

EFFECTS OF SODIUM CHLORIDE AND POLYETHYLENE GLYCOL
ON THE WATER RELATIONS, GROWTH, AND MORPHOLOGY
OF CITRUS ROOTSTOCK SEEDLINGS

By

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In the name of God,
Most Gracious,
Most Merciful.

"It is He Who has let free the two bodies of flowing water: one palatable and sweet and the other salt and bitter: yet has He made a barrier between them, a partition that is forbidden to be passed."

Glorious Quran
Sura XXV (Furquan), or The Criterion
Verse #53

In the name of God
Most Gracious,
Most Merciful.

"It is He Who sendeth down rain from the skies: with it We produce vegetation of all kinds: from some We produce green (crops), out of which we produce grain, heaped up (at harvest); out of the date-palm and its sheaths (or spathes) (come) clusters of dates hanging low and near: and (then there are) gardens of grapes, and olives, and pomegranates, each similar (in kind) yet different (in variety): when they begin to bear fruit, feast your eyes with the fruit and the ripeness thereof. Behold! in these things there are signs for people who believe.

Yet they make the Jinns equals with God, though God did create the Jinns; and they falsely, having no knowledge, attribute to Him sons and daughters. Praise and glory be to Him! (for He is) above what they attribute to Him!

To him is due the primal origin of the heavens and the earth: how can He have a son when He hath no consort? He created all things, and He hath full knowledge of all things.

That is God, your Lord! There is no god but He, The Creator of all things: then worship ye Him: and He hath power to dispose of all affairs."

Glorious Quran
Sura VI (An'am), or Cattle
Verses #99-102

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The effects of sodium chloride (NaCl) and polyethylene glycol (PEG) on the growth, water relations, and leaf mineral content of citrus rootstocks were investigated. Significant growth reduction and physiological disturbances occurred even at NaCl and PEG concentrations of -0.10 MPa. Growth reduction and physiological changes were found to precede visible damage. Growth was reduced up to 30% without being accompanied by visible leaf injury symptoms. Leaf burn symptoms developed only after a threshold value of chloride accumulation (1%) was reached. Leaf burn symptoms developed too slowly to accurately evaluate salt damage. Root conductivity correlated better with salinity tolerance among rootstocks than did total fibrous root length.

Sodium chloride usually caused less damage than PEG. Unlike PEG, NaCl significantly increased leaf thickness and succulence along with leaf sodium and chloride concentrations, but reduced calcium and zinc contents in the leaves. Both NaCl and PEG reduced leaf magnesium and potassium contents but increased leaf phosphorus and manganese contents.

Differences in sodium and chloride exclusion capacities among rootstocks were found. Sour orange, rough lemon, and Milam were sodium and chloride accumulators. Poncirus trifoliata, Swingle citrumelo, and Carrizo citrange were sodium excluders but chloride accumulators. Cleopatra mandarin was a chloride excluder but a sodium accumulator. Differences in NaCl sensitivity among rootstocks were also found. Cleopatra mandarin and sour orange were the least sensitive, Milam and Poncirus trifoliata were the most sensitive, and rough lemon, Swingle citrumelo, and Carrizo citrange were intermediate in sensitivity. Cleopatra mandarin tolerated high concentrations of NaCl by partial exclusion of chloride while sour orange tolerated NaCl even though it accumulated sodium and chloride in its leaves. Sour orange might have the ability to compartmentalize these ions and exclude them from the cytoplasm where they may inhibit metabolic processes.

Seedlings receiving NaCl or PEG produced small and shallow root systems with the majority of the roots occurring in the top layer. Addition of calcium sulfate to saline irrigation water was found to be beneficial in overcoming the detrimental effects of NaCl on citrus. The split-root experiment showed that citrus could withstand substantial amounts of stress as long as half of the root system was growing in a non-stressed environment.

INTRODUCTION

It is well established that salt can impair the performance of many agricultural plants. Salts present in the soil and irrigation water are a serious problem for commercial agriculture particularly in arid and semi-arid regions. However, the potential for salinity damage also exists in humid climates. Controlling or reducing salt injury is usually achieved either through soil management practices and irrigation with good quality water or by combining these practices with the use of salt-tolerant plants.

Citrus is a fruit crop of international significance. It is grown in over 50 countries and ranks among the top 3 tree fruit crops in world production. In certain areas where citrus is grown, salinity is already a problem of some importance. In other areas, the future of citriculture is threatened by salinity largely because agriculture is being forced to use lower quality land and water for irrigation. In agricultural areas with salinity problems, citrus is particularly vulnerable because there is relatively little salt tolerance in the genus.

Salinity studies have shown that among species, cultivars, and various selections, only 2 rootstocks, Cleopatra mandarin and Rangpur lime, have a limited capacity to tolerate certain salts. However, rootstocks are usually selected for other attributes such as yield and fruit quality. Rootstocks deficient in these characteristics are not likely to be commercially used despite favorable salt tolerance.

In Florida, there are many citrus plantings located in coastal areas where saline water is being used for irrigation. Citrus planting in these and other southern Florida areas has been accelerated by extensive freeze damage in more northern areas. These changes in the citrus industry, as well as the diseases triteza and blight, have greatly affected interest in rootstock characteristics including salt tolerance.

In the past, virtually all evaluations of citrus response to salinity were based on visual leaf injury and correlations with leaf chloride content. There were no root system observations recorded and no detailed physiological studies conducted. Such observations and measurements of physiological responses are necessary for a complete understanding of salt injury and tolerance in plants. This information is particularly valuable for efficient breeding and screening of new germplasm for salt tolerance.

The objectives of this research are the following:

1. To compare the salt tolerance of citrus rootstocks commercially important in Florida and to determine which rootstocks are salt excluders or salt accumulators.
2. To determine the salt concentrations at which growth is depressed, water balance is disturbed, and leaves are injured.
3. To separate specific ion effects of salts from their osmotic effects by comparing growth, water relations, and plant chemical analyses under NaCl and PEG stresses.
4. To measure the effects of several NaCl and PEG concentrations on root growth and distribution.
5. To study citrus growth and water relations under non-uniform salinity (split-root system).
6. To examine the importance of calcium in reducing NaCl damage.

LITERATURE REVIEW

Salts

Many hectares of land throughout the world are too saline for profitable agriculture (Carter, 1975). Large amounts of arable lands are being removed from crop production every year due to increasing soil salinity (Chapman, 1975; Epstein et al., 1980). Saline irrigation water combined with fertilizer application are the factors most responsible for increasing soil salinity (Epstein et al., 1980; Jones et al., 1952; Stewart et al., 1977).

The ions in soil waters which contribute significantly to salinity problems are principally sodium, chloride, calcium, magnesium, sulfate, potassium, bicarbonate, carbonate, nitrate, and occasionally borate ions (Bernstein and Hayward, 1958; Peck, 1975; Shainberg, 1975). However, most salinity research has involved NaCl because it is the most common salt in saline soils and irrigation waters.

Mechanisms of Salt Tolerance in Plants

Salt-tolerant plants are generally thought to be protected from salt stress by either ion accumulation or ion exclusion. Accumulation of high concentrations of ions in halophyte leaves has been known to be a salt tolerance mechanism (Flowers et al., 1977; Greenway and Munns, 1980). Salts can be tolerated because ions are compartmentalized in the vacuole and not in the cytoplasm. Hence, metabolic processes are not inhibited. These ions in the vacuoles balanced with neutral organic solutes in the cytoplasm lower the leaf osmotic potential. This allows

the plant to extract water from saline solutions. However, salt tolerance in glycophytes (nonhalophytes) is related to ion exclusion because of the plant's inability to compartmentalize toxic ions in a useful way and to adjust osmotically (Greenway and Munns, 1980).

Mechanisms of Salt Injury

Salt damage to plants is caused by the decrease in the water potential of the soil solution or by the toxicity of specific ions. Some workers attribute most of the salt damage to osmotic stress (Bernstein, 1961, 1963; Bernstein and Hayward, 1958; Bielorai et al., 1978, 1983; Bohn et al., 1979). Others favor the idea that toxic effects of specific ions predominate in restricting growth and yields (Babaeva et al., 1968; Gollek, 1973; Strogonov, 1964).

A common method of distinguishing between osmotic and ion toxic effects of salts is to compare the effects of isosmotic solutions of the salt with those of non-toxic organic substances. If the salt injury is simply osmotic, all solutes should produce the same injury at the same osmotic potential (Levitt, 1980). Polyethylene glycol (PEG), a non-ionic compound, has been successfully used as an osmoticum for subjecting plants and plant tissues to known levels of water stress (Janes, 1966; Kaufmann and Eckard, 1971; Kawasaki et al., 1983a, b).

Osmotic Effect

Water is osmotically more difficult to extract from saline solutions. Pair et al. (1975) pointed out that the addition of 0.4% salts had the effect of reducing the total available water in the soil by approximately 33%. Salt addition is analogous to soil drying since both result in reduced water uptake. In extreme circumstances, salinity can prevent water uptake even when the soil is at field capacity (Hartz, 1984). Water uptake by mature grapefruit trees, mature Valencia orange

trees, and Valencia orange seedlings was reduced as salinity increased (Bielorai et al., 1983; Hayward and Blair, 1942; Plessis, 1985).

Ion Toxic Effect

Ion toxic effect of salt is attributed to excess accumulation of certain ions in plant tissues and to nutritional imbalances caused by such ions. Ion excess has been defined as a condition where high internal ion concentrations reduced growth (Greenway and Munns, 1980). In many crops, salt injury increases with increased salt uptake. Raspberries were found to accumulate chloride ions more rapidly and consequently were more severely injured than blackberry (Ehlig, 1964). Tagawa and Ishizaka (1963) found that the primary cause of injury to rice by NaCl was chloride accumulation in the shoots. When treated with NaCl, a less resistant barley variety accumulated higher levels of chloride and sodium than a more resistant variety (Greenway, 1962).

Salt damage to citrus has been mainly attributed to excessive accumulation of chloride and sodium in the leaves (Abdel-Messih et al., 1979; Chapman et al., 1969; Cooper, 1961; Cooper et al., 1951; 1952b; Cooper and Peynado, 1953; El-Azab et al., 1973; Furr and Ream, 1968; Grieve and Walker, 1983). Goell (1969) suggested that salt ions such as chloride in citrus leaves might shorten the life span of leaves by increasing chlorosis (loss of chlorophyll and photosynthetic potential) and by promoting senescence and abscission. Sulfate and other ions also caused damage to citrus (Bhambota and Kanwar, 1970; Bingham et al., 1973; Cerda et al. 1979; Hewitt and Furr, 1965a; Peynado and Young, 1964). It has been suggested that the accumulation of ions in large amounts in the leaves is the main factor causing leaf burn and inhibition of certain metabolic processes.

Sodium can also cause injury to plants through its deleterious effect on the soil. When the proportion of exchangeable sodium is relatively high, clay particles in the soil tend to disperse and block the pores through which water flows. This phenomenon decreases the hydraulic conductivity of the soil (Bohn et al., 1979; Shainberg, 1975) and causes poor aeration. Studies by Aldrich et al. (1945) demonstrated that inferior performance of orange trees was caused primarily by poor water penetration resulting from sodium accumulation on the exchange complex.

Nutritional Imbalance

Salt can also damage plants by causing nutritional imbalances. High sodium levels can lead to calcium and magnesium deficiencies (Bohn et al., 1979). In spinach and lettuce, sodium salts decreased dry matter production as well as leaf potassium, magnesium, and calcium contents (Matar et al., 1975). Pumpkin and sweet clover plants subjected to NaCl showed potassium deficiency (Solov'ev, 1969). A decrease in potassium uptake at higher concentrations of sodium was found in sugarcane (Nimbalkar and Joshi, 1975) and rice (Paricha et al., 1975). With increased salinity, potassium and phosphorus uptake decreased in grapes, guava, and olive plants (Taha et al., 1972), in wheat (Sharma and Lal, 1975), and in barley (Kawasaki et al., 1983b).

In citrus, nutritional imbalance has been also attributed to depressed absorption of some nutrients. A decrease in the concentration of calcium, magnesium, and sometimes potassium was found when salt concentration in the irrigation water was increased (Jones et al., 1957; Patil and Bhambota, 1980; Pearson et al., 1957).

Plant Responses to Salinity

Salinity has been known to adversely affect all stages of plant development such as germination, vegetative growth, and fruiting. Salinity has also been found to depress chlorophyll content, photosynthesis, stomatal conductance, root conductivity, and transpiration of many crops. For example, growth of citrus (Furr and Ream, 1968), Vicia faba (Helal and Mengel, 1981), pepper (Hoffman et al., 1980), alfalfa (Keck et al., 1984), bean (Meiri and Poljakoff-Mayber, 1970), and corn (Siegal et al., 1980) was significantly depressed under saline conditions.

Yield of grapefruit (Bielorai and Levy, 1971; Bielorai et al., 1978, 1983), orange (Bingham et al., 1973, 1974; Chapman et al., 1969), celery (Francois and West, 1982), and muskmelon (Shannon and Francois, 1978) was severely reduced due to salinity stress. Salinity was found to alter fruit quality by decreasing the "pack out" of oranges at a commercial packing shed (Bingham et al., 1974) and by decreasing the marketable yield of tomato and melon (Mizrahi and Pasternak, 1985; Shannon and Francois, 1978). It was found that the relative amount of the premium grade fruit decreased with use of saline water even though there was a trend toward higher soluble solids and better taste (Bingham et al., 1974; Mizrahi and Pasternak, 1985; Shannon and Francois, 1978).

Salinity reduced leaf chlorophyll content in grapevine, bean, barley, citrus and mangrove (Downton and Millhouse, 1985), spinach (Downton et al., 1985), and Acacia saligna (Shaybany and Kashirad, 1978). Leaf chlorophyll content declined only when certain amounts of salt ions accumulated in the leaves. Salinity reduced photosynthesis in spinach (Downton et al., 1985), rice (Flowers et al., 1985), Xanthium strumarium (Schwarz and Gale, 1983), beans (Seemann and Critchley,

1985), and Acacia saligna (Shaybany and Kashirad, 1978). Under most circumstances, photosynthetic reduction was attributed to ion accumulation in the leaves and to reduction in stomatal conductance.

Salinity was found to reduce root conductivity in white lupin (Munns and Passioura, 1984) and beans (O'Leary, 1969; 1974). However, salinity did not affect root conductivity in barley (Munns and Passioura, 1984), sunflower and tomato plants (Shalhevet et al., 1976). Reduced hydraulic conductivity of roots has been attributed to root suberization and to reduced root membrane permeability.

Salinity and Citrus

Citrus is generally classified as a salt sensitive crop because physiological disturbances and growth and fruit yield reductions can occur at relatively low salinity levels (Bernstein, 1969; Bielorai et al., 1978, 1983; Boaz, 1978; Cherif et al., 1982; Cooper and Shull, 1953; Francois and Clark, 1980; Furr et al., 1963; Kirkpatrick and Bitters, 1969; Marsh, 1973; Patil and Bhambota, 1980; Pehrson et al., 1985; Walker et al., 1982).

Citrus Salinity Research

The response of citrus to salinity is a topic of concern in many regions where citrus is grown especially the United States, Israel, Egypt, India, Spain, and Tunisia. In the United States, salinity studies essentially began in Texas during the 1940s. Investigations were led by W.C. Cooper with emphasis on differences in salinity tolerance among citrus rootstocks (Cooper, 1948; Cooper and Gorton, 1952; Cooper and Peynado, 1959; Cooper and Shull, 1953; Cooper et al., 1951). The work was conducted mostly on young budded trees grown in the field. Salinity treatments consisted of $\text{NaCl} + \text{CaCl}_2$ added to Rio Grande river water. These studies led to the observation that chloride

exclusion was strongly correlated with salt tolerance. Chloride accumulation or exclusion and leaf injury symptoms were used to classify salt tolerant and salt sensitive rootstocks.

Salinity studies on citrus were started in California in the 1950's (Harding et al., 1958a; Janes et al., 1952; Pearson and Goss, 1953), in Israel in the 1970s (Bielorai et al., 1973; Heller et al., 1973), and in Australia in the 1970s (Cole and Till, 1977). Most of these studies were conducted in the field on mature citrus trees and were focused on yield reduction and fruit quality alteration as a function of salt concentration in irrigation waters (Bielorai et al., 1978, 1983; Bingham et al., 1973, 1974; Boaz, 1978; Francois and Clark, 1980; Levy et al., 1979; Pehrson et al., 1985; Shalhevet et al., 1974).

Recent salinity work in Israel was directed to plant breeding using cell culture techniques (Ben-Hayyim and Kochba, 1983; Ben-Hayyim et al., 1985). Recent work in Australia was conducted mainly with young rootstock seedlings grown in pots under glasshouse conditions (Behboudian et al., 1986; Grieve and Walker, 1983; Walker and Douglas, 1983; Walker et al., 1982, 1983, 1984, 1986). Salinity treatments consisted of NaCl added to a nutrient solution. These studies were focused on sodium and chloride exclusions mechanisms, water relations, and photosynthesis. Photosynthesis was severely reduced and photosynthetic reduction was attributed to a loss of turgor in salt excluder rootstocks and to chloride accumulation in salt accumulator rootstocks.

Some salinity work on citrus conducted in Egypt (Abdel-Messih et al., 1979; Minessy et al., 1973), India (Bhambota and Kanwar, 1970; Patil and Bhambota, 1980), Spain (Cerdeja et al., 1979; Guillen et al., 1978), and Tunisia (Cherif et al., 1981; 1982; Zid, 1975; Zid and

Grignon, 1985, 1986) on budded trees and rootstock seedlings involved ion analysis and nutrient absorption. These studies showed that salinity caused nutritional imbalance, growth reduction, and leaf burn. Growth reduction was attributed to potassium deficiency and foliar necrosis to sodium accumulation in the leaves.

Salinity is of increasing concern in Florida. Salt water intrusion into groundwater in areas where citrus is grown has increased the need for salinity studies in Florida. Many citrus rootstocks are being used in Florida such as sour orange, Swingle citrumelo, Carrizo citrange, and Milam without knowing their salt tolerance. As a result, there is an incentive to study the salinity tolerance of these and other rootstocks which are commercially important.

Physiologists often concentrate on the activities of shoots and neglect roots because they are out of sight and more difficult to study than shoots (Kramer, 1983). Roots play an important role in the growth and development of the entire plant. Their health, vigor and activity can be an index of the functioning of the above-ground parts (Cridler, 1927). It is important to investigate root growth and distribution because roots are directly in contact with salts in the soil. Detailed information on the growth behavior and morphological development of citrus root systems under salt conditions is not available.

The two major resistances to water movement through the soil-plant-atmosphere continuum are the roots and the stomata (Kramer, 1969; Kriedemann and Barrs, 1981). Root conductivity and stomatal conductance are important variables to be monitored in salinity studies because they can provide information on the water balance disturbance caused by salt. Root conductivity of some in citrus rootstocks under salinity stress has not been previously studied. Furthermore,

information relating root conductivity to stomatal conductance and transpiration as a function of different osmotic concentrations is lacking.

Under field conditions, the roots of an individual plant grow in soil which varies in water content and salt concentration both in space and with time. In assessing the suitability of water for irrigation, it is usually assumed that plants respond to the mean root zone salinity (Shalhevet and Bernstein, 1968). However, some workers suggest that the least saline part of the rooting zone controls the overall plant growth and yield (Lunin and Gallatin, 1965). Responses of citrus to non-uniform salinity or to zonal salinization are not known.

Citrus Tolerance to Salinity

Scion. Differences in salt tolerance among citrus varieties or scions have been shown. Boaz (1978) concluded that Valencia orange had a lower tolerance to salinity than grapefruit on sweet orange rootstock. Bernstein (1969) reported that lemon was more sensitive to salinity than orange which was more sensitive than grapefruit. Miwa et al. (1957) also found that lemon was the most susceptible variety to foliar spray injury from sea water. Results of Pearson and Huberty (1959) showed that navel orange trees were more sensitive to irrigation water quality than Valencia orange trees. Budded on rough lemon, salt tolerance decreased in the following order: Hamlin, Valencia, Pineapple and Blood red sweet orange (Bhambota and Kanwar, 1969). Valencia seemed to be more sensitive to salinity than Shamouti when both were grafted on sour orange rootstock (Shalhevet et al., 1974).

Rootstock. Some studies have indicated a wide range in salt tolerance among citrus rootstocks (Cooper, 1948; Cooper and Edwards, 1950; Cooper et al., 1952b, 1958). Cooper et al. (1951) found that

Cleopatra mandarin and Rangpur lime are relatively salt-tolerant rootstocks. They classified sour orange, rough lemon, sweet lemon, tangelo and sweet lime as sensitive rootstocks and Florida sweet orange and trifoliolate orange as very sensitive. In another study, Cleopatra mandarin and Rangpur lime were also found to be the most tolerant rootstocks and Carrizo citrange was the most sensitive rootstock (Joolka and Singh, 1979; Patil and Bhambota, 1978). Trifoliolate orange and rough lemon were found to be very salt sensitive (Bhambota and Kanwar, 1969). Although some selections of sour orange differed in salt tolerance, Ream and Furr (1976) found that none of them was as salt tolerant as Cleopatra mandarin.

Salt Exclusion. Exclusion of certain ions has been demonstrated in some citrus rootstocks. Rangpur lime and Cleopatra mandarin appear to be chloride excluders (Cooper, 1961; Cooper and Gorton, 1952; Cooper and Peynado, 1959; Douglas and Walker, 1983; Grieve and Walker, 1983; Hewitt and Furr, 1965b; Walker, 1986; Walker et al., 1983; Wutscher et al., 1973). Trifoliolate orange appears to be a sodium excluder (Elgazzar et al., 1965; Grieve and Walker, 1983; Walker, 1986) and Citrus macrophylla a boron excluder (Cooper and Peynado, 1959; Embleton et al. 1962). This suggests the existence of a blocking mechanism in the transport of these ions (Fernandez et al., 1977). It also indicates the existence of apparently separate mechanisms which regulate the uptake and transport of ions (chloride and sodium) in salt-stressed citrus (Fernandez et al., 1977; Grieve and Walker, 1983; Walker et al., 1983).

Ion concentration. Citrus is a nonhalophyte, and its tolerance to salinity is correlated with its ability to restrict the entry of ions into the shoots (Greenway and Munns, 1980). Injury to citrus from NaCl has been attributed to excess chloride accumulation (Ben-Hayyim and

Kochba, 1983; Cooper, 1961; Cooper and Gorton, 1952; Furr and Ream, 1969). In an effort to screen young citrus trees for salt tolerance, Hewitt et al. (1964) found that the leaves could be analyzed for chloride after 3 to 4 weeks of treatment with highly saline irrigation water. Fernandez et al. (1977) considered foliar chloride content as a suitable index of the soil salinity status and toxicity levels. However, Ben-Hayyim et al. (1985) showed the difficulty in determining if any particular ion could serve as a reliable marker for salt tolerance in citrus.

Citrus Responses to Saline Conditions

Photosynthesis. Photosynthetic rates were reduced by 50 to 75% after 70 days of NaCl stress (Behboudian et al., 1986; Walker et al., 1982). A decrease in photosynthesis is often caused by a drop in leaf turgor, but studies have shown different turgor responses to salinity. In one study with Rangpur lime, photosynthesis reduction was attributed to low turgor pressures in rangpur lime and not to leaf chloride or sodium concentrations since there was no significant difference in concentrations of these ions between salt-stressed and control leaves. In contrast to Rangpur lime, photosynthetic reduction during salt treatment in Etrog citron was associated with a marked increase in leaf chloride since turgor was not reduced. Their work established that a plant's capacity for salt exclusion alone or turgor maintenance alone was unable to protect citrus seedlings against photosynthetic reduction. Therefore, to improve salt tolerance in citrus, studies need to be focused not only on salt excluding rootstocks but also on the ability of scions to maintain turgor. It appears that the inability to osmotically adjust and exclude toxic ions is related to citrus sensitivity to salinity (Zid and Grignon, 1986).

Yield. Citrus yield has been related to salt concentration in the soil (Bielorai et al., 1978; Harding et al., 1958b). According to Boaz (1978) and Maas and Hoffman (1977), the threshold salinity is an electrical conductivity of the soil saturation extract of 1.8 dS/m (1.8 mmhos/cm) for oranges and grapefruit. Above this threshold, yield is reduced at a rate of 16% per dS/m. Pehrson et al. (1985) stated that 10 and 50% yield reductions for citrus were associated with electrical conductivities of the soil saturation extract of 2.3 and 4.8 dS/m, respectively.

Salinity was found to significantly reduce citrus yield without visual symptoms (Pehrson et al., 1985). The use of moderately saline irrigation water (2.5 dS/m) decreased orange yield by about 30% without any visible leaf injury symptoms (Bingham et al., 1974). Within a concentration range of 2 to 2.7 dS/m, 9 to 18% yield reduction in grapefruit occurred without apparent toxicity symptoms (Bielorai et al., 1978, 1983). When irrigated with moderately saline water (15 to 30 mM, $\text{CaCl}_2 + \text{Na}_2\text{SO}_4 + \text{MgSO}_4$), Valencia orange had yield reductions of 34 to 54% with no visible leaf injury symptoms (Francois and Clark, 1980).

Leaf injury. Salinity effects develop slowly so that leaf injury symptoms appear after a certain period of time. However, the length of this time period is shortened by higher salt concentrations. Grown in the field, two-year-old Ruby red grapefruit on sour orange rootstock irrigated with salt solutions of 2500 mg/L (50:50 NaCl and CaCl_2) showed no visible symptoms of salt injury during a one year period. Trees irrigated with 4000 mg/L salt solution developed leaf bronzing within 1 month and marginal burning of the leaves within 2 months. Trees irrigated with 5000 mg/L salt solution were completely defoliated within a one year period (Cooper, 1961; Cooper et al., 1952a).

Salinity and high water table. Relatively few studies have been conducted to investigate the effects of a combination of water table and salinity on citrus even though this condition exists in many parts of the world. Studying the effects of salinity and water table on the growth and mineral composition of young grapefruit trees, Pearson and Goss (1953) found that the rates of defoliation and twig dieback due to salinity were greatly accelerated by a frequently fluctuating water table. In a more detailed report of the same study, Pearson et al. (1957) concluded that the salinity factor accounted for approximately 90% of the variance in growth while the water table factor accounted for only about 4%. They found that sodium and chloride accumulated in toxic amounts in the leaves and were responsible for the decrease in growth. However, while investigating the effect of different water table depths and salinity levels on sweet orange, Kanwar and Bhambota (1969) observed that the adverse effect of water table was more pronounced than that of salinity. Both studies agreed that the interaction of water table and salinity affected the trees more severely than either condition alone.

The fact that Cleopatra mandarin is more sensitive to flooding (Ford, 1964) but more salt tolerant (Cooper et al., 1951) than sour orange raises the question about the performance of these two rootstocks under saline conditions associated with high water table or flooding problems.

Irrigation. Citrus is relatively sensitive to salinity, but can withstand high salt concentrations depending on the variety, rootstock, and irrigation management. Good irrigation management should consider the salinity factor in the irrigation water, in the soil, and in the root zone (Boaz, 1978). Methods of irrigation scheduling which do not account for salinity are not sufficiently accurate for scheduling

irrigation in areas with a saline high water table. Irrigation water containing about 250 mg chloride per liter reduced grapefruit yield by 28 to 32% when trees were irrigated at intervals of 40 days compared to intervals of 18 days (Bielorai and Levy, 1971; Bielorai et al., 1973). These studies demonstrated that the effect of salinity is more severe at lower soil water content.

Overhead sprinkler irrigation should be avoided when using water containing high levels of salts because salt residues can accumulate on the foliage and seriously injure plants. Navel orange accumulated injurious amounts of chloride and sodium from sprinkler-applied water having 500 to 900 ppm total dissolved solids (Harding et al., 1958a). Considerable leaf burn and defoliation of these trees were found to be correlated with excessive amounts of sodium and chloride and lower amounts of potassium in the leaves. Leaf injury of navel orange trees developed at concentrations of 5 to 10 mmol/L of NaCl, CaCl₂ or Na₂SO₄ in the sprinkler-applied waters (Ehlig and Bernstein, 1959). Salt content of up to 1300 mg/L caused defoliation of sprinkler-irrigated citrus trees in Texas (Lyons, 1977). In Australia, during periods of high salinity in the irrigation water, foliar absorption of sodium and chloride occurred when using overhead sprinklers on citrus. It was believed that this problem caused poor tree health, low yield, and possibly poor fruit quality in citrus (Cole and Till, 1977).

Frequency rather than duration of sprinkler irrigation is perhaps more important in foliar absorption of salts. Salt injury was higher under higher evaporation conditions and with short and frequent periods of overhead sprinkling (Eaton and Harding, 1959; Ehlig and Bernstein, 1959; Harding et al., 1958a).

Micro-irrigation is gaining in popularity not only in arid regions but also in humid subtropical areas. Micro-irrigation refers to both drip and microsprinkler irrigation. Micro-irrigation enables the use of poorer quality water that cannot be tolerated with overhead sprinklers. Direct foliar uptake of salts, and hence leaf injury, is avoided with drip irrigation (Calvert and Reitz, 1966). Nevertheless, saline water cannot be used indiscriminately with micro-irrigation systems. Comparative studies between overhead sprinklers and drip systems using saline water showed that vegetative growth, root development, and yield were greater with drip than with sprinkler irrigation (Goldberg and Shmueli, 1971; Shmueli and Goldberg, 1971). In a comparison of flood and drip systems, water high in chloride and boron was applied to young grapefruit trees on many rootstocks (Wutscher et al., 1973). More chloride and boron accumulation was found in trees that were flood irrigated than in those that were micro-irrigated.

Drip irrigation at frequent intervals maintains a low soil water tension and prevents salt accumulation within the wetted zone. Consequently, water with higher salinity levels may be used without significantly affecting the yield. Nevertheless, salt accumulation under drip irrigation must be considered because salts may accumulate both at the periphery of the wetted zone and on the soil surface (Bielorai, 1977, 1985; Goldberg et al., 1976; Hoffman et al., 1985; Yaron et al., 1973).

Reducing Salt Damage

Role of Calcium

Calcium has been known to have an ameliorating effect on the growth of plants under saline conditions (Deo and Kanwar, 1969; Epstein, 1972; Hyder and Greenway, 1965). This effect has been attributed to calcium

preventing the uptake of the sodium ion to injurious levels, and allowing the uptake of potassium (Waisel, 1962). In the presence of adequate concentrations of calcium, bean plants were able to exclude sodium and to withstand the effects of relatively high NaCl concentrations (LaHaye and Epstein, 1969, 1971). In barley, inhibition of the absorption and translocation of potassium and phosphorus by NaCl was found to recover dramatically in the presence of calcium (Kawasaki et al., 1983b). Application of gypsum to the soil or in the irrigation water markedly reduced the percentage of soluble sodium in the soil (Harding et al., 1958b) and reduced the percentage of sodium in citrus leaves and roots (Jones et al., 1952; Pearson and Huberty, 1959).

Calcium amendments are commonly used for replacement of exchangeable sodium (Richards, 1954). Calcium can flocculate soil in which clay particles and aggregates have been dispersed by sodium. Salt-affected soils can therefore be made productive by chemical amendment, drainage, and irrigation with high quality water, but sometimes the cost of these operations exceeds the expected returns from the land.

Genetic Improvement

In recent years, adapting plants to saline environments through breeding and genetic manipulation have been attempted (Epstein et al., 1980). The genetic basis for salt tolerance, using information from studies with whole plants, has allowed the identification of plants with increased salt tolerance. Another approach is to increase salt tolerance through cell culture (Croughan et al., 1981).

In some species, the variability in salt tolerance may not be adequate for a successful breeding program because it may not be possible to find salt-tolerant wild relatives and use them as sources of germplasm. Suspension of cells from salt-sensitive plants in solutions

having various degrees of osmotic stress was found to be a promising technique to select salt-tolerant cells from salt-sensitive cells. This implies that the genetic information for growth in a saline environment may be present in salt-sensitive cells but is not expressed. Selection of salt-tolerant cells may provide genetic material that will help improve our understanding of salinity resistance at the cellular level.

MATERIALS AND METHODS

General Procedures

This study consisted of 5 experiments involving citrus seedlings grown in greenhouses in central Florida. Seeds were sown in plastic trays composed of individual cells. The trays were filled with PROMIX BX [60% Canadian peat, 20% perlite, and 20% vermiculite with dolomitic limestone, superphosphate, calcium nitrate and fritted trace elements added]. The seeds were irrigated with tap water twice a week until emergence. Seedlings were irrigated with tap water every other day and fertilized with 20-20-20 (N,P,K) fertilizer once a week. The temperature and relative humidity in the greenhouses were controlled by both heating and evaporative cooling systems with conventional end-wall air circulation fans. The minimum and maximum temperature and relative humidity ranged from 20 to 35°C and from 40 to 100%, respectively.

Three to 6 months after emergence, uniform seedlings were selected and transplanted into pots or wooden boxes containing fine sand taken from the top 30 cm of a citrus orchard soil. The soil was Astatula fine sand (hyperthermic, uncoated Typic Quartzipsamments) with a pH of 6.5 and a field capacity and a wilting percentage of 7.2% and 1.2% (volume basis), respectively. Seedlings were irrigated every 2 to 3 days with half strength Hoagland's solution #1 (Hoagland and Arnon, 1950) for at least one month before starting salt and polyethylene glycol (PEG) treatments. Treatments were started by adding NaCl, PEG, or other salts to the Hoagland solution.

The water holding capacity of the soil in the containers was about 18% (volume basis). The irrigation frequency was 2 to 3 days. The amount of solution added each time was based on bringing the soil to slightly more than the water holding capacity of the soil in the containers to prevent salt accumulation in the growth medium and to prevent plants from undergoing a drought stress.

Standard curves (Fig. 1, 2) of osmotic potential versus solute concentration were developed for NaCl and PEG 4000 by measuring vapor pressure and freezing point depression. The values obtained were similar to those of Steuter et al. (1981) who compared freezing point depression and vapor pressure methods for determination of water potential of PEG solutions. Electrical conductivities of the different treatments were determined with a conductivity meter. Electrical conductivity values were converted to TDS (Richards, 1954).

Sodium chloride and PEG treatments were continued for at least 4 months, after which the plants were harvested and the roots were washed briefly with tap water to free them of sand particles. Shoots were separated into stems and leaves, and roots were separated into taproots, lateral roots, and fibrous roots (roots less than 2 mm in diameter). The material was oven-dried for 3 days at 60°C, weighed, ground, and retained for ion analysis.

Analysis of variance (F-test) was used to determine significant differences and Duncan's multiple range test was employed for mean comparison at $P < 0.05$.

Experiment 1: Effects of NaCl and PEG on the Root Conductivity and Leaf Ion Content of Seedlings of 7 Citrus Rootstocks

The objective of this experiment was to compare the growth, ion content, and water relations of 7 rootstocks treated with different

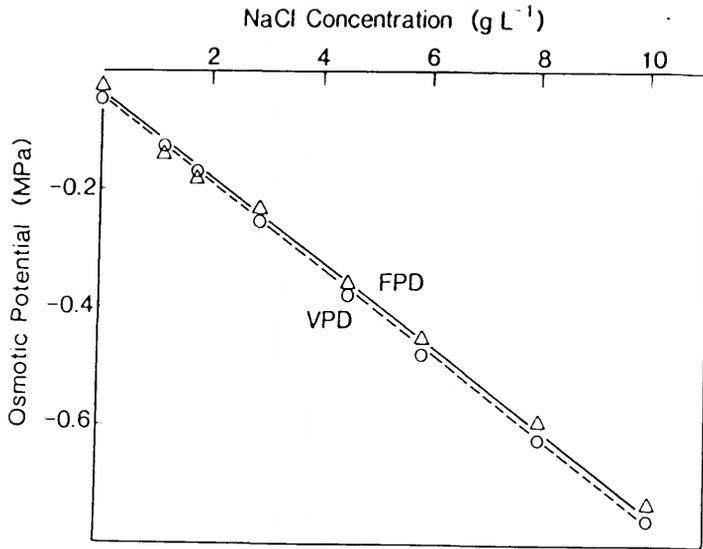


Fig. 1. Osmotic potential versus NaCl concentration as determined by vapor pressure (VPD) and freezing point depression (FPD).

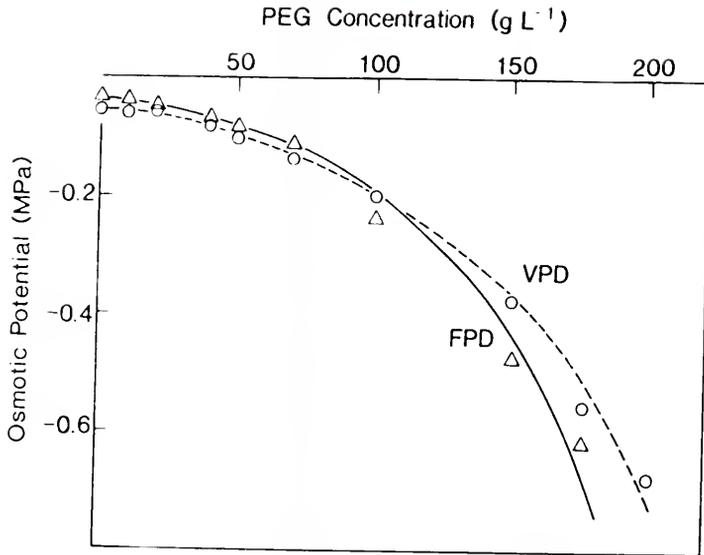


Fig. 2. Osmotic potential versus PEG concentration as determined by vapor pressure (VPD) and freezing point depression (FPD).

levels of NaCl and PEG. On October 20, 1985, 5-month-old uniform seedlings of 7 rootstock cultivars were transplanted into 33 cm-tall black plastic pots containing about 2.2 L of fine sand. Rootstocks studied were the following: sour orange (Citrus aurantium), Cleopatra mandarin (C. reshni), Swingle citrumelo (C. paradisi x Poncirus trifoliata), Carrizo citrange (P. trifoliata x C. sinensis), rough lemon (C. jambhiri), Milam (C. jambhiri variant) and trifoliolate orange (P. trifoliata). The plants were watered with a half strength Hoagland's solution and were grown with this control solution for 2 months. Sodium chloride and PEG treatments were started on December 19, 1985, and nutrient solutions for treated plants were identical to that of the control plants except for the addition of NaCl and PEG. Sodium chloride and PEG were added to the half strength Hoagland's solution to achieve final concentrations of -0.10, -0.20, and -0.35 MPa. The basic nutrient solution (control) had an osmotic potential (OP) of -0.05 MPa.

Treatments were as follows:

<u>Treatment</u>	<u>TDS</u> (mg L ⁻¹)	<u>OP</u> (MPa)	<u>EC</u> (dS m ⁻¹)	<u>NaCl</u> (mmol)
1. NS control : ½ Hoagl. sol.	550	-0.05	1.1	0
2. NaCl (0.10) : 1.0 g NaCl/L ½ Hoagl. sol.	1600	-0.10	3.1	17
3. PEG (0.10) : 55 g PEG/L ½ Hoagl. sol.	460	-0.10	0.9	0
4. NaCl (0.20) : 2.2 g NaCl/L ½ Hoagl. sol.	3000	-0.20	5.4	38
5. PEG (0.20) : 105 g PEG/L ½ Hoagl. sol.	400	-0.20	0.8	0
6. NaCl (0.35) : 4.2 g NaCl/L ½ Hoagl. sol.	4900	-0.35	8.8	72
7. PEG (0.35) : 144 g PEG/L ½ Hoagl. sol.	350	-0.35	0.7	0

Plants were adjusted to their final NaCl and PEG concentrations through a progression of -0.10, -0.20, and -0.35 MPa solutions at 2-day intervals to avoid osmotic shock. Plants were then maintained at their

final osmotic levels for 5 months. The experimental unit was a single seedling arranged in a split plot with 4 replications. The 7 salt treatments were assigned to the main plots and the 7 rootstocks to the subplots.

At the end of the experiment, root hydraulic properties were evaluated while in situ on 4 seedlings of each rootstock as previously described (Graham and Syvertsen, 1984, 1985; Levy et al., 1983; Syvertsen and Graham, 1985). Before measuring, the soil was wetted to field capacity to minimize possible differences in soil hydraulic conductivity and equilibrated to 25°C in the laboratory. Each pot and intact plant were placed in a pressure chamber. The stem was then cut 10 cm above the soil and the chamber was sealed around the cut stem. The pressure within the chamber was increased gradually to a constant value of 0.5 MPa. After an initial equilibration time of 10 minutes, the weight of the liquid exuded from the cut end was measured at least 5 times at 1 minute intervals. Osmotic potential of the exudate was measured by a Wescor vapor pressure osmometer calibrated with NaCl solutions.

Each root system was washed free of soil, and the total length of fibrous roots of each plant was determined by the line-intersect method (Tennant, 1975). Water flow per root system measured in this way included a soil conductivity component and was expressed as weight of exudate per unit time and pressure ($\mu\text{g s}^{-1} \text{MPa}^{-1}$). Root conductivity for each rootstock was calculated by dividing the water flow by the total fibrous root length. Thus, the root conductivity was expressed in $\mu\text{g/s/MPa}$ per meter of fibrous roots ($\mu\text{g m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$).

Prior to measuring root conductivity, the trunk circumference of each seedling was measured at a point 5 cm above the soil surface and

converted to stem cross sectional area. Dry weights of leaves, stems, fibrous roots, and tap roots were determined. Shoot root ratio and specific root weight (root weight per unit length) were calculated. Leaf chloride content was measured using a Buchler-Cotlove chloridometer after extracting the leaf samples with a nitric-acetic acid solution. Measurement of leaf Na, Ca, Mg, K, P, Zn, Mn, Cu, and Fe content was performed using an inductively coupled argon plasma spectrophotometer after a wet digestion of the samples in a nitric-perchloric acid mixture.

Experiment 2: Water Relations of Sour Orange and Cleopatra Mandarin Seedlings under NaCl and PEG Stresses

The objective of this experiment was to study the effects of NaCl and PEG on the root conductivity, plant growth, stomatal conductance, and chlorophyll content of seedlings of 2 rootstocks differing in chloride accumulation characteristics, sour orange and Cleopatra mandarin (Cooper et al., 1951).

Six-month-old uniform seedlings of sour orange and Cleopatra mandarin were transplanted on November 13, 1985, into 19-cm tall black plastic pots containing 5.5 L of Astatula fine sand. Plants were then watered to excess every 2 to 3 days with half strength Hoagland's solution for one month before NaCl and PEG treatments were started. The treatments were the same as in Experiment 1. The treatments were replicated 7 times in a split plot design with 2 main plots (rootstocks) and 7 subplots (solutions). All variables measured in Experiment 1 with the exception of the chemical analysis were also measured similarly in this experiment. Seedling height from the soil surface to the terminal bud was measured every 2 weeks. Leaf conductance to water vapor was measured on abaxial leaf surfaces with a Li-cor 1600 steady state

porometer at 2-hour intervals from 0700 to 1700 hours for 3 consecutive days.

After 5 months of NaCl and PEG treatments, two 1-cm diameter disks were removed from the central area of 2 mature leaves per seedling to determine leaf chlorophyll content using N, N-dimethyl formamide as a solvent (Moran and Porath, 1980; Syvertsen and Smith, 1984). Two millimeters of N, N-dimethyl formamide were placed in a small bottle and the 2 leaf disks which were removed from the same seedling were weighed and then immersed in the solvent. The bottles were firmly closed and stored in the dark in a freezer for 2 months. The bottles were then removed from the freezer and left in the dark to equilibrate to the temperature of the laboratory prior to spectrophotometer examination. One millimeter of the chlorophyll extract from each bottle was diluted with deionized water and examined by means of a scanning spectrophotometer. The optical density of the extract was measured at wavelengths of both 663 μ and 644 μ , and chlorophyll content was calculated following the equations used by Arnon (1949). Leaf chlorophyll content was expressed as mg of leaf chlorophyll per gram fresh weight.

New shoot growth was determined by counting leaf number and measuring leaf area over a 3-month period. The plants were harvested after 6 months of NaCl and PEG treatments. Total leaf area was measured by a Li-cor leaf area meter. Fresh and dry weights of leaves were determined. Specific leaf weight (SLW), expressed on a fresh and dry weight basis per unit of leaf area, was calculated. Leaf succulence was expressed as grams of water per gram of leaf dry weight.

Experiment 3: Fibrous Root Density and Distribution of Sour Orange
Seedlings under NaCl and PEG Stresses

The objective of this experiment was to determine the effect of NaCl and PEG on the root growth and distribution of sour orange seedlings. Five-month-old seedlings were transplanted on October 1, 1985, into root boxes filled with Astatula fine sand. The root boxes were similar to those described by Bevington and Castle (1982, 1985). Each container consisted of one plexiglas sheet (6.4 mm thick) attached to the front of a wooden box. The plexiglas was covered with a removable metal shutter to exclude light. The internal dimensions of a root box were 87 cm high, 27 cm wide, and 5 cm thick. The viewing surface was 23 dm² and the volume was about 11.5 L. Drainage was provided by 3 mesh-covered outlets in the bottom of the box. The boxes were vertically oriented. Seedlings were allowed to adjust in their containers for 2 months. During this period, they were watered every other day with half strength Hoagland's solution. Plants were then treated with 2 concentrations of NaCl and PEG (total osmotic potential equal to -0.12 and -0.24 MPa). The experimental design was a randomized complete block with 3 replications using a single seedling per box. Treatments were as follows:

<u>Treatment</u>	<u>TDS</u> (mg L ⁻¹)	<u>OP</u> (MPa)	<u>EC</u> (dS m ⁻¹)	<u>NaCl</u> (mmol)
1. NS control : ½ Hoagland's sol.	550	-0.05	1.1	0
2. NaCl (0.12) : 1.1 g NaCl/L ½ Hoagl. sol.	1700	-0.12	3.3	19
3. PEG (0.12) : 60 g PEG/L ½ Hoagl. sol.	450	-0.12	0.9	0
4. NaCl (0.24) : 2.8 g NaCl/L ½ Hoagl. sol.	3300	-0.24	5.9	48
5. PEG (0.24) : 110 g PEG/L ½ Hoagl. sol.	390	-0.24	0.8	0

Root growth was recorded at 2-week intervals by using colored pencils to trace the root system onto transparent acetate sheets. Plant height was measured at 2-week intervals. Stomatal conductance was measured about every 2 weeks and for 2 consecutive days at 2-hour intervals from 0700 to 1700. After 6 months of NaCl and PEG treatments, the plants were taken from their boxes by removing the plexiglas wall and inserting a needle board to hold the root system in place. Leaves, stems, and roots were separated and roots were divided in place into 3 equal compartments (top, middle, and bottom). Shoot and root dry weight, shoot root ratio, leaf number, plant height, root length, specific root weight, and stomatal conductance were determined as described in Experiment 2.

Experiment 4: Response of Split-Root Sour Orange Seedlings to Salinity

The objective of this experiment was to determine and quantify the growth and water relations of sour orange seedlings when only a portion of the root system was exposed to NaCl or PEG. A split-root system was initiated using the technique of Koch and Johnson (1984). The tap root of each seedling at the 3-leaf stage was cut to a 1 cm length and all other roots were removed. The remaining portion of the tap root was dipped into a 50% ethanol solution containing 5 grams of IBA (indolebutyric acid) per liter. Seedlings were then placed in PROMIX BX, watered daily and fertilized weekly for 2 months. Seedlings which had 2 uniform adventitious root systems were selected and transplanted when 5 months old into 2.2 L square plastic containers stapled together along one side (Fig. 3). These seedlings were left to adjust in their double pots for 1 month before NaCl and PEG treatments were imposed. The treatments were replicated 4 times in a randomized complete block design and are shown below:



Fig. 3. Sour orange seedlings with a split-root system.
a. Root development after 2 months.
b. Container system used to grow split-root seedlings.

<u>Treatment</u>	<u>TDS</u>	<u>OP</u>	<u>EC</u>
	(mg L ⁻¹)	(MPa)	(dS m ⁻¹)
1. NS/NS (no salt)	550/550	-0.05/-0.05	1.1/1.1
2. NS/NaCl (0.10)	550/1600	-0.05/-0.10	1.1/3.1
3. NaCl (0.10)/NaCl (0.10)	1600/1600	-0.10/-0.10	3.1/3.1
4. NS/NaCl (0.20)	550/3000	-0.05/-0.20	1.1/5.4
5. NaCl (0.20)/NaCl (0.20)	3000/3000	-0.20/-0.20	5.4/5.4
6. NS/NaCl (0.35)	550/4900	-0.05/-0.35	1.1/8.8
7. NaCl (0.35)/NaCl (0.35)	4900/4900	-0.35/-0.35	8.8/8.8
8. NS/PEG (0.20)	550/400	-0.05/-0.20	1.1/0.7
9. PEG (0.20)/PEG (0.20)	400/400	-0.20/-0.20	0.7/0.7

Water relations variables were monitored on 4 successive days during the fourth month of salt treatment. Leaf water potential was measured at sunrise and at midday on fully expanded leaves using a pressure chamber. Leaves were then removed from the chamber, wrapped in double plastic bags and rapidly frozen at -20°C . Leaves were subsequently thawed after 48 hours and their osmotic potential was determined with a vapor pressure osmometer. Turgor potential was obtained by subtracting the osmotic potential value from the water potential value. Morning and midday stomatal conductance and leaf transpiration rates were measured with a steady state porometer. For anatomical study, 2 mature leaves per plant from NS/NS and NaCl (0.35)/NaCl (0.35) treatments were selected from about half-way between the first leaf and the shoot apex. Two small rectangles were cut at mid-lamina of each leaf, frozen immediately, and cut by a Cryostat minot rotary microtome in sections 10 microns thick. Sections were then thawed in a phosphate buffer saline solution. Twenty randomly selected leaf cross sections per treatment were fixed for a light microscopy study.

After 4 months of NaCl and PEG treatment, the plants were harvested, and shoot and root dry weights were determined.

Experiment 5: Effects of Calcium on Sour Orange Seedlings Grown under Saline Conditions

The objective of this experiment was to determine if the addition of calcium to saline irrigation water would reduce salt damage. Three-month-old sour orange seedlings were transplanted on August 10, 1986, into the same pots used in Experiment 2. Salt treatments (Table 1) were started after 1 month of adjustment, and seedlings were irrigated every 2 to 3 days for 4 months. The treatments were replicated 8 times in a randomized complete block design. The plants were watered the night before harvest and leaves were removed the following morning. Fresh and dry weights of leaves, stems, and roots were recorded. The succulence of new and old leaves was computed. The dried, mature, fully expanded leaves were ground and their mineral content was determined as in Experiment 1.

Table 1. Salt treatments and chemical properties of the different treatments--Experiment 5.

Treatment	Na (mmol)	Ca (mmol)	Sodium calcium ratio	TDS (mg L ⁻¹)	EC (dS m ⁻¹)	Osmotic potential (MPa)
1 (NS)	0	2.5	0:2.5	550	1.1	-0.05
2 NaCl	40	2.5	16:1	3000	5.4	-0.21
3 NaCl + 7.5 mM CaSO ₄	40	10.0	4:1	3500	6.3	-0.23
4 NaCl + 13.5 mM CaSO ₄	40	16.0	2.5:1	3800	6.8	-0.26
5 NaCl + 8.75 mM CaSO ₄ + 8.75 mM CaCl ₂	40	20.0	2:1	4200	7.5	-0.26
6 NaCl + 7 mM KCl	40	2.5	16:1	3400	6.1	-0.23
7 NaCl + 7 mM KCl + 7.5 mM CaSO ₄	40	10.0	4:1	3800	6.8	-0.21
8 NaCl + 17.5 mM CaCl ₂	40	20.0	2:1	4700	8.4	-0.30
9 (NS)--no calcium	0	0	0:1	450	0.9	-0.03
10 NaCl--no calcium	40	0	40:0	2800	5.0	-0.19
11 NaCl + 1 mM CaSO ₄	40	1.0	40:1	2900	5.2	-0.19
12 NaCl + 5 mM CaSO ₄	40	5.0	8:1	3100	5.5	-0.21

RESULTS

Experiment 1: Effects of NaCl and PEG on the Root Conductivity and Leaf Ion Content of Seedlings of 7 Citrus Rootstocks

The results of the analysis of variance showed that salt treatments and rootstocks were significant and independent factors; i.e., the interaction of these 2 factors was not significant.

Significant differences in growth due to NaCl and PEG treatments were found among rootstocks. Shoot dry weight generally decreased as NaCl and PEG concentration increased in the nutrient solution (Table 2). Shoot dry weight at the low, medium, and high NaCl concentrations was 18 to 36%, 30 to 55%, and 58 to 82% lower, respectively, than the control plants. Shoot dry weight of sour orange (SO) and Cleopatra mandarin (CM) seedlings was the least affected while Milam (ML) and Poncirus trifoliata (PT) seedlings showed the greatest response. Sodium chloride and PEG effects on root dry weight were similar to those on shoot dry weight (Table 3). However, roots were less affected than shoots so that the shoot-root ratio decreased with increasing NaCl and PEG concentration (Table 23, Appendix). Total plant dry weight (Table 24, Appendix) and stem cross sectional area (Table 25, Appendix) were proportionally reduced by NaCl and PEG concentrations and reductions were usually greater with PEG than with NaCl. Fibrous root length was also reduced by NaCl (Fig. 4) but specific root weight (SRW, dry weight per unit length) increased with increasing NaCl concentration (Table 4).

Table 2. Shoot dry weight (g) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatment (-MPa)	Sour		Cleopatra		Swingle		Carrizo		Rough		Milam		Poncirus	
	orange		mandarin		citrumelo		citrange		lemon				trifoliata	
	Mean ²	NS	Mean	NS	Mean	NS	Mean	NS	Mean	NS	Mean	NS	Mean	NS
NS control	21.0a ^y	0	22.1a	0	13.9a	0	17.8a	0	30.2a	0	24.6a	0	8.6a	0
NaCl (0.10)	17.3ab	18	17.9ab	19	9.8b	30	12.5b	30	21.0b	30	16.7b	32	5.5b	36
NaCl (0.20)	13.2b	37	15.4b	30	7.7bc	45	9.1c	49	14.8c	51	11.0c	55	4.3bc	50
NaCl (0.35)	8.8c	58	9.1c	59	4.1c	70	4.5d	75	8.6d	72	4.3e	82	2.0e	76
PEG (0.10)	14.2b	32	12.5bc	44	8.4b	40	8.3c	54	15.9c	48	11.9c	52	4.3bc	50
PEG (0.20)	9.5c	55	8.8c	61	5.9c	58	6.0d	66	10.6d	65	8.0d	68	3.7cd	57
PEG (0.35)	6.7c	69	7.2c	68	4.7c	67	4.9d	72	8.0d	74	7.1d	71	2.8de	67

^yMean of 4 plants.

^zMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 3. Root dry weight (g) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatment (-MPa)	Sour orange		Cleopatra mandarin		Swingle citrumelo		Carrizo citrange		Rough lemon		Milam		Poncirus trifoliata	
	%	Mean ²	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean
NS control	0	9.24a ^y	0	8.59a	0	6.14a	0	6.71a	0	12.01a	0	9.72a	0	3.77a
NaCl (0.10)	16	7.76ab	18	7.05ab	18	4.62ab	25	5.44ab	19	8.66ab	28	7.54ab	22	2.88ab
NaCl (0.20)	36	5.92b	26	6.32ab	26	3.60bc	41	4.14bc	38	6.25bc	48	5.09bc	48	2.28bc
NaCl (0.35)	56	4.03bc	54	3.98c	54	2.34c	62	2.44c	64	4.56c	62	2.59d	73	1.66c
PEG (0.10)	29	6.53b	30	6.02ab	30	4.70ab	24	4.57ab	32	8.73ab	27	5.50bc	43	3.00ab
PEG (0.20)	45	5.10bc	43	4.93bc	43	3.88bc	37	3.44bc	49	6.83bc	43	4.91bc	50	2.57ab
PEG (0.35)	58	3.93c	49	4.38bc	49	3.56bc	42	3.36bc	50	5.79bc	52	4.29cd	56	1.98bc

²Mean of 4 plants

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

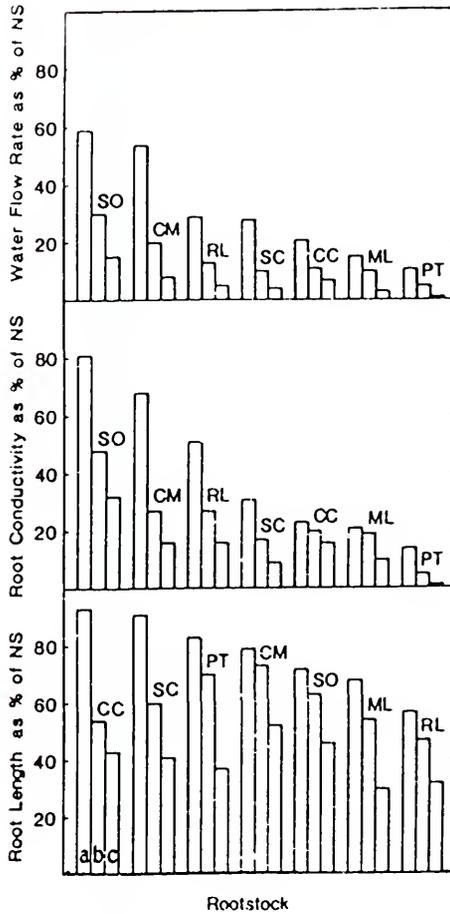


Fig. 4. Effect of 3 NaCl concentrations (a = -0.10 MPa, b = -0.20 MPa, c = -0.35 MPa) on the total fibrous root length, root hydraulic conductivity, and water flow rate for seedlings of 7 citrus rootstocks.

Table 4. Specific fibrous root weight (mg m^{-1}) of seedlings of 7 rootstocks grown for 5 months under different NaCl concentrations-- Experiment 1.²

Treatments (-MPa)	Sour orange	Cleopatra mandarin	Swingle citrumelo	Carrizo citrange	Rough lemon	Poncirus trifoliata
NS control	71 a ^y	70 a	68 c	59 b	68 c	71 c
NaCl (0.10)	72 a	71 a	70 bc	61 b	70 bc	74 bc
NaCl (0.20)	73 a	71 a	73 ab	63 ab	73 b	77 ab
NaCl (0.35)	73 a	72 a	75 a	66 a	78 a	81 a
						54 c
						56 bc
						59 b
						73 a

²Mean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

The increase in SRW of rough lemon (RL), ML, and PT was greater than that of the other rootstocks.

Root hydraulic variables were affected by rootstock and NaCl. Significant differences in root conductivity among rootstocks were found under non-stressed conditions (Table 5) as well as under NaCl stress conditions (Fig. 4). Sour orange and CM had the smallest reduction in hydraulic conductivity and ML and PT had the greatest. There was a significant negative relationship between root hydraulic conductivity and SRW of the 7 rootstocks studied (Fig. 5). As root weight per unit length increased, conductivity decreased.

Water flow through the root system decreased as much as 41 to 89% at the first NaCl level (Fig. 4). Osmotic potential of root exudate due to NaCl stress followed the same trend as root hydraulic conductivity (Fig. 20, Appendix). Water flow and osmotic potential of root exudate were reduced the least in SO and CM and the most in ML and PT. However, when NaCl was not added to the irrigation water, PT and Swingle citrumelo (SC) had the highest osmotic potential of root exudate, and SO and CM had the lowest potentials (Table 5).

Leaf burn symptoms appeared in the NaCl (0.35) treatment in PT and ML after 5 weeks. In RL, SC, Carrizo citrange (CC), and SO, leaf burn symptoms occurred after 6 weeks at the highest NaCl concentration (-0.35 MPa). Just before harvest, final evaluation of the different rootstocks based on tree appearance and performance was made (Table 6, Fig. 6).

Leaf ion content of the seedlings of the 7 rootstocks was affected by the NaCl and PEG concentrations. Sodium (Table 7) and chloride (Table 8) contents in the leaves of all rootstocks increased with increasing NaCl in the nutrient solution. Cleopatra mandarin accumulated the least chloride while PT, SC, and CC accumulated the

Table 5. Root length, root conductivity, water flow rate, and osmotic potential of root exudate of seedlings of the 7 rootstocks under non-stressed conditions. Osmotic potential of the nutrient solution was -0.05 MPa--Experiment 1.

Rootstock	Root length (m)	Root conductivity ($\mu\text{g s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)	Water flow rate ($\mu\text{g s}^{-1} \text{MPa}^{-1}$)	OP of root exudate (MPa)
Sour orange	73.1 b ^y	9.9 d	724 c	-0.23 c
Cleopatra mandarin	78.0 b	10.4 d	811 c	-0.20 c
Swingle citrumelo	45.6 c	24.2 b	1104 b	-0.13 a
Carrizo citrange	53.1 c	26.6 b	1413 a	-0.17 b
Rough lemon	107.4 a	14.2 c	1525 a	-0.17 b
Milam	70.3 b	15.7 c	1104 b	-0.17 b
<u>Poncirus trifoliata</u>	37.4 c	31.4 a	1174 b	-0.12 a

^zMean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

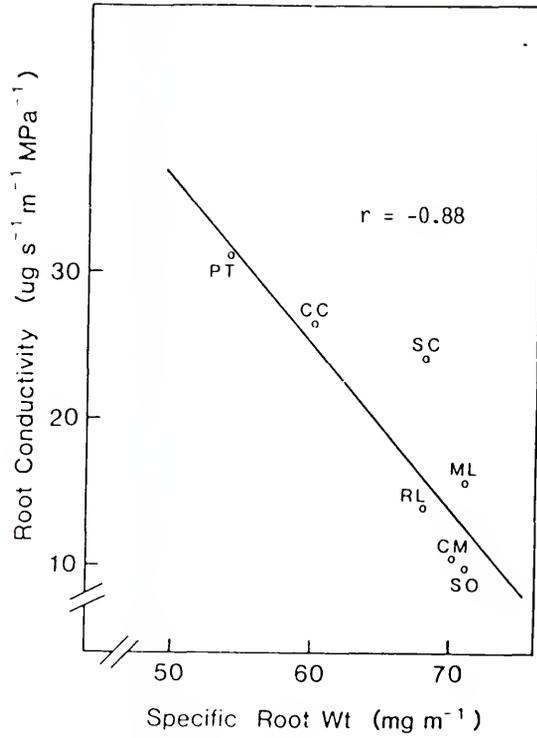


Fig. 5. Relationship between root hydraulic conductivity and specific root weight of seedlings of 7 citrus rootstocks under non-stressed conditions.

Table 6. Visible injury in seedlings of 7 rootstocks after 5 months of NaCl treatments--Experiment 1.

Rootstock	-0.10	-0.20	-0.35
	Osmotic potential of the irrigation water (MPa)		
Cleopatra mandarin	No leaf burn	No leaf burn	Leaf burn Leaf drop
Sour orange	No leaf burn	Light leaf burn	Leaf burn Leaf drop
Svingle citrumelo Carrizo citrange	No leaf burn	Leaf burn Leaf drop	Leaf burn Leaf drop
Rough lemon Milam	Leaf burn	Leaf burn Leaf drop	Leaf burn Leaf drop Branch die back
<u>Poncirus trifoliata</u>	Leaf burn Leaf drop	Leaf burn Leaf drop	Leaf burn Complete defoliation Branch die back

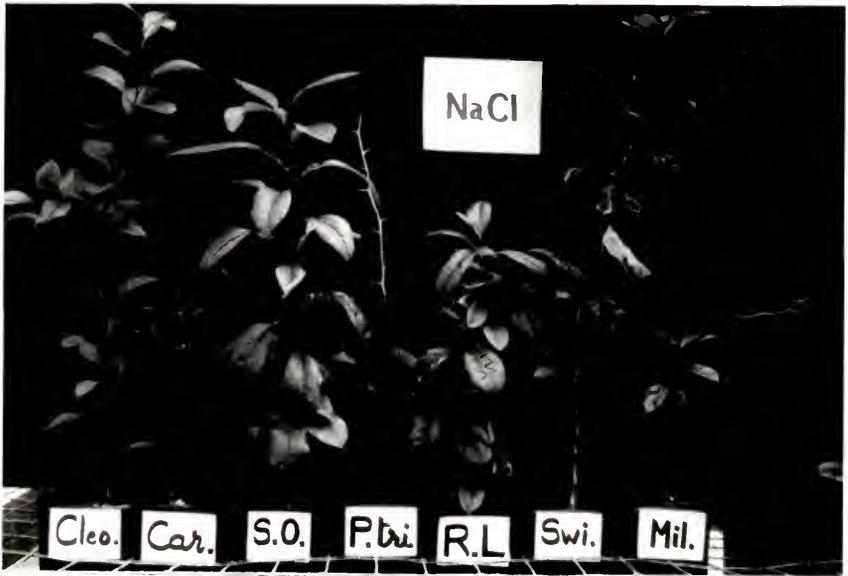


Fig. 6. Effect of NaCl at an osmotic potential of -0.35 MPa on the 7 rootstocks after 5 months of salinity treatments.

Table 7. Leaf sodium content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.^z

Treatment (-MPa)	Sour		Cleopatra	Swingle	Carrizo	Rough	Poncirus	
	orange	mandarin	citrumelo	citrange	lemon	Milam	trifoliata	
NS control	0.02 d ^y	0.03 c	0.03 d	0.02 d	0.03 c	0.02 d	0.02 d	
NaCl (0.10)	0.47 c	0.81 b	0.29 c	0.18 c	1.40 b	1.19 c	0.18 c	
NaCl (0.20)	1.38 b	1.96 a	1.32 b	1.12 b	1.69 b	2.19 b	0.67 b	
NaCl (0.35)	1.57 a	1.98 a	1.89 a	1.74 a	2.65 a	2.76 a	1.59 a	
PEG (0.10)	0.03 d	0.04 c	0.03 d	0.02 d	0.03 c	0.02 d	0.02 d	
PEG (0.20)	0.02 d	0.04 c	0.02 d	0.02 d	0.02 c	0.02 d	0.02 d	
PEG (0.35)	0.02 d	0.03 c	0.02 d	0.02 d	0.02 c	0.02 d	0.02 d	

^zMean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 8. Leaf chloride content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.^z

Treatment (-MPa)	Sour orange	Cleopatra mandarin	Swingle citrumelo	Carrizo citrange	Rough lemon	Milan	<u>Poncirus trifoliata</u>
NS control	0.02 d ^y	0.03 d	0.02 d	0.03 d	0.04 d	0.05 d	0.06 d
NaCl (0.10)	1.77 c	0.42 c	0.87 c	0.99 c	2.33 c	1.53 c	1.38 c
NaCl (0.20)	2.49 b	1.37 b	2.57 b	2.67 b	2.64 b	3.07 b	2.81 b
NaCl (0.35)	3.61 a	2.62 a	3.70 a	3.79 a	4.06 a	4.48 a	4.04 a
PEG (0.10)	0.02 d	0.02 d	0.01 d	0.03 d	0.03 d	0.03 d	0.04 d
PEG (0.20)	0.03 d	0.03 d	0.01 d	0.02 d	0.03 d	0.03 d	0.03 d
PEG (0.35)	0.04 d	0.03 d	0.02 d	0.02 d	0.03 d	0.04 d	0.03 d

^zMean of 4 plants.

^yMean separatin within columns by Duncan's Multiple Range Test, 0.05 level.

least sodium. Even at a relatively low NaCl concentration (-0.10 MPa), large amounts of chloride were accumulated in SO, RL, ML, and PT leaves. Large amounts of sodium were also accumulated in RL and ML leaves. The accumulation or exclusion characteristics of sodium and chloride for each rootstock are summarized in Table 9.

Sodium chloride at -0.35 MPa reduced leaf calcium of all rootstocks 10 to 40% with the exception of PT while PEG generally increased calcium content (Table 10). Both NaCl and PEG reduced magnesium (Table 26, Appendix). Magnesium reduction varied among rootstocks and ranged from 28 to 50% and from 22 to 41% under NaCl and PEG, respectively.

Potassium decreased significantly in SO, CM, RL, and ML but did not in SC, CC, and PT with NaCl treatments (Table 27, Appendix). Potassium seemed to be more strongly reduced in PEG treatments than in NaCl treatments.

Both NaCl and PEG had similar effects on leaf phosphorus content but the effect was more pronounced with PEG (Table 28, Appendix). Sodium chloride and PEG significantly increased phosphorus in CM, SC, CC, RL, and ML, reduced phosphorus in PT, and did not affect phosphorus in SO.

Both zinc and manganese were significantly increased under PEG stress. In some rootstocks, PEG more than doubled the zinc and manganese levels. Zinc was reduced in SC, CC, RL, ML, and PT but was not in SO and CM under NaCl stress (Table 29, Appendix). Manganese tended to increase in the leaves of NaCl-treated plants except for RL (Table 30, Appendix).

Table 9. Ion exclusion and accumulation in the leaves of citrus rootstock seedlings.

Sour orange	Cleopatra mandarin	Swingle citrumelo	Carrizo citrange	Rough lemon	<u>Poncirus</u> <u>trifoliata</u>
Cl accum.	Cl exclu.	Cl accum.	Cl accum.	Cl accum.	Cl accum.
Na accum.	Na accum.	Na exclu.	Na exclu.	Na accum.	Na exclu.

Table 10. Leaf calcium content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatment (-MPa)	Sour orange	Cleopatra mandarin	Swingle citrumelo	Carrizo citrange	Rough lemon	Milam <u>trifoliata</u>	Poncirus <u>trifoliata</u>
NS control	2.0 b ^y	2.7 a	2.8 a	3.0 ab	2.3 b	3.1 b	2.3 c
NaCl (0.10)	1.7 c	2.3 c	2.2 b	2.6 c	1.8 c	2.2 c	2.3 c
NaCl (0.20)	1.6 c	2.2 c	1.8 c	2.5 c	1.8 c	2.1 cd	2.1 c
NaCl (0.35)	1.3 d	1.4 d	1.8 c	2.5 c	1.4 d	1.9 d	2.1 c
PEG (0.10)	2.1 b	2.3 c	2.9 a	3.2 a	2.4 ab	3.2 ab	3.0 a
PEG (0.20)	2.3 a	2.7 a	2.9 a	2.9 b	2.7 a	3.5 a	2.5 b
PEG (0.35)	2.5 a	2.7 a	3.0 a	3.1 a	2.6 a	3.5 a	2.5 b

^z Mean of 4 plants.

^y Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Experiment 2: Water Relations of Sour Orange and Cleopatra Mandarin
Seedlings under NaCl and PEG Stresses

As in Experiment 1, the results of the analysis of variance showed significant differences among salt treatments and between rootstocks but there were no significant interactions between these 2 factors.

The growth rate of SO and CM seedlings was significantly reduced with increasing NaCl and PEG concentrations in the nutrient solution. A NaCl concentration as low as -0.10 MPa (1600 mg L^{-1}) reduced shoot and root dry weight, root length, and stem cross sectional area by 50% after 6 months of treatment (data not presented). For both rootstocks, seedling height was 26 to 39% and 33 to 50% lower, respectively, at the first 2 NaCl concentrations (Table 31, Appendix). Total leaf area was reduced by more than 40% at the -0.10 MPa NaCl level (Table 32, Appendix). All these growth variables were more severely reduced under PEG than under NaCl stress.

No significant difference in growth reduction was found between SO and CM. Similar to Experiment 1, shoot root ratio decreased and SRW increased with increasing NaCl and particularly PEG in the nutrient solution (data not shown).

Sodium chloride reduced new shoot growth of SO (Tables 11, 12). Leaf size of new shoots was smaller for salt-treated plants than for control plants (Table 11). Sodium chloride-treated plants had 59 to 86% fewer leaves than those grown without salt (Table 12).

Root hydraulic conductivity and water flow of the 2 rootstocks were reduced at the first salinity level by about 50% and more than 70%, respectively. Water flow through the root system to the shoot in the PEG treatment was reduced by more than 95% (data not shown). Similar to Experiment 1, no significant differences in root conductivity, water

Table 11. Monthly new flush growth--area/leaf (cm^2)--of sour orange seedlings--Experiment 2.

Treatment (-MPa)	February		March		April	
	Mean ^z	% lower than NS	Mean	% lower than NS	Mean	% lower than NS
NS control	16.7 a ^y	0	20.4 a	0	40.3 a	0
NaCl (0.10)	11.6 b	31	14.9 b	27	31.9 b	21
NaCl (0.20)	9.6 b	43	11.0 bc	46	18.0 c	55
NaCl (0.35)	8.5 b	49	9.8 c	52	16.0 c	60

^zMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 12. Monthly new flush growth--leaf number--of sour orange seedlings--Experiment 2.

Treatment	February		March		April	
	Mean ^z	% lower than NS	Mean	% Lower than NS	Mean	% lower than NS
NS control	17 a ^y	0	27 a	0	43 a	0
NaCl (0.10)	7 b	59	10 b	63	13 b	70
NaCl (0.20)	5 b	71	7 bc	74	10 bc	77
NaCl (0.35)	4 b	77	5 c	82	6 c	86

^zMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

flow and osmotic potential of root exudate were found between SO and CM. There was a positive correlation between water flow through the root system and osmotic potential of root exudate (Fig. 7). With NaCl, less water flow corresponded to higher ion concentrations in the root exudate and consequently to a lower osmotic potential of the root exudate. Both NaCl and PEG increased SLW when expressed on a dry weight basis (Table 33, Appendix). However, unlike NaCl, PEG decreased SLW when expressed on a fresh weight basis. Consequently, leaf succulence was decreased by PEG and increased by NaCl (Table 13). Among PEG treatments, succulence was more reduced in SO than in CM seedlings.

Leaf chlorophyll content was reduced by NaCl and PEG treatments. A significant difference in chlorophyll content due to NaCl was found between SO and CM with a greater reduction occurring in SO (Table 14). Polyethylene glycol generally reduced chlorophyll level in CM more than did NaCl.

Stomatal conductance was also affected by NaCl (Figs. 21, 22, Appendix) and PEG (Figs. 23, 24, Appendix). No significant difference in stomatal conductance was found between SO and CM under NaCl and PEG stresses. Again, the effect of PEG was more pronounced on this variable than that of NaCl. There was a significant positive linear correlation between root hydraulic conductivity and midday stomatal conductance (Fig. 8).

Addition of NaCl and PEG to the nutrient solution reduced seedling water use or evapotranspiration. Water use could be approximated because the amount of water added each time was based on bringing the soil to slightly more than field capacity. Estimated water use for NaCl (0.10), NaCl (0.20), NaCl (0.35), PEG (0.10), PEG (0.20), and PEG (0.35)

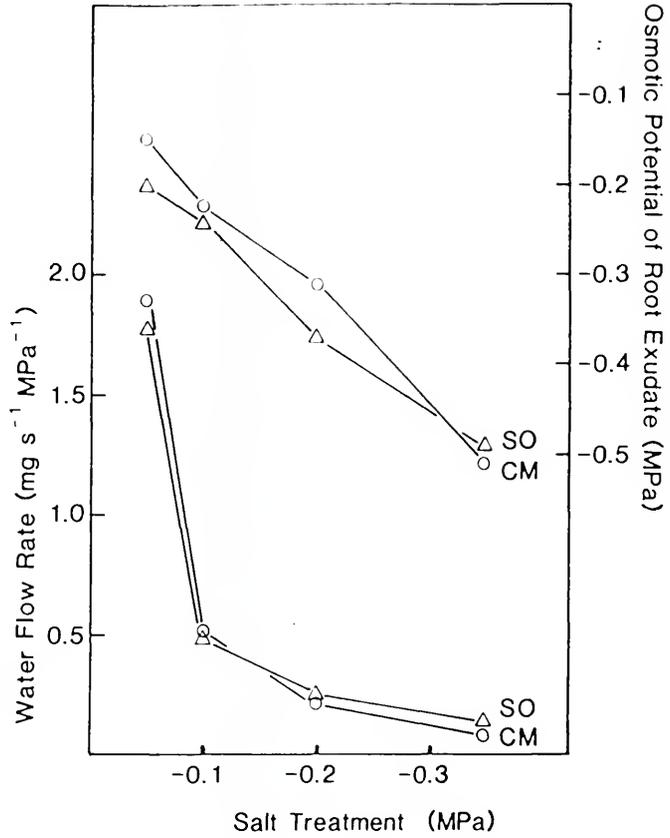


Fig. 7. Relationship between water flow rate and osmotic potential of root exudate of sour orange and Cleopatra mandarin seedlings.

Table 13. Leaf succulence [(g water/g dry wt) x 100] of seedlings of 2 rootstocks grown for 6 months under different NaCl and PEG concentrations--Experiment 2.

Treatment (-MPa)	<u>Sour orange</u>		<u>Cleopatra mandarin</u>	
	Mean ^z	% difference than NS	Mean	% difference than NS
NS control	179 b ^y	0	125 b	0
NaCl (0.10)	190 ab	+6	125 b	0
NaCl (0.20)	191 ab	+7	125 b	0
NaCl (0.35)	194 a	+8	144 a	+15
PEG (0.10)	63 c	-65	81 c	-35
PEG (0.20)	51 c	-72	50 d	-60
PEG (0.35)	27 d	-85	52 d	-58

^zMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 14. Total chlorophyll (mg g^{-1} fresh wt) of seedlings of 2 rootstocks grown for 6 months under different NaCl and PEG concentrations--Experiment 2.

Treatment (-MPa)	<u>Sour orange</u>		<u>Cleopatra mandarin</u>	
	Mean ^z	% lower than NS	Mean	% lower than NS
NS control	1.99 a ^y	0	2.42 a	0
NaCl (0.10)	0.88 b	56	2.15 a	11
NaCl (0.20)	0.61 c	69	1.64 b	32
NaCl (0.35)	0.59 c	70	1.12 c	54
PEG (0.10)	0.88 b	56	1.20 c	50
PEG (0.20)	0.58 c	71	0.95 c	61
PEG (0.35)	0.56 c	72	0.83 c	66

^zMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

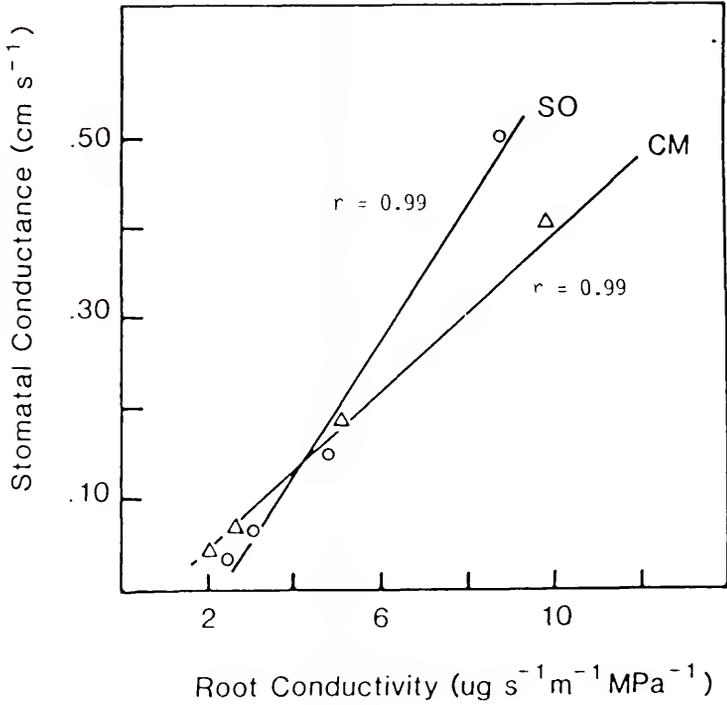


Fig. 8. Relationship between midday stomatal conductance and root conductivity of sour orange and Cleopatra mandarin seedlings.

treatments were, respectively, 50, 25, 17, 25, 12, and 12% of that for the control (NS) treatment.

Experiment 3: Fibrous Root Density and Distribution of Sour Orange Seedlings under NaCl and PEG Stresses

Plant responses in this experiment to NaCl and PEG treatments were similar to those obtained in Experiment 2. Shoot and root dry weight, shoot root ratio, and leaf number generally decreased with increasing NaCl and PEG concentrations in the nutrient solution (data not shown). Significant differences among treatments were found in stomatal conductance during different months (Fig. 9) as well as in daily stomatal conductance (Fig. 10). Stomatal conductance also decreased as leaf age increased (Fig. 9). Throughout the growing period, shoot and root growth rate increased with time, but the growth rate of stressed seedlings was less than that of non-stressed seedlings. After 4 weeks, measurements of seedling height (Fig. 11) and root length (Fig. 12) showed a significant reduction in plant growth due to NaCl and PEG treatments. Cycling between shoot and root growth was noticed under stressed and non-stressed conditions (Fig. 13).

When the portion of the root system in each compartment (top, middle, and bottom) of the root box was compared, root density decreased with depth and was significantly higher in the top compartment than in either of the lower 2 sections (Table 15, Fig. 14). Seedlings receiving NaCl or PEG treatments developed a shallow root system as compared to the control (Fig. 14). Stressed seedlings had a higher percentage of the total root system in the top of the root boxes. About 65% of the roots of the PEG-stressed seedlings, but less than 50% of the roots of control seedlings, were located in the upper section (Table 15). In the

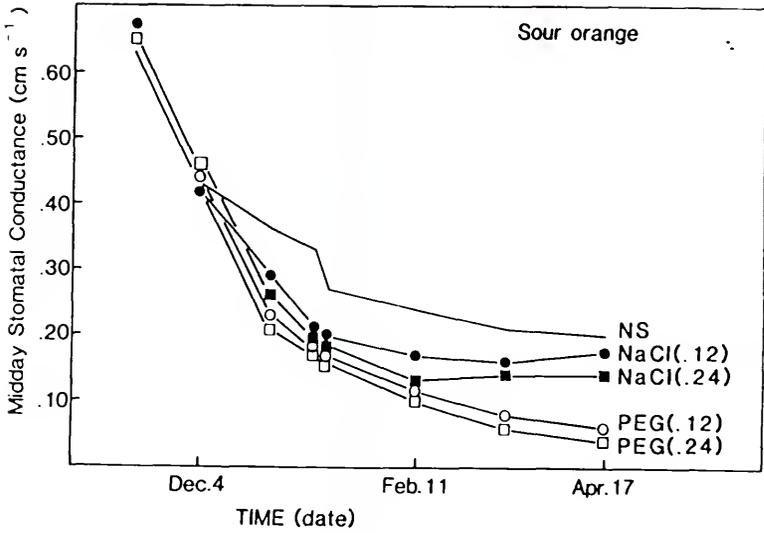


Fig. 9. Midday stomatal conductance of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl or PEG.

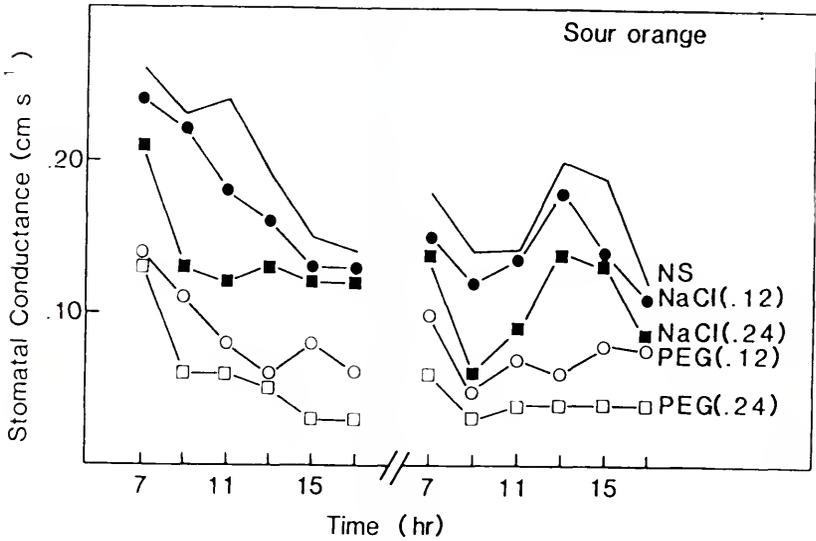


Fig. 10. Relationship of time of day to stomatal conductance of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl or PEG during 2 consecutive days. Measurements were started on April 17, 1986. Seedlings were irrigated the day before measurements were started and not irrigated until after measurements were completed on Day 2.

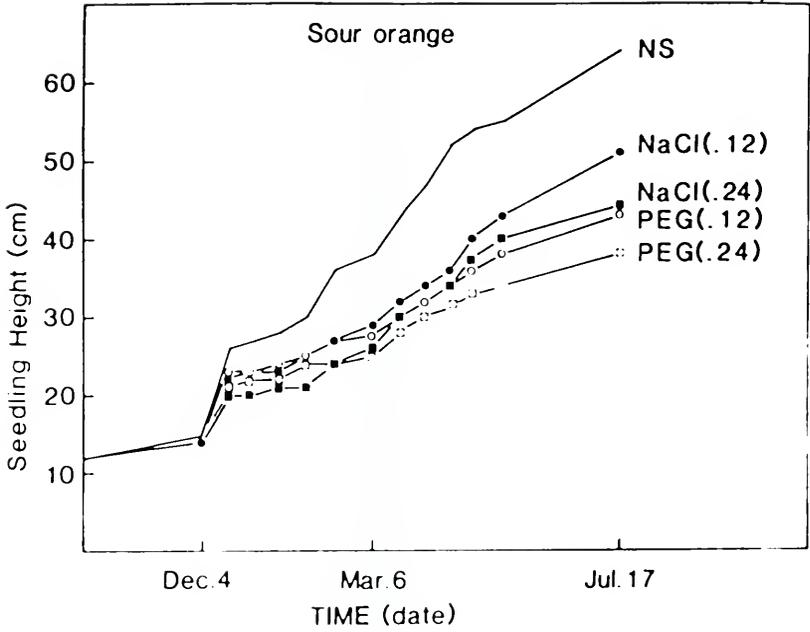


Fig. 11. Growth of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl or PEG.

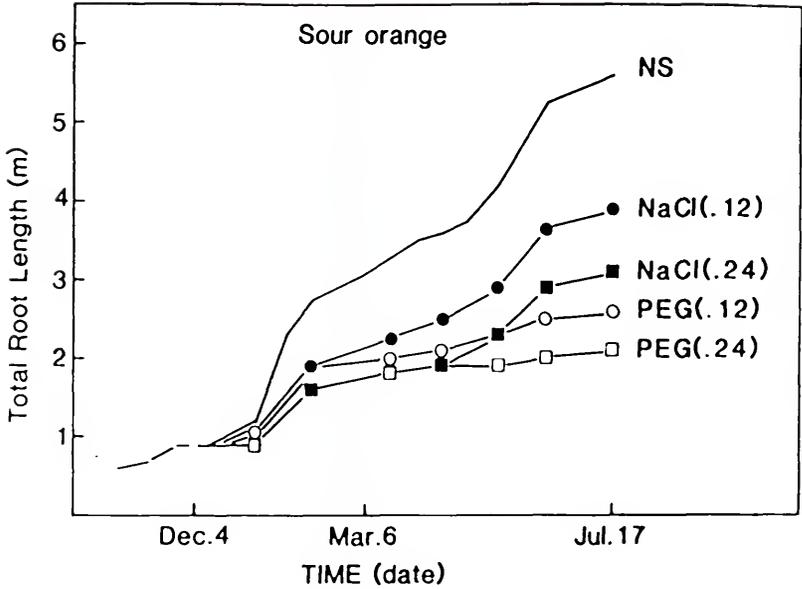


Fig. 12. Fibrous root length of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl or PEG.

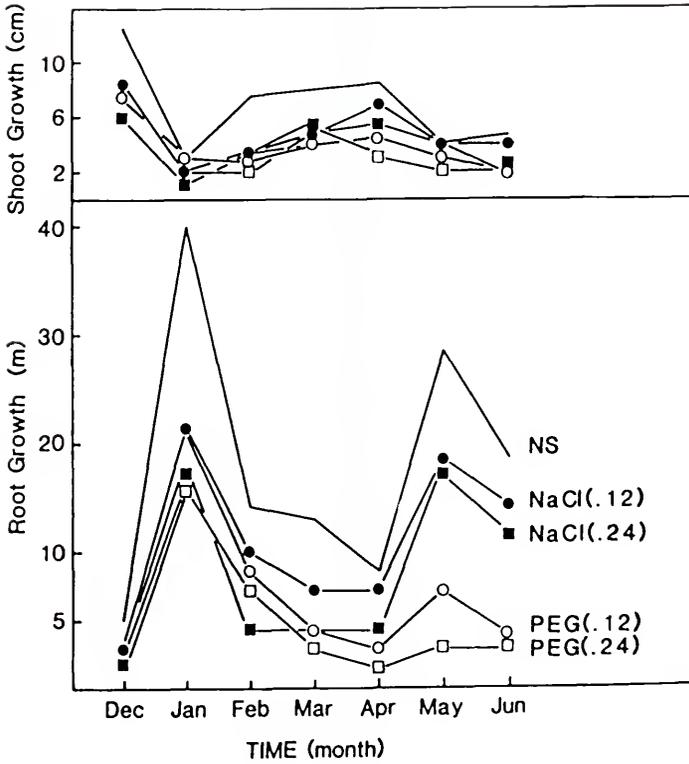


Fig. 13. Fluctuations in shoot and root growth of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl or PEG.

Table 15. Fibrous root length (m and %) in the 3 compartments of the root boxes for seedlings under different NaCl and PEG treatments--Experiment 3.

Treatment	Top			Center			Bottom			Total		
	Mean ^z	% lower than NS	% lower than NS	Mean	% lower than NS	% lower than NS	Mean	% lower than NS	% lower than NS	Mean	% lower than NS	% lower than NS
NS control	80.8 a ^y	0	0	48.1 a (28%)	0	0	45.1 a (26%)	0	0	174.0 a (100%)	0	0
NaCl (0.12)	68.4 ab	15	15	36.7 ab (29%)	24	24	19.4 b (16%)	57	57	124.5 b (100%)	29	29
NaCl (0.24)	54.4 bc	33	33	29.1 bc (29%)	39	39	15.5 bc (16%)	66	66	99.0 bc (100%)	43	43
PEG (0.12)	54.2 bc	33	33	21.6 bc (26%)	55	55	7.4 bc (9%)	84	84	83.2 cd (100%)	52	52
PEG (0.24)	44.8 c	45	45	20.5 c (30%)	57	57	3.1 c (5%)	93	93	68.4 d (100%)	61	61

^zMean of 3 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

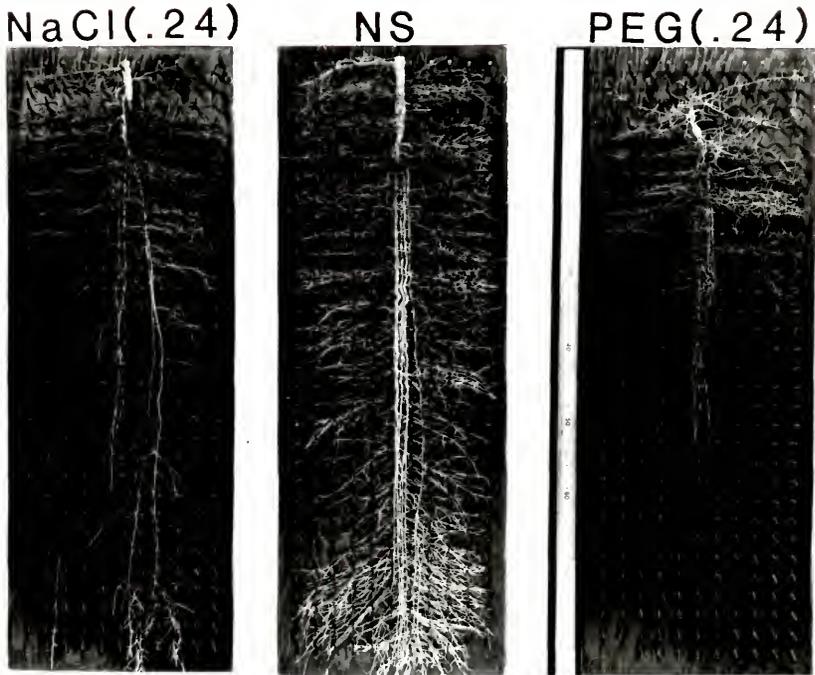


Fig. 14. Root density and distribution of sour orange seedlings growing in root boxes under non-stressed (NS) and stressed (NaCl, PEG) conditions. NaCl and PEG treatments were at -0.24 MPa osmotic potential.

bottom section, only 5 to 16% of the roots developed in the stressed chambers as compared to 26% in the controls.

Fibrous root length at the plexiglas face, measured from tracings made on acetate sheets with colored pencils, was compared to the total fibrous root length measured at the end of the experiment. Root length against the plexiglas represented 3 to 4%, 2 to 3%, and 4 to 5% of the total root length in the top, middle, and bottom of the root boxes, respectively. From the comparison of root lengths at the plexiglas and in the box, it was concluded that growth and distribution of citrus roots at the plexiglas-soil interface correlated satisfactorily with growth and distribution of roots in the bulk soil.

Experiment 4: Response of Split-Root Sour Orange Seedlings to Salinity

Uniform salinity was significantly more damaging to sour orange seedlings than non-uniform salinity (Table 16; Fig. 15). Shoot dry weight was reduced only slightly (9 to 21%) when half of the root system was irrigated with saline solutions. When both halves of the root system were irrigated with saline solutions, shoot dry weight was reduced 45 to 81% (Table 16). The trend was similar with root dry weight in that stressing one-half of the root system resulted in only a moderate reduction (16 to 31%) in root dry weight. Stressing both halves gave a much larger reduction in root dry weight (43 to 79%).

In the split-root test, shoot growth did not correlate well with the average salt stress of the total root system. The average osmotic potential of the NS/NaCl (0.20) treatment was -0.12 MPa. Even though this was slightly greater than the average osmotic potential of the NaCl (0.10)/NaCl (0.10) treatment, shoot dry weight was 35% (10.7 g) less in the NaCl (0.10)/NaCl (0.10) treatment. Similarly, shoot dry weight in the NaCl (0.20)/NaCl (0.20) treatment was 50% (14.5 g) less than that in

Table 16. Shoot and root dry wt of split-root sour orange seedlings under NaCl and PEG stresses--Experiment 4.

Treatment	Average OP of solution (MPa)	Shoot dry wt (g)		Root dry wt (g)	
		Mean ^z	% lower than NS/NS	Mean	% lower than NS/NS
NS/NS	-0.05	37.1 a ^y	0	9.29/9.41 a	0
NS/NaCl (0.10)	-0.08	33.6 ab	9	9.64/6.12 ab	16
NaCl (0.10)/NaCl (0.10)	-0.10	20.4 d	45	5.33/5.27 cde	43
NS/NaCl (0.20)	-0.13	31.1 bc	16	9.49/4.22 bc	27
NaCl (0.20)/NaCl (0.20)	-0.20	14.9 f	60	3.85/3.98 ef	58
NS/NaCl (0.35)	-0.20	29.4 bc	21	9.74/3.21 bcd	31
NaCl (0.35)/NaCl (0.35)	-0.35	7.1 gh	81	1.97/2.01 g	79
NS/PEG (0.20)	-0.13	26.9 c	27	9.79/2.15 cd	36
PEG (0.20)/PEG (0.20)	-0.20	3.6 h	90	1.67/1.81 g	81

^zMean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

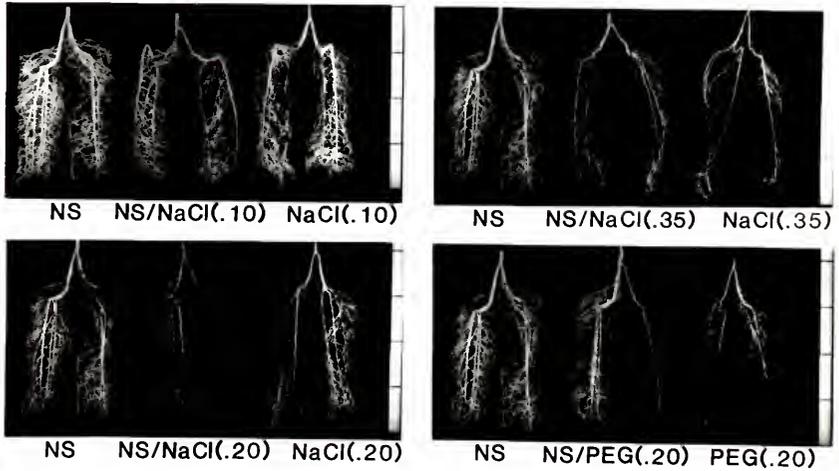


Fig. 15. Split-root treatment of sour orange seedlings under uniform and non-uniform NaCl and PEG stresses. NaCl treatments were at -0.10 , -0.20 , and -0.35 MPa osmotic potentials. PEG treatments were at -0.20 MPa osmotic potential.

the NS/NaCl (0.35) treatment, even though both of these treatments had the same average NaCl stress (-0.20 MPa).

Under uniform salinity similar to Experiments 1, 2, and 3, shoot growth was more reduced than root growth. However, under non-uniform salinity, root dry weight on a percentage basis appeared to be more reduced than shoot dry weight (Table 16).

Partial leaf burn occurred after 4 weeks in the NaCl (0.35)/NaCl (0.35) treatment and after 5 weeks in the NaCl (0.20)/NaCl (0.20) treatment. No leaf damage symptoms were noticed in the remaining treatments until the end of the experiment.

Water relations variables were monitored on 4 successive days during the fourth month of salt treatment. Data were combined because no significant differences were found from day to day. Similar to growth, water relations variables were also significantly more disturbed under uniform salinity than under non-uniform salinity conditions. With uniform salinity, leaf water and turgor potentials decreased significantly from morning to midday, but leaf osmotic potential did not (Fig. 16). Leaf water potential, osmotic potential, stomatal conductance, and transpiration decreased with increasing NaCl and PEG concentrations in the irrigation water (Tables 17, 18). Turgor potential significantly increased in response to NaCl treatments particularly during the morning. A significant positive correlation was found between stomatal conductance and transpiration (Fig. 17). Similar to findings of the preceding experiments, PEG at -0.20 MPa was more damaging than NaCl at the same osmotic potential.

Cross sections of leaves from control (NS/NS) and from NaCl (0.35)/NaCl (0.35) treatments, compared by light microscopy, showed that the number of cell layers in the epidermis, the palisade, and the spongy

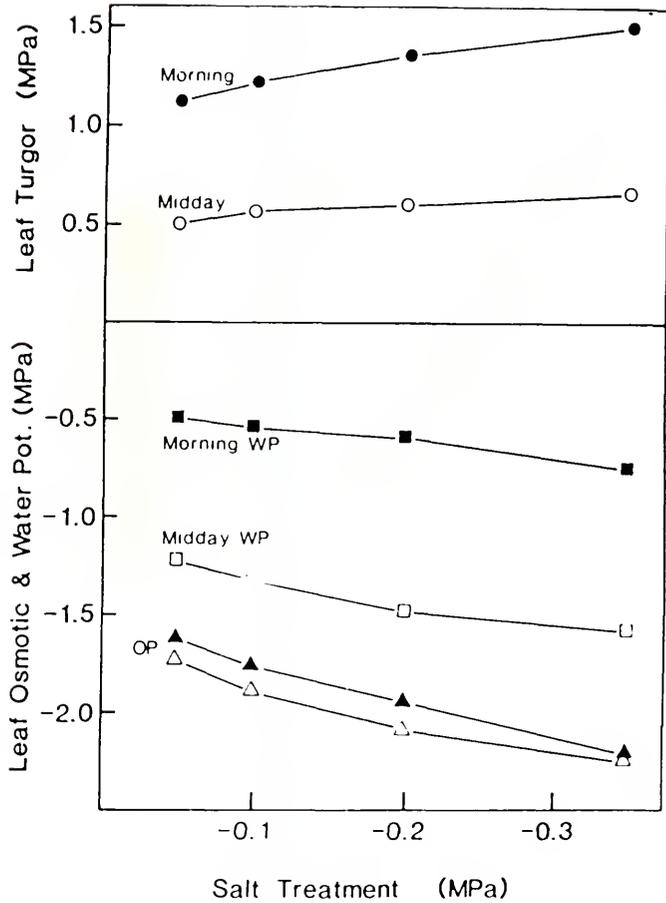


Fig. 16. Leaf water, osmotic, and turgor potential of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with NaCl added to both root halves. Solid figures are morning values and open figures are midday values.

Table 17. Midday leaf water, osmotic, and turgor potentials (MPa) of split-root sour orange seedlings under NaCl and PEG stresses--Experiment 4.

Treatment	Water potential		Osmotic potential		Turgor potential	
	Mean ^z	% lower than NS/NS	Mean	% lower than NS/NS	Mean	% higher than NS/NS
NS/NS	-1.23 a ^y	0	-1.73 a	0	0.50 a	0
NS/NaCl (0.10)	-1.22 a	-1	-1.74 a	1	0.52 a	4
NaCl (0.10)/NaCl (0.10)	-1.32 ab	7	-1.89 bc	9	0.57 a	14
NS/NaCl (0.20)	-1.26 ab	2	-1.81 ab	5	0.55 a	10
NaCl (0.20)/NaCl (0.20)	-1.48 abc	20	-2.08 d	20	0.60 a	20
NS/NaCl (0.35)	-1.32 ab	7	-1.89 bc	9	0.57 a	14
NaCl (0.35)/NaCl (0.35)	-1.60 c	30	-2.26 e	31	0.66 a	32
NS/PEG (0.20)	-1.29 ab	5	-1.85 ab	7	0.56 a	12
PEG (0.20)/PEG (0.20)	-1.43 abc	16	-1.98 cd	14	0.55 a	10

^zMean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 18. Midday stomatal conductance and transpiration of split-root sour orange seedlings under NaCl and PEG stresses--Experiment 4.

Treatment	Stomatal conductance (cm s^{-1})		Transpiration ($\mu\text{g cm}^{-2} \text{s}^{-1}$)	
	Mean ²	% lower than NS/NS	Mean	% lower than NS/NS
NS/NS	0.26 a ^y	0	0.63 a	0
NS/NaCl (0.10)	0.22 ab	15	0.55 ab	13
NaCl (0.10)/NaCl (0.10)	0.20 ab	23	0.45 bc	29
NS/NaCl (0.20)	0.21 ab	19	0.53 ab	16
NaCl (0.20)/NaCl (0.20)	0.15 abc	42	0.36 bc	43
NS/NaCl (0.35)	0.21 ab	19	0.46 abc	27
NaCl (0.35)/NaCl (0.35)	0.13 bc	50	0.33 c	48
NS/PEG (0.20)	0.18 abc	31	0.37 bc	41
PEG (0.20)/PEG (0.20)	0.08 c	69	0.31 c	51

²Mean of 4 plants.

^yMean separatin within columns by Duncan's Multiple Range Test, 0.05 level.

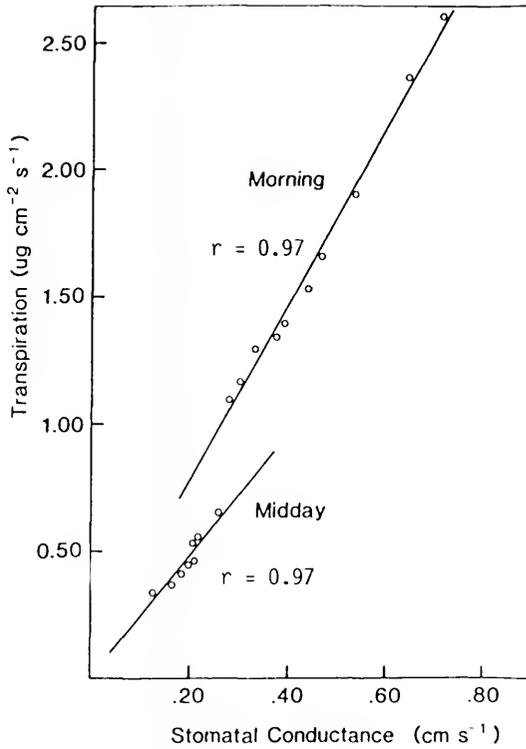


Fig. 17. Relationship between transpiration and stomatal conductance of sour orange seedlings.

mesophyll in control leaves and NaCl-treated leaves were similar. Epidermal and palisade cells of the control and NaCl-grown leaves were also similar in size; however, the spongy mesophyll cells of the NaCl-treated leaves were about 3 times larger than those of the control (Fig. 18). The overall increase in leaf thickness due to NaCl was relatively small (23%) because the enlarged cells of the spongy mesophyll were tightly packed with much less intercellular space. Cells of the spongy mesophyll in NaCl-treated leaves also had fewer chloroplasts than those in the control leaves.

Experiment 5: Effects of Calcium on Sour Orange Seedlings Grown under Saline Conditions

Addition of NaCl to half strength Hoagland's solution significantly reduced growth of sour orange seedlings. Shoot, root, and total plant dry weights were reduced by about 30% (treatments 2 and 10) when 40 mM NaCl was added to the nutrient solution (Tables 19, 20). However, addition of 7.5 mM CaSO_4 (treatment 3) to the salty solution decreased the adverse effect of NaCl on growth. Furthermore, addition of only 5 mM CaSO_4 (treatment 12) completely inhibited the adverse effect of NaCl. Addition of either KCl (treatments 6 and 7) or CaCl_2 (treatments 5 and 8) to the salty solution did not improve plant growth.

In the leaves of the sour orange seedlings, addition of NaCl to the nutrient solution significantly increased sodium and chloride, decreased calcium, magnesium, and potassium but had little or no effect on phosphorus, zinc, manganese, copper, and iron (Table 21). Sodium and chloride accumulation in the leaves usually reduces growth. Addition of CaSO_4 (treatments 3, 4, 11, and 12) to the saline solution reduced sodium and chloride content and, therefore, improved plant growth. Addition of KCl (treatment 6) did not reduce sodium and chloride; hence,

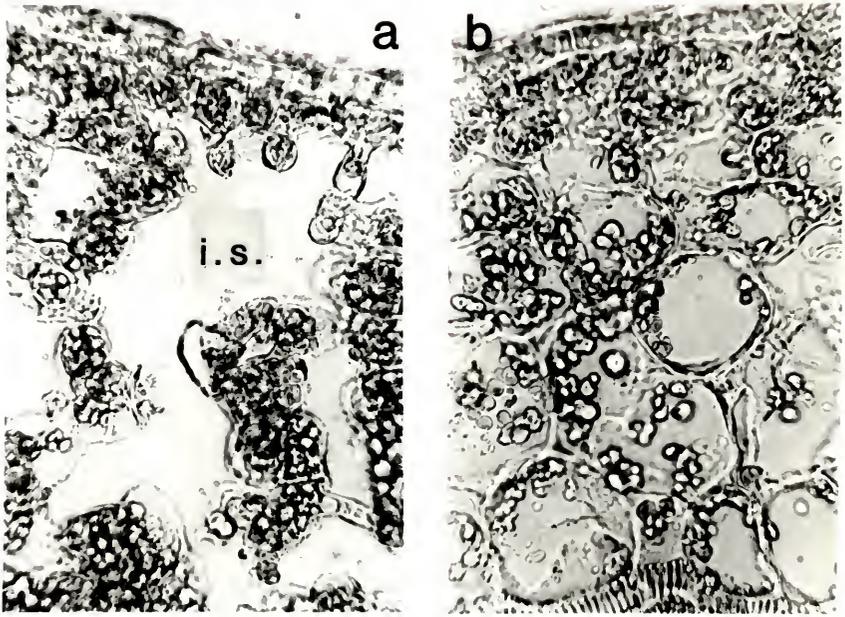


Fig. 18. Cross sections of sour orange leaves.
a. Leaf cross section of non-stressed seedling.
b. Leaf cross section of NaCl-stressed seedling.
i.s. = intercellular space.

Table 19. Root and shoot dry wt of sour orange seedlings under different salt treatments--Experiment 5.

Treatment	Sodium calcium ratio	Root dry wt (g)		Shoot dry wt (g)	
		Mean ^z	% lower than NS	Mean	% lower than NS
1 (NS)	0:2.5	9.44 a ^y	0	36.62 a	0
2 NaCl	16:1	6.80 a	28	25.91 cde	29
3 NaCl + 7.5 mM CaSO ₄	4:1	9.15 a	3	33.41 ab	9
4 NaCl + 13.5 mM CaSO ₄	2.5:1	7.54 a	20	29.22 bcd	20
5 NaCl + 8.75 mM CaSO ₄ + 8.75 mM CaCl ₂	2:1	6.94 a	26	25.06 de	32
6 NaCl + 7 mM KCl	16:1	6.86 a	27	27.04 cd	26
7 NaCl + 7 mM KCl + 7.5 mM CaSO ₄	4:1	7.65 a	19	28.34 cd	23
8 NaCl + 17.5 mM CaCl ₂	2:1	6.84 a	28	23.17 e	37
<hr/>					
9 (NS)--no calcium	0:0	9.45 a	0	35.27 ab	0
10 NaCl--no calcium	40:0	7.36 a	22	26.12 cde	26
11 NaCl + 1 mM CaSO ₄	40:0	8.18 a	13	32.15 ab	9
12 NaCl + 5 mM CaSO ₄	8:1	9.32 a	1	36.99 a	-5

^zMean of 8 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 20. Total plant dry wt and leaf succulence (water content as % dry wt) of sour orange seedlings under different salt treatments--Experiment 5.

Treatment	OP (MPa)	Mean ^z	% lower than NS	Total plant dry wt (g)		Succulence = (g water/g dry wt) x 100	
				Mean ^z	% lower than NS	New leaves	Old leaves
1 (NS)	-0.05	46.06 a ^y	0	341	210		
2 NaCl	-0.21	32.71 cde	29	307	222		
3 NaCl + 7.5 mM CaSO ₄	-0.23	42.56 ab	8	322	215		
4 NaCl + 13.5 mM CaSO ₄	-0.26	36.76 bcd	20	319	217		
5 NaCl + 8.75 mM CaSO ₄ + 8.75 mM CaCl ₂	-0.26	32.00 de	31	320	244		
6 NaCl + 7 mM KCl	-0.23	33.90 cde	26	315	258		
7 NaCl + 7 mM KCl + 7.5 mM CaSO ₄	-0.21	35.99 cd	22	339	241		
8 NaCl + 17.5 mM CaCl ₂	-0.30	30.01 e	35	304	252		
9 (NS)--no calcium	-0.03	44.72 ab	0	357	222		
10 NaCl--no calcium	-0.19	33.48 cde	25	319	238		
11 NaCl + 1 mM CaSO ₄	-0.19	40.33 ab	10	321	236		
12 NaCl + 5 mM CaSO ₄	-0.21	46.31 a	-4	321	215		

^zMean of 8 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 21. Leaf mineral analysis of sour orange seedlings under different salt treatments--Experiment 5.

Treatment	Ca (%)	Mg (%)	Na (%)	Cl (%)	K (%)
1 (NS)	2.1 c ^y	0.30 b	0.02 d	0.02 g	2.8 b
2 NaCl	1.7 d	0.21 c	0.47 ab	0.97 cd	2.0 c
3 NaCl + 7.5 mM CaSO ₄	2.7 b	0.20 cd	0.24 c	0.43 f	1.9 c
4 NaCl + 13.5 mM CaSO ₄	2.7 b	0.20 cd	0.24 c	0.39 f	1.9 c
5 NaCl + 8.75 mM CaSO ₄ + 8.75 mM CaCl ₂	3.4 a	0.20 cd	0.26 c	0.73 de	2.0 c
6 NaCl + 7 mM KCl	1.3 ef	0.15 e	0.43 b	1.21 b	3.6 a
7 NaCl + 7 mM KCl + 7.5 mM CaSO ₄	2.1 c	0.17 de	0.20 c	0.56 ef	2.9 b
8 NaCl + 17.5 mM CaCl ₂	3.5 a	0.21 c	0.20 c	1.52 a	1.9 c
9 (NS)--no calcium	1.6 de	0.36 a	0.02 d	0.04 g	2.9 b
10 NaCl--no calcium	1.1 f	0.23 c	0.61 a	1.13 bc	2.2 c
11 NaCl + 1 mM CaSO ₄	1.7 d	0.22 c	0.43 b	0.48 f	2.1 c
12 NaCl + 5 mM CaSO ₄	2.4 bc	0.21 c	0.27 c	0.41 f	1.9 c

(Cont'd)

Table 21. (Cont'd)

Treatment	P (%)	Fe (ppm)	Mn (ppm)	Zn (ppm)	Cu (ppm)
1 (NS)	0.13 ab	113 a	9 b	32 a	7 a
2 NaCl	0.13 ab	87 ab	11 ab	30 a	6 a
3 NaCl + 7.5 mM CaSO ₄	0.13 ab	97 ab	10 ab	27 a	6 a
4 NaCl + 13.5 mM CaSO ₄	0.12 abc	73 ab	9 b	28 a	5 a
5 NaCl + 8.75 mM CaSO ₄ + 8.75 mM CaCl ₂	0.11 c	90 ab	10 ab	24 a	6 a
6 NaCl + 7 mM KCl	0.13 ab	113 a	9 b	25 a	5 a
7 NaCl + 7 mM KCl + 7.5 mM CaSO ₄	0.3 ab	90 ab	10 ab	31 a	6 a
8 NaCl + 17.5 mM CaCl ₂	0.11 c	103 ab	12 a	24 a	6 a
9 (NS)--no calcium	0.12 abc	83 ab	10 ab	35 a	6 a
10 NaCl--no calcium	0.11 bc	63 b	11 ab	27 a	6 a
11 NaCl + 1 mM CaSO ₄	0.13 ab	97 ab	12 a	29 a	7 a
12 NaCl + 5 mM CaSO ₄	0.14 a	80 ab	12 a	30 a	5 a

² Mean of 8 plants.

³ Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

growth was not improved. Addition of CaCl_2 (treatments 5 and 8) reduced sodium but did not reduce chloride sufficiently to improve growth.

Significant growth reduction occurred without any visible symptoms of salt damage. Although total plant dry weight was reduced by more than 28% in some treatments after 4 months of salinity stress, none of these treatments caused any apparent leaf damage symptoms.

Comparison of Citrus Seedling Responses to NaCl and PEG Treatments

The effects of NaCl and PEG on citrus seedlings differed in the degree and the type of damage. When considering NaCl and PEG at similar osmotic potentials, the damaging effects on all measured variables generally appeared to be larger in the PEG treatment than in the NaCl treatment. Citrus seedling responses to NaCl and PEG compared to the no salt control are summarized in Table 22. The higher salinity damage occurring in Experiment 2 in comparison to Experiment 1 was thought to be mainly due to the more rapid onset of salt treatment and to the longer duration of salt treatment.

Differences in damage and leaf burn symptoms were also found between NaCl and PEG. Leaves from NaCl-treated seedlings appeared abnormally thickened. Leaf symptoms in the NaCl treatment were initially similar to nitrogen deficiency (uniform loss of the green color over the entire leaf). Later, leaf burn occurred as large spots merged together. Leaf scorch and areas of dead tissue extended inward from the margins of the leaf. Sodium chloride-damaged leaves readily abscised and dropped as soon as visual burn symptoms appeared. Sometimes leaves fell off before they reached this stage. Leaf symptoms in PEG treatment first appeared similar to iron-manganese deficiency (interveinal chlorosis). Then, leaf burn appeared at the edges and particularly at the tip of the leaf. Later, the dead area extended inward from the tip (Fig. 19).

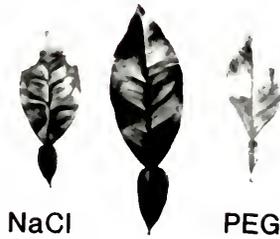
Table 22. Summary of citrus rootstock responses to NaCl and PEG as compared to the no salt control.

Variable	NaCl	PEG
<u>Growth</u>		
Total fibrous root length	decrease	decrease
Leaf number	decrease	decrease
New shoot growth	decrease	decrease
Total root dry weight	decrease	decrease
Total shoot dry weight	decrease	decrease
Seedling height	decrease	decrease
Stem cross sectional area	decrease	decrease
Total leaf area	decrease	decrease
<u>Water Relations</u>		
Root conductivity	decrease	decrease
Water flow rate	decrease	decrease
OP of root exudate	decrease	decrease
Stomatal conductance	decrease	decrease
Transpiration	decrease	decrease
Water use	decrease	decrease
Leaf water potential	decrease	decrease
Leaf osmotic potential	decrease	decrease
Leaf turgor potential	increase	increase
Leaf succulence	increase	decrease
<u>Leaf Mineral Analyses</u>		
Chloride	increase	no change
Sodium	increase	no change
Calcium	decrease	increase
Magnesium	decrease	decrease
Potassium	decrease	decrease
Phosphorus	increase	increase
Zinc	decrease	increase
Manganese	increase	increase
Copper	no change	no change
Iron	no change	no change
<u>Other Variables</u>		
Shoot root ratio	decrease	decrease
Specific root weight	increase	increase
Specific leaf wt (Dry wt basis)	increase	increase
Specific leaf wt (Fresh wt basis)	increase	decrease
Leaf chlorophyll	decrease	decrease

Sour orange



Control NaCl-damaged leaves



NaCl

PEG

Control

Fig. 19. Sour orange leaves from non-stressed (control) and stressed (NaCl, PEG) seedlings.

DISCUSSION

Leaf Ion Content and Salinity Tolerance

Rootstock Tolerance

Important differences in salt tolerance among citrus rootstocks were demonstrated in this study. Based on various measurements of plant growth (shoot, root, and total plant dry weight), on plant water relations factors (root hydraulic conductivity, water flow rate, and osmotic potential of root exudate), and on seedling appearance and performance (leaf burn, leaf drop, and dieback), S0 and CM seedlings were the least affected while the most damage occurred in ML and PT seedlings. Rough lemon, SC, and CC had an intermediate response. From these results, S0 as well as CM were classified as relatively tolerant rootstocks, RL, SC, and CC were sensitive, and ML and PT were very sensitive rootstocks to NaCl. Cooper et al. (1951) and Ream and Furr (1976), who based their conclusions on visual leaf burn symptoms and leaf chloride content, found that CM appeared to be more salt tolerant than S0. The current study, which was mainly based on growth and water relations measurements, showed that S0 was as tolerant as CM. This overall classification agreed with Cooper et al. (1951) who reported that PT was a very salt sensitive rootstock and with others who found that CC was a salt sensitive rootstock when compared to CM (Joolka and Singh, 1979; Patil and Bhambota, 1978).

Ion Exclusion and Accumulation

Sour orange seemed to behave differently from the other rootstocks. Even though SO accumulated higher amounts of sodium and chloride than PT and its hybrids (SC and CC) at the first salinity level (Tables 7, 8), plant growth and physiological activities of SO were relatively unaffected as compared with those of RL, ML, SC, CC, and PT. Rough lemon and ML were sodium and chloride accumulators similar to SO. However, salt damage was more severe and tree growth and appearance were poorer in RL and ML than in SO. Since excess accumulation of both chloride and sodium in SO leaves caused relatively minor damage to this rootstock, SO might have the ability to partially exclude these ions from the cytoplasm where they could inhibit metabolic functions. Salinity studies at the cellular level could further clarify ion exclusion and compartmentalization ability in citrus.

The citrus rootstocks tested in this study are considered to be salt sensitive because no rootstock has the ability to exclude both chloride and sodium. Rough lemon, ML, and SO are chloride and sodium accumulators. Poncirus trifoliata, SC, and CC are chloride accumulators but sodium excluders. Cleopatra mandarin is a chloride excluder but a sodium accumulator. Furthermore, sodium exclusion capacity in PT, SC, and CC and chloride exclusion capacity in CM are limited. This study (Tables 7, 8) showed the inability of PT, SC, and CC to exclude sodium and the inability of CM to exclude chloride at moderate salinity levels (-0.2 MPa). It is suggested that in any program where plants are being screened for salt tolerance on the basis of salt exclusion, chloride exclusion as well as sodium exclusion should be considered because the chloride and sodium accumulating properties of a particular species are quite different (Grieve and Walker, 1983).

Leaf Ion Content and Ion Toxicity

Sodium chloride was found to reduce potassium in SO, CM, RL, and ML but not in SC, CC, and PT leaves (Table 27, Appendix). Sour orange, CM, RL, and ML are sodium accumulators (Table 9). Sodium accumulation in these rootstocks might be the main factor which depressed leaf potassium. Poncirus trifoliata, SC, and CC are sodium excluders (Table 9). The unaffected leaf potassium in these rootstocks might be attributed to sodium exclusion.

There was an inverse relationship between chloride ion accumulation in the leaves and salt tolerance. Usually chloride accumulation was associated with more damage. Since PT and its hybrids (SC and CC) accumulated large amounts of chloride, their ability to exclude sodium (particularly at -0.10 MPa) and to maintain adequate potassium did not help prevent these rootstocks from showing severe growth reduction and water relation disturbances. Furthermore, although CM accumulated excess sodium in its leaves, growth and water relations of CM were not as severely affected at -0.10 MPa since it was a chloride excluder.

The levels of chloride and sodium accumulation at which leaf burn symptoms developed were found to be higher than the upper limits set by earlier investigators. Such differences are mainly attributed to different experimental conditions. Comparison between leaf chloride content (Table 8) and visual symptoms (Table 6) shows that a leaf chloride content of about 1% in SC and CC and even 1.7% in SO did not cause any leaf burn symptoms. Similarly, when comparing leaf sodium content (Table 7) to visual symptoms (Table 6), leaf sodium content up to 1.9% in CM did not cause visible leaf burn. However, growth and water relations were severely altered.

Leaf chloride and sodium analysis is thought to provide useful information on toxicity limits as well as on rootstock tolerance. Harding and Chapman (1951) recommended that a leaf chloride content exceeding 0.25% be considered indicative of chloride toxicity. Bernstein (1969) stated that although 0.25% might not lead to obvious chloride toxicity symptoms, it might affect the longevity of leaves and reduce the yield. Chapman et al. (1969) suggested that 0.30% chloride in the dry matter was regarded as the threshold value of injury and leaf levels over 0.75% chloride would be indicative of serious growth retardation and yield reduction. According to Abdel-Messih et al. (1979), sodium leaf content higher than 0.36% would be critical for developing burn symptoms in citrus leaves. These threshold values were lower than those found in this study because of the higher degree of stress under field and dry climate conditions.

Importance of Calcium under Saline Conditions

Under salinity conditions, addition of calcium to irrigation waters resulted in different responses in citrus. The present study on S0 seedlings showed that the beneficial effect of calcium depended on the anion associated with the calcium salt. Calcium sulfate was found to be significantly more effective than calcium chloride in reducing the deleterious effect of NaCl on growth (Tables 19, 20). Walker and Douglas (1983) did not observe any improvement in citrus growth by increasing calcium chloride in the growth medium. However, the earlier work on citrus by others showed the effectiveness of calcium sulfate, calcium nitrate, and calcium carbonate on reducing sodium concentrations in plant tissues, in preventing the deflocculation effect of sodium and in improving tree appearance and growth (Cooper, 1961; Harding et al., 1958b; Jones et al., 1952). LaHaye and Epstein (1969, 1971)

demonstrated that an increase in calcium levels by adding either calcium sulfate or calcium chloride protected bean plants from salt injury by restricting sodium absorption and translocation to the leaves. Failure in effectiveness of calcium chloride in our work might have been due to the chloride accompanying the calcium and to the sensitivity of citrus to chloride.

Physiological Effects of NaCl and PEG

Effect of NaCl on Root Conductivity

The present study showed that root hydraulic conductivity in citrus seedlings was severely reduced due to NaCl stress and that root conductivity varied significantly among rootstocks under stressed and non-stressed conditions. Under non-stressed conditions, these results were consistent with data obtained by others (Graham and Syvertsen, 1985; Syvertsen and Graham, 1985; Syvertsen et al., 1981). Under salinity stress, root conductivity of different citrus rootstocks has not been thoroughly studied.

Reduced hydraulic conductivity of roots has been attributed to several factors. Bielora et al. (1983) suggested that reduced water uptake by mature citrus trees irrigated with saline water was a result of soil solute potential reduction and to root suberization. Hayward and Blair (1942) observed a condition resembling dormancy caused by suberization of epidermal and root cap cells of Valencia orange seedlings irrigated with NaCl solutions. They also noted reductions in water uptake and development of lateral roots and root hairs as salinity increased. Walker et al. (1984) studied the anatomy and the ultrastructure of roots from two citrus genotypes (Rangpur lime and Etrog citron) with different abilities for chloride exclusion. They found that NaCl increased suberization of the hypodermis and endodermis

closer to the root tip. This increase in suberization associated with the lower extension rate of the root tips might be of prime importance in reducing root permeability and root hydraulic conductivity.

O'Leary (1974) found that the reduction in root conductivity of beans could be reversed after a 2-day exposure to high NaCl by removing the NaCl. This short time reversibility suggested that biochemical or membrane changes were responsible for the reduced conductivity because root suberization may not have yet occurred. Thus, differences in root hydraulic conductivity may arise from anatomical and biochemical features.

Effect of PEG on Root Conductivity

Polyethylene glycol was found to reduce root hydraulic conductivity more severely than NaCl. Similar to NaCl, reduction in root conductivity due to PEG was attributed to reduced root permeability. Reduction in root permeability might result from root suberization, inhibited root hair formation, and oxygen deficiency around the roots. Growth of root hairs in redtop grass seedlings and in Vicia faba was completely inhibited by a PEG concentration of -0.2 MPa (Jackson, 1962; Zahran and Sprent, 1986). It was suggested by Mexal et al. (1975) that the main damage of PEG to plants was caused by low oxygen solubility and slow oxygen transport to the roots. In the present study, after the termination of the first 4 experiments when the roots were removed and washed from the soil, there was an indication that the root system in PEG treatments suffered aeration deficiency since PEG-treated soil was found to be firmer and sticky. Furthermore, under osmotic stress, citrus roots exhibited early suberization of the endodermis and root hairs were directly affected by soil water conditions (Cossmann, 1940).

Effect of NaCl on Stomatal Conductance

In all experiments, stomatal conductance was reduced significantly with an increase in NaCl or PEG concentrations. It is apparent from Fig. 8 that there is a strong correlation ($R = 0.99$) between stomatal conductance and root conductivity. Even though there was a strong correlation, closure of stomata might not be caused entirely by salinity-induced water stress. This possibility was based on the data presented in Table 17 which showed leaf turgor maintenance in salt treated plants. Stomatal closure was similarly reported in certain glycophytes when grown under saline conditions, even when leaf turgor was maintained (Gale et al, 1967; Meiri and Poljakoff-Mayber, 1970). O'Leary (1969) also found that stomatal conductance of beans grown in salinized solutions was also lower than that of control plants. He suggested that the increase in resistance (or decrease in conductance) in the water flow pathway could result in the bean leaves experiencing physiological drought even if osmotic adjustment occurred.

The work of Walker and his coworkers showed more clearly the importance of sodium concentration in affecting stomata of citrus under salinity stress. Stomatal recovery occurred in leaves of stress-relieved Etrog citron (C. medica) even though the leaves retained high chloride concentrations and low sodium concentrations (Walker et al., 1982). There was a failure of stomatal recovery of Valencia leaves on other citrus rootstocks which was associated with retention of high sodium concentration (Walker et al., 1983). It is possible that high amounts of sodium replaced potassium in the vacuoles and guard cells and caused stomata to close (Behbondian et al., 1986).

Stomatal behavior in citrus under NaCl stress is mainly affected by ion accumulation and therefore, better associated with the leaf osmotic potential and not the bulk turgor potential of the leaves.

Effect of PEG on Stomatal Conductance

Stomatal conductance in citrus was more reduced under PEG stress than under NaCl stress (Figs. 9, 10). These results agreed with those of Plaut and Federman (1985) and with Sanchez-Diaz et al. (1982) who found that PEG decreased leaf conduction and carbon dioxide fixation rate in tomato and legume plants more severely than did NaCl. Reduction in stomatal conductance due to PEG might be attributed to several factors such as drought stress caused by reduced water flow to the shoots and to translocation of PEG to the leaves. It was suggested by Lawlor (1970) that PEG blocked the water pathway and induced desiccation in plants. It was also concluded that PEG damage was due to its uptake and translocation throughout the plant (Emmert, 1974; Kaufmann and Eckard, 1971; Lagerwerff et al., 1961; Lawlor, 1970). It is possible that PEG was absorbed and translocated in leaves of citrus seedlings since PEG caused leaf necrosis.

Effect of NaCl and PEG on Chlorophyll

Leaf chlorophyll content was the only variable more significantly affected in S0 than in CM (Table 14). For S0 seedlings, chlorophyll reduction due to NaCl was similar to that due to PEG. However, for CM, chlorophyll reduction was more severe under PEG than under NaCl treatments. Since NaCl did not reduce chlorophyll as much in CM, and since CM is a chloride excluder, chlorophyll reduction could be mainly attributed to chloride accumulation in the leaves. Contrary to this, Bhamkota and Kanwar (1970) attributed salt induced chlorophyll reduction in sweet orange to sodium uptake and to a reduction in magnesium and

iron uptake. Leaf chlorophyll content has also been found to be reduced in many other crops such as beans (Seemann and Critchley, 1985) and spinach (Downton et al., 1985; Robinson et al., 1983). In other photosynthetic related processes, NaCl was found to inhibit the Hill reaction (Sivtsev, 1973) and increase the hydrolytic activity of chlorophyllase (Sivtsev et al., 1973) in tomato leaves.

Effect of NaCl on Leaf Thickness and Succulence

Increases in leaf succulence and thickness have been attributed to changes in cell size, cell layer number, or a combination of both. In the present study, examination of leaf sections by light microscopy (Fig. 18) suggested that an increase in spongy mesophyll cell size rather than an increase in cell number caused the greater leaf thickness and succulence. Similar conclusions were made with tobacco (Flowers et al., 1986), spinach (Robinson et al., 1983), and beans (Wignarajah et al., 1975). However, in Atriplex, cotton, and Salicornia herbacea, leaf thickness and succulence increased not only due to a development of larger cells but also to an increase in cell layers of the mesophyll. In most circumstances, increase in succulence was accompanied by an increase in sodium and chloride concentrations in the leaves.

Growth of Citrus Rootstock Seedlings under NaCl and PEG Stresses

The results of this study are consistent with those of other investigators who classified citrus as a salt sensitive crop. Growth was reduced at least 20% in the rootstocks ranked as tolerant when irrigated with a nutrient solution containing as little as 1 g NaCl/L (-0.1 MPa). The higher salinity damage occurring in Experiment 2 in comparison to Experiment 1 was thought to be mainly due to the more rapid onset of salt treatment and to the longer duration of salt treatment.

Relationship of Leaf Damage Symptoms to Growth Reduction

Significant growth reduction and physiological disturbances were found to precede visible leaf symptoms. When comparing shoot dry weight (Table 2) to visual symptoms (Table 6), growth reduction up to 30% occurred without being accompanied by visible leaf damage symptoms. Similar to this, the use of saline irrigation water decreased grapefruit and orange yields from 18 to 54% without apparent toxicity symptoms (Bielorai et al., 1978, 1983; Bingham et al., 1974; Francois and Clark, 1980). Salinity effects develop slowly so that leaf injury symptoms appear only after a certain period of time. Leaf symptoms are, therefore, a poor parameter for evaluating salt damage.

Root Growth and Distribution under NaCl and PEG Stresses

The present study showed that root growth of citrus was severely reduced even at relatively low concentrations of NaCl and PEG in the nutrient solution. The average daily root growth rate was reduced by 30 to 50% at -0.12 MPa NaCl and PEG, respectively (Table 15). Nevertheless, these results showed that citrus roots were able to grow slowly at an osmotic potential of -0.24 MPa. Bevington and Castle (1985) reported that citrus root growth was significantly reduced at a soil matric potential of -0.05 MPa and Monselise (1947) reported that citrus root growth was very limited at soil water potentials of -0.75 to -0.80 MPa. Within the limited range of NaCl and PEG used in the current study, it is not possible to specify a water potential value at which growth stopped completely.

Root distribution of stressed seedlings was altered in comparison to root distribution of control seedlings. Stressed seedlings had a higher percentage of the total root system in the top and a much lower percentage at the bottom of the root boxes (Table 15). Seedlings

receiving NaCl or PEG treatments produced, therefore, a shallow root system.

Root and shoot growth was found to be cyclic (2-month cycle) in young citrus seedlings even when the plants were under NaCl or PEG stress (Fig. 13). It was observed that immediately following the cessation of shoot elongation, a rapid increase in root growth occurred and continued until the initiation of the next shoot growth flush. Alteration of root and shoot growth activity in citrus has been described earlier under non-stressed conditions by other investigators (Bevington and Castle, 1982, 1985; Marloth, 1949).

Effect of Non-Uniform Salinity and Water Stress

Soil water content and salinity levels are seldom uniform in the field, particularly with the use of microsprinklers which may irrigate only a portion of the root zone. A split-root experiment was designed to determine if non-stressed portions of the root system compensated for the decrease in water and nutrient uptake by the stressed portions so that plants could withstand substantial amounts of stress.

The non-stressed roots were found to partially compensate for the decrease in water by the stressed roots. Water uptake from each of the 2 sides was estimated since the amount of water added each time was based on bringing the soil to slightly above field capacity. Water uptake by the unsalinized half of the root system increased when the other half of the root system was subjected to salinity stress. Similar results were obtained on corn (Bingham and Garber, 1970) and alfalfa (Shalhevet and Bernstein, 1968). Watering one part of the root system of wheat (Lawlor, 1973) and tomato (Tan et al., 1981) resulted in a compensatory increase in water uptake by other parts of the root system so that plant water relations remained relatively unaffected. However,

compensation was not seen in beans and barley because plants with half their roots in saline solutions had growth and water relations values intermediate between those of plants grown in non-saline solutions and plants grown in saline solutions (Kirkham et al., 1969, 1972). Only partial compensation occurred in SO seedlings since plants with half their root systems in either NaCl or PEG solutions had shoot and root dry weight and leaf water and osmotic potential values closer to those of the non-stressed control than to those with completely stressed root system (Tables 16,17).

No soil water measurements were recorded in the split-root experiment. However, the root dry weight data (Table 16) might indicate that some water could have been transported through roots from the non-stressed half to the stressed half. Several investigators have demonstrated that plant roots can absorb water from a wet soil, transport the water, and build up the moisture of a dry soil. In a study using wheat plants with roots split between soil and nutrient solution, Kirkham (1980) showed transport of water from the solution to the soil suggesting that roots were acting like wicks.

While the present study was carried out under greenhouse conditions, it provided several useful observations which are relevant to field conditions. Citrus as a deep and dense rooted crop may tolerate certain levels of salinity as long as a portion of the root system remains in a relatively non-saline soil.

Comparative Effects Between NaCl and PEG

Although PEG-induced water stress is osmotic in nature and may not be exactly the same as the water stress occurring in soils, it is a sensitive method that can create small degrees of water stress on a continuous basis not easily induced in soils (Gergely et al., 1980).

Polyethylene glycol was used satisfactorily by several investigators for various species (Janes, 1966; Kaufmann and Eckard, 1971; Kaul, 1966) in which the response to PEG was attributed to a decrease in osmotic potential with no obvious toxic effects.

Injuries to citrus rootstock seedlings by PEG were greater than the osmotic effects per se. Damage due to ionic effects of sodium and chloride were less than the damage from non-ionic PEG. Excess damage might be attributed to insufficient transport of oxygen to the root system due to high PEG viscosity and its effect on soil stickiness and firmness. Damage could also be caused by PEG uptake and transport to the leaves where it caused dehydration and leaf damage. Oxygen availability could be significantly reduced at relatively low PEG concentrations (Mexal et al., 1975). Absorption and secretion of PEG 4000 and 6000 by Solanaceae species was observed (Yaniv and Werker, 1983), as well as the appearance of white material on the upper surface of bean leaves grown in PEG 20000 (Lagerwerff et al., 1961).

Studies with other species have shown NaCl to be either more damaging or less damaging than PEG. Similar to results of the present investigation, the damaging effect of PEG was found to be higher than NaCl at equal osmotic potentials in tobacco (Heyser and Nabors, 1981) and tomato (Plaut and Federman, 1985). However, growth of beans, maize, and barley was substantially better with PEG than isosmotic salt solutions (Lagerwerff and Eagle, 1961; Storey and Wyn Jones, 1978). The matter of separating toxic ion effects from osmotic effects of salts on citrus was not clearly determined in this study. This important question merits continued investigation involving the testing of other non-ionic compounds or nutrient solutions at different concentrations.

SUMMARY AND CONCLUSIONS

The conclusions from this study are summarized below:

1. Differences in sodium and chloride exclusion capacity were found among citrus rootstocks. This study was the first to show that ML was a chloride and sodium accumulator while SC and CC were chloride accumulators but sodium excluders.

2. Citrus rootstocks were found to be sensitive to NaCl since none of these rootstocks was able to exclude both chloride and sodium. Furthermore, sodium and chloride exclusion capacities were lost at a concentration of -0.20 MPa. Differences in NaCl sensitivity among rootstocks were also found. Cleopatra mandarin and SO were the least sensitive, ML and PT were the most sensitive, and RL, SC, and CC were intermediate in sensitivity.

3. This study was also the first to show that salt tolerance in citrus rootstocks was not strongly correlated with chloride and sodium exclusion. Even though SO accumulated higher amounts of chloride and sodium than PT, SC, and CC at an osmotic potential of -0.10 MPa NaCl, growth of SO was as good as CM and significantly better than the remaining rootstocks. Water relations measurements also showed that SO was similar to CM but less stressed than the other rootstocks. Sour orange and CM acted through 2 different mechanisms to tolerate salinity stress. Cleopatra mandarin tolerated high concentrations of NaCl by partial exclusion of chloride. Sour orange tolerated NaCl by possible

compartmentation of sodium and chloride and their exclusion from the cytoplasm where they could inhibit metabolic processes.

4. Sodium chloride usually caused less damage than PEG to seedlings of 7 citrus rootstocks. Both NaCl and PEG caused significant growth depression and physiological disturbances even at a concentration of -0.10 MPa. The response of citrus rootstocks to the 2 compounds was different suggesting that NaCl and PEG acted through different mechanisms. Addition of PEG to the irrigation water probably reduced aeration and also moved to the shoots where it caused plant dehydration and leaf damage. Addition of NaCl reduced water uptake but increased leaf sodium and chloride concentrations. This increased leaf thickness and succulence and caused leaf burn.

5. Growth reduction and physiological disturbances were found to precede visible damage. Growth was reduced up to 30% without being accompanied by visible leaf injury symptoms. Leaf burn symptoms developed only after a threshold value of chloride accumulation (1%) was reached. Leaf burn symptoms developed too slowly to accurately evaluate salt damage.

6. In all NaCl and PEG treatments, growth was depressed and water balance was disturbed. Growth depression was shown by plants that had lower dry weight, fewer leaves per plant, smaller area of individual leaves, shorter height, smaller stem cross sectional area, and smaller root systems. Disturbance in water balance was shown by reductions in root hydraulic conductivity, stomatal conductance, transpiration, water use, and leaf water and osmotic potentials.

7. Root observation boxes were used to follow root growth and distribution under stressed and non-stressed conditions. Root growth usually alternated with shoot growth but this alternating pattern was

not shifted by NaCl and PEG stresses. However, root growth and distribution were significantly affected. Seedlings receiving NaCl or PEG treatments, produced smaller and shallower root systems with the majority of the roots occurring in the top layer.

8. Although roots were in direct contact with NaCl and PEG solutions, shoot growth was more reduced than root growth. The monthly or daily amount of new flush area was found to be a sensitive measure of the effects of NaCl on plants. Root conductivity correlated better with salinity tolerance among rootstocks than did total fibrous root length.

9. Stomatal conductance was greatly reduced even though leaf turgor was maintained. This reduction was attributed to a decrease in water flow to the shoots and to a suggested lack of osmotic adjustment of the guard cells. Reduction in stomatal conductance correlated with an accumulation of sodium and chloride in the leaves and depressed transpiration and water use. Reduction in water consumption of the stressed seedlings was attributed to lower transpiration rate per leaf and also to smaller total transpiring area per plant.

10. Examination of leaf sections by light microscopy suggested that an increase in cell size rather than cell number was responsible for the increased leaf thickness. Leaf succulence and thickness increased due to the development of larger cells in the spongy mesophyll in response to ion accumulation. Microscopic examination also showed a decrease in leaf intercellular space and the number of chloroplasts under NaCl stress. Leaf chlorophyll content decreased in salt-treated seedlings which agreed with microscopic observations. Chlorophyll reduction was mainly attributed to chloride accumulation in the leaves.

11. The split-root experiment demonstrated that citrus shoot growth did not correlate with the average osmotic potential of the 2 root

halves. It demonstrated also that citrus could withstand substantial amounts of stress as long as half of the root system was growing in a non-stressed environment.

12. Sodium chloride reduced calcium and magnesium contents but increased phosphorus content in the leaves. Sodium chloride decreased leaf potassium content only in sodium-accumulator rootstocks (SO, CM, RL, and ML).

13. This study showed that the beneficial effect of adding calcium to saline irrigation water depended on the anion accompanying the salt. Calcium sulfate but not calcium chloride was found to overcome the detrimental effects of NaCl by decreasing the concentrations of sodium and chloride in the leaves.

APPENDIX

Table 23. Shoot root ratio (g/g) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatments (-MPa)	Sour orange	Cleopatra mandarin	Swingle citrumelo	Carrizo citrange	Rough lemon	Milam	Poncirus trifoliata
NS control	2.27 a ^y	2.58 a	2.27 a	2.67 a	2.51 a	2.53 a	2.28 a
NaCl (0.10)	2.23 a	2.54 a	2.12 a	2.30 b	2.43 a	2.21 b	1.91 b
NaCl (0.20)	2.23 a	2.44 ab	2.14 a	2.19 b	2.37 a	2.16 b	1.90 b
NaCl (0.35)	2.19 a	2.28 b	1.77 b	1.85 c	1.88 b	1.67 c	1.23 c
PEG (0.10)	2.18 a	2.07 c	1.78 b	1.85 c	1.82 b	2.16 b	1.44 c
PEG (0.20)	1.86 b	1.78 d	1.52 c	1.76 c	1.55 c	1.62 c	1.44 c
PEG (0.35)	1.71 b	1.63 d	1.31 c	1.47 d	1.38 c	1.65 c	1.43 c

^z Mean of 4 plants.

^y Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 24. Total plant dry weight (g) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatment (-MPa)	Sour orange		Cleopatra mandarin		Swingle citrumelo		Carrizo citrange		Rough lemon		Milam		Poncirus trifoliata	
	Mean ^z	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%
NS control	30.2a ^y	0	30.7a	0	20.1a	0	24.5a	0	42.2a	0	34.3a	0	12.4a	0
NaCl (0.10)	25.0ab	17	24.9ab	19	14.4b	28	18.0b	27	29.7b	30	24.2b	30	8.4b	32
NaCl (0.20)	19.1b	37	21.7bc	29	11.3cd	44	13.2c	46	21.0de	50	16.1c	53	6.6cd	47
NaCl (0.35)	12.9de	57	13.0d	58	6.5e	68	7.0e	72	13.1f	69	6.9e	80	3.7e	70
PEG (0.10)	20.7b	31	18.5c	40	13.1bc	35	12.9c	47	24.6cd	42	17.4c	49	7.3bc	41
PEG (0.20)	14.6cd	51	13.7d	55	9.8d	51	9.5d	61	17.4ef	59	12.9d	62	6.3cd	49
PEG (0.35)	10.7e	65	11.5d	63	8.2de	59	8.3de	66	13.8f	67	11.4d	67	4.8de	61

^z Mean of 4 plants.

^y Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 25. Stem cross sectional area (cm²) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatment (-MPa)	Sour orange		Cleopatra mandarin		Swingle citrumelo		Carrizo citrange		Rough lemon		Milam		Poncirus trifoliata	
	Mean ^z	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%
NS control	0.35a ^y	0	0.33a	0	0.56a	0	0.42a	0	0.67a	0	0.59a	0	0.36a	0
NaCl (0.10)	0.29b	17	0.28b	15	0.42b	25	0.33b	21	0.48b	28	0.45b	24	0.27b	25
NaCl (0.20)	0.25c	29	0.22cd	33	0.29d	48	0.25c	41	0.33d	51	0.39c	34	0.22c	39
NaCl (0.35)	0.19d	46	0.16e	52	0.20f	64	0.17d	60	0.28e	58	0.21f	64	0.14e	61
PEG (0.10)	0.25c	29	0.22cd	33	0.36c	36	0.27c	36	0.40c	40	0.36c	39	0.25b	31
PEG (0.20)	0.18d	49	0.19d	42	0.25e	55	0.17d	60	0.26ef	61	0.30d	49	0.21c	42
PEG (0.35)	0.14e	60	0.15e	55	0.19f	66	0.13e	69	0.23f	66	0.25e	58	0.18de	50

^zMean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 26. Leaf magnesium content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.

Treatment	Sour orange	Cleopatra mandarin	Swingle citrumelo	Carrizo citrange	Rough lemon	Milam trifoliata	Poncirus trifoliata
NS control	0.27 a ^z	0.24 a	0.28 a	0.25 a	0.28 a	0.33 a	0.22 a
NaCl (0.10)	0.23 b	0.20 b	0.16 d	0.18 b	0.23 bc	0.22 d	0.12 c
NaCl (0.20)	0.19 c	0.15 d	0.16 d	0.18 b	0.19 e	0.23 cd	0.12 c
NaCl (0.35)	0.16 d	0.12 e	0.17 d	0.19 b	0.15 f	0.21 d	0.12 c
PEG (0.10)	0.21 bc	0.21 b	0.20 c	0.20 b	0.21 de	0.27 bc	0.13 bc
PEG (0.20)	0.23 b	0.18 c	0.21 c	0.19 b	0.22 cd	0.25 cd	0.13 bc
PEG (0.35)	0.25 a	0.17 c	0.23 b	0.20 b	0.24 b	0.30 ab	0.15 b

^z Mean of 4 plants.

^y Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 27. Leaf potassium content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.^z

Treatment	Sour		Cleoapatra		Swingle		Carrizo		Rough		Poncirus	
	orange	mandarin	citrumelo	citrange	lemon	Milam	trifoliata					
NS control	3.0 a ^y	3.1 a	2.4 a	2.5 a	3.0 a	3.1 a	2.6 a					
NaCl (0.10)	2.8 a	2.0 c	2.4 a	2.4 a	2.4 b	2.4 b	2.7 a					
NaCl (0.20)	2.5 b	1.5 d	2.4 a	2.5 a	2.1 c	2.1 cd	2.7 a					
NaCl (0.35)	2.2 c	1.5 d	2.3 a	2.5 a	2.0 c	2.0 d	2.6 a					
PEG (0.10)	2.0 cd	2.0 c	2.0 c	2.0 b	1.9 c	2.3 bc	1.9 b					
PEG (0.20)	1.8 d	2.2 b	2.1 bc	1.8 b	2.0 c	2.3 bc	1.8 b					
PEG (0.35)	1.8 d	1.9 c	2.1 bc	1.8 b	1.9 c	2.2 bc	1.8 b					

^z Mean of 4 plants.

^y Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 28. Leaf phosphorus content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.²

Treatment	Sour		Swingle		Carrizo		Rough		Poncirus	
	orange	mandarin	citrumelo	citrange	lemon	Milam	<u>trifoliata</u>			
NS control	0.09 ab ^y	0.08 c	0.10 de	0.15 b	0.08 c	0.09 d	0.21 a			
NaCl (0.10)	0.08 b	0.09 bc	0.09 e	0.17 a	0.10 b	0.11 cd	0.18 c			
NaCl (0.20)	0.08 b	0.12 a	0.12 c	0.17 a	0.11 b	0.13 bc	0.18 c			
NaCl (0.35)	0.09 ab	0.11 ab	0.14 ab	0.17 a	0.15 a	0.17 a	0.19 b			
PEG (0.10)	0.10 a	0.12 a	0.13 bc	0.15 b	0.14 a	0.11 cd	0.16 d			
PEG (0.20)	0.10 a	0.11 ab	0.13 bc	0.16 ab	0.15 a	0.14 b	0.15 d			
PEG (0.35)	0.10 a	0.11 ab	0.15 a	0.17 a	0.15 a	0.16 a	0.15 d			

²Mean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 29. Leaf zinc content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.^z

Treatment	Sour orange		Cleopatra mandarin		Swingle citrumelo		Carrizo citrange		Rough lemon		Poncirus trifoliata			
NS control	40	c ^y	49	c	59	c	52	b	59	b	76	c	93	bc
NaCl (0.10)	37	c	50	c	53	cd	49	bc	57	b	49	d	85	c
NaCl (0.20)	35	c	50	c	43	d	42	c	55	b	43	de	41	d
NaCl (0.35)	39	c	53	c	37	d	41	c	43	c	39	e	38	d
PEG (0.10)	76	a	127	a	150	b	91	a	96	a	140	a	145	a
PEG (0.20)	81	a	125	a	155	ab	83	a	104	a	123	ab	128	a
PEG (0.35)	62	b	75	b	170	a	86	a	92	a	114	ab	106	ab

^z Mean of 4 plants.

^y Mean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 30. Leaf manganese content (%) of seedlings of 7 rootstocks grown for 5 months under different NaCl and PEG concentrations--Experiment 1.^z

Treatment	Sour orange		Cleopatra mandarin		Swingle citrumelo		Carrizo citrange		Rough lemon		Poncirus trifoliata	
	13 d ^y	23 c	27 c	32 c	21 e	23 d	27 d	41 c	25 c	28 c	21 f	
NS control	13 d ^y	23 c	27 c	32 c	21 e	23 d	27 d	41 c	25 c	28 c	21 f	
NaCl (0.10)	20 c	27 c	27 c	32 c	20 e	27 d	27 d	41 c	25 c	29 c	42 e	
NaCl (0.20)	21 c	32 c	32 c	32 c	26 de	41 c	41 c	41 c	24 c	31 c	45 e	
NaCl (0.35)	24 c	28 c	28 c	28 c	36 de	44 c	44 c	44 c	25 c	38 c	65 d	
PEG (0.10)	72 a	115 a	115 a	115 a	173 a	93 b	93 b	93 b	72 a	102 b	165 a	
PEG (0.20)	69 a	112 a	112 a	112 a	150 b	108 a	108 a	108 a	76 a	120 a	105 b	
PEG (0.35)	49 b	55 b	55 b	55 b	85 c	94 b	94 b	94 b	58 b	91 b	73 c	

^zMean of 4 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 31. Seedling height (cm) of seedlings of 2 rootstocks grown for 6 months under different NaCl and PEG concentrations--Experiment 2.

Treatment (-MPa)	Sour orange		Cleopatra mandarin	
	Mean ^x	% lower than NS	Mean	% lower than NS
NS control	104 a ^y	0	106 a	0
NaCl (0.10)	64 b	39	79 b	26
NaCl (0.20)	52 c	50	71 c	33
NaCl (0.35)	48 cd	54	55 d	48
PEG (0.10)	60 b	42	63 c	41
PEG (0.20)	41 de	61	54 d	49
PEG (0.35)	38 e	64	43 e	59

^xMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 32. Total leaf area (cm²) of seedlings of 2 rootstocks grown for 6 months under different NaCl and PEG concentrations--Experiment 2.

Treatment (-MPa)	<u>Sour orange</u>		<u>Cleopatra mandarin</u>	
	Mean ^z	% lower than NS	Mean	% lower than NS
NS control	3595 a ^y	0	3601 a	0
NaCl (0.10)	2002 b	44	1782 b	51
NaCl (0.20)	1381 c	62	1421 bc	61
NaCl (0.35)	881 d	76	725 de	80
PEG (0.10)	1019 cd	72	913 cd	75
PEG (0.20)	431 e	88	498 de	86
PEG (0.35)	213 e	94	294 e	92

^zMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

Table 33. Specific leaf weight (mg/cm²) of seedlings of 2 rootstocks grown for 6 months under different NaCl and PEG concentrations--Experiment 2.^z

Treatment	<u>Sour orange</u>		<u>Cleopatra mandarin</u>	
	Fresh wt	Dry wt	Fresh wt	Dry wt
	basis	basis	basis	basis
NS control	25.1 a ^y	9.0 b	18.7 b	8.3 c
NaCl (0.10)	27.5 a	9.5 b	18.9 b	8.4 c
NaCl (0.20)	27.9 a	9.6 b	19.1 b	8.5 c
NaCl (0.35)	28.2 a	9.6 b	21.1 a	8.7 c
PEG (0.10)	18.2 b	11.2 a	18.3 b	10.1 b
PEG (0.20)	17.4 bc	11.5 a	18.2 b	12.1 a
PEG (0.35)	14.4 c	11.3 a	18.1 b	11.9 a

^zMean of 7 plants.

^yMean separation within columns by Duncan's Multiple Range Test, 0.05 level.

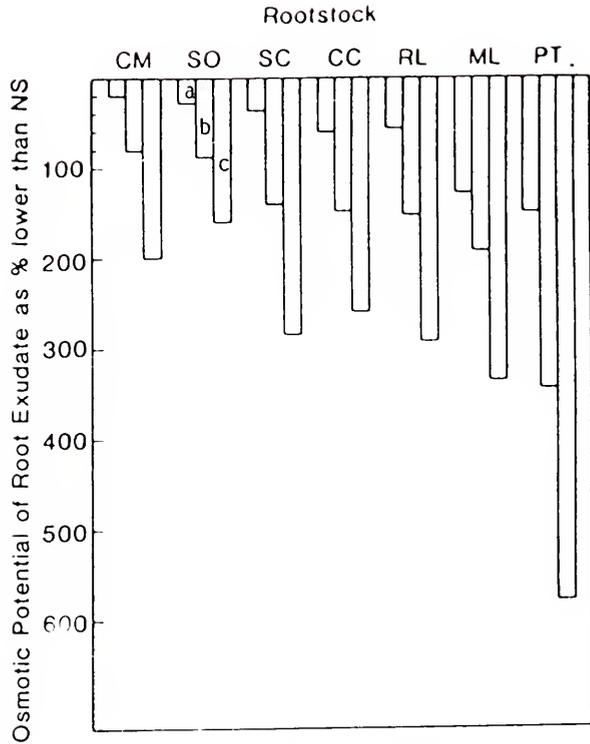


Fig. 20. Effect of 3 NaCl concentrations (a = -0.10 MPa, b = -0.20 MPa, c = -0.35 MPa) on the osmotic potential of root exudate collected from seedlings of 7 citrus rootstocks.

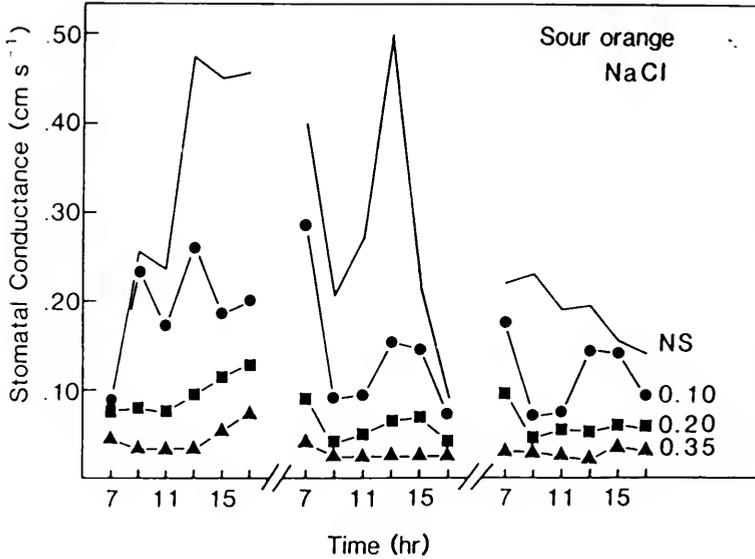


Fig. 21. Relationship of time of day to stomatal conductance of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl during 3 consecutive days. Measurements were started on April 9, 1986.

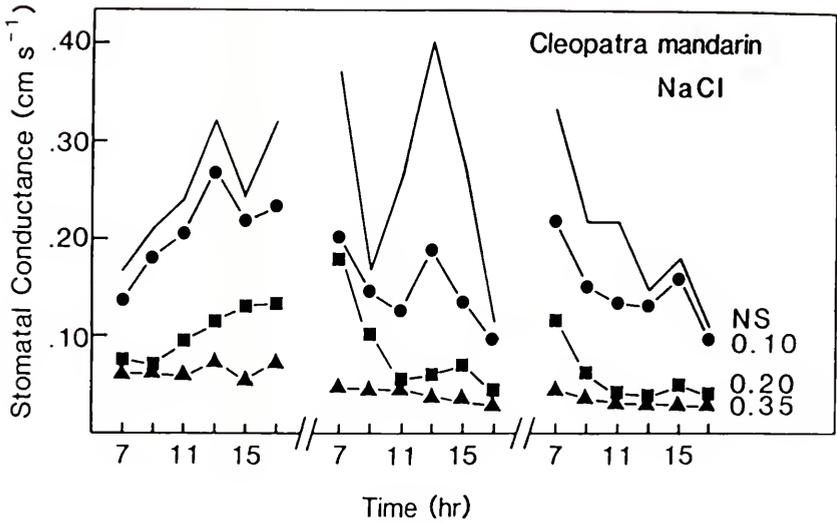


Fig. 22. Relationship of time of day to stomatal conductance of Cleopatra mandarin seedlings irrigated with nutrient solution containing no salt (NS) or with added NaCl during 3 consecutive days. Measurements were started on April 9, 1986.

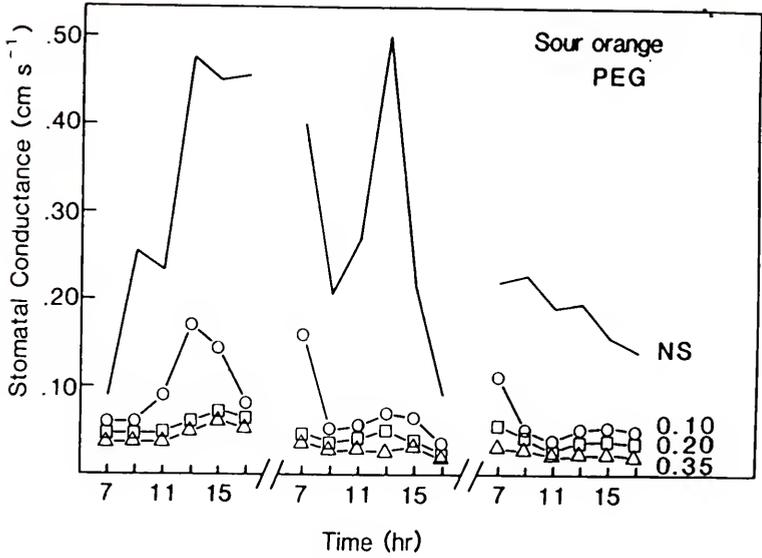


Fig. 23. Relationship of time of day to stomatal conductance of sour orange seedlings irrigated with nutrient solution containing no salt (NS) or with added PEG during 3 consecutive days. Measurements were started on April 9, 1986.

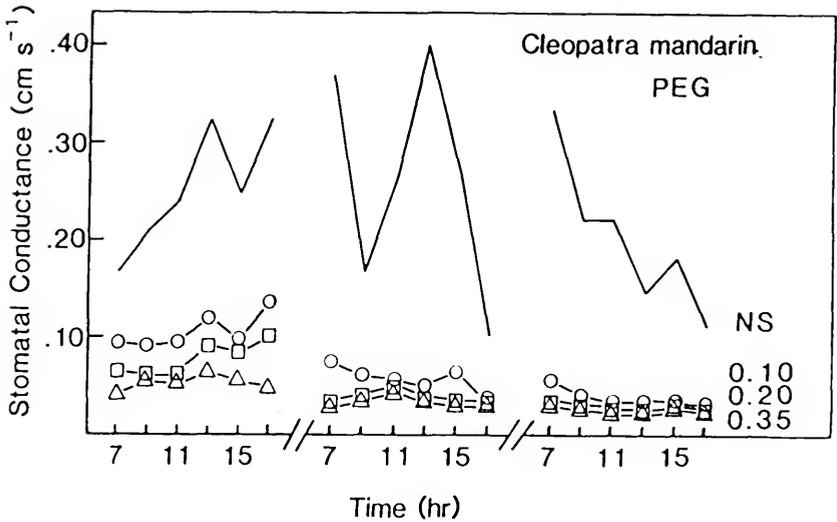


Fig. 24. Relationship of time of day to stomatal conductance of Cleopatra mandarin seedlings irrigated with nutrient solution containing no salt (NS) or with added PEG during 3 consecutive days. Measurements were started on April 9, 1986.

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BIOGRAPHICAL SKETCH

Mongi Zekri was born in Kerkennah, Tunisia, on December 3, 1955. He received his secondary education and graduated from Chott-Mariem High School, Sousse, in June 1972. He obtained the diplome of Baccalaureat of Science in September 1972.

He entered the National Institute of Agronomy in Tunis in October 1972 and graduated with the degree of Bachelor of Engineering in June 1976. Upon graduation, he was employed by the Office of Cereals under the Ministry of Agriculture as an inspector and a researcher on wheat for two and a half years. He served in the Army from March 1977 to March 1978 and obtained the rank of lieutenant in August 1977.

He was awarded a scholarship to pursue graduate studies in the United States. He attended the Intensive English Program in the spring and summer of 1980 at the University of Missouri-Columbia. In the fall of 1980, he enrolled at the University of Florida as a graduate student in the Fruit Crops Department and earned the degree of Master of Science in April 1984.

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He is married to the former Leila Atia. They have one daughter, Dhoha.

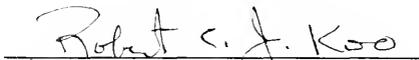
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Lawrence R. Parsons, Chairman
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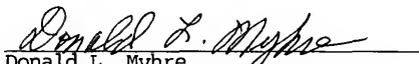
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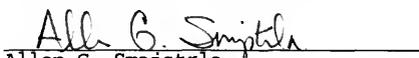
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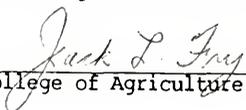

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