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Water relations of Fino lemon plants on two rootstocks under flooded conditions

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Abstract

Potted two-year-old Fino lemon plants (*Citrus limon* (L.) Burm. fil.) grafted on two different rootstocks: sour orange (*C. aurantium*) (SO), and *C. macrophylla* (CM) were submitted to two different treatments: non-flooded (control) and flooded for 8 days, under field conditions. Lemon/CM plants had lower plant plus soil resistance to water flow ($R_{(p+s)}$) values for both treatments. The decrease in leaf water potential (Ψ_l) and leaf turgor potential (Ψ_p) values, observed in the last part of the flooding period, in both flooded scion/rootstock combinations, can be related to the increase in the resistance to water flow. The maintenance in Ψ_l and Ψ_p values in flooded plants at values similar to those of the control plants, at the beginning of the flooding period and during the recovery period, can be ascribed to the stomatal control observed (decrease in leaf conductance (g_l) values). The later g_l recovery in lemon/CM than in lemon/SO flooded plants, could explain the lower vegetative growth of lemon/CM plants by flooding effect. The observed g_l response to soil flooding suggested that porometry is a reliable indicator of the altered behaviour caused by flooding in lemon plant.

Keywords: Lemon plants; Flooding stress; Water relations

Abbreviations: CM, *Citrus macrophylla*; E_l, leaf transpiration rate; g_l, leaf conductance; soil-O_2, soil oxygen concentration; Ψ_l, leaf water potential; Ψ_m, soil matric potential; Ψ_s, leaf osmotic potential; Ψ_p, leaf turgor potential; $R_{(p+s)}$, plant plus soil resistance to water flow; SO, sour orange.

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1. Introduction

Fino lemon trees grafted on sour orange or *Citrus macrophylla* are widely cultivated along the Mediterranean coast of Spain. The semi-arid cli-

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mate of this area, with an annual rainfall of ca. 250 mm, means irrigation practices are necessary for commercial crop culture. However, occasional very heavy rainfall occurs in spring and autumn. This induces detrimental effects on fruit trees [1].

The overriding effects of soil flooding are to limit the availability of oxygen to the roots [2] and to reduce root permeability to water uptake [3]. The stress symptoms are similar to those reported for drought stress, although mechanisms and causes differ [4]. The symptoms include stomatal regulation [5], changes in leaf water status [6], decrease in leaf gas exchange parameters [7,8], leaf abscission and epinasty [5,9], anatomical and morphological adaptations [6,10], chlorosis, necrosis and reduction in growth [3,11].

Citrus flood resistance is considered intermediate in relation to other fruit trees [12]. Scion/rootstock interactions on citrus tree tolerance/intolerance to flooding stress are basic to successful citriculture under these occasional situations [13]. In this sense, Vu and Yelenosky [8] indicated that under prolonged soil flooding conditions leaf photosynthetic capacity decreased, fibrous roots were damaged and leaf abscission was induced more when sweet orange plants were grafted on sour orange than on rough lemon rootstocks. The ability of the former to develop adventitious roots could be responsible for this more favourable response [14].

According to Ortíz and García-Lidón [15] and Bender [16], citrus plants grafted on sour orange are more resistant to flooding than those grafted on *C. macrophylla*. However, there are no studies about the mechanisms developed for lemon plants, on these two rootstocks, to confront flooding stress situations. The genetic basis of this information could provide critical data on developing superior rootstocks to cope with this problem in the Mediterranean citrus culture [8].

For these reasons, the aim of this study was to characterise, under flooding conditions of a duration similar to the effect of a heavy rainfall, the tolerance mechanisms of Fino lemon plants grafted on sour orange and *C. macrophylla*. Leaf conductance, leaf water potential, leaf turgor potential, plant plus soil resistance to water flow and shoot growth were used as stress indicators.

2. Material and methods

2.1. Plant material and treatments

The experiment was carried out on two-year-old lemon plants (*Citrus limon* (L.) Burm. fil.) cv. Fino grafted on two different rootstocks: sour orange (*C. aurantium* L.), lemon/SO, and *C. macrophylla*, lemon/CM. They were grown under field conditions in 35 l pots (40 cm diameter) filled with a mixture of a clay loam top soil and peat, containing 4% of organic matter. Pots were buried in the soil in order to protect them against high temperature.

Lemon plants were drip irrigated, using one emitter of 4 l/h/tree, over a year. Soil water potential was maintained around field capacity (-15 to -25 kPa), monitored by tensiometers placed at 20 cm depth. A routine fertilisation and pest programme was applied.

In October 1992, twenty lemon plants of each rootstock were submitted to two different treatments: control plants, irrigated daily as indicated, and flooded plants for a period of 8 days. Ten plants of each rootstock were flooded by placing their pots in a water tank, maintaining the water level 4 cm above soil surface during the flooding period. A similar number of plants were used for the control treatment. After being submerged for 8 days, the plants were removed from the water, drained over three days, then placed in the same conditions as the control plants. Recovery was studied over a period of 43 days.

During the experimental period the mean air temperature ranged from 24.1 to 11.5°C, the mean daily evaporation, from a class A pan evaporimeter on grass, was 4 mm/day, and the mean air vapour pressure deficit, from dry and wet bulb temperature data, ranged from 3.5 to 1.5 kPa.

2.2. Measurements

The oxygen content of the soil water surrounding the roots (soil-O_2) was measured with an oxygen-electrode YSI, model 58. One suction probe (5 cm diameter) was installed in four plants per treatment of each rootstock type. The oxygen-electrode was carefully introduced in the probes for the oxygen concentration measurements.

Leaf water potential (Ψ_l) was measured on mature and sun exposed leaves from the middle third of the trees, using a pressure chamber and following the recommendations of Turner [17]. Two measurements per tree and four trees per treatment of each rootstock were taken at each sampling.

Leaf conductance (g_l) and transpiration rate (E_l) were measured on the abaxial surface on a similar number of mature sun exposed leaves to Ψ_l, using a steady-state porometer (LICOR, LI-1600). All measurements were made at midday ($\approx$ 12 solar time) every 1–3 days during the flooding period, and less frequently during the recovery period.

Leaves from Ψ_l measurements were frozen in liquid nitrogen. After thawing, the osmotic potential (Ψ_s) was measured in the expressed sap using the HR-33T dew point microvoltimeter attached to the C-52 chamber (WESCOR) following the procedure reported by Slavik [18]. Leaf turgor potential (Ψ_p) was derived as the difference between Ψ_l and Ψ_s.

Plant plus soil resistance to water flow ($R_{(p+s)}$) was derived according to Sands and Theodorou [19]:

$$E_l = -(\Psi_l - \Psi_m)/R_{(p+s)}$$

where Ψ_m is the soil matrix potential. Since the matric potential is zero in the flooded treatment and close to zero in the control treatment, plant plus soil resistance can be expressed (following Savé and Serrano [6]) as:

$$R_{(p+s)} = -\Psi_l/E_l$$

Terminal shoot growth of four tagged shoots per tree, one from each compass point, was measured on four trees per treatment of each rootstock type at the beginning and at the end of the experiment.

3. Results

The concentration of oxygen in the soil water surrounding the roots (soil-O_2) was similar in both scion/rootstock combinations studied (lemon/SO and lemon/CM), so, the average values are shown in Fig. 1. Soil-O_2 levels in control plants ranged between 0.19 and 0.25 mmol/l during the experimental period.

A rapid decrease in soil-O_2 was found from the beginning of the stress period, with a 50% of reduction in the first 24 h. From day 2 to the end of the flooding period, the soil-O_2 levels remained constant (around 0.06 mmol/l). The complete recovery of these levels occurred 16 days after the end of the flooding period (Fig. 1).

Vegetative growth, based on shoot elongation measurements, during the experimental period was 37.9 and 23.7 mm, in control and flooded lemon/SO plants, respectively. In lemon/CM plants shoot elongation was 93.8 and 25.8 mm, in control and flooded plants, respectively (data not shown). These results indicated that vegetative growth was higher in lemon/CM than in lemon/SO control plants, with an increase of 28% with respect to the initial length for lemon/SO plants, as opposed to 73% for lemon/CM ones. Vegetative growth of lemon plants on SO rootstock was unaffected by flooding, whereas in those grafted on CM, a statistically significant reduction in shoot growth (70%) was noted.

Leaf water potential (Ψ_l) in control plants presented some fluctuations during the experimental period. These were of greater magnitude in lemon/SO plants (Fig. 2). The overall Ψ_l levels were statistically significant higher in lemon/CM than in lemon/SO plants.

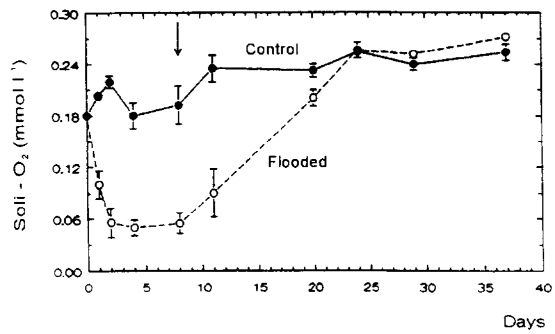

Fig. 1. Changes in oxygen content of the soil water surrounding the roots (soil-O_2) in lemon plants on CM and SO rootstocks during the experimental period in control (closed symbols) and flooded (open symbols) treatments. Each point is the mean of eight measurements. Arrow indicates the end of the flooding period. Vertical bars are $\pm$ SE of the mean.

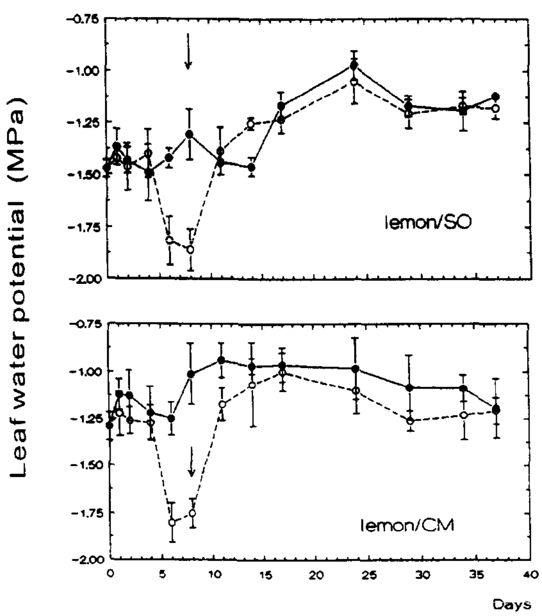

Fig. 2. Effect of flooding stress during the experimental period on leaf water potential (Ψ_l) in lemon/SO and lemon/CM plants in control (closed symbols) and flooded (open symbols) treatments. Arrows indicate the end of the flooding period. Each point is the mean of eight measurements. Vertical bars are ± SE of the mean.

During the first four days of the flooding period non-significant differences in Ψ_l values were found between control and flooded plants in both scion/rootstock combinations. Thereafter, a drastic Ψ_l reduction was observed, reaching minimum Ψ_l values of around -1.8 MPa, with no differences between both scion/rootstock combinations, although the reduction, with respect to the control Ψ_l levels, was greater in lemon/CM plants (Fig. 2).

The recovery of leaf water potential, after the plants were removed from the water, occurred rapidly. Flooded lemon/SO plants reached similar levels of Ψ_l to that of control plants just three days after the end of the flooding period, and three days after that in lemon/CM ones (Fig. 2).

Flooding stress did not induce a Ψ_p decrease in either scion/rootstock combinations, during the first four days of the stress period (data not shown). Afterwards, a Ψ_p decrease was observed. Minimum Ψ_p values were obtained at the end of the stress period (around 0.5 MPa). The recovery of Ψ_p after flooding period was discontinued was similar to that of Ψ_l.

Control plants showed higher overall leaf conductance (g_l) values when they were grafted on CM than on SO (Fig. 3). Flooding caused a progressive reduction of g_l values from the beginning of this period, reaching minimum values of 15 and 30 mmol/m^2/s, for lemon/SO and lemon/CM plants, respectively, at the end of the stress period.

Leaf conductance recovery in flooded plants was very slow (Fig. 3), reaching values similar to those of the control plants 26 days after Ψ_l was recovered, in lemon/SO plants (Fig. 3). In lemon/CM plants the g_l recovery occurred 2 weeks latter than that of lemon/SO plants (data not shown).

Both treatments of lemon/SO plants had higher plant plus soil resistance to water flow ($R_{(p+s)}$) values than the lemon/CM ones (Table 1). The flooding effect caused an increase in $R_{(p+s)}$, which was consistent from day 2 of the stress period in

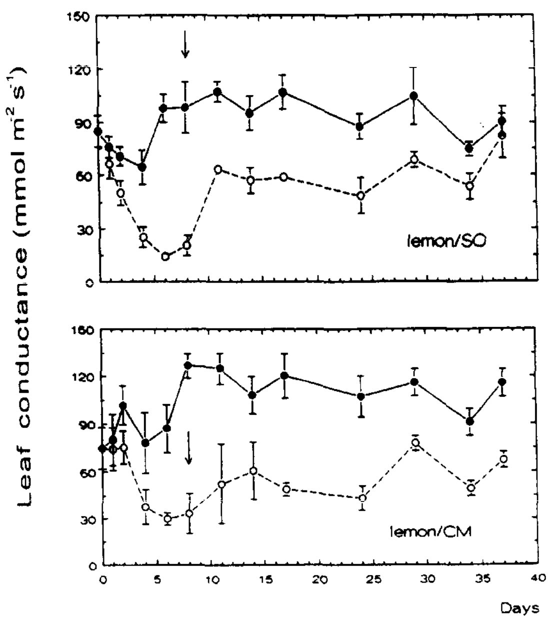

Fig. 3. Effect of flooding stress during the experimental period on leaf conductance (g_l) in lemon/SO and lemon/CM plants in control (closed symbols) and flooded (open symbols) treatments. Arrows indicate the end of the flooding period. Each point is the mean of eight measurements. Vertical bars are ± SE of the mean.

Table 1
Plant plus soil resistance to water flow ($R_{(p+s)}$, MPa/mol/m^2/s) of Fino lemon/CM and lemon/SO plants in control and flooded treatments throughout the experimental period

Day	Lemon/CM		Lemon/SO	
	Control	Flooded	Control	Flooded
0	529.6	—	693.4	—
1	476.3 a	516.7 a	790.1 a	794.8 a
2	436.4 a	637.9 a	760.6 a	1070.2 b
4	568.0 a	1015.1 b	906.0 a	1387.4 b
6	621.5 a	1880.0 b	670.1 a	3921.4 b
8↓	456.8 a	2368.1 b	523.1 a	3709.3 b
11	403.2 a	1264.0 b	764.3 a	1255.2 b
14	499.4 a	958.6 b	781.0 a	1203.6 b
27	460.9 a	876.7 b	490.9 a	1299.4 b
34	637.2 a	1027.9 b	690.0 a	980.2 b
37	646.5 a	1427.2 b	781.0 a	810.0 a
45	654.7 a	845.0 b	700.4 a	824.0 a
49	592.7 a	680.1 b	719.3 a	851.2 a
51	537.5 a	526.1 a	693.4 a	751.0 a

Each value is the mean of eight measurements. The arrow indicates the end of the flooding period. Means within a row for each scion/rootstock combination that do not have a common letter are significantly different by the $LSD_{0.05}$ range test.

both scion/rootstock combinations. At the end of the flooding period lemon/SO flooded plants presented a higher $R_{(p+s)}$ increase than lemon/CM ones.

After the flooding period ended, $R_{(p+s)}$ values in flooded plants remained higher than control plants during a period of 29 and 43 days for lemon/SO and lemon/CM plants, respectively (Table 1). Total $R_{(p+s)}$ recovery did coincide with that of the g_l (Fig. 3).

4. Discussion

It is clear that the overriding effect of flooding is to limit the diffusion rate of oxygen in the soil [2] (Fig. 1). The fact that the depletion in the soil-O_2 concentration was similar in the both scion/rootstock combinations studied, together with the greater sensitivity of vegetative growth of lemon/CM plants, is in line with the ideas pointed out by Ortíz and García-Lidón [15] and Bender [16], who indicated that sour orange rootstock tolerate soil flooding better than *C. macrophylla*.

During the first four days of flooding there was, in comparison with the non-flooded plants, a maintenance in Ψ_l (Fig. 1) and Ψ_p (data not shown) values and an increase in $R_{(p+s)}$ values (Table 1) in flooded plants. These behaviours coincided with a progressive g_l reduction (Fig. 2). These facts show that partial stomatal closure of lemon/SO and lemon/CM flooded plants can occur without a decrease in leaf turgor, despite the high $R_{(p+s)}$ values. This stomatal response may be considered as an adaptive mechanism to prevent leaf dehydration [20]. Similar behaviours have been reported in other plant species such as kiwi fruit [6], forest plants [9], tomato [21] and mango [22].

In this sense, stomatal regulation under flooding stress can be related to other processes, according to Savé and Serrano [6], such as low soil oxygen concentration, increase in leaf ABA levels, increase in CO_2 concentration caused by import of gas from the soil, or by injury of the photosynthetic apparatus. Other authors [3,10] indicated that this stomatal closure can be related to the suppression of synthesis and translocation of gibberellins and cytokinins in the roots by root injury resulting from flooding.

On the other hand, it is important to note that in the last part of the flooding period (4–8 days), when the highest $R_{(p+s)}$ and lowest g_l values occurred in flooded plants (Table 1 and Fig. 3), a Ψ_l and Ψ_p decrease was noted (Fig. 2). The cause of this leaf tissue dehydration could be ascribed to a prevailing effect of the high plant plus soil resistance to water flow values, as has been pointed out in flooded almond plant [5].

The fact that $R_{(p+s)}$ values were lower in lemon/CM than in lemon/SO control plants (Table 1) explains the higher overall Ψ_l values in lemon/CM plants (Fig. 3), since the water flow through soil and plant is more favoured in these plants.

After flooding was discontinued, Ψ_l and Ψ_p values in flooded plants recovered (Fig. 2), but the $R_{(p+s)}$ increase and g_l decrease took longer than the recovery of Ψ_l and Ψ_p in both scion/rootstock flooded combinations (Table 1 and Fig. 3). This indicated that during the recovery period there was no close relation between these parameters, with a prevailing behaviour similar to that which operated in the first phase of the flooding period.

The longer g_l recovery time in lemon/CM versus lemon/SO flooded plant (Fig. 3), after soil-O_2 reached control levels (Fig. 1), could indicate that in lemon/CM plants the hormonal imbalance and/or the adverse effects on the photosynthetic apparatus took longer. As a consequence, the overall lower g_l values (lower net photosynthesis) could explain the inhibitory effect of flooding on vegetative growth in lemon/CM plants [23,24].

The results of this study indicated that the two studied rootstocks induced qualitatively similar mechanisms at leaf water relations level to confront a flooding stress period of 8 days. However, the later leaf conductance recovery in lemon/CM plants after the stress period, may indicate that Fino lemon plants grafted on sour orange is a more appropriate combination to resist an occasional very heavy rainfall situation, which is in agreement with the related literature [16,17].

Two different situations could be identified in the stomatal response to flooding. In the first four days of the flooding period and during the recovery period, the stomatal regulation (lower g_l) prevented leaf tissue dehydration, despite the higher $R_{(p+s)}$ values in flooded than in control plants. In consequence, in the first case (0–4 days), the g_l reduction could be mediated by the low soil-O_2, the increase in leaf CO_2 concentration, as well as the effects of chemical signals from roots or adverse effects on the photosynthetic apparatus. During the recovery period, however, when soil-O_2 levels were recovered, only the last mentioned causes could operate.

In the last part of the flooding period (4–8 days) a second situation operated. The highest $R_{(p+s)}$ values could be responsible for the Ψ_l and Ψ_p decrease, therefore, the minimum g_l values registered in this phase, can be produced by leaf dehydration and/or by the causes involved in the first described situation.

The g_l response early in the flooding during the two described situations, could suggest that porometry is a reliable indicator of the altered behaviour caused by flooding in lemon plants.

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