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Research Paper

Short-term responses to flooding stress of three *Prunus* rootstocks

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ABSTRACT

In fruit trees, flooding stress can affect plant survival and growth, and tolerance to root anoxia is determined by rootstock characteristics. Similarly to almond, peach trees are also among the *Prunus* species proving most susceptible to root anoxia in flooded soils. The aim of our study was to investigate the short-term responses to flooding of different *Prunus* rootstocks, in terms of growth and development and physiological variables. Flood treatments were continuously applied for 6 days to myrobalan plum Sansavini 2/5 (Mr. S. 2/5), Monegro and Nemared peach rootstocks. Trees that were not exposed to flooding served as controls. Physiological and growth variables were evaluated. Flooding negatively affected net photosynthesis (Pn), leaf conductance (gs) and water potential (Ψ_w) in Monegro and Nemared but not in Mr. S. 2/5 rootstock. However, flooding treatments did not affect the intercellular concentration of CO_2 (Ci) in any of the rootstocks. We propose that the lack of alterations in Ci indicates that the processes related to photosynthetic metabolism are affected simultaneously with stomatal closure. Flooding only reduced the leaf growth of Monegro and Nemared rootstocks. The Mr. S. 2/5 rootstock had the highest constitutive root porosity, which increased its tolerance to flooding compared to the other rootstocks. The differences in the responses to flooding of various rootstocks should be considered in production settings where it is not possible to properly control irrigation to prevent short periods of flooding or in soils that do not drain irrigation or rain water quickly.

1. Introduction

Crops are vulnerable to flooding, which can occur unexpectedly and with varying intensity and frequency. This problem is expected to increase as a result of global climate change (Alpert et al., 2002). Floods are usually caused by excessive rainfall or irrigation mismanagement; their effects are particularly damaging in soils with high clay content and poor drainage (Jackson, 2004; Kijne, 2006; Holzapfel et al., 2009). When flood irrigation is used to grow fruit trees, a poor drainage design can cause waterlogging of the soil for short periods of time. Floods create conditions of anaerobiosis for the root system that can adversely affect root function, growth and development, depending on the degree of tolerance presented by the cultivated fruit species (Domingo et al., 2002; Arbona et al., 2008, 2009; Amador et al., 2012; Pistelli et al., 2012; Insausti and Gorjon, 2013). Even short periods of flooding can cause mortality among many species with agricultural use (Vervuren et al., 2003), causing high losses in both yield and quality of the harvested fruit (Insausti and Gorjon, 2013).

Soil flooding affects physiological, morphological, anatomical and growth characteristics of plants, with different fruit species exhibiting varying intensities (Arbona et al., 2009; Insausti and Gorjon, 2013; Martinazzo et al., 2011; Nicolás et al., 2005; Pimentel et al., 2014). Flooding can cause changes in a plant's water and carbon balance (Arbona et al., 2009; Insausti and Gorjon, 2013; Martinazzo et al., 2011; Nicolás et al., 2005; Pimentel et al., 2014) in sensitive species, by adversely affecting the root hydraulic conductivity (Syvertsen et al., 1983; Ruíz-Sánchez et al., 1996), water potential (Ψ_w), leaf conductance (gs), chlorophyll content and net photosynthesis (Pn) g(Davies and Flore, 1986; Domingo et al., 2002; Insausti and Gorjon, 2013; Martinazzo et al., 2011; Ranney, 1994). In general, the responses to flooding of sensitive species vary with plant age, season and the degree of stress caused by anaerobic conditions (Bailey-Serres and Voesenek, 2008).

In fruit trees, tolerance to root anoxia is determined by the rootstock characteristics (Ranney, 1994; Domingo, 2002; Pimentel et al., 2014). A useful strategy for growing fruit trees intolerant to root anoxia in areas that are prone to flooding could be growing them on rootstocks that are tolerant to this type of stress (Ranney, 1994; Domingo et al., 2002). Among *Prunus* rootstocks, *P. cerasifera Ehrh.* and *P. domestica* (L.) are

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considered relatively tolerant to flooding (Ranney, 1994), whereas *P. persica* as well as hybrid rootstocks of *P. persica* × *P. dulcis* [Mill.] D. A. Webb are considered sensitive to this type of stress (Martinazzo et al., 2011; Insausti and Gorjon, 2013). The peach-almond hybrid rootstock Monegro experienced the highest tree mortality (80% of dead trees) in a long-term study with twelve rootstocks, and it could be attributed to its sensitivity to root anoxia in compact soils (Mestre et al., 2015). In contrast, other plum or plum based rootstocks (Replantpac as a *P. cerasifera* based rootstock) mostly survived or their mortality rate was low in this type of soils. The myrobalan plum Sansavini 2/5 (Mr. S. 2/5) rootstock has a high tolerance to soil flooding (Dichio et al., 2004) and can be used as rootstock for peach tree cultivars (Muleo et al., 2006). Iacona et al. (2013) used a clonal variant (S.4) of the rootstock Mr. S. 2/5, which provided the grafted peach with increased tolerance to flooding compared to the wild type, after 21 days of continuous flooding. However, the authors noted that further studies were needed to assess the phenotypic plasticity that could potentially induce rapid changes in the short term.

A common response underlying the tolerance to flooding of some species is the development of aerenchyma, which facilitates oxygen diffusion from the atmosphere to the roots and towards the rhizosphere and the outward diffusion of potentially toxic compounds such as ethanol, acetaldehyde and CO_2 (Calvo-Polanco et al., 2012; Le Provost et al., 2012). I Evaluating the presence of aerenchyma from histological sections (Vartapetian and Jackson, 1997; Parent et al., 2008) is common practice; however, it is important to test the role that aerenchyma plays in the transport of air because the intercellular spaces in the aerenchyma could contain water (Sojka, 1988; Grimoldi et al., 1999). Thus, it would be appropriate to assess the content of air in root tissues (porosity) if related to flood tolerance (Sojka, 1988; Grimoldi et al., 1999). There are two types of aerenchyma: one is inducible aerenchyma, which forms in low-oxygen environments; the other is constitutive aerenchyma, which fundamentally forms in the absence of external environmental stress as an integral part of ordinary root development (Jackson et al., 1985).

The aim of our study was to investigate the short-term responses to flooding expressed by different *Prunus* rootstocks. In fruit trees, the chances of brief flooding events are much higher than prolonged flooding events, and growth of sensitive species may be affected by those short flooding events.

We propose the hypothesis that in rootstocks that are sensitive to flooding, the physiological variables associated with water and carbon balance are affected within 24 h and that this behaviour has an effect on growth, which is also rapidly and differentially expressed compared with tolerant rootstocks. Furthermore, we predict that roots of tolerant rootstocks are constitutively porous and have higher air content in their tissues than non-tolerant ones. Thus, we suggest that rootstocks with higher porosity express greater tolerance to flooding, based on the differential response to flooding of their physiological and growth variables compared to sensitive rootstocks.

2. Materials and methods

2.1. Plant material and experimental design

Six-month-old *Prunus* rootstocks of the following cultivars were used: 1) Monegro, peach-almond hybrid, (*P. persica* (L.) Batsch × *P. dulcis* [Mill.] D. A. Webb), 2) Mr. S. 2/5 (*P. cerasifera Ehrh.*), both of which were obtained through clonal propagation, and 3) Nemared peach (*P. persica* (L.) Batsch), which was obtained through sexual reproduction, the most common form of propagation of this material (Ramming and Tanner, 1983; Loreti and Morini, 2008). The selected plants were homogeneous as regards dimensions (height, stem diameter and number of stems) and were placed in 40 L pots containing a mixture of perlite (30%), peat (35%) and grape marc (35%) as substrate. Pots were randomly distributed on the ground using a completely randomized design and were watered regularly; pests, diseases and weeds were strictly controlled. In addition, water-soluble fertilizer containing NPK 15-10-15 was applied once a week during the growing period. At the beginning of the experiment, trees were 150 cm high and the roots occupied the entire volume of soil in the pot. The treatments were as follows: (1) control, trees irrigated at field capacity to prevent water stress, and (2) flooding, water level kept at 50 mm above the soil surface. To avoid water loss from flooded pots, pots were placed in 50 L containers without drainage. Control tree pots were also placed in 50 L pots, but with drainage.Seven repetitions of each rootstock were used per treatment for a total of 42 plants under trial. Flooding treatment was continuous and lasted for 6 days. Soil anoxia was characterized by measuring the oxygen diffusion rate (ODR) at a 5-cm depth according to the methodology proposed by Letey and Stolzy (1964) with slight modifications, using platinum microelectrodes with a reference calomel electrode (Sojka and Scott, 2002; Insausti and Gorjon, 2013). The ODR measurement was carried out on the first day of the flood treatment.

2.2. Physiological measurements

Pn and intercellular concentration of CO_2 (Ci) were measured under saturated irradiances (2000 μmol m^{-2} s^{-1} PPFD) in mature and fully expanded leaves that were located in the middle third of the shoot of each plant, using an open infrared gas analysis system (Li-Cor 6400, Li-Cor Inc, Lincoln, NE, USA). Irradiances were provided via a 6400–02 B LED light source chamber. Air flow and CO_2 concentration in the reference cell (CO2R) were automatically controlled by the equipment at 300 mmol s^{-1} and 400 mmol mol^{-1} (ppm), respectively.

Gs was also measured in mature, fully expanded leaves located in the middle third of central axis of each plant. The measurement was performed using a diffusion porometer (Delta T AP4, Delta-T Devices, Cambridge).

Ψ_w was measured in the same leaf that was used to measure gs, using a Biocontrol 4 pressure chamber (Bio-Control, Argentina). All the physiological measurements were made at 0, 24 and 48 h after starting the flooding treatment.

2.3. Growth measurements

Length and width of one leaf from each tree were measured at the third node from the apex. Measurements were made at the beginning of the experiment and then, every two days until the sixth day after starting the flooding treatment, using a digital caliper.

2.4. Root porosity measurements

To evaluate the functionality of root tissues with regard to oxygen carrying capacity, constitutive root porosity was assessed. This variable was quantified using the pycnometer method (Sojka, 1988), which is based on the incremental weight change that occurs when the air volume in roots or leaves is replaced by water, after maceration with a mortar. Young roots were used for this analysis. Root porosity (*RP*) was calculated as follows: $RP\ (\%) = 100 \times (P_G - P_R)/(P + R - P_R)$, where P is the weight of the pycnometer only filled with water, R is the fresh weight of intact roots, P_R is the weight of the pycnometer with water and intact roots, and P_G is the weight of the pycnometer filled with water and the previously macerated roots. Measurements were made 6 days after the experiment was started.

2.5. Statistical analysis

The data were analysed using analysis of variance (ANOVA). The assumptions of normality and homogeneity of variance were previously verified. A repeated measures test was used to analyse the response variables recorded (Moser et al., 1990). The data of ODR was tested by *t*-test and root porosity was analysed using 1-way ANOVA. All results