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How Salinity Damages Citrus: Osmotic Effects and Specific Ion Toxicities

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SUMMARY. There are two ways salinity can damage citrus: direct injury due to specific ions, and osmotic effects. Specific ion toxicities are due to accumulation of sodium, chloride, and/or boron in the tissue to damaging levels. The damage is visible as foliar chlorosis and necrosis and, if severe enough, will affect orchard productivity. These ion accumulations occur in two ways. The first, more controllable and less frequent method, is direct foliar uptake. Avoiding irrigation methods that wet the foliage can easily eliminate this form of specific ion damage. The second way specific ion toxicity can occur is via root uptake. Certain varieties or rootstocks are better able to exclude the uptake and translocation of these potentially damaging ions to the shoot and are more tolerant of salinity. The effect of specific ions, singly and in combination, on plant nutrient status can also be considered a specific ion effect. The second way salinity damages citrus is osmotic effects. Osmotic effects are caused not by specific ions but by the total concentration of salt in the soil solution produced by the combination of soil salinity, irrigation water quality, and fertilization. Most plants have a threshold concentration value above which yields decline. The arid climates that produce high quality fresh citrus fruit are also the climates that exacerbate the salt concentration in soil solution that produces the osmotic effects. Osmotic effects can be slow, subtle, and often indistinguishable from water stress. With the exception of periodic leaching, it

is difficult to control osmotic effects and the cumulative effects on woody plants are not easily mitigated. This review summarizes recent research for both forms of salinity damage: specific ion toxicity and osmotic effects.

Salinity has been a problem since irrigated agriculture began thousands of years ago. It is most common in the arid and semiarid areas where evapotranspiration, the combination of evaporation from the soil with transpired water from plants, exceeds annual precipitation, making irrigation necessary. Salts occur naturally in soils, and they accumulate further as they are introduced in irrigation waters and fertilizers. The combination of the three in irrigated agriculture in arid zones, particularly if water is limited in quantity and quality, will eventually produce salinity problems. As most citrus is produced in arid climates, and since citrus and its commercial rootstocks are classified as salt sensitive, salinity damage is a problem in citrus production (Maas, 1993). This problem manifests in two forms: specific ion damage and osmotic effects.

Salinity tolerance of citrus

The general term “salinity” refers to the presence of the dissolved cations sodium, calcium, boron, magnesium and potassium, and the anions: chloride, sulfate, and carbonate in the soil solution in concentrations high enough to reduce crop growth.

The salinity tolerance of any crop is defined as the ability to endure the effects of excess salt in the root zone. The crop salt tolerance is best described by plotting its relative yield as a function of increasing soil salinity (Maas, 1990). This relationship between relative yield and soil salinity is described by the following equation:

$$Y = 100 - B(EC_e - A)$$

where Y is relative yield; A is the threshold value or the maximum soil salinity, in $dS \cdot m^{-1}$, at which 100% yield is still realized; B is the slope or percent reduction in yield per unit increase in soil salinity ($dS \cdot m^{-1}$); and EC_e is the average root zone salinity expressed as the electrical conductivity of the saturated soil paste, in $dS \cdot m^{-1}$. This formula describes the level of soil salinity where plant productivity begins to decline (A) and how rapidly it declines in productivity (B) as soil salinity in-

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creases. With woody crops, these two values generally reflect only the osmotic effects of salinity, not specific ion toxicities. Generally, specific ion toxicities produce injury and, potentially, yield losses, above what is predicted based on osmotic effects alone.

Using the above formula, Maas and Grattan (1999) ranked grapefruit (*Citrus paradisi*), lime (*C. aurantifolia*), sweet orange (*C. sinensis*), and pummelo (*C. grandis*) as salt sensitive relative to other crops. They all have a salinity threshold (A) of 1.2 to 1.5 dS·m⁻¹ and slopes (B) of 12.8% to 13.5%. Therefore, for soil salinities that exceed 1.5 dS·m⁻¹, yield would decline at the rate of about 13% to 13.5% with each additional increase in ECe. Shalhevet and Levy (1990) and Pearson et al. (1957) reported similar values.

While all fruit-producing citrus cultivars are classified as salt sensitive, this is not true of citrus rootstocks, which vary widely in their salt uptake and translocation from shoots to roots. For example, Rangpur lime (*C. reticulata* var. *austera* × *C. limon*) excludes chloride and sequesters sodium in basal parts, and Cleopatra mandarin (*C. reticulata*) excludes both sodium and chloride, while trifoliolate orange (*Poncirus trifoliata*) excludes only sodium but translocates chloride to leaves (Grieve and Walker 1983). The few long-term studies using rootstock–scion combinations further demonstrate the salinity management potential rootstock selection can provide (Cooper et al., 1956; Vardi et al., 1988).

Mechanisms of salinity damage

Salinity damages crops two ways: by osmotic effects and specific-ion toxicities. Both types of damage can occur in citrus production.

Salinity damage from osmotic effects occurs when the concentration of salts in the soil water are high enough to reduce crop growth. This concentration varies from crop to crop. Most crops, including citrus, are glycophytes and are unable to absorb salts from the soil water and accumulate them in their tissue as a means of adjusting osmotically. Rather, they accumulate organic solutes in their cells, along with nontoxic ions, as a means of adjusting to the saline conditions (Lauchli and Epstein, 1990).

Specific ion toxicities are the result of boron, sodium, and chloride ion accumulation in plant tissues, either from leaf absorption and/or root uptake, and are more common in woody plants, especially evergreens, where the leaves have longer lives and transpire longer (Lauchli and Epstein, 1990; Maas and Grattan, 1999). Very little is known about the specific mechanism of tissue injury by salts. Since injury usually occurs in the older leaves, where concentrations of specific ions are generally higher than in younger leaves, it is often thought injury is due to direct cell injury and tissue desiccation due to high concentrations of accumulated salts. Older leaves have higher specific ion concentrations because they have transpired longer. This damage manifests as visible leaf or stem “burn.” Visible symptoms of salt injury in citrus are generally referred to collectively as “chloride effect” because chloride is the most common cause of specific ion toxicity in citrus, whether generated by foliar absorption or root uptake (Maas, 1993).

Chloride also is more problematic than sodium. Sodium tends to be sequestered in roots and woody tissue more than chloride. Moreover, an adequate supply of free calcium in the soil solution improves membrane integrity and is a factor in controlling specific ion toxicities (Grattan and Grieve, 1999). In citrus grown under saline conditions, calcium was effective in reducing sodium and chloride transport from roots to leaves, thus avoiding specific ion toxicities (Zekri, 1993; Zekri and Parsons, 1990a).

Embleton et al. (1973) and Bernstein (1965) summarized the effects of the anions and cations that contribute to specific ion toxicities in citrus. The following descriptions are from their summaries.

Chloride toxicity manifests as slight leaf bronzing and leaf tip yellowing followed by tip burn and necrosis, all proceeding downward leaf chloride concentrations must generally be above 0.7% dry matter, produce chloride toxicity. However, injury is dependent upon not only the tissue ion concentration but on environmental conditions as well. For example, a crop can contain high concentrations of a specific ion to potentially toxic levels but injury will not become evident until the crop experiences another

stress, such as a hot, dry wind (Maas and Grattan, 1999).

Boron toxicity produces a mottled yellowing of the leaf tip followed by interveinal chlorosis (Embleton et al., 1973). The boron levels in leaves required to produce boron toxicity range from 0.005% to 0.17% dry weight, depending upon the part of the citrus leaf. Levels are highest in the leaf parts to first show toxicity.

Sodium toxicity starts as a marginal yellowing followed by a progressive necrosis beginning at the leaf margins. The advancing spread of the sodium burn imparts a rippled appearance to the burned areas. The sodium levels in citrus leaves required to produce toxicity start at 0.04% leaf dry weight (Bernstein, 1965).

Specific ion toxicity from foliar absorption

Chloride, boron, and sodium can all be absorbed by leaves when wetted by sprinkler irrigation and produce toxicity (Stolzy et al., 1966). A citrus tree’s susceptibility to foliar specific-ion toxicity depends upon how quickly leaves absorb these ions, which is a function of leaf structure, leaf retention time, how frequently and for how long the crop is irrigated, evaporative demand, and concentration of salts in the irrigation water. As an evergreen, citrus has leaves with long retention times, and thus may accumulate ions to high concentrations even if ion levels in irrigation water are moderate, particularly if foliar irrigation is frequent and the climate arid. Harding et al. (1956) first described severe foliar damage to the skirts of citrus trees from under tree sprinklers even when the irrigation water was of good quality, as low as 2.0 to 3.3 mol·m⁻³ Cl⁻. Specific ion toxicities in citrus can be exacerbated by overhead sprinkler irrigation and hot, dry climates, more than would occur otherwise if irrigated in more moderate climates by methods that do not wet the leaves. Therefore, changing irrigation methods, frequency and timing, and sprinkler angles can eliminate or at least reduce this form of specific ion toxicity. If overhead sprinklers must be used, irrigation intervals and duration should be longer, and done during periods of low evaporative cooling, preferably at night. The objective is to avoid the short, repeated irrigations during hot, dry conditions that favor maximum foliar uptake.

Specific ion toxicity from root uptake

For citrus orchards that are not irrigated by overhead sprinklers, specific ion toxicities are usually the result of root uptake of sodium, chloride, or/and borate and translocation and accumulation in the leaves. In these instances, chloride is most often the major culprit. Generally chloride is the dominant anion in soil solution, and if it is readily absorbed by the rootstock, its toxicity will generally build upon the adverse effects induced by osmotic effects alone. As with chloride ion toxicity from foliar uptake, chloride accumulation in leaves by root uptake only is not a definitive indicator of potential total chloride stress in a given microclimate. Raveh and Levy (2000) suggest both leaf accumulation and current chloride uptake status must be determined to give an accurate measure of total potential of chloride stress. They suggest an integration of average leaf transpiration rate through the season, and leaf and xylem sap chloride levels, will generate the best indicator of potential chloride status, and thus potential toxicity (Raveh and Levy, 2000).

Specific ion effects on plant nutrient status

Accumulations of specific ions, singly or in combination, can produce nutritional imbalances in plants. Traditionally, this has not been regarded as specific ion toxicity as the criterion, visible damage, is not present. However, as with osmotic effects, these specific ion accumulations do decrease growth as well as affect nutrient balance. In three experiments Zekri and Parsons (1990, 1992) and Zekri (1993) demonstrated sodium chloride delayed and depressed seedling emergence, reduced shoot and root biomass, and altered mineral concentration in a range of young citrus seedlings, but did not produce the leaf necrosis commonly associated with specific ion toxicity. Zekri and Parsons (1990) demonstrated sodium chloride increased the leaf sodium and chloride content of while decreasing the calcium, magnesium and potassium. Zekri (1993) later reported sodium chloride applied before seedling emergence through young seedling growth increased sodium, chloride, nitrogen, phosphorus, and potassium content of young seedlings

while again reducing calcium and magnesium. The major difference between the two reports was the effect sodium chloride had on potassium concentration. Levitt (1980) attributed some of the adverse effects of salinity in citrus to its ability to generate a potassium deficiency. However, this effect has not always been reproducible (Behboudian et al., 1986; Walker and Douglas, 1983). Potassium content appears to be linked to sodium accumulation. Zekri and Parsons (1992) reported sodium chloride reduced leaf potassium in rootstocks that sequestered sodium, Cleopatra mandarin, rough lemon (*C. jambhiri*), and Milam lemon (*C. jambhiri* hybrid), and increased it in leaves of rootstocks that excluded sodium, Swingle citrumelo (*C. paradise* x *P. trifoliata*), Carrizo citrange (*C. sinensis* x *P. trifoliata*) and trifoliata orange. However, they also reported the ability to exclude sodium broke down at higher salinity levels. Addition of calcium sulfate always improved seedling growth with the best results in sour orange (*C. aurantium*), rough lemon or Swingle citrumelo seedlings. Generally, Zekri (1993), and Zekri and Parsons (1990, 1992) found the nutrient imbalances caused by specific ion toxicity, and amelioration of it, to be strongly dependent upon rootstock and growth stage. Their results are consistent with those of Jones et al. (1957) and Pearson et al. (1957).

Osmotic effects of salinity damage

The other way salinity harms citrus is through osmotic effects imposed by salts in the soil solution (Lauchli and Epstein, 1990; Hanson et al., 1999). These effects are the processes by which salinity most commonly reduces citrus tree growth and yield. Normally the concentration of solutes in the root cells is higher than that in the soil solution. This differential allows water to move freely into the plant root. As salinity in the soil solution increases the differential between soil and root cell solution increases and the soil water initially becomes less available to the plant. To counter increasing soil salinity the plant root cells must adjust osmotically, either by accumulating salts, or by increasing synthesis of organic compounds, primarily sugars and organic acids. These processes use energy that would otherwise be used for growth and yield production.

The result of prolonged but effective osmotic adjustment is a smaller plant that may appear healthy. Some species adjust osmotically more readily or efficiently than others. Frequently, osmotic adjustment to increased salinity is incomplete and the plants respond as if water stressed.

Plants that adjust osmotically are classified as either halophytes or glycophytes (Lauchli and Epstein, 1990). Halophytes adjust and thrive under saline conditions by accumulating absorbed salts creating a salinity differential which facilitates water uptake from a saline soil. Citrus is classified as a glycophyte; a plant affected by moderate levels of salinity. Glycophytes adjust osmotically by increasing production of sugars and organic acids that increase the osmolarity of constituents in the root cells. This process demands more energy than the osmotic adjustment through salt accumulation halophytes, which results in greater yield and growth suppression. Thus, glycophytes are more affected by salinity than halophytes.

Most of the pre-1990s literature investigating the response of commercial citrus to salinity was, as Spiegel-Roy and Goldschmidt (1996) observed, short-term responses of ungrafted rootstocks. The more recent literature detailing the effects of salinity on citrus growth and yield, fruit quality, and nutritional balance more frequently incorporates rootstock–scion combinations but is generally still short-term studies on trees in containers or grown hydroponically (Fernandez-Ballester et al., 2003; Garcia et al., 2002; Garcia-Agustin and Primo-Millo, 1995; Grieve and Walker, 1983; Levy and Syvertsen, 2004). Collectively, the above literature demonstrates citrus is saline sensitive, and that both growth and yield will suffer from sustained salinity. This literature also demonstrates that the ability to tolerate salinity is associated with the ability of individual rootstock genotypes to either exclude chloride by restricting entry, to accumulate sodium in the basal sections of the rootstock, to adjust osmotically, or decrease water uptake, all with the net result of protecting the scion from ion accumulation.

A number of more recent studies have focused on specifically how, physiologically, sustained salinity impacts water uptake, net gas exchange and photosynthesis, ion partitioning,

and the metabolism of citrus species (Almansa et al., 2002; Bañules et al., 1995; Ben-Hayyim et al., 2001; Garcia-Sanchez et al., 2002a, 2002b; Moya et al., 1999, 2002, 2003; Nolte et al., 1997; Piqueras et al., 1996). Collectively, these papers demonstrate that salinity affects most stages of citrus physiology and metabolism, with the most detrimental and measurable effects occurring on root water and nutrient uptake, hydraulic conductivity, gas exchange, photosynthesis, chlorophyll content, some metabolites such as proline, and leaf anatomy. Thus far, the accumulated knowledge of the physiology and metabolism of salt-affected and salt-tolerant citrus suggests few horticultural manipulations, other than irrigation timing and quantity, which could possibly alleviate salinity stress for the long-term, bearing life of a mature citrus tree.

Two major problems are encountered when investigating the effects of salinity on long-term plant physiology and productivity of any species. The first is distinguishing the effects of salinity from its effects on soil water availability. The second is the soil saturation produced by a saline soil when applying salinity treatments. Different approaches have been taken with each problem.

To separate the effects of salinity from its effects on soil water availability, polyethylene glycol has been used to simulate the osmotic pressure of a saline soil solution. At equal osmotic potential levels, polyethylene glycol reduced stomatal conductance and growth of sour orange seedlings more strongly than saline soil solutions with higher levels of electrical conductivity. This suggests the osmotic pressure produced by salinity is less harmful to citrus than that produced by direct water stress (Zekri and Parsons, 1990b). However, numerous studies with polyethylene glycol suggest it has toxic effects on plants apart from its ability to produce decreased soils moisture deficits (Krizek, 1985). As a result, studies with polyethylene glycol have decreased in recent decades.

In the second case—attempts to determine the effects of salinity without the confounding factor of soil saturation—the studies have been conducted in sand or hydroponic tanks where salinity level and root exposure can be controlled while drainage or aeration eliminates soil saturation (Garcia et al.,

2002). These studies generally produce good physiological data on uptake and exclusion but cannot integrate the effect of long-term salinity on tree growth and development. There are virtually no long-term studies investigating the effects of sustained salinity on long-term growth and yield.

Breeding citrus for salinity tolerance

Both the earlier literature demonstrating the effects of sustained salinity on citrus tree growth and yield, and the later studies investigating the physiology and metabolism, suggest only genetic manipulation will provide citrus that is tolerant of sustained salinity stress. Early identification of traits for predicting salt tolerance has been elusive. Zekri (2001) investigated the ability of seedling salinity tolerance to predict the tolerance of mature, bearing citrus. His results suggest rootstock seedling trials are not a good indicator of later salinity tolerance, perhaps because the effects of salinity are long term and cumulative in maturity. It is likely that specific ion toxicities become more dominant over the years. The evaluation of rootstock seedlings for salinity tolerance by Garcia et al. (2002) supports using Cleopatra mandarin as a donor of salt tolerance in traditional breeding programs, because it possesses the three mechanisms of salt tolerance in citrus: chloride exclusion, water saving, and accumulation of soluble solids (Garcia et al., 2002). Spiegel-Roy and Saad (1997) have had some success regenerating salt-tolerant callus in citrus. Noat et al. (1995a, 1995b) have demonstrated induction of a gene encoding an oleosin homologue in cultured citrus cells exposed to salt stress. Tozlu et al. (2002) have completed a QTL analysis of the salt stress-related traits in citrus and the genus *Poncirus* and are now breeding for citrus salt tolerance. Undoubtedly, breeding for salinity tolerance in citrus will continue, particularly as this crop, like many others, is introduced to more marginal lands where saline water is the only source of irrigation.

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