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Rootstock and nitrate involvement in 'Ettinger' avocado response to chloride stress*

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Abstract

The damage caused by excess chloride in 'Ettinger' avocado plants grown on the Mexican rootstock, Schmidt appeared mainly in the leaves and shoots, whereas the main toxic influence of chloride on the West Indian rootstock, Zriphin 99 rootstock appeared in the root system which showed a strong peroxidative activity. The dry weight of the roots of Zriphin 99 was also reduced and shoot/root ratio was increased, whereas the roots of Schmidt rootstock were much less affected. An increased level of chloride ion was detected in the leaves of 'Ettinger'/Schmidt compared with plants on Zriphin 99. The level of nitrate ion was higher in leaves of 'Ettinger'/Zriphin 99 than in those of plants grown on Schmidt. The activity of nitrate reductase was correlated with the damage caused by excess chloride level to 'Ettinger' cultivar grown on either rootstock. The study demonstrates and evaluates the parts played by rootstock and nitrate in avocado response to chloride stress.

Keywords: Avocado; Chloride; Nitrate; Nitrate reductase; Peroxidase; Rootstock; Stress

1. Introduction

Avocado (*Persea americana*) is one of the most sensitive fruit trees to excess chloride ion in the irrigation water (Haas, 1950; Bingham and Fenn, 1966; Bingham et al., 1968). Similar to the findings for many plant species (Munns et al., 1988), chloride stress reduces vegetative growth and yield of avocado trees (Oster et al., 1985). Necrotic spots, starting at the leaf margin, is a prompt and typical symptom of chloride stress in avocado (Haas, 1950; Oster et al., 1985).

Ben Ya'acov (1966) characterized the response curve of different avocado rootstocks to increased chloride level and reported that avocado rootstocks of the Mexican race transfer

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Abbreviations: Cl^- = Chloride ion; R = Nitrate reductase; NRA = Nitrate reductase activity

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greater chloride sensitivity to the scion than do rootstocks of the West Indian race. Similar results were reported in many other studies (Haas, 1950; Bingham and Fenn, 1966; Bingham et al., 1968; Ben Ya'acov, 1988). This acceptance was based on the observation that avocado cultivars grafted on rootstocks of the Mexican race usually show much more of the typical chloride stress symptoms at the tops of the trees than the same cultivars grafted on rootstocks of the West Indian race.

The root system has not received enough attention in the past. However, in the last few years, evidence has accumulated for the importance of the role of the roots in the response of avocado to chloride stress (Ben Ya'acov, 1988; Stienhardt et al., 1991). Recently it has been suggested that nitrogen fertilization of avocado trees irrigated with increased levels of chloride ion can reduce the damage (Bar, 1989; Lovatt, 1989), but there is still a lack of information about the mechanism that controls this effect.

Syvertsen and Yelenosky (1988) reported that the effect of chloride ion on the nitrate composition of citrus tissues was rootstock-dependent and their results indicated that in the presence of excessive chloride concentration, there was a marked influence of rootstock on the uptake of both chloride ion and essential nutrients, particularly nitrate. The relationship between chloride and nitrate ions has been studied in various plant systems and it has been shown that these two anions compete with one another for transport and metabolism in the plant (Cram, 1973; Kafkafi et al., 1982; Glass and Siddqi, 1985). Chloride levels in irrigation water are increasing, to the extent that it has been hypothesized that its toxicity dominates salt damage in avocado in many areas of world (Bar, 1989). This increases the need to understand the relationship between nitrate and chloride ions in relation to this important fruit tree.

In this study, we attempted to demonstrate the response to chloride stress of the leaf and root systems of 'Ettinger' avocado grown on two different rootstocks. We also tried to show the involvement of nitrate composition and the activity of nitrate reductase in the response of avocado grown under chloride stress conditions.

2. Material and methods

2.1. Experimental protocol

The plant material for this study included 32 2-year-old, similarly developed, avocado plants of the cultivar 'Ettinger', grafted on two rootstocks: Schmidt and Zriphin 99. In addition, 32 9-month-old ungrafted seedlings of the same rootstocks were used. The grafted plants were grown in 6 l and the seedlings in 2 l sand and soil filled pots and placed in a completely randomized design in an environmentally controlled greenhouse at the Volcani Center, Bet Dagan, Israel. Eight plants on each rootstock were treated with either NaCl (450 mg l^{-1} Cl^{-1}) or H_2O (200 mg l^{-1} Cl^{-1}). One hundred and five milliliters of each solution were applied twice weekly, by irrigation, to the two groups of plants.

Chloride damage was determined in the below- and above-ground parts of the plants. The number of leaves was recorded and the size and percentage of necrotic leaves was calculated for each individual plant. For the evaluation of root damage, the plants were carefully taken out of the pots twice during the study. The percentage of white and necrotic

roots was recorded and the plants returned to their pots until the end of the study. The growth of the central shoot was determined for each plant and the fresh weight of the root system of each plant was measured after washing it and removing the soil; later, the dry weight was determined. Ninety days after the beginning of the study, fresh and dry weight of all the leaves, shoots and roots were determined in the seedlings used in the study.

2.2. Chloride and nitrate analysis

For chemical analysis, leaf samples consisting of ten fully mature leaves free of necrosis were taken from each plant, 45 and 90 days after the beginning of the study.

$N\text{-}NO_3^-$ was analyzed by nitration of salicylic acid under highly acidic conditions. Absorbance of the complex formed was determined at 410 nm in basic solutions (Cataldo et al., 1975). Absorbance of the chromophore is directly proportional to the amount of nitrate-N present. The advantage of this method is that ammonium, nitrite and chloride do not interfere.

Leaf and root chloride was extracted with water and measured potentiometrically (Chapman and Pratt, 1961).

2.3. Enzyme assay

In vivo nitrate reductase activity (NRA) was analyzed in 250 mg leaf or root disks using a modification of the procedure of Hageman and Reed (1980) as described by Reddy and Menary (1990). Activity of the enzyme was expressed as nmol NO_2^- g^{-1} (fresh weight) h^{-1}, as determined spectrophotometrically at 540 nm.

Peroxidase activity was assayed by the method described by Bar-Akiva and Lavon (1968) with some adaptations (Dunford, 1990). A 50 mg fresh weight tissue sample was placed in a 2 ml reaction cuvette with 0.1 M K-phosphate buffer pH 6.0 that contained 0.5 M pyrogallol as a reductant. H_2O_2 was added and the time needed for pyrogallin production was measured at an optical density of 470 nm.

Plant tissues of the same age and free of necrosis were taken for all the assays. The enzyme assays were performed in three separate experiments with at least three replicates in each plant. Unless stated differently, each plant of the study is a replicate, with a total of eight replicates. Statistical analysis was performed using Student's *t*-test or Duncan's multiple range test ($P = 5\%$) to compare treatment effects. In regressions, all data were used but for clarity only the means were plotted in Fig. 3.

3. Results

3.1. Rootstock effect on avocado response to chloride stress

The percentage of necrotic leaves of avocado cv. 'Ettinger' grown on the Mexican rootstock, Schmidt is significantly higher than of 'Ettinger' grown on the West Indian rootstock, Zriphin 99 (Fig. 1). The difference between the percentages of necrotic leaves on the two rootstocks was evident by 45 days after the beginning of the study. Even in the

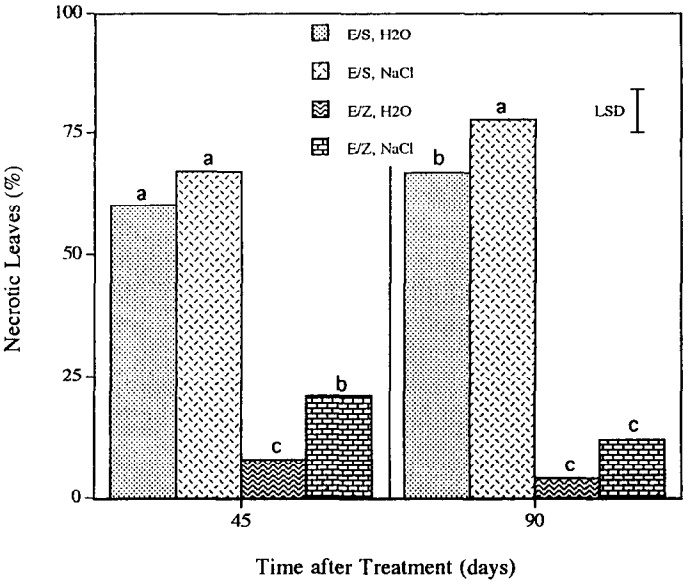

Fig. 1. Leaf necrosis of 'Ettinger' avocado grown on two rootstocks as affected by H_2O (200 mg l^{-1} Cl^-) or NaCl (450 mg l^{-1} Cl^-) treatments. The necrosis was measured 45 and 90 days after the beginning of the study. Means followed by the same letter within each time after treatment are not significantly different at the 5% level according to Duncan's multiple range test. Each plant was a replicate, with a total of eight replicates. E/S, 'Ettinger'/Schmidt; E/Z, 'Ettinger'/Zriphin 99; LSD, least significant difference at $P = 5\%$ for the entire experiment, over both experiment times.

H_2O treatment that contained a chloride level of 200 mg l^{-1}, 60% of the leaves of 'Ettinger'/Schmidt trees were necrotic, while only about 10% of 'Ettinger'/Zriphin 99 trees showed any necrosis 45 days after the beginning of the experiment. NaCl treatment significantly elevated the percentage of necrotic leaves of the trees grown on Schmidt only after 90 days.

Peroxidase activity was assayed in leaves of 'Ettinger' grown on both rootstocks (Table 1). The activity of the enzyme in both treatments was higher in leaves of 'Ettinger'/Schmidt than that of 'Ettinger'/Zriphin 99. NaCl treatment increased peroxidase activity in leaves of plants grown on both rootstocks (F test, $P = 1\%$). The roots of Zriphin 99 showed an

Table 1
Peroxidase activity in 'Ettinger' avocado grown on two rootstocks as affected by H_2O (200 mg l^{-1} Cl^-) or NaCl (450 mg l^{-1} Cl^-) treatments. The enzyme activity (10^{-3} unit min^{-1} ml^{-1}) was measured 90 days after the beginning of the study. Each plant was a replicate, with a total of eight replicates

Rootstock	H_2O		NaCl	
	Leaves	Roots	Leaves	Roots
Schmidt	109a	37a	163a	48b
Zriphin 99	39b	53a	114b	85a

Means in columns followed by the same letter are not significantly different by Duncan's multiple range test, at the 5% level.

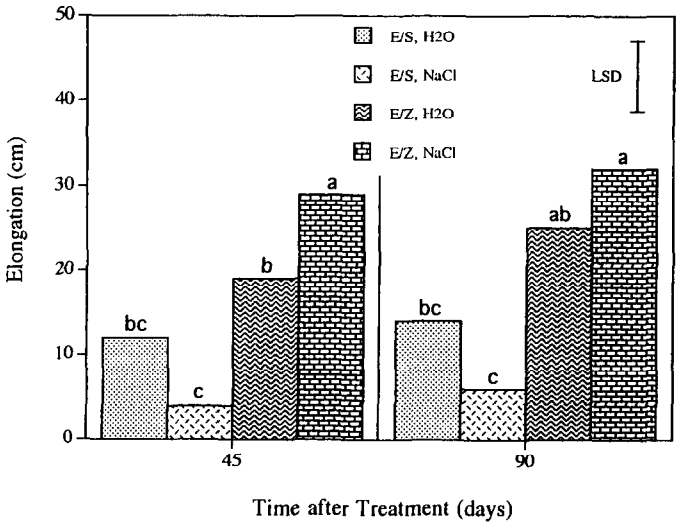

Fig. 2. Shoot elongation of 'Ettinger' avocado grown on two rootstocks as affected by H_2O (200 mg l^{-1} Cl^-) or NaCl (450 mg l^{-1} Cl^-) treatments. Shoot elongation was determined for the first 45 days and 90 days after the beginning of the study. Means followed by the same letter within each time after treatment are not significantly different at the 5% level according to Duncan's multiple range test. Each plant was a replicate, with a total of eight replicates. E/S, 'Ettinger'/Schmidt; E/Z, 'Ettinger'/Zriphin 99; LSD, least significant difference at $P = 5\%$ for the entire experiment, over both experiment times.

increased oxidation response to chloride application, which was expressed by peroxidase activity (Table 1). The difference in the enzyme activity between the two rootstocks was significantly increased by NaCl treatment. The roots of Zriphin 99 were more necrotic and lignified than those of Schmidt rootstock (data not shown).

The central shoot of plants of 'Ettinger'/Zriphin 99 in both treatments (H_2O and NaCl) elongated during the present study (Fig. 2), whereas elongation of the central shoot of plants 'Ettinger'/Schmidt was much less and occurred mainly in H_2O treatment. The major change in the growth of the central shoot in both rootstocks occurred during the first period of the experiment (45 days from the beginning of the study).

Table 2
Root dry weight and shoot/root ratio (on dry weight basis) in two avocado rootstocks as affected by H_2O (200 mg l^{-1} Cl^-) or NaCl (450 mg l^{-1} Cl^-) treatments. Shoot and root weight was determined 90 days after the beginning of the study. Each plant was a replicate, with a total of eight replicates

Rootstock	H_2O		NaCl	
	Root dry weight (g)	Shoot/root	Root dry weight (g)	Shoot/root
Schmidt	53a	1.7b	47a	1.6b
Zriphin 99	21b	2.3a	18b	2.8a

Means in columns followed by the same letter are not significantly different by Duncan's multiple range test, at the 5% level.

Table 3
Chloride and nitrate concentration of 'Ettinger' avocado plants as affected by H_2O (200 mg l^{-1} Cl^-) or NaCl (450 mg l^{-1} Cl^-) treatments. Leaves and roots of 'Ettinger' plants grown on Schmidt and Zriphin 99 rootstock were used to determine chloride and nitrate levels 90 days after the beginning of the study. The values are expressed as a percentage of dry weight of leaf or root. Each plant was a replicate, with a total of eight replicates

Rootstock	H_2O		NaCl	
	Leaves	Roots	Leaves	Roots
Chloride conc.				
Schmidt	1.05a	0.46b	1.34a	0.53b
Zriphin 99	0.58b	0.89a	0.83b	0.86a
Nitrate conc.				
Schmidt	0.21b	0.17b	0.25b	0.11a
Zriphin 99	0.41a	0.23a	0.39a	0.05b

Means in columns followed by the same letter are not significantly different by Duncan's multiple range test, at the 5% level.

Table 4
Changes in nitrate concentration and nitrate reductase activity in leaves and roots of 'Ettinger' avocado plants as affected by NaCl treatment. The undamaged part of five chloride-damaged leaves and roots from each plant was used. Cl^- was expressed as meq mg^{-1}, NO_3^- as $\mu g\ g^{-1}$ and nitrate reductase activity (NRA) as nmol NO_2^- g^{-1} (fresh weight) h^{-1}. Each plant was a replicate, with a total of eight replicates

Rootstock	Cl^-		NO_3^-		NRA	
	Leaves	Roots	Leaves	Roots	Leaves	Roots
Schmidt	0.16a	0.11a	2043b	1355a	200a	55b
Zriphin 99	0.09b	0.08a	3216a	544b	124b	151a

Means in columns followed by the same letter are not significantly different by Duncan's multiple range test, at the 5% level.

The dry weight of the root system of H_2O-treated (200 mg l^{-1} Cl^-) Schmidt plants, was significantly higher than that of the root system of Zriphin 99 plants (Table 2). NaCl treatment (450 mg l^{-1} Cl^-) had no effect on the dry weight of the roots of both rootstocks (F test, $P = 5\%$). The shoot/root ratio was significantly higher in Zriphin 99 plants than in Schmidt plants in both treatments. NaCl treatment had no significant effect on the shoot/root ratio (F test, $P = 5\%$).

3.2. Chloride and nitrate level in leaves and roots of 'Ettinger' avocado plants

The level of chloride was higher in leaves of both H_2O- and NaCl-treated 'Ettinger'/Schmidt plants than in 'Ettinger'/Zriphin 99 plants, whereas roots of Zriphin 99 contained higher level of chloride than roots of Schmidt (Table 3). NaCl treatment significantly increased the chloride content in the leaves of 'Ettinger' plants grown on both rootstocks (F test, $P = 5\%$), but had no effect on the content of chloride in the roots.

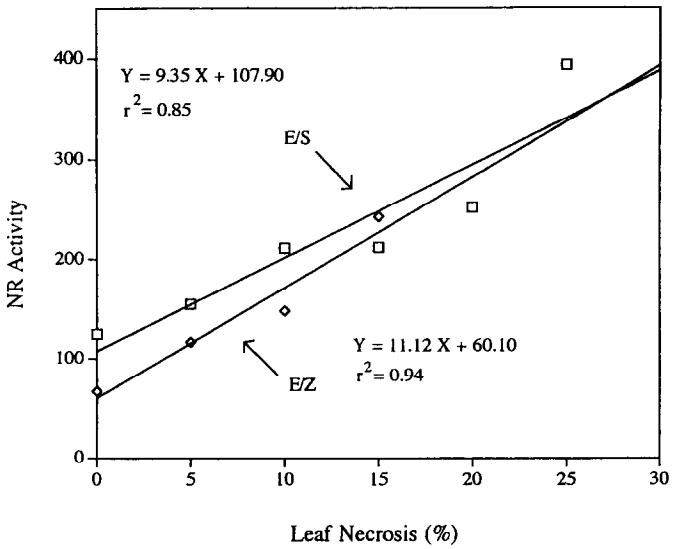

Fig. 3. Relationship between the extent of leaf necrosis and nitrate reductase activity as affected by NaCl treatment. Leaves showing necrosis of 0–25% of the whole leaf were sampled. Points are mean of eight values. Each plant was a replicate. The assays were done 90 days after the beginning of the study. NRA was expressed in nmol NO_2^- g^{-1} (fresh weight) h^{-1}. E/S, 'Ettinger'/Schmidt; E/Z, 'Ettinger'/Ziphin 99.

Nitrate concentration was significantly higher in the leaves of 'Ettinger'/Ziphin 99 plants in both H_2O and NaCl treatments, than that in 'Ettinger'/Schmidt plants (Table 3). In H_2O-treated plants, nitrate level was higher in roots of Ziphin 99 than in Schmidt. In NaCl-treated plants, Schmidt roots contained significantly higher nitrate level in comparison to Ziphin 99. Interestingly, after 90 days the level of nitrate was reduced in roots of NaCl-treated Ziphin 99 plants to a greater extent than in H_2O-treated plants (F test, $P = 1\%$).

3.3. Nitrate involvement in 'Ettinger' avocado response to chloride stress

In NaCl-treated leaves of 'Ettinger'/Schmidt plants which contained a relatively high chloride concentration and were severely damaged (Fig. 1), the nitrate level was lower than in those of 'Ettinger'/Ziphin 99 leaves (Table 4). However, the NRA was higher in leaves of 'Ettinger'/Schmidt compared than in 'Ettinger'/Ziphin 99 leaves. In general, a similar pattern was also observed in roots. Although the chloride level was not higher in roots of Ziphin 99 than in those of Schmidt, the former seem to be more sensitive (Tables 1 and 2) and nitrate level was lower in Ziphin 99 than in Schmidt.

A high correlation was observed between the activity of nitrate inducible enzyme, nitrate reductase (NR) and the size of necrotic spots caused to 'Ettinger' leaves by chloride toxicity (Fig. 3). In most cases, NRA was higher in leaves of 'Ettinger' plants grown on Schmidt rootstock than in those of 'Ettinger'/Ziphin 99. An increased degree of necrosis in leaves of 'Ettinger'/Ziphin 99 plants led to their abscission, which is why NRA was not assayed in leaves showing necrosis higher than 15% (Fig. 3).

4. Discussion

Mainly because of chloride toxicity, increased salinity of the irrigation water reduces the vegetative growth and productivity of avocado trees in most scion–rootstock combinations (Oster et al., 1985; Bingham et al., 1968), but the level of damage is type-dependent. At present, it is generally accepted that rootstocks of the Mexican race are the most sensitive to chloride, those of the West Indian race are the most tolerant and the Guatemalan rootstocks fall in between (Haas, 1950; Ben Ya'acov, 1988). Until recently, the sensitivity of avocado trees to salinity was characterized mainly in terms of the appearance of the necrosis in the leaves, which is a typical symptom of salinity (Oster et al., 1985; Ben Ya'acov, 1988). The results of the present study are in agreement with previous reports, based on leaf criteria, and clearly show that the leaves of avocado cv. 'Ettinger' grown on the Mexican rootstock Schmidt are more damaged by increased chloride level than those of the same cultivar grown on the West Indian rootstock Zriphin 99. The damage was characterized by the visible appearance of necrotic spots on the leaves (Fig. 1) and peroxidase activity (Table 1) that has been reported to be activated in plants in response to chloride stress (Corpas et al., 1993; Hernandez et al., 1993) and has been suggested to be a major causative factor of necrosis. It is of interest that the percentages of necrotic leaves on the 'Ettinger'/Zriphin trees was lower at 90 days than at 45 days, in both the H_2O and the NaCl treatments, whereas the percentage in NaCl-treated 'Ettinger'/Schmidt trees was higher at 90 days. This was a result of extensive leaf abscission which occurred in avocado cultivars grown on Zriphin 99 rootstock in response to irrigation with saline water (Oster et al., 1985; Bar, 1989).

During the last few years, several reports (Ben Ya'acov, 1988; Stienhardt et al., 1991) have indicated that the yield is reduced even in avocado trees without leaf necrosis and that many trees, including those grown on West Indian rootstocks, have collapsed in the orchard (A. Ben Ya'acov, personal communication and unpublished data, 1994). Based on these data, it has been suggested that the performance of avocado trees is influenced by exposure to increased chloride level in the irrigation water. The investigation of the response of the 'Ettinger' plant root system to chloride stress clearly demonstrated that roots of Zriphin 99 are more sensitive than roots of Schmidt (Tables 1 and 2) and their dry weight was reduced even in 'ordinary' H_2O, which contained 200 mg l^{-1} Cl^-. Further increase of the level of chloride (450 mg l^{-1} Cl^-) only slightly reduced root dry weight of both rootstocks and the difference between them was maintained. Peroxidative activity was markedly higher in Zriphin 99 roots in comparison with Schmidt roots (Table 1). The peroxidative activity of the roots of Zriphin 99 was followed by intensive necrosis and lignification, as was reported by McDougall (1992). The lignification was clearly localized in the cortex cell layer of Zriphin 99 roots, whereas a different pattern of chloride damage was obtained in Schmidt roots (Wiesman, unpublished data, 1994).

Munns et al. (1988) reported that chloride did not directly inhibit plant growth and suggested that it might affect production and translocation of hormones and some other essential factors which regulate plant growth and productivity. The data of the present study suggest that the different tissues that are most damaged by excess chloride levels in 'Ettinger' plants grown on the respective rootstocks (leaves in Schmidt and roots in Zriphin 99) influence the shoot/root ratio differently (Table 2). This may explain why the growth of the central shoot of 'Ettinger'/Zriphin 99 plants is not reduced and may even be further

elongated in response to NaCl treatment. A similar response to salinity was also described by Munns et al. (1988). In the case of 'Ettinger'/Zriphin 99, the diminution of the root system reduces its competition with the shoot and a temporary visual tolerance can be seen in this scion/rootstock combination. An opposite effect, which reduced shoot growth, occurred in the case of Schmidt. We suggest that the initial event of chloride stress, which mainly damages the underground part of 'Ettinger'/Zriphin 99 plants, masks the real toxic effect of chloride, and it is only after a period of vigorous growth of the top of the plants that the plant performance declines, owing to the retardation of root system development and reduction of its activity, that reduces its ability to supply the hormonal and nutritional essential factors for the whole plant growth.

Our data indicated a higher uptake of chloride by Schmidt than Zriphin 99 rootstock (Table 3). Chloride accumulated mainly in the leaves of 'Ettinger'/Schmidt, to a higher level than in the West Indian grown plant. In NaCl-treated plants on both rootstocks, chloride level was increased; however, in the leaves of 'Ettinger'/Zriphin 99 it reached to a much lower level. Interestingly, chloride level was slightly reduced in roots of NaCl-treated Zriphin 99 compared with H_2O-treated roots. Similar results were reported by Ben Ya'acov (1966) for West Indian rootstocks treated with increased NaCl levels. It might suggest of a reduction in the activity of the roots in conditions of high salinity. Our analysis of chloride in the avocado plant system showed a similar pattern to that reported by Syvertsen and Yelenosky (1988) for the salt-tolerant citrus rootstock, Kleopatra, in which most of the chloride was localized in the root system, in contrast to sensitive citrus rootstocks, in which an increased level of chloride was found in the leaves. These findings are in agreement with the data on the different tissues that are most damaged by chloride in the two avocado rootstocks studied.

The competition between chloride and nitrate in uptake and transport has been reported in several studies of various plant species (Cram, 1973; Kafkafi et al., 1982; Glass and Siddqi, 1985) that suggested a negative feedback regulation between these two anions. After a period of adaptation to the soil conditions, an increased uptake of nitrate was found in Zriphin 99, compared with the Schmidt rootstock (Table 3). Even after 90 days, by which time the roots of the Zriphin 99 rootstock were heavily damaged by chloride, the level of nitrate in this plant was higher than that in the plant on the Schmidt rootstock, and most of the nitrate was localized in its leaves. These data can explain the relatively low level of chloride in the leaves of 'Ettinger'/Zriphin 99 in comparison with the combination with Schmidt.

Nitrate reductase is a substrate-inducible enzyme (Beevers and Hageman, 1980) and therefore NRA is assumed to reflect the long-term nitrate supply of a plant in its respective habitat (Stadler and Gebaner, 1992). The results of the present study clearly demonstrate a correlation between NRA and chloride damage in leaves of 'Ettinger' plants grown on both Schmidt and Zriphin 99 rootstocks (Fig. 3). Taking the data of chloride and nitrate contents and NRA all together (Table 4) suggests that in case of nitrate accumulation without a high rate of its reduction, as in 'Ettinger'/Zriphin 99 leaves and 'Ettinger'/Schmidt roots, low chloride damage occurs. The opposite is also true as is shown in 'Ettinger'/Schmidt leaves and 'Ettinger'/Zriphin 99 roots, which show major chloride damage in both combinations.

The difference in NRA in 'Ettinger' grown on the respective rootstocks is interesting, since NRA is induced by an increased nitrate level, so the question is why NRA is relatively lower in leaves of Schmidt plants, that show decreased level of nitrate, than in leaves of plants grown on Zriphin 99, which show an increased level of nitrate (Table 4). This contradiction can be explained in two ways: the decreased level of nitrate in leaves of Schmidt plants is a result of the reducing activity of NR that converts the nitrate to nitrite or from an inactivation of NR in leaves of plants grown on Zriphin 99 rootstock. It is well documented that NR proteins from different plant sources differ in their sensitivity to protease degradation and to some other environmental factors (Solomonson and Barber, 1990). The difference in NRA between 'Ettinger' grown on the respective rootstocks may be of high importance because this enzymatic system may be used as a selection tool for new avocado clones with increased tolerance to chloride stress, as was also suggested by Lovatt (1989).

In summary, the results of the present study clearly demonstrated that the root system of the West Indian avocado rootstock, Zriphin 99 is more sensitive to increased level of chloride than the Mexican rootstock Schmidt. In addition, a correlation between high nitrate level and low NRA, on the other hand, and low chloride sensitivity, on the other hand, was demonstrated. These last data suggest that nitrate together with NRA and peroxidase activity may be used for determination of avocado sensitivity to chloride stress, but much more study is still needed in this field before a selection program based on this system could be conducted.

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