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Carbohydrate depletion in roots and leaves of salt-stressed potted *Citrus clementina* L.

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Abstract

In citrus, damage produced by salinity is mostly due to toxic ion accumulation, since this salt-sensitive crop adjusts osmotically with high efficiency. In spite of this observation, the putative role of sugars as osmolites under salinity remains unknown. In this work, we have studied carbohydrate contents (total hexoses, sucrose and starch) in leaves and roots of citrus grown under increasing salinity. The experimental system was characterized through the analyses of several parameters known to be strongly affected by salinity in citrus, such as chloride accumulation, photosynthetic rate, ethylene production and leaf abscission. Three-year-old plants of the Clementina de Nules cultivar grafted on Carrizo citrange rootstock were watered with three different levels of salinity (NaCl was added to the watering solutions to achieve final concentrations of 30, 60 and 90 mM). Data indicate that salt stress caused an accumulation of chloride ions in a way proportional to the external increase in NaCl. The adverse conditions reduced CO_2 assimilation, increased ethylene production and triggered abscission of the injured leaves. Data also show that salinity induced progressive depletions of carbohydrates in leaves and roots of citrus plants. This observation clearly indicates that sugar accumulation is not a main component of the osmotic adjustment machinery in citrus.

Introduction

Salt stress induces drastic changes in the physiology of plants (Munns 2002). During initial exposure to salinity, plants experience water stress, which in turn reduces leaf expansion. During long-term exposure to salinity, plants experience ionic stress, which can lead to premature abscission or senescence of adult leaves, and thus to a reduction in the photosynthetic area available to support continued growth (Cheeseman 1988; Munns 2002). Plants growing in salinized media may reduce internal water deficits through the absorption of inorganic ions and the synthesis of organic solutes for osmotic adjustment. The role of carbohydrates as active osmolytes has been studied in many plant species with contrasting results depending on the genotype, the severity and duration of the stress, and the tissue studied (Rathert 1984; Cheeseman 1988; Gucci et al. 1998; Kerepesi et al. 1998; Sultana et al. 1999; Balibrea et al. 2000; Martínez-Ballesta et al. 2004). Surprisingly, in citrus, which

can be included among the most sensitive crops to salinity (Storey and Walker 1999; Ferguson and Grattan 2005), little information is available on carbohydrate changes during salt stress. Thus, Lloyd and Howie (1989a) showed consistently reduced levels of soluble sugars and starch in leaves of 24-year-old trees salinized for several years, while Walker et al. (1984) found suberization of root tissues associated to a decrease in root reducing sugar concentrations in salt-stressed citrus plants. On the other hand, it is well known that citrus adjust osmotically with high efficiency. Although the involvement of inorganic ions and also of compatible solutes such as proline in this process appears to be well documented (Maas 1993; Gómez-Cadenas et al. 1998), the role of sugars as possible osmolytes has not been either well established or discarded.

An important trait of salt-sensitive genotypes is that they are unable to exclude salt ions from the shoots (Munns 1993). Certain citrus genotypes such as Cleopatra mandarin or Rangpur lime rootstocks can be classified as relatively tolerant due to their ability to restrict chloride ions to roots while others, such as Carrizo citrange, proved to be more sensitive to salinity (Storey and Walker 1999). It is also well known that in citrus physiological disturbances produced by salinity are associated with leaf chloride build-up rather than with sodium accumulation (Romero-Aranda et al. 1998) and it has been proposed that chloride absorption and, hence, salt tolerance in citrus depends to a great extent upon water use (Moya et al. 2003). Salinity causes suberization of root tissues (Walker et al. 1984), a decrease in root hydraulic conductivity, an impaired assimilation of mineral nutrients (Ruiz et al. 1997), visual toxicity symptoms (Chapman 1968) and eventually leaf abscission (Gómez-Cadenas et al. 1998, 2002). Furthermore, chloride accumulation in citrus leaves decreases net photosynthetic rate, transpiration and stomatal conductance while activates plant antioxidant machinery (Arbona et al. 2003; Iglesias et al. 2004). Abscisic acid and ethylene have been involved as modulators of some of these responses of citrus to high salinity (Gómez-Cadenas et al. 1998).

To evaluate whether an accumulation of leaf carbohydrates can contribute to adjust the osmotic potential of citrus under salt stress, in the present work, citrus plants were watered with three different levels of salinity (NaCl was added to the watering solutions to achieve final concentrations of 30, 60 and 90 mM). Results are discussed in terms of physiological relevance.

Materials and methods

Plant material

Experiments were carried out on 3 year-old plants of the Clementina de Nules cultivar (*Citrus clementina* L. cv Nules) grafted on Carrizo citrange rootstock (*Poncirus trifoliata* L. Raf. × *Citrus sinensis* L. Osb.) obtained from a commercial nursery. Plants were immediately transplanted to 10 l pots filled with perlite as a substrate and allowed to acclimate for 6 months. Greenhouse conditions were the following: day temperature, 24–29 °C; night temperature, 17–19 °C; relative humidity, 50–85%. During the acclimation period, plants were watered three times a week with 1 l of a modified Hoagland solution for citrus (Bañuls et al. 1997). After the acclimation period, actively-growing new vegetative flushes were found in all plants.

Treatments

Plants were divided into 4 groups of 30 plants, randomly distributed along the experimental area in the greenhouse. Each group of plants was watered three times a week with 1 l of a modified Hoagland solution that did not contain chloride salts. Furthermore, distilled water was used to make this solutions. The measured chloride concentration of the watering solution used for control plants was 0.17 mM. Different groups of plants were watered with the same solution but NaCl (Reagent grade, JTBaker, Madrid, Spain) was added to reach final concentrations of 30.17, 60.17 and 90.17 mM, respectively. From this point on, and to facilitate the reading of the paper, the different treatments will be referred as control, 30, 60 and 90 mM.

The whole experiment was completely carried out in greenhouse conditions. Five plants per group were marked and used for leaf abscission measurements. Sampling was always performed at same time in the morning and three to five plants

per treatment used each day. Intermediate leaves and young roots were excised, minced and frozen in liquid nitrogen, immediately placed in hermetic bottles and lyophylized. After lyophylization dry material was ground to powder and kept dry until analysed.

Photosynthesis measurements

Net photosynthetic rate was measured with a LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) equipped with a 18 cm^3 prismatic leaf chamber (see Iglesias et al. 2002).

Chloride analysis

Analysis of chloride anions was performed as described in Moya et al. (1999). Briefly, plant dry tissue was incubated overnight with a mixture of glacial acetic acid and nitric acid in water. Supernatant was filtered and an aliquot used for the automatic titration in a chloridemeter (model 926, Sherwood Scientific Ltd. Cambridge, UK).

Ethylene production

Detached intermediate citrus leaves were kept for 4 h with their petioles submerged in water in tubes sealed with a silicone cap. One ml of headspace gas was extracted and injected into a gas chromatograph type Agilent 4890D, (Agilent technologies, Inc. Wilmington, DE, USA) equipped with an activated alumina column and a flame ionization detector (Gómez-Cadenas et al. 1996).

Carbohydrate analysis

Samples were extracted with 80% ethanol and purified sequentially by cation and anion exchange columns, and by C-18 cartridges. Sucrose and total hexoses were analyzed with a Waters-Millipore HPLC system (Milford, MA, USA) equipped with a high performance carbohydrate column (4.6×250 mm, Waters-Millipore) and a R401 differential refractometer. Starch was determined in the remaining pellets as glucose released.

Statistical analyses

When appropriate, means were compared by using the least significant difference (LSD) test ($p \leq 0.05$). Statistical analyses were performed using StatGraphics Plus (V. 2.1.) for Windows (Statistical Graphics Corp., MD, USA).

Results

Chloride accumulation

Control Clementine plants showed levels of chloride in leaves ranging between 3.9 and 8.7 mg g dry weight^{-1} (DW) throughout the experimental period (Figure 1). Leaf chloride levels in treated plants increased uniformly during the first 30 days of salt stress despite the amount of NaCl added. Afterwards, the rate of ion accumulation in 90 mM-treated plants increased rapidly, reaching 33.9 mg g DW^{-1} 60 days after the onset of the experiment (4.7-fold higher than control plants). In 60 mM-treated plants, leaf chloride accumulation was lower but still important (2.3-fold of accumulation regarding control plants at day 60). Plants watered with 30 mM NaCl showed a slight but constant increase in leaf chloride levels throughout the period studied (Figure 1).

Chloride content in roots increased rapidly after salt treatments to reach distinct maximums depending upon the intensity of the stress (Figure 2). Sixty and 90 mM NaCl treatments

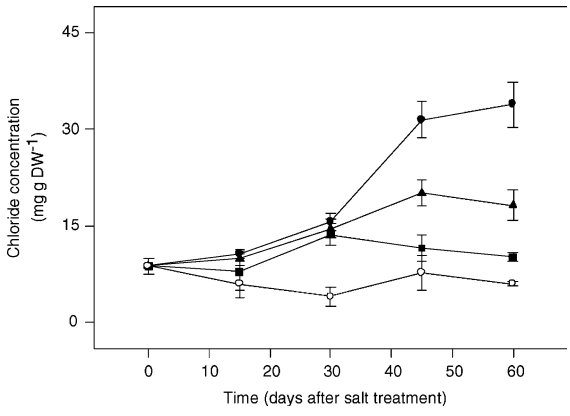

Figure 1. Leaf chloride concentration in citrus plants under salt stress: Control plants (○); plants treated with, 30 mM NaCl (■); 60 mM NaCl (▲); 90 mM NaCl (●). Data are means ± standard errors.

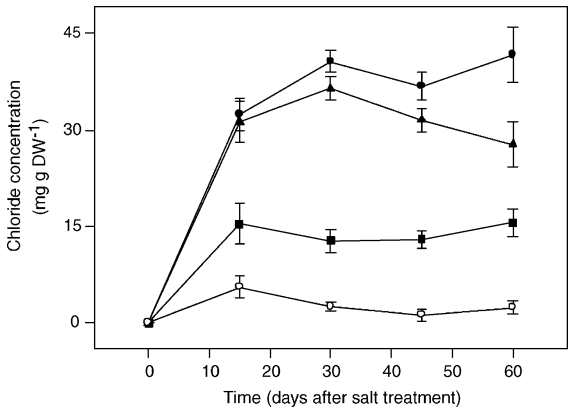

Figure 2. Root chloride concentration in citrus plants under salt stress: Control plants (○); plants treated with, 30 mM NaCl (■); 60 mM NaCl (▲); 90 mM NaCl (●). Data are means ± standard errors.

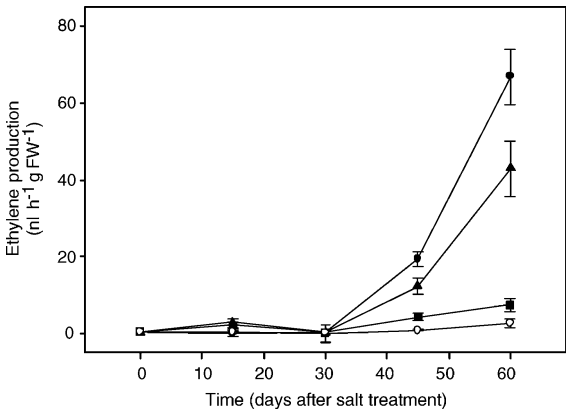

Figure 3. Leaf ethylene production in citrus plants under salt stress: Control plants (○); plants treated with, 30 mM NaCl (■); 60 mM NaCl (▲); 90 mM NaCl (●). Data are means ± standard errors.

caused large accumulations of this ion (about 5.5-fold of increase compared with control plants 15 days after the onset of the treatments). Afterwards, chloride levels in roots of both groups of plants remained high although at the end of the experiments 90 mM-treated plants showed higher concentration (41.6 vs. 27.6 mg g DW^{-1} in 60 mM-watered plants). In plants watered with 30 mM NaCl, lower accumulation of chloride was found in roots. However, levels were still 2.6-fold higher than control plants after 15 days of salt stress and remained constant but higher than controls until the end of the experiment.

Ethylene production

Leaf ethylene production (Figure 3) remained at basal levels in control plants during the whole period studied (ranging between 0.2 and 2.7 nl h^{-1} g^{-1}). Salt treatments caused increases in ethylene release that were significant after 30 days of salinization. Thus, 60 days after the onset of the experiment, levels in 30, 60 and 90 mM NaCl-treated plants were 2.6-, 15.0- and 23.9-fold higher than those in control plants.

Leaf abscission

Plant defoliation increased proportionally to the extent of sodium chloride added to the watering solution (Figure 4). Plants under the three levels of salinity kept most of their leaves attached until day 35. After this date, abscission increased dramatically in 90 mM NaCl-treated plants to reach 90% of leaves after 60 days of salinization. Plants treated with 60 mM NaCl showed the same pattern of leaf abscission although lower percentages were observed (57% at day 60). At the end of the experiment, leaf abscission reached a 20% in plants watered with 30 mM NaCl. It is interesting to note that the ethylene production and leaf abscission followed parallel patterns along the experimental period.

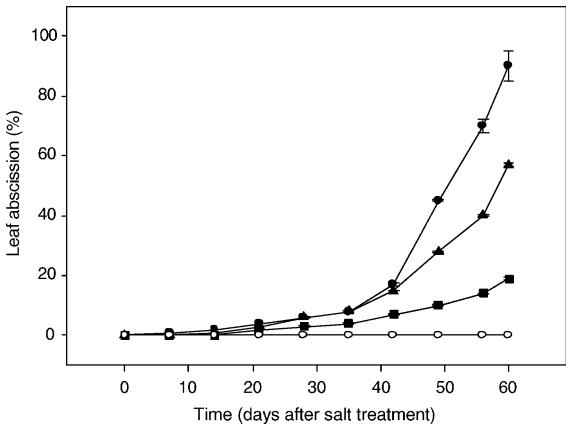

Figure 4. Leaf abscission in citrus plants under salt stress: Control plants (○); plants treated with, 30 mM NaCl (■); 60 mM NaCl (▲); 90 mM NaCl (●). Data are means ± standard errors.

Photosynthesis rate

Table 1 shows data on photosynthetic rates of the different groups of plants studied. High salinity in the watering solution caused important reductions in this parameter that were proportional to the NaCl concentration. After 45 days of salt stress, photosynthesis was reduced and values remained low at the end of the experimental period. In this way, plants treated with 30, 60 and 90 mM NaCl showed net photosynthetic rates that in average were 11.0%, 33.1% and 44.5% lower than control plants, respectively.

Carbohydrate content

All soluble leaf carbohydrates were impaired by salinity (Figure 5). Total hexose (glucose plus fructose) levels decreased proportionally to the extent of salt added to the watering solution. In comparison with control plants, those treated for 60 days with 30, 60 and 90 mM NaCl showed reductions of 33.5, 56.5 and 78.9% in hexose concentration, respectively (Figure 5a). Sucrose content was similarly affected by salinity (Figure 5b) and levels in leaves of all treated plants decreased linearly, achieving the lowest concentration on the last day of sampling (decreases of 44.1, 63.1 and 76.1% in plants treated with 30, 60 and 90 mM NaCl, respectively). Starch levels in salinized plants were also lower than those in control plants (Figure 5c). Starch contents in 30 mM NaCl-treated plants decreased 21% with respect to control plants 45 days after the onset of the salinization and remained at the same level the rest of the experimental period. Starch concentration reductions were more drastic in 60 and 90 mM-NaCl treated plants reaching the lowest levels (41 and 44% reductions, respectively compared with control plants) on the last day of sampling.

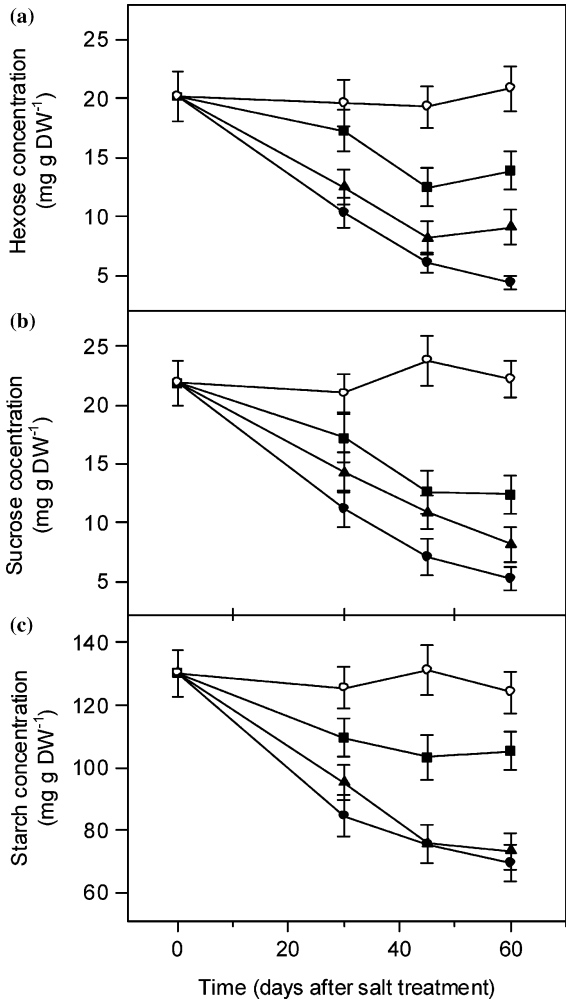

Figure 5. Leaf carbohydrate contents in citrus plants under salt stress, (a) Hexoses; (b) Sucrose; (c) starch: Control plants (○); plants treated with, 30 mM NaCl (■); 60 mM NaCl (▲); 90 mM NaCl (●). Data are means ± standard errors.

Table 1. Effect of salinity on net photosynthetic rate in *Citrus clementina*. Measurements were performed at environmental humidity and CO_2 at 750 μmol m^{-2} s^{-1}. Within the cuvette, average temperature was 23.5 ± 0.8 °C and leaf-to-air vapour pressure deficit was 1.5 ± 0.2 kPa. Data, expressed in μmol CO_2 m^{-2} s^{-1}, are means ± standard errors. Values in each column noted with different letters differ significantly at $p < 0.05$.

Treatment	Time after treatment	
	45 days	60 days
Control	9.3 ± 0.3^{a}	8.5 ± 0.5^{a}
30 mM NaCl	8.3 ± 0.4^{b}	7.6 ± 0.7^{b}
60 mM NaCl	6.8 ± 0.2^{c}	5.2 ± 0.6^{c}
90 mM NaCl	5.1 ± 0.5^{d}	4.9 ± 0.6^{c}

In roots, the different salt treatments caused similar reductions in hexose levels (Figure 6a). The average reduction in hexose concentration was 16% after 30 days of stress and remained constant during the whole experimental period with only slight differences among treatments. The pattern of root sucrose depletion in response to

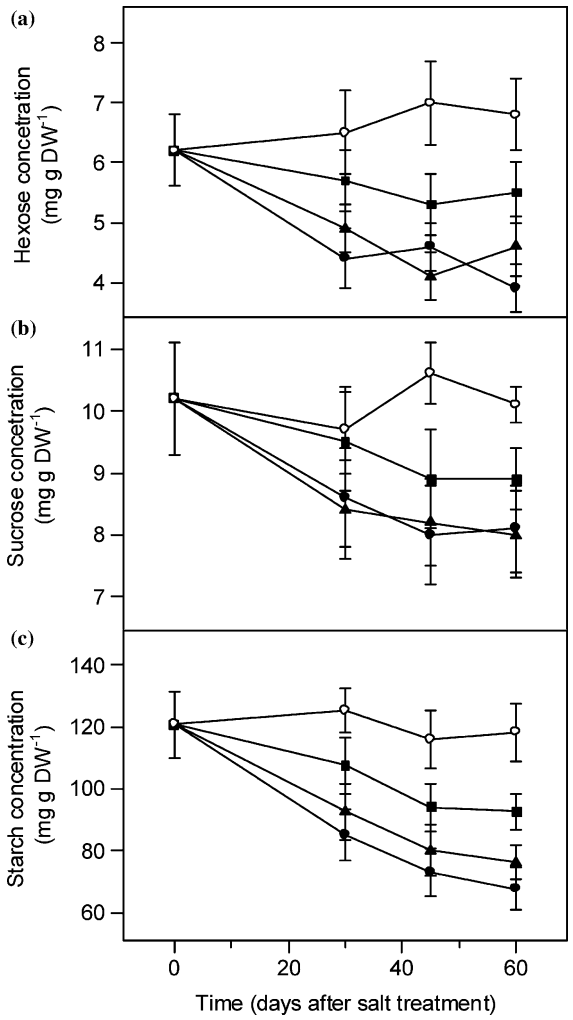

Figure 6. Root carbohydrate contents in citrus plants under salt stress, (a) Hexoses; (b) Sucrose; (c) starch: Control plants (○); plant treated with, 30 mM NaCl (■); 60 mM NaCl (▲); 90 mM NaCl (●). Data are means ± standard errors.

salinity was similar to that followed by hexose content (Figure 6b) and no important differences were found among salt treatments. The reduction in root sucrose contents reached an average of 21%. In terms of root starch concentration (Figure 6c), differences between control and salt-treated plants were observed after 30 days of stress. Salinized plants showed decreases in starch accumulation in a way proportional to the extent of salt stress imposed. Thus, although no important differences between 60 and 90 mM-NaCl treated plants were found, both groups of plants showed levels of starch in roots very low at the end of the experiment (reductions of 35.4% and 42.6% regarding control plants in 60 and 90 mM NaCl-treated plants, respectively) while 30 mM NaCl-treated plants showed intermediate levels (21.7% of reduction).

Discussion

The injuries of salinity on citrus physiology are caused by two main effects, an osmotic stress due to the high concentration of saline ions nearby the root zone and a toxic effect promoted by chloride ion accumulation in plant tissues (Gómez-Cadenas et al. 1998; Ferguson and Grattan 2005). Data shown in Figures 1 and 2 indicate that, in the experiments reported in this work, Clementine plants exposed to high levels of salinity in the watering solution clearly increased chloride content both in roots and leaves. In roots (Figure 2), the pattern of accumulation can be divided into two phases, an early linear increase (until 18 days after the onset of salt treatment) and a subsequent period of stabilization (until the end of the studied period). It is worth to note that the pattern of chloride accumulation in leaves (Figure 1) could be adjusted to a sigmoidal curve where, the exponential increase started after 18 days of salinization. Taken in consideration that the amount of chloride accumulated was proportional to the NaCl added to the watering solution in both roots and leaves, the model seems to indicate that when the equilibrium between root chloride concentration and external medium was reached, translocation to the shoots was enhanced. Chloride accumulation in leaves, apparently led to a progressive intoxication and to leaf abscission, when ion concentration reached deleterious levels. Leaf abscission (Figure 4) was proportional to the rate of leaf ethylene production (Figure 3) and also parallel to the amount of chloride accumulated in these organs (Figure 1). These data demonstrate that the physiological behavior of plants in these experiments was similar to that previously reported for our group in citrus under severe salt stress (Gómez-Cadenas et al. 1998, 2002). Furthermore, current data expand previous findings to lower concentrations of NaCl in the watering solution.

In terms of osmotic adjustment, it is known that the accumulation of salts in the substrate triggers a

transient water deficit that induces an increase in ABA accumulation and stomatal closure (Gómez-Cadenas et al. 1998, 2002). In these conditions, plants accumulate proline and ions in the leaves to decrease water potential and maintain a proper water flux and leaf turgor (Bañuls et al. 1997; Gómez-Cadenas et al. 1998; Arbona et al. 2003). The significant contribution of the results reported here, relays in the observation that salinity reduced carbohydrate content in citrus leaves (Figure 5). This allows us to discard the hypothesis that assigns a role for carbohydrates in maintaining high turgor potential in leaves of citrus under prolonged stress. Despite the contrasting information found in the literature on the role of carbohydrates as osmolytes (Rathert 1984; Cheeseman 1988; Gucci et al. 1998; Kerepesi et al. 1998; Sultana et al. 1999; Balibrea et al. 2000; Martínez-Ballesta et al. 2004), data presented in this work together with previous research (Bañuls et al. 1997; Gómez-Cadenas et al. 1998; Arbona et al. 2003) seem to indicate that the osmotic adjustment in citrus under salt stress is mostly dependent upon accumulation of proline and inorganic ions.

The important reductions in hexoses, sucrose and starch in leaves (Figure 5) proportional to the degree of salinization could be a consequence of the decrease in CO_2 assimilation (Table 1, see also Bañuls et al. 1997; Gómez-Cadenas et al. 2002) and might account for the impairment in plant growth and metabolism generally found in response to salt stress. Another implication of the starch and sucrose depletion promoted by the different levels of salinity is that leaves could change from source to sink under these adverse conditions. Lloyd and Howie (1989a, b) proposed that this change in leaf behavior can be responsible for a reduction of flowering in citrus. In 24-year-old citrus trees growing under moderate salt stress for 5 years, these authors observed reductions in carbohydrates that correlated with a greater number of vegetative flushes in spring at the expense of reproductive and mixed ones.

The root system has always been, and still is the 'hidden part' of the plant. However, its function in citrus physiology is crucial. Besides the acknowledged role in provision of water and mineral nutrients, citrus roots are probably the most important storage organ. Roots accumulate carbohydrates in winter and play a critical role in exporting them to the developing fruitlets during the early steps of fruit set (Goldschmidt and Koch 1996). Figure 6 shows that in roots of salt-stressed citrus, reductions of hexoses, sucrose and starch were similar to those detected in leaves although less marked differences between treatments and a delay in time were observed. The concomitant reductions in leaves and roots seem to discard a massive transport of sucrose from the aerial part to the roots. On the contrary, the depletion in soluble and non-soluble root carbohydrates has to be explained in terms of disturbances in translocation of sucrose from shoots to roots and/or in carbohydrate metabolism.

In conclusion, data shown in this work indicate that salt stress causes progressive depletion of carbohydrates in leaves and roots of citrus plants. This observation, excludes a significant contribution of carbohydrates in the long-term maintenance of leaf turgor and seems to discard massive transports of photoassimilates from leaves to roots under these conditions. Data also show an accumulation of chloride ions in a way proportional to the external increase in NaCl. Tissue intoxication by ions seems to be related to a depletion in CO_2 assimilation and sugar contents both in leaves and roots. When the adverse conditions persist in time and/or intensity, hormonal signals trigger abscission of the injured leaves.

Acknowledgements

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