

The effects of intermittent flooding on seedlings of three forest species

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Abstract

Under greenhouse conditions, seedlings of three forest species, baldcypress (*Taxodium distichum*), nuttall oak (*Quercus nuttallii*), and swamp chestnut oak (*Quercus michauxii*) were subjected to an intermittent flooding and subsequent physiological and growth responses to such conditions were evaluated. Baldcypress showed no significant reductions in stomatal conductance (g_s) or net photosynthetic rate (P_N) in response to flood pulses. In nuttall oak seedlings g_s and P_N were significantly decreased during periods of inundation, but recovered rapidly following drainage. In contrast, in swamp chestnut oak g_s was reduced by 71.8 % while P_N was reduced by 57.2 % compared to controls. Baldcypress displayed no significant changes in total mass while oak species had significantly lower leaf and total mass compared to their respective controls. Thus baldcypress and nuttall oak showed superior performance under frequent intermittent flooding regimes due to several factors including the ability for rapid recovery of gas exchange soon after soil was drained. In contrast, swamp chestnut oak seedlings failed to resume gas exchange functions after the removal of flooding.

Additional key words: bottomland forests; leaf conductance; net photosynthetic rate; *Quercus michauxii*; *Quercus nuttallii*; *Taxodium distichum*.

Introduction

Flooding in wetland soils decreases the available oxygen content while imposing various degrees of stress on plants depending on the species, age class, the timing, the intensity, and the duration of flooding (Pezeshki 1994). Subsequent removal of floodwater allows for the diffusion of oxygen and increased soil redox potential. There is a potential for competitive advantage for seedlings of species that can

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survive the periodic flooding as well as those species that can recover rapidly after flooding recedes.

Previous studies on gas exchange responses of woody species to flooding have mostly focused on the responses to stagnant continuous flooding (Sena Gomes and Kozlowski 1980, Shanklin and Kozlowski 1985, Pezeshki 1990, 1993, Angelov *et al.* 1996, Wibbe and Blanke 1997) while little is known about responses to short-term flood pulses (Megonigal and Day 1992). It is not clear how flood-sensitivity or different degrees of sensitivity under continuous flooding would be reflected in plant responses under a series of pulse flooding. We asked the question whether plant species considered flood-sensitive would display similar sensitivity or response criteria if subjected to frequent periodic inundation. This is important because the seedlings transplanted for bottomland forest reforestation/restoration must be able to survive intermittent flooding that is so typical in bottomland forests of the lower Mississippi floodplain forests. Thus, the main objective of the present study was to characterize the physiological and growth responses of seedlings of key bottomland forest species in south-central USA to a series of intermittent flood periods that mimic the fluctuating water levels encountered in the natural, undisturbed bottomland forest environments. A second objective was to evaluate recovery responses after flooding was removed during each cycle as well as over the experimental period.

Materials and methods

We have studied species within the Mississippi River alluvial plain areas that are important economically and ecologically and are target species for reforestation. The species represent a range of flood-sensitivity in order of lowest to highest, baldcypress (*Taxodium distichum* L.), nuttall oak (*Quercus nuttallii* Palmer), and swamp chestnut oak (*Quercus michauxii* Nutt.) (Monte 1978, Hook 1984, Angelov *et al.* 1996). Baldcypress seed cones and nuttall oak acorns were collected from Rapides Parish, Louisiana, USA. Swamp chestnut oak acorns were collected from the Tigrett Wildlife Management Area near Dyersburg, Tennessee. Seeds were stratified between January and March of 1996 according to current stratification protocol (Schopmeyer 1974). Seedlings were germinated in propagation flats containing commercial potting soil. Germination began during the second week of April and all plants used for the study had germinated by April 27. In June 1996, seedlings were transplanted from propagation flats to containers (30 cm depth, 22 cm width, one plant per pot). Seedlings were planted in soil collected from the Ap horizon of a Falaya silt loam soil from an old agricultural field in Shelby County, Tennessee. To allow for mortality due to transplanting, plants were monitored closely for two weeks and any dead seedlings were replaced. Seedlings were grown in a ventilated greenhouse on campus of the University of Memphis. Average temperatures throughout the study period ranged from 23.8 to 41.4 °C.

Plants were watered daily and fertilized weekly with 20-20-20 Peters fertilizer. After a 12 d period of acclimation, seedling with a mean height of 10.0, 21.8, and

21.6 cm for baldcypress, nuttall oak, and swamp chestnut oak, respectively, were subjected to two soil treatments: (1) Control (C), well watered and well drained, (2) intermittent flooding (IF), flooded for 5 d and drained for 5 d. The IF treatment was imposed for 3 complete cycles ending with the plants drained. Treatment effects on soil conditions was quantified by measuring soil redox potential (Eh, mV) throughout the experiment. Twenty-four seedlings per species were randomly assigned to each treatment, for a total of 48 plants per species. The experiment followed a factorial design with three species and two levels of soil moisture (C, IF). In addition, the experiment followed a completely randomized block design to compensate for any differences in environmental conditions within the greenhouse.

Soil Eh was measured periodically (every 3 or 4 d) using platinum tipped electrodes, a millivolt meter (*Orion* model 250A), and a calomel reference electrode. Soil Eh was measured in 6 pots from each treatment at 10 cm below the soil surface.

Photosynthetic photon flux density (PPFD), g_s , and P_N were measured using a portable photosynthesis system (model *CIRASI*, *PP Systems*, Hertfordshire, UK). Gas exchange measurements were conducted on 12 plants per treatment (one per each plant) on each sunny sample day between 10:00-14:00 h, on intact, well-developed leaves in the upper third of the canopy. When possible, measurements were taken on the first and final day of each flooded and drained period. Measurements were conducted on 11 sample days throughout the experiment: days 0, 1, 4, 6, 10, 14, 16, 19, 23, 26, and 30.

Height, diameter, and biomass of all study plants were recorded at the beginning (day 0) and conclusion (day 30) of the experiment. Samples were divided into leaves, stems, and roots and were oven dried at 80 °C.

Root porosity, a measure of the percentage air space within a root, was conducted at the conclusion of the study on the 12 destructive samples used for final biomass analysis. Root porosity was measured using a 25 mm³ pycnometer as described by Jensen *et al.* (1969). The pycnometer was first filled with water only and weighed. A sample (0.2-0.3 g) of root was cut from the tip portion and weighed. The root material was then placed in the water filled pycnometer and weighed. The root sample was then extracted and ground to a powder with mortar and pestle. The ground powder was returned to the pycnometer and weighed. Root porosity was calculated according to Jensen *et al.* (1969).

Counts of number of leaves on each plant were supplemented with height and diameter measurements. Leaf area was measured on ten sample leaves of different sizes for each species using a leaf area analysis system (*AgVision, Decagon Devices*, Pullman, Washington, USA). Leaf area was then regressed by dry mass. Total dry mass of leaves was used to calculate total leaf area. The models used to calculate leaf area were:

$$T. distichum \text{ LA} = 0.06 + (16.60) \text{ LDM} \quad (r^2 = 0.98)$$

$$Q. nuttallii \text{ LA} = 0.01 + (24.22) \text{ LDM} \quad (r^2 = 0.98)$$

$$Q. michauxii \text{ LA} = 0.64 + (15.78) \text{ LDM} \quad (r^2 = 0.98)$$

where LA = leaf area [cm²] and LDM = leaf dry mass [g].

The *t*-tests procedure of the Statistical Analysis System (SAS) was used to test for differences between treatments within species for growth, biomass, root porosity, and

leaf area. *SigmaPlot* was used for computing regression models for leaf area. Repeated measures analysis of variance was used to test differences in means of gas exchange data (SAS 1990).

Results

Soil Eh under control treatment remained above +500 mV indicating well-aerated conditions during the experiment (Fig. 1). In IF pots, soil Eh fluctuated with periods of flooding and draining. During the first flooding/drained cycle, Eh dropped to as low as +175 mV by the second day of flooding but recovered to aerobic levels after 5 d of being drained. In the subsequent flooding periods, soil Eh decreased with each flooding period. In the second and third draining periods soil Eh did increase but never to above +350 mV.

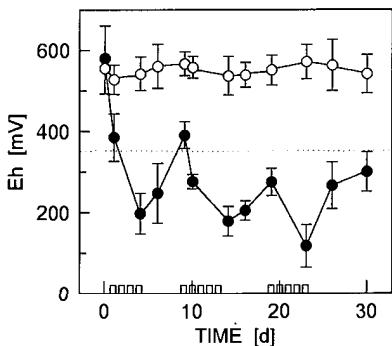


Fig. 1. Changes in soil redox potential (Eh) conditions for two soil treatments (○ - control, ● - intermittently flooded, □ - flooding days) during the experiment. An Eh value of +350 mV represents the value at which oxygen disappears from the soil. Vertical lines represent SE. Vertical bars represent days flooded for the intermittently flooded treatment ($n = 6$).

Survival rates of baldcypress and nuttall oak were 100 % in both treatments at the conclusion of the experimental period. Mortality of intermittently flooded swamp chestnut oak was first noted on day 4 of the experiment. By the conclusion of the experiment survival rates of swamp chestnut oak were 100 and 96 % for C and IF treatments, respectively. No morphological changes were evident during the experiment for any of the study species.

Gas exchange responses: Stomatal conductance and P_N of IF baldcypress were not significantly different from controls on any measurement day (Fig. 2). Initially, g_s decreased by 29 % on day 6 but recovered to levels similar to controls by day 10 (Fig. 2) and remained high for the remainder of the study. P_N initially decreased to 85 % of controls on days 1 and 4. By day 14, P_N values were comparable to control plants. P_N decreased during the third flooding period and during the third drained period but remained within 90 % of control plants (Fig. 2).

Stomatal conductance of flooded nuttall oak seedlings showed no reduction compared to controls till the first draining period (day 6) (Fig. 2). Throughout the second flooded and drained period, g_s was not significantly reduced compared to controls. During the final flooding period, g_s was reduced and remained low throughout the final drained period (Fig. 2). Decreases in P_N of IF nuttall oak followed the flood-

ing/drained regime throughout the study. During the first flooding period P_N was decreased by 25 and 32 % of controls on days 1 and 4, respectively (Fig. 2). P_N during the first drained period was comparable to controls, thus indicating a recovery. During the second and third flooded periods P_N was 39 and 56 % of controls, respectively (Fig. 2). During both the second and third drained periods P_N was not significantly different from controls (Fig. 2). This indicates rapid recovery of photosynthetic activity in response to flood-water removal.

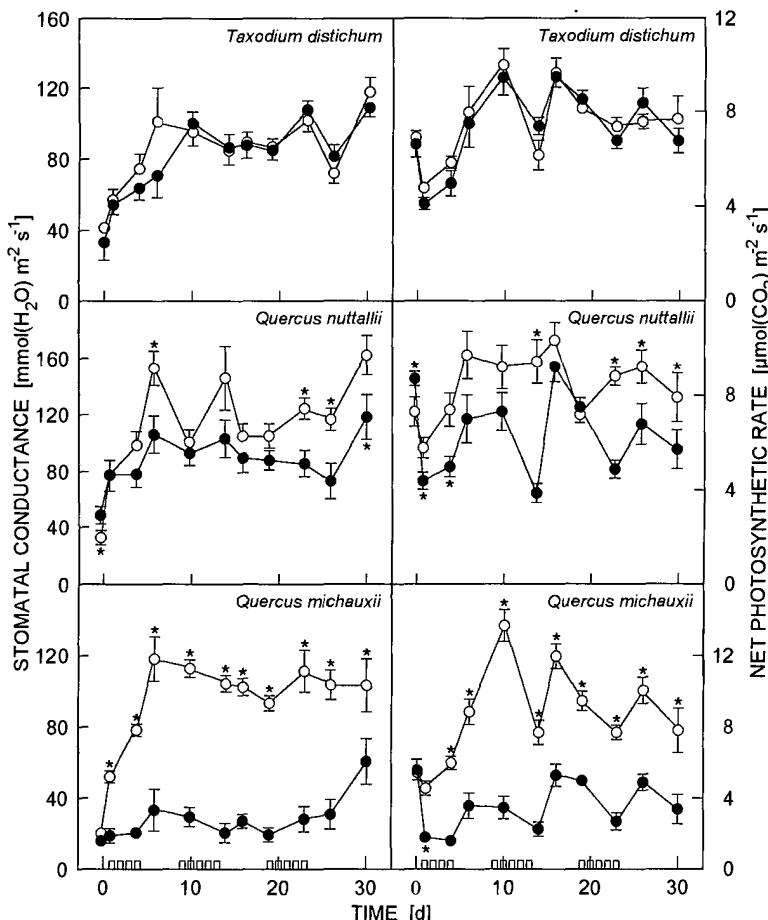


Fig. 2. Daily mean stomatal conductance and net photosynthetic rates for *Taxodium distichum*, *Quercus nuttallii*, and *Quercus michauxii* (C) seedlings under control (○) and intermittent flooding (●) treatments. For each measurement day an asterisk represents significant differences at $p < 0.05$. Vertical lines represent SE. Vertical bars represent days flooded for the intermittently flooded treatment ($n = 12$).

In swamp chestnut oak, g_s decreased to 35 % of control after 1 d of flooding and remained low throughout the study period, but showed a slight recovery trend at the conclusion of the experiment (58 % of controls on day 30) (Fig. 2). This was the only

Table 1. Mean stomatal conductance, g_s [mmol(H₂O) m⁻² s⁻¹] and net photosynthetic rate, P_N [μmol(CO₂) m⁻² s⁻¹] over the study period, height [cm], diameter [mm], root, stem, leaf, total dry mass [g], total leaf area per plant [cm²], number of new leaves (the number of leaves emerged over the study period) per plant, and root porosity [%] for *Taxodium distichum*, *Quercus nuttallii*, and *Quercus michauxii* under control (C) and intermittently flooded (IF) treatments. Means are followed by standard error. For each species, means in each column followed by an * are significantly different at the $p<0.05$ level.

Variable	<i>T. distichum</i>		<i>Q. nuttallii</i>		<i>Q. michauxii</i>	
	C	IF	C	IF	C	IF
g_s	81.4±2.9	78.5±2.9	103.0±4.3	84.4±3.3*	86.6±3.6	25.3±1.9*
P_N	7.6±0.2	7.2±0.2	8.2±0.2	6.5±0.2*	8.5±0.3	3.6±0.2*
Height growth	18.0±1.3	16.8±1.3	17.8±2.3	10.5±1.2*	11.7±1.3	5.2±2.1*
Diameter growth	11.8±1.71	14.8±1.1	14.4±2.1	15.4±3.2	12.3±3.5	11.8±3.8
Root dry mass	0.05±0.01	0.04±0.01	0.82±0.20	0.48±0.10	0.41±0.30	0.28±0.10
Shoot dry mass	0.18±0.02	0.21±0.02	1.04±0.30	0.58±0.10	0.99±0.10	0.48±0.20*
Leaf dry mass	0.24±0.02	0.19±0.04	1.40±0.20	0.73±0.10*	2.14±0.50	0.49±0.20*
Total dry mass	0.47±0.04	0.44±0.06	3.26±0.60	1.79±0.20*	3.54±0.50	1.25±0.40*
Leaf area/plant	5.46±0.40	4.51±0.64	2.7±7.72	6.50±3.60*	56.40±5.92	28.3±1.50*
New leaves/plant	12.4±1.0	10.8±0.6	15.8±3.0	7.8±0.8*	19.4±4.1	5.1±1.5*
Root porosity	11.7±1.7	27.8±4.5*	16.1±2.4	19.7±4.3	16.0±2.3	14.6±2.7

indication of g_s recovery for this species that otherwise had a constant depressed g_s . In swamp chestnut oak P_N was also sensitive to flooding, dropping to 35 % of control following 24 h of flooding and remained below 55 % of control for the remainder of the experiment (Fig. 2). Higher values of P_N were recorded on drained days showing marginal recovery from flooding.

Mean gas exchange values for baldcypress over the experimental period showed no significant reduction in g_s and P_N in response to periodic flooding. In contrast, nuttall and swamp chestnut oak showed significant decreases in g_s and P_N in the IF plants compared to their respective controls (Table 1).

Growth and biomass: The height growth increment (final values-initial values) in IF baldcypress was not significantly different compared to control plants (Table 1). Height growth in nuttall and swamp chestnut oak decreased in the IF treatment compared to their respective controls (Table 1). Diameter growth was not significantly different between treatments in any of the study species (Table 1).

Baldcypress showed no significant differences in biomass allocation patterns or total biomass between treatments (Table 1). Intermittently flooded nuttall and swamp chestnut oaks had significantly lower leaf and total mass compared to control (Table 1). Stem dry mass of IF swamp chestnut oaks was also significantly lower than in control (Table 1).

Total leaf area and the number of leaves per plant was not significantly different for baldcypress under different treatments (Table 1). In oaks, decreased leaf number and leaf area were found in IF plants compared to controls (Table 1). Root porosity of IF baldcypress was significantly higher compared to control plants. No significant

differences in root porosity were found between treatments for the oak species (Table 1).

The relationship between soil Eh conditions and plant gas exchange: The effect of reduced soil Eh on g_s and P_N was investigated using regression analysis. In baldcypress there was no significant correlation between g_s and Eh ($r^2 = 0.01$, $p = 0.918$). Stomatal conductance in nuttall oak and swamp chestnut oak was significantly correlated with soil Eh, *i.e.*, g_s decreased as soil Eh became more reduced with r^2 values of 0.29 and 0.80 and p values of 0.02 and 0.001, respectively. There was no significant correlation between P_N of baldcypress and soil Eh ($r^2 = 0.01$, $p = 0.9540$). In both oak species, P_N was significantly correlated with soil Eh, decreasing as soil Eh became reduced with $r^2 = 0.38$ and $p = 0.002$ in nuttall oak and $r^2 = 0.53$ and $p = 0.001$ for swamp chestnut oak.

Discussion

Literature suggest that species from a broad range of flood-sensitivity show reductions in gas exchange upon exposure to continuous flooding (*e.g.*, Kozlowski 1982, 1984, Pezeshki and Chambers 1986). A species' specific flood-tolerance capability seems to determine if and how long gas exchange remains reduced (Pezeshki *et al.* 1996). Previous studies reported that baldcypress seedlings grown in stand still anoxic conditions had initial reductions in g_s and P_N but recovered within two to three weeks (Pezeshki 1991). In our study, intermittently flooded baldcypress seedlings had initial reductions in g_s and P_N during the first flood period followed by a recovery of gas exchange function for the remainder of the study. In nuttall oak seedlings, gas exchange decreased during periods of flooding but recovered rapidly following drainage. The reduction in P_N during the flooding cycles followed the reduction in g_s , suggesting that stomatal closure and the subsequent diffusional limitation of CO_2 was partially responsible for the lower carbon fixation rates. The rapid recovery of g_s and P_N in response to drainage indicated that decreased gas exchange in nuttall oak is temporary when exposed to short periods of soil flooding. In contrast, the IF swamp chestnut oak had decreased g_s and P_N after one day of flooding; little or no recovery noted for this species. Gardiner and Hodges (1996) found that the g_s in four bottomland oak species was significantly reduced under continuous flooding. The relationship between plant gas exchange and Eh further indicated the difference in sensitivity to periodic flooding among the study species. The gas exchange rates in baldcypress did not change in response to reduced soil conditions while decreases in g_s and P_N in oak species were closely correlated to the reducing soil conditions.

Under flooding, reductions in shoot growth occur due to a variety of factors including anaerobic respiration of the root and the disruption in translocation of root metabolites (Reid and Bradford 1984, Pezeshki 1994). Although height growth reduction in baldcypress subjected to continuous flooding regimes has been reported (Shanklin and Kozlowski 1985, Conner 1994), height growth of intermittently

flooded baldcypress in our study was not decreased significantly suggesting that height growth in this species is less sensitive to intermittent flooding than to continuous flooding (Yamamoto 1992, Pezeshki and Anderson 1997). In the present study, height growth of both oak species was reduced in response to IF significantly. Decrease in height growth in seedlings exposed to continuous flooding is a common response in oaks such as *Quercus nigra*, *Q. phellos* (Gardiner and Hodges 1996), and *Q. nuttallii* (Pezeshki and Anderson 1997). While many tree species may exhibit reduced height growth in response to flooding, some flood-tolerant species such as baldcypress show increased stem diameter growth (Yamamoto 1992). However, in the present study stem diameter of the study species was not significantly affected by the intermittent flooding treatment.

Prior work has shown decreased biomass accumulation in baldcypress in response to continuous flooding. Baldcypress seedlings continuously flooded for 8 or 12 weeks had decreased root and shoot biomass compared to control (Shanklin and Kozlowski 1985, McLeod *et al.* 1986). In contrast, periodic flooding increased baldcypress biomass over the short-term (Megonigal and Day 1992). In the present study, no significant differences were found in biomass production of baldcypress in response to intermittent flooding. In oak species, leaf biomass and total biomass were significantly reduced in the IF treatment. In addition, leaf area and number of leaves in baldcypress did not change significantly while oak species had decreased leaf area and leaf number indicating that baldcypress showed very little sensitivity to cyclical flooding events. However, leaf area decreased in baldcypress seedlings subjected to continuous flooding (Shanklin and Kozlowski 1985, Nash and Graves 1993). Reduction in leaf area in response to continuous flooding has been shown for other species (Smit 1988, Peterson and Bazzaz 1984). Our results suggest that carbon fixation was reduced in oak species due to reduced leaf area and low P_N . The culmination of decreased P_N and decreased leaf area in the oak species exposed to intermittent flooding could affect the survival of these species in areas subjected to frequent IF, particularly for the swamp chestnut oak.

Our root porosity values further indicated some major differences in responses of the study species to periodic flooding. Increased root porosity through the development of aerenchyma tissue allows for deeper rooting and enhanced survival associated with wetland plants because of the diffusion of photosynthetic and atmospheric O₂ to the roots (Kozlowski 1984, Armstrong *et al.* 1994). Previous work with baldcypress has shown increases in root porosity in response to continuous flooding (Kladze *et al.* 1994, Pezeshki 1996). In the present study, root porosity was increased by 137 % in IF baldcypress seedlings compared to control. The increased root porosity in response to periodic flooding facilitated O₂ diffusion which in turn allowed for continued functioning and growth of the root system (see also Pezeshki 1996). In contrast neither of the flooded oak species had increased root porosity compared to their respective controls.

In conclusion, the patterns of gas exchange and growth responses to periodic soil flooding for each species differed from those previously reported under continuous flooding. In addition, gas exchange and growth responses differed among the study species. Baldcypress was the most insensitive species to IF followed by nuttall oak

and swamp chestnut oak. Hence short-term flood pulses adversely affect plant gas exchange and growth in certain forest species that represent a range of flood sensitivity. Baldcypress and nuttall oak showed superior performance under IF that is likely to be due to the ability for rapid recovery of gas exchange functions after floodwater was drained. In contrast, swamp chestnut oak seedlings failed to resume gas exchange functions during the drained cycles. The observed differences in response to flood cycles among the study species further demonstrated the importance of taking into account the species-specific flood response characteristics whenever a bottomland forested site is targeted for reforestation. Our results show that baldcypress and nuttall oak would be excellent choices for reforestation in areas exposed to frequent intermittent flooding. In addition, baldcypress seedlings, if treated with short-term intermittent flooding in the nursery prior to field transplanting, may have a better chance for survival due to increased root porosity. This hypothesis, however, requires additional testing.

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