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# Pruning after flooding hastens recovery of flood-stressed avocado (*Persea americana* Mill.) trees

Maria Angelica Sanclemente[a,b], Bruce Schaffer[a,*], Pilar M. Gil[c], Ana I. Vargas[a], Frederick S. Davies[b]

[a] *University of Florida, Tropical Research and Education Center, 18905 S.W. 280 Street, Homestead, FL 33031, USA*
[b] *Department of Horticultural Sciences, University of Florida, P.O. Box 110690, Gainesville, FL 32611, USA*
[c] *Departamento de Fruticultura y Enología, Facultad de Agronomía e Ingeniería Forestal, Pontificia Universidad Católica de Chile, Vicuña Mackenna 4860, Macul, Santiago, Chile*

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A B S T R A C T

Two experiments (Expts. 1 and 2) were conducted at different times with avocado (*Persea americana* Mill. cv. Choquette) trees in containers to test the effects of leaf pruning immediately after removing trees from short-term flooding on tree recovery. Trees in each experiment were divided into two flooding treatments: (1) flooded, or (2) non-flooded. Trees in each flooding treatment were divided into two pruning treatments: (1) pruned; approximately two-thirds of the canopy removed by pruning immediately after trees were removed from flooding (unflooded), or (2) non-pruned. In each experiment, net $CO_2$ assimilation ($A$), stomatal conductance of water vapor ($g_s$), transpiration ($E$), water use efficiency (WUE, calculated as $A/E$) and xylem sap flow (in Expt. 2) were determined daily during the flooding period and periodically after trees were unflooded until harvest time in each flooding/pruning treatment. Tissue dry weights were determined for trees in all treatments at the end of the experiment (several weeks after trees were unflooded). Net $CO_2$ assimilation, $g_s$, $E$ and WUE of flooded trees decreased after 2 and 5 days and trees were unflooded after 3 and 6 days in Expts. 1 and 2, respectively. After trees were unflooded, $A$, $g_s$, $E$ and WUE were lower in flooded trees than in non-flooded trees for a few weeks, but these reductions were greater for pruned than non-pruned trees. Eventually, $A$, $g_s$, $E$ and WUE of flooded trees in both the pruned and non-pruned treatments returned to values similar to those of non-flooded trees. After trees were unflooded, for trees in the pruned treatment, xylem sap flow was generally not significantly affected by flooding. However, for non-pruned trees, xylem sap flow was usually lower in the flooded than non-flooded trees. In each experiment, leaf dry weight and total plant dry weight were significantly lower for flooded than non-flooded trees only in the non-pruned treatments. In Expt. 2, root and stem dry weights were also lower in flooded than non-flooded trees only in the non-pruned treatment. The results indicate that pruning the canopy of avocado immediately after trees are removed from short-term flooding hastens plant recovery. It is postulated that the hastened recovery was due to pruning bringing the shoot to root ratio of flooded trees (with damaged roots) and the subsequent supply and demand for water and nutrients into better equilibrium in flooded trees, allowing pruned trees to recover more quickly from flooding compared to non-pruned trees.

## 1. Introduction

Avocado production is rapidly increasing worldwide (FAOSTAT, 2011). This rapid expansion has resulted in avocado orchard establishment on marginal sites that are prone to flooding or poor soil drainage (Schaffer et al., 2013). Moreover, increasing occurrences of catastrophic weather events such as tropical storms or hurricanes as a result of global climate change are expected to increase the potential for severe periodic flooding throughout the world (IPPC, 2009; Vörösmarty et al., 2000). In areas such as southern Florida, a high water table (1–2 m below the soil surface; Barquin-Valle et al., 2011) coupled with heavy rains can lead to water remaining above the soil surface in avocado orchards for several days (Crane et al., 1994; Schaffer, 1998). Furthermore, avocado orchards are often over-irrigated (Du Plessis, 1991) which can result in hypoxic conditions in the root zone.

Avocado trees have a relatively shallow root system that does not spread much beyond the tree canopy (Wolstenholme, 2013).

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*Abbreviations:* $A$, net $CO_2$ assimilation; $g_s$, stomatal conductance of water vapor; $E$, transpiration; WUE, water use efficiency.

[*] Corresponding author. Tel.: +1 305 246 7001x362; fax: +1 305 246 7003.
*E-mail address:* bas56@ufl.edu (B. Schaffer).

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Roots are extensively suberized, with low hydraulic conductivity, few root hairs, poor water uptake and sensitivity to low soil oxygen concentrations (Ferreyra et al., 2006). These characteristics make avocado one of the most susceptible fruit trees to soil flooding (Ferreyra et al., 2006; Schaffer et al., 1992, 2006). Flooding produces hypoxic or anoxic conditions in the root zone by displacing oxygen in the soil (Drew, 1997; Geigenberger, 2003). Hypoxic conditions caused by short periods (a few days) of standing water in the root zone of avocado trees has been shown to negatively impact physiological processes such as net $CO_2$ assimilation ($A$), stomatal conductance of water vapor ($g_s$), and transpiration ($E$) and cause tree mortality (Schaffer, 1998; Schaffer et al., 1992, 2006, 2013).

Tree mortality in flooded avocado orchards has been attributed to a reduction in root volume as a result of oxygen starvation of the roots (Schaffer et al., 2007, 2013). The reduction of root volume caused by flooding can be exacerbated by Phytophthora root rot caused by the oomycete *Phytophthora cinnamomi* (Schaffer et al., 2013), the major disease of avocado worldwide (Dann et al., 2013). In flooded avocado trees, a reduction in root volume due to root mortality occurs before the canopy is affected (Schaffer et al., 1992). This results in a high canopy volume relative to root volume (Schaffer, 1998). The high shoot/root ratio as a result of orchard flooding has led to the recommendation in some areas, such as south Florida, of pruning avocado trees soon after flood waters subside to bring the shoot/root ratio back into equilibrium (Crane et al., 1994). It has been suggested that removing a portion of the canopy of trees exposed to flooded conditions decreases total tree transpiration, which compensates for decreased water absorption due to less root volume as a result of root mortality. Therefore, sufficient water and nutrients can be supplied by the remaining roots to the canopy (Crane et al., 1994). Reducing canopy size in flooded orchards also decreases tree weight, thereby facilitating re-establishment of trees that may topple as a result of strong winds and flooded soils resulting from tropical storms or hurricanes (Crane et al., 1994).

Recommendations related to pruning of avocado trees to reduce flooding stress are based mainly on observations (Gil et al., 2008). Thus, there is a need to quantify the effects of leaf area removal and timing (pre- or post-flooding) of leaf area removal relative to the occurrence of flooding on physiology, growth and survival of avocado trees. Sanclemente et al. (2013) found that removing a portion of avocado leaves immediately prior to flooding actually increased tree stress and mortality as a result of decreased carbohydrate production and translocation to the roots of flooded trees resulting in less substrate for root respiration during flooding. However, quantitative data on the effects of pruning immediately after a flooding event on tree recovery have not been reported. The objective of this study was to quantify the effects of pruning immediately after avocado trees were removed from flooding (unflooded) on tree physiology. The hypothesis was that pruning avocado trees immediately after they are removed from flooding (unflooded) hastens tree recovery by decreasing the shoot/root ratio so that flood-damaged roots can still adequately supply sufficient water to the reduced (pruned) canopy.

## 2. Materials and methods

### 2.1. Study site description

This study was conducted at the University of Florida, Tropical Research and Education Center in Homestead, Florida, USA (25.5°N and 80.5°W). Two experiments were conducted at different times with avocado trees in plastic containers to assess the effects of pruning a portion of the canopy immediately after flooded plants were removed from flooding (unflooded) on plant stress (determined by leaf gas exchange measurements) and recovery (determined by plant biomass measurements) from short-term (days) flooding. Expt. 1 was conducted in a shade-house with a clear polyethylene roof and shade cloth (30% light exclusion) on all four sides. Air temperature in the shade-house was recorded with a StowAway TidbiT sensor/data logger (Onset, Bourne, Massachusetts, USA) located above the tree canopies. In Expt. 1, daily air temperature in the screen-house ranged from 24.6 to 30.7 °C with a mean of 29.0 °C. During the flooding period (when roots were submerged), the mean daily temperature was 30.6 °C, with a maximum temperature of 40.1 °C.

Based on the results of Expt. 1, a second experiment (Expt. 2) was subsequently conducted in which the effect of flooding and pruning on plant water consumption was also assessed by continuous xylem sap flow measurements. Also, to reduce the amount of temperature fluctuation and high maximum temperature that occurred in the shade-house during the flooding period in the first experiment, Expt. 2 was conducted in a completely enclosed greenhouse with fans and cooling pads to reduce the ambient temperature. Air temperature in the greenhouse in Expt. 2 was recorded in the same manner as described for Expt. 1. In Expt. 2, daily air temperature in the greenhouse ranged from 25.1 to 31.5 °C with a mean of 28 °C. During the flooding period (when roots were submerged), the mean daily temperature was 27.0 °C with a maximum temperature of 28.3 °C.

### 2.2. Plant material

Two-year-old 'Choquette' avocado trees on Waldin seedling rootstock, the most common rootstock for avocado trees in Florida (Crane et al., 2013), were used in each experiments. Trees in potting medium (40% Canadian peat, 10% sand, 40% pine bark and 10% perlite) in 11.3 L plastic containers were obtained from a commercial nursery. The potting medium had been steam sterilized prior to planting trees. Prior to initiating treatments, trees in each experiment were also treated with fungicide; Ridomyl® (Syngenta International AG, Basel, Switzerland) in Expt. 1 or Alliete® (Bayer Crop Science, Morganville, North Carolina, USA) in Expt. 2 as a soil drench to help prevent Phytophthora root rot.

### 2.3. Experimental design

Each experiment was set up as a completely randomized design with a 2 × 2 factorial arrangement of treatments. There were two flooding treatments: (1) flooded, and (2) non-flooded. There were two pruning treatments: (1) pruned; approximately two-thirds of the canopy cut off (pruned) immediately after plants were unflooded, and (2) non-pruned. There were five single-tree replications for each treatment combination in Expt. 1 and six single-tree replications per treatment combination in Expt. 2.

Prior to initiating treatments, tree height and stem diameter (10 cm above the graft union) were measured on each tree and the means were compared among assigned treatment groups. In each experiment, mean tree height and stem diameter at the beginning of the experiment did not statistically differ (tree size was uniform) among assigned treatment groups (as determined by ANOVA, $P > 0.05$). Prior to initiating treatments, the mean ± SE of tree height and stem diameter, respectively were 76.6 ± 2.0 cm and 12.8 ± 0.3 mm for all treatments combined in Expt. 1. In Expt. 2, the initial tree height and stem diameter were 96.3 ± 1.7 cm and 12.7 ± 0.2 mm, respectively for all treatments combined.

### 2.4. Flooding treatments

In each experiment, trees were flooded by submerging each plant container into a 19 L plastic bucket filled with tap water to about 5 cm above the soil surface. Buckets were refilled each day with stagnant water collected on the same day that the flooding treatment was initiated to avoid re-oxygenation of the medium and to maintain a constant water level. Trees in the control treatment were not flooded. Plants were removed from flooding (unflooded) after a statistically significant difference ($P \leq 0.05$) in $A$ or $g_s$ between flooded and non-flooded trees was observed in any of the pruning treatments for 2 consecutive days. In each experiment, trees were manually irrigated throughout the entire study (with the exception of flooded trees during the flooding period). Tensiometers (Irrometer Company, Riverside, California, USA) were installed in five randomly selected containers for plants in the non-flooded treatments, and soil suction was maintained at 10–15 KPa to ensure that non-flooded trees were not drought stressed (Kiggundu et al., 2012).

### 2.5. Pruning treatments

In each experiment, branches were pruned immediately (within minutes) after flooded plants were unflooded (plants and containers were removed from the 19 L buckets of water). Trees in the control treatments were not pruned. In each experiment, approximately two-thirds of the canopy was removed by counting the leaves and pruning branches until only about one-third of the initial canopy remained. There were insufficient numbers of branches to remove entire branches, so often the outer two-thirds of a branch was removed. This resulted in a higher proportion of older leaves than young leaves remaining on the pruned trees, because the younger leaves were on the exterior portions of the branches.

### 2.6. Soil redox potential

In both experiments during the flooding period, soil redox potential of trees in the flooded treatment was measured with a metallic ORP indicating electrode (Accumet model 13-620-115, Fisher Scientific, Pittsburg, Pennsylvania, USA) connected to a voltmeter. Measurements were made daily in each container by placing the electrode into a polyvinyl chloride (PVC) pipe inserted 10 cm deep into the media of each container.

### 2.7. Leaf gas exchange parameters

As physiological indicators of plant stress in the absence of visible symptoms, net $CO_2$ assimilation ($A$), stomatal conductance of water vapor ($g_s$), transpiration ($E$) and plant water use efficiency (WUE; calculated as $A/E$) were determined for all trees in each experiment with a CIRAS-2 portable gas analyzer (PP Systems, Amesbury, Massachusetts, USA) at a light saturated photosynthetic photon flux (PPF) of 1000 $\mu$mol quanta $m^{-2}\,s^{-1}$, a reference $CO_2$ concentration of 375 $\mu$m $CO_2$ $mol^{-1}$ and an air flow rate into the leaf cuvette of 200 mL $min^{-1}$. Leaf gas exchange measurements were made between 0900 HR and 1200 HR. Measurements were made one or two days prior to the initiation of flooding, daily during the flooding period, and 3 times per week after trees were unflooded to monitor tree recovery from flooding.

### 2.8. Xylem sap flow

In Expt. 2, xylem sap flow was monitored continuously in a subsample of 4 plants in each treatment combination with a Dynagage Flow 32-1KTM Sap Flow System (Dynamax, Inc., Houston, Texas, USA). Measurements started 7 days before the initiation of the flooding treatments and stopped a few days before trees were harvested.

### 2.9. Plant biomass measurements

Trees were harvested at the end of each experiment and tissue dry weights were determined. Roots were separated from the rooting medium and carefully washed with tap water. Tissue samples were then oven dried at 70 °C to a constant weight, and leaf, stem, root and total plant dry weights were determined.

### 2.10. Statistical analyses

Data were analyzed by a two-way analysis of variance (ANOVA) to assess statistical interactions between flooding and pruning treatments. If there were significant interactions, flooding treatments were analyzed separately within each pruning treatment. Differences between flooding treatments were compared within each pruning treatment by repeated measures ANOVA for $A$, and $g_s$, and xylem sap flow and by a non-paired $T$-test for plant dry weights using the SAS statistical software package (SAS 9.2, SAS Institute, Cary, North Carolina, USA).

## 3. Results

### 3.1. Soil redox potential

In Expt. 1, mean soil redox potential of all flooded plants was 141.2 mV beginning one day after flooding and decreased to 100.6 mV by day 3 (the day plants were unflooded). In Expt. 2, mean soil redox potential for the flooded treatment was 423.4 mV beginning on day 1 and continued to decrease to −55.0 mV by day 6 (the day plants were unflooded).

### 3.2. Leaf gas exchange

In both experiments, there was a significant statistical interaction ($P \leq 0.05$) between flooding and pruning treatments for $A$, $g_s$, $E$ and WUE on several measurement dates. Therefore, flooding treatments were compared separately within each pruning treatment.

In Expt. 1, all 5 trees (replications) in each treatment combination survived the continuous flooding period. Two days after plants were submerged, there were significant reductions in $A$, $g_s$, $E$ and WUE due to flooding (Figs. 1 and 2). These differences were significant on day 3, so trees were unflooded after 3 days of continuous flooding.

In Expt. 1, $A$ of trees in both the pruned and non-pruned treatments was significantly lower for flooded than non-flooded trees for up to 20 days after the flooding treatment began (17 days after trees were unflooded). However, the reductions in $A$ due to flooding were greater for the non-pruned than pruned trees (Fig. 1). On day 20, there was a significant difference in $A$ between flooding treatments for the non-pruned trees, but not for the pruned trees. For non-pruned trees, $g_s$ (Fig. 1), $E$ and WUE (Fig. 2) were significantly lower for flooded than non-flooded trees up to day 20, whereas for pruned trees there was no significant reduction in $g_s$, $E$ or WUE after day 4 (1 day after plants were unflooded).

In Expt. 2, significant differences in $A$, $g_s$, $E$ and WUE between flooded and non-flooded trees were first observed 5 days after trees were flooded (Figs. 3 and 4). These same differences were also observed on day 6. Therefore, flooded trees were unflooded after 6 days of continuous flooding. At that time, 3 trees had died as a result of continuous flooding (as indicated by dead leaves and buds, and a brown color of the vascular tissue). Those trees were removed from the experiment prior to initiating the pruning treatments because the objective of the study was to follow the rate of recovery from flooding of surviving pruned and non-pruned trees.

In Expt. 2, $A$, $g_s$ (Fig. 3) and $E$ (Fig. 4) were significantly lower for flooded than non-flooded trees in both the pruned and non-pruned treatments for up to 20 days after flooding began (14 days after trees were unflooded); WUE was lower for flooded plants for up to 15

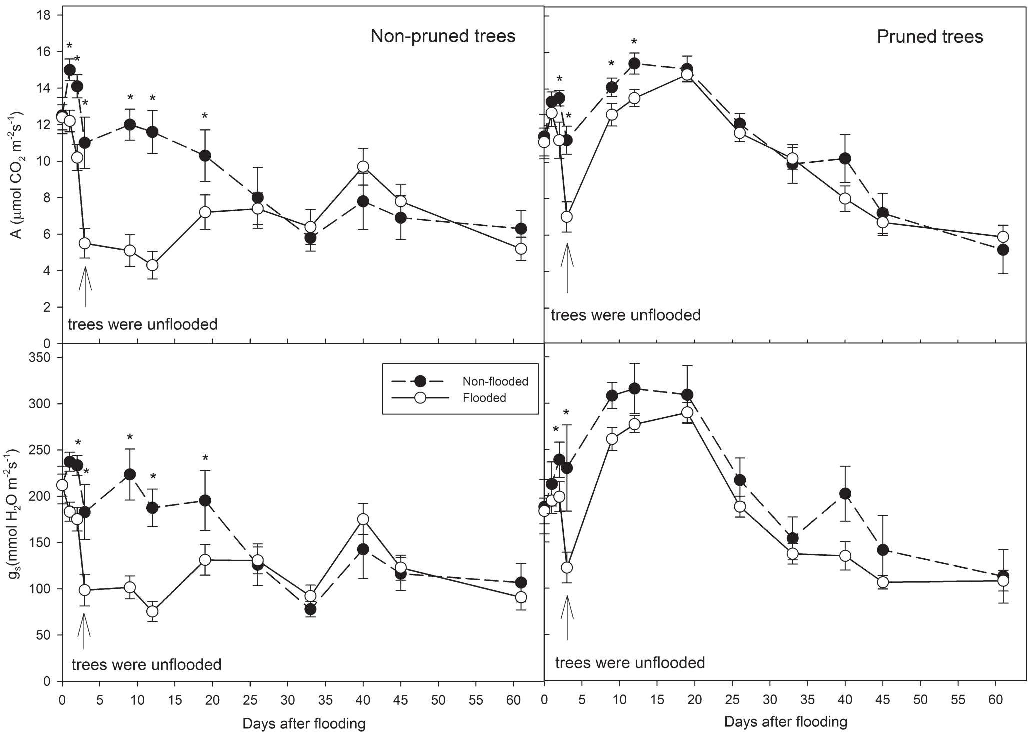

**Fig. 1.** Effect of flooding on net $CO_2$ assimilation ($A$) and stomatal conductance ($g_s$) of two-year-old 'Choquette' avocado trees on Waldin seedling rootstock pruned immediately after plants were unflooded or non-pruned (Expt. 1). Symbols represent means and bars represent ±1 standard error. An asterisk indicates a significant difference between treatments according to repeated measures ANOVA ($P \leq 0.05$).

days after flooding began (11 days after trees were unflooded). However, reductions in $A$, $g_s$, $E$ and WUE (Figs. 3 and 4) as a result of flooding were greater for trees in the non-pruned than in the pruned treatment. Flooding did not negatively impact $A$, $g_s$ or $E$ after day 20 or WUE after day 15, except on day 40 when $A$ and $g_s$ were actually higher for the flooded than non-flooded trees and on day 55 where $A$, $g_s$ and $E$ were slightly but significantly lower for the flooded than non-flooded trees (Figs. 3 and 4).

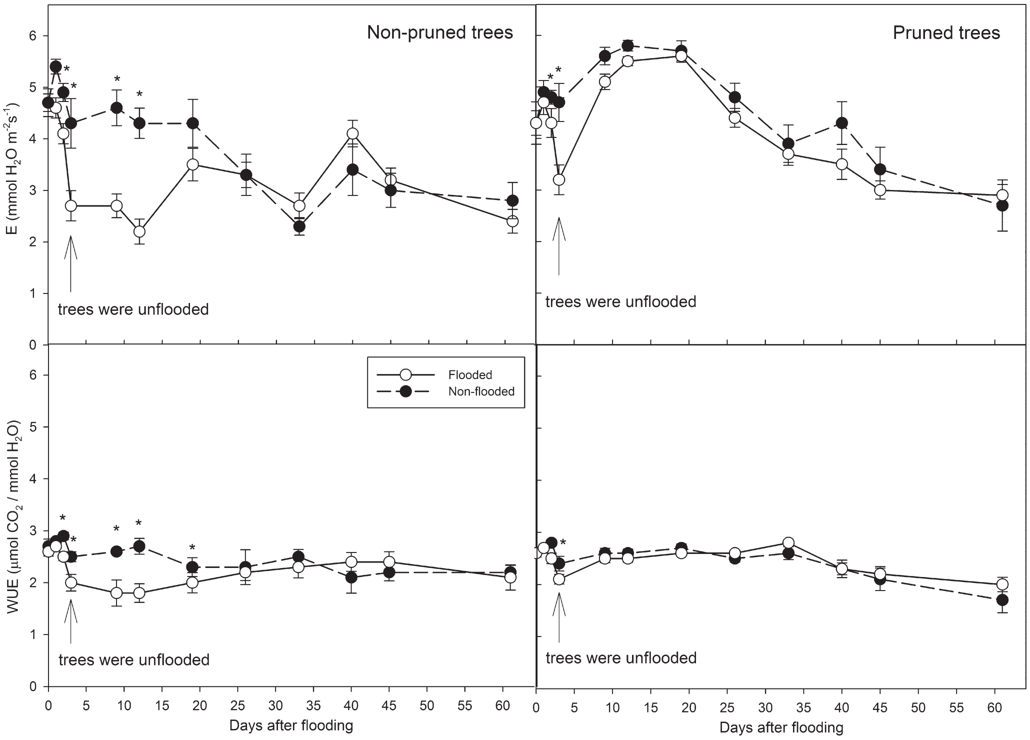

**Fig. 2.** Effect of flooding on transpiration ($E$) and water use efficiency (WUE) of two-year-old 'Choquette' avocado trees on Waldin seedling rootstock pruned immediately after plants were unflooded or non-pruned (Expt. 1). Symbols represent means and bars represent ±1 standard error. An asterisk indicates a significant difference between treatments according to repeated measures ANOVA ($P \leq 0.05$).

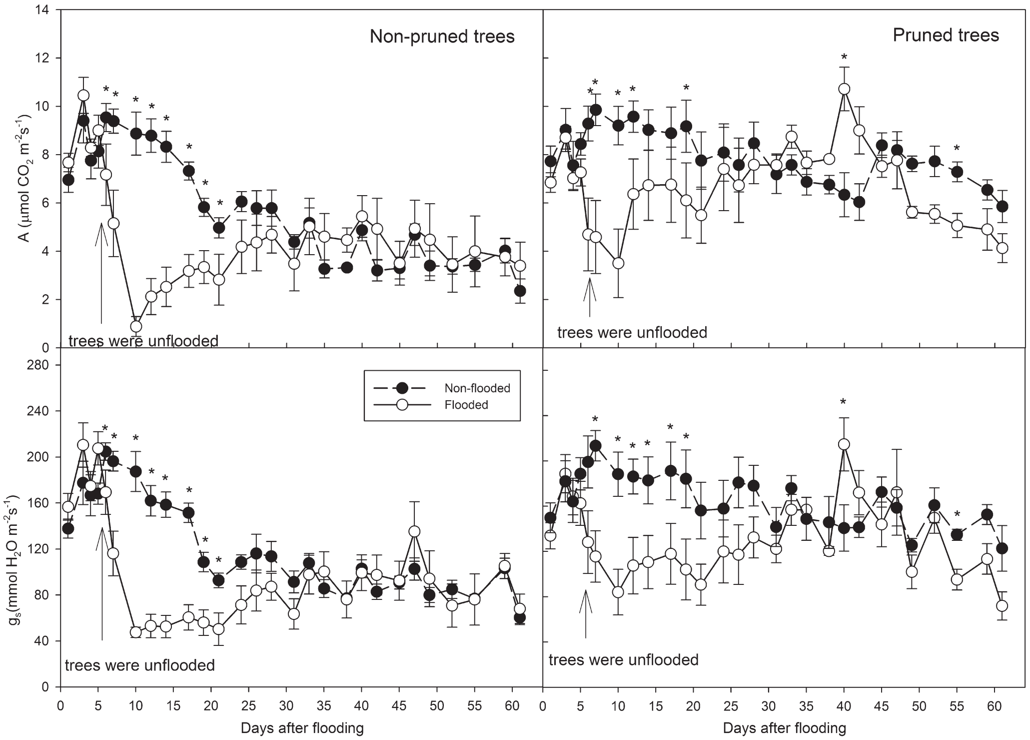

**Fig. 3.** Effect of flooding on net $CO_2$ assimilation ($A$) and stomatal conductance ($g_s$) of two-year-old 'Choquette' avocado trees on Waldin seedling rootstock pruned immediately after plants were unflooded or non-pruned (Expt. 2). Symbols represent means and bars represent ±1 standard error. An asterisk indicates a significant difference between treatments according to repeated measures ANOVA ($P \leq 0.05$).

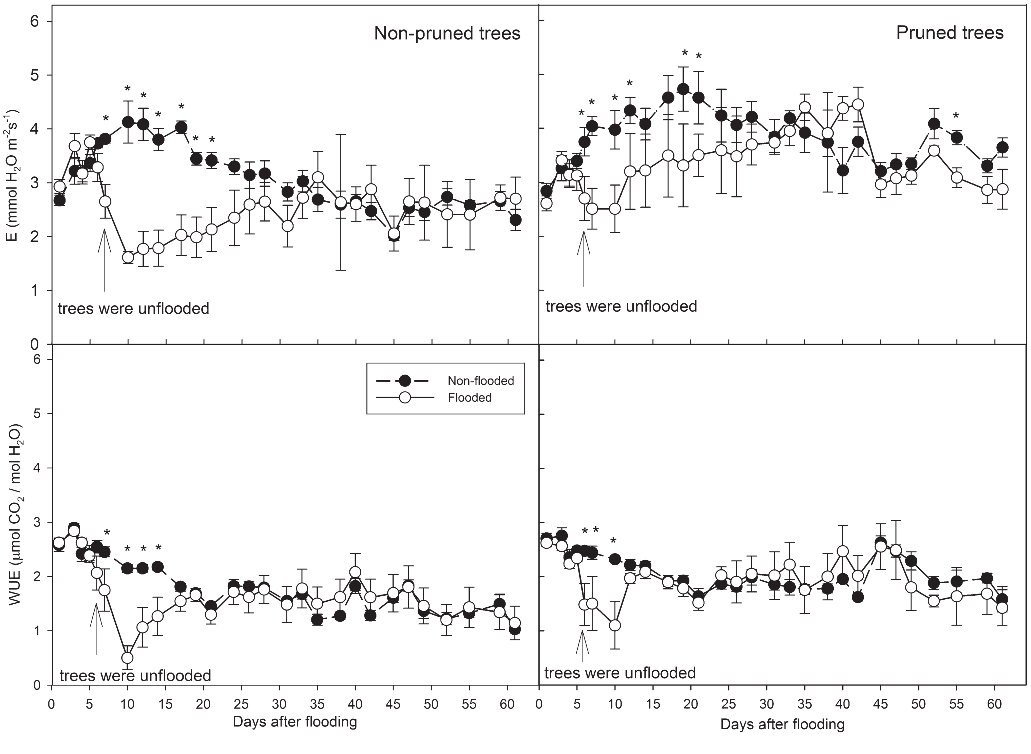

**Fig. 4.** Effect of flooding on transpiration ($E$) and water use efficiency ($WUE$) of two-year-old 'Choquette' avocado trees on Waldin seedling rootstock pruned immediately after plants were unflooded or non-pruned (Expt. 2). Symbols represent means and bars represent ±1 standard error. An asterisk indicates a significant difference between treatments according to repeated measures ANOVA ($P \leq 0.05$).

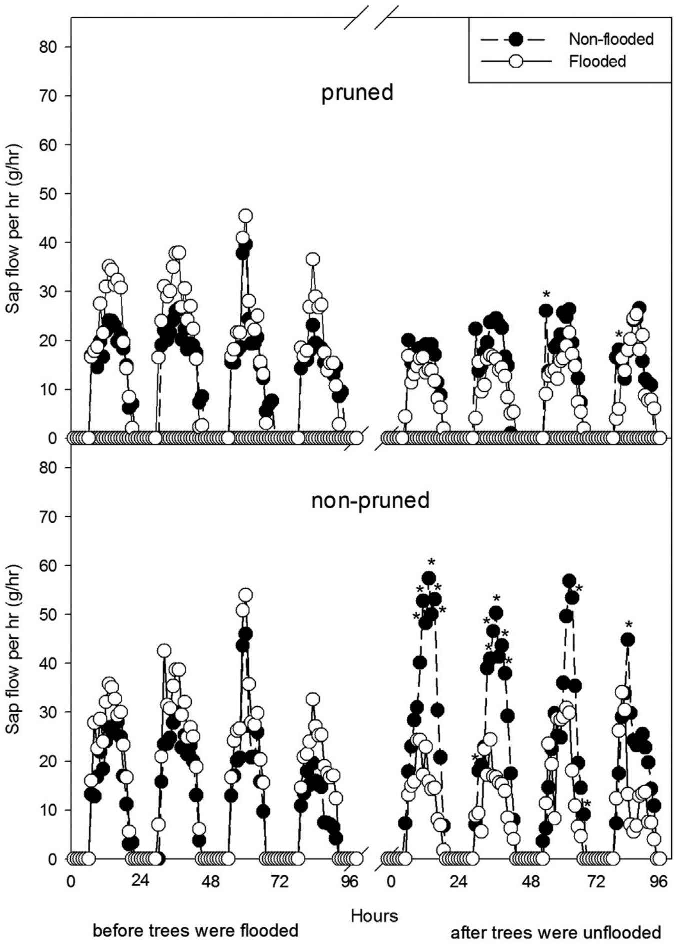

**Fig. 5.** Effect of flooding on hourly xylem sap flow rates of pruned and non-pruned two-year-old 'Choquette' avocado trees on Waldin seedling rootstock. Trees were pruned immediately after plants were removed from 6 days of flooding (unflooded). The graph shows hourly sap flow for 4 days before plants were flooded and 4 days after plants were unflooded. An asterisk indicates a significant difference in hourly sap flow between flooding treatments according to repeated measures ANOVA ($P \leq 0.05$).

### 3.3. Xylem sap flow

There was a significant interaction ($P \leq 0.05$) between flooding and pruning treatments for xylem sap flow. Therefore flooding effects were analyzed separately within each pruning treatment.

After trees in the flooded treatment were unflooded and pruned, the hourly sap flow rate was generally significantly lower in flooded than non-flooded trees in the non-pruned treatment, whereas for trees in the pruned treatment there was generally no difference in the hourly sap flow rate between flooded and non-flooded trees (Fig. 5).

After flooded trees were unflooded and trees in the pruned treatment were pruned (after day 6) until they were harvested, total daily sap flow rate was generally lower for flooded than non-flooded trees only in the non-pruned treatment, but not in the pruned treatment (Fig. 6). Due to considerable between-tree (between-replication) variability within each treatment, these differences were usually significant at the 10% (0.1) significance level but not at the 5% (0.05) significance level (Fig. 6).

### 3.4. Plant dry weight

In both experiments, there was a significant interaction ($P \leq 0.05$) between flooding and pruning treatments for dry weights of some plant tissues. Therefore, flooding effects on plant tissue dry weights were analyzed separately within each pruning treatment for both experiments.

At the end of Expt. 1, in the non-pruned treatment, flooded trees had significantly lower leaf, root, stem and total plant dry weights than non-flooded trees (Table 1). For pruned trees, leaf dry weight was lower for the flooded than non-flooded trees. However, there was no significant difference in stem, root or total plant dry weight between the flooded and non-flooded treatments for the pruned trees (Table 1).

In Expt. 2, in the non-pruned treatment, flooded trees had significantly lower leaf and total plant dry weights than non-flooded trees (Table 2). In contrast, for pruned trees, root and total plant dry weight were significantly higher for flooded than non-flooded trees (Table 2). In Expt. 2, in the non-pruned treatment, there were no significant differences in root or stem dry weights between flooded and non-flooded trees, although root and stem dry weights of flooded trees tended to be lower than those of non-pruned, non-flooded trees (Table 2). For pruned trees, leaf and stem dry weights tended to be lower for non-flooded than flooded trees, but those differences were not statistically significant (Table 2).

## 4. Discussion

In Expt. 1, flooding reduced leaf gas exchange within 2 days after roots were submerged, whereas in Expt. 2, flooding did not result in reductions in leaf gas exchange until 5 days after roots were submerged. These differences were presumably due to the higher maximum air temperature during the flooding period (40.1 °C) in the shade-house used for Expt. 1 (which had no cooling system)

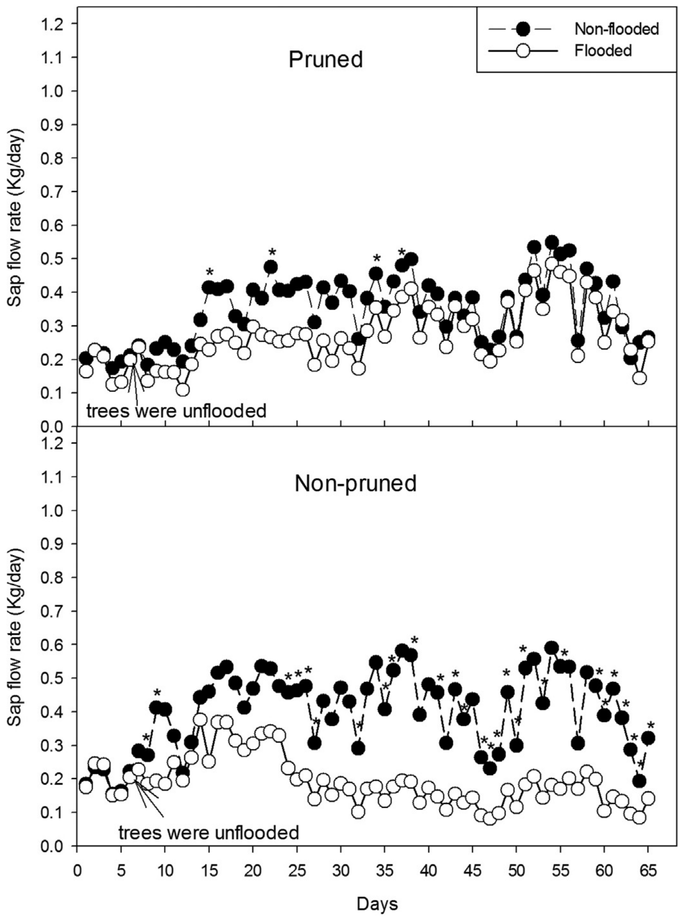

**Fig. 6.** Effect of flooding on daily xylem sap flow rate of non-pruned and pruned two-year-old ‘Choquette’ avocado trees on Waldin seedling rootstock. Plants were pruned immediately after they were unflooded. An asterisk indicates a significant difference between treatments according to a repeated measures ANOVA ($P \leq 0.10$).

**Table 1**
Root, leaf, stem, and total plant dry weight of flooded and non-flooded 2-year-old ‘Choquette’ avocado trees on Waldin seedling rootstock in each of two pruning treatments (pruned or non-pruned) (Expt. 1).

| | Flooding treatment | Leaf dry wt. (g) | Root dry wt. (g) | Stem dry wt. (g) | Total plant dry wt. (g) |
|---|---|---|---|---|---|
| Non-pruned | Non-flooded | 102.3 | 62.3 | 62.4 | 226.9 |
| | Flooded | 74.1 | 35.0 | 46.2 | 155.4 |
| | *P* value | ** | * | * | * |
| Pruned | Non-flooded | 44.2 | 23.7 | 30.4 | 98.4 |
| | Flooded | 31.7 | 25.3 | 24.3 | 81.3 |
| | *P* value | * | NS | NS | NS |

Mean separation between flooding treatments was by *T*-test; *indicates significance at $P \leq 0.01$; **indicates significance at $P \leq 0.05$, within each pruning treatment.

**Table 2**
Root, leaf, stem, and total plant dry weight of surviving flooded and non-flooded 2-year-old ‘Choquette’ avocado trees on Waldin seedling rootstock in each of two pruning treatments (pruned or non-pruned) (Expt. 2).

| | Flooding treatment | Leaf dry wt. (g) | Root dry wt. (g) | Total plant dry wt. (g) |
|---|---|---|---|---|
| Non-pruned | Non-flooded | 145.6 | 112.1 | 374.4 |
| | Flooded | 128.3 | 98.1 | 338.6 |
| | *P value* | ** | ns | *** |
| Pruned | Non-flooded | 108.0 | 105.8 | 323.7 |
| | Flooded | 114.0 | 118.0 | 345.8 |
| | *P value* | ns | *** | ** |

Mean separation between flooding treatments was by *T*-test; **indicates significance at $P \leq 0.05$; ***indicates significance at $P \leq 0.10$, within each pruning treatment.

compared to the lower maximum air temperature (28.3 °C) in the glasshouse used for Expt. 2 (which was cooled by fans and cooling pads). Increased air temperatures and concomitant increases in plant respiration can exacerbate the negative effects of flooding on physiology and growth of fruit trees (Schaffer et al., 1992). When flooded soil becomes hypoxic or anoxic, root respiration shifts from aerobic to anaerobic respiration, which produces considerably less energy in the form of ATP than aerobic respiration (Drew, 1997; Geigenberger, 2003). Anaerobic respiration can also result in a build-up of lactic acid which reduces the pH of the cells (called cytoplasmic acidosis) leading to root cell death (Drew, 1997; Schaffer et al., 1992). Thus, the higher ambient temperatures during the flooding period in the shade house compared to the greenhouse may have increased root respiration and exacerbated the negative impact of anaerobic root respiration on plant metabolic processes, including leaf gas exchange.

In Expt. 1, the mean soil redox potential decreased to 100.6 mV whereas in Expt. 2 it decreased reduced to −55.1 mV by the end of the flooding period. The greater decrease in redox potential in Expt. 2 than in Expt. 1 was a result of the longer flooding period in Expt. 2 (6 days) than in Expt. 1 (3 days). Soil redox potentials below 200 mV indicate anaerobic soil conditions (Ponnamperuma, 1972). Thus, in both experiments, the soil was anaerobic at the end of the flooding period prior to unflooding and pruning the trees.

In both experiments, flooding reduced $A$, $g_s$, $E$ and WUE of avocado trees. This has been observed in several other studies (Gil et al., 2007, 2009; Schaffer et al., 1992, 2007, 2013). Gil et al. (2007) observed that flooding of avocado trees decreased the amount of open stomata to 20%, and that $g_s$ of avocado trees was positively correlated with the percentage of open stomata when data for flooded and non-flooded trees were pooled. In avocado trees, reductions in transpiration have been attributed to reductions in $g_s$ (Schaffer et al., 1992, 2006). Similar results have been observed in other tropical fruit trees including mamey sapote (*Pouteria sapota*) (Nickum et al., 2010) and carambola (*Averrhoa carambola*) (Ismail and Noor, 1996). The mechanisms for decreased $g_s$ in avocado trees as a result of flooding have not been elucidated (Gil et al., 2009). It has been hypothesized for other woody plants that an increase in abscisic acid (ABA) concentration in leaves is the root-to-shoot signaling mechanism inducing stomatal closure in flooded plants (Kozlowski, 1997). In the present study, ABA concentration was not measured. However, Gil et al. (2009) could not relate stomatal closure to differences in ABA concentrations between flooded and non-flooded avocado trees. In the present study, initial reductions in leaf gas exchange for several days after trees were unflooded, were greater for non-pruned than pruned trees. This was presumably because the decreased leaf area from pruning resulted in reduced transpirational demand by the canopy and thus less water uptake was required by pruned trees. Therefore for pruned trees, roots damaged by flooding were able to supply sufficient water to sustain the trees. This is confirmed by the fact that flooding caused a significant reduction in xylem sap flow in non-pruned trees, whereas in pruned trees there was generally no significant differences in xylem sap flow between flooded and non-flooded trees. Internal regulation of $g_s$ and xylem sap flow has generally been interpreted as mechanisms to restrict water movement during drought or flooding (Nicolás et al., 2005; Ruiz-Sanchez et al., 1996). Low oxygen concentration in the root zone as a result of flooding has been shown to reduce the permeability of roots to water (Smith et al., 1990) increasing the resistance to water uptake (Domingo et al., 2002). Under these conditions, water loss from the shoots exceeds the supply from the roots, leading to a reduction in leaf water potential and $g_s$ (Domingo et al., 2002). In woody plants, the differences between water loss via transpiration and water uptake, and short-term dynamics associated with changes in water status can be determined from measurements of xylem sap flow. For example, lemon (*Citrus limon*) trees subjected to 3 days of flooding exhibited a progressive reduction in xylem sap flow and stomatal closure (Ortuño et al., 2007). Similarly, in young apricot (*Prunus armeniaca*) trees, 3 h of flooding caused a decrease in sap flow and a strong reduction in plant hydraulic conductance, decreasing water absorption by the roots (Nicolás et al., 2005). In the same experiment, a close relationship was observed between leaf water potential, leaf conductance and plant hydraulic conductance, indicating that hydraulic signals likely play a dominant role in coordinating the observed responses of the shoot. In the present study, pruning apparently brought the shoot to root ratio of flooded trees (with damaged roots) and the subsequent supply and demand for water and nutrients into better equilibrium, allowing pruned trees to recover more quickly from flooding compared to non-pruned trees.

There was a significant reduction in leaf dry weight due to flooding in non-pruned trees in both experiments and in pruned trees in Expt. 1. A typical response of avocado trees to flooding is leaf abscission due to increased ethylene accumulation in leaves in response to flooding (Schaffer et al., 1992; Gil et al., 2009). For pruned trees, the lack of significant differences in leaf dry weight between flooded and non-flooded trees in Expt. 2 was presumably the result of a large portion of leaves of flooded trees pruned off before they had a chance to abscise. The much higher maximum air temperature during the flooding period in Expt. 1 compared to Expt. 2 probably hastened leaf abscission due to increased ethylene concentration resulting in a significantly lower leaf dry weight for flooded than for non-flooded trees in the pruned treatment in Expt. 1. Gil et al. (2009) observed that hypoxia in the root zone of avocado after 3 days of flooding resulted in increased ethylene emission from leaves that was associated with increased leaf abscission. Sawada et al. (1989) found that the rate of leaf shedding due to ethylene was positively correlated with air temperature in trees sensitive to ethylene.

In both experiments, the significantly lower total plant dry weights (and lower root and stem dry weights in Expt. 1) of flooded compared to non-flooded trees that were not pruned was most likely due to relatively greater flooding induced decreases in $A$ for non-pruned than pruned trees for several days after trees were unflooded. Although in both the pruned and non-pruned treatments, leaf gas exchange values of flooded trees recovered to those of non-flooded trees a few weeks after unflooding, the temporary greater reductions in leaf gas exchange of the non-pruned trees were apparently sufficient to reduce total tree biomass of non-pruned trees.

Pruning about 2/3 of the canopy immediately after trees were removed from short-term (3–5 days) flooding brought the shoot/root ratio into better equilibrium allowing leaf gas exchange and xylem sap flow rates of flooded trees to recover more rapidly in pruned than non-pruned trees. The results of this study support the observation that leaf removal by pruning avocado trees immediately after flooding can hasten recovery of flooding-stressed trees (Crane et al., 1994; Gil et al., 2008). However, further studies are necessary to quantify the relationship between the quantity of canopy removed by pruning and survival and recovery of flooded trees. Also, the present study was conducted with young trees in containers. Further studies are needed to assess the effects of pruning after flooding on recovery of large fruiting trees in an orchard and to determine if an increased rate of recovery from short-term flooding in an orchard is sufficient to offset the costs of pruning. We speculate that pruning after flooding may be more beneficial in an orchard than for trees in containers due to the greater shoot volume relative to root volume that often occurs in orchards in regions such as southern Florida where root restriction as a result of hard bedrock underlying the soil coupled with marginal root damage by Phytophthora root rot reduces the amount of root volume resulting in high shoot/root ratios (Schaffer et al., 2013).

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