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Original article

Growth, gas exchange, water relations, fresh and dry matter partitioning in young fig (*Ficus carica* L.) plants irrigated with saline water

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Summary

Background – **Salinity tolerance of *Ficus carica* L. is still poorly quantified.** *Objectives* – **We subjected container-grown fig plants (cv. 'Dottato') to salt stress to determine survival, growth, biomass distribution, leaf gas exchange, and water relations.** *Methods* – **In a typical experiment plants were irrigated with saline water at either 50, 100, or 200 mM NaCl concentration for seven-eight weeks. In year 1 we added two additional concentrations: 300 (then adjusted after one week to 250 for the remaining six weeks) and 400 mM NaCl.** *Results* – **Salinity rapidly modified plant water status. Leaf photosynthetic rate (*A*) and stomatal conductance (g_s) decreased as salinity was increased beyond 50 mM NaCl after 18 days of stress in both years. Leaf chlorophyll concentrations were unaltered by salinity. Shoot growth stopped after two weeks of salinization at 100 mM NaCl and beyond. Leaf area and number decreased significantly for the 200 mM-treated plants starting from five weeks after the beginning of salinization due to extensive leaf drop. Plant dry weight for the 50, 100, and 200 mM NaCl ranged 91–92%, 63–80%, 52–60% of the controls, respectively. The canopy-to-root ratio (both fresh and dry weight) did not change over the 0–100 mM NaCl range.** *Conclusions* – **Our study expands the interval of safe growth beyond previously reported thresholds. There are good perspectives to grow fig trees under saline conditions provided tolerant cultivars are planted.**

Keywords
chlorophyll, leaf area, osmotic potential, photosynthesis, root, survival

Significance of this study

What is already known on this subject?
- Fig trees are considered moderately tolerant to salinity, but survival, growth and physiological responses have been poorly quantified.

What are the new findings?
- This study expands the interval of safe growth beyond previously reported thresholds.

What is the expected impact on horticulture?
- Fig trees are suitable for areas where brackish or saline waters are used for irrigation provided tolerant cultivars are used.

Introduction

Ficus carica L. trees are harvested both for fresh and dried fruits on 290,000 ha worldwide (FAOSTAT, 2019). Since ancient times fig cultivation mostly occurs in arid and semi-arid climates of the Mediterranean region and Middle East, where production is limited by water deficit and/or salt stress (Flaishmann et al., 2008; Gholami et al., 2012) and modern orchards are often irrigated with brackish or saline water. Fig trees are considered moderately tolerant to salinity (Flaishmann et al., 2008; Metwali et al., 2014; Zarei et al., 2016), similarly to olive and pomegranate (Maas and Hoffmann, 1977; Rhoades et al., 1992; Sun et al., 2018). However, the survival, growth and physiological response of fig trees to saline conditions has been poorly quantified (Maas, 1986; Maas and Hoffmann, 1977). Only few studies, limited in duration and/or interval of saline concentrations, have been conducted so far (Golombek and Lüdders, 1993; Maas, 1986; Okubo and Utsunomiya, 1996, 1997; Zarei et al., 2016).

Woody species may adapt to salinity via a number of physiological mechanisms. A decrease in stomatal conductance (g_s), which reduces transpiration and increases water use efficiency (WUE), is a common response in plants of medium tolerance to salinity and leads to a reduced accumulation of toxic ions into the leaves and prolonged leaf longevity (Gucci and Tattini, 1997; Khayyat et al., 2014; Melgar et al., 2008; Olmo et al., 2019; Sun et al., 2018). Both non-stomatal and stomatal factors were responsible for the short-term changes in leaf photosynthetic rate (*A*) of two fig cultivars induced by exposure to salinity for one week (Golombek and Lüdders, 1993). Decreased g_s and increased WUE enhanced salt tolerance during the first few days of salinization with only slight differences in the stomatal response between the two cultivars (Golombek and Lüdders, 1993). The extent of stomatal closure induced by salinity has been shown to be genotype dependent (Zarei et al., 2016). The suppression of *A* and g_s was documented after two weeks of salinization in fig plants exposed to 50 mM NaCl without apparent symptoms of leaf injury (Okubo and Utsunomiya, 1996).

Salinity also affected the water relations of most woody species including fig (Gucci et al., 1997; Hasegawa et al., 2000; Melgar et al., 2008; Olmo et al., 2019; Zarei et al., 2016). In olive, a crop that shares similar environmental and cultural conditions with fig, early changes in leaf water potential

(LWP) and relative water content occurred even at low levels of salinity (Gucci et al., 1997), albeit symptoms of toxicity and permanent damage appeared at higher NaCl than those causing comparable damage in other fruit trees (Rhoades et al., 1992). In olive and citrus plants the salt-induced decrease in LWP was compensated for by a parallel decrease in osmotic potential (LOP), thus the turgor of salinized plants was maintained at levels similar or even higher than control ones (Gucci et al., 1997; Melgar et al., 2008). Plant tissues adjust osmotically by accumulating inorganic and organic ions that draw cytoplasmic water from adjacent cells, maintain tissues well hydrated, preserve membrane integrity and avoid plasmolysis. The decrease in LOP may either reflect the different ability of genotypes to exclude Na^+ and Cl^- from the shoot (Gucci et al., 1997; Khayyat et al., 2014; Melgar et al., 2008; Ruiz et al., 1997) or the inherent trait of salt-induced accumulation of osmolytes and osmoprotectants like mannitol and proline (Gucci et al., 1998; Khayyat et al., 2014; Metwali et al., 2014; Storey and Walker, 1999; Tattini et al., 1996). The leaf proline content of two fig cultivars has been shown to increase after six weeks of salinization (Nejad and Shekafandeh, 2014).

The objective of our work was to determine the effect of salinization on survival, vegetative growth, water relations, gas exchange, fresh and dry matter partitioning of young fig plants of cv. 'Dottato', one of the most widely grown cultivars in Italy (known as 'Kadota' in California). The 'Dottato' bears medium-sized fruits with green to yellow skin and honey flavoured flesh (Flaishmann et al., 2008). We used a wide range of NaCl concentrations to identify thresholds for the different vegetative and physiological responses.

Materials and methods

Plant material and salt treatments

Micropropagated plants of cv. 'Dottato' were used over two growing seasons. In year 1, 120 plants were grown in a glasshouse in 3.9-L pots containing sand and topped with peat to avoid water percolation along the sides. At the beginning of the growing season plants were less than one-year old, they had at least six fully-expanded leaves and a well lignified stem at least 0.10 m high. Only the apical shoot was left to grow (where necessary lateral shoots were removed). Prior to the beginning of saline treatments plants had been grown outdoor, selected homogeneous in size and then randomly assigned to saline treatments (12 plants per treatment). Six additional plants were enclosed in plastic bags sealed around the stem to prevent evaporative losses from the soil surface to measure daily water consumption as plant weight loss, and irrigation volumes scheduled accordingly.

Salinization lasted from June 30 through August 17. The experiment was partially conducted outdoor (June 30–July 8), then plants were taken to a glasshouse due to rain. In year 1 plants were irrigated four days a week for seven weeks with 250 mL of deionized water (0) or saline water (50, 100, 200, 300–250, and 400 corresponding to 50, 100, 200, 300–250 and 400 mM NaCl concentration, respectively). Plants of the 300–250 treatment were irrigated with 300 mM NaCl solution for the first week, then with 250 mM NaCl solution for the remaining six weeks. This change in saline concentration was due to extensive leaf necrosis that had developed after only one week of exposure at 300 mM concentration. The 400 mM NaCl treatment was suppressed after one week of stress because of the rapid development of severe symptoms of toxicity (leaf necrosis and abscission) and thereafter plants received only good quality water. Saline water solutions were obtained by adding different amount of pure (≥99.8%) NaCl (Sigma-Aldrich Co., St. Louis, MO, U.S.A.).

In year 2, 48 plants from the same batch of those used in year 1 were grown in 5-L pots filled with a mixture of 6.4% clay, 8.6% silt, and 85% sand. All plants were 0.6–0.8 m high and had at least six fully expanded leaves when the experiment was started. Twelve plants per treatment were irrigated with 400 mL per plant three times a week until June 28, then with 700 mL until July 24. Plants were kept outdoor and subjected to four concentrations (0, 50, 100, and 200 mM NaCl) from June 2 through July 31. In case of rain events plants were brought into a glasshouse and then back outdoors as soon as precipitations ended. Unlike year 1 when final salt concentrations were supplied from the beginning of the experiment, in year 2 the four NaCl concentrations (0, 50, 100 and 200 mM) were reached gradually by step increments of 50 mM per irrigation. Therefore, the 100 mM and 200 mM concentrations were achieved two and seven days after the 50 mM treatment had reached its final concentration. Fertilizers were not added prior to or during the course of the experiment.

Growth analysis, fresh and dry matter distribution

Stem elongation and the number of fully-expanded leaves (including leaves used for water relations measurements) of 12 plants per treatment were measured during the salinization period every week. The leaf area of individual leaves was calculated using a regression equation preliminarily obtained by measuring leaf length and leaf area of a sample of 12 leaves using image analysis (Supplemental Information – Figure S1). Stem elongation was measured non-destructively after tagging the last fully-expanded leaf with a woolen string every week. The number of fully-expanded leaves with toxicity symptoms (chlorosis, leaf blotch, browning of the leaf margin) and that of healthy ones was also measured. At the end of the experiment, six plants per treatment were destructively harvested and partitioned into leaves, stem and roots, and their fresh and dry weights determined (DW after drying at 70°C until constant weight). Roots were carefully recovered, gently washed, then blotted dry and their fresh and dry weights determined. In the second growing season six plants were harvested eight weeks after the beginning of salinization and partitioned as in year 1.

Water relations

In year 1 the stem water potential (SWP) was measured at six dates using a Scholander-type pressure chamber (PMS Instruments, Albany, OR, U.S.A.). Prior to SWP measurements the transpiration of the youngest fully-expanded leaf of four plants per treatment was blocked by enclosing the leaf into a plastic bag wrapped with aluminium foil for 120 min until the SWP reached equilibrium with the xylem. The latex exuding from the petiole cut-end after leaf excision was immediately blotted dry, and then the leaf was pressurized at a rate of 0.02 MPa s^{-1}. The SWP was measured between 11 am and 13 pm solar time. After SWP determination, leaf blades were frozen and kept at -20°C for determination of LOP using a Wescor 5500 vapour pressure osmometer (Gucci et al., 1997). Turgor pressure was calculated as the difference between SWP and LOP. In year 2 the protocol was similar, except that entire plants were enclosed in black plastic bags the evening before measurement and maintained in the dark until pressurized. All measurements were taken between 6:30 and 7:30 am.

Gas exchange and chlorophyll content

Gas exchange parameters of the last fully-expanded leaf of six replicate plants per treatment were measured on nine dates, using a portable gas exchange system (CIRAS-1, PP Systems, Hitchin, U.K.). Measurements were taken on cloudless days between 7:30 am and 9:30 am (solar time) at photosynthetic photon flux density higher than 900 µmol m^{-2} s^{-1}, ambient CO_2 ranging from 380 to 390 µL L^{-1}, and air temperature of 29.8 ± 1.3°C (mean + standard deviation). On July 11, gas exchange was measured under partially cloudy conditions and at lower temperatures than at other dates. On dates when plants were kept in the glasshouse, gas exchange was measured after they had been acclimated outdoors under saturating light conditions for at least two hours. In year 2, gas exchange parameters of six plants per treatment were measured at six dates under similar environmental conditions as in the first year.

The leaf chlorophyll content was determined non-destructively using a SPAD-502 unit (Konica Minolta, Osaka, Japan) that measured transmission at 600–700 nm and 900–1,000 nm wavelength, following standard protocols. Readings were taken on the central part of the blade away from main veins on the same leaves measured for gas exchange parameters. SPAD units had been previously correlated with chlorophyll concentrations determined using N,N-dimethylformamide (DMF), as in Moran and Porath (1980). In brief, 100 mg of leaf lamina was transferred to a tube containing 3 mL of DMF and kept in the dark at 4°C for 72 h. The absorbance was then read at 647 and 664 nm using a spectrophotometer (Hitachi U-2000, Tokyo, Japan). The relationship between greenness index and chlorophyll content of leaf tissue is shown in Supplemental Information - Figure S2.

Experimental design and statistical analysis

Plants were arranged according to a completely randomized design, each saline treatment consisting in 12 plants. The SWP was measured on four plants, leaf gas exchange and biomass determinations on six plants, vegetative growth on 12 plants per treatment. Means of salt treatments were separated by least significant differences (LSD) at $P > 0.05$ after analysis of variance (ANOVA) within each year. The NaCl concentration at which biomass was 50% that of controls (Conc50), and was calculated by regression analysis over the 0–250 mM range in year 1 and the 0–200 mM range in year 2 using Costat (CoHort Software, Monterey, CA, U.S.A.).

Results

Salinity rapidly modified the water status of fig plants. While the SWP of control plants remained stable at about -0.65 and -0.3 MPa in year 1 and year 2, respectively, those of salt-treated ones declined as the NaCl concentration increased (Figures 1A, 2A). Increasing saline concentrations progressively decreased SWP. Values of -1.5 MPa and below were measured for the 300–250 mM treatment starting from one week after the onset of salinization (Figure 1A). Significant differences from the control appeared for the SWP of 200 mM NaCl-treated plants about 10–14 days after salt stress was imposed. Differences in SWP between control and 100 mM NaCl-treated plants were significant after about four weeks, whereas for the 50 mM treatment they were not significantly different (albeit lower of the control) throughout the experiment (Figures 1A, 2A).

The LOP of control plants ranged between -1.5 and -1.2 MPa (Figure 1B), but it remained relatively stable and then declined at the last two dates of measurement in year 2 (Figure 2B). In both years the LOP of 200 mM treatment gradually decreased over time and reached similar values at the end of the experiment; the LOP of 50 and 100 mM were stable in year 1, whereas they decreased rapidly after four weeks of salinization in year 2 (Figures 1B, 2B). The lowest LOP values were measured for the 300–250 mM treated plants (Figure 1B). As a result of changes in SWP and LOP, turgor pressure remained above 0.5 MPa for all treatments and quite similar across treatments except for the 200 and 250–300 treatments (Figures 1C, 2C).

Leaf *A* and g_s decreased as salinity was increased beyond 50 mM NaCl after 18 days of stress in both years (Figures

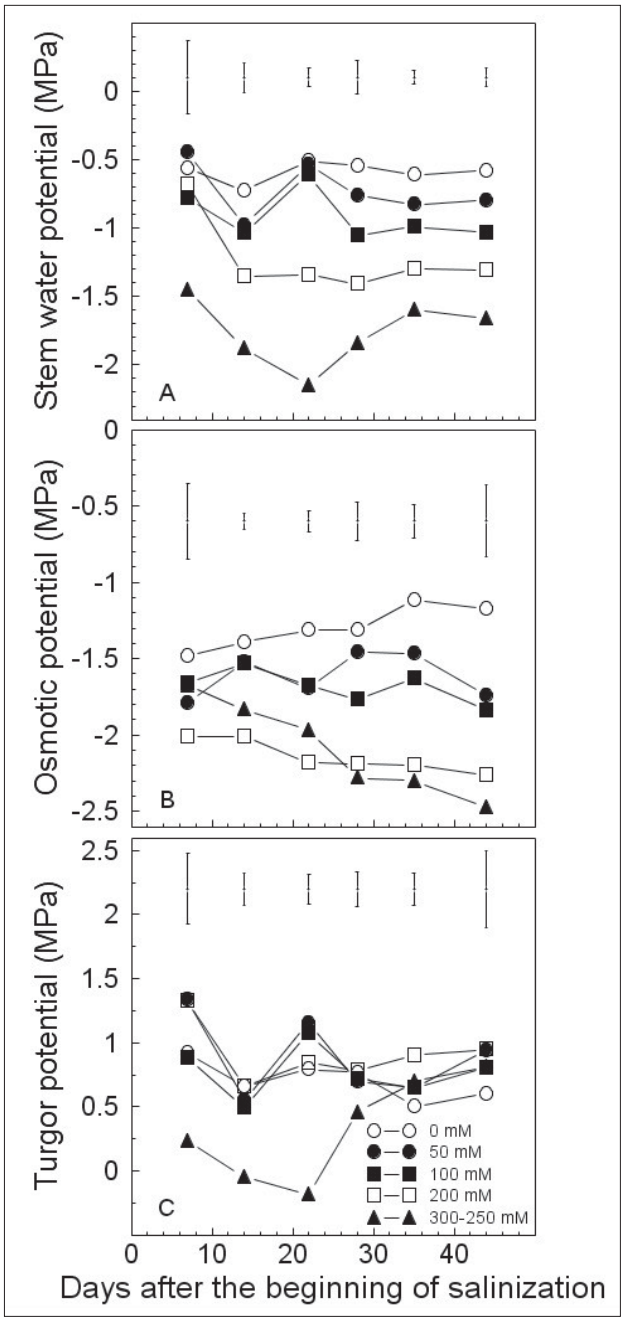

Figure 1. Stem water potential (A), leaf osmotic potential (B) and turgor potential (C) measured on fig plants irrigated with saline water (0, 50, 100, 200 and 300–250 mM NaCl) for seven weeks in year 1. Vertical bars represent least significant differences (LSD) calculated after analysis of variance (ANOVA) for a randomized block design with four replicate plants.

3, 4). At 21 days after the beginning of salinization *A* of the 50 mM NaCl was lower than that of control plants. The course of gas exchange parameters remained relatively stable during the following weeks and similar for 50- and 100-mM NaCl-treated plants and for 200- and 300–250 mM ones in year 1 (Figure 3). The *A* of 200 mM-treated plants decreased for about two weeks and then remained similar to values of the 300–250 mM treatment. After three weeks of stress the *A* of 100-mM treated plants was similar to that of 50-mM NaCl ones in year 1, but not in year 2 (Figures 3, 4). In general, *A* paralleled g_s including after 18 days of salinization when both parameters increased in year 1 (we ignore

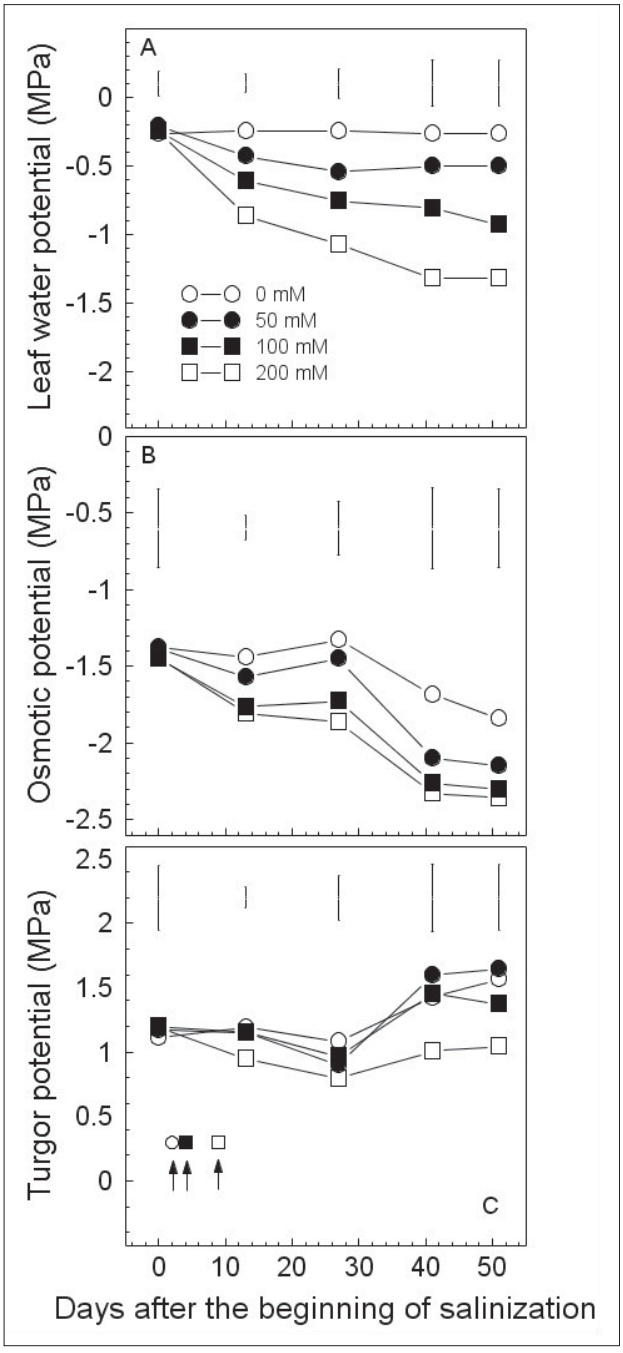

FIGURE 2. Stem water potential (A), leaf osmotic potential (B) and turgor potential (C) measured on fig plants irrigated with saline water (0, 50, 100 and 200 mM NaCl) in year 2. Vertical bars represent least significant differences (LSD) as in Figure 1. Arrows indicate when final concentrations were reached.

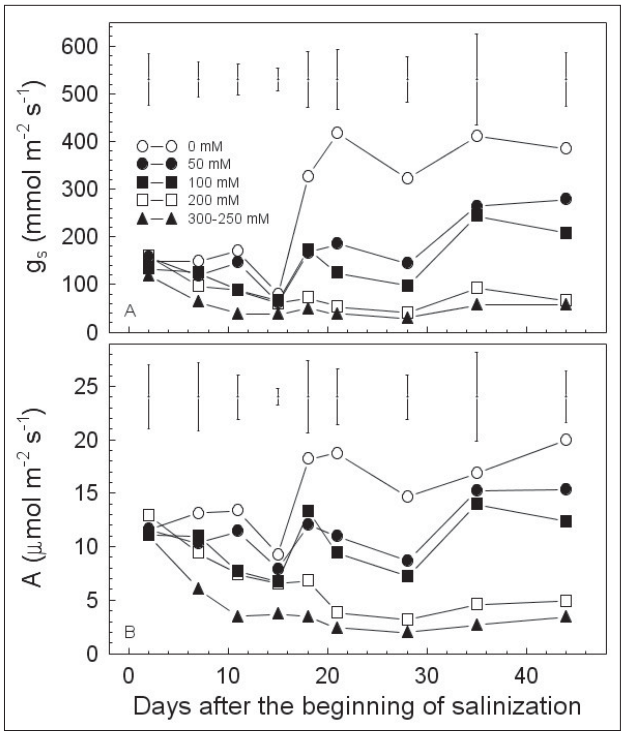

FIGURE 3. Leaf photosynthesis (*A*) and stomatal conductance (g_s) of fig plants irrigated with saline water (0, 50, 100, 200 and 300–250 mM NaCl) for seven weeks in year 1. Vertical bars represent least significant differences (LSD) calculated after analysis of variance (ANOVA) for a randomized block design with plants as replication ($n = 6$).

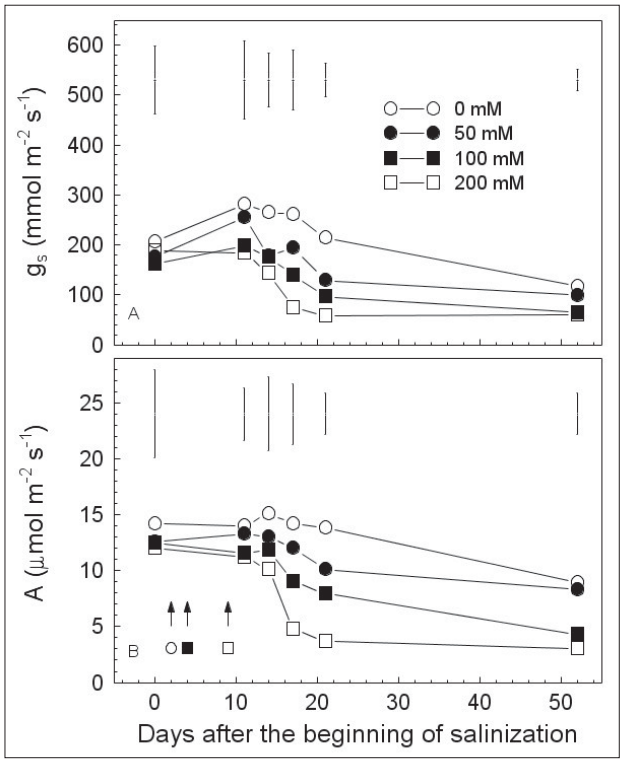

FIGURE 4. Stomatal conductance (g_s) and leaf photosynthesis (*A*) measured on fig plants irrigated with saline water (0, 50, 100 and 200 mM NaCl) for seven weeks in year 2. Vertical bars represent least significant differences (LSD) as for Figure 3. Arrows indicate when final concentrations were reached.

the reason for this rise). In year 2, when salinization was gradually imposed, the first differences in gas exchange over the 0–100 mM range of NaCl concentrations were measured after 17 days of salinization (Figure 4). Leaf chlorophyll concentrations were slightly lower for the 100 and 200 mM NaCl treatments in year 2, but differences were not significant (Figure 5).

The effect of salinity on growth parameters was similar in both years and, therefore, we report only results from year 1 (Figure 6). Shoot growth stopped after two weeks of salinization for the 100 mM treatment and beyond, whereas that of control plants continued until five weeks after the beginning of the experiment. Shoot length was similar across the 50–200 mM NaCl interval, whereas leaf area and number of leaves decreased significantly for the 200 mM treated plants due to extensive leaf drop (Figure 6A, B). Leaf drop was preceded by necrosis that started along the leaf margin and then spread to the inner part of the leaf lamina. By the end of the 7th week of salinization with 100 mM NaCl new shoot length was about 70% that of the controls (Figure 6C). Growth decreased as salinity increased and ceased at 200 mM NaCl and beyond. At those concentrations wide browning of leaf margins and burn tip of the apices were evident after two-three weeks of treatment.

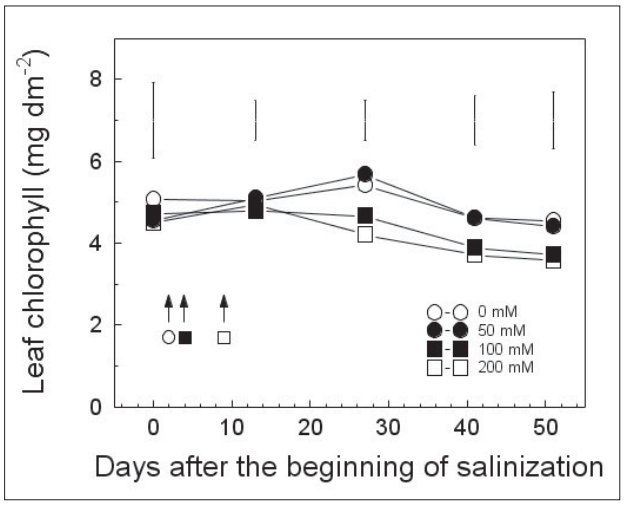

Figure 5. Leaf chlorophyll measured in year 2 on fig plants irrigated with saline water (0, 50, 100 and 200 mM NaCl) for seven weeks. Vertical bars represent least significant differences (LSD) calculated after analysis of variance (ANOVA) for a randomized block design with plants as replication (n = 6). Arrows indicate when final concentrations were reached.

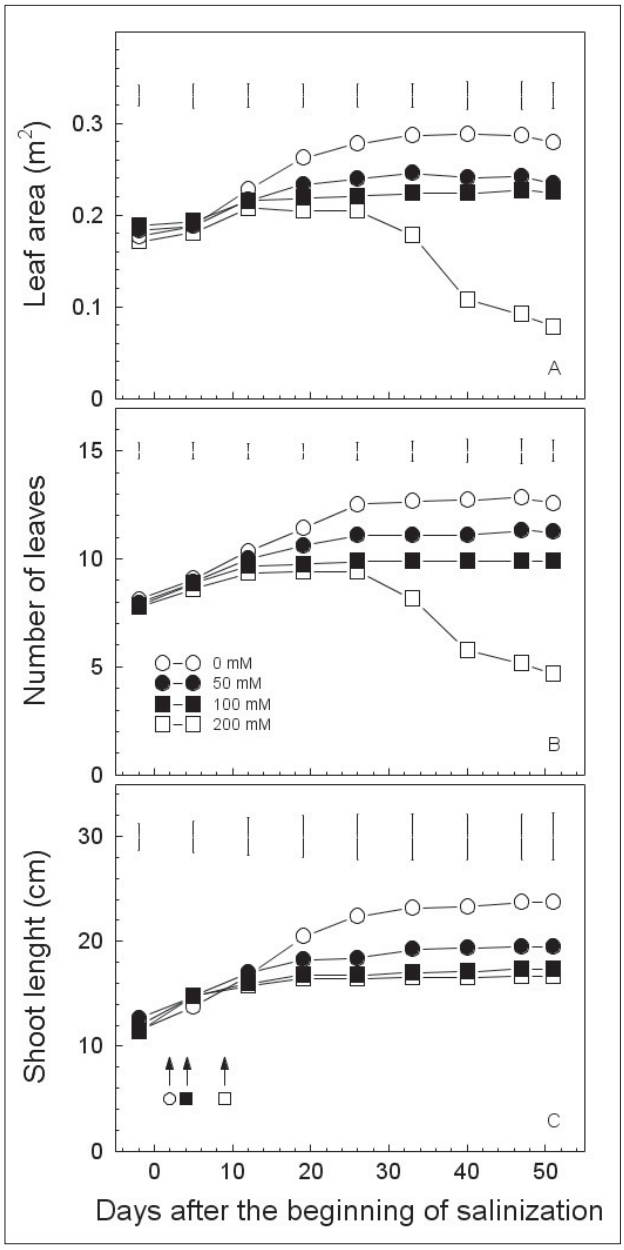

Figure 6. Leaf area, number of leaves and shoot length of fig plants irrigated with saline water (0, 50, 100 and 200 mM NaCl) in year 2. Vertical bars represent least significant differences (LSD) calculated after analysis of variance (ANOVA) for a randomized block design with plants as replication (n=6). Arrows indicate when final concentrations were reached.

Table 1. Fresh and dry matter distribution, canopy-root biomass ratio and DW/FW ratio of fig plants after seven weeks of irrigation with saline water (0, 50, 100, 200 and 300–250 mM NaCl) in year 1. Abscised leaves were not included. Least significant differences (LSD) were calculated after analysis of variance (ANOVA) for a completely randomized design (n = 6). Legend: FW, fresh weight; DW, dry weight.

NaCl	FW (g)				DW (g)				Canopy/Root		DW/FW
	Leaf	Stem	Root	Total	Leaf	Stem	Root	Total	FW	DW	(total)
0	18.2 a	12.0 a	28.1 a	58.2 a	5.6 a	4.2 a	8.4 a	18.3 a	1.2 a	1.1 a	0.31
50	13.9 b	10.1 a	25.6 a	49.6 a	4.5 b	4.2 a	8.2 a	16.9 a	1.1 a	1.0 a	0.34
100	10.7 c	6.2 b	17.4 b	34.4 b	3.2 c	2.6 b	5.8 b	11.6 b	1.1 a	1.1 a	0.34
200	4.9 d	5.2 b	18.0 b	28.2 bc	1.5 d	2.0 b	6.0 b	9.6 bc	0.6 b	0.6 b	0.34
300–250	1.3 e	4.6 b	14.9 b	20.9 c	0.4 e	1.7 b	4.9 b	6.9 c	0.4 b	0.4 b	0.33
LSD (0.05)	3.01	2.69	6.35	8.86	0.99	1.03	2.04	2.99	0.29	0.30	0.014

Table 2. Fresh and dry matter distribution, canopy-root biomass ratio and DW/FW ratio of fig plants after seven weeks of irrigation with saline water (0, 50, 100 and 200 mM NaCl) in year 2. Abscised leaves were not included. Statistical analysis and legend as in Table 1. FW, fresh weight; DW, dry weight.

NaCl (mM)	FW (g)				DW (g)				Canopy/Root		DW/FW (total)
	Leaf	Stem	Root	Total	Leaf	Stem	Root	Total	FW	DW	
0	65.2 a	117.8 a	86.6 a	269.6 a	16.4 a	46.5 a	20.6 a	83.5 a	2.16 a	3.1 a	0.31
50	52.1 ab	105.7 ab	79.0 ab	236.8 ab	14.0 ab	44.4 a	17.2 a	75.6 ab	2.05 a	3.4 a	0.32
100	44.5 bc	92.8 bc	73.6 ab	210.9 b	11.4 b	39.5 ab	16.0 ab	66.8 b	1.96 ab	3.2 a	0.32
200	10.3 c	79.4 c	62.0 b	151.8 c	3.2 c	32.8 b	14.3 b	50.2 c	1.53 b	2.6 b	0.33
LSD (0.05)	3.51	3.40	7.86	45.9	4.28	8.11	3.90	13.7	0.48	0.41	0.03

In year 2 the FW of all leaves of control plants was about three times greater than that of the controls of year 1 (Tables 1 and 2). At the end of the salinization experiment, the fresh weight of 50, 100, 200, and 300–250 mM NaCl treated plants was 85, 59, 48 and 36% of that of control plants (Table 1). The greatest reduction in fresh and dry weight was measured for leaves, mainly due to the increasing leaf abscission induced by salinity as the concentration increased and to a minor extent to the inhibition of leaf expansion. In year 1 the leaf FW of 50, 100, 200, and 300–250 mM-treated plants was 76, 59, 27, and 7% that of the controls respectively, whereas in year 2 it was 80, 68, and 16% (300–250 treatment non present), respectively. The FW of roots ranged 91%, 62-85%, 64–72% of the controls for the 50, 100, and 200 mM NaCl (Tables 1, 2). Salinity did not significantly affect the DW/FW of leaves, stems, and roots (Tables 1, 2). The leaf dry weight was significantly lower than that of control plants even for the 50-mM treatment; higher concentrations further decreased the DW of leaves. The dry weights of stem and root were significantly less than those of the controls only from the 100 mM treatment and beyond (Table 1). The canopy-root ratio (both fresh weight and dry weight) was similar in the 0–100 mM NaCl range (Tables 1 and 2). In year 1 the NaCl Conc50 were 145 and 256 mM for canopy and root FW, respectively, and 155 and 302 mM for the canopy and root DW. For the whole plant Conc50 was 184 and 197 mM for FW and DW, respectively in year 1, and 229 and 251 mM for FW and DW in year 2.

Discussion

The main objective was to identify the range of NaCl concentrations compatible with survival, vegetative growth and basic physiological parameters of young fig plants. Therefore, we tested a wide range of NaCl concentrations up to 400 mM to simulate worst case scenarios. Young plants could survive irrigation water up to 200 mM NaCl for seven weeks, but extensive leaf damage and drop, absence of any growth, stomatal closure and drastic inhibition of photosynthesis made us conclude that irrigation water of 200 mM NaCl was definitely beyond the tolerance limit for growing fig as a crop. Previous studies on salinity tolerance of fig plants focused on the physiological response in the 0–120 mM NaCl range (Golombek and Lüdders, 1993; Nejad and Shekafandeh, 2014; Zarei et al., 2016), except Soliman and Abd Alhady (2017) that spanned a wider interval (0–12,000 ppm NaCl) in tissue culture and concentrations above 10,000 ppm proved lethal for sensitive cultivars. In our study 300–250-treated plants were still alive after seven weeks of salinization and even those exposed to 400 mM NaCl for one week survived and recovered growth and gas exchange parameters upon relief of stress with good quality water (data not shown; Caruso et al., 2017). These results confirm that *Ficus carica* is one of the most resistant fruit trees of the temperate zone to salt stress (Hasanuzzaman et al., 2013; Rhoades et al., 1992).

The next question was to identify the safe range for growing healthy plants. Irrigation with saline water at 50 mM NaCl affected neither colour, wilting, abscission of leaves nor other visible symptoms of the canopy. At this concentration shoot growth and leaf area were slightly (but not significantly) decreased; fresh and dry weights were well above 80% those of the controls. Treatment with saline water at 100 mM NaCl did not induce major symptoms of toxicity, nor leaf wilting. Marginal necrosis or chlorotic areas appeared occasionally in basal leaves (Caruso et al., 2017) but plants were functionally viable. The time course of shoot growth and leaf area also confirmed that young fig plants could tolerate salinity up to 100 mM NaCl. Injury symptoms on leaf tips of potted fig plants had been observed after five days of exposure at 12–15 dS m^{-1} or after two weeks at 6.9 dS m^{-1} (Nejad and Shekafandeh, 2014), that is earlier or at lower concentrations than in our study. Greater sensitivity in growth parameters was also reported by Okubo and Utsonomiya (1996), who found that stem elongation and the increase in node number of plants treated with 50 mM NaCl for four weeks were only 37 and 59% of the controls. Zarei et al. (2016) calculated the electrical conductivity at which growth was 50% of the controls (EC50) in 8-month old seedlings of four genotypes. They reported EC50 values above 8 dS m^{-1} for shoot FW and DW of all genotypes and for root FW and root DW of two and three genotypes, respectively, leaving the actual values undetermined. In year 1 we calculated Conc50 of 184 and 197 mM NaCl for fresh and dry whole plant biomass, respectively. As we repeated the experiment with bigger plants in the second year Conc50 rose, but shoot growth (both FW and DW) was impaired more than that of the root. An increase in root-canopy ratio is a common adaptive response of higher plants to salinity (Hasegawa et al., 2000; Gucci and Tattini, 1997). These results indicate higher tolerance of fig plants than that previously reported. One explanation lies in the small size of plants (seedlings or rooted cuttings less than one-year-old) used in previous studies (Nejad and Shekafandeh, 2014; Okubo and Utsonomiya, 1996). It is well known that plant age and stage of development play a role in resistance to abiotic stresses such as freezing or salinity, and that young plants are usually more tender than adult trees (Gucci and Tattini, 1997; Levitt, 1980). An alternative explanation lies in genotypic sensitivity (Soliman and Abd Alhady, 2017; Zarei et al., 2016). Based on symptoms appearance, growth, and gas exchange, 'Dottato' stands out as a tolerant cultivar (Soliman and Abd Alhady, 2017; Zarei et al., 2016), which can partially explain the maintenance of biomass accumulation at NaCl concentrations that otherwise

were inhibitory for the growth of other genotypes. Similarly to previous investigations, there was a negative correlation between canopy biomass and NaCl concentration (Zarei et al., 2016) or internode length and the number of expanded leaves *in vitro* (Metwali et al., 2014).

Species of medium tolerance to salinity decrease LOP to maintain a favourable gradient for the uptake of water and nutrients (Gucci and Tattini, 1997; Hasanuzzaman et al., 2013; Hasegawa et al., 2000). We found a decrease in LOP as the saline concentration was increased within the 0–200 mM range of concentrations. The salt-induced decrease in LOP compensated for the lower LWP and allowed to maintain turgor of 50 mM-treated plants to the levels of controls and that of the 100 mM-treated ones above 0.5 MPa. Turgor is the main drive for cell expansion in growing tissues, so positive pressures are needed to continue growth (Hasegawa et al., 2000). A reduction in growth implies using fewer resources that can be potentially destined to activate mechanisms of stress adaptation. The decrease in LOP was likely due to the accumulation of salts and osmotically active solutes caused by salt stress, as it happens in most crops (Rhoades et al., 1992; Gucci et al., 1997, 1998; Hasegawa et al., 2000; Melgar et al., 2008; Storey and Walker, 1999). Previous studies reported that salt tolerant fig genotypes were able to exclude Na^+ and Cl^- from the shoot and leaf (Okubo and Utsonomiya, 1996; Zarei et al., 2016).

Gas exchange parameters of control 'Dottato' plants were higher than those measured in field-grown Greek cultivars 'Fracasana' and 'Mission', but similar to cv. 'Kalamon' (Vemmos et al., 2014). We measured *A* values ranging between 15 and 20 µmol m^{-2} s^{-1} for control plants; g_s was also high and reached values up to 400 mmol m^{-2} s^{-1}. Since gas exchange is influenced by environmental conditions and our data also showed fluctuations that we cannot fully explain (see *A* and g_s of controls in Figure 3), we are unable to conclude whether those high values were inherent to 'Dottato' or caused by experimental conditions. However, the effect of increasing salt concentrations on *A* and g_s confirmed results from Golombek and Lüdders (1993) and Zarei et al. (2016). The courses of *A* of the 50- and 100 mM treatments and their gap with respect to the controls were consistent with dry matter accumulation, which ranged 91–92% (50 mM) and 63–80% (100 mM) of the controls in both years (Figures 3, 4; Tables 1, 2). Stomatal conductance paralleled the course of *A*, but the decrease in g_s was greater than that of *A* as salt stress increased. This resulted in increased WUE (Golombek and Lüdders, 1993), an effective mechanism to reduce water consumption. The increase in root-canopy ratio, a common adaptive response of higher plants to salinity, contributed to enhance water uptake (Hasegawa et al., 2000; Gucci and Tattini, 1997). Although we have evidence of stomatal components affecting gas exchange parameters we cannot quantify the contribution of non-stomatal factors. There were no differences in chlorophyll content across the 0–200 mM salt treatments confirming results by Golombek and Lüdders (1993). Significant losses in chlorophyll occurred for treatments exceeding 200 mM NaCl.

In conclusion, increased water use efficiency, biomass accumulation, maintenance of turgor and chlorophyll, dynamics of gas exchange within the 0–100 mM NaCl range are evidence that young fig plants can probably tolerate long periods of salt stress. Fig fruits provide a number of bio-active compounds as they are rich in anthocyanins, flavonols, flavones, phenolic acids (Russo et al., 2014; Solomon et al., 2016; Francini et al., 2021) and supply minerals, vitamins, carbohydrates and calories with low levels of fat, cholesterol or sodium (Barolo et al., 2014). Major organic volatile compounds from the peel and pulp have also been characterized (Gündeşli et al., 2020). The nutraceutical value of fruits is currently a potential drive for the development of the fig industry in dry areas characterized by calcareous and/or saline soils. This species well tolerates NaCl concentrations of 50 mM, and up to 100 mM with reduced growth. Concentrations between 50 and 100 mM are compatible with cultivation in soils or with water of medium salinity (Rhoades et al., 1992). The electrical conductivity of saturated soil paste extract at which there is no reduction in yield has been estimated as 2.7 dS m^{-1}, a threshold similar to that reported for olive (2.6 dS m^{-1}) (NSW-DPI, 2016), whereas a 10% yield decrease should occur at 4–6 dS m^{-1} (Bernstein, 1980), an interval compatible with our results and values reported for other moderately tolerant woody species (Gucci and Tattini, 1997; Sun et al., 2018). Our study expands the interval of safe growth and performance beyond what had been previously reported. *Ficus carica* can be considered not only a perennial crop of medium tolerance to salinity, but also suitable for areas where brackish or saline waters are used for irrigation or salinity develops as a transient stress over the summer months, as it occurs in Mediterranean climates. Although the long-term effects on yield and fruit quality remain to be ascertained, there are good perspectives for growing fig trees under saline conditions provided tolerant cultivars are used.

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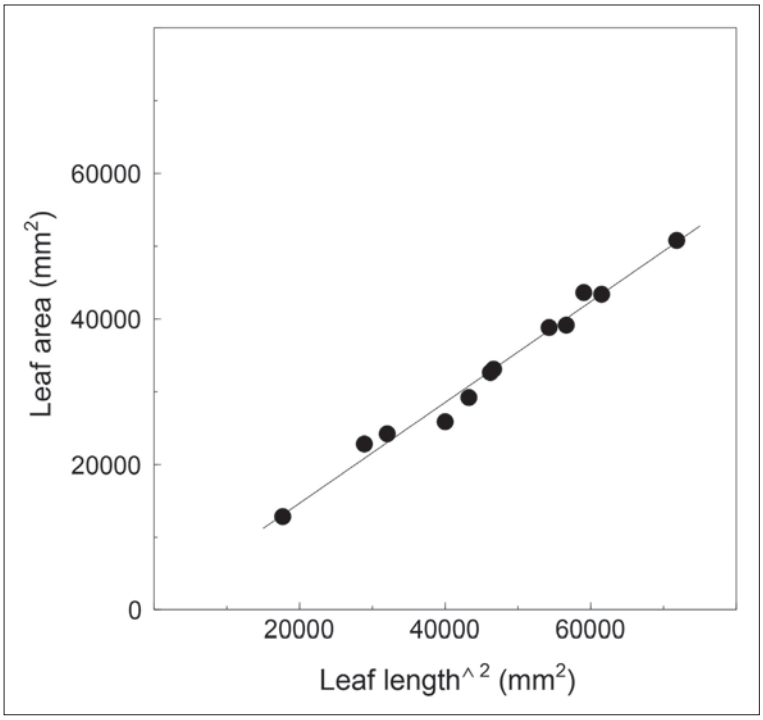
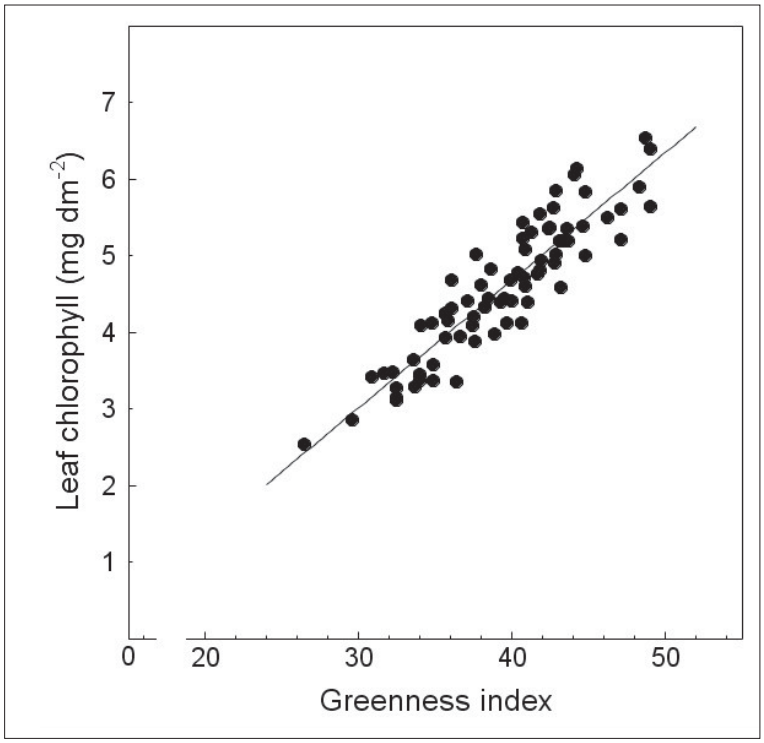
Supplemental Information



Supplemental Information – Figure S1. The relationship between leaf length squared and leaf area of leaves of cv. 'Dottato'. Regression equation: Leaf area = 0.69 • Leaf length^2 – 864; R^2 = 0.984.



Supplemental Information – Figure S2. The relationship between greenness index and leaf chlorophyll content determined using the method by Moran and Porath (1980). Regression equation: y = 0.17x – 1.99; R^2 = 0.83.