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ON THE MECHANISM OF CHLORIDE TOXICITY

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The sandculture experiment with chloride as a variable has provided an excellent opportunity for detailed examination of the effects of excessive chloride on bearing avocado trees. Hass avocado trees have been under chloride treatment for the past four years. A summary of the more practical considerations of investigation such as leaf symptoms, mineral nutrition, growth and fruit characteristics have been published in a recent issue of the California Avocado Society Yearbook (1967). The present report covers some of the more fundamental aspects of chloride toxicity - the mechanism(s) of injury.

Experimental Procedures

Avocado trees (Hass scion — Mexican root stock) were transferred from a commercial nursery in the San Diego County to large, outdoor sandculture units located at the Riverside campus. For the first two years all trees received uniform, complete nutrient solution. Differential treatment consisted of amending the nutrient solutions with chloride salts of calcium, magnesium and potassium in amounts sufficient to produce a range of chloride extending to 20 meq Cl/l. However, the total salt concentration of all treatment solutions were equalized by adjusting the composition of the nutrient solutions. The differential treatments (5 chloride concentrations, replicated 4-fold) have been in effect for over four years at this rime. Details of the construction and general operational procedure of the sandculture apparatus are available in the California Avocado Society Yearbook (1967).

The general procedure consisted of collecting leaf samples every two months for complete chemical analysis of all nutrients (Ca, Mg, K, P, S, B, Cu, Fe, Mn, Mo, Zn, and Cl) to follow seasonal variations as well as to note effects of chloride on nutrition of the tree as determined by leaf analysis. In addition, the effects of chloride on leaf symptoms, tree growth, water relationships, fruit characteristics, etc., were noted and subsequently reported. (1, 2)

As for the techniques employed in the study of injury mechanisms, they were varied, but in general, were designed to determine the distribution of chloride in the plants. In particular, the leaf was carefully examined by several techniques to determine the distribution pattern of chloride therein — not only as to leaf position such as the tip or margin, but also as to cellular or extracellular concentrations. Additional details will be given below.

Results and Discussion

Leaf Analysis-—Mineral Nutrition: Although incipient chloride injury symptoms create the appearance of a chlorosis associated with a deficiency of iron or zinc, no abnormalities were observed in the leaf analysis. The leaf analysis program clearly established that no nutritional disorders were being induced by the chloride treatment as all levels of the macro- and micronutrients were above deficiency levels, nor was there an interaction between leaf chloride and any of the other elements analyzed. Unquestionably, the effects of excessive chloride in the substrate on the avocado tree were due to chloride specifically.

Specific Chloride Effects: Examination of the leaf chloride vs substrate chloride relationship illustrated in figure 1 reveals a clue to accounting for the avocado tree's unusual sensitivity to chloride. The above relationship is sometimes referred to as the "absorption isotherm," the character of the curve indicating something of the absorption process. Referring to figure 1, we note that chloride uptakes as indicated by leaf chloride increases in proportion to the substrate concentration up to a concentration of 15 meq Cl/l; however, increasing the substrate further results in a marked increase in chloride uptake. We may speculate that exceeding a critical substrate concentration disrupts the absorption process in some manner, permitting greater amounts, possibly excessive amounts, of chloride to enter the root system. Chloride does not accumulate in the roots; actually, the concentrations therein are comparable to those of the substrate. Apparently, the chloride is conducted rather directly from the root surfaces to the leaf tissue where it concentrates as the water is transpired. Under conditions of high moisture demand and excessive chloride in the substrate, the tree would rapidly accumulate substantial quantities of chloride in the leaf tissue.

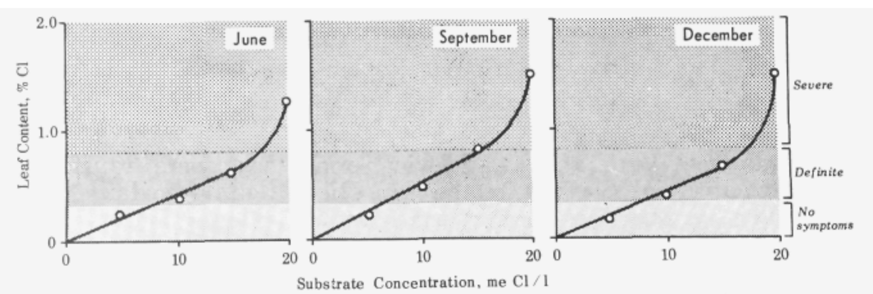

Figure 1. Leaf chloride of the most recently matured leaf in relation to substrate chloride and season of year.

Leaf Chloride Distribution: Examination of leaf sections for chloride reveal that under conditions of excessive chloride in the substrate a pattern of chloride accumulation coincided with the necrosis or leaf burn pattern. A. R. C. Haas (3) called attention to the above pattern some forty years ago. The fundamental question though is about the specific location of the chloride, i.e., is the chloride exclusively contained within the cells? We were able to resolve the question by using a special technique which enabled us to force the zylem fluids or extracellular fluids out of a leaf for chemical analysis. The procedure consisted of placing a leaf inside a pressure chamber in such a manner that the petiole extended out of the chamber; the blade was, of course, sealed in. Pressure was applied to force zylem fluid out the petiole where it could be collected for examination. The first few drops represent the zylem fluid present within the petiole at time of collecting the leaf for examination and accordingly, the chloride content would be quite low. However, subsequent drops attain a maximum chloride concentrate perhaps representative of the extracellular fluids initially present in the leaf margin tissue. Representative data are given in table 1. Substantial extracellular salt concentrations are associated only with the high chloride treatment and with chloride specifically. Unquestionably, chloride accumulates outside of the cell to the extent of creating osmotic pressures (related to the total dissolved solids) which may restrict movement of water into the cell.

TABLE 1. Electrical conductivity (E.C.) and chloride content of zylem fluid from the most recently matured leaves from trees with and without excessive chloride treatment. Leaves were collected during the fall season.

Fraction of Zylum Fluid	Zylem fluid from trees receiving: Trace Chloride Substrate		20 meq C1/1 Substrate	
Drops	E.C. mmhos/cm	C1 meq/1	E.C. mmhos/cm	C1 meq/1
1st	1.0	1.5	3	25
10th	0.7	1.7	25	300
20th	0.7	1.5	30	315

The matter of extracellular chloride was also approached by an independent method with essentially the same conclusion. Specifically, avocado leaves from trees under excessive chloride treatment were desorbed with water for various periods of time. The chloride desorbed as a function of the desorbing time, indicates that same 25 to 30% of the total chloride initially present in the leaf desorbs rapidly and that a substantial portion of the leaf chloride resist desorption even after a period of 50 hours. While there is not complete agreement as to the significance of such a desorption curve, it indicates without question different release rates, presumably due to the source (extracellular or cellular). Measurements of the "free space" within a leaf (void space between cells primarily) are lacking for the avocado tree; but on the assumption of the volume being 25% of that of the entire leaf, we may visualize concentrations of chloride external to the cells being essentially equal to that of the cells. For example, 25% of the leaf chloride assigned to free space volume constituting 25% of the leaf volume indicates an extracellular chloride concentration equal to or greater than that of the cells.

The significance of extracellular salts concentrations becomes evident upon considering the water relations of the cell. Restricted water entry may lead to a dehydration and disrupted metabolic activity such that the leaf develops a leaf burn and if severe enough abscisses prematurely.

Proposed Mechanism

Under conditions of excessive chloride being present in the substrate, the avocado tree absorbs chloride at a rate exceeding the rate (and capacity) that chloride may be absorbed by the leaf cells, causing chloride to acccumulate extracellularly to levels inhibiting the transfer or movement of sufficient water to the adjacent cells to sustain a satisfactory rate of metabolism. The restriction of water flow into the cells may bring about a dehydration of the cells, interfering with metabolic processes and manifesting leaf burn and defoliation. The reduced leaf area for photosynthesis would curtail energy production. In addition, the energy expenditure for chloride accumulation within cells would be at the expense of energy required for growth processes.

The above hypothesis on chloride injury is, of course, specific for the avocado tree under chloride stress. Similar or much higher concentrations of other common anions found in the soil solution are not injurious to the tree. Regarding the plant species factor, no chloride injury specificity is observed with field crops and vegetable crops in general.

LITERATURE CITED

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