

Root Growth of Avocado is More Sensitive to Salinity than Shoot Growth

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ABSTRACT. In most crop species, growth of the shoot is more sensitive to salt stress than root growth. Avocado [*Persea americana* Mill.] is very sensitive to NaCl stress. Even low concentrations of salt (15 mM) inhibit tree growth and decrease productivity. Observations in experimental orchards have suggested that root growth in avocado might be more restricted by salinity than shoot growth. In the present study, we evaluated quantitatively the inhibitory effects of salt stress on growth of the avocado root in comparison to the shoot. Seedling plants of the West-Indian rootstock 'Degania 117' were grown in complete nutrient solution containing 1, 5, 15, or 25 mM NaCl. The threshold NaCl concentration causing root and shoot growth reduction occurred between 5 and 15 mM. At all concentrations, root growth was much more sensitive to salinity than shoot growth. A concentration of 15 mM NaCl, which did not affect the rate of leaf emergence on the plant and decreased leaf biomass production only 10%, induced a 43% reduction in the rate of root elongation and decreased root volumetric growth rate by 33%. Under 25 mM NaCl, leaf biomass production, leaf initiation rate and leaf elongation rate were reduced 19.5%, 12%, and 5%, respectively, while root volumetric growth and root elongation rate were reduced 65% and 75%, respectively. This strong root growth inhibition is expected to influence the whole plant and therefore root growth under salinity should be considered as an important criterion for rootstocks' tolerance to NaCl.

Salt stress is one of several environmental stresses that induces changes in growth and morphology of plants. Inhibition of vegetative development of shoots and roots is the primary response to salt stress (Lazof and Bernstein, 1998; Munns, 1993). Root growth is usually less sensitive to the stress than is growth of the shoot (Bernstein and Kafkafi, 2002; Cheeseman, 1988; Rawson et al., 1988) and root to shoot ratio therefore typically increases under salinity.

Avocado is known to be the most salt-sensitive cultivated fruit tree. Even low levels of salt inhibit the vegetative growth of the avocado shoot (Bar et al., 1997; Bernstein et al., 2001; Bingham and Fenn, 1966; Haas, 1950) and its fruit production (Ayers et al., 1951; Bingham et al., 1968; Downton, 1978; Steinhardt et al., 1995.) Chloride and sodium concentrations in irrigation water, which are considered tolerable for many crops, induce severe leaf damage in avocado. Salt-induced leaf damage is considered to reduce the photosynthetic leaf area and hence yield potential in avocado (Ayers et al., 1951; Bingham et al., 1968). The extent of sensitivity of avocado rootstocks to salt stress is therefore conventionally quantified by stress impact on the appearance of chloride and sodium-induced leaf-burn damage. However, the extent of stress induced leaf damage did not correlate with stress-induced inhibition of shoot vegetative development (Bernstein et al., 2001). Additionally, in a long-term selection project, minimizing leaf damage under salt stress did not prevent the negative effects on avocado productivity (Ben-Ya'acov et al., 1979; Ben-Ya'acov and Michelson, 1995). This suggests that the utilization of leaf damage as a major marker for salt tolerance should be reevaluated, and other plant factors might contribute significantly to the tree response to salinity, and to decreased productivity.

Very little is known about the effects of salt stress on growth, development and function of the avocado root system. The few reports available demonstrate inhibitory effects of salinity on root development (Bingham and Fenn, 1966; Haas, 1950). Inhibition of root growth, and hence root surface area, is also suggested from the reduced capacity of trees under salt stress to take-up water (Steinhardt et al., 1987, 1995; Meiri Bernstein and Zilberstaine, unpublished data). Interestingly, root to shoot ratio was reported to decrease under salt stress (Bar et al., 1997) suggesting that, contrary to most crop species, the avocado root system might be more sensitive to salt stress than its shoot. Substantial root growth inhibition might conceivably be an important component in the tree's response to the stress.

If indeed growth and function of avocado roots are very sensitive to salt stress, then it might be advantageous to add root growth criteria in evaluation of avocado rootstock salt sensitivity, which currently emphasizes shoot characteristics (such as leaf-burn damages).

The objective of this study was to investigate the effect of salt stress on avocado root growth. Specifically, we tested the hypothesis that in rootstocks selected for resistance to salt, growth of roots is more sensitive to salinity than is growth of shoots.

Materials and Methods

PLANT MATERIALS AND GROWTH CONDITIONS. 'Degania 117', a West-Indian avocado rootstock, commonly used in Israel and relatively resistant to salt stress (Ben-Ya'acov, personal communication) was chosen for the study. Four-month-old seedlings, germinated in a commercial nursery, were grown in a screen house in 2-L pots filled with a tuff (Scoria, granulated volcanic ash) and peat mixture (1:3) for a period of 4 months. In the beginning of the spring, the plants were transferred to a growth chamber where the temperature was maintained at 25 °C during the day and 21 °C at night in a photoperiod of 13 h, light intensity of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 50% to 70% humidity. Following 10 d of

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acclimation, individual plants were transplanted into 10 L plastic containers containing quarter-strength aerated modified Hoagland nutrient solution (Bernstein et al., 1995), of pH 5.7. The nutrient solution was changed twice weekly throughout the experiment.

SALINIZATION TREATMENTS. Salinization treatments were started 30 d after the plants were transferred to solution culture, 2 weeks after new roots had emerged. Two experiments were carried out. The first experiment was designed to determine the salt concentration at which growth sensitivity occurred for 'Degania 117'. For this experiment, the plants were divided into two groups, control and salt, eight plants per treatment. The control solution was kept at 1 mM NaCl. The salt treatment solution was elevated in three steps to 25 mM NaCl. NaCl was therefore elevated to 5, 15, and 25 mM NaCl in 6-week intervals. Starting one week after each increase in salt concentration, root and shoot growth of plants from both treatments were monitored. At each measurement duration, growth of the stressed plants was thus compared to that of the nonstressed plants of same age. The effect of the different salt concentrations was hence studied in one plant population to avoid the possible variability in response to the stress expected between heterozygous seedling avocado plants. The comparison of stressed and nonstressed plants at each salt concentration was intended to standardize the effect of plant age on the measured response to the stress.

In a following experiment the growth response of the root and the shoot to the different salt treatments was evaluated in plants of same age (and developmental stage), with the duration of exposure to stress kept identical in all treatments. Similar to the first experiment, salinization treatments were started 30 d after the plants (8 months old) were transferred to solution culture. The plants were exposed to 1, 15, or 25 mM NaCl (eight plants per treatment). The NaCl concentration was elevated in steps of 5 mM, every 24 h. Accordingly, the final salt concentrations of the 15 and the 25 mM treatments were reached 3 and 5 d after salinization had started. Analysis of the root and shoot growth responses was initiated 12 d after commencement of salinization. Both experiments were designed to follow a completely randomized pattern.

ROOT GROWTH ANALYSIS. In the first experiment, periodic measurements of root length were used for the analyses of root elongation rate. In each plant, 20 roots were marked with threads of different colors, loosely tied to the oldest mature part of the roots. Roots selected for analysis were of the first order that had emerged after the plants had been transferred to solution culture. 30–40 mm long roots were marked one week after each elevation of salt concentration. Root length was measured as the distance from the point of root emergence from the higher order (more mature) root, to its tip. The length of the roots was measured 5 times, in time intervals of 24, 36, or 48 h. Root elongation rate was calculated as the slope of the regression of root length vs. time. The data were analyzed by the General Linear Model procedure of SAS (SAS Institute, Cary, N.C.). Linear regression lines of length of roots vs. time were fitted to the control and salt treatment. The homogeneity of the two lines was tested. The analysis was conducted for each of the three salt concentrations.

In the second experiment, growth of the entire root system was also evaluated, in addition to the analysis of individual root tip elongation growth. The volume of the root system was measured nondestructively 1 and 5 weeks after the salt concentration of the highest salinity treatment had been achieved. Roots, still attached to the plant, were gently blotted and dipped into a glass cylinder containing the appropriate nutrient solution. Changes

of solution height were measured with a micrometer and used for calculation of root system volume growth, presented in cubic centimeters per month.

SHOOT GROWTH ANALYSIS. In the first experiment, the effect of salinity on leaf biomass deposition was quantified. One week after start of salinization, the youngest leaf to have reached the reference length of 1.5 cm was marked on each plant with a colored thread loosely tied around the leaf petiole. At the termination of the experiment seventeen weeks later, the cumulative weight of leaves that had developed during the experiment was measured destructively.

In the second experiment, in addition to total leaf biomass production, leaf emergence rate and leaf length increase were also analyzed. One week after the final salt concentration was reached, the youngest leaf on the plant that had reached the reference length of 1.5 cm was marked as described above for the first experiment. Once a week, the number of new leaves that had reached the reference length was recorded. Concomitantly, in nondestructive measurements, leaf growth was monitored. The length of the two youngest leaves on each plant which had reached the reference length of 1.5 cm one week after the highest salinity concentration had been reached (i.e., the leaf described above in relation to leaf biomass production analyses and the second youngest leaf) was measured over time throughout the experiment. Results from the two leaves on each plant ($n=8$) were averaged to give the single plant value. A *t* test was performed to test whether the difference in leaf length between control and the salinity treatment at each measurement-duration was significant. At the termination of the experiment, the weights of all the young leaves that had emerged on the plant, after the marked leaf, were measured destructively to give fresh leaf biomass deposition, data are presented in units of g/month.

Results

'Degania 117' is a relatively salt-resistant rootstock (Ben-Ya'acov, personal communication). Nonetheless, the present study demonstrates that root growth of this West-Indian rootstock is very sensitive to salt stress. During 8 d of elongation, roots that were exposed to 15 mM NaCl grew 6 mm less (45%) than roots grown under 1 mM NaCl (control), and roots exposed to 25 mM NaCl grew 10.6 mm less (71%) than the control roots (Fig. 1). The lowest salinity concentration, 5 mM NaCl, did not affect root elongation growth. In the three salt treatments, the rate of root length increase was linear throughout the measurement period (Fig. 1). Test for homogeneity of the slopes of the fitted linear regression lines indicated that the rate of root elongation at the lowest salinity treatment (5 mM NaCl) was not significantly different from the control ($p = 0.745$, Fig. 2.). Exposure to the intermediate salinity treatment (15 mM NaCl) induced a 43% reduction in the rate of root elongation ($p < 0.0001$). The highest salinity treatment, 25 mM NaCl, resulted in a 75% reduction of elongation rate ($p < 0.001$, Fig. 2).

Unlike root growth that was greatly inhibited by salinity, the growth of the shoot was much less affected. The total biomass of new leaves produced during 17 weeks of growth (in the first experiment) was reduced only $15\% \pm 0.7$ by exposure to salinity (absolute data of shoot biomass accumulation are presented for the second experiment in Fig. 4).

It is apparent from Fig. 2 that the rate of root elongation in the control treatment increases linearly with time ($r^2 = 0.9981$). It increased by 0.9 and 0.8 mm·d⁻¹ from the first to the second, and

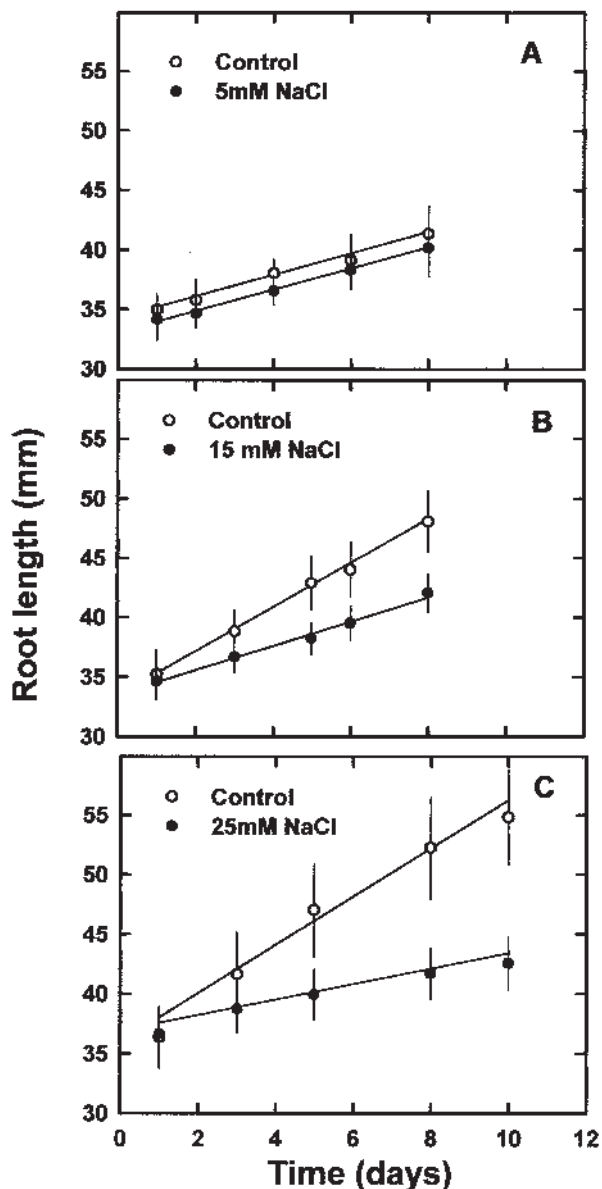


Fig 1. Elongation growth of roots from plants exposed to 5 (A), 15 (B), and 25 mM NaCl (C), in comparison to roots from control plants (grown under 1 mM NaCl). The effect of the different salt concentrations was studied in a single plant population, the salt concentration was elevated from 5 to 15 and then to 25 mM NaCl in 6-weeks intervals. Time is marked as days from the beginning of the nondestructive growth monitoring (one week following each increase in salt concentration). Presented results are cumulative root lengths over time; an average \pm SD ($n = 8$ plants), with 20 root tips averaged to give the single plant value. The fitted linear regression lines are $y = 34.1346 + 0.8940x$ for the control, $y = 33.1300 + 0.8741x$ for 5 mM NaCl, $r^2 = 0.9938$ (A); $y = 33.3732 + 2.8328x$ for the control, $y = 33.4235159 + 1.03735x$ for 15 mM NaCl, $r^2 = 0.9967$ (B); $y = 35.30713 + 2.05239x$ for the control, $y = 36.4436 + 0.6382x$ for 25 mM NaCl, $r^2 = 0.9862$ (C).

second to the third measurement periods, respectively. Unlike the control, the elongation rate of the salinized roots did not increase and even decreased with time (i.e., with increased salt concentration). A 38% decrease in root elongation rate (from 1.06 to 0.66 $\text{mm}\cdot\text{d}^{-1}$) was measured between the second (15 mM NaCl) and third (25 mM NaCl) measurements. As a result, normalization of the rate of root growth data to 'percent of control' demonstrated a near linear decrease with salt concentration, with a slope of 0.38/ mM ($y = 117.975 - 3.797x$, $r^2 = 0.9917$).

The results of the first experiment suggest that the threshold

NaCl concentration causing root growth reduction in the rootstock 'Degania 117', falls in the NaCl concentration range between 5 and 15 mM. The relatively small variability between the individual seedling rootstock responses to the stress (standard deviation for shoot and root responses smaller than 5% and 4.7% respectively, depicted in Fig. 1, and details in the text) indicated that root and shoot growth responses to different salt level could also be tested with different seedling populations for each treatment. Such an experimental design, which was applied in the second experiment, prevents complications in interpretation of experimental results arising from exposure to varied duration of stress, history of stress levels, and changes in plant age.

Results from the second experiment demonstrate that salinity induces a small inhibition of shoot growth. Leaf appearance rate for plants grown under 15 mM NaCl was not statistically different than that of control plants; as a result, the cumulative leaf number per plant was similar over time for both treatments (Fig. 3A). Exposure to 25 mM NaCl delayed the appearance of new leaves. During 60 d of exposure to the stress, the number of new leaves that appeared on plants of the 25 mM NaCl treatment was 12% smaller than the number of new leaves that appeared on the nonstressed plants (Fig. 3A).

Salinization also reduced the length of the mature leaf (Fig. 3B). In the highest salinity treatment, the length of mature leaves was 16.5% smaller than length of mature leaves of the nonstressed plants (173 and 207 mm in stressed and nonstressed plants, respectively). The rate of leaf elongation was also affected by salinity but only slightly. Exposure to 25 mM NaCl reduced the rate of leaf elongation by 5% (calculated from a linear regression of the data in Fig 3B, for the rapid period of leaf growth, $r^2 = 0.9921$ and 0.9862 for the control and salt treatment, respectively). The reduction of final leaf size was a combined result of the slight reduction in leaf elongation rate, and a shortened duration of rapid leaf growth (Fig. 3B).

Smaller leaf size, and slower leaf appearance rate are thought to result in decreased photosynthetic leaf area under salinity stress and hence reduced yield potential. The cumulative production of leaf biomass during 30 d of growth was indeed reduced by salinity (10% by exposure to 15 mM NaCl, and 19.5% by exposure to 25 mM NaCl, Fig. 4).

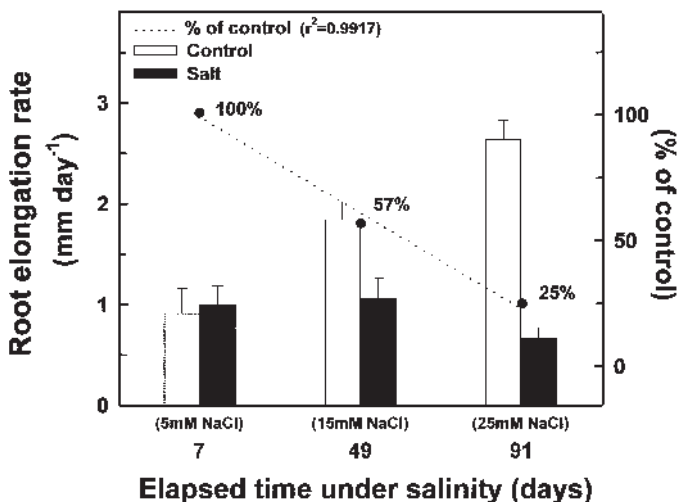


Fig 2. Elongation rates of roots from plants exposed to salinity 7 d (5 mM NaCl), 49 d (15 mM NaCl) and 91 d (25 mM NaCl) in comparison to roots from control plants (grown under 1 mM NaCl), presented as $\text{mm}\cdot\text{d}^{-1}$ and percent of the control. Results calculated from data presented in Fig 1. The fitted linear regression line for percent of control is $y = 117.975 - 3.797x$.

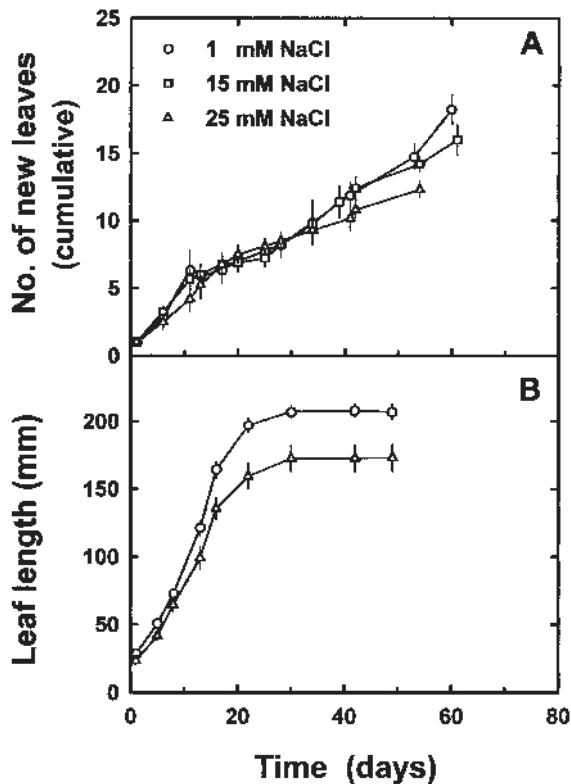


Fig 3. Cumulative leaf number (A) and leaf length (B) of plants exposed to 1, 15, or 25 mM NaCl. Time is marked as days from the beginning of the nondestructive growth monitoring, 12 d after commencement of salinization, in the second experiment. Data are the average \pm SD ($n = 8$ plants). Length of the control leaves was significantly higher than of the 25 mM NaCl treatment from day 15 to 50 ($P < 0.01$). No significant difference (at $p = 0.01$) could be demonstrated for days 1 to 8. Leaf length of the 15 mM NaCl treatment was not significantly different than the control ($p < 0.01$), data omitted for clarity.

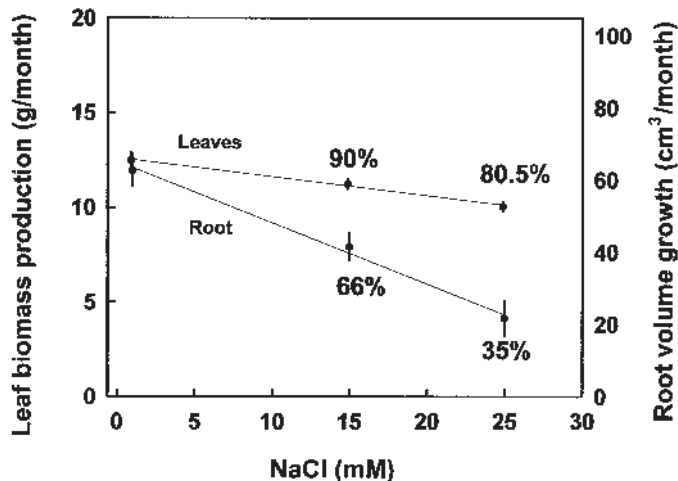


Fig 4. Leaf biomass production rate, and root volumetric growth rate over time in response to 1, 15, or 25 mM NaCl (second experiment). Numbers adjacent to the treatment symbol represent percent of control. Leaf biomass production data are average \pm SD ($n = 8$ plants). Root volume increase was calculated from nondestructive measurements of root volume at the second and sixth weeks of salinization, and are averages \pm SD ($n = 8$ plants).

The relative growth responses of the avocado root and shoot to salinity were found to be similar in the two experimental setups of this study. Unlike shoot growth that was only slightly affected by salinity, root growth measurements demonstrated a strong sensitivity of the root to salinity. A concentration of 15 mM NaCl,

inhibited shoot biomass production rate by only 10%, but induced a 35% reduction in the rate of root volume increase (Fig. 4). The highest salinity tested, 25 mM NaCl, induced a 19.5% reduction in shoot biomass deposition rate, but a 65% reduction in root volume growth rate (Fig. 4). The effect of 15 and 25 mM NaCl on root elongation rates in this experiment (data not presented) was similar to that in the first experiment (Fig. 2). The extent of root growth inhibition due to salinity was similar whether the measured parameter was root elongation rate or entire root system volumetric growth. The measured extent of growth inhibition was also similar between the two experiments, suggesting that, within the time frame tested in this study (18 weeks of salinization) the sensitivity of root growth to salinity might not change with duration of exposure to salinity.

Discussion

It is commonly known for a large variety of plants that root growth is usually less sensitive to salt stress than is growth of the shoot (Cheeseman, 1988; Lazof and Bernstein, 1998; Rawson et al., 1988). Root to shoot ratio therefore often increases under salinity (Delane et al., 1982; Weimberg et al., 1984). The results of the present study, which demonstrate that growth of the avocado root is much more sensitive to salt stress than growth of the shoot, identify avocado as a unique crop species.

The avocado root is characterized by a unique morphology. It has few root hairs, demonstrates a low degree of root branching and, in soil grown plants, the main root mass is found in the top soil layer (Borys et al., 1985). These root characteristics might result in heightened sensitivity to soil salinity. First, the shallow root system results in exposure to large fluctuations in environmental conditions (soil water content, salt concentration, temperature), which might exacerbate stress conditions even under moderate salt concentrations, in soil-grown plants. Second, nutrient acquisition under salt stress might be reduced. The scarcity of root hairs dictates that water and nutrient uptake takes place only in the limited surface area of the young growing root tips. The low degree of root branching restricts the number of root tips active in absorption. Accordingly, inhibition of root growth and root proliferation, if takes place under stress, could considerably reduce the surface area of young roots and hence the uptake capacity of the root system. This in return might reduce nutrient supply to the shoot. The shallow, relatively inefficient root system of avocado, (Moore-Gordon et al., 1997; Wolstenholme and Whiley, 1999) might hypothetically contribute to the extreme sensitivity of the tree to salt stress via an effect on nutrient acquisition.

Additionally, reduction of developing root tissue mass under stress might also result in reduced transport of growth regulators from the root to the shoot which may affect shoot growth and productivity.

Rootstocks are known to be of importance in the resistance of grafted fruit trees to salt stress (Maas, 1990). Previous studies with grafted avocado trees demonstrated the effect of the rootstock in resistance of the grafted tree to salinity (Ben-Ya'akov, 1970; Cooper, 1951; Embelton et al., 1962; Haas, 1950; Kadman, 1970). Differences between rootstocks affected the extent of shoot (scion) growth reduction under salinity in grafted trees (Oster and Arpaia, 1992). The large sensitivity of the root to salt stress, demonstrated in the present study, suggests that the extent of resistance induced by a specific rootstock on the grafted tree might be related to the growth sensitivity of the rootstock itself. On the other hand, the response of the root to salinity might be

affected by the scion. The tolerance level of the scion and its responses to salinity might affect root responses.

'Degania 117', the rootstock selected for this study, was previously ranked as relatively tolerant to salinity, based on selection criteria which emphasized shoot responses (Ben-Ya'acov, personal communication). In the present study, growth of the Degania 117 shoot was indeed found to be relatively insensitive to salt stress. On the other hand, root growth, which was not considered in the selection program for salt tolerance, demonstrated extreme sensitivity to saline conditions. It is not known at this time if the extreme sensitivity of the root growth relative to the sensitivity of the shoot is characteristic only of avocado rootstocks which were selected for salt tolerance based on shoot performance under stress, or alternatively, if it is characteristic of avocado rootstocks in general. Additionally, it is not known if the surprising difference between the sensitivities of the root growth and the shoot growth to salinity is typical of grafted avocado trees as well. Observations from field studies suggested that root factors might play a central role in tree response to salt stress. Salinity induced damage to trees grafted on resistant rootstocks was also suggested to be related to root damage (Steinhardt et al., 1995).

We suggest that it is important to evaluate the significance of the prominent inhibition of root growth under salinity to the function of the entire root system and the plant shoot in both grafted and ungrafted trees. If root growth inhibition is found to be directly involved with whole plant damage or with reduced productivity, current evaluation practices for rootstock sensitivity should include evaluation of root responses.

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