Scientia Horticulturae, 36 (1988) 1-15
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

Shade Reduces the Foliar Symptoms of 'Fuerte' Avocado Affected by Salt, without Significantly Changing the Concentration of Na, K or Cl in the Leaves

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(Accepted for publication 5 February 1988)

ABSTRACT

Chirachint, W. and Turner, D.W., 1988. Shade reduces the foliar symptoms of 'Fuerte' avocado affected by salt, without significantly changing the concentration of Na, K or Cl in the leaves. *Scientia Hortic.*, 36: 1-15.

The effect of shade on the response of 'Fuerte' avocado plants to NaCl was studied because it was thought to be an important factor influencing the response of the plants in the field. Potted plants were exposed to 20 mM NaCl for 6 weeks in shaded (50%) or fully sunlit conditions in a glasshouse.

Shading reduced the amount of necrosis on the leaves of salt-treated plants from $27 \pm 7\%$ of the leaf area to $6 \pm 2\%$. It did not significantly change the concentration of Cl, Na or K in the tissues. Plants which received NaCl had 20% less dry matter and leaf area and 20% lower leaf conductance than control plants. Cl accumulated in the tissue water of the tops, especially the old leaves, while sodium tended to accumulate in the woody tissues of the main root, scion and branches. Potassium accumulated less in the roots and more in the tops of salt-affected plants.

Chemical analysis of the tissues is a more reliable indicator of the presence of high salt than the presence of symptoms, which depends on the level of irradiance experienced by the leaves.

Keywords: avocado; chloride; potassium; salinity; shade; sodium.

INTRODUCTION

The avocado is a salt-sensitive species and numerous reports have associated high concentrations of chloride in the leaves with necrosis (Haas, 1950; Ayers et al., 1951; Kadman, 1963, 1964). The first systematic study of the effect of salt on avocado was that of Bingham et al. (1968). Downton (1978) studied

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0304-4238/88/$03.50

the effect of salt stress on growth and flowering of 'Fuerte' on three different rootstocks.

Leaf necrosis on avocado trees at Carnarvon, Western Australia, has been associated with high concentrations of chloride in the leaves. The expression of symptoms vary considerably among cultivars, within trees and between sites. This suggested that salinity may not be the only factor associated with the expression of symptoms, and external factors, such as the microclimate around the tree, and plant factors may be important. Bernstein (1980) drew attention to the fact that leaf necrosis of many plants subjected to saline soils was more severe when they experienced hot and dry weather, which is a feature of the Carnarvon environment.

The experiment reported here was performed on 'Fuerte' avocado. At Carnarvon, its productivity is intermediate compared with other cultivars (Burt, personal communication). The experiment was designed to see whether leaf necrosis was more severe on salt-affected plants exposed to full sunlight than on those grown at lower irradiance, and whether this was associated with changes in the concentration of Na, K and Cl in the plant tissues, as reflected in leaf conductance.

MATERIALS AND METHODS

Plants and growing conditions. – 'Fuerte' scions grafted onto seedling rootstocks of 'Topa Topa' were chosen to evaluate the effects of NaCl and irradiance on growth, nutrient concentration, nutrient content and distribution among plant organs. 'Fuerte' avocado is widely grown in Australia and is a hybrid cultivar between Mexican and Guatemalan races. 'Topa Topa', of the Mexican race, is a rootstock used in Australia (Hawson, 1982).

The plants used were about 2 years old and had been grafted 1 year previously. They were transplanted to 13.5-l black plastic pots filled with 8 kg of steam-sterilized sand pine bark, peat and sawdust in equal parts, and kept under shadecloth (50% irradiance). Field capacity ($56 \pm 3\%$) and wilting point ($35 \pm 2\%$) of the media were determined using a pressure-plate apparatus at 0 and -1500 kPa (Richards, 1941).

The experiment was carried out in a sunlit glasshouse at Nedlands (latitude 30°S). Plants were watered with overhead sprinklers twice daily for 4 weeks without the addition of nutrients, and then moved into a sunlit glasshouse in which the day/night temperature was set to 35/25°C. The chloride concentration in the water used for overhead irrigation was not measured, but the leaves had concentrations of 0.038% Cl, 0.63% K and 0.36% Na in their dry matter at the start of the experiment. On occasions the maximum temperature rose to 40°C, but the minimum was 24–26°C throughout the experimental period. At noon on a clear day, the photon flux density inside the glasshouse was 1350 ± 50 μE m^{-2} s^{-1}. Relative humidity inside the glasshouse at 09.00 h was

approximately 60%. Polythene beads on the top of the media reduced water loss. Treatments commenced on 26 December 1984, 2 weeks after the plants were introduced into the glasshouse, and ceased on 6 February 1985.

Experimental design and treatment application. – The four treatments were (i) 2 levels of NaCl (0 and 20 mM), and (ii) 2 levels of irradiance (50 and 100%). The irradiance was reduced by placing black shadecloth over the plants. Irradiance and NaCl treatments were applied at the same time. A factorial arrangement in a randomized complete block design was used with 4 replications. One plant was used as one replication, so 24 plants were used in the experiment.

The NaCl treatments were applied daily in 1/10-strength commercial nutrient solution (Aquasol, 120 mg l^{-1}, Hortico Ltd., Port Melbourne, Vic.). Before treatment application, the pots were copiously leached with deionized water to prevent salt accumulation in the root zone. The nutrient solution to which the salt was added contained (mM of nutrient) 1.9 N, 0.2 P, 0.6 K, 0.3 Cl and a trace of sodium.

Measurements. – Height (from media to the apex) and stem diameter (10 cm above the graft union) were measured every 2 weeks. Stomatal resistance was measured on the abaxial surface with an automatic porometer (Delta, Mk 3) and leaf temperature was measured on the adaxial surface of the fourth youngest fully mature leaf between 09.00 and 10.00 h. An infrared thermometer (Everest interscience, Model 110) was used to measure leaf temperature. The porometer was calibrated before each series of measurements, which were made every second day. Measurements were made on a single leaf on each plant. The choice of the fourth youngest fully mature leaf meant that at the beginning of the experiment the measured leaves had been present on the plants before treatments commenced, while at the end of the experiment the measured leaves were part of the new flush of growth produced during the experimental period. The leaves on which stomatal resistance and conductance were measured had symptoms present in appropriate treatments.

Harvesting. – At the end of a 6-week treatment period, all the plants were destructively harvested. Each plant was partitioned into 11 organs (Fig. 1), as shown below.

Plant organs	Abbreviation used
Flush leaves	FL
Petioles of flush leaves	FP
Flush branches (primary and secondary branches)	FB
Old leaves	OL
Petioles of old leaves	OP
Old branches (secondary branches)	OB
Scion	SC
Stock	ST
Main root	MR
Old roots (brown in colour)	OR
New roots (white in colour)	NR
Whole plant	WHOLE

FL, FP and FB were produced during the experiment.

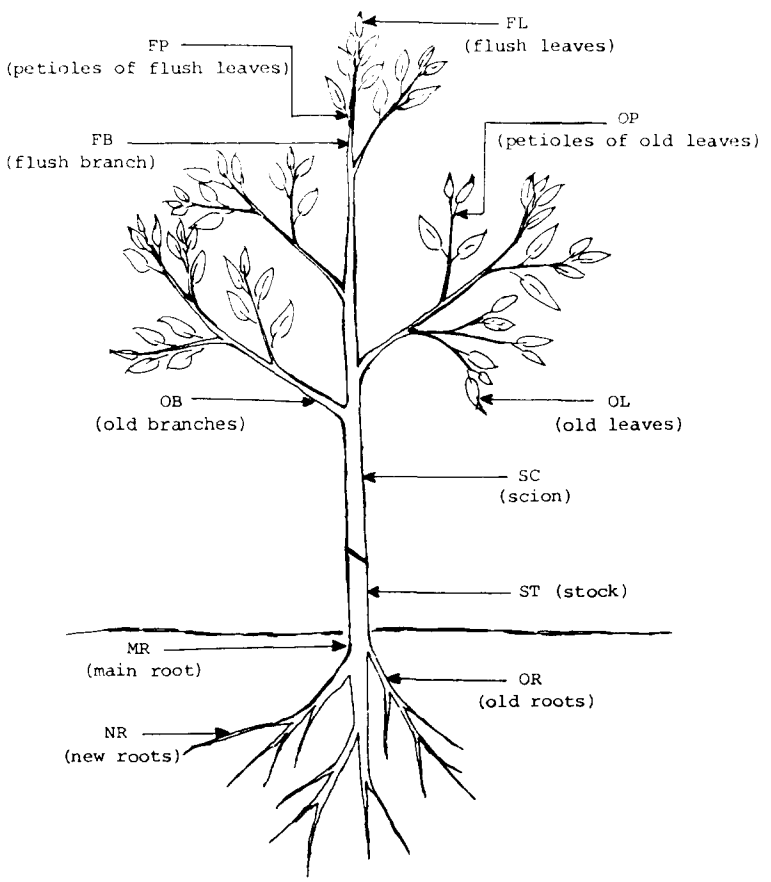

Fig. 1. The partitioning of avocado plants at harvest.

Roots were washed for 1–2 min with deionized water at 4 °C to minimize ion loss. Each organ was blotted dry and weighed immediately to determine fresh weight (FW). Leaf area and root length were measured using a leaf area meter (Liser model Li-3000) and a root length scanner (Comair), respectively. Fresh samples were cut into small pieces and oven-dried at 70 °C for 24 h. Material was weighed after 24 and 48 h drying. With small pieces of plant parts, 24 h drying was found to be satisfactory. Dry weight (DW) was obtained before grinding in a stainless steel mill.

The water content and succulence of each organ were calculated from the following equations:

$$\text{Water content} = \text{FW} - \text{DW}$$

$$\text{Succulence} = (\text{FW} - \text{DW})/\text{FW}$$

Changes in the proportional distribution of dry weight were studied using the ratio of the dry weight of each organ (DW_o) to that of the whole plant (DW_w). The specific root length (S_R) for each root category as well as for the whole root system was calculated as

$$S_R = (\text{root length})/(\text{root fresh weight})$$

Chemical analyses. – The concentrations of sodium and potassium in the dry matter of each organ were determined using atomic absorption spectrometry (AAS — Perkin Myer 403) after the ground samples were digested in nitric and perchloric acid (Johnson and Ulrich, 1959). Chloride was extracted in boiling weak sulphuric acid (pH 3.5) and was determined with a Buchler–Cotlove chloridometer.

The ratio of concentration in each organ (C_o) to that in the whole plant (C_w) for each element was used to express the effect of treatments on the change in distribution of each ion among organs. C_o was measured and C_w was calculated from M_w/D_w, where M_w was the mass of nutrient in the plant and D_w was the whole plant dry weight. It can be shown that C_o/C_w is the same as the ratio of the proportion of nutrient in the organ to the proportion of dry matter in the organ (Turner and Lahav, 1986).

The proportional distribution of each nutrient was calculated from the ratio between the content in each organ (CT_o) and that in the whole plant (CT_w).

As symptoms of necrosis occurred, degrees of damage were graded from 0 to 100%, where 0% represented no damage and 100% represented the whole of each leaf scorched.

Statistical analyses. – Transformations were used where data were not normally distributed. An angular transformation was used for the proportional

distribution, $\log_{10}$ for K/Na ratios and square root for the other data (Snedecor and Cochran, 1980). The same transformations were used on all the plant parts for the purpose of comparison, although significant reductions in variance were not achieved in all cases. Transformed values, with the appropriate LSD, are presented on the left-hand side of the figures. Back-transformed values are presented on the right-hand side of the figures.

Means of treatments were compared using the least significant difference (LSD) calculated from

$$LSD = SEd \times t_{0.05} \text{ or } t_{0.01}$$

where SEd represented the standard error of the difference between means.

RESULTS

Plant weight and leaf area. – Shading did not significantly change either dry weight or fresh weight in any of the individual organs of the plants. The 20 mM NaCl reduced dry weight of the whole plant from 75 to 60 g, primarily through its influence on FL and NR (Fig. 2).

Over all treatments the OR and NR were the most succulent organs. Shading tended to reduce succulence in most organs, but the effects were not significant. 20 mM NaCl increased the succulence of the new roots, but the remainder of the plant was largely unaffected (Fig. 3).

Neither shading nor NaCl changed top:root ratios of either fresh weight (1.17 ± 0.09) or dry weight (2.20 ± 0.20).

Leaf area of the FL of salt-treated plants was approximately one-third of the OL. Shading had no significant effect on the leaf area, but NaCl signifi-

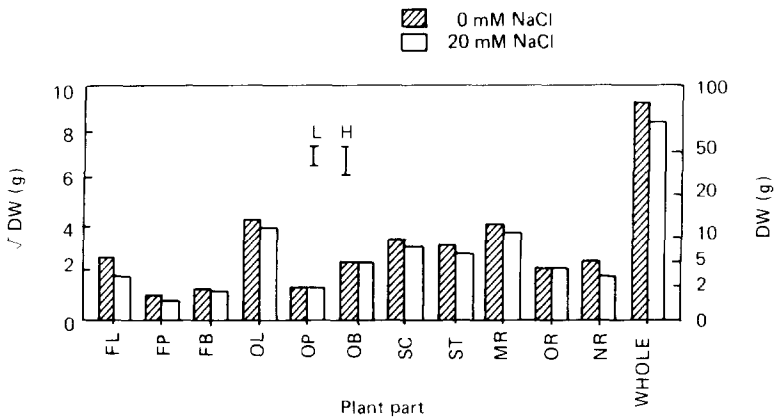

Fig. 2. The effect of 20 mM NaCl on dry weight of each organ and of the whole plant of 2-year-old 'Fuerte' avocados treated with NaCl in a glasshouse for a 6-week period. Bars L and H represent the LSD at 5 and 1%, respectively.

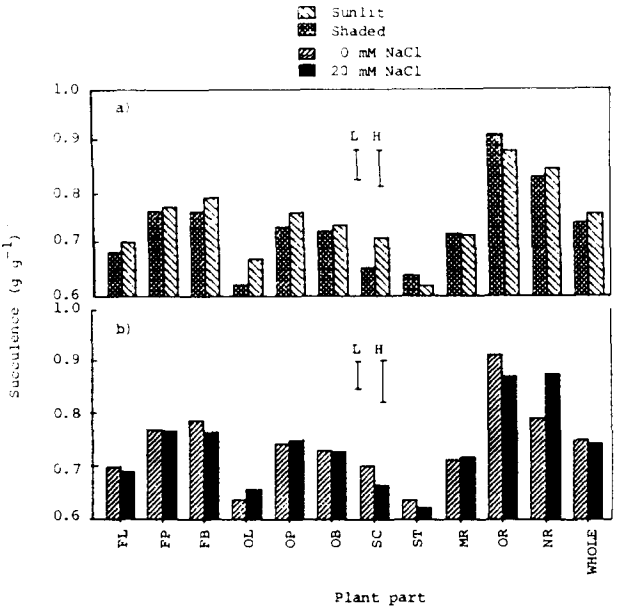

Fig. 3. The effect of (a) shading and (b) 20 mM NaCl on the succulence of each organ and of the whole plant of 2-year-old 'Fuerte' avocados grown in a glasshouse for a 6-week period. Bars L and H represent the LSD at 5 and 1%, respectively.

cantly reduced the area of FL by 25%. The interaction between shading and NaCl was not significant.

Root length. – NaCl decreased specific root length (S_R) of the NR by 17% (from 2.0 to 1.66 m g^{-1}) and the effect of NaCl was greater than that of shading (7% decrease), which did not cause any significant changes.

Leaf conductance and temperature. – Shading did not change leaf conductance on the abaxial surface of old avocado leaves (0.34 ± 0.02 cm s^{-1}). Increasing the concentration of NaCl from 0 to 20 mM NaCl in the root media lowered the leaf conductance from 0.38 to 0.31 cm s^{-1}. Apart from shading and NaCl, differences in leaf conductance were found at different periods of time and varied from 0.18 to 0.52 cm s^{-1}.

Leaf temperatures increased from 28.4 to 29.2 °C with an increase in NaCl from 0 to 20 mM, and while leaves of 20 mM NaCl plants were warmer than the air and leaves of 0 mM NaCl plants were cooler than the air, the differences were small (< 0.5 °C).

Nutrient responses

Concentration of chloride, sodium and potassium expressed on a dry weight basis. – Shading had no significant effect on the concentrations of chloride, sodium or potassium. Increasing NaCl increased the concentration of chloride in all organs and of sodium in most organs, except in FL, FB, OL and OP (Fig. 4a and b). The effect of NaCl on the concentration of chloride was greater than that of sodium. In OL, for instance, the concentration of chloride rose more than 6-fold, from 0.10 to 0.64%. Marked effects of NaCl on the concentration of sodium were in OB, SC, ST and in all root organs where the concentration increased more than 100%. 20 mM NaCl increased the concentration of potassium in some top organs (FL, FB and OB) but depressed the concentration in OR and NR (Fig. 4c). The effects were much stronger in the roots, where the

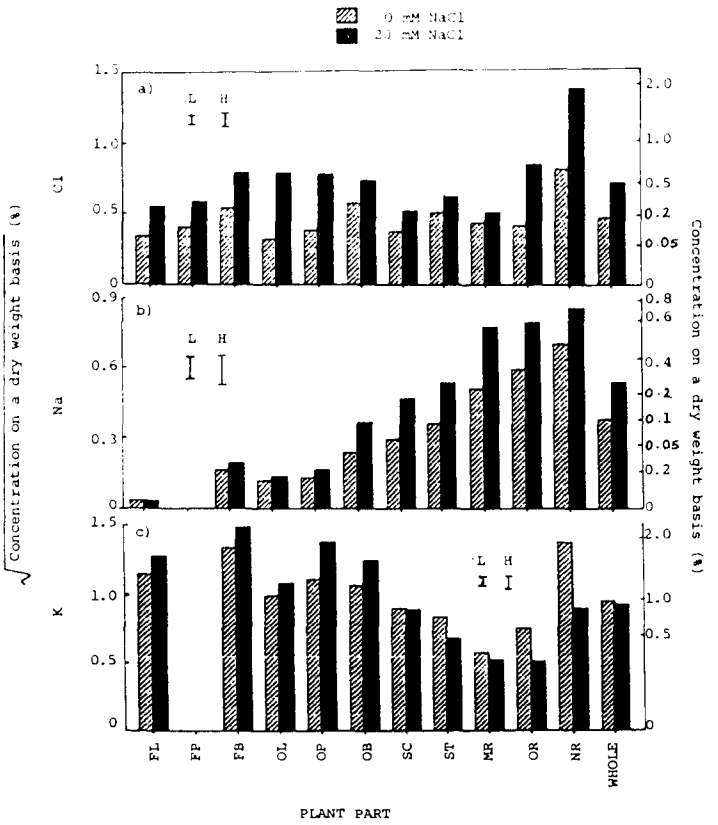

Fig. 4. The effect of 20 mM NaCl on the concentration of (a) chloride, (b) sodium and (c) potassium on a dry weight basis in each organ and in the whole plant of 2-year-old 'Fuerte' avocados treated with NaCl in a glasshouse for a 6-week period. Bars L and H represent the LSD at 5 and 1%, respectively.

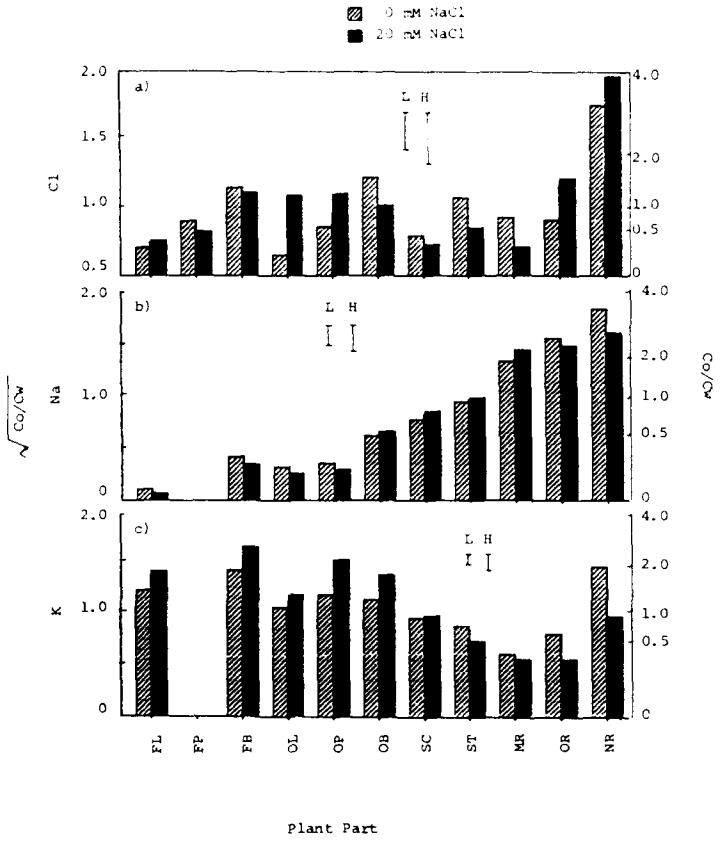

Fig. 5. The effect of 20 mM NaCl on the ratio of the concentration of (a) chloride, (b) sodium and (c) potassium in each organ to that in the whole plant of 2-year-old 'Fuerte' avocados treated with NaCl in a glasshouse for a 6-week period. Bars L and H represent the LSD at 5 and 1%, respectively.

reduction was about 55% in OR and NR compared with 50% increase in OP, 30% in OB and 25% in OL.

Shading did not change the ratio of the concentrations of any ions in each organ to that of the whole plant. By contrast, 20 mM NaCl increased the ratio of the concentration of chloride in OL from 0.4 to 1.2, and tended to increase the ratio in OP, OR and NR. There was a tendency towards a decrease in the woody organs such as in SC, ST and MR (Fig. 5a). The 20 mM NaCl increased the ratio of the concentration of potassium in tops but it decreased it in the ST and in all roots (Fig.5c). Although NaCl changed the ratio of concentrations of chloride and potassium, it had no effect on ratio of the concentration of sodium (Fig. 5b).

Concentration of chloride, sodium and potassium in the tissue water. – As shading and NaCl affected the succulence of some plant parts, it was worthwhile looking at the concentrations of chloride, sodium and potassium in the tissue water. Shading had no significant effect on concentrations of any ions.

NaCl increased the concentration of chloride in the tissue water of all organs (Fig. 6a) and increments were almost 3-fold in OR and OL. There was only a 1.5-fold increase in the whole plant.

The 20 mM NaCl increased the concentration of sodium, especially in the tissue water of the woody organs (Fig. 6b). There was a marked difference in the OR and NR, Na concentration increasing in the tissue water of OR but tending to decrease in NR as NaCl increased.

Shading did not change the concentration of potassium in any organs. By contrast, NaCl increased the concentration of potassium in the tissue water of

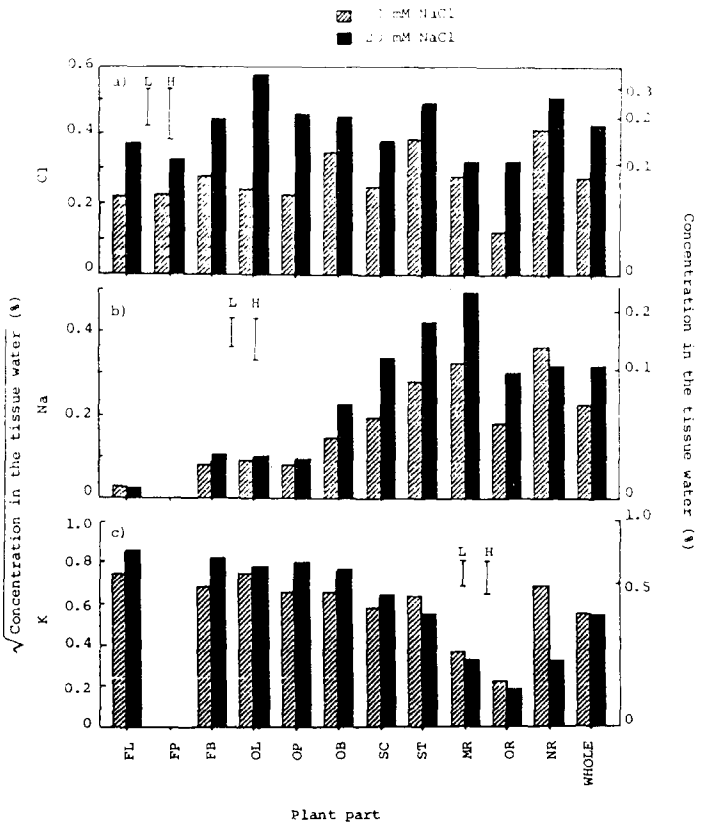

Fig. 6. The effect of 20 mM NaCl on the concentration of (a) chloride, (b) sodium and (c) potassium in the tissue water in each organ and in the whole plant of 2-year-old 'Fuerte' avocados treated with NaCl in a glasshouse for a 6-week period. Bars L and H represent the LSD at 5 and 1%, respectively.

the tops and tended to decrease it in roots (Fig. 6c). However, there was no effect on the concentration in the tissue water of the whole plant.

K/Na ratios. – The K/Na ratios changed over several orders of magnitude from near 1000 in FL to near 100 in FB, OL and OP, to near 10 in OB, SC and ST, and to near 1 in the roots (Fig. 7). The K/Na ratio in MR of plants subjected to 20 mM NaCl was about 50% less than in those subjected to 0 mM NaCl, but it decreased even more in the OR (from 2.0 to 0.4) and in the NR (from 4.0 to 1.0, Fig. 7). However, the effects of NaCl on the K/Na ratios in tops were not statistically significant.

Symptoms. – Symptoms of necrosis at the leaf margin and necrotic spots between the leaf veins were observed on the plants given 20 mM NaCl. The severity of the leaf necrosis on shaded plants was about 6% of the leaf area, and

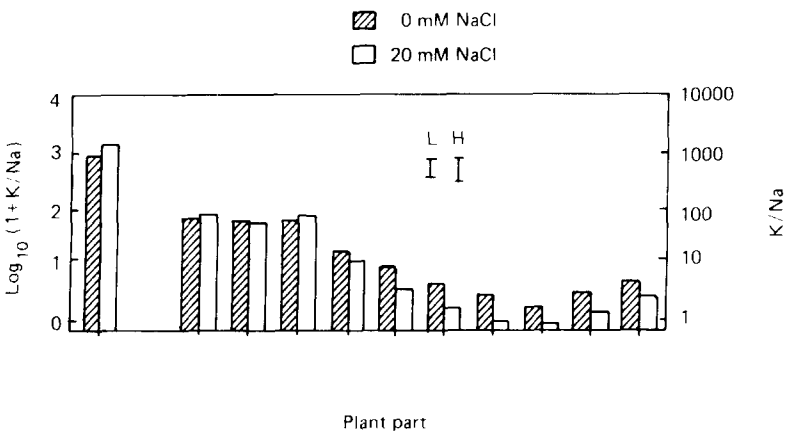

Fig. 7. The effect of 20 mM NaCl on the K/Na ratio in each organ and in the whole plant of 2-year-old 'Fuerte' avocados treated with NaCl in a glasshouse for a 6-week period. Bars L and H represent the LSD at 5 and 1%, respectively.

TABLE 1

The symptoms of leaf necrosis on avocado leaves at harvesting time. The degrees of necrosis were graded from 0 to 100% of leaf-area burnt

	Treatments (mM NaCl)	Necrosis (%)
No shade	0	2.50 ± 1.71
	20	26.67 ± 7.15
Shade	0	1.67 ± 1.05
	20	5.83 ± 2.01

was much greater on sunlit plants which had about 27% of the leaf area burnt (Table 1). Symptoms of leaf necrosis also occurred on the plants which had not received NaCl but the degree of severity was much less, and the values were not greater than 6%.

DISCUSSION

Expression of symptoms. – In our experiment increased necrosis of old leaves was associated with high concentrations of Cl, but only in full sunlight. At tissue water concentrations of 0.15% (42 mM) or less (0.5% dry matter) necrosis was less than 10%, but at higher concentrations necrosis varied from 0 to 50% on individual plants depending on the amount of sunlight being received (Fig. 8). The presence of symptoms on plants receiving 0 mM NaCl was not expected and cannot be explained on the basis of concentrations of Na, Cl or K in the leaf dry matter (Robinson, 1986).

In the field some parts of the tree are more exposed to the sun than others. The importance of shade in the expression of symptoms demonstrated here may explain some of the variation in symptom expression observed in the field. It would also indicate that "scorched" and "healthy" leaves sampled from the same tree may have very similar concentrations of Cl. One may then be unable to discern the cause of the "scorched" leaves, but chemical analysis of the tissue would be a more reliable indication of high salt than the appearance of symptoms.

We thought that the increased necrosis in sunlit leaves might be caused by their having a higher concentration of chloride. While there is some suggestion in the data that this might be true (Fig. 8), shading did not significantly influence the concentration of Cl in the leaves. An alternative explanation is the changed water status of the leaves leading to reduced conductance, higher leaf temperatures and heat damage. While NaCl reduced conductance and increased leaf temperatures, the changes were not thought to be large enough to cause significant changes in the rate of necrosis. However, leaf energy balance is very sensitive to changes in radiation and damage may occur over short time-periods. Air temperatures of 40°C were recorded in the glasshouse for short periods and these may have contributed to the necrosis.

Effect on growth. – Since shading did not reduce dry weight accumulation or leaf conductance, we assume that photosynthetic rate was not reduced by shading. This is supported by the data of Scholefield et al. (1980), which suggest a low light saturation for individual leaves of avocado.

The reduction in dry weight in plants which experienced 20 mM NaCl was proportional to the reduction in leaf conductance. Both components could have been influenced by changes in the internal water status of the leaves, a parameter which was not examined in this experiment. Thus, high salt may have

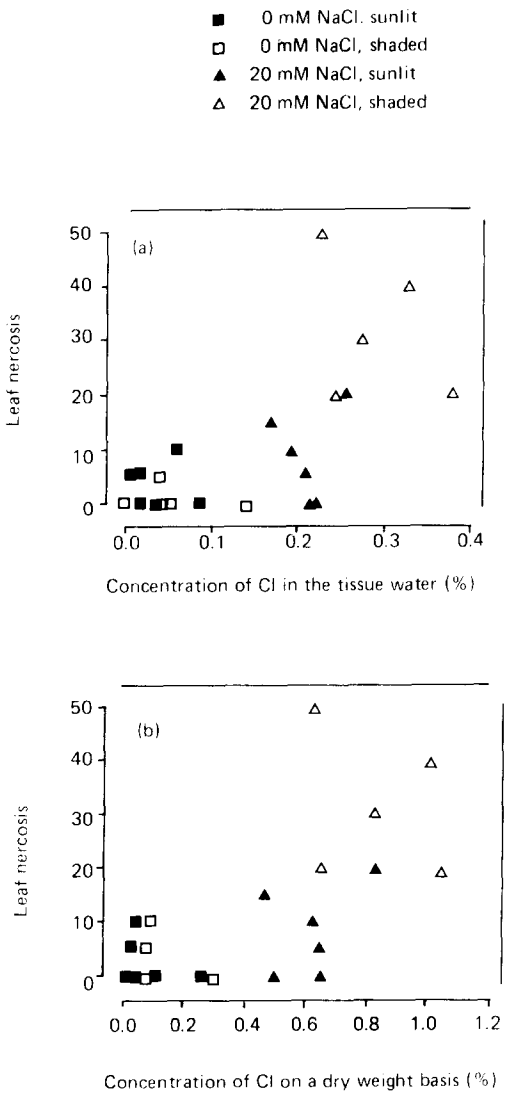

Fig. 8. The relationship between leaf necrosis and the concentration of chloride (a) in the tissue water and (b) on a dry weight basis in the old leaves of 2-year-old 'Fuerte' avocados grown in a glasshouse for a 6-week period.

reduced photosynthesis although the distribution of dry matter between flush leaves and new roots was unaffected by salinity (Fig. 2). In some other species water stress changes the dry matter distribution, e.g. Hoffman et al. (1971) found that water stress increased root growth at the expense of tops in cotton. The lack of response in this experiment may have been due, in part, to the short time-period involved for a woody species; 6 weeks.

We expected plants treated with NaCl to be more succulent, as found by Downton (1978), but in our experiment shading rather than NaCl increased succulence.

The new roots produced by plants treated with salt were thicker than the controls. These roots would then explore a smaller volume of soil, but this may be unimportant for mobile elements such as chloride.

Nutrient responses. – On a dry weight basis, high concentrations of chloride and sodium were found in the NR. Similar effects were observed by Haas (1950). The distribution of sodium within the plants — high concentrations in the roots and low concentrations in the tops — was similar to observations of Kadman (1964) on avocado and Townsend (1980) on several other species.

The 20 mM NaCl increased the concentration of Cl in all organs, with the old leaves being the most sensitive. The concentration was greater than the 0.25% regarded as toxic (Cooper and Gorton, 1950). Similar effects have been observed in avocado by Ayers (1950) and Downton (1978).

Although the concentration of sodium in plant parts increased, it did not reach toxic concentrations ($> 0.25\%$ in leaves (Robinson, 1986)).

Overall, the NaCl treatments caused Cl to accumulate in the tops, Na to accumulate in the woody organs and a greater proportion of K to be allocated to the tops.

Differences among organs in the concentration of nutrient in the dry matter were not accounted for by expressing ion concentration on a tissue-water basis (Cassidy, 1966). The effect of NaCl on the concentration of chloride was greatest in the tissue water of old leaves and least in the NR, where no effect was observed. When avocado was subjected to high salt, chloride was shifted from the tissue water in the OB to OL. This allowed the plant to remove salt, but at the expense of loss of leaves. Thus organs differed in their ability to accumulate chloride.

ACKNOWLEDGEMENT

W.J. Simmons provided helpful technical advice on the mineral analysis of plant samples.

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