

Running title: Flooding response of apricot on two rootstocks

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Physiological responses of apricot plants grafted on two different rootstocks to flooding conditions

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Summary

The effects of soil flooding on plant water relations and vegetative growth was studied in potted two-year-old apricot plants (*Prunus armeniaca* L., cv. Búlida) grafted on two different rootstocks: Pollizo prune (*P. insititia* L.) (P) and Real Fino apricot (RF). Plants were submitted outdoors to three treatments: T0, not flooded (control), and two flooded treatments for 3 (T1) and 6 (T2) days. Apricot water relations were seen to be adversely affected from first day of the flooding onwards. These effects were more pronounced in Búlida/RF than in Búlida/P plants. The T1 plants developed an early stomatal regulation (decrease in leaf conductance (g_l)), which prevented leaf tissue dehydration, together with decrease in net photosynthesis (Pn) and the increase in resistance to water flow ($R_{(p+s)}$). This early g_l and Pn response suggests that porometric and/or photosynthetic changes are reliable bio-indicators of the altered behaviour caused by flooding in apricot plants. The lowest g_l and Pn, and highest $R_{(p+s)}$ values occurred with more prolonged flooding (6 days), when a decrease in leaf water potential (Ψ_l) and leaf turgor was noted, together with epinasty, which in Búlida/RF plants led to a decrease in Ψ_l to -6.0 MPa, and the death of all plants. These results indicate Búlida apricot plants grafted onto Pollizo prune rootstock is a more appropriate combination than Búlida/Real Fino to resist occasional soil flooding situations.

Key words: Flooding stress - Gas exchange - *Prunus armeniaca* - Water relations.

Abbreviations: C_i internal CO_2 concentration. - E_l leaf transpiration rate. - g_l leaf conductance. - J water flow rate. - L root length. - L_p root hydraulic conductivity. - LIA leaf insertion angle. - P hydrostatic pressure. - P_n net photosynthesis. - Ψ_l leaf water potential. - Ψ_m soil matrix potential. - Ψ_o leaf osmotic potential. - Ψ_{os} leaf osmotic potential at full turgor. - Ψ_p leaf turgor potential. - $R_{(p+s)}$ plant plus soil resistance to water flow. - soil- O_2 soil oxygen concentration.

Introduction

Apricot (*Prunus armeniaca* L.) is widely cultivated along the Mediterranean coast of Spain. The semi-arid climate of this area is characterised by occasional very heavy rainfall occurring in spring and autumn. Most of the soils, which are developed from Miocene lime marl, have clay-loam to clay textures and a low organic matter content. Such soils frequently have poor drainage and heavy rain or excessive irrigation causes them to become waterlogged; air space is displaced by the water and O_2 in the soil is quickly depleted, which induces a water stress situation in plants (Kawase 1981).

Research into the effects of water deficit on agricultural crops has been extensive, whereas less attention has been focused on plant responses to soil flooding. The physiological responses to flooding represent a wide range of

metabolic, hormonal, developmental and physiological processes. Among these, may be mentioned ethylene accumulation, stomatal closure, wilting, changes in the leaf insertion angle, reduced growth, and adventitious root formation (Bradford and Yang 1981, Kramer 1983, Fitter and Hay 1987).

In fruit trees, the resistance to oxygen deficiency in roots is mediated by the characteristics of the rootstock. Differences in the level of soil aeration tolerated by the more commonly used rootstocks of apricot trees have been described (Egea 1970, Crossa-Raynaud and Audergon 1987). Although Egea (2000) indicated that Pollizo prune rootstock tolerate soil flooding better than Real Fino apricot, there have been no studies concerning the response of these apricot rootstocks to different soil flooding treatments.

For these reasons, the aim of the present paper was to study the effects of soil flooding on the plant water relations and vegetative growth of young apricot plants grafted onto apricot and prune rootstocks, as well as to evaluate the effect of rootstock on the degree of resistance of apricot plants to flooding conditions.

Materials and Methods

Plant material and experimental conditions

The experiment was carried out on two-year-old apricot trees (*Prunus armeniaca* L.), cv. Búlida, on two rootstocks: Pollizo prune (*P. insititia* L.) (P) and Real Fino apricot (RF), growing outdoors in 35 litre pots (40 cm diameter) containing a mixture of clay loam topsoil and peat (4:1 v/v). Plants were drip

irrigated daily using one emitter of 4 l h^{-1} per tree, maintaining the soil matrix potential at about -20 kPa (monitored with tensiometers placed at 15 cm depth). Routine fertilization was applied (65 g N , $48 \text{ g K}_2\text{O}$, $72 \text{ g P}_2\text{O}_5$ and 1.5 g Fe (Fe-EDDHA) per plant and year) through the drip irrigation system every 2 weeks. No root emergence from pots into the surrounding soil was observed.

At the end of July 1999, 30 apricot plants of each rootstock, of similar size and appearance were submitted to three treatments: T0, nonflooded (control treatment), irrigated daily as indicated, and two flooded treatments, for a period of 3 days (T1) and 6 days (T2). Ten plants of each rootstock were flooded by submerging the pots in a water tank (70 cm depth), maintaining the water level 4 cm above soil surface during the flooding period. A similar number of plants (ten) were used for the control treatment. After being submerged for 3 and 6 days, the plants were removed from the water, drained, then placed in the same conditions as the control plants. Irrigation was reinitiated when soil matrix potential values reached -45 kPa , which occurred three and four days after the end of the flooding period, for T1 and T2 treatment, respectively. Recovery was studied over a period of 40 days.

During the experimental period the climatic conditions were typical of a Mediterranean climate, with mean air temperature ranging from 24 to $28 \text{ }^\circ\text{C}$, while the mean daily evaporation, from a class A pan evaporimeter on grass, was around 7.5 mm d^{-1} , and the mean air vapour pressure deficit, from dry and wet bulb temperature data, ranged from 2.5 to 3.5 kPa .

Measurements

Soil and plant water status, and leaf gas exchange were measured daily during the flooding period, and every 2-4 days during the recovery period. The oxygen content of the soil water surrounding the roots (soil-O₂) was measured with an oxygen-electrode Orion, model 810. One suction probe (5 cm diameter) was installed in three plants per treatment of each rootstock type. The oxygen-electrode was carefully introduced in the probes for the oxygen concentration measurements.

Soil matrix potential (Ψ_m) were determined in three pots per treatment using tensiometers at 15 cm depth. Leaf water potential was measured at midday (12:00 h solar time) (Ψ_l) for one mature leaf per plant and five plants per treatment, using a pressure chamber, following the recommendations of Turner (1981). Fully expanded leaves were selected at random from the middle third of the shoots. After measuring Ψ_l , the leaves were frozen in liquid nitrogen and osmotic potential (Ψ_o) was measured after thawing the samples and extracting the sap, using a Wescor 5500 vapour pressure osmometer. Leaf turgor potential (Ψ_p) was derived as the difference between leaf osmotic and water potentials.

Leaf osmotic potential at full turgor (Ψ_{os}) was measured on leaves adjacent to those used to measure leaf water potential. Five leaves per treatment were rehydrated to full saturation, following the same methodology as for Ψ_o . Osmotic adjustment was estimated as the difference between the Ψ_{os} of flooded and control plants.

Leaf conductance (g_l), net photosynthesis (P_n), leaf transpiration rate (E_l) and internal CO_2 concentration (C_i) were measured at mid-day, for a similar number (five) and type of leaves as for leaf water potential, using a field-portable, closed gas-exchange photosynthesis system (LI-6200) incorporating IRGA (LI-6250). Each leaf was enclosed within a fan-stirred one-litre chamber. The mean return flow rates of air circulating within the closed system and the leaf to air vapour pressure deficit for all measurements were around $450 \mu\text{mol s}^{-1}$, and -2.1 kPa, respectively. The CO_2 analyser was calibrated daily with two standard CO_2 /air mixtures.

The angle between leaf petiole and stem (leaf insertion angle, LIA) was measured with a transparent protractor to determine epinasty, the change in petiole angle. Ten randomised leaves per plant and five plants per treatment were measured.

Plant plus soil resistance to water flow ($R_{(p+s)}$) was derived, according to Sands and Theodorou (1948):

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

Since the matrix 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 1986) as:

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

Root hydraulic conductivity (L_p) was measured according to Ramos and Kaufmann (1979) at the end of the two flooding periods on three plants of

each rootstock. The root system was carefully washed, and a portion was immediately submerged in a container of water before being placed in the pressure chamber with the cut stump exposed. A small piece of tubing was fitted to the stump and connected to an Eppendorf micro tube. After obtaining a good seal, the air pressure was increased at a rate of 0.4 MPa min^{-1} up to final pressure of 1.0 MPa . Every three min the exudate was collected and its volume measured. This was repeated four times, the first exudate was not included in the calculation of the mean exudate volume. Subsequently, total root length was estimated using an Image Analysis System (Delta-T Devices Ltd.). Root hydraulic conductivity was calculated using the formula:

$$L_p = J / (P \cdot L)$$

where L_p is expressed in $\text{mg MPa}^{-1} \text{ m}^{-1} \text{ s}^{-1}$, P is the applied hydrostatic pressure (MPa), L is the root length (m) and J is the water flow rate through the entire root system (mg s^{-1}).

Vegetative growth was evaluated by measuring the trunk diameter 10 cm above the graft union, using an electronic digital calibre. Measurements were taken on all the selected trees at the beginning of the experiment and at the end of the flooding and recovery periods. At the end of the experimental period, three plants per treatment and rootstock were separated into roots, stems and leaves, and the fresh and dry weights (oven-dried at $75 \text{ }^\circ\text{C}$ to constant weight) of each component were determined. Total and average leaf area were determined using the Delta-T measurement system described above.

Results

Water relations

The concentration of oxygen in the soil water surrounding the roots (soil-O₂) was similar in both rootstocks studied; the average values are shown in figure 1. Soil-O₂ values in the control plants were around 6 mg l⁻¹ throughout the experimental period.

Soil-O₂ values rapidly decreased from the beginning of the flooding period, with a 50 % reduction being observed in the first 24 hours. After three days this value decreased to 2.5 mg l⁻¹ (T1 treatment), and around 0.5 mg l⁻¹ after 6 days of flooding in the T2 treatment (Fig. 1). These values recovered to reach the levels of the control 3 and 18 days after the end of the flooding period, for T1 and T2 treatments, respectively (Fig. 1).

Leaf water potential (Ψ_1) values in the control plants presented similar values of around -1.5 MPa in both P and RF rootstocks (Fig. 2). During the first three days of flooding non-significant differences in Ψ_1 values were found between control and flooded plants in both rootstocks. At day 4 of the experimental period, the treated (T1 and T2) plants grafted onto RF showed a significant Ψ_1 decrease (Fig. 2 a, c), whereas those grafted onto P showed similar Ψ_1 values to those of the control treatment (Fig. 2 b, d).

Minimum Ψ_1 values of around -2.7 MPa were reached in T1 treatment two days after the end of the flooding period, with no differences between rootstocks. In the T2 Búlida/P plants Ψ_1 remained constant from day 4 to 6,

then decreased to reach a minimum of -2.9 MPa four days after the end of the flooding period (Fig. 2 d). However, plants on RF rootstock showed a drastic decrease in Ψ_1 (< -6 MPa) (Fig. 2 c), which caused the death of all the plants of this treatment.

The leaf water potential recovered slowly after the plants were removed from the water. In the T1 treatment, recovery was faster in plants grafted on P than on RF rootstock (13 and 21 days after the end of the flooding period, respectively) (Fig. 2 a, b). In T2 plants grafted on P rootstock Ψ_1 recovered after 23 days (Fig. 2 d).

Leaf osmotic potential at full turgor was similar in plants of both rootstocks, with values of -1.8 MPa in both the control plants and those submitted to flooding (data not shown).

Leaf conductance (g_i) showed slight fluctuations during the experimental period both in the control and flooded plants (Fig. 3). Control plants showed slightly higher overall g_i values when they were grafted on P than on RF (Fig. 3). Flooding caused a progressive reduction of these g_i values from the outset, which was significant from day 1 in Búlida/RF plants (Fig. 3 a) and from day 2 in Búlida/P plants (Fig. 3 b).

Minimum g_i values coincided with those of Ψ_1 (Fig. 2), on day 5 for the T1 treatment of both rootstocks (g_i values 30 % of the control) (Fig. 3 a, b), and on day 10 for the T2 treatment on Búlida/P plants (g_i values 18 % of the control) (Fig. 3 d). T2 plants grafted on RF rootstock showed g_i values near

zero from day 5 of flooding (Fig. 3 c).

Leaf conductance was slow to recover in flooded plants (Fig. 3), reaching values similar to those of the control plants 5-8 days after Ψ_1 had recovered (Fig. 2). This was particularly so in Búlida/RF plants in which g_l recovered later than in Búlida/P plants.

Net photosynthesis showed a similar behaviour to that of g_l , with overall values slightly higher in plants grafted on P than on RF rootstock. A greater reduction in Pn was observed in plants grafted on RF rootstock (Fig. 4 a, c). In T2 plants grafted on RF net photosynthesis reached negative after day 4 (Fig. 4 c). However Pn values recovered to reach control values more rapidly than g_l (Fig. 3), coinciding with the recovery of leaf water potential values (Fig. 2). All flooded plants showed simultaneous decreases in Pn and g_l , and an increase in internal CO₂ concentration values (Table 1).

Flooding caused a downward growth of the petioles known as epinasty, which was statistically significant from day 6 of the experimental period in plants of both rootstocks (Table 1), whether in the T2 treatment (still immersed in water) or in the T1 treatment (during the recovery period). Epinasty was more pronounced in plants grafted on RF than on P rootstock (Table 1).

By day 3 of the flooding period an increase in plant plus soil resistance to water flow ($R_{(p+s)}$) had occurred (Table 1). At the end of the flooding periods Búlida/RF flooded plants showed greater increases than Búlida/P plants. It should be noted that maximum $R_{(p+s)}$ values did not coincide with the end of

the flooding periods (Table 1). Recovery was similar to that of leaf conductance and occurred more rapidly in plants grafted on P than on RF (Table 1).

Root hydraulic conductivity (L_p) was around 170 and 90 $\text{mg MPa}^{-1} \text{m}^{-1} \text{s}^{-1}$ for control plants grafted on RF and P, respectively. A greater reduction was observed in Búlida/RF plants (37 and 29 % of control values, for T1 and T2 treatments, respectively), whereas the L_p values of Búlida/P only decreased after 6 days of flooding (T2 treatment) (data not shown).

Vegetative growth

After three days of flooding, plants did not exhibit any evidence of wilting. However, on day 3 of the recovery period the plants on both rootstocks in the T1 treatment began to show visual wilting symptoms, which was more severe in Búlida/RF plants. On day 5, 20 % of these plants showed shoot desiccation, provoking slight leaf abscission, which did not affect Búlida/P plants. In the T2 treatment, leaf wilting and desiccation were observed in Búlida/RF plants, 2-4 days after flooding was discontinued. This led to total leaf shedding in the RF plants, whereas only 20 % of the Búlida/P plants lost their leaves (data not shown).

Total biomass was reduced by flooding in Búlida/RF plants, with a reduction with respect to non-flooded plants, of 22 and 41 % for T1 and T2 treatments, respectively (Table 2). However, the dry weights of the shoots, leaves and roots of flooded plants were similar in flooded and control plants of

the Búlida/P combination.

Trunk growth was also negatively affected by flooding, with negative values being observed in plants of the T2 treatment, at the end of the experiment (Table 2). No significant differences on trunk growth in Búlida/P plants were found, although a tendency to decrease by flooding effect was observed (Table 2).

Discussion

In flooded soils, air space is displaced by water, and the oxygen remaining in the soil is quickly depleted (Fig. 1) by respiration of plant roots and soil microorganisms (Kawase 1981). When plants in this experiment were removed from water, soil-O₂ recovery was slow (Fig. 1). A similar slow recovery period was found in citrus plants flooded for 8 days (Ruiz-Sánchez et al. 1996).

Flooding had no influence on the leaf water potential of apricot plants during the first three days of the flooding period (Fig. 2), while leaf conductance and net photosynthesis were more affected, decreasing from the beginning of flooding (Figs. 3 and 4). No osmotic adjustment was found in flooded plants. Nor were we able to detect differences in leaf turgor potential between the leaves of flooded and control plants (data not shown) at a time when leaf conductance was obviously affected (Fig. 3).

For these reasons, stomatal regulation, which has been recognised as

one of the earliest responses to flooding in fruit trees (Kozłowski 1982, Syvertsen et al. 1983, Davies and Flore 1986, Smith and Ager 1988, Schaffer and Ploetz 1989, Larson et al. 1991), appears to have had a positive impact on the water balance of both apricot rootstocks during the early stages of flooding (McNamara and Mitchell 1989, Ruiz-Sánchez et al. 1996), and may be considered as an adaptive mechanism to prevent leaf dehydration (Bradford and Hsiao 1982).

This stomatal regulation did not occur as a result of a water deficit in the leaf, but as a hormonal imbalance caused; it has been proposed by an increase in abscisic acid as well as a deficiency in such factors from the roots as cytokinins and gibberellins, which promote stomatal opening (Wright 1972, Bradford and Yang 1981).

During the recovery period, leaf conductance of treated plants remained lower than leaf conductance of control plants, although the stomata remained responsive to environmental changes (Fig. 3). Similar observations were made in blueberry plants submitted to periodic flooding during 2-7 days, although over longer periods leaf conductance did not respond to environmental changes, and did not recover pre-flood levels after flooding was discontinued (Crane and Davies 1988).

Several studies have pointed to a parallel reduction in photosynthetic capacity and leaf conductance caused by flooding (Wong et al. 1979, Kozłowski and Pallardy 1984). In our study, the concomitant increase in internal CO₂ concentration (Table 1), and decrease in net photosynthesis (Fig.

4) suggested that carbon assimilation was also affected by nonstomatal factors (Farquhar and Sharkey 1982, Larson et al. 1991).

Together with stomatal regulation, epinasty is one of the earliest responses of plants to soil flooding, and has been observed in a variety of herbaceous and woody species (Bradford and Yang 1981, Sánchez-Blanco et al. 1994). Ethylene has been established as an important mediator in this response (Drew et al. 1979).

Low concentrations of oxygen in the root zone have been shown to reduce the permeability of roots to water (Smith et al. 1990, Zang and Tyerman 1991), increasing the resistance to water uptake (Table 1). Under these conditions loss of water from the shoots exceeds the supply from the root, leading to a drop in leaf water potential (Fig. 2).

Leaf abscission reduced the leaf area in flooded Búlida/RF plants (Table 2), thus limiting transpiration, which is a mechanism to conserve soil water (Kozłowski 1985, Nash and Graves 1993).

Trunk growth in T2 Búlida/RF plants was adversely affected by flooding (Table 2). Similarly, Nash and Graves (1993) observed that flooding induced negative RGR (relative growth rate) values in red apple, pawpaw and black tupelo plants, indicating that these plants were senescing. Larson et al. (1991) indicated that stem radial growth measurement is a more sensitive indicator of the effects of flooding on mango tree growth than the measurement of shoot length growth.

Conclusions

The data obtained in this study indicate that apricot water relations were adversely affected by soil flooding, and the differences between control and flooded plants were evident from the first day of the flooding.

Plants grafted onto Real Fino apricot and Pollizo prune rootstocks developed similar mechanisms to confront short term soil flooding conditions (3 days), based on an early stomatal regulation, which prevented leaf tissue dehydration. Under long term soil flooding (6 days) severe leaf tissue dehydration were noted (as a result of root system deterioration), which, in the case of plants grafted on Real Fino rootstock caused wilting and the death of all plants.

The early leaf conductance and net photosynthesis response seems to suggest that porometric and/or photosynthetic changes are reliable bio-indicators of the altered behaviour caused by flooding in apricot plants, as has been proposed in lemon (Ruiz-Sánchez et al. 1996) and kiwi fruit (Savé and Serrano 1986).

Flooding effects were more pronounced in apricot plants grafted onto Real Fino rootstock than in the plants grafted onto Pollizo prune. Also, flooding reduced the total biomass of Búlida/RF plants. Neither wilting nor desiccation was observed in Búlida/P plants. This indicates that the selection of rootstock is critical in reducing the impact of flooding in apricot plantations.

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Table 1. Internal CO₂ concentration (Ci), epinasty and plant plus soil resistance to water flow (R_(p+s)) in young apricot plants grafted onto Pollizo prune (P) and Real Fino apricot (RF) rootstocks in control (T0) and flooding treatments for 3 (T1) and 6 (T2) days, during the experimental period.

Day	Treat.	Ci (mg L ⁻¹)		Epinasty (°)		R _(p+s) (MPa mol ⁻¹ m ² s ⁻¹)	
		P	RF	P	RF	P	RF
0	T0	320.2	340.3	79.9	77.6	265.3	199.6
1	T0	308.9 a	337.6 a	78.2 a	76.5 a	251.5 a	259.4 a
	T1	350.9 a	358.7 a	81.2 a	79.7 a	284.5 a	385.0 a
3	T0	299.4 a	321.2 a	80.0 a	76.9 a	179.0 a	171.3 a
	T1*	423.5 b	458.0 b	77.1 a	76.5 a	470.0 b	582.1 b
6	T0	322.5 a	328.5 a	76.4 a	73.0 a	240.0 a	204.2 a
	T1	395.5 b	440.5 b	62.6 b	63.6 b	1200.0 c	1487.5 b
	T2*	411.0 b	569.4 c	62.0 b	54.0 b	547.4 b	10940.0 c
10	T0	336.0 a	320.3 a	79.1 a	76.3 a	158.9 a	183.2 a
	T1	313.8 a	401.4 b	66.3 b	61.1 b	493.6 b	640.0 b
	T2	462.2 b	-	68.2 b	-	1611.0 c	-
24	T0	353.3 a	342.7 a	75.0 a	75.0 a	180.9 a	185.3 a
	T1	351.6 a	356.0 a	70.5 a	71.3 a	191.1 a	334.7 b
	T2	357.3 a	-	72.7 a	-	464.3 b	-
33	T0	347.0 a	378.0 a	74.1 a	70.4 a	221.3 a	219.5 a
	T1	356.1 a	371.5 a	68.3 a	69.4 a	226.9 a	208.9 a
	T2	339.0 a	-	67.1 a	-	255.8 a	-

*indicates the end of the flooding period. Each value is the mean of five measurements. Means, for each day, followed by different letter indicate the existence of significant differences by the LSD_{0.05} range test.

Table 2. Total biomass on dry weight basis, root dry weight, total leaf area and trunk diameter increase of young apricot plants grafted onto Pollizo prune (P) and Real Fino apricot (RF) rootstocks in control (T0) and flooded treatments for 3 (T1) and 6 (T2) days, at the end of the experimental period.

Treat.	Biomass		Root		Leaf area		Trunk diameter	
	(g)		(g)		(cm ²)		increase (%)	
	P	RF	P	RF	P	RF	P	RF
T0	1189 a	1180 a	455 a	399 a	5565 a	5313 a	3.88 a	6.40 a
T1	1241 a	918 b	445 a	319 ab	4830 a	2917 b	3.08 a	0.79 b
T2	1048 a	696 c	352 a	237 b	4148 a	0 c	1.71 a	-3.39 c

Each value is the mean of three (biomass) or five (trunk) measurements. Means followed by different letter indicate the existence of significant differences by the LSD_{0.05} range test.

Legend to figures

Figure 1. Changes in oxygen content of the soil water surrounding the roots (soil-O₂) of young apricot plants on Real Fino and Pollizo rootstocks not flooded (T0, —●—) or flooded for 3 (T1, —○—) and 6 (T2, ⋯▽⋯) days during the experimental period. Each point is the mean of six measurements. Vertical bars represent standard error of the mean. ●— flooding period.

Figure 2. Leaf water potential (Ψ_l) of young apricot plants grafted onto Real Fino (a, c) and Pollizo (b, d) rootstocks not flooded (T0, —●—) or flooded for 3 (T1, —○—) and 6 (T2, ⋯▽⋯) days during the experimental period. Each point is the mean of five measurements. Vertical bars represent standard error of the mean. ●— flooding period.

Figure 3. Leaf conductance (g_l) of young apricot plants grafted onto Real Fino (a, c) and Pollizo (b, d) rootstocks not flooded (T0, —●—) and flooded for 3 (T1, —○—) and 6 (T2, ⋯▽⋯) days during the experimental period. Each point is the mean of five measurements. Vertical bars represent standard error of the mean. ●— flooding period.

Figure 4. Net photosynthesis (P_n) of young apricot plants grafted onto Real Fino (a, c) and Pollizo (b, d) rootstocks not flooded (T0, —●—) or flooded for 3 (T1, —○—) and 6 (T2, ⋯▽⋯) days during the experimental period. Each point is the mean of five measurements. Vertical bars represent standard error of the mean. ●— flooding period.

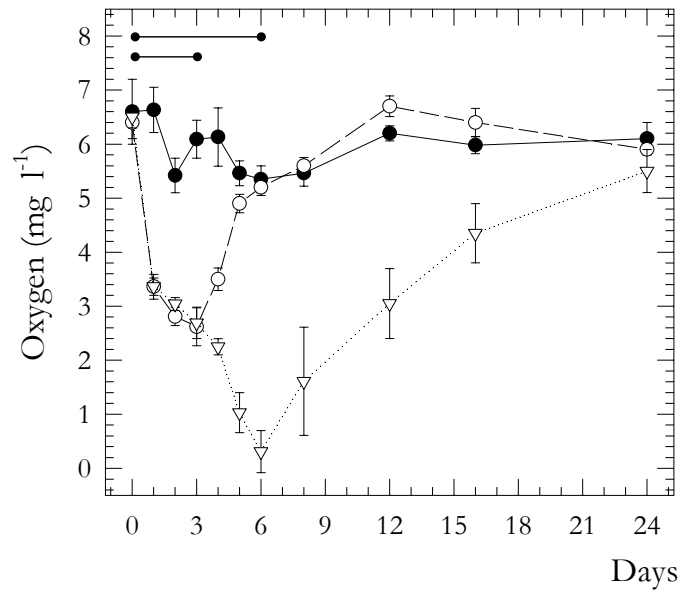


Figure 1

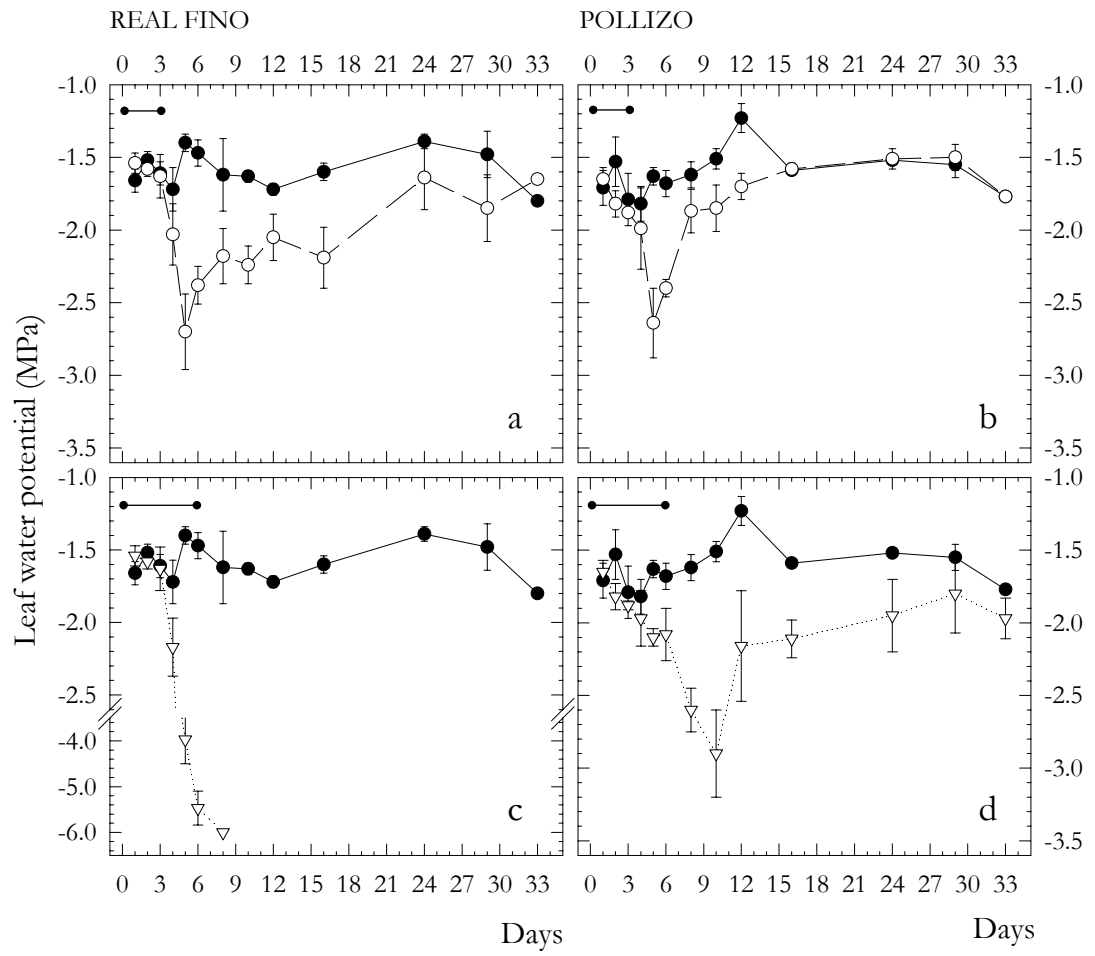


Figure 2

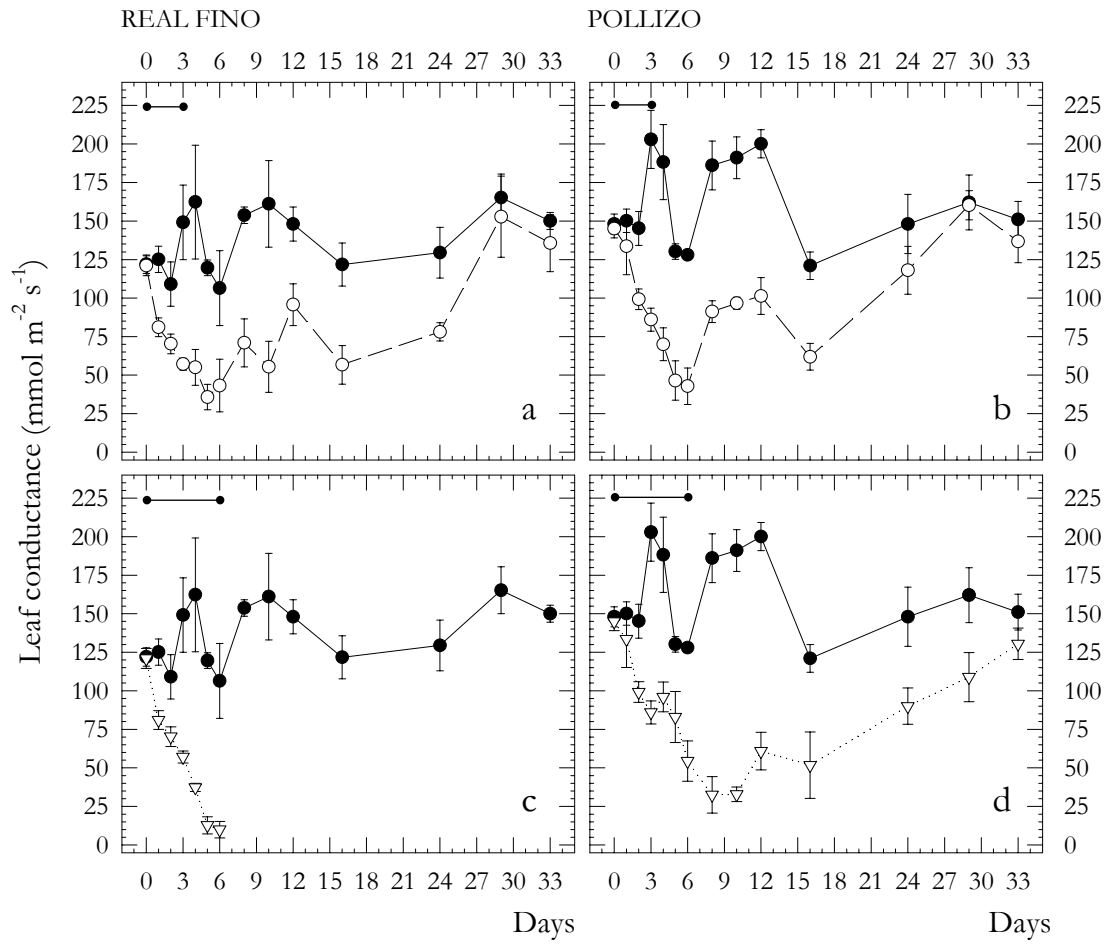


Figure 3

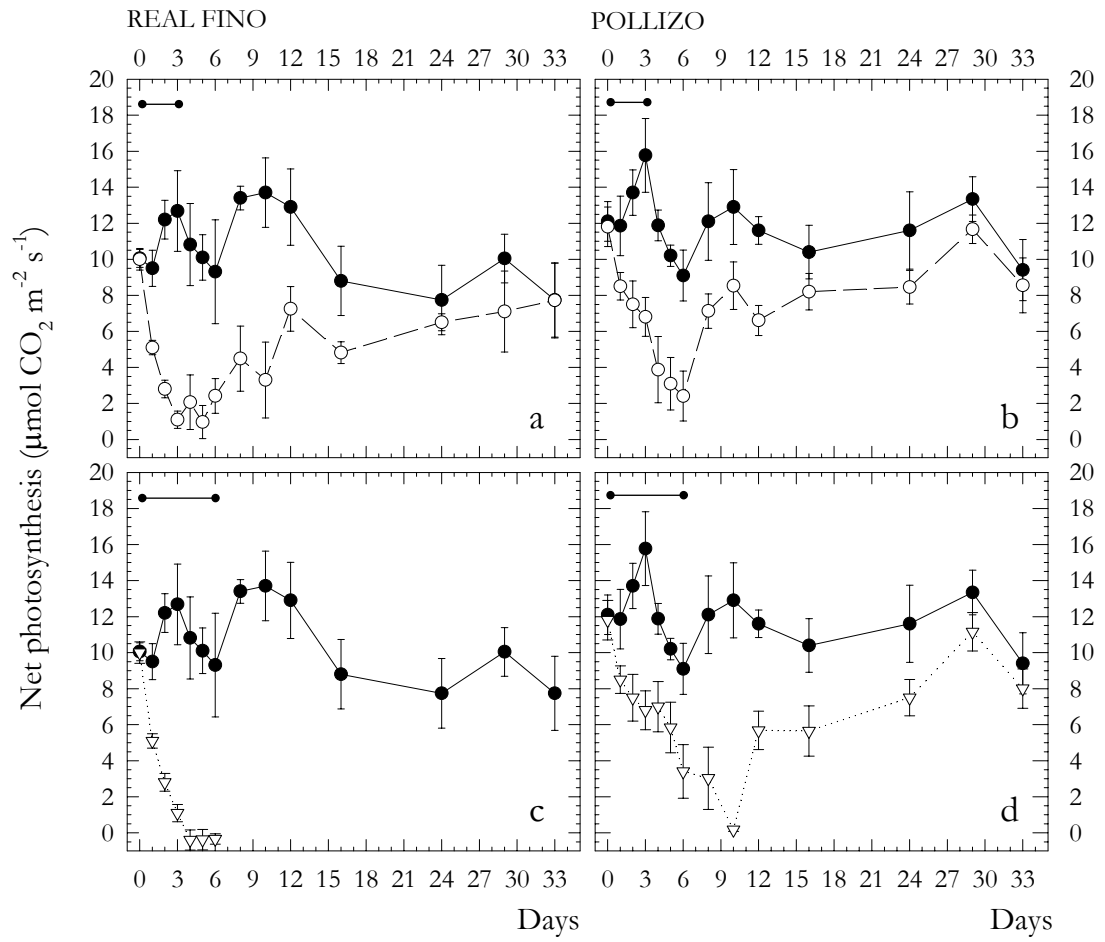


Figure 4