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Effect of Flooding on Elemental Uptake and Biomass Allocation in Seedlings of Three Bottomland Tree Species

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ABSTRACT

Seedlings of baldcypress *(Taxodium distichum)*, nuttall *oak (Quercus nuttallii)*, and cherrybark oak *(Quercus falcata* var. *pagodaefolia)* were subjected to flooding for 70 days in a greenhouse. The treatment imposed was reducing soil conditions characterized by low soil redox potential (Eh), and replicated three times. Plant elemental uptake, allocation and growth in response to the treatment were evaluated. For baldcypress, element uptake was not significantly influenced by low soil Eh conditions except for significant iron (Fe) decrease in the roots. In contrast, both oak species showed significant decreases in element uptake under low Eh treatment. In nuttall oak seedlings, uptake of aluminum (Al), boron (B), potassium (K), magnesium (Mg), phosphorus (P), and zinc (Zn) was significantly lower in the shoot and root of flooded plants as compared to controls. In flooded plants, Fe uptake was

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significantly lower in roots while manganese (Mn) was significantly higher in shoots compared to controls. In cherrybark oak, uptake of many elements was lower under low Eh treatments as compared to controls. However, Fe uptake was significantly greater in flooded roots compared to controls. Little evidence of changes in biomass allocation patterns in response to low soil Eh was found in baldcypress but total biomass decreased significantly under low soil Eh conditions. In oaks, total biomass decreased significantly under low soil Eh conditions. The present findings demonstrated that plant elemental uptake and biomass allocation are affected by low soil Eh conditions in woody species with a wide range of flood-sensitivity ranging from highly sensitive such as cherrybark oak to tolerant species such as baldcypress.

INTRODUCTION

Substantial forest within the Mississippi River floodplain is subjected to alterations in hydrology, in many cases due to human activities, leading to prolonged soil flooding. Such conditions promote soil reduction (low soil redox potential, Eh) imposing significant stress on woody plants particularly seedlings. Seedlings and saplings are more vulnerable to low soil Eh conditions during early stages of establishment than mature trees.

Tree nutrition under low soil Eh conditions is affected by many factors, including the soil physicochemical characteristics, soil nutrient pools, plant developmental and physiological status and flood-tolerance capabilities (Kozlowski, 1984). Inhibition of nutrient uptake and transport in flood-sensitive species is caused by root disfunction and/or death of root system in flooded soils. Oxygen stress may also change the permeability of cell membranes in the roots causing nutrient leaching (Rosen and Carlson, 1984). For many species, flooding results in low tissue concentrations of nutrients such as nitrogen(N), P, and K (Letey et al., 1965; Trought and Drew, 1980). In flooded soils, Fe and Mn availability increases due to the reduction processes (Ponnamperuma, 1972). Increased tissue Fe concentrations (Lal and Taylor, 1970; Slowik et al., 1979) and Mn concentrations (Lal and Taylor, 1970) during flooding have been reported in some crop species.

Understanding nutritional responses of seedlings of bottomland forest species to soil reduction following flooding is important in formulating management plans for proper utilization and conservation of these ecosystems. However, to date, little literature exists about this topic. We examined the influence of low soil Eh conditions on elemental uptake and growth of three bottomland forest species that exhibit a range of flood-sensitivity, e.g., Baldcypress *(Taxodium distichum* L.), Nuttall oak (*Quercus nuttallii* Palmer), and Cherrybark oak (*Q. falcata* var. *pagodaefolia* Ell.). Baldcypress is a flood-tolerant species that occupies sites with a wide range of flooding regimes. Nuttall oak is a moderately flood-tolerant species typically found in areas flooded IO-21% of the growing season. The seedlings of this species can survive two months of inundation (Hook, 1984). In contrast, Cherrybark oak is a flood-sensitive species that suffers high mortality, even among mature trees, if exposed to partial inundation (Hook, 1984). The differences in the reported responses suggest potential differences in physiological and nutritional responses among these species. Although the general aspects of nutrient uptake of woody species under soil flooding has been investigated (Pezeshki, 1994; Kozlowski, 1997 and the references cited therein), nutrient uptake of seedlings of bottomland tree species under reducing soil conditions need further studies because much of the previous work did not quantify the intensity of soil reduction (Eh conditions). We hypothesized that under strongly reducing conditions (low soil Eh) element uptake decreases regardless of the species' flood-sensitivity ranking. The objective of the present study, therefore, was to evaluate and compare elemental uptake and growth responses of study species under low soil Eh conditions.

MATERIALS AND METHODS

Seedlings were obtained from the Tennessee State Forest Nursery, Pinson, TN and were transplanted into containers (30 cm depth, 22 cm width). The soil was collected from the A_p horizon of a Sharkey Clay soil obtained from a bottomland forest in west Tennessee. The plants (one plant in each pot) were grown in a ventilated greenhouse, watered daily and fertilized with a commercial water soluble fertilizer (23N-19P-17K) once per week. Pots were modified to allow drainage through tubes attached to the bottom of each container; any leachate was collected in designated traps and returned to the container daily.

After the initial 10 days acclimation period, the seedlings, with mean heights of 52.2, 54.4, and 27.8 cm, for baldcypress, nuttall oak, and cherrybark oak, respectively, were subjected to two soil treatments: (1) control, well-watered but not flooded and (2) permanently flooded to two cm above the soil surface.

Treatment effect on soil conditions was quantified by measurements of soil redox potential (Eh) using redox electrodes installed at 15 cm below the soil surface. Twelve seedlings per species were randomly assigned to each treatment. The experiment followed a completely randomized block design using three replications each containing 4 plants per species-treatment combination.

Biomass dry weight and partitioning were determined at the conclusion of the experiment (day 70) by harvesting the plants and separating each sample plant into leaf, stem, and root components. Plant components were then dried at 70°C to a constant weight and dry weights were recorded.

At the conclusion of the study, tissue samples from foliage and roots were collected from the study plants for nutrient determination. Samples were dried in an oven at 70°C for 72 hours, and ground. Plant tissue samples (0.5 g) were acid digested and elemental analysis [Al, B, calcium (Ca), cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu), Fe, K, Mn, Mg, sodium (Na), nickel (Ni), P, lead (Pb), sulfur(S), silicon (Si), and Zn] was conducted on the samples utilizing an inductively coupled argon plasma emission spectrophotometer (ICAP).

The general linear models (GLM) and T-test procedures of the Statistical Analysis System (SAS, 1990) were used to test for differences in biomass and nutrient means for each species between treatments.

RESULTS

The mean soil Eh values were +508±86 and +6±115 mV for control and flooded pots, respectively. Soil Eh measurements indicated that aerated soil conditions prevailed in control treatment while reducing soil conditions characterized by low soil Eh were dominant in flooded treatment. The flooded soil conditions in this study represent conditions where oxygen (0), nitrate, Mn, and Fe are reduced. These soil Eh levels reflect a mid-range in soil Eh values encountered in flooded soils representing a poorly drained, moderately reducing soil conditions. Survival rates in baldcypress and nuttall oak were 100% under both control and low soil Eh treatments. In contrast, in cherrybark survival was 100% and 16% under control and low soil Eh condition, respectively.

In baldcypress, leaf biomass did not change significantly in response to low soil Eh treatment (Figure 1A). Stem and root biomass were lower under low soil Eh conditions, however, statistical analysis showed that the difference was not significant at the 0.05 level (Figure 1 A), but total biomass decreased significantly ($p<0.01$) under low soil Eh conditions. Biomass data indicated little evidence of any detectable, consistent changes in biomass allocation patterns in baldcypress in response to low soil Eh. In contrast, nuttall oak and cherrybark oak showed significant reductions in leaf, stem, and root biomass under low soil Eh condition (Figure 1B, 1C).

Elemental uptake data indicated that in baldcypress, uptake was not significantly influenced by low soil Eh conditions except for significantly lower uptake of Cd and Fe in roots and Ni in shoot of plants grown under low soil Eh compared to controls (Table 1 and Figure 2). In contrast, both oak species showed significant changes in elemental uptake rates in response to the low Eh treatment as evidenced by shoot and root tissue analysis (Table 1). For instance, in nuttall oak seedlings, uptake of Al, B, Ca, Cd, K, Mg, S, Si, and Zn was significantly lower in shoot of flooded plants as compared to controls (Table 1). Similarly, root uptake of Al, B, Cd, Co, K, Mg, Na, Pb, and Zn was significantly lower in roots of flooded plants as compared to controls (Table 1). Iron uptake was significantly lower in roots (Figure 2) while Mn was significantly lower in shoots (Figure 3) of plants subjected to low soil Eh treatment as compared to controls. Phosphorus uptake was significantly lower in roots and shoots of nuttall oak under low soil Eh as compared to controls (Figure 4). In chenybark oak uptake of many elements was adversely affected by

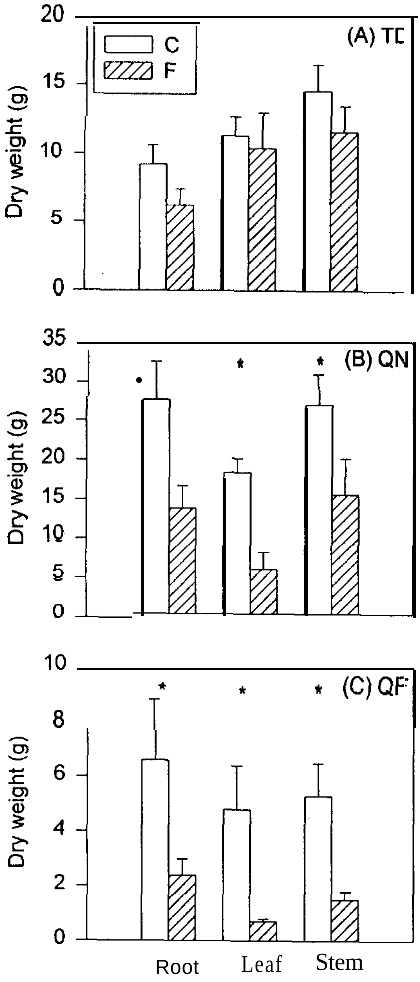

FIGURE 1. Dry weights of biomass components in (A) ***Taxodium distichum*** (TD), (B) ***Quercus nuttallii*** (QN), and ***(C) Q. falcata*** (QF) var. ***pagodaefolia*** seedlings under aerated (C) and low soil Eh conditions (F). For each species, * denotes significant differences for biomass between treatments at the $p<0.05$ level.

TABLE 1. Elemental uptake and allocation to shoot and root ($\mu g\ day^{-1}$) for *Taxodium distichum, Quercus nuttallii,* and Q. *falcata var. pagodaefolia* grown under aerated control (C) and low soil Eh (F) conditions. Significant effects are denoted as: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

		Baldcypress *T. distichum*		**Nuttall** oak *Q. nuttallii*		**Cherrybark** oak *Q. falcata*	
Nutrient		C	F	C	F	C	F
Al	Shoot	14.4	8.3	19.1	**8.9***	41.4	**0.7***
	Root	48.7	6.3	403.5	**2.4***	12.5	8.8
B	Shoot	12.8	10.3	19.7	**5.5*****	4.4	**0.4***
	Root	3.6	2.2	9.5	**3.6***	1.3	0.8
Ca	Shoot	1843.4	1564.3	1738.6	**602.0*****	635.3	**49.9***
	Root	576.4	494.2	1372.5	771.7	399.4	336.1
Cd	Shoot	0.03	0.001	0.3	0.12 **	0.13	0.01
	Root	0.23	**0.06***	0.44	0.08”	0.03	0.06
co	Shoot	0.16	0.11	0.1	0.08	0.04	0.01
	Root	0.29	0.47	0.57	0.17 **	0.07	0.08
Cr	Shoot	0.12	0.06	0.2	0.17	0.10	0.01
	Root	0.17	0.07	0.63	0.07	0.04	N/A
CU	Shoot	0.86	0.73	1.3	0.7	0.44	0.06
	Root	1.1	0.81	2.9	0.97	0.37	0.34
K	Shoot	2853.7	2558.5	2104.8	**975.1****	637.9	**77.2***
	Root	1269.2	1294.9	2252.2	**703.7***	459.7	242.0
Mg	Shoot	537.7	452.5	675.3	**326.8***	267.9	23.5’
	Root	228.4	201.4	405.3	**146.3***	84.4	40.8
Na	Shoot	27.1	31.2	29.8	35.7’	12.3	4.2
	Root	221.9	182.0	290	**98.4***	53.7	26.8
Ni	Shoot	0.61	**0.26***	19.6	0.5	0.36	0.16
	Root	3.2	0.64	2.3	**5.3****	1.57	6.24
Pb	Shoot	0.2	0.2	0.4	0.12	0.16	0.01
	Root	0.43	0.4	1.44	**0.4***	0.28	0.06’
S	Shoot	440.7	388.6	377.1	**188.1***	128.3	**20.1***
	Root	192.0	134.5	332.6	210.7	87.0	58.9
Si	Shoot	140.2	100.8	156.1	86.9’	31.6	**5.8***
	Root	149.0	123.5	270.8	180.4	53.1	**33.5**
Zn	Shoot	11.5	13.6	16.4	**5.5****	8.2	1.5
	Root	0.66	0.66	1.1	**0.33***	0.1	0.1

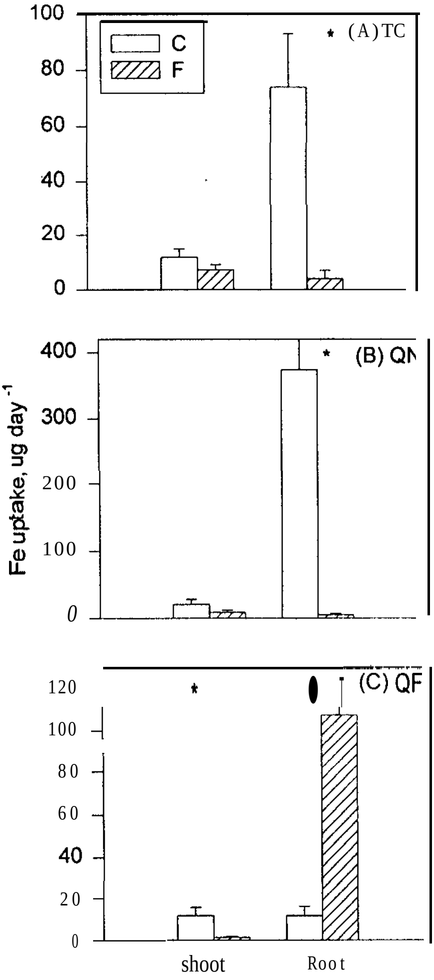

FIGURE 2. Shoot and root iron uptake for (A) *Taxodium distichum* (TD), (B) *Quercus nuttallii* (QN), and (C) *Q. falcata* (QF) var. *pagodaefolia* seedlings under aerated (Control) and low soil Eh conditions. For each species, * denotes significant differences for total biomass between treatments at the $p<0.05$ level.

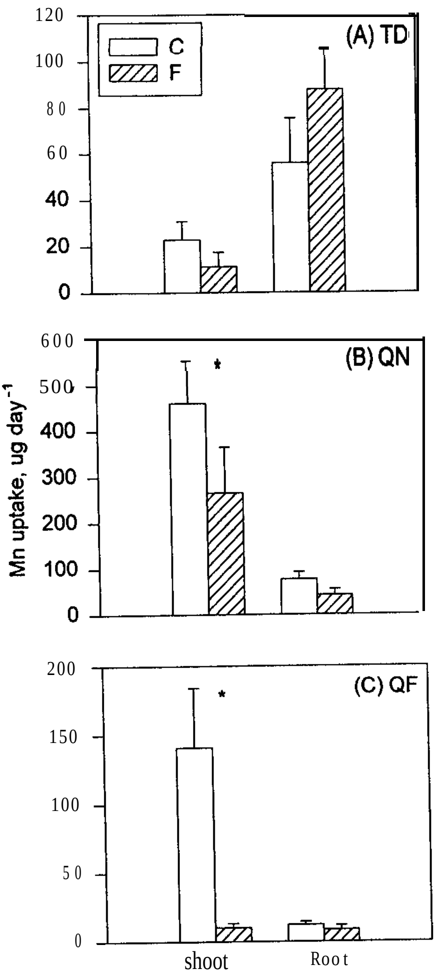

FIGURE *3.* Shoot and root manganese uptake for (A) ***Taxodium*** *distichum* (TD), (B) ***Quercus nuttallii*** (QN), and *(C)* ***Q. falcata*** (QF) var. ***pagodaefolia*** seedlings under aerated (Control) and low soil Eh conditions. For each species, * denotes significant differences for total biomass between treatments at the $p<0.05$ level.

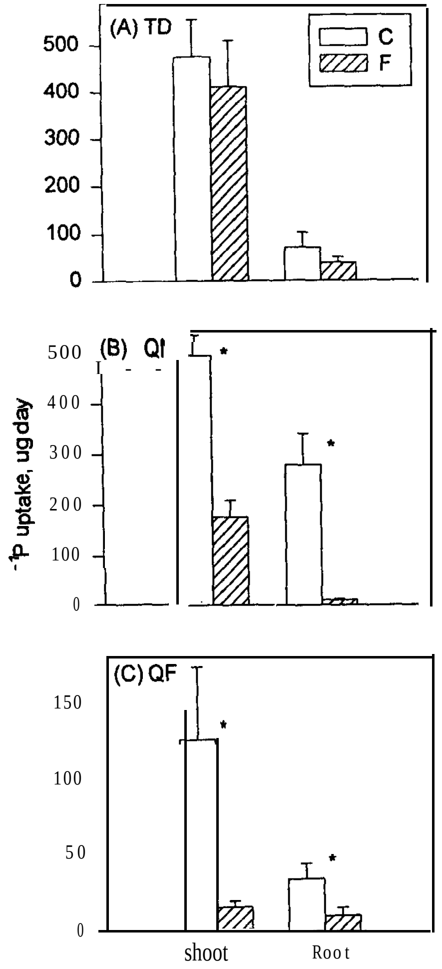

FIGURE 4. Shoot and root phosphorus uptake for (A) ***Taxodium*** *distichum* (TD), (B) *Quercus* ***nuttallii*** *(QN),* and (C) ***Q. falcata*** (QF) *var. pagodaefolia* seedlings under aerated (Control) and low soil Eh conditions. For each species,* denotes significant differences for total biomass between treatments at the $p<0.05$ level.

the low Eh treatments including some nutrients (Table 1). For instance, Mn uptake rates were significantly lower in shoots while P was significantly lower in shoots and roots of flooded plants as compared to controls (Figures 3 and 4). In contrast, while Fe uptake was significantly decreased for shoot in plants subjected to flooding, it was significantly greater in flooded roots compared to controls (Figure 2).

DISCUSSION

In the present study, the average soil Eh for the flooded conditions was below the level of +350 mV that signifies the onset of oxygen disappearance from the soil system (DeLaune et al., 1990). Elemental uptake including many nutrients remained largely unaffected in baldcypress, the most flood-tolerant species among our study species (Table 1 and Figures 2-4). However, root Fe was significantly lower under flooded conditions. This finding was attributed to baldcypress ability for root oxygenation thus, Fe oxidation in the rhizosphere (Pezeshki, 1994). In contrast, uptake of many elements including nutrients was profoundly affected by low soil Eh conditions in oaks. Generally, plant nutrition under flooded and low soil Eh conditions is affected by many factors including plant developmental and physiological status and flood-tolerance characteristics (Kozlowski, 1984; Kozlowski, 1997). Inhibition of nutrient uptake and transport in flood-sensitive species due to dysfunction and/or death of root system has been reported in the literature. Nutrient uptake for most part is an energy dependent process thus is impacted by oxygen stress (Kozlowski, 1997).

For numerous species, flooding results in low foliage concentrations of many nutrients including P and K (Letey et al., 1965; Trought and Drew, 1980). Phosphorus uptake is influenced by soil reduction processes. Plant tissue P content decreases in response to low soil Eh conditions during long-term flooding episodes presumably due to the suppressed uptake capability of roots (Kozlowski and Pallardy, 1984). Decreased shoot P content has been reported for seedlings of *Pinus clausa*, ***P. serotina***, and ***P. taeda*** (Topa and McLeod, 1986) and *Carya illinoensis* (Smith et al., 1989) subjected to low rhizosphere oxygen conditions. Literature, however, is not consistent. For instance, seedlings of *P.* ***taeda***, submitted to flooding had higher root P concentrations than control plants (McKee et al., 1984).

In bottomland tree species adapted to wetland conditions ion uptake may continue partly because of the internal O_2 supply system (John et al., 1974). For instance, seedlings of *T.* ***distichum*** and ***Nyssa aquatica*** grown under flooded (but aerated) conditions had higher tissue concentrations of P, Ca, K, and Mg compared to plants under non-flooded conditions (Dickson et al., 1972). Flood-tolerant species develop adventitious roots and internal aerenchyma system allowing oxygen transport from aerial tissues to the roots and root-soil interface (Armstrong, 1968; Coutts and Armstrong, 1976). Flood-induced development of aerenchyma tissue in baldcypress and to a lesser extent in nuttall oak has been reported previously (Pezeshki, 1991). In the present study, adventitious roots and hypertrophied lenticels were present on the submerged portions of stems in baldcypress. In contrast, little morphological change was observed in cherrybark oak in response to flooding. The observed morphological responses to low soil Eh conditions in baldcypress may partially explain the apparent continuation of nutrient uptake under low soil Eh conditions. Flood-tolerant species may also maintain selective nutrient uptake capability; Fe uptake in flooded baldcypress remained similar to controls in the shoot while it was significantly lower in the root (Figure 2). Tissue Fe content *in N. aquatica* and *N. sylvatica* var. *biflora* (swamp tupelo) was significantly greater in root under flooded conditions, but not in foliage indicating internal mechanisms for Fe immobilization (Hook et al., 1983; McKevlin et al., 1995). Decreased K in foliage, increased P in roots and stem and K in roots was reported for *N. aquatica* subjected to flooding (McKevlin et al., 1995).

In flood-sensitive woody species, nutrient uptake and accumulation at toxic levels may occur under reduced soil conditions due to higher availability of certain nutrients and root dysfunction (Hook et al., 1983). For instance, during prolonged flooding, ferric and manganic forms are reduced to ferrous and manganous forms that are soluble (Ponnamperuma, 1972). Thus tissue Mn and Fe concentrations may be greater than found in plants under aerated conditions (Tanaka and Yoshida, 1970). Plant tissue Fe, Mn, and S content may reach toxic levels under low soil Eh conditions (Good and Patrick, 1987; McKevlin et al., 1987; Gries et al., 1990). In the present study, Fe uptake was significantly greater in flooded roots of cherrybark oak seedlings as compared to controls indicating the potential loss of selective nutrient uptake capability (Figure 2). In flooded *Pinus sylvestris*, P, Ca, Mn, Na, and S concentrations were increased (Heiskanen, 1995). However, Fe was lower in baldcypress and nuttall oak roots while shoot Fe remained unchanged.

In the present study, all study species showed decreases in total biomass in response to low soil En treatment. Shanklin and Kozlowski (1985) found decreased biomass accumulation in flooded baldcypress seedlings after 14 weeks of flooding above the soil surface. Similarly, flooded baldcypress seedlings had reduced root and shoot biomass after 12 weeks (McLeod et al., 1986). Flynn (1986) reported that baldcypress seedlings under non-flooded condition had significantly greater biomass than seedlings flooded to a depth of 15-20 cm for 18 weeks. In both nuttall oak and cherrybark oak, various biomass components were also lower under flooded treatment than control plants, showing additional susceptibility to flooding. Oaks with comparable flood-sensitivity ranking have shown similar reductions in biomass due to flooding in laboratory studies (Pezeshki et al., 1996).

The present findings support the hypothesis that plant elemental uptake is affected by soil flooding (and the resultant low soil Eh conditions); the extents of such effects may depend on many factors including the species' flood-response characteristics. Management plans concerning utilization, restoration, or conservation of bottomland forested ecosystems should consider the species flood-response profile as well as the timing and duration of flooding, soil nutrient pool, and soil reduction characteristics at a specific site prior to the initiation of such efforts.

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