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Floods affect physiological and growth variables of peach trees (*Prunus persica* (L.) Batsch), as well as the postharvest behavior of fruits

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ABSTRACT

Flooding is a case of abiotic stress that can affect plant growth, yield and fruit quality of many fruit trees species. The peach tree is recognized as highly susceptible to this stress factor. The aim of this study was to investigate the effects of flood periods on some physiological variables directly related to the growth and development of different organs of the peach tree and to evaluate the response to flooding by the plant with respect to postharvest fruit ripening. Flood cycles of 12 h per day were applied for two months to 'Red Globe' peach plants, comparing them with other plants with no flooding. Physiological variables, growth and behavior of the fruits after harvesting were evaluated. Flooding affected negatively leaf conductance and water potential and significantly decreased the chlorophyll content of leaves compared to controls. The trees subjected to flooding had branches with lower diameter and length growth, as well as smaller fruits, than control trees. The fruits from flooded trees produced ethylene earlier after harvest and responded with a faster softening. The results of this study proved that stress due to flooding produces responses that not only affect the plant but also the fruits after harvest.

1. Introduction

Plants have a generalized response to stress, which is expressed in reduced growth and biomass production (Chapin, 1991; Wang et al., 2003). However, in agricultural production activities such as fruit growing, post-harvest fruit quality is as important as harvest yield and maintaining that quality over time after harvest is of the utmost importance. However, there is little information on the relationship between abiotic stresses in general, when acting on the plant, and the effects it produces on the fruits in later stages of the agricultural production cycle (post-harvest).

Flooding is a case of abiotic stress that occurs frequently in both natural and agricultural systems, affecting growth and often causing the death of many species of plants (Voesenek et al., 2006; Bailey-Serres and Voesenek, 2008; Colmer and Voesenek, 2009). The negative impact of flooding on terrestrial plants is due to the low rate of gas diffusion in the water and the relatively low solubility of oxygen in water (Armstrong and Drew, 2002). Oxygen concentration in the roots decreases sharply with flooding (Armstrong et al., 1994), resulting in an "energy crisis" (Colmer and Voesenek, 2009). It is widely known that the energy deficit caused by anaerobiosis, following inhibition of mitochondrial respiration, is one of the most important factors affecting plants during flooding (Gibbs and Greenway, 2003; Wegner, 2010); its effects can be very damaging to the carbon and water economy in non-tolerant plants. The rhythm of photosynthesis decreases with flooding due to the closure of the stomata and to a decrease in the activity of the Rubisco enzyme and the destruction of chlorophyll (Pezeshki, 2001). Floods affect the water relations of susceptible plants. Flooded roots have a slower water flow than aerated ones, as stomatal closure is one of the faster responses to soil flooding (Pezeshki, 2001). In many species, it is common that stomatal closure occurs in response to flooding even when the water potential does not decreases significantly; this fact, as with responses to drought, would be mediated by the action of abscisic acid (ABA) (Koslowski and Pallardy, 1984; Jackson, 2002).

In response to a wide range of environmental stressors, including hypoxia, an increase in the production of ethylene is observed (Alonso and Stepanova, 2004) which results, in many species, in a decreased growth rate (Voesenek and Van der Veen, 1994). Ethylene production is induced by hypoxia, which is caused by flooding through the increase in the activity of enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, which controls the rate-limiting step in biosynthesis (Zarembinski and Theologis, 1993; Jackson, 2008). An increase in the concentration of ethylene in all plant tissues in response to flooding is observed (Stünzi and Kende, 1989; Jackson, 2008). Throughout the life cycle of higher plants, ethylene affects germination, cell elongation, cell fate, flowering, fruit ripening, senescence and abscission (Lin et al., 2009). However, there is no history linking increased ethylene

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production in the fruit after harvest and its influence on postharvest maturation as a result of flooding.

Among fruit trees the peach is one of the most susceptible to hypoxia in soil (Rowe and Beardsell, 1973; Amador et al., 2012) and it is common that cultivated peach trees are subjected to frequent flooding periods in soil due to heavy rainfall, poor soil drainage or irrigation mismanagement. Morphological symptoms on the tree due to flooding are often similar to those caused by water deficit, such as loss of turgidity, leaf wilting, desiccation of shoots, and tissue death (Couts, 1981). Expected peach responses to flooding would be similar to those recorded in other susceptible trees and could include effects on the carbon economy, water relations, the growth of different plant organs, high ethylene production and premature leaf senescence (Pereira and Kozlowski, 1977). On the other hand, a poor fruit set can also occur in peach, as well as fruits having less weight (Alvino et al., 1986). However, there are no known studies that evaluate how flooding stress on the tree can affect the post-harvest behavior of fruits.

The aim of this study was to investigate the effects of flooding periods on some physiological variables directly related to the growth and development of different plant organs of peach and to evaluate postharvest fruit ripening behavior in response to flooding before harvest.

2. Materials and methods

2.1. Plant material and experimental design

This research was conducted on an orchard of 8-year-old peach plants (*Prunus persica* (L.) Batsch) cv. Red Globe, grafted on 'Nemaguard' (*P. persica x P. davidiana*) rootstocks. Ten trees with similar characteristics (height, handling, etc.) planted at 4 × 4 m distance were studied, during the growing season in Buenos Aires (Argentine) (34°35′S, 58°29′W). The experiment was carried out on an Argiudoll soil of vertic characteristics, with an outstanding Bt horizon that has 35–38% of clay.

Treatments

(1) Controls: Water availability was subjected to the rainfall that occurred during the experiment, to which supplemental irrigation was added to keep the trees at field capacity, with special care to maintain adequate soil aeration conditions.
(2) Flooding: trees were subjected to daily flooding for 12 hours. Treatment began in the middle of the lignification of the fruit endocarp (Stage II), and lasted 60 days, until the harvest of the fruit. Treatment consisted in keeping the water level 50 mm above the ground for 12 h (08:00 to 20:00 h). The flooding was not continuous but in recovery pulses to simulate how the flood actually affects the peach in production systems.

To achieve water stagnation and prevent lateral displacement, a trench with a depth of 1 m was dug around each plant where a polyethylene film was placed. Polyethylene was also placed around control trees watered to field capacity. At night, during which time the plants were not flooded, there was a period of partial oxygenation of the root system of treated plants.

Soil anoxia by flooding was characterized by measuring the oxygen diffusion rate (ODR) at a soil depth of 5 cm with platinum microelectrodes (Letey and Stolzy, 1964).

2.2. Measurements of physiological variables of the plant

Leaf conductance was measured at midday on two leaves from each tree, from branches similar to those in which growth was subsequently measured: (a) one day before the start of treatment; (b) approximately at half the period of flooding; (c) at the end of the experiment, before harvest. A Delta T diffusion porometer, model AP4 (Delta-T Devices, Cambridge), was used.

Leaf water potential was evaluated at midday in the same leaves and at the same times in which leaf conductance was measured. A pressure chamber (Scholander pump) Biocontrol, model 6 (Biocontrol Argentina) was used.

Chlorophyll content in the leaf was evaluated with a Konica Minolta SPAD 502 meter (Spectrum Technologies Inc.) in ten leaves per tree, after 30 days of flooding.

2.3. Plant growth variables

Ten shoots per tree were marked at the start of the flood for measuring branch length and diameter growth and five previous season fruits from ten branches per tree were marked at the beginning of the flood for measuring the diameter of the fruits on each branch.

Growth variables were measured from the beginning of the flood every 20 days, approximately, until the end of the experiment.

2.4. Postharvest fruit variables

Ethylene production of the fruit was measured using the gas chromatography technique of "Headspace" (Restek corporation, 2000) using a Hewlett Packard Series II chromatograph-5890. Six fruits per tree were used, with five repetitions for both flooding and control treatments. The fruits were harvested at the time they started to change color. Ethylene production was evaluated every two days in the same fruits stored at 20 °C.

The firmness of the fruit was measured with an "Effegi" penetrometer equipped with 8.9 mm diameter plunger and expressed as kg. Measurements were made during one week in fruits stored at 20 °C temperature. Eight fruits from each tree were used for the five repetitions of each measurement for every treatment. The first measurement was at harvest, the second 3 days later, and the third 7 days after harvest.

2.5. Statistical analysis

Five flooded peach trees and five control trees were used. The experiment was conducted using a completely randomized design, thanks to the experimental material and soil being perfectly homogeneous. The obtained data were analyzed by analysis of variance (ANOVA). We used a repeated measures test for analyzing response variables periodically recorded (Moser et al., 1990).

3. Results

3.1. Soil oxygen diffusion rate

The ODR decreased quickly during flooding treatment from $102 \pm 2\ \mu g\ m^{-2}\ s^{-1}$ to $0.5 \pm 0.1\ \mu g\ m^{-2}\ s^{-1}$. When flooding was discontinued, the ODR recovered its original values during the first 6 h of the recovery phase.

3.2. Effect of periods of flooding on water potential and leaf conductance

Water potential measurements showed significant differences ($P < 0.01$) between treatments at the last measurement date, which corresponded to day 60 of undergoing 12 h of flooding daily (Fig. 1A). The water potential was more negative in flooded plants than in controls and although after 25 days of flooding this response was evidenced as a small non-significant trend, at 60 days the difference was highly significant (Fig. 1A). Leaf conductance, evaluated

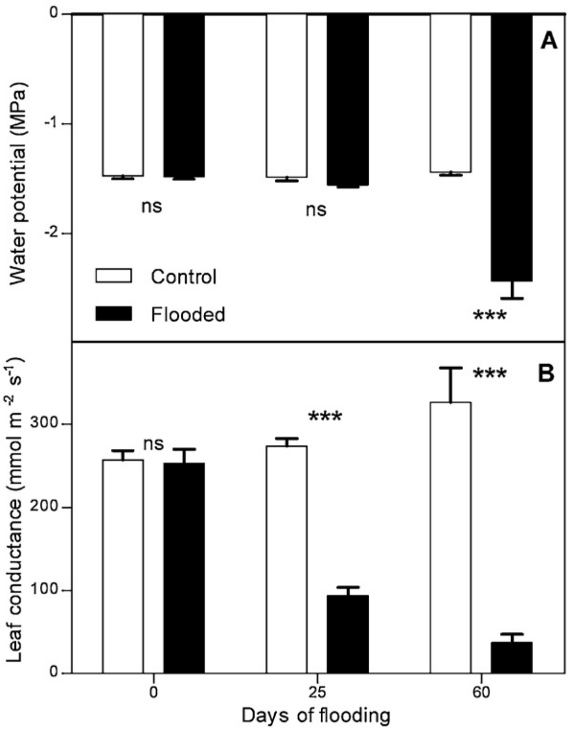

Fig. 1. Leaf water potential (A) and leaf conductance (B) of peach leaves growing in control and flooded soils. All measurements were taken at midday on clear days. References: (ns) no significant difference ($P > 0.05$); (***) very significant difference ($P < 0.01$). The bar indicates the standard error.

in the same leaves and at the same times as water potential, was more affected by the flood (Fig. 1B). Highly significant differences against the flooding treatment were evident after 25 days, and the same response, with more significant differences, was recorded at 60 days ($P < 0.001$) (Fig. 1B).

3.3. Effect of flooding on chlorophyll content in leaves

The flood severely affected the chlorophyll content of leaves. After 30 days of daily flooding periods, chlorophyll content in leaves was three times lower in the flooded trees than in controls (9.8 v. 29.6 SPAD units, respectively) ($P < 0.001$).

3.4. Responses to flooding with respect to branch growth

Both the increase in length (Fig. 2A) and in diameter of the branches during the year (Fig. 2B) were affected by the flood ($P < 0.05$). The highest growth rate for both treatments was recorded during the first 20 days after the beginning of the flood. Although there was a trend of lower growth in length and diameter in the branches of flooded trees during this period, it was not significantly apparent until 40 days of flooding. From that moment on the differences in the response variables between the treatments remained until the end of experiment.

3.5. Effects of flooding on fruit growth

Between the middle of the lignification of the fruit endocarp until the beginning of its exponential growth period fruit diameter growth was low under both treatments (Fig. 3). In the treatment in which flood pulses were applied at this period there was a non-significant trend of smaller fruit diameter. This response variable became significant ($P < 0.05$) in the following two measurements. (Fig. 3)

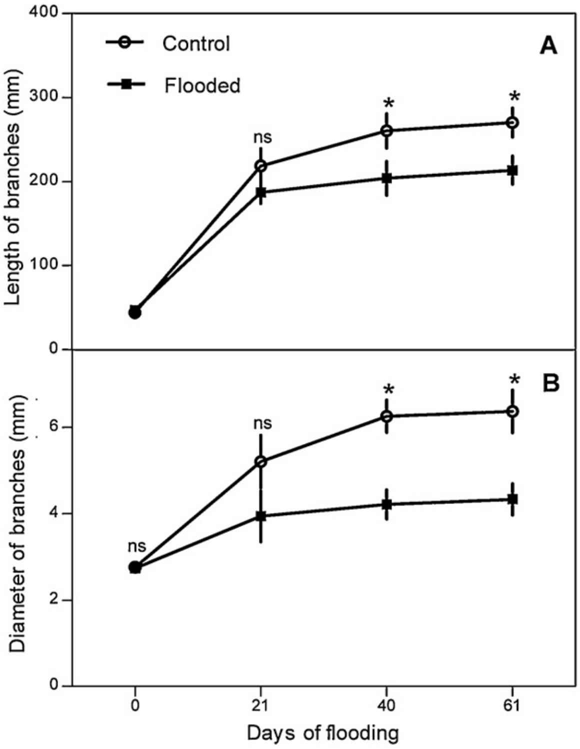

Fig. 2. Length (A) and diameter (B) of growing branches of peach plants growing under control and flooded conditions. References: (ns) no significant difference; (*) significant difference ($P < 0.05$). The bar indicates the standard error.

3.6. Effect of flooding on the postharvest ethylene production of fruits

At the first evaluation date, immediately after harvest, there was no production of ethylene in harvested fruits from flooded trees or from controls (Table 1). At the second evaluation date (in the same fruits, two days after harvest) there were significant differences in ethylene production ($P < 0.001$) between fruits from flooded trees and from controls. The fruits harvested from flooded trees showed high ethylene production while the fruits harvested from control trees did not produced ethylene (Table 1). Four days after harvest, at the third ethylene measurement date in the same fruits, no

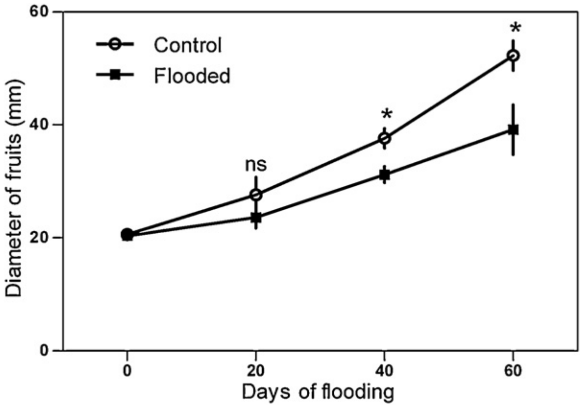

Fig. 3. Effects of flooding on fruit diameter growth of peach trees. References: (ns) no significant difference; (*) significant difference ($P < 0.05$). The bar indicates the standard error.

Table 1
Ethylene production (μl kg^{-1} h^{-1}) in peach fruit from flooded and control plants, evaluated at the time of harvest (0 days) and at 2 and 4 days post-harvest on the same fruit. References: (ns) no significant difference; (***) very significant difference ($P < 0.001$); (SE) mean standard error.

Days after harvest	Control		Flooded		
	Ethylene (μl kg^{-1} h^{-1})	SE	Ethylene (μl kg^{-1} h^{-1})	SE	
0	0	0	0	0	ns
2	0	0	287.12	108.47	***
4	235.83	112.12	243.76	102.73	ns

significant differences were found ($P > 0.05$) between treatments (Table 1). At that time fruit from controls produced as much ethylene as fruit from flooded trees.

3.7. *Effect of flooding on postharvest fruit firmness*

At the time of harvest there was no significant differences ($P > 0.05$) in the firmness of fruit between those which came from flooded trees and those which came from controls (Table 2). Three days after harvest fruits from flooded plants showed less firmness than those from control trees ($P < 0.05$) (Table 2). At 7 days the differences were more significant ($P < 0.01$). The post-harvest loss of firmness was much higher in fruits from flooded trees than those from controls (Table 2).

4. Discussion

The results presented in this paper show that flooding affected the analyzed physiological variables of peach plants. Flooding severely affected the water relations of plants not adapted to flooded soil environments (Jackson and Drew, 1984; Parent et al., 2008). According to our results, this happened for peach; as in other species sensible to flooding, the explanation could lie in the effect of anoxia on the water uptake by the roots (Pezeshki, 2001; Islam and Macdonald, 2004). Roots under hypoxia suffer severe damage due to the low diffusion of oxygen in the water, which inhibits cell mitochondrial respiration and affects the normal operation of the root (Brändle and Crawford, 1987). Also, the reduction of water absorption under flooding is a consequence of a reduction of the root hydraulic conductivity (Else et al., 2001; Islam and Macdonald, 2004) that seems to be associated with the gating of aquaporins (Tournaire-Roux et al., 2003). Moreover, the roots may be severely affected by the accumulation of toxic products in the soil and by the anaerobic metabolism of cells (Pezeshki, 2001; Fiedler et al., 2007). This causes the plant roots to stop absorbing water or to have a much slower water flow than aerated roots, resulting in on of faster responses of plants subjected to flooding, which is stomatal closure mediated by the increase in ABA concentration (Jackson and Drew, 1984; Jackson, 2002). In citrus, 28 days of flooding produce significant effects on the hydraulic conductivity of the roots and in stomatal conductance (Syvertsen et al., 1983). According to these authors, the decrease in hydraulic conductivity due to a flood is sufficient to generate a significant closure of stomata. In our experiment this effect was recorded at day 25 of the daily flood cycles. However, the effect of flooding on leaf conductance that was recorded at that time did not occur with respect to water potential; the stomatal response anticipated that of the water potential. The closure of the stomata is an early response of plants susceptible to flooding (Pezeshki, 2001). It is known that the closure of the stomata in the leaves of flooded plants is caused by ABA, which accumulates rapidly after flooding and affects stomata before significant hydraulic changes occur in the leaves (Jackson, 1991; Jackson et al., 2003). In *Pyrus* the anaerobiosis of the root induces the partial closure of stomata before the water potential gets altered; a longer time under anoxia markedly reduces the leaf water potential and the hydraulic conductivity of the roots in this species (Andersen et al., 1984).

Table 2
Firmness (kg) of fruit from flooded and control plants, stored at 20 °C, evaluated at the time of harvest (0 days) and at 3 and 7 days post-harvest. References: (ns) no significant difference; (*) significant difference ($P < 0.05$); (***) very significant difference ($P < 0.01$).

Days after harvest	Firmness (kg)			
	Control		Flooded	
0	6.5	ns	6	ns
3	5.8	*	4.2	*
7	4.5	**	1.2	**

The very significant differences in water potential and leaf conductance caused in peach trees by 60 days of 12-h flooding cycles are similar to those reported by many authors in plants sensitive to flooding (Jackson, 1991; Pezeshki, 2001).

Moreover, chlorophyll content decreases in leaves of plants grown in reduced soils due to the anaerobic effect of a flood (Webb and Fletcher, 1996; Yordanova and Popova, 2001). This response underlies generalized chlorosis, a symptom that was evident in the trees studied in this work. The destruction of chlorophyll and stomatal closure, both of which were recorded in our experiment, would adversely affect the photosynthetic capacity of flooded plants (Pezeshki, 2001; Colmer and Voesenek, 2009).

Water potential is the hydraulic force that, through its pressure component, is involved in the elongation of cells (Lambers et al., 2008). The significant reduction of this variable, and possibly of photosynthesis, due to stomatal closure and to the lower chlorophyll content in plant leaves of flood plants are evidenced as the main causes of the smaller diameter and elongation growth of the branches of flooded plants in our experiment. The branches were growing branches of the same year in full growth and development, the main destination of photoassimilates from the branches themselves, developing buds and leaves (DeJong and Moing, 2008). The effect of flooding on growing branches is an important response that could affect the fruit production of the plant the following year.

The same cause-effect relationship could be seen in the differences in fruit growth between those from flooded plants and from controls starting at the stage of greatest cell expansion in peach fruit (Roth, 1977).

The effect of flooding on the overall growth of the peach trees, in this experiment, was not as marked as that observed by other authors (Mizutani et al., 1979). Moreover, those authors reported the death of trees two weeks after the flooding ended. The difference between the two experiments is that in the present work, flooding was intermixed with daily recovery periods, as often happens during soil flooding in peach production areas as a result of irrigation mismanagement or excessive rainfall. However, these recovery periods of soil aeration were not enough to reverse the effects generated by the flood periods.

Another variable that showed a clear difference between treatments was the greater ethylene production in fruit of flooded plants two days after harvest. This result explains the observed fact that fruits harvested from flooded trees matured faster than those harvested from control trees. It is widely known that phytohormone ethylene accelerates the ripening of climacteric fruits such as peaches (Kader, 2002). This response may be due to the increased production in flooded plants of ethylene precursor ACC synthase (Voesenek et al., 2006), which, when moving to the fruits of these plants causes, through the action of ACC oxidase, the increased production of ethylene recorded in fruits from flooded plants when compared with fruits from control plants (Zarembinski and Theologis, 1993). It would be interesting to test this hypothesis in another experiment. The early production of ethylene in fruits from flooded plants is the most likely factor to have affected the firmness of those fruits in our experiment. The synthesis and activity of hydrolytic enzymes in the cell wall which contribute to the process of fruit softening are dependent on ethylene (Sozzi, 2004). According to our data the postharvest loss of firmness in fruits from flooded plants was very significant, compared with the fruits from control plants.

5. Conclusions

Flood-induced reduction of growth of peach branches and fruits was accompanied by multiple concurrent physiological dysfunctions in plants. Therefore, flooding events in a peach growing plantation may have relatively high impacts on fruit production, so this hypothesis should be tested at crop level. However, it is important to note that the results of this work allowed to relate the stress on the plant, in this case from flooding, with the postharvest behavior of fruits. In our case, fruits from flooded trees produced ethylene earlier after harvest and responded with a faster softening. The results of this study proved that stress due to flooding produces responses that not only affect the plant but also its fruits after harvest.

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