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 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 μmol 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. 2C). 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. 2A).

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