM plants of 'CARZ' and 'SO' accumulated more Cl^- in leaves than non-mycorrhizal plants. Cl^- was higher in non-mycorrhizal roots of 'SwO' and 'CARZ' than in mycorrhizal roots (Hartmond et al. 1987). Graham and Syvertsen (1989) reported that VAM increased the concentrations of Cl^- in leaves and roots of 'SwO' and 'SO' seedlings irrigated with high-salinity water. This increase could not be attributed to increased transpiration in the VAM plants. Na^+ concentrations, on the other hand, were not affected by VAM. There were no significant growth or physiological interactions between mycorrhizae and salinity. Natural VAM in relatively saline soils may be sensitive to salinity and its population decreased with increased soil salinity (Levy et al. 1983). VAM strains that originated in soils of different salinities may differ in this respect (Copeman et al. 1996; Juniper and Abbott 1993).

VI. BENEFITS OF MODERATE SALINITY

Other than the benefits from moderate applications of fertilizer salts, salinity is usually not beneficial for citrus in the long run. Since citrus can tolerate moderate salinity and produce a profitable yield using

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proper cultural practices and tolerant cultivars, there may be some short-term benefits from salinity.

A. Chilling and Freezing Tolerance

Moderate salinity at levels of 1065 to 2130 mg Cl⁻¹ L⁻¹ (30 to 60 mol m⁻³ of NaCl) applied for 2 months, reduced growth and total plant transpiration but enhanced cold hardiness of 'SwO' and 'CLEO' seedlings (Syvertsen and Yelenosky 1988) even though leaf Ψ_{π} and leaf proline concentration did not change significantly. Thus, controlled salinity stress under greenhouse conditions can substitute for cool temperature-induced freeze tolerance in seedlings by reducing physiological activity and growth. However, when freeze injury was determined for young grapefruit trees on different rootstocks, trees with high Cl⁻ content were more susceptible to freeze injury than those with low Cl⁻ (Peynado 1982).

B. Leaching

Du Plessis (1985) suggested that reduced transpiration from salinity stress could potentially be a benefit in reducing the accumulation of soil salinity, since the lower water uptake should increase the leaching fraction. This scenario implies that an increase in the leaching fraction occurs when irrigating with increasingly saline water when water applications are scheduled similarly to those for non-saline conditions. However, soil salinity can increase proportionally to the salinity in the irrigation water and thereby reduce growth and yield.

C. Increase Flowering, Yield

Just as drought stress can substitute for cool wintertime temperatures to enhance flower induction (Nir et al. 1972; Southwick and Davenport 1986), it is possible that moderate salinity stress will also increase flowering. In a warm, wet climate with inadequate chilling or drought stress to maximize flower induction, controlled salinization might offer a substitute to induce flowering as is practiced for inducing flowering of litchi in Thailand (E. Tomer, pers. commun. 2001). If saline irrigation water could be applied during induction followed by adequate rainfall or irrigation with good-quality water during fruit set, yields might be increased. The successful economic use of such a practice, however, remains to be tested. As discussed above, effects of moderate salinity on fruit quality are usually subtle (Boman 2000).

VII. SUMMARY

Since decreases in the quality of the world's water resources are inevitable, it is important that growers continue to improve production practices and genetic varieties to deal with poor-quality water to sustain production. Citrus can use reclaimed water better than other crops since fruit are either processed for juice or thoroughly washed and disinfected in the packinghouse prior to peeling (Parsons et al. 2002). However, reclaimed waters are higher in salinity than unused water and salinity will increase as urban water use efficiency improves.

There are many things citrus growers can do to ameliorate problems associated with salinity stress, from choosing the best rootstock and scion cultivars to appropriately managing irrigation and fertilizer application methods. To help citrus growers cope with salinity problems, researchers should not only understand the mode of action of salinity stress but also understand the underlying mechanisms of salinity tolerance. Salinity reduces water use through osmotic effects but the gradual accumulation of Cl^- , Na^+ , and B to toxic levels are equally or even more important in citrus trees.

Fortunately, the different species of *Citrus* and their relatives differ in susceptibility to salinity, and future breeding may produce better rootstocks than are available today. Salinity tolerance is a whole plant phenomenon that requires an appreciation of citrus rootstock/scion interactions in the field. Such relationships are complicated by interactions between salinity and physical environmental factors as well as between salinity, pests, and diseases. The study of interactions between salinity, drought, and elevated CO_2 can yield insights into salt exclusion/uptake, growth, and plant water use. New rootstocks or even salt-tolerant cultivars, together with improved cultural practices, such as nutrition, irrigation, drainage, and perhaps altering the physical environment, such as shading or raising humidity, may enable future citriculture to utilize lower-quality water. Not all effects of salinity are negative, however, as moderate osmotic stress can reduce physiological activity and growth, allowing citrus seedlings to survive cold stress. Short-term salinity can even enhance flowering after the salinity stress is relieved.

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