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THE INFLUENCE OF NaCl STRESS ON PLANT TISSUE NUTRIENT CONCENTRATIONS AND COMPARTMENTALIZATION OF Na AND Cl WITHIN LEAF SURFACE AREA OF PERSEA AMERICANA MILL (CV. 'FUERTE')

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ABSTRACT

Avocado is a salt sensitive fruit tree species that often faces serious problem of saline toxicity in many coastal areas, including those of Greece. Salinity cause negative effects on avocado yields and fruit quality, as well as on the survival of young plantlets. In order to investigate this problem, a 75-day pot experiment, inside an experimental greenhouse, with 6 NaCl treatments (0, 5, 10, 15, 20 and 30 meq NaCl /L) was conducted. The objectives of this study were to investigate the effects of NaCl stress on: i) the nutrition of 'Fuerte' avocado plants and Na and Cl distribution in different vegetative tissues (Top leaves, Basal leaves, Graft stem, Rootstock stem and Root), ii) the compartmentalization of Na and Cl within the following leaf surface area zones: Apex (1), Margin (2), Centre (3) and Base (4), in mature, as well as in young leaves. It was found that the highest Cl and K concentrations in the top and basal leaves were found in 30 meq NaCl / L. Na concentration was significantly higher in graft stem, rootstock stem and root, in the treatments 15-30 meq NaCl / L. Compartmentalization in mature leaves indicated that Cl concentration was significantly higher in the Apex leaf zone, in the treatments 15, 20 and 30 meq NaCl / L. With regard to Na compartmentalization, neither in the young leaves, nor in the mature ones were found significant differences in Na concentration among the leaf zones 1-4.

KEYWORDS:
Salt stress, avocado, leaf surface zone

INTRODUCTION

Avocado (Persea americana Mill.) is a profitable tree crop (FAO, 2019), with a total world production of more than 7 million tons in the year 2019. The last fifteen years, avocado has become an economically dynamic crop in the island of Crete, Greece, where several economically important cultivars, such as cv. 'Hass' and cv. 'Fuerte', are grown on more than 1,000 ha [1].

Salinity is a serious problem, particularly in fruit tree crops, due their long-life. The total area in the world affected by saline soils is 397 million ha [2]. The last decades it represents challenges for agriculture due to natural phenomena, extreme climatic changes and human activities [3]. Salinity affects stomatal conductance immediately [4]. At high salinity, salts can concentrate in leaves to excessive levels, and it is more likely that the damage is caused by Na+ rather than Cl- [5]. Salinity significantly reduces growth, productivity, and quality of crops, by affecting their physiology and biochemical attributes [6]. Due to increase in Na and Cl uptake, it was found that nutrient uptake (mainly those of N, Ca and K) is disturbed, which ultimately reduces plant growth [7].

Avocado is classified among the most sensitive to salinity stress fruit tree species [8]. Yield begins to decline at irrigation water EC above 0.75 dS/m with chloride concentrations>100 ppm [9]. Under salinity stress, several negative physiological and growth responses have been reported, such as decline in aerial biomass and Chl a/b concentrations, as well as leaf necrosis [10, 11], and yield decrease of more than 63% [12]. Due to the increasing establishment of avocado orchards in saline areas in Greece, it is important to study the salinity effects on the growth, yields, physiology and nutrition of *Persea americana* Mill. However, despite the studied physiological (gas exchange, chlorophyll concentration and fluorescence, tocopherols, water use efficiency), yield and growth responses of avocado plants to salinity stress [13, 10, 14, 12], a few published information exists on the effects of NaCl stress on the nutrition of *Persea americana* Mill. According to our knowledge, only Alvarez-Acosta [15] studied the NaCl stress on the nutrient metabolism (leaf, stem and root Na+, Cl-, K+,

Ca^{2+} and Mg^{2+} concentrations) of avocado trees, while [14] evaluated the salt stress tolerance of 13 avocado rootstocks (including plant nutrition data) with regard to their ability to restrict the absorption and transport of Cl- to the scion (cv. 'Hass'). In addition, more work has been published for genotype 'Hass' [11], than for cv. 'Fuerte', for which relatively limited published information on its tolerance to salt stress exists.

The objectives of this study were the following: i) to investigate the effect of NaCl stress on the nutrition of the avocado genotype 'Fuerte' plants, ii) to study the time variation of foliar Na, Cl, P and K concentrations to salt stress, iii) to investigate the compartmentalization of Na and Cl within the leaf surface area zones 1-4 (from the edge to the base of leaves) (Figure 2).

MATERIALS AND METHODS

Plant material and greenhouse conditions. The plant material of the experimentation consisted of two-year-old avocado plants (Persea americana Mill., cv. 'Fuerte'), which were grafted on 'Zutano' rootstock. The experiment was conducted in a greenhouse of the Aristotle University of Thessaloniki, faculty of Agriculture, in Thessaloniki (40◦32'_04.16''_N and 22◦59'_41.33''_E) for 75 days (from the middle of December to early March). The plants were grown in 35-L pots, filled with a mixture of sand and perlite (1:1). One month before the beginning of the experiment, the plants were irrigated only with high quality tap water, in order them to be acclimatized inside the greenhouse. During the experimental period, the temperature of the greenhouse was set at approximately 20-21 °C.

NaCl treatments. Six NaCl treatments were applied: The plants were randomized (based on their initial height and weight) and separated into 6 similar groups, each one irrigated with 50% modified Hoagland nutrient solution, containing 0, 5, 10, 15, 20 or 30 meq NaCl / L. In each treatment, 8 plants-replicates were included. All the plants were irrigated 3 times per day (every 4 h), for 30 sec, with an automated irrigation system. The water in the containers was checked and supplemented with extra water every three days. The experiment ended when the first salinity symptoms appeared on the avocado plants irrigated with 30 meq NaCl / L.

Leaf sampling and determination of tissue nutrient concentrations. During the experiment, the foliage of the plants was divided in three zones; upper (young leaves), middle (mature leaves, recently taken their final size) and bottom layer foliage (old mature leaves). Leaf samples were taken: i) from the middle layer foliage (zone) on the 13th, 26th, 39th, 57th and 75th day after the beginning of the experiment, ii) from the upper layer foliage on the 57th and 75th day (end) of the experiment. For the distribution (compartmentalization) of Na, Cl, K and P in leaf surface area, samples were taken from the bottom and the upper layer foliage at the end of the experiment. Each leaf was divided in four zones; Apex (1), Margin (2), Centre (3) and Base (4). At the end of the experiment (75th day) each plant was divided into 5 parts: a) top leaves, b) basal leaves, c) graft stem, d) rootstock stem and e) root. After being received, all the parts were double washed with tap and distilled water, and afterwards they were dried at 75°C for 3 days. Then, the samples were ground to a fine powder, in order to pass a 30-mesh screen.

A portion of 0.5 g. of the fine powder of each sample was dry-ashed in a muffle furnace, at 515 °C, for 5 h. Then, the ash was dissolved with 3 mL of 6 N HCl and diluted with double distilled water up to 50 mL. Potassium (K) and Na concentrations were determined by the atomic absorption spectroscopy (Perkin-Elmer 2340, Waltham MA, USA), while P was determined in 470 nm, using the vanado-molybdo-phosphate yellow method [16]. Finally, Cl determination was performed according to the method of AgNO3, 0,01N, together with the presence of K_2CrO_4 [17]).

Statistical analysis. The experimental design was a 6X1 factorial, consisting of 6 NaCl treatments and one genotype; in each treatment, eight plants-replicates were included. Thus, the total number of the experimental plants was 48. The data were statistically analyzed by the SPSS statistical program (SPSS, Inc., Chicago, IL, USA). In order to compare the mean values among the treatments, ONE-WAY ANOVA, and particularly the Duncan's multiple range test, for $P \leq 0.05$, was followed.

RESULTS

Plant tissue nutrient concentrations. Our experiment in avocado plants identified varying levels of nutrient concentration in individual parts of the plant, as response to salinity stress.

Foliar Na concentration was significantly increased in 30 meq NaCl / L, at 57 days from the beginning of the experiment (it was found approximately 0.09% d.w.), compared to the other treatments and the previous sampling dates, while it reached its highest concentration (0.21% d.w.) also in the same treatment, at the end of the experiment (75th day) (Figure 1a). Significant differences among the treatments in Cl concentration of mature leaves from the middle zone were found from the 13th day of the experiment and afterwards (Figure 1b). From the 26th day, the highest leaf Cl concentration was recorded in 30 meq NaCl / L, while only at the end of the experimentation period (75th day) were found significant differences among the level

of 30 meq NaCl / L and the other treatments (Figure 1b). In addition, for all the 6 treatments foliar Cl showed an increasing trend from the beginning until the end of the experiment; indicatively, in 30 meq NaCl / L, leaf Cl was 0.30% d.w. on the 13th day and reached approximately 1.10% d.w. on the 75th day (Figure 1b).

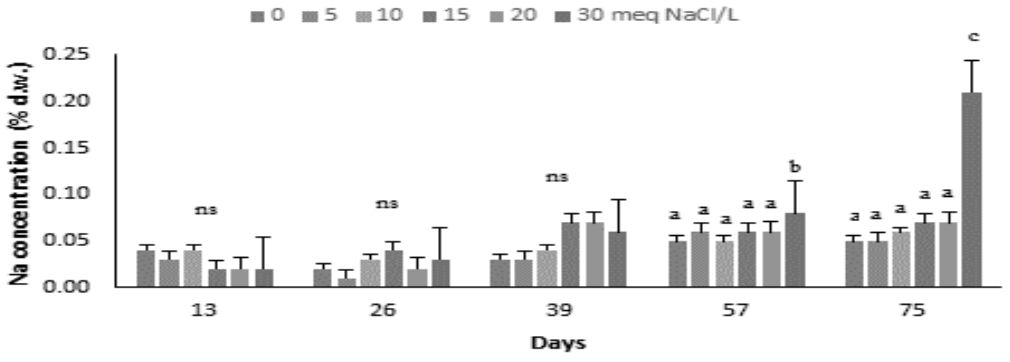
Leaf P did not significantly vary among the treatments and sampling dates and fluctuated from 0.07 to 0.10% d.w. (Figure 1c). Thus, the level of NaCl (from 5 to 30 meq / L) did not significantly affect foliar P nutrition, for the duration of our experiment (75 days). Foliar K showed an increasing trend, for all the treatments, between the 13th and the 26th day of the experiment; after the 26th day, a significant decline was observed (Figure 1d). However, between the 57th and the 75th day a constant or increasing trend in leaf K concentrations was found only in the high NaCl treatments (20 and 30 meq NaCl / L) (Figure 1d). This phenomenon may be ascribed to an antagonism between K+ and Na+ for common uptake by plants. Indeed, other researchers have also found that K+ may play a beneficial role in suppressing Na+ uptake, in order to alleviate the harmful effect of NaCl stress [18, 19].

At the end of the experiment, the highest Cl and K concentrations in the top (young) leaves were found in 30 meq NaCl / L (2.11% and 0.29% d.w., respectively) (Table 1). Especially for Cl, significant differences were found between the highest treatment (30 meq NaCl / L) and those of 0-15 meq NaCl, but not between 30 meq NaCl / L and 20 meq NaCl / L (Table 1). With regard to Na, surprisingly the highest concentration in the top leaves was found in the treatment of 15 meq NaCl / L, while in the basal leaves the highest Na concentration was determined in 30 meq NaCl / L (0.20% d.w.) (Table 1). Similarly, in the same treatment, in basal leaves were detected the highest Cl and K concentrations (1.19% and 1.10% d.w., respectively), as happened in the top leaves, while P concentrations in basal leaves were approximately two times higher in 10 and 15 meq NaCl / L (0.21% d.w.), compared to the other treatments (Table 1). Graft stem and rootstock stem Na concentrations were significantly higher in 15, 20 and 30 meq NaCl / L, compared to the 0, 5 and 10 meq NaCl / L treatments. Finally, significantly lower root K concentrations were determined in 20 and 30 meq NaCl / L (0.32% and 0.34% d.w.), compared to the other treatments, while significantly higher root Cl was found in 15-30 meq NaCl / L (0.11-0.23% d.w.), compared to 0-10 meq NaCl / L (Table 1).

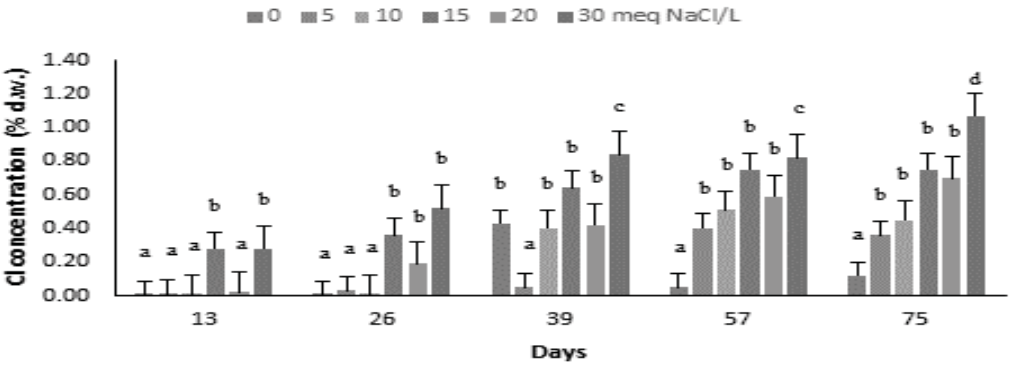
TABLE 1
Effect of NaCl stress in the tissue nutrient concentration of five different parts of P. americana (var. Fuerte) plants.

	Top Leaves				Basal Leaves				Graft Stem				Rootstock Stem				Root			
meq NaCl/ L	Na	K	P	Cl	Na	K	P	Cl	Na	K	P	Cl	Na	K	P	Cl	Na	K	P	Cl
0	0.01a	1.64a	0.21a	0.02a	0.03a	0.76a	0.11a	0.02a	0.04a	1.09ab	0.09a	0.02a	0.02a	0.47a	0.07a	0.03a	0.14a	0.67b	0.13a	0.01a
5	0.03a	1.47a	0.19a	0.01a	0.06a	0.63a	0.10a	0.17ab	0.06a	1.15ab	0.10a	0.06a	0.03a	0.59a	0.08a	0.06a	0.21a	0.50b	0.13a	0.02a
10	0.04a	1.86a	0.26a	0.07ab	0.06a	0.64a	0.21b	0.47b	0.06a	1.07ab	0.06a	0.12ab	0.06a	0.48a	0.07a	0.07a	0.30a	0.50b	0.11a	0.01a
15	0.13b	1.59a	0.21a	0.17b	0.09a	0.74a	0.21b	0.65bc	0.24b	1.01ab	0.14a	0.14ab	0.12b	0.53a	0.08a	0.05a	0.38b	0.57b	0.11a	0.23c
20	0.07a	1.91a	0.25a	0.24bc	0.04a	0.92ab	0.10a	0.86c	0.19b	1.02ab	0.07a	0.09a	0.11b	0.58a	0.09a	0.08a	0.31b	0.32a	0.10a	0.11b
30	0.09a	2.11b	0.27a	0.29c	0.20b	1.10b	0.11a	1.19d	0.32b	0.86a	0.09a	0.15ab	0.11b	0.48a	0.07a	0.07a	0.27b	0.34a	0.13a	0.19c

*Data were recorded at the end of the experiment. Values within the column followed by the same letter are not significantly different, according to Duncan's multiple range test, at P≤0.05.



(a)



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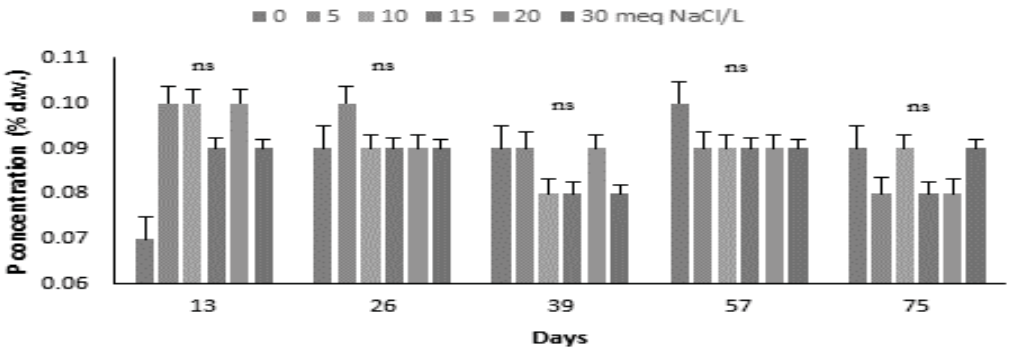

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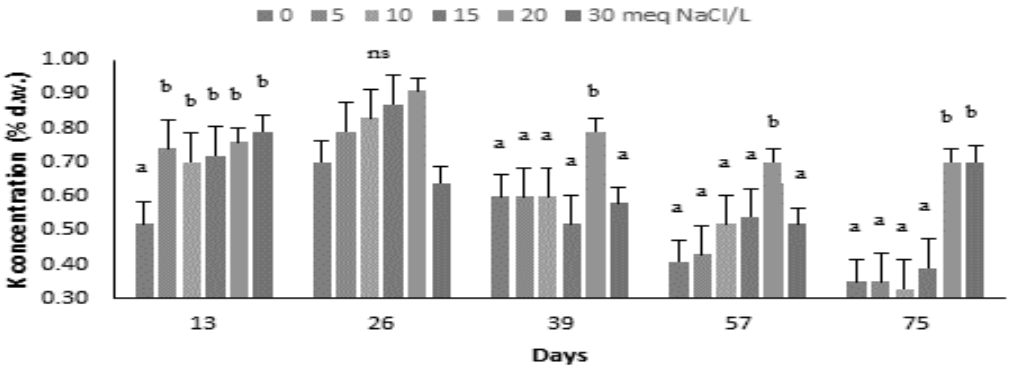

(d)

FIGURE 1

Effect of NaCl stress in the Na (a), Cl (b), P (c) and K (d) concentration of middle layer foliage of P. americana (var. Fuerte) after 13, 26, 39, 57 and 75 days. Bars represent standard error. The different letters reported above the bars grouped for each single treatment indicate statistically significant differences according to Duncan's multiple range test at P≤0.05; ns not significant.

It is quite remarkable from the results of Table 1 that the highest Cl concentrations were determined in the basal leaves (reaching up to 1.19% d.w.), while the highest Na concentrations (up to 0.38% d.w.) were detected in root (Table 1). The increased Cl concentrations in basal leaves should be ascribed to the fact that the mature leaves of basal foliage had already taken their final size, while Cl- uptake was increasing from 0 to 30 meq NaCl / L; in contrast, in the upper foliage the younger leaves had not been received their final size yet, and this was probably the reason why Cl concentrations did not exceed 0.29% d.w. (Table 1). In contrast to our results for significantly higher Na concentrations in root system, compared to the other vegetative tissues, Tsabarducas [19] found lower Na concentrations in root, than in leaves of the Citrus limon genotypes Nouvel Athos, Lisbon and Maglini, under NaCl stress (80 mM NaCl). Maybe the difference between our data and those of Tsabarducas [19] could be ascribed to the different plant species used for experimentation, i.e. maybe the higher Na translocation from root system to leaves in Citrus limon, compared to Persea americana Mill, is a species characteristic, showing probably higher sensitivity to NaCl stress for the Citrus linon plants. Alvarez-Acosta [15] found that Na+ was concentrated to a higher degree than Cl- in the root system of avocado plants, as a self-protection against Na+ toxicity. The differences among rootstocks in absorption and transport of Na+ and Cl- highly influence the salt stress tolerance of fruit trees and Vitis vinifera L. [20].

Na, and Cl compartmentalization in leaf surface area. Very close to the end of the experimental period, leaf samples from the bottom and upper foliage of the plants were taken, in order to investigate if significant differences existed among the leaf surface zones 1, 2, 3 and 4 (Figure 2). Chlorine concentrations in the treatments 15, 20 and 30 meq NaCl / L were significantly higher at the leaf zone 1 (Apex), compared to the zones 2 (Margin), 3 (Centre) and 4 (Base), but only in the bottom (mature) leaves (Table 2); in contrast, in the upper (young) leaves insignificant differences among the leaf zones 1-4 were recorded (Table 2).

With regard to Na compartmentalization in bottom (mature) leaves, only in 30 meq NaCl / L, significantly higher concentration was determined in the leaf zone 4 (base of the leaf). However, insignificant differences in Na concentration were found in the upper (young) leaves (Table 2).

In the bottom leaves significant differences were found in K concentration in 20 meq NaCl / L, at the edge (leaf zone 1), while in P concentration in 30 meq NaCl / L, in the leaf zone 3 (Table 2; Figure 3). The fact that the highest Cl concentrations were detected at the Apex (zone 1) of the bottom leaves should be ascribed to the easy and quick transport of Cl-, after taken up by roots, to the aerial parts of the plants [21]. Thus, since Cl- is relatively mobile and it is easily transported in the xylem [22] via transpiration, it is mainly accumulated at the edge of the leaves, where the symptoms of Cl toxicity (e.g. leaf burns and injuries) usually appear [14]. As it can be concluded from the data of Table 2, Cl concentration at the edge of bottom leaves (zone 1) exceeded 1% d.w. (it varied from 1.02% to 1.37% d.w.) (Table 2). Since the minimum foliar Cl requirements for normal plant growth is within the range from 0.02 to 0.04% d.w. [23], in our study Cl concentrations at the Apex (edge of leaves) was 25.5 to 68.5 times higher, compared to those quoted as optimum ones in literature.

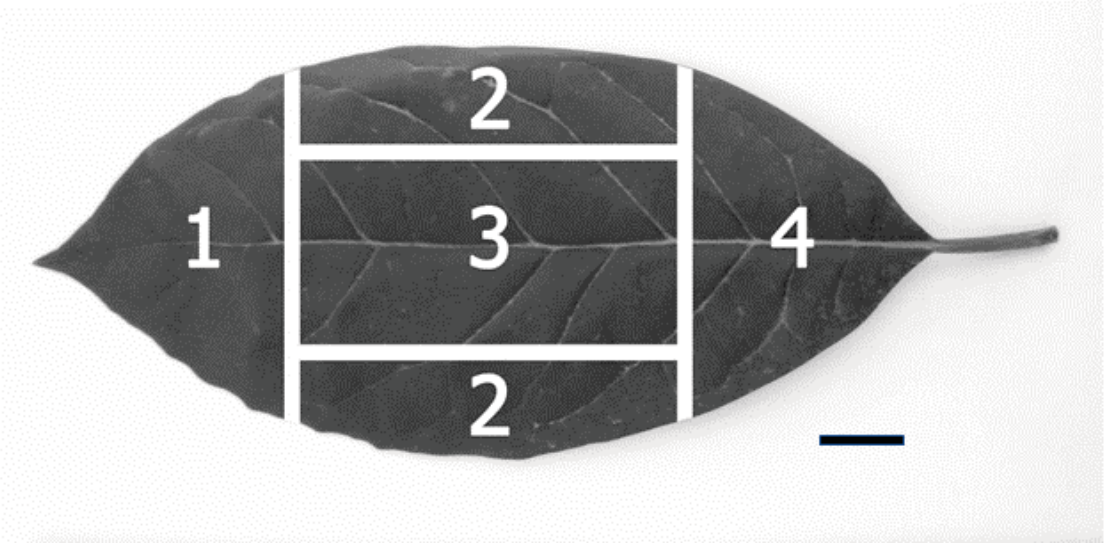

FIGURE 2
Compartmentalization of P. americana (var. Fuerte) leaf in four zones; Apex (1), Margin (2), Centre (3) and Base (4), for the definition of Na, Cl, K and P concentration in mature and young leaves. Scale bar 2 cm.

TABLE 2
Effect of NaCl stress in the compartmentalization of Na, Cl, K and P in leaf surface area of bottom and upper leaves of P. americana (var. Fuerte) plants.

		Bottom Leaves				Upper Leaves			
meq NaCl/L	Leaf Zone	Na	K	P	Cl	Na	K	P	Cl
0	1	0.02a	0.74a	0.08a	0.65a	0.06a	0.83a	0.15a	0.02a
	2	0.02a	0.70a	0.12ab	0.38a	0.04a	1.03a	0.18a	0.02a
	3	0.02a	0.39a	0.08a	0.01a	0.09ab	1.20a	0.17a	0.02a
	4	0.02a	0.60a	0.08a	0.36a	0.03a	1.51ab	0.17a	0.02a
5	1	0.02a	0.70a	0.11a	0.86a	0.03a	1.03a	0.17a	0.02a
	2	0.03a	0.52a	0.10a	0.54a	0.03a	1.14a	0.17a	0.02a
	3	0.03a	0.25a	0.06a	0.08a	0.05a	1.26a	0.16a	0.02a
	4	0.05a	0.64a	0.09a	0.64a	0.03a	1.76b	0.17a	0.02a
10	1	0.05a	0.83a	0.10a	0.77a				
	2	0.04a	0.60a	0.10a	0.49a				
	3	0.03a	0.25a	0.07a	0.03a				
	4	0.04a	0.79a	0.09a	0.59a				
15	1	0.04a	0.95ab	0.11a	1.26bc	0.02a	1.22a	0.17a	0.02a
	2	0.02a	0.60a	0.09a	0.74a	0.01a	1.32a	0.17a	0.02a
	3	0.03a	0.25a	0.06a	0.06a	0.02a	1.51ab	0.16a	0.02a
	4	0.07a	0.60a	0.08a	0.63a	0.11ab	1.76b	0.15a	0.11b
20	1	0.04a	1.18b	0.13a	1.02b	0.02a	1.80b	0.16a	0.04a
	2	0.04a	0.79a	0.11a	0.68a	0.10ab	1.70ab	0.19a	0.02a
	3	0.03a	0.43a	0.08a	0.18a	0.03a	1.12a	0.18a	0.02a
	4	0.04a	1.03ab	0.10a	0.59a	0.05a	2.40bc	0.20a	0.02a
30	1	0.09ab	0.87a	0.10a	1.37bc	0.04a	1.03a	0.17a	0.02a
	2	0.1ab	0.79a	0.09a	0.95a	0.03a	1.51ab	0.18a	0.02a
	3	0.07a	0.48a	0.22b	0.48a	0.02a	1.32a	0.18a	0.04a
	4	0.18b	0.79a	0.08a	0.83a	0.02a	1.90b	0.20a	0.03a

*Data were recorded at the end of the experiment. Values within the column followed by the same letter are not significantly different, according to Duncan's multiple range test, at P≤0.05.

Salt stress adversely affects plant growth, both above, and belowground. Our pot experiment, provide an indication of how well avocado trees of productive orchards respond under salt stress. Although water quality to prevent yield reduction in avocado is considered to be EC=0.75 dS/m [24], avocado growers in western Crete use water with EC > 1.5 dS/m. Still, currently, a great number of avocado trees using "Zutano" rootstock are planted every year in Greece. Since we the adverse effects of saline stress cannot be reduced, future use of salinity tolerant rootstocks is required to improve yield when poor quality soil or water is used.

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