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Effects of flooding on susceptibility of *Taxodium distichum* L. seedlings to drought

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Abstract

Responses of baldcypress (*Taxodium distichum*) seedlings to soil moisture were studied to test the hypothesis that flooding may lead to seedling's higher susceptibility to drought. Treatments included a well-watered but drained control (C), continuously flooded (CF), control followed by drought (CD), and flooded followed by drought (FD). Gas exchange values revealed no significant effects on net photosynthetic rate (P_N) in response to flooding. In contrast, after the onset of drought, P_N was significantly reduced in CD and FD plants. Significant growth reductions under mild drought conditions indicated that baldcypress seedlings were drought sensitive. However, comparison of gas exchange rates and growth responses between CD and FD plants indicated that prior flooding had no detectable effect on subsequent sensitivity of baldcypress to drought. These findings explain baldcypress persistence in wetland habitats characterized by periodic flooding and mild drought.

Additional keywords: baldcypress; dry mass; leaf; photosynthesis; redox potential; root; stem; stomatal conductance; transpiration rate; wetlands.

Introduction

Baldcypress, *Taxodium distichum* (L.) Rich., is a flood-tolerant tree species found in forested wetlands of the southeastern United States. Although baldcypress persists across a range of hydrologic regimes, early growth and survival of regenerated seedlings appear to be directly related to the frequency of substrate exposure to air (Klimas 1987, Pezeshki 1991, Mitsch and Gosselink 2000). Currently, many wetlands and associated water bodies in the region are experiencing problems due to limited water level fluctuations primarily imposed by human-induced changes in hydrology (USFWS 1989). In certain areas, regulatory agencies are proposing to re-instate water level fluctuations including extreme drawdowns (USFWS 1989). However, the implications of such plans for the survival of woody seedlings growing in adjacent wetlands are not well known. First, tree seedlings grown in such areas are subjected to frequent soil flooding and, thus, usually develop flood-induced characteristics such as adventitious roots. A drawdown could expose these roots to air. Second, drawdowns during the growing season may create severe drought.

Despite frequent precipitation, droughts of sufficient severity occur frequently during the growing season across this region. Although no data exist for the probable number of drought days in the region for trees (because of their deep rooting), the probable number of drought days for crop plants 5 years out of 10 is 70 to 80 (Kozlowski *et al.* 1991, Kozlowski and Pallardy 1997). Thus, it is reasonable to expect a high probability of drought during the growing season. Additionally, root systems of seedlings of woody species that are grown under flooded conditions are shallow as compared to non-flooded plants and may be more susceptible to drought stress.

In general, plant responses to flooding and drought include stomatal closure (Pezeshki and Chambers 1985, Smith and Ager 1988, Kozlowski and Pallardy 1997) and decreases in net photosynthetic rate, P_N (Pezeshki and Chambers 1985, Pezeshki *et al.* 1986, Pezeshki 1993). However, previous research on responses of baldcypress have focused primarily on gas exchange responses to soil flooding (see Pezeshki 1993, 1994, Anderson and Pezeshki 1999 and the references cited therein) while relatively little is known about gas exchange responses to intermittent flooding and drought cycles. The purpose of this research was to quantify responses of baldcypress seedlings to such a cycle. The main objective was to determine whether or not flooding has any effect on seedling susceptibility to a subsequent drought and to quantify the physiological functions and growth following re-watering. To meet this objective we tested the hypothesis that flooding of baldcypress seedlings may lead to seedling's higher susceptibility to drought as compared to seedlings that had not been exposed to flooding.

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Materials and methods

Baldcypress seeds, collected from local sources in west Tennessee, USA were germinated following the stratification protocol described by Pezeshki and Santos (1998). Newly germinated seedlings were transplanted in pots 15 cm in diameter and 30 cm in height and filled with soil collected from the A_p horizon of a Falaya silt loam. Seedlings were placed in a greenhouse and allowed to acclimate for one week prior to treatments. All treatments were fertilized weekly with a commercial soluble fertilizer (20-20-20 %, N : P : K, respectively). At the initiation of the study, seedlings averaged 34.7±0.9 cm in height. Well-watered controls were watered daily with 1 000 cm^3 of tap water to achieve field capacity while flooded treatments were subjected to saturated soils with water level maintained at 5 cm above the soil surface.

The experimental design was a complete randomized block design. Initially, using two treatments with 3 blocks per treatment and 14 seedlings per block, there were a total of 84 randomly selected seedlings; 42 were randomly assigned to control (C) and 42 to continuous flooding (CF). The study was divided into three phases. Phase I was carried out in order to induce initial flood responses beginning on day 0 and ending on day 62. At the end of the phase I, seedlings were assigned randomly to two subsets and four treatments: C (control), CF (control followed by flooding), FD (flood followed by drought), and CD (control followed by drought); thus, 21 seedlings per each treatment combination. Phase II began on day 63.

Soil water potential was monitored using pre-dawn leaf water potential measurements. Seedlings in the drought treatments received 500 cm^3 water once pre-dawn leaf water potential measurements approached –0.5 MPa in order to maintain a mild (moderate) drought stress.

Phase III began on day 99 with the re-watering of the drought-stressed seedlings; bringing the soil to field capacity and maintaining it at this level for two weeks. Plant measurements continued in order to determine the degree of resumption of plant functioning. The entire study lasted for 114 d (June through October, 1999).

Soil measurements included soil redox potential, Eh [mV] using platinum-tipped electrodes built according to Patrick and DeLaune (1977). The electrodes were placed at 15 cm below the soil surface in six randomly chosen pots per treatment. A portable millivoltmeter and a calomel reference electrode were used to determine Eh (Pezeshki and DeLaune 1998). The study was conducted in an air-conditioned greenhouse where temperature ranged from 23.5 to 41.2 °C and natural light provided a daily maximum of photosynthetic active radiation (PAR) around 1 600-1 750 $\mu mol\ m^{-2}\ s^{-1}$ at the top of plant canopy during sunny days.

Plant measurements included P_N and stomatal conductance (g_S) using a portable field photosynthetic system (*CIRAS1*, *PP Systems*, Hitchin, England). These measurements were conducted weekly on well-developed, intact attached leaves (needles) from the upper portion of branches of ten randomly selected seedlings per treatment. Leaf water potential was measured on five randomly selected seedlings within each treatment using a pressure chamber (model *1003*, *PMS Instruments*, Corvallis, OR, USA). Height measurements were conducted at the conclusion of each phase. Final biomass was collected at the conclusion of the study and separated into plant parts of either dead or live leaf, stem, and root. Fresh masses were determined immediately after harvesting. Plant parts were then dried at 70 °C to a constant mass in order to determine dry mass.

Analyses of the data employed GLM procedures of the Statistical Analysis System (*SAS Institute*, Cary, NC, USA) to determine any significant differences between different treatment groups under flood and drought conditions. GLM procedures including multiple pair-wise comparisons (Tukey's HSD) were used to determine significant differences at the 0.05 level between treatment groups in gas exchange responses, biomass allocation patterns, and leaf water potential.

Results

Plant responses to flooding (phase I): Soil Eh was reduced in flooded treatments ranging between +18 to +172 mV while Eh values indicative of oxidized soil conditions ranging between +408 to +485 mV were recorded for controls (Fig. 1).

Both transpiration rate (E) and g_S increased in CF plants as compared to C plants after 14 d of flooding ($p = 0.0001$). For instance, g_S remained significantly higher than control plants through day 53 of the study ($p = 0.0008$, Fig. 2*C*). Two days after flooding, P_N decreased significantly ($p = 0.0014$) as compared to controls. However, P_N rates recovered after fourteen days of flooding to values comparable to controls ($p = 0.5457$). Mean P_N for phase I showed no significant treatment effects (Fig. 2*A*).

Mean height (±SE) was 73.80 (±1.84) and 74.30 (±2.09) cm in C and CF plants, respectively. Percent survival was 100 % for both treatments. Thus, flooding had no significant effects on height growth or survival rate at the end of phase I.

Plant responses to flooding followed by drought (phase II): During phase II, the continuously flooded (CF) pots remained flooded, thus, continued to exhibit reduced soil Eh conditions ranging from −73 to −118 mV. In contrast, following initiation of drought, soil returned to aerated condition as Eh in FD pots (flooded in phase I followed by drought in phase II) exhibited values comparable to C (control) and CD (control in phase I followed by drought in phase II).

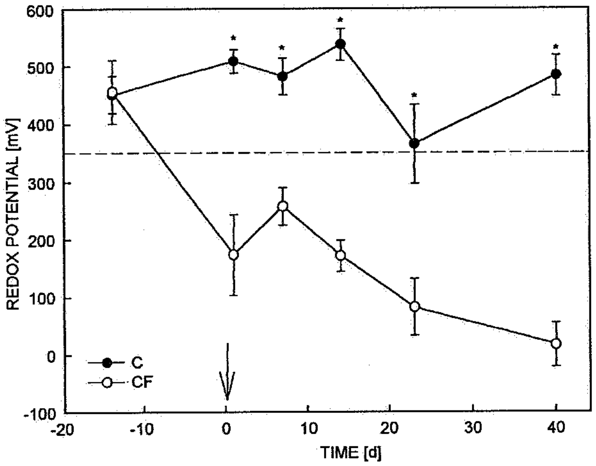

Fig. 1. Soil redox potential [Eh] before and during phase I of the study period. *Arrow* indicates the initiation of flooding. *Dashed line* indicates Eh of +350 mV, the approximate Eh at which O_2 disappears from the soil. Significant differences at the 0.05 level between flooded and control conditions are noted by *. *Bars* indicate ±SE.

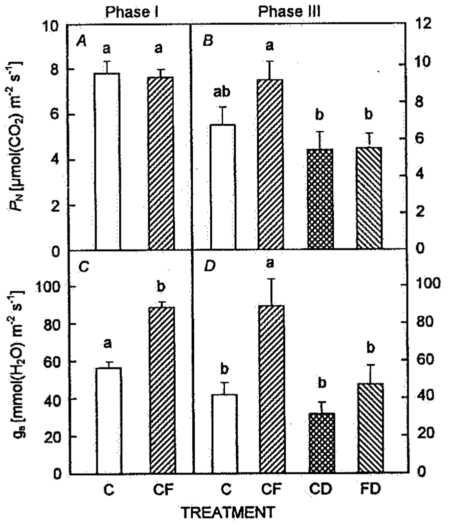

Fig. 2. (*A, B*) Mean net carbon assimilation (P_N) and (*C, D*) stomatal conductance (g_S) during phase I (*A, C*) and phase III (*B, D*) of the study period. Significant differences at the 0.05 level between continuously flooded (CF), control (C), control followed by drought (CD), and flood followed by drought (FD) are noted by different letters. *Bars* indicate ±SE.

After five days of draining (day 68) and withholding water, predawn leaf water potentials (Ψ_{PD}) in FD and CD plants were −0.437 and −0.443 MPa, respectively. Leaf Ψ_{PD} measurements exhibited no significant differences between FD and CD plants throughout phase II as both treatments were designed to impose mild drought conditions (Fig. 3*C*) while C and CF plants did not experience water stress.

Significant reductions in mean g_S and P_N were found at the conclusion of phase II (Fig. 3*A,B*). Values of g_S, *E*, and P_N in CD and FD plants were significantly lower compared to C and CF plants. However, no significant differences were observed between CD and FD plants (Fig. 3*A,B*), thus, flooding during phase I had no detectable effects on plant gas exchange responses to drought during phase II.

Recovery from stresses (phase III): Six days after re-watering, no significant differences in Ψ_{PD} were found between treatments. Mean Ψ_{PD} was −0.020±0.002, −0.020±0.002, −0.040±0.004, −0.030±0.004 MPa in C, CF, CD, and FD, respectively.

During phase III, P_N in CD and FD plants recovered substantially after re-watering (Fig. 2*B*). Mean g_S in CF plants remained significantly higher than all other treatments (Fig. 2*D*).

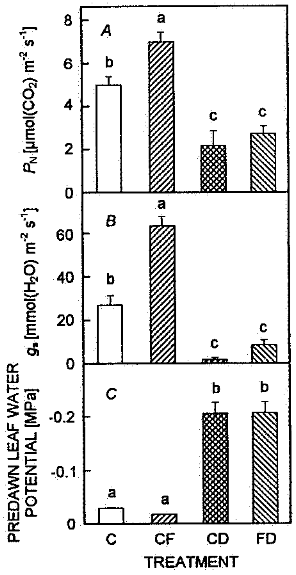

Fig. 3. (*A*) Mean net carbon assimilation (P_N), (*B*) stomatal conductance (g_s), and (*C*) predawn leaf water potential [MPa] during Phase II. Significant differences at the 0.05 level between continuously flooded (CF), control (C), control followed by drought (CD), and flood followed by drought (FD) are noted by different letters. *Bars* indicate ±SE.

At the conclusion of phase III, mean heights were 79.40±2.70 cm in C, 85.90±4.30 cm in CF, 76.50±3.09 cm in CD, 80.50±3.01 cm in FD and showed no significant differences across treatments ($p = 0.2571$). Under drought, root masses in CD and FD plants were significantly reduced compared to controls (Table 1). However, no significant differences in shoot or root mass were observed between CD and FD plants. Shoot mass in CF was significantly higher than under other treatments at the conclusion of the study. Stem dieback was observed in CD and FD plants. In addition, live leaf mass significantly decreased under CD and FD treatments (Table 1). Significant differences were found in root/shoot ratios (RSR) at the conclusion of the study. Control plants had the highest RSR of 1.79 while RSR was 1.48, 1.16, and 0.96 in CF, FD, and CD plants, respectively.

Table 1. Means (±SE) of final total shoot dry mass [g], total root dry mass [g], and biomass components of live stem, dead stem, live leaf, dead leaf, live root and dead root mass at the conclusion of the study. Treatments: control (C), continuously flooded (CF), flood followed by drought (FD), and control followed by drought (CD). Significant differences across treatments at the 0.05 level noted by different letters.

Variable	C	CF	FD	CD
Shoot dry mass	16.29 ± 1.63^{b}	24.15 ± 2.52^{a}	12.93 ± 1.20^{b}	14.58 ± 0.98^{b}
Root dry mass	26.63 ± 3.53^{a}	36.71 ± 6.37^{a}	11.17 ± 1.43^{b}	11.80 ± 1.73^{b}
Dead leaf mass	0.52 ± 0.13^{bc}	0.32 ± 0.10^{c}	1.81 ± 0.41^{b}	3.45 ± 0.54^{a}
Live leaf mass	6.23 ± 0.60^{a}	5.47 ± 0.53^{a}	2.31 ± 0.43^{b}	2.24 ± 0.44^{b}
Live stem mass	9.49 ± 1.11^{b}	18.33 ± 1.99^{a}	6.17 ± 0.97^{b}	7.07 ± 0.69^{b}
Dead stem mass	0.06 ± 0.03^{b}	0.03 ± 0.03^{b}	2.64 ± 0.82^{a}	1.80 ± 0.63^{ab}
Live root mass	26.62 ± 3.52^{a}	36.34 ± 6.37^{a}	11.10 ± 1.42^{b}	11.68 ± 1.74^{b}
Dead root mass	0.006 ± 0.004^{b}	0.080 ± 0.020^{ab}	0.09 ± 0.030^{ab}	0.120 ± 0.030^{a}

Discussion

Gas exchange rates in flood-tolerant species such as baldcypress usually resumes rapidly following a flood event (Kozlowski 1982, Pezeshki *et al.* 1986, Pezeshki 1990, 1993) as was noted in this study. In fact, despite the initial reductions (values not shown), enhanced g_S relative to controls was noted in continuously flooded plants (Fig. 2*C,D*). Maintenance of high g_S during flooding may have contributed to the observed maintenance of high P_N rates during this study. The gas exchange response pattern observed in part reflects an important flood-tolerance characteristic allowing for continued photosynthetic carbon fixation under reduced soil Eh. Although soil Eh in flooded treatments remained reduced (Fig. 1), Eh values did not reflect a highly reduced soil environment that can adversely impact plant functioning (Pezeshki and DeLaune 1998).

Pezeshki and Anderson (1997) and Conner and Flynn (1989) reported continued height growth in baldcypress in both intermittent and continuously flooded soil conditions. In contrast to these findings, reduced height growth in baldcypress was found in seedlings exposed to continuous flooding (Yamamoto 1992, Conner 1994, Yamamoto *et al.* 1995). Many of these studies did not report soil redox potential, therefore, it is not clear how reduced the soil became, thus, making it difficult to compare these results directly. Nevertheless, the present study indicated that baldcypress seedlings are well suited for sustaining height growth under mildly reduced soil conditions created by soil flooding.

Leaf water potentials in CF plants remained similar to controls. Satisfactory maintenance of water status in CF plants suggests that there were no changes in resistance to water movement across root membranes as compared to controls. Interestingly this "normal" internal water status was maintained in CF plants without development of any visible adventitious roots.

Soil flooding influences numerous aspects of root and shoot physiology that may inhibit growth or alter biomass allocation (Kozlowski 1982, Pezeshki 1994). Biomass allocation in baldcypress was modified in response to flooding. A significant increase in shoot growth of CF plants was noted as compared to controls (Table 1). Allocating photosynthate to shoot growth enhances seedling's survival against future flooding events because portions of shoots must be maintained above floodwaters or death of baldcypress seedlings will likely occur. Root biomass in CF plants, however, was similar to that found in controls. Some species grown in flooded conditions experience reductions in root growth (McLeod *et al.* 1986, Pezeshki *et al.* 1996). Aboveground biomass, however, was greatest in CF plants as compared to controls. Greater biomass accumulation under continuous flooding in *Nyssa aquatica*, a highly flood-tolerant tree species has been reported by McKelvin *et al.* (1995).

Responses to drought: At the onset of mild drought conditions, substantial reductions in g_S and P_N in CD and FD plants were observed. Stomatal closure prevents excess water loss during periods of limited water availability and/or high evaporative demand but reduces photosynthesis through diffusion limitations and the resultant decreasing intercellular concentrations of CO_2 (Epron *et al.* 1992). Reductions in g_S and P_N in CD and FD plants indicated that under mild drought conditions P_N was reduced, at least partially, due to stomatal closure.

Our results did not support the hypothesis that prior flooding of baldcypress plants may lead to greater susceptibility to drought as compared to well-watered seedlings that were exposed to the same degree of drought. No significant differences in P_N and g_S between CD and FD plants were found (Fig. 3*A,B*), thus, prior flooding of baldcypress seedlings apparently did not affect gas exchange responses to drought. However, gas exchange rates in both CD and FD plants were reduced substantially when predawn leaf water potentials reached –0.5 MPa or less (more negative). Decreases in gas exchange also coincided with partial wilting that occurred at predawn leaf water potentials of less than –0.5 MPa. These findings suggest that baldcypress seedlings were susceptible to drought regardless of prior exposure to soil flooding.

Midday leaf water potentials decreased significantly in CD as compared to C plants during mild drought. Leaf water potential of –2.1 MPa observed in CD plants and –1.7 MPa in FD plants may explain reduced root growth and inhibition of P_N in both treatments since as plant water content decreases, vital functions such as P_N are suppressed (Larcher 1995). Although observations of reduced g_S have been made in response to drought without apparent leaf water deficits (Liu and Dickmann 1992), reductions in gas exchange rates in this study can be attributed to leaf water deficits under drought as indicated by low (more negative) leaf water potentials as compared to controls.

Recovery from drought: Upon resumption of regular watering of the FD and CD seedlings during phase III, significant increases in gas exchange rates were observed. This response to removal of mild water stress is typical of many species (Bradford and Hsiao 1982). Although gas exchange rates in baldcypress were adversely affected by drought, lowering of the soil water potential (–0.5 MPa or more negative) was not detrimental to survival of CD and FD plants as survival was 100 % for both treatments.

Biomass allocation patterns at the conclusion of the study indicated significant reductions in root mass for CD and FD plants as compared to control plants (Table 1). Water stress can decrease growth directly through its effect on turgor, or indirectly by limiting carbon gain. Water availability can also alter the allocation of saccharides between the root and shoot (Teskey and Hinckley 1986). Deep and extensive root systems have been identified as advantageous for successful plant growth on dry sites (Kozlowski and Pallardy 1979a,b, Dougherty and Hinckley 1981). Lowered root/shoot ratios compared to controls, as observed in CD and FD plants during this study, may leave seedlings susceptible to extended drought. However, root growth was comparable between FD and CD plants, therefore, FD plants were not left more susceptible to drought as compared to CD plants.

In conclusion, within its natural range, baldcypress persists across a range of soil moisture regimes found in periodically flooded wetlands such as bottomland forests of the southern United States. In addition to enduring flood, seedlings must also endure periodic mild drought. Continuation and/or rapid recovery of gas exchange under conditions of flooding or mild drought reflect an important attribute allowing for continued photosynthetic carbon fixation as was demonstrated in this study. We noted, however, that prior flooding of seedlings did not affect their subsequent responses to drought. Thus, our results did not support the hypothesis that flooding of baldcypress seedlings may lead to more drought-susceptible plants as compared to non-flooded seedlings. However, seedlings were able to survive moderately reduced soil conditions followed by a mild drought.

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