The impact of prolonged flood-irrigation on leaf gas exchange in mature pecans in an orchard setting

J.C. Kallestad[a], T.W. Sammis[a,*], J.G. Mexal[a], V. Gutschick[b]

[a]Department of Plant and Environment Science, New Mexico State University, Las Cruces, NM 88003.
[b]Department of Biology, New Mexico State University, Las Cruces, NM 88003.
*Corresponding author. Email: tsammis@nmsu.edu

Abstract

Woody perennials subjected to root oxygen-stress often respond with varying levels of reduced assimilation and leaf gas exchange. Yet in most of these studies, seedlings grown in pots were subjected to experimental conditions that rarely exist in nature for mature trees. To determine if flooding mature orchard-grown pecan (*Carya illinoiensis* (Wangh) K. Koch) results in a similar depressed photosynthetic rate (P_n), transpiration (E), and stomatal conductance (g_s) as found in potted seedling studies, 27 year-old trees were continuously flooded for 35 days during which gas exchange measurements were compared with non-flooded controls. Flood-treated trees exhibited a continuous decline in P_n, g_s, and E without any apparent recovery throughout the treatment period, and progressively higher levels of intercellular CO_2 (C_i). Flooded trees also exhibited widespread interveinal 'bronzing' in subtle blotchy patterns, sporadic adaxial interveinal scorching, and simultaneously put on a flush of new growth, not seen in the control trees. Mechanisms are considered relating a putative disruption in carbohydrate export to the reduced levels of photosynthesis

Keywords: *Carya illinoiensis*; Oxygen stress; Soil water; Hypoxia; Photosynthesis.

Introduction

Researchers have looked for associations between the natural distribution of the tree species and the hydrological or edaphic factors in their habitats to support a hypothetical flooding tolerance or sensitivity (Hosner and Boyce, 1962; Hook and Brown, 1973; Loucks and Keen, 1973; Tang and Kozlowski, 1982; Kozlowski, 1997; Sparks, 2002). A generally accepted consensus for pecan distribution is that they tend to be confined on the lowest-lying portions of river bottomlands in well-drained loamy ridges near moving water, and are rarely found on low, poorly drained clayey flats, or in coarse textured, excessively-drained, shallow soils (Bryson 1974; Wolstenholme, 1979; Sparks, 2002). However, before the advent of flood-control, seasonal flooding along the waterways where native pecans are

currently found was probably more common. Shade intolerance (Baker, 1950), a long juvenile period (Woodroof and Woodruff, 1934), and seed predation may also contribute to pecans inability to effectively compete with sympatric species in wetter habitats. Nonetheless, pecan can be found in low abundance in alluvial depressions and backwater swamps where soil is saturated for more than 3 months (Heimann and Mettler-Cherry, 2004).

There are few reports on the effects of soil water logging on mature orchard-grown pecan trees. Alben (1957) reported widespread foliar scorching and early defoliation in trees grown in poorly drained orchards in Louisiana that received frequent episodes of heavy rainfall. The effect was restricted to a select group of cultivars, and occurred primarily in the tops of the trees. It was proposed that this leaf disorder was related to root injury and an inability to meet high transpiration demand. When the rootzone was waterlogged only until April or May no injury was observed, but if saturation persisted into the early summer months, early defoliation would occur.

Studies using seedling pecans have shown that net photosynthesis(P_n), stomatal conductance (g_s), and transpiration (E) are reduced when subjected to hypoxic soil conditions, and that P_n is not entirely coordinately regulated with g_s and E. Loustalot (1945) found that P_n in 4 month-old 'Burkett' seedlings flooded in either silty loam or sandy soil reached 50% of the expected rate (arbitrary standard) in 8 or 9 days of treatment while reduction in the transpiration rate (E) lagged behind and did not consistently decrease for 12 to 14 days of the treatment, suggesting that P_n was not solely controlled by stomatal aperture. Smith and Ager (1988) found a net decrease in assimilation and E after only one day of flooding 53 day-old 'Dodd' seedlings. The P_n and g_s values were depressed for the 15 day flood treatment but intracellular carbon dioxide partial pressure (C_i) did not vary from control seedlings, suggesting that reduced stomatal aperture in combination with a metabolically controlled reduction of photosynthetic capacity contributed to lower P_n. In an experiment where 'Dodd' pecan seedlings were grown in sealed pots and treated with 13% (mole percent), and 0% gas-phase oxygen in the potting media, smaller leaf area and root length in the hypoxia-treated plants suggested reduced assimilation, and stomatal resistance to water vapor exchange increased 2.7 fold when treated with 13% O_2 for 7 days, and 4 fold when treated with 0% O_2 for 7 days (Smith et al., 1989). Similarly, Smith and Huslig (1990) found reduced leaf area and lower g_s in 'Dodd' seedlings flooded for 14 days. However, when the plants were subsequently transferred to well-drained conditions they exhibited a short-term 2-fold increase in E that returned to normal levels after 15 days of drainage. Flooding had no persistent impact on P_n after drainage.

Pecan orchards in the Mesilla Valley of New Mexico are routinely flooded (border-irrigated). Infiltration rates in these alluvial soils vary from 0.15 to 51 cm hr^{-1} (Bulloch and Neher, 1980). Slow draining tight clay soils, common in the valley, can impede the recharge of oxygen into the root zone and may lead to hypoxic conditions for roots. The purpose of this study is to determine: *i*) if photosynthesis and leaf gas exchange in mature trees are effected by prolonged flooding, and *ii*) the extent and duration of soil hypoxic conditions resulting from continuous flooding required to impact photosynthesis and gas exchange.

Methods and Materials

Study site

The study area was located at the pecan orchard of the New Mexico State University Leyendecker Plant Science Research Center, 18.5 km south of Las Cruces New Mexico. Two groups of 29 year-old 'Wichita' variety pecan trees, approximately 6 m high and having an average breast height diameter of 18.5 cm were chosen for the treatments. The trees are spaced approximately 4.6 m within the row, with rows spaced approximately 9.25 m apart. The soil is classified as clayey over loamy, montmorillonitic (calcareous), thermic, Typic Torrifluvent: Belen series (Bulloch and Neher, 1980). The top 60 cm of the soil is clay (55-60% clay, 31-39% silt, and 1-8% sand), with layers of silty clay, clay, and silty clay loam stratified between 60 and 90cm, and fine sand below 90-100 cm. The orchard has been irrigated on a 21-25 day cycle with either well or Rio Grande water depending on availability. The quantity of applied irrigation water was not metered.

Treatments

A 195 m^2 flood-treatment plot measuring 18.4 m by 10.6 m, centered on the centerline of the row and between 2 study trees was constructed (Figure 1). A border was built around the perimeter by digging a 14 cm wide trench to a depth of approximately 67 cm to prune roots and to install 4 mil plastic sheeting to prevent water infiltration out of the plot. The trench was backfilled and additional soil was added to build a 16 cm high berm around the perimeter. Water was applied to the plot daily beginning July 13, 2004 such that 1 to 4 cm of water was continuously standing on the surface. A 2.08 m^3 water tank was used to slowly supply water to the plot at night. The measured saturated infiltration rate was 0.08 ± 0.02 cm hr^{-1} (n=14). The duration of the treatment period was predetermined to terminate when the averaged photosynthesis rate for the flooded trees fell below 50% of the maximum rate. The plot was drained August 18, 2004.

The control trees were located in a plot 20 m from the flood-treatment plot in an adjacent row (Figure 2). The control trees were irrigated on May 5, June 1, June 25, July 26, and September 8, 2004. The irrigation timing likely resulted in soil moisture stress during part of the study time period.

To provide access to the middle south-facing tree canopy for leaf gas exchange measurements, standard construction scaffolding was erected to a height of 3 m between the study trees on both flooded and control plots.
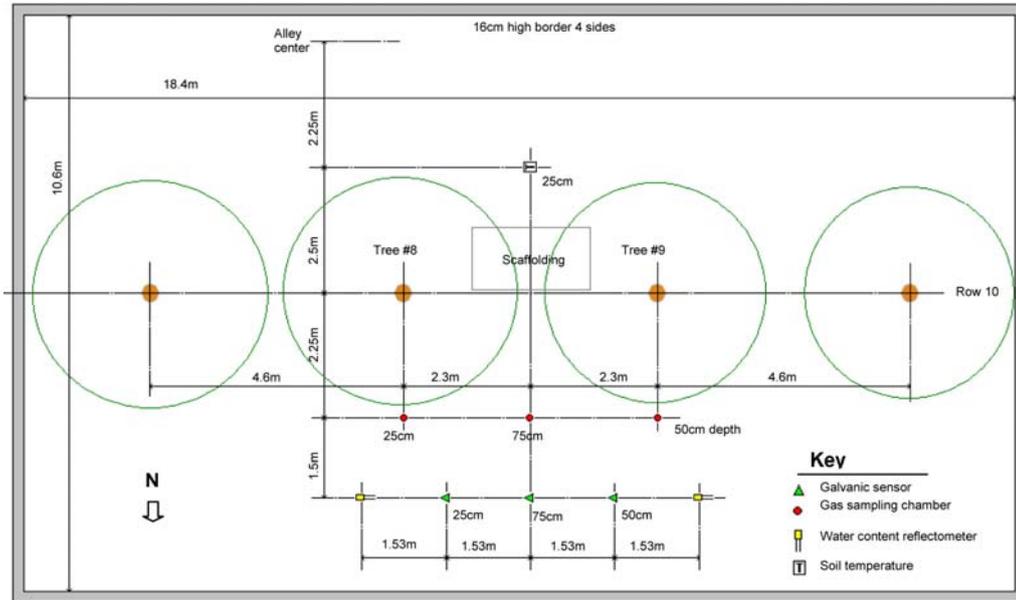
Figure 1. Flooded plot tree and instrument locations.
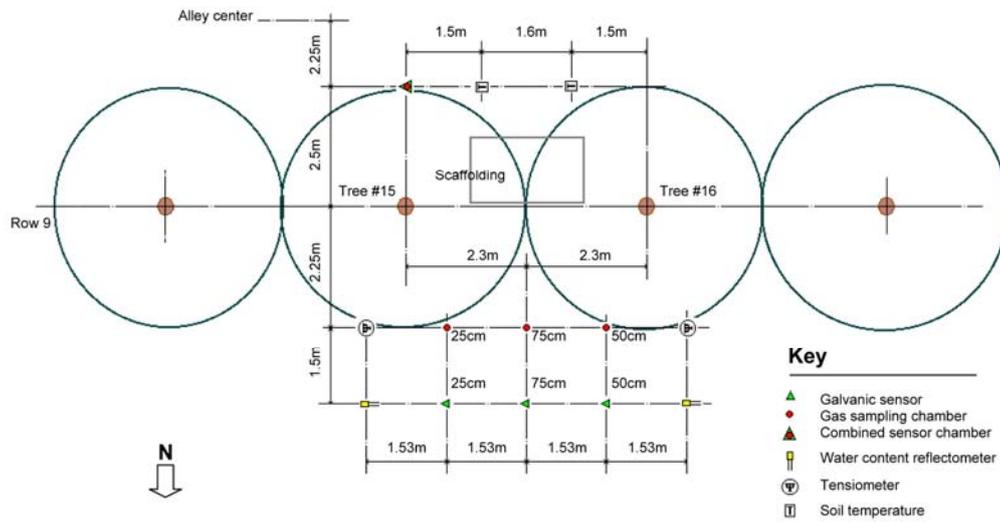
Figure 2. Control plot tree and instrument locations.

Soil measurements

Two soil moisture content reflect meters (model CS616, Campbell Scientific, Logan UT) placed vertically measured average volumetric soil moisture from 0-30 cm and 30-60 cm depth at each plot. Soil temperature probes (model L-107, Campbell Scientific, Logan UT) were buried at 25 cm and 50 cm depth in the control plot and at 25 cm in the flooded plot. Soil matric potential measurements were made only in the control plot using tensiometers (Irrometer Co., Riverside CA) buried at 30 cm and 45 cm. Soil matric potential measurements were typically taken before 09:30 hr. Gas-phase soil oxygen concentration was measured at 25, 50, and 75 cm depths using galvanic sensors housed in buried diffusion chambers (Kallestad et al., 2006). Soil moisture content readings were collected hourly and oxygen concentration voltages were measured every 10 seconds and averaged over each hour using a CR10x data logger (Campbell Scientific, Logan UT) at each plot. Gas sampling diffusion chambers used in conjunction with the FOXY optical oxygen sensor (Kallestad et al., 2006) were also installed in both flood and control plots at 25, 50 and 75cm depth. Optically sensed oxygen concentrations were used primarily for verifying the reliability of the galvanic oxygen sensors. Placement of the instruments in the control and treatment plots are indicated on the site maps (Figures 1, 2).

Leaf gas exchange measurements

Measurements of photosynthetic rate, conductance, intercellular carbon, transpiration, and vapor pressure deficit at the leaf surface, were made on individual leaflets using a portable gas exchange system (model 6400, LI-COR Biosciences, Lincoln, NE). Measurements were gathered periodically from mid-June to mid-September, and every other day beginning at 09:30 and 13:30 hours throughout the flood-treatment period. During each measurement period, a total of 10 -15 leaflets were unsystematically chosen from the 7 terminal leaflets on separate full-sun leaves, on 2 flooded trees and 2 non-flooded controls (20-30 measurements per treatment per time point). Readings were taken on clear cloudless days using the sun and sky as light source. Photosynthetic active radiation (PAR) was typically between 1600 and 2010 μmol quanta m^{-2} s^{-1} and not less than 950 μmol quanta m^{-2} s^{-1}. The system was adjusted so that the reference CO_2 stream to the leaf chamber received 400 μmol CO_2 mol^{-1} air; flow rate was set to 400 μmol s^{-1}; and chamber humidity was not controlled. No distinction was made between leaves on fruiting versus vegetative branches. New leaf growth occurred between the second and third week of treatment only on the flooded trees. Since these leaves were not in the initial sampling population they were not included in the flood-treated leaf measurements. However, four days after the flooded plot was drained separate measurements were made on these new leaves to compare with other populations of leaves in the flood-treated and control trees.

Leaf tissue analysis

Leaf samples (30 third position leaflets per sample) were collected on one occasion at the end of the treatment period. Samples were collected for 3 discrete populations of leaves

based on treatment and appearance to determine if nutrient deficiencies or salt toxicity were associated with visible disorders. Elemental analysis was performed on acid digested plant material using ICP-OES spectroscopy, except for chloride, which was determined by acetic acid extraction according to Gavlak et al., (1998). Elemental analysis was performed by the New Mexico State University Soil Water and Air Testing Laboratory.

Statistical analysis

LICOR 6400 data were analyzed with SAS® version 9.3.1 statistical software (SAS Institute Inc, Cary NC). A Mixed model was used to compare the fixed effect of treatment on the response variables P_n and C_i. To account for the covariance structure resulting from clusters of repeated measurements (sub sampling within a tree), the model incorporated a random effect for tree within treatment. Degrees of freedom were computed using the Kenward and Rodger adjustment. Since the treatments were not applied to each tree independently, each of the two trees in a treatment group is essentially a pseudo replicate of an experimental unit. The results were also used to identify the time at which separation of mean photosynthesis rate between control and flood-treated trees became significant.

Results and Discussion

Gas-phase soil oxygen concentrations at 25 and 50 cm depth in the flood treated plot fell to near 0%, and the concentration at 75 cm was less than 2% (Figure 3 shows only 50 cm probe) for approximately 40 days, whereas, soil oxygen levels at 50 cm depth in the control plot fell below 10% for a period of 8 to 10 days in response to irrigations or heavy rainfall from 14 August to 16 August. Maximum soil oxygen levels at 50 cm in the control plot declined in response to increased soil moisture from precipitation events that followed irrigations. Several soil and plant-related factors contribute to differences in oxygen availability between mature trees and young potted seedlings that may delay the onset of reduced leaf gas exchange after flooding of mature trees. The volume of soil involved in the root system of orchard grown pecan is much greater and the root density is likely to be much lower than in the medium used in potted seedling. The sandy layer below 90 cm also may have provided a reserve of oxygen to deep roots. In this experiment, it took 5 days to deplete O_2 below 2% in the top 50cm of soil, and possibly longer at deeper depths.

During the treatment period, minimum soil temperature at 25 cm depth in the control plot ranged from 24° to 31 °C, and 23 and 30 °C in the flooded plot soil. The soil temperatures were in the range of normal pecan growth and would not have contributed to any change in transpiration and P_n measurements.
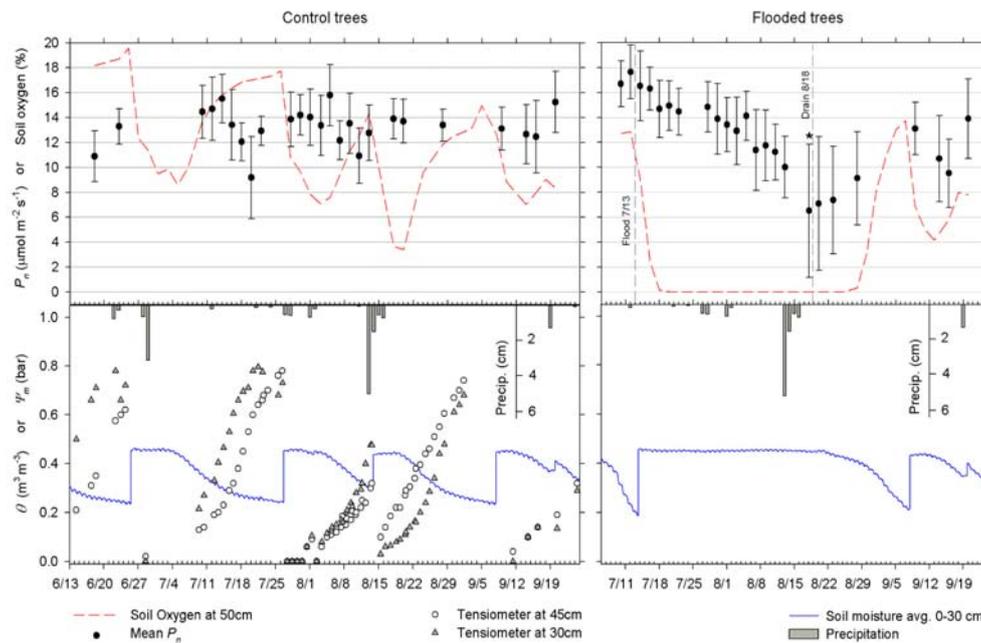
Figure 3. Morning photosynthetic rate measurements taken from control and flood-treated trees. P_n values represent the mean and standard deviation of subsamples from two trees per treatment (flood-treated avg. n=23.1, control avg. n=20.). Flood-treated P_n values significantly different from controls are marked (*). Soil O_2 concentration curve was plotted through the 12:00 time point every other day.

The average morning P_n in leaves of the control trees was approximately 14.1 µmol m^{-2} s^{-1} (Figure 3). When the average rootzone soil moisture fell below 0.34 m^3 m^{-3} from 14 July to 21 July, afternoon readings of P_n declined to 3.25 µmol m^{-2} s^{-1} (Figure 4). Meteorological factors in combination with reduced soil moisture contributed to the observed decline in control tree leaf gas exchange. The minimum relative humidity from 14 July to 21 July ranged from 9.4% to 22% (avg = 17.2%), afternoon air temperatures ranged from 35 to 37 °C, and afternoon leaf vapor pressure deficits ranged from 3.3 to 5.5 kPa. Stomatal regulation of P_n under soil moisture stress is also apparent in the control trees in the afternoon readings (Figure 4). Transpiration in control trees also declined from 14 July to 21 July in response to these environmental conditions (Figure 5). Similar decreases in P_n, g_s and E in response to high vapor pressure deficit and low soil water potential have been described by Rigger and Daniell (1988) and Mielke (1981) for pecan. Based on a water balance irrigation scheduling model, the pecan orchard should have been watered on 14 July to prevent soil moisture stress conditions. After irrigation on 26 July, increases in afternoon readings of P_n, E and Ci were observed in the control trees (Figures 4, 5). The pattern of P_n fluctuations in the control trees correlate strongly with low soil moisture, low relative humidity, and high matric potential rather than low soil oxygen levels (Figure 3).
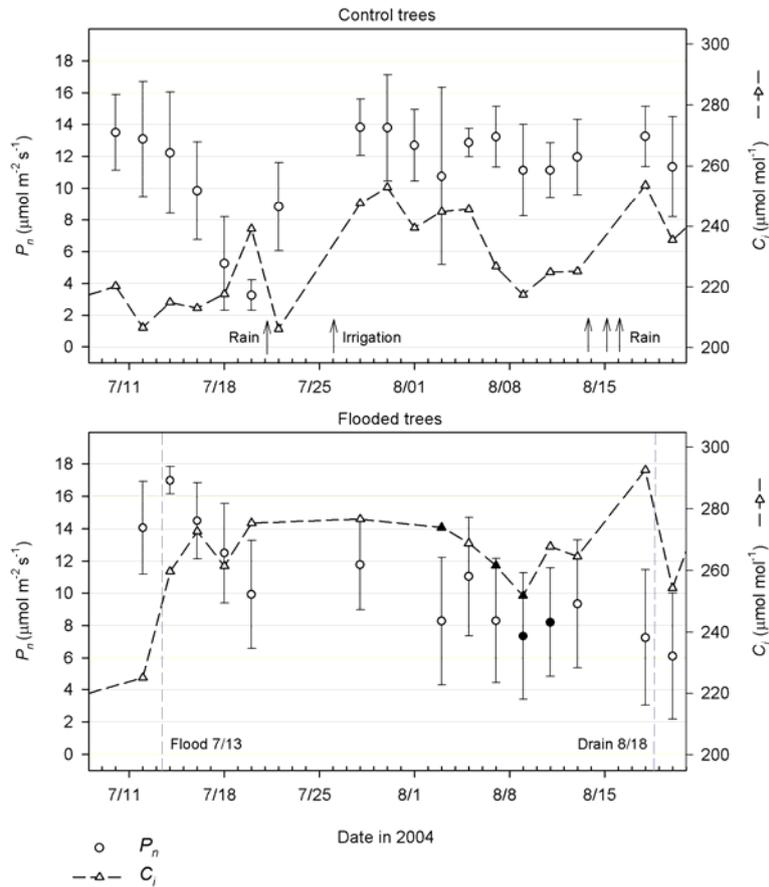
Figure 4. Afternoon P_n and C_i measurements of flood-treated and control tree leaflets. P_n values represent mean and standard deviation from two trees per treatment (flood-treated avg. n=23.1, control avg. n=20.). Flood-treated P_n and C_i means significantly different from controls at the $\alpha = 0.05$ level are marked with filled symbols.

Flood-treated mature pecans exhibited a morning decline in P_n, and g_s (Figure 3) without any recovery during the treatment period. Greater decreases in gas exchange were evident in the afternoon readings (Figure 4). Transpiration also decreased progressively in the flood treated trees (Figure 5), although, it appeared to level out after 14 days of flooding. Photosynthetic rate fell to 50% of maximal after 34 days of flood-treatment, based on the morning readings, and after 25 days based on the afternoon readings.
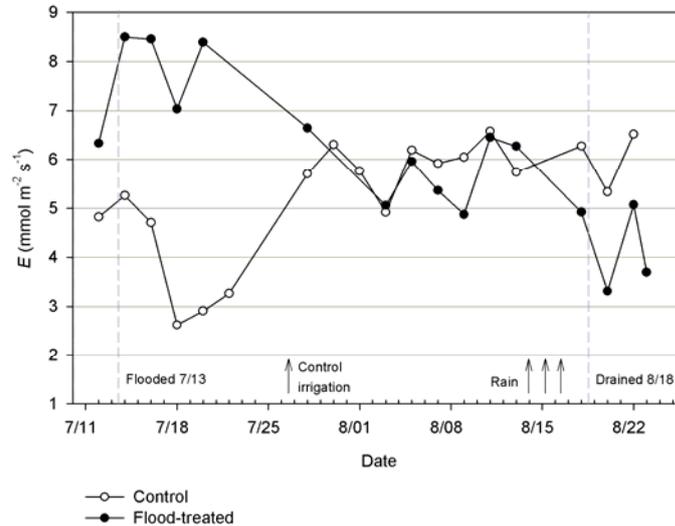
Figure 5. Afternoon *E* measurements of flood-treated and control tree leaflets. Values represent the mean of two trees per treatment (flood-treated avg. n=23.1; control avg. n=17.4)

In the flood-treated trees, there is a high correlation between P_n - g_s and P_n - C_i ($r^2 =$ 0.95), but the downward shift in the curve (Figure 6) compared to the control trees, along with higher C_i levels, suggests that photosynthetic capacity is reduced. As light and ambient CO_2 were not limiting in the current study, one explanation for elevated levels of C_i associated with depressed rates of photosynthesis, especially in the afternoon readings, is that photosynthesis is limited by the *utilization* of photosynthates. The utilization of triose phosphate for the production of starch, sucrose, or the regeneration of RuBP must occur at a rate such that the concentration and flux of inorganic phosphate (P_i) regenerated in these steps is able to keep pace with the demand from photophosphorylation (Sharkey, 1985; Paul and Foyer, 2001).

The extent to which flooding disrupts assimilate transport to the roots or alters source-sink relations appears to be related to hypoxia sensitivity (Hook and Brown, 1973). Many reports of non-stomatal limitation of photosynthesis with elevated C_i tend to be associated with flood-sensitivity. Smith and Ager (1988) reported that flooded pecan seedlings showed no significant change in C_i compared to non-flooded controls, whereas mature trees in this study show an increase in Ci under flood conditions.
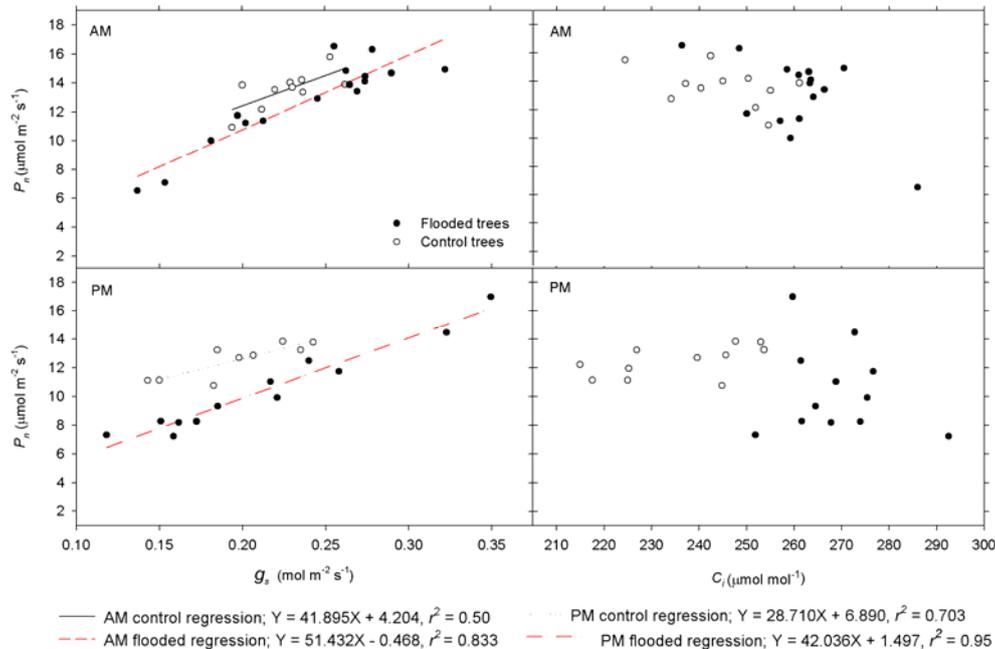
Figure 6. Relationship of net photosynthetic rate with stomatal conductance and intercellular CO_2. Data points represent means grouped by treatment and measurement time within the treatment period. Data for control trees were excluded from 7/14 to 7/22.

Trees that are supposedly sensitive to flood vary in their C_i response. Pezeshki (1993) found elevated C_i levels associated with reduced P_n in *Quercus lyrata* and *Q. falcata* but decreased C_i in the flood-tolerant *Taxodium distichum*, which was able to recover 91% of control P_n levels after the second week of flooding. Zude-Sasse et al (2001) found C_i was not elevated above control until 28 hours of flooding *Mangifera indica*, even though P_n was reduced within 2.5 hours of root anoxia.

In contrast, decreased C_i associated with decreased P_n, and g_s in response to flooding have been reported in flood-tolerant species. Beckman et al (1992) found reduced C_i in flooded *Prunus cerasus*, but non-stomatal limitation of P_n, that was about equal to the stomatal limitation initially, became more dominant as flooding continued. Similarly, decreased C_i has been reported for *Vaccinium ashei* in response to flooding (Davies and Flore, 1986).

Variance in gas exchange measurements tended to increase in the flooded trees as the treatment progressed (Figure 3). This is thought to be associated with the development of leaf disorders. Approximately 21 days (August 7) after the flood- treatment began; flooded trees exhibited leaf bronzing and simultaneously put on a flush of new growth, which was not seen in the control trees. Leaf disorders included widespread subtle interveinal 'bronzing' in blotchy patterns, and to a much lesser extent, adaxial interveinal scorching most plausibly resulting from heat stress related to reduced transpiration. Bronzing and

scorching were observed primarily on full-sun leaves of south-facing branches, but bronzing could be seen on interior leaves to a lesser degree (Figure 7). These disorders were not necessarily associated with a particular main branch, but could occur on select secondary or tertiary branches adjacent to other secondary or tertiary branches with apparently normal leaves. Four days after the flooded plot was drained, gas exchange measurements were made on discrete populations of leaves based on their treatment and appearance (Table 1). Photosynthetic rate and g_s were depressed in all flooded leaves, and the extent of the reduction (and variance) followed the severity of the disorder. Averaged transpiration was lower in flooded bronzed leaves but not significantly. Intercellular CO_2 showed an inverse relationship with P_n, with highest values occurring in the bronzed leaves.

Figure 7. Leaf coloration on control and flood-treated trees.

Table 1. Mean and standard deviation for photosynthesis (P_n), stomatal conductance (g_s), intercellular CO_2 (C_i), and transpiration (E) in appearance-classified leaflet subsamples of flooded and control trees on Aug.22nd 2004.

Treatment, leaf condition	P_n ($\mu mol\ m^{-2}\ s^{-1}$)	g_s ($mol\ m^{-2}\ s^{-1}$)	C_i ($\mu mol\ mol^{-1}$)	E ($mmol\ m^{-2}\ s^{-1}$)	Subsample size
Control, normal	14.21 ± 1.44	0.232 ± 0.040	247.5 ± 12.1	5.87 ± 0.85	24
Flooded, new growth	11.98 ± 2.68	0.214 ± 0.098	251.0 ± 25.4	5.52 ± 1.49	11
Flooded, 'normal'	10.23 ± 2.55	0.189 ± 0.065	262.8 ± 13.2	5.74 ± 1.57	23
Flooded, bronzed	4.80 ± 3.71	0.128 ± 0.060	317.1 ± 49.3	4.46 ± 1.62	20

Table 2. Leaf elemental analysis.

		Treatment, leaf condition			
Element	Unit	Control, normal	Flooded, bronzed	Flooded, new growth	Published range
P	%	0.10	0.07	0.11	.08 - 0.18 [a]
K	%	1.04	0.87	1.12	0.99 - 1.55 [a]
S	%	0.20	0.20	0.16	
Ca	%	1.61	1.36	1.10	1.55 - 2.43 [a]
Mg	%	0.43	0.32	0.41	0.40 - 0.60 [a]
Fe	mg/kg	117	82	59	39 - 72 [a], 116 [b]
Zn	mg/kg	34	30	34	53 - 283 [a]
Mn	mg/kg	33	35	29	146 - 597 [a]
B	mg/kg	331	277	105	57 - 173 [a], 300 [b]
Cu	mg/kg	10	10	10	4.8 - 12.2 [a]
Al	mg/kg	116	115	62	376 [b]
Na	%	0.01 [c]	0.01 [c]	0.0 [d]	0.0163 [b]
Cl⁻	%	0.294	0.335	0.385	

a. Based on Arizona survey, Univ. of AZ Cooperative Extension
b. Based on Sparks & Madden (1977)
c. Measured concentration at the minimum detectable limit.
d. None detected

   In addition to leaf bronzing, the flooded trees a break in dormancy and new leaf flush on a limited number of branches, typically subtended by mature, fully expanded leaves with the bronze discoloration. Leaves of new growth were easily distinguished from the mature

leaves by being slightly chlorotic, slow to expand, and thicker. The new flux of leaf growth observed in the flood pecan tress due to anaerobic stress has also been described by Erez et al. (1980), who found that treating the roots of pre-chilled *Prunus persica* cuttings with 2.5 or 5% O_2 for up to 6 days released a greater percentage of buds from winter rest and more rapidly than roots treated with high O_2 atmosphere.

Leaf tissue elemental analysis collected for control, flooded-bronzed, and flooded-new growth (Table 2) indicate that phosphorus, potassium, calcium and magnesium levels were marginally deficient and chloride was elevated in flooded-bronzed leaves. Both flooded and control trees have levels of manganese that are considered deficient (Sparks, 1978), and boron levels considered borderline toxic. However, visible B toxicity resulting in leaf tip and margin burn, and interveinal chlorosis are thought to occur at concentrations ≥ 500 mg kg^{-1} (Blackmon and Winsor 1946; Picchioni et al., 1991). The lower levels of iron and manganese in flooded–bronzed and flooded-new growth leaves suggest that Fe and Mn were becoming increasingly reduced in the soil and not available for transport, and probably contributed to chlorosis in the new growth. Chloride levels are higher in flood-treated trees, suggesting impaired chloride exclusion by the roots. While levels above 0.3% are thought to contribute to leaf scorch in almond, walnut, and pistachio, optimal levels have not been determined for pecan (Sibbett, 2000). The elevated levels of K in flooded-new growth leaves is consistent with K following assimilate translocated to new sinks and its requirement for stem elongation (Marschner, 1995).

In our study, it is not known whether the lower levels of phosphorus, potassium, magnesium and iron in the flooded-bronzed leaves (Table 2) represent diminished uptake throughout the whole plant, or a localized response in branches involved in nutrient remobilization during the flush of new growth. Wood (1988) found significantly lower levels of K in leaves of fruit-bearing pecan branches than in leaves of nonbearing branches. Smith et al (1989), and Vu and Yelenosky (1991) reported no changes in leaf K in flood-treated trees but significant reductions in the roots. In contrast, Close and Davidson (2003) found a 50% reduction in foliar K and P in *Eucalyptus nitens* saplings in response to flooding. The reserves of stored K in mature trees may take considerable time to deplete and manifest itself as a widespread deficiency in the leaves with accompanying effect on photosynthesis.

Also, the patchiness of the bronzing symptom suggests that source of the disorder may be local to specific leaves rather than a systemic response that might arise from high levels of ethylene, or chloride throughout the transpiration stream. Although, physiological compartmentalization of root and limb, which becomes more entrenched as a tree ages (Wood, 1991), may explain why some branches were affected more than others if ethylene did contribute to the disorder.

Conclusions

As with potted seedling pecan, flooded mature pecan trees exhibit decreasing P_n, but unlike seedlings, continuous flooding along with high ambient temperatures resulted in higher C_i and leaf disorders. The regulation of photosynthesis in response to the environment is highly dynamic and involves cross-talk within a complex network of signal transduction pathways. Gas exchange measurements made after the 35 day treatment period indicate g_s fully recovered after the treatment, and P_n regained 85% of levels measured in July. However, the appearance of marginal leaf necrosis on select branches, and a greater incidence of shuck die-back in flooded trees in late October indicate that senescence may have been induced earlier, possibly from elevated levels of ethylene or root damage on selected roots.

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