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Relationship Between Chloride and Nitrate and Its Effect on Growth and Mineral Composition of Avocado and Citrus Plants

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ABSTRACT

Two rootstocks of avocado (*Persea americana* Mill.), the salt-tolerant 'Degania-113' and the salt-sensitive 'Smith', and two rootstocks of citrus, the salt-tolerant 'Cleopatra' mandarin (*Citrus reshni* Hort. ex Tan) and the salt-sensitive 'Troyer' citrange (*Poncirus trifoliata x Citrus sinensis* [L.] Osbeck), were grown in a sandy soil and irrigated daily with nutrient solutions containing various chloride concentrations. Increasing the concentration of chloride resulted in elevated chloride levels in all avocado plant parts, and toxic symptoms that were more pronounced in the 'Smith' than in the 'Degania-113' avocado rootstock. When leaves of both rootstocks had accumulated similar chloride levels and showed scorching damage, the leaves of 'Degania-113' abscised, while those of 'Smith' did not. High chloride reduced the total dry matter yield of the root more than that of the shoot, decreasing the "root: shoot" dry weight ratio in both rootstocks. Addition of nitrate to the irrigation water reduced chloride accumulation in the plant and alleviated its adverse effects. Accumulation of nitrogen in the plant exceeded that of chloride in all cases. High nitrate reduced phosphorus levels in the plant and caused chlorosis in young leaves. High chloride partially reversed this effect. Citrus rootstocks responded similarly, but leaves of the chloride-sensitive 'Troyer' accumulated more chloride than 'Cleopatra'. High chloride resulted in scorching damage in the leaves and branches of 'Troyer', but not in 'Cleopatra'. Nitrate reduced chloride accumulation and toxic symptoms as well as boron levels in the leaves. The results of this study suggests that water containing high chloride levels may be used to irrigate avocado and citrus orchards, provided that nitrate is supplied continuously at a molar concentration equivalent to half that of chloride. Our results also suggest that a nitrate supplement applied to citrus will reduce the undesirable uptake of boron. The difference in mode of resistance to chloride between avocado and citrus rootstocks is discussed.

INTRODUCTION

Avocado is known to be the most salt-sensitive of the cultivated fruit trees. Salt damage in avocado orchards has been reported in California (Branson and Gustafson, 1972), Texas (Cooper, 1948), Australia (Downton, 1978), and Israel (Ben-Yaacov, 1976). Chloride concentrations in the irrigation water which are considered tolerable for many crops are detrimental to avocado. Foliar accumulation of chloride induces necrosis, early leaf shedding, and decreased yield (Bingham et al., 1968). The Mexican avocado race is considered to be the most salt-sensitive and the West Indian is relatively salt-tolerant (Ben-Yaacov, 1976).

Generally, citrus trees are also salt-sensitive (Zekri, 1993). Large quantities of chloride have been found to accumulate in their leaves and in the juice of fruit from trees irrigated with water containing high chloride concentrations (Syvertsen et al., 1993). Citrus trees are also very sensitive to high boron (Chapman, 1986) which poses a serious problem in areas affected by salinity (Peynado and Sluis, 1979).

Increased nitrogen nutrition has been shown to decrease chloride toxicity in avocado (Embleton et al., 1958; Haas, 1929; Haas and Bruska, 1955) and citrus (Lips et al., 1990). Competition between chloride and nitrate uptake has also been observed in other species (Kafkafi, 1984). Chloride uptake and its toxicity has been found to be reduced by increasing the nitrate concentration of the nutrient solution for tomatoes (Kafkafi et al., 1982), melon, lettuce (Feigin, 1985), wheat (Soliman et al., 1994), and strawberry (Awang and Atherton, 1994).

The need to devise practical methods for the optimal irrigation of avocado and citrus orchards in arid regions, where chloride concentrations in the water are high, led us to study the quantitative relationship between chloride and nitrate and their effects on the growth and mineral uptake in young plants of salt-tolerant and salt-sensitive avocado and citrus rootstocks.

MATERIALS AND METHODS

Avocado Plants

One-year-old avocado plants of two rootstocks, 'Degania-113' (West Indian, relatively salt-resistant) and 'Smith' (Mexican salt-sensitive), were grown in 10-liter containers filled with a sandy soil. The field capacity of the soil was determined and the plants were irrigated with 40% excess of the water required to reach field capacity, and at a frequency that did not allow more than 25 to 30% water loss by evapotranspiration. The plants were placed under a 40% shade net. The minimum temperatures during the experimental period ranged between 15 and 20°C and the maximum temperatures between 25 and 30°C. The minimum relative humidity ranged between 40 and 50% and the maximum between 75 and 95%. Plants were irrigated for 126 days with solutions containing 2, 4, 8, or 16 mM chloride. Each chloride concentration was combined with 2, 8, or 16 mM nitrate, resulting in a total of 12 treatments. Half of the treatments were conducted with iso-osmotic nutrient solutions with reciprocal chloride:nitrate molar concentrations of 16:2 and 2:16, 8:2 and 2:8, and 16:8 and 8:16. This experimental design enabled separation of the osmotic effects from the specific anion effects. To isolate the chloride anion effects, sodium was excluded from the nutrient solutions. The only source of sodium was tap water, which contained 0.81±0.09 mM sodium and had an EC of 0.830±0.05 $dS{\cdot}m^{-1}$. The tap water also contained 0.19±0.07 mM nitrate and 0.98±0.04 mM chloride. The relevant chloride and nitrate concentrations were obtained with chloride and nitrate salts of magnesium, calcium, and potassium, at a charge equivalent ratio of 1:5:3, respectively. All solutions also contained 0.6 mM potassium dihydrogen phosphate, 0.2 mM magnesium sulfate, 1 mM calcium sulfate, and a commercial mix of chelated micro elements. The chloride content of the tap water was taken into account during preparation of the nutrient solutions. Each treatment was applied to eight plants of each rootstock. Four of them were sampled on day 57, and the other four 126 days after the beginning of the treatments. For growth evaluation and mineral analysis, each plant was separated into leaves, roots, cotyledons, and lower (10 cm) and upper stems. The stem bark was separated from the wood so that four different stem samples were analyzed.

Citrus Plants

One-year-old plants on two different citrus rootstocks, the salt-tolerant 'Cleopatra' mandarin and the salt-sensitive 'Troyer' citrange, were grown in a greenhouse in 8-liter containers filled with a sandy soil. The minimum temperatures during the experimental period ranged between 18 and 23°C and the maximum temperatures between 27 and 33°C. The minimum relative humidity ranged between 40 and 50% and the maximum between 75 and 95%. The field capacity of the soil was determined and the plants were irrigated with 40% excess of the water required to reach field capacity, at a frequency that did not allow more than 25 to 30% water loss by evapotranspiration. The plants were irrigated for three months with nutrient solutions containing 2, 16, or 48 mM chloride. Each chloride concentration was supplemented with 2, 8, or 16 mM nitrate, resulting in a total of nine treatments. The nutrient solutions were prepared as in the avocado experiment, except that 10% of the nitrogen in the nutrient solution was supplied as ammonium to prevent high pH near the root.

Mineral Analysis

The various collected plant parts were oven dried for 48 h at 70°C, weighed, ground, and the nitrogen, phosphorus, calcium, and sodium were determined following wet digestion with sulfuric acid and hydrogen peroxide. Nitrogen was determined by colorimetry using the Nessler's reagent and sodium by flame photometry. Phosphorus was determined colorimetrically with ammonium molybdate after reduction with ascorbic acid. Calcium was determined by atomic absorption spectrophotometry. Chloride was extracted with 0.1N nitric acid and determined using a chloridometer.

TABLE 1. Effects of chloride and nitrate concentrations in the irrigation water on chloride levels and scorching in leaves of young plants of 'Degania-113' (West Indian) and 'Smith' (Mexican). Data are means of four replicates ±SE for chloride.

Cl : NO_3 (mM)	Cl^- ($g \cdot 100gDM^{-1}$)		Leaf scorching[z]	
	'Degania'	'Smith'	'Degania'	'Smith'
2 : 2	1.14 ±0.17	0.85 ±0.11	0.50	1.00
2 : 8	0.71 ±0.05	0.41 ±0.08	0.50	1.25
2 : 16	0.43 ±0.05	0.45 ±0.09	0.38	1.50
4 : 2	1.75 ±0.34	1.23 ±0.15	1.25	2.75
4 : 8	0.44 ±0.08	0.84 ±0.11	0.50	2.00
4 : 16	0.43 ±0.05	0.55 ±0.05	0.50	1.50
8 : 2	1.71 ±0.17	1.37 ±0.17	2.00	3.25
8 : 8	1.06 ±0.13	1.03 ±0.09	1.25	2.75
8 : 16	0.66 ±0.09	0.73 ±0.07	1.00	2.00
16 : 2	2.64 ±0.17	2.31 ±0.19	2.75	4.75
16 : 8	2.39 ±0.16	2.02 ±0.23	2.25	4.50
16 : 16	1.26 ±0.26	1.02 ±0.08	1.50	3.00

[z] Leaf scorching was evaluated on a scale of values ranging from 0 (no scorching) to 5 (severe scorching).

RESULTS

Effects of Chloride on Avocado Plants

Increasing the chloride concentration in the nutrient solution containing 2 mM nitrate resulted in an increase in chloride levels in the leaves (Table 1), roots, cotyledons, bark and wood of both rootstocks (not shown). The chloride levels in the leaves of the salt-tolerant 'Degania-113' plants were in most cases slightly higher than those in the salt-sensitive 'Smith'. Increasing the chloride level resulted in leaf scorching which was more pronounced in the 'Smith' than in 'Degania-113' plants (Table 1). The two rootstocks differed in their abscission response to high chloride. Leaves of 'Smith' did not abscise, even when almost entirely scorched. In contrast, leaves of 'Degania-113' abscised even when only one-third of the leaf area had been scorched. The increase in chloride content in the plants was associated with a decrease in dry matter yield of the whole plant (Table 2). However, the dry matter yield of 'Degania-113' plants was in all cases higher than that of 'Smith' (Table 2). The dry weight of the root system in both rootstocks was decreased to a greater extent than that of the shoots in plants irrigated with solutions containing 2 mM nitrate, while increasing the chloride concentrations from 2 to 16 mM decreased the dry weight of the roots in both rootstocks by about 70%. This resulted in a 60% decrease in the root:shoot dry weight ratio (Table 2). Increasing the concentration of chloride had no effect on the leaf content of nitrogen (Table 3), phosphorus, or calcium (not shown).

Effects of Nitrate Supplement on Avocado Plants

An eight-fold increase in nitrate concentration in the irrigation water (from 2 to 16 mM) resulted in an increase of only 20 to 30% in the level of nitrogen in the leaves of both rootstocks, but resulted in an increase of two to four-fold in the level of nitrogen in the wood tissue (Table 3). Increasing the nitrate concentration in the nutrient solution led to a decrease in the chloride level in the leaves (Table 1), roots, cotyledons, bark, and wood of both rootstocks (not shown). Addition of 2 to 16 mM nitrate to the solutions reduced chloride levels in the leaves of 'Degania-113' by 53-76% and in 'Smith' by 47-56% (Table 1), and consequently reduced the severity of damage and growth inhibition (Table 2). When the nitrate concentration in solution containing 16 mM chloride was increased from 2 to 16 mM, the dry matter yield of the whole plant significantly increased (Table 2).

Addition of nitrate to the solutions containing 2 or 4 mM chloride reduced root growth by 40% in 'Degania-113', whereas shoot growth increased slightly, resulting in a decreased value of the "root:shoot" dry weight ratio. Plants of both rootstocks irrigated with iso-osmotic solutions, composed of reciprocal molar concentrations of chloride:nitrate of 16:2 and 2:16, 8:2 and 2:8, 16:8 and 8:16, showed reduced dry matter yield (Table 2) and/or displayed severe leaf scorching (Table 1) only when chloride was the dominant anion.

TABLE 2. Effects of chloride and nitrate concentrations in the irrigation water on the total dry weight and the ratio of "root dry weight:shoot dry weight" (R:S) of young plants of 'Degania-113' (West Indian) and 'Smith' (Mexican). Data are means of four replicates ±SE for the total dry plant weight.

Cl : NO_3 (mM)	DRY PLANT WEIGHT (grams)		R : S ratio	
	'Degania'	'Smith'	'Degania'	'Smith'
2 : 2	130 ±3.6	63 ±5.4	0.34	0.34
2 : 8	134 ±6.9	69 ±6.0	0.29	0.38
2 : 16	121 ±7.6	72 ±9.0	0.22	0.34
4 : 2	131 ±8.2	63 ±7.1	0.39	0.28
4 : 8	130 ±6.4	72 ±2.9	0.27	0.24
4 : 16	117 ±6.0	74 ±7.2	0.22	0.23
8 : 2	130 ±5.6	56 ±3.0	0.18	0.20
8 : 8	127 ±8.4	61 ±2.9	0.18	0.24
8 : 16	115 ±9.2	68 ±5.0	0.20	0.22
16 : 2	76 ±7.4	39 ±9.0	0.19	0.15
16 : 8	95 ±4.2	47 ±7.6	0.17	0.18
16 : 16	104 ±8.0	70 ±6.3	0.17	0.18

TABLE 3. Effects of chloride and nitrate concentrations in the irrigation water on nitrogen levels in leaves and wood of young plants of 'Degania-113' (West Indian) and 'Smith' (Mexican). Data are means of four replicates ±SE.

Cl : NO_3 (mM)	Nitrogen in leaves ($g \cdot 100gDM^{-1}$)		Nitrogen in wood ($g \cdot 100gDM^{-1}$)	
	'Degania'	'Smith'	'Degania'	'Smith'
2 : 2	1.82 ±0.03	2.28 ±0.28	0.27 ±0.03	0.35 ±0.04
2 : 8	2.30 ±0.03	2.16 ±0.08	0.64 ±0.08	0.63 ±0.09
2 : 16	2.38 ±0.13	2.57 ±0.10	1.13 ±0.19	1.11 ±0.10
4 : 2	1.81 ±0.03	1.91 ±0.19	0.31 ±0.02	0.32 ±0.01
4 : 8	2.40 ±0.08	2.31 ±0.21	0.61 ±0.08	0.63 ±0.04
4 : 16	2.61 ±0.20	2.35 ±0.19	0.91 ±0.13	1.13 ±0.15
8 : 2	2.00 ±0.07	2.19 ±0.10	0.64 ±0.11	0.53 ±0.06
8 : 8	2.40 ±0.07	2.39 ±0.11	0.90 ±0.07	0.70 ±0.08
8 : 16	2.57 ±0.12	2.36 ±0.10	0.95 ±0.09	0.96 ±0.06
16 : 2	1.82 ±0.16	2.17 ±0.22	0.64 ±0.12	0.53 ±0.06
16 : 8	2.11 ±0.07	2.42 ±0.05	0.74 ±0.02	0.72 ±0.09
16 : 16	2.38 ±0.05	2.62 ±0.08	1.25 ±0.10	1.01 ±0.11

The ratio of chloride to nitrate uptake by the plants of both rootstocks showed a positive linear relationship to the ratio of chloride to nitrate in the nutrient solutions, within the anion ratio range of 0.125 to 2.0 (Figure 1). The only case where the uptake ratio was similar to the ratio in the nutrient solution was in the solution composed of 2 mM chloride and 16 mM nitrate (0.125 ratio). Increasing the anion ratio in the solution from 2 to 8 led to a disproportionate increase in uptake of nitrate over chloride. Even though the chloride concentration was eight-fold higher than that of nitrate, the ratio of chloride:nitrate taken up by the plant was less than 1 (Figure 1).

A decrease in phosphorus level was found in all plant parts of both rootstocks as a response to increased nitrate concentration in the nutrient solution (Figure 2). The calcium content of 'Degania-113' leaves was higher than that of 'Smith' in all the treatments with an average of 1.89% and 1.47% in dry matter, respectively (not shown).

As indicated earlier, the only source of sodium in the nutrient solution was the tap water which contained about 0.8 mM sodium. Sodium was found to accumulate mainly in the lower plant parts of both rootstocks (not shown). The distribution

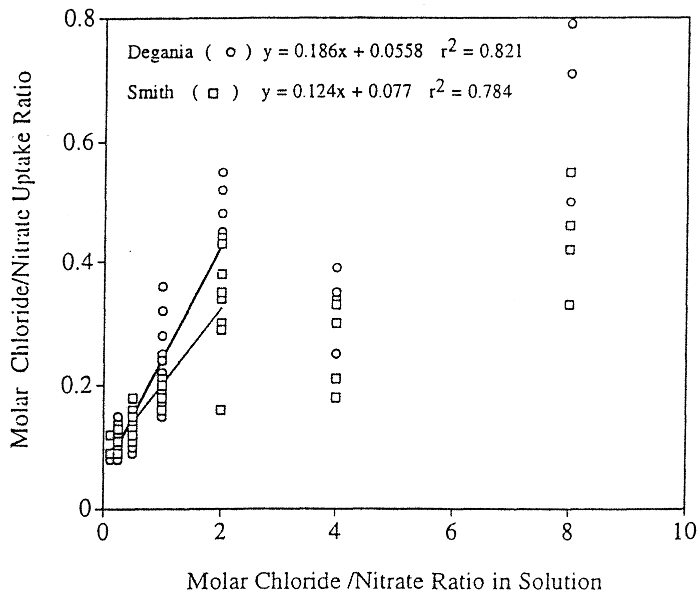

FIGURE 1. Influence of the chloride:nitrate ratio in the nutrient solution on the molar ration of Cl:N uptake in 'Degania-113' and 'Smith' plants after 126 days of treatment. Each point represents one replicate.

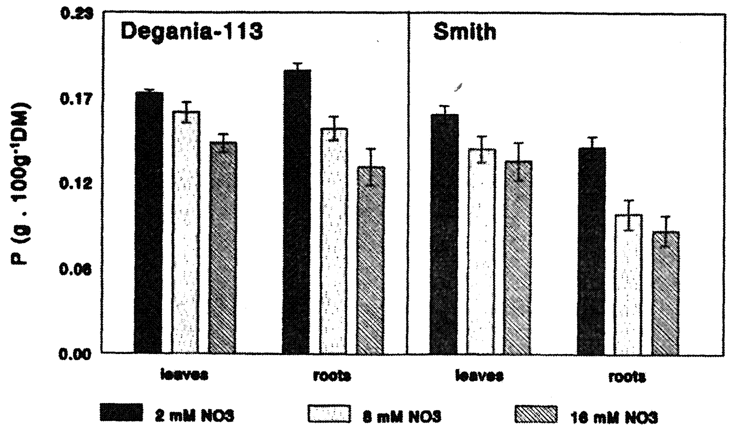

FIGURE 2. Effect of nitrate supplementation of irrigation water on the phosphorus content of leaves and roots of 'Degania-113' and 'Smith' after 126 days of treatment. Data are means ±SE of 16 replicates.

of sodium in 'Degania-113' differed from that in 'Smith'. At the end of the experiment, 69% of the sodium was found in the roots of 'Degania-113' and 52% in the roots of 'Smith'. This is especially striking in light of the fact that in both rootstocks, the roots comprise only about 20% of the total plant dry matter. Only 7.4% of the total sodium taken up by 'Degania-113' and 17.4% taken up by 'Smith' reached the leaves, although leaves comprise about 41% of the total plant dry plant matter (not shown).

Effect of Chloride on Citrus Plants

Irrigation of 'Cleopatra' and 'Troyer' plants for 90 days with water containing increasing concentrations of chloride resulted in increasing chloride contents in the leaves (Figure 3). When irrigated with water containing only 2 mM chloride, which is considered prime irrigation water, the chloride content of 'Troyer' leaves was four-fold higher than that of 'Cleopatra' irrigated with the same solution. When the irrigation water contained 16 mM chloride, the chloride content of 'Troyer' leaves was seven-fold higher than that of 'Cleopatra' (Figure 3).

High concentrations of chloride in the water inhibited branch growth in 'Troyer' more than in 'Cleopatra' (Figure 4). Leaves and branches of 'Troyer' displayed severe damage as a response to increased chloride concentrations in the water (Figure 4), but no damage was detected in 'Cleopatra' leaves, even at 48 mM chloride, except for some slight yellowing.

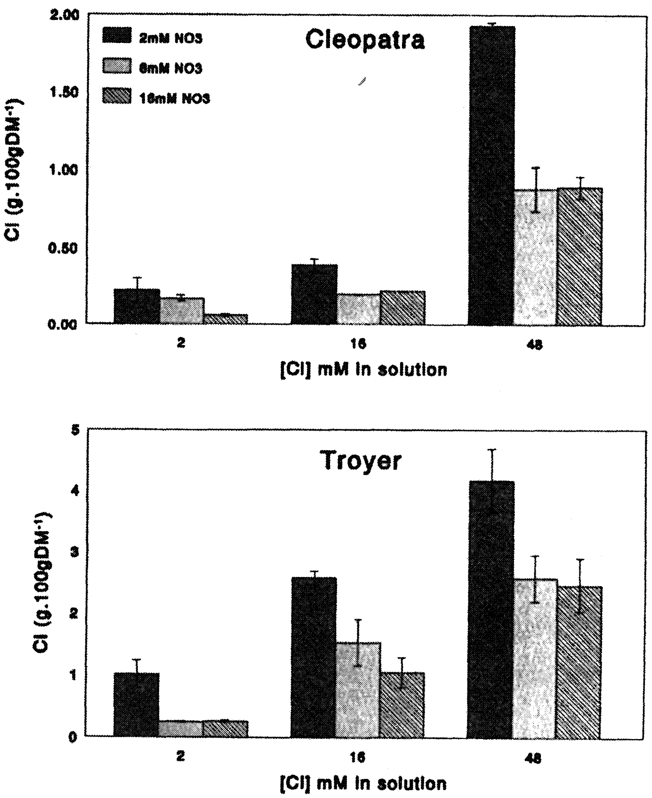

FIGURE 3. Effect of nitrate supplementation of irrigation water on the chloride content of leave of 'Cleopatra' and 'Troyer' plants irrigated with water containing increasing concentrations of chloride. Note the different scales of the y axis in the two figures. Data are means ±SE of three replicates.

Effect of Nitrate Supplement on Citrus Plants

Addition of 8 or 16 mM nitrate to the irrigation water containing 2, 16, or 48 mM chloride resulted in decreased chloride contents in the leaves of both 'Troyer' and 'Cleopatra' plants (Figure 3). This effect was already noticeable at the lower chloride concentration in 'Troyer', but only at the higher chloride concentration in 'Cleopatra'. The severity of damage to 'Troyer' leaves and branches was decreased with the addition of nitrate to the irrigation waters containing either 16 or 48 mM chloride (Figure 4). Addition of 8 mM nitrate to water containing 16 mM chloride slightly enhanced branch growth in 'Cleopatra' (Figure 4). However,

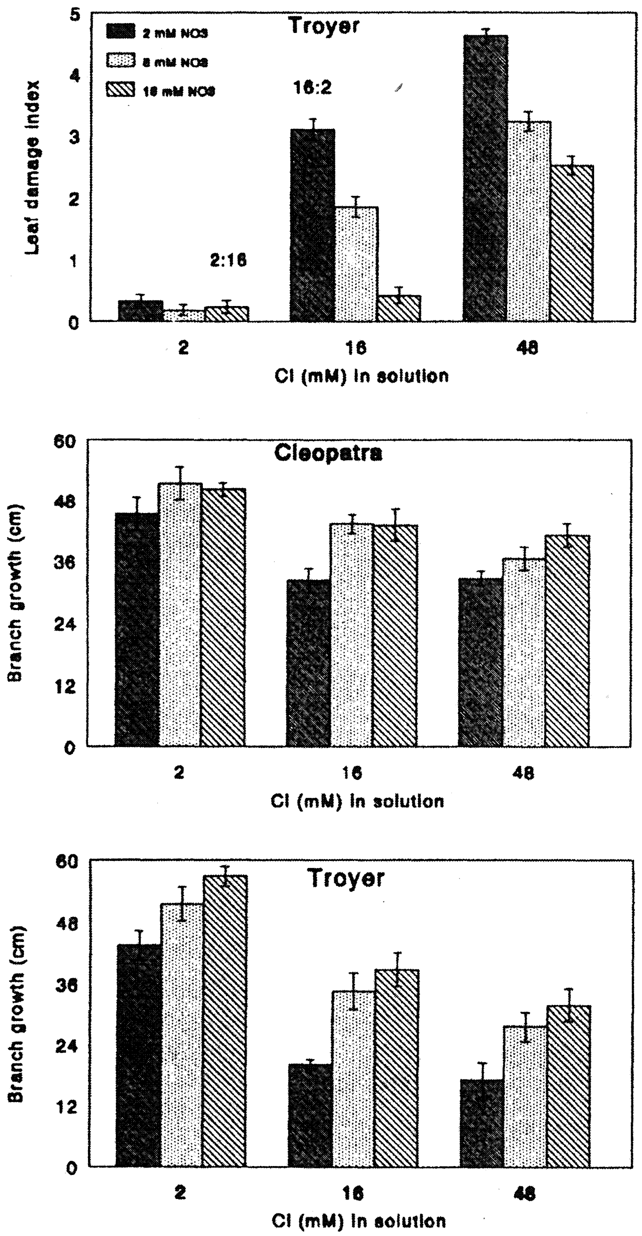

FIGURE 4. Effect of nitrate supplementation of irrigation water on shoot damage in 'Troyer' plants irrigated with water containing increasing concentrations of chloride. Visual symptoms of shoot damage were evaluated on a scale of values ranging from 0 (no damage) to 5 (severe damage, including leaf scorching and branch-tip burning). Data are means ±SE of 18 replicates. The values 2:16 and 16:2 on top of bars refer to the reciprocal molar concentrations of chloride:nitrate in two iso-osmotic treatments.

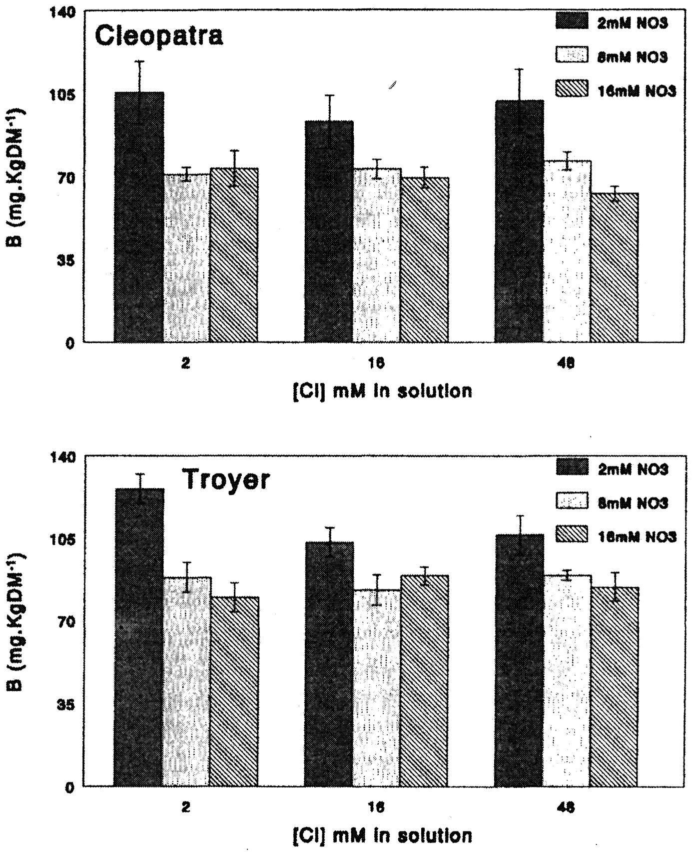

FIGURE 5. Effect of nitrate supplementation of irrigation water on the boron content of leaves of 'Cleopatra' and 'Troyer' plants irrigated with water containing increasing concentrations of chloride. Data are means ±SE of three replicates.

the chloride-induced inhibition of growth of 'Troyer' branches was strikingly reversed by the addition of 8 mM nitrate to water containing 2, 16, or 48 mM chloride (Figure 4). A further increase in nitrate concentration had no significant effect.

Increasing the nitrate concentration in the water from 2 to 16 mM resulted in decreased boron levels in the leaves of both citrus rootstocks (Figure 5). Signs of chlorosis were apparent in leaves of 'Troyer' plants irrigated with water containing a high nitrate concentration (16 mM).

DISCUSSION

Since chloride is the ion responsible for the immediate adverse effects of saline water used for crop irrigation, we attempted to isolate and characterize the effect of the chloride anion in saline water on avocado and citrus plant growth and mineral composition. We, therefore, excluded the sodium cation from the nutrient solutions.

An increase in chloride levels in the plant tissues and damage in response to increased chloride concentrations in the irrigation water have been demonstrated in avocado (Bingham et al., 1968) and citrus (Zekri, 1993). Similar responses were obtained in this study using 'Degania-113' as a representative of the West Indian salt-tolerant avocado rootstocks and 'Smith' as a representative of the salt-sensitive Mexican rootstocks. However, in contrast to other previously reported findings (Kadman and Ben-Yaacov, 1970), we observed that chloride levels in the leaves of 'Degania-113' were higher than in 'Smith'. We also found that the leaf tissue of 'Degania-113' is more tolerant than that of 'Smith' to high chloride. In addition, the two rootstocks responded differently to high chloride with respect to abscission behavior: The salt-tolerant 'Degania-113' plants shed their leaves when the chloride content exceeded a certain level, whereas the salt-sensitive 'Smith' did not. Thus, leaf shedding in 'Degania-113' may be a mode of adaptation to high chloride. The higher rate of growth in 'Degania-113' than in 'Smith' enables it to rapidly replace the old chloride-loaded leaves with a new flush. Therefore, the chloride tolerance of 'Degania-113' plants is not due to reduced chloride accumulation in the leaves, but rather stems from three other properties, the ability of its leaf tissue to withstand high chloride levels, the capacity to shed its chloride-loaded leaves prematurely, and its higher growth rate, which enables accelerated growth after leaf shedding. Our results show that chloride lowered the "root:shoot" dry weight ratio of both rootstocks by reducing root growth to a greater extent than that of the shoot. These findings are in agreement with those in other species (Kuiper et al., 1989). The enhancement of shoot growth by irrigation water containing 8 mM chloride is probably a result of reduced root growth which lowers root demand for carbohydrates, and thus allows a more abundant supply to the shoot. The nitrate-induced inhibition of root growth in 'Degania-113' irrigated with lower chloride concentrations could result from the nitrogen-enhanced shoot growth favoring translocation of carbohydrates to the shoot. This explanation was suggested by Brouwer (1983) who coined the term "functional equilibrium" to describe the phenomenon of mutual influence of two organs via nutrient supply.

Our results showed that nitrogen levels in the wood tissue of avocado plants correlated better than nitrogen levels in the leaves with nitrate concentrations in the water. This is in line with our earlier findings suggesting that the avocado wood tissue serves as a reservoir for nitrogen in the tree (Lahav et al., 1990).

Nitrogen analysis of wood tissues could, therefore, supply the information obtained from leaf analysis with regard to the nitrogen status of the avocado tree.

The results of our study confirm the observations of others (Embleton et al., 1958; Haas and Bruska, 1955) that under low nitrate nutrition, chloride levels in avocado trees are higher than in trees grown under ample nitrate conditions. In an early study, Bingham et al. (1968) were puzzled by the fact that increasing the chloride concentration in the nutrient solutions caused "a disproportionately greater chloride uptake" and consequent injury. Our findings can explain their result as follows: while keeping a fixed total molar concentration they increased the chloride level at the expense of nitrate, creating relatively low nitrate conditions resulting in a disproportionately accelerated chloride uptake and accumulation.

We showed that increasing the nitrate concentration in solutions containing 16 mM chloride increased the dry matter yield which may create a "dilution effect". Under these conditions, however, chloride uptake almost ceased. We suggest, therefore, that in this case, the reduction of chloride levels by nitrate cannot be explained merely by a chloride "dilution effect", but involves inhibition of chloride uptake.

In our study, plants preferentially took up nitrate from the nutrient solution. Chloride and nitrate anions are taken up by the roots against the electrochemical gradient (Runge, 1983). Nitrate is reduced after uptake, whereas chloride maintains its negative charge. The active uptake of chloride is reduced as the chloride electrochemical potential gradient builds up during its accumulation (Cram, 1973). Thus, the chloride:nitrate ratio in the plant is always higher than that in the nutrient solution, resulting in a preference for nitrate uptake over chloride. In addition, high nitrate concentrations in the water may inhibit chloride uptake due to an allosteric influence of nitrate on chloride uptake sites (Cram, 1973) further reducing chloride accumulation by the plant.

The rate of calcium translocation to leaves in the salt-tolerant 'Degania-113' was higher than in the salt-sensitive rootstock. This is in line with findings of Embleton et al. (1962) in avocado and of Gorton and Cooper (1954) in citrus. This characteristic can be linked to the capacity of salt-tolerant plants to accumulate sodium in their roots and lower organs. Accumulation of sodium in the roots allows more calcium to reach the leaves. It might be possible to use those characteristics of salt-tolerant rootstocks as indicators for rapid primary screening of rootstock tolerance to salinity.

In an earlier study, we showed that high nitrate concentrations caused a decrease in iron uptake and translocation (Bar and Kafkafi, 1992). The present study demonstrates reduced phosphorus uptake as well, which is in line with, previous observations (Kafkafi, 1990). The decrease in phosphorus levels can be attributed to the nitrate-induced enhancement of growth which may "dilute" the phosphorus in the plant (Martin-Prevel et al., 1987). In addition, high pH of the rhizosphere, caused by enhanced nitrate uptake, increases the content of monohydrogen phosphate in the soil solution relative to the more available dihydrogen phosphate (Mengel and Kirkby, 1987). Phosphorus deficiency was not observed in our study, even at very high nitrate levels, because of the ample supply of phosphate in the nutrient solutions. Nevertheless, under field conditions, mainly in sandy soils, phosphorus and micro-element deficiencies may develop as a result of high nitrate nutrition.

In the chloride-sensitive citrus rootstock, inhibition of branch growth and scorching of leaves and branch tips were apparent even at 2 mM chloride, which is considered good quality water. In contrast, the salt-tolerant 'Cleopatra' showed some growth inhibition only at the higher chloride concentrations and slight yellowing only at 48 mM chloride. The mode of resistance to chloride in citrus differs from that in avocado. Leaves of 'Cleopatra' plants accumulated much less chloride than those of 'Troyer' plants irrigated with water containing the same concentration of chloride. Furthermore, no injuries were observed in 'Cleopatra' leaves, even when their leaf chloride level was two-fold higher than that found in severely scorched 'Troyer' leaves. Thus, chloride resistance in 'Cleopatra' may be attributed to both its ability to restrict chloride uptake and transport to the leaves and the ability of its leaf tissue to withstand high chloride concentrations.

Addition of nitrate to irrigation water containing high chloride concentrations resulted in decreased chloride levels in citrus leaves, and might therefore accounted for the alleviation of the chloride-induced toxic effects. Citrus trees are known to be very sensitive to high boron levels in the soil (Chapman, 1986; Peynado and Sluis, 1979). It might, therefore, be possible to use the nitrate-induced reduction of boron uptake in order to reduce the detrimental effects of boron in citrus orchards.

The detrimental effects of salinity on plants can be attributed to either an increase in the osmoticum of the nutrient solution or ion-specific toxicity. Our results with citrus and avocado plants grown in iso-osmotic solutions with reciprocal molar ratios of chloride:nitrate showed that toxic symptoms appear only when chloride is the main anion. This suggests that within the range of salinity and chloride concentrations used in our studies, the toxic symptoms are not due to osmotic effects, but rather to chloride-specific toxicity.

In light of the observed nature of the competition between nitrate and chloride, and the clear preference for nitrate absorption, we suggest that the molar nitrate concentration in the soil solution be maintained at about 50% of that of the chloride to ensure the reduction of chloride uptake and avoid the negative effects of the nitrate. Field experiments should be conducted to determine whether addition of nitrate to the irrigation water in avocado and citrus orchards would improve growth and yield under conditions of high salinity. As the chloride:nitrate ratio influences the levels of phosphorus and iron in the plant, these effects should be considered when planning to employ the nitrate supplement method. In any event, when applying the results of this research, one must bear in mind the possible danger to the environment from the increased use of nitrate fertilizers. It is important to employ appropriate techniques in order to prevent leaching of nitrate from the rhizosphere.

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