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EFFECTS OF FLOODING ON ROOT AND SHOOT PRODUCTION OF BALD CYPRESS IN LARGE EXPERIMENTAL ENCLOSURES[1]

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Abstract. Effects of hydroperiod on the root production of bald cypress (*Taxodium distichum*) saplings were determined in large (8.0 m^2 × 1.5 m deep) watertight enclosures over three growing seasons. Our objectives were to determine the effect of continuous and periodic flooding regimes on biomass production, carbon allocation to roots and shoots, and root-system morphology. The effect of the flooding treatments on plant biomass was different for 1-yr-old seedlings and 3-yr-old saplings. After one growing season, root and shoot biomass was highest in the periodically flooded (PF) treatment. After three growing seasons there were no significant differences in total biomass but there were differences in root-to-shoot ratios. Improved growth in the continuously flooded (CF) treatment began in the second growing season and coincided with morphological adaptations to flooding. Such adaptations include the production of water roots, development of intercellular air spaces, and distinctly different root-system morphologies.

Periodically flooded cypress allocated more carbon to roots than did continuously flooded cypress and developed deeper root systems. A relatively deep rooting zone may have provided the PF saplings access to water and dissolved nutrients within the water table (50–60 cm deep during summer). Continuously flooded plants had low root-to-shoot ratios and shallow root systems. A relatively shallow rooting zone with ample water and nutrients allowed CF cypress to allocate relatively more biomass to leaves.

After 3 yr, total productivity in the two treatments was not significantly different, yet belowground production was greater in periodically flooded saplings ($P = .05$) and there was a tendency for higher aboveground production in continuously flooded saplings ($P = .14$). Without the belowground production estimates we might have concluded that CF plants were more productive than PF plants. Most plants can respond to changing resource availabilities by shifting the allocation of carbohydrates to roots or shoots. Because resource availability in freshwater forested wetland ecosystems can be highly variable, studies of production should include estimates of root production.

Key words: adventitious roots; aerenchyma; carbon allocation; flooding; productivity; rhizotron; rooting depth; root production; roots; root : shoot; root system morphology; Taxodium distichum.

INTRODUCTION

The magnitude, duration, and timing of flood events are important factors regulating primary productivity in wetland forests. The effects of flooding on primary productivity have been investigated in many wetland forest ecosystems. Few such studies have considered root production, despite evidence that it comprises a significant portion of primary production in forest ecosystems (Harris et al. 1980, Megonigal and Day 1988, Raich and Nadelhoffer 1989). Carbon is allocated to roots at the expense of leaves, stems, reproductive tissues, and secondary compounds (Mooney 1972, Waring and Schlesinger 1985, Tilman 1988). Factors that promote the allocation of energy and nutrient resources to roots necessarily reduce potential aboveground production. A thorough understanding of the factors affecting the productivity of wetland forests requires knowledge of their effect on carbon allocation to roots (Brinson et al. 1981, Vogt et al. 1986).

It is difficult to assess root production without severely disturbing the soil (Bohm 1979). Root production studies in wetland forests are particularly problematic because it is difficult to manipulate the water table and flooding depth. Greenhouse or growth-chamber experiments offer control over flooding depth, but usually they are of short duration and suffer from a limited soil volume.

In greenhouse studies, most tree species respond to continuous flooding with reduced rates of growth relative to periodic flooding treatments (Kozlowski 1984); however, extremely flood-tolerant tree species such as bald cypress (*Taxodium distichum* [L.] Richard) occasionally have shown improved growth under contin-

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TABLE 1. Biomass of flooded bald cypress seedlings relative to the driest treatment in the study. Flooding increased (+), decreased (−), or had no effect (0) on biomass. Flooding treatments are relative to the soil surface. All differences are significant at $P \leq .05$.

		Effect relative to the driest treatment			
Driest treatment	Treatment for comparison	Shoot	Root	Total	Citation
Field capacity	1 cm above surface, O_2	+	0		Dickson and Broyer 1972
	1 cm above surface, no O_2	+	−		Dickson and Broyer 1972
10 cm below surface	At the surface			0	McLeod and Sherrod 1981
	5 cm below surface			0	McLeod and Sherrod 1981
Drained, watered	2 cm above surface	−	−	−	Shanklin and Kozlowski 1985
6 cm below surface	At the surface	0	−	−	McLeod et al. 1986
	6 cm above surface	−	−	−	McLeod et al. 1986
6 cm below surface	At the surface	0	−		Donovan et al. 1988
	6 cm above surface	0	−		Donovan et al. 1988
Drained, watered	6 cm above surface	−	−	−	Donovan et al. 1989
	12 cm above surface	−	−	−	Donovan et al. 1989

uous flooding (Table 1). Field studies have shown that bald cypress production decreases on extremely wet or extremely dry sites, but most do not consider belowground production. Thus, it is reasonable to ask: Is the net primary production (shoots + roots) of extreme hydrophytes such as bald cypress comparable on continuously flooded and periodically flooded sites?

The objectives of our study were to determine experimentally the effects of periodic and continuous flooding on (1) biomass allocation to roots and shoots, (2) vertical root distribution, and (3) root system structure in young bald cypress trees over a 3-yr period.

MATERIALS AND METHODS

Rhizotron cell design

Two wetland rhizotron cells (enclosures for root-growth experiments) were constructed during the winter and spring of 1986 in the Rhizotron Facility at the University of Georgia's Savannah River Ecology Laboratory (Day et al. 1989). The two cells were directly adjacent, and there was no differential shading or protection from wind. The cells were in full sunlight. Each cell was 2.83 × 2.83 × 1.5 m deep, impermeable to water, and open to the atmosphere. A pipe in the bottom of each cell allowed soil water to drain at a controlled rate. The cells were leached with water and checked for leaks before they were filled with soil. The reconstructed soil profiles consisted of 100 cm of a sapric Histosol underlain by 10 cm of sand and 10 cm of gravel. The soil was from a former cypress wetland near Jacksonboro, South Carolina. Two oxygen chambers (Carter et al. 1984) and three fused platinum–copper redox probes (Faulkner et al. 1989) were installed in the soil profile of each cell at 20 cm depth intervals. This interval was considered adequate to describe the soil profile. Rainfall was measured adjacent to the cells.

Because hydroperiod is the most important factor affecting wetland structure and function, we gave special attention to the hydraulic design of the experiment and to the hydroperiod treatments. One cell was continuously flooded and one was periodically flooded in a manner typical of many southeastern forested wetlands (Fig. 1). Natural seepage and turnover of soil water was simulated by allowing ≈20 L/d to drain from each cell. Based on output and storage volumes (Table 2), the soil water pool turned over at roughly 9-mo intervals. Creek water was pumped from a polyethylene storage tank and sprinkled onto the soil surface to replace water draining from the bottom of the cells. A system of wells, floats, solenoid switches, and pumps prevented the water table from falling below a prescribed depth. The prescribed depth was +20 cm (above the soil surface) in the CF cell and variable in the PF cell according to the following schedule: −20 cm from March to May and October to December, −50 cm from June to September, and +20 cm from January to February. However, the water table often was higher than the scheduled level because of rainfall events (Fig. 1). The hydroperiod treatments were initiated on 23 May 1986 and maintained until 20 October 1988.

Experimental design

Bald cypress seeds were germinated in January 1986. The seedlings were grown in a greenhouse and conditioned to above-surface flooding for 1 mo before they were transplanted to the rhizotron cells on 9 May 1986. Twenty-five seedlings were randomly assigned to each cell using a random numbers table. Another 25 plants were used for initial biomass estimates. There was no significant difference in height (mean ± 1 SD = 34 ± 5 cm) among the three groups (ANOVA, $P = .23$). To minimize competitive effects, the seedlings were regularly spaced at 51-cm intervals in a matrix of 5 columns and 5 rows; seedlings on outside rows were 51 cm from the wall.

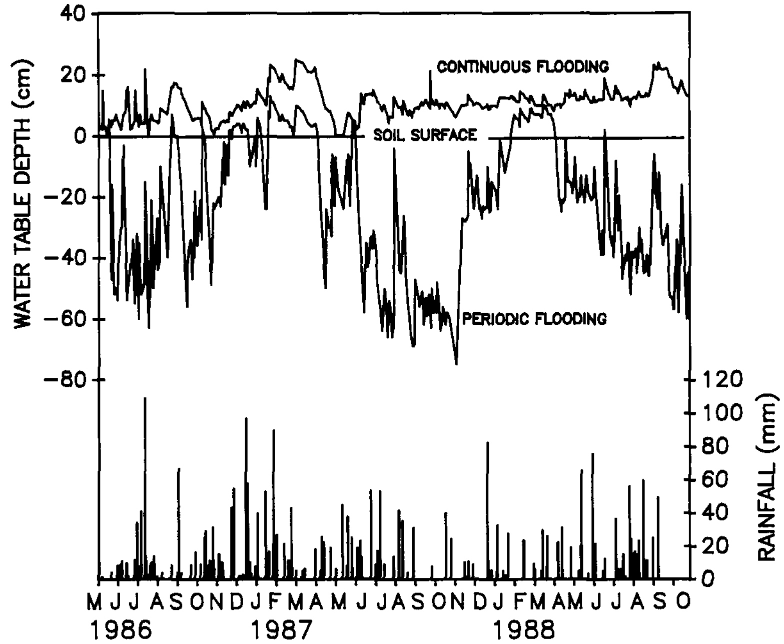

FIG. 1. Water table depth and rainfall volume for the 30-mo study period.

Soil oxygen content and redox potential (Eh) were determined at 20 cm depth intervals both prior to the initiation of hydroperiod treatments and at 2-wk intervals after treatment initiation. A sample of plants ($n = 8$ in 1986 and 1988; $n = 9$ in 1987) was harvested each October, at the end of the growing season but prior to leaf abscission. Plants were harvested in a pattern designed to maximize inter-plant distances among the remaining individuals. Shoots were separated into leaves, branches, and stems. Roots and soil were removed from a 30 × 30 cm plot, centered on the bole of the plant, to a soil depth of 30 cm. Excavation was by hand with a small trowel. The holes were back-filled with fresh soil from the original source. Samples were frozen and stored until they could be processed; freezing had no apparent effect on the color or tensile strength of the roots. After thawing, the roots were washed, separated from organic debris, air-dried, and separated into size classes. Soil samples were washed gently with tap water through a standard no. 10 (2 mm-mesh) sieve. Care was taken during the washing process to recover (with tweezers) most of the fine roots; however, an unknown fraction of the 1–2 mm root size class was undoubtedly lost. Dead roots were separated from a subset of the samples taken in the third year. Dead roots occurred in the fine size class

TABLE 2. Total inputs and outputs of water and selected nutrients for the two rhizotron cells (enclosures for root-growth experiments) during the 30-mo study. CF = continuously flooded, PF = periodically flooded.

Component of soil solution†	Input		Output		Storage*	
	CF	PF	CF	PF	CF	PF
Rain water (m^3)	23.8	23.8				
Creek water (m^3)	49.9	47.4				
Total water (m^3)	73.7	71.2	18.6	18.8	5.9	5.8
Total N (g)	0.517	0.505	12.8	12.7		
NH_4-N (g)	0.220	0.161	5.48	5.57	59.2	51.9
PO_4-P (g)	0.134	0.134	2.79	2.77	18.9	8.3
Ca (g)	1.33	1.32	6.57	6.71	36.1	27.2
Mg (g)	0.853	0.820	10.0	10.5	57.5	54.0
Fe (g)	0.197	0.204	11.6	11.0	15.7	8.8
Mn (g)	0.019	0.017	0.091	0.086	0.210	0.160

* Storage is the product of average nutrient concentration and total soil water mass as determined from saturated bulk density cores.

† Total N was determined by Kjeldahl digestion. Concentrations of the other nutrients were determined after filtration (0.45-μm mesh filter) by inductively coupled plasma emission spectroscopy (Ca, Mg, Fe, and Mn) or colorimetric absorbance (NH_4-N and PO_4-P). See Day et al. (1989) for details on nutrient analyses.

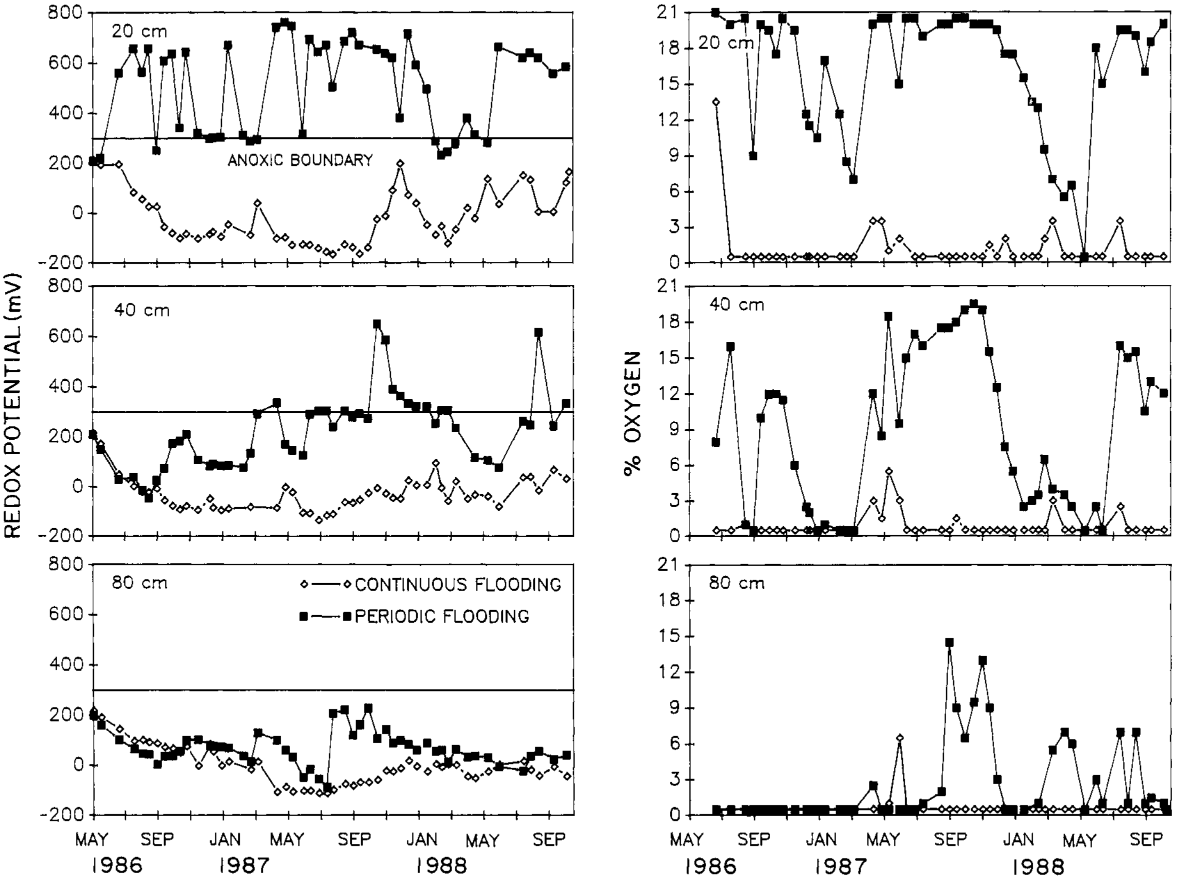

FIG. 2. Redox potential and oxygen content at three depths. Redox potentials below 200–400 mV (——) generally reflect anaerobic conditions (Bohn 1971). ■ = periodic flooding; ◇ = continuous flooding.

(< 1 mm) only and accounted for an insignificant fraction of the total fine root mass. All samples were oven-dried at 65°C and cooled in a desiccator before weighing.

In October 1988 the cells were completely excavated to determine the total root biomass of each plant. The soils were removed in three depth increments (0–30 cm, 30–60 cm, and 60–100 cm). Roots were not severed until they were entirely exposed so that all root biomass estimates could be associated with individual plants. The roots of plants removed in 1987 were identified by their location, color, and flexibility. They were collected as a single batch sample. These roots were included in the production estimates but not the biomass estimates. Fine root biomass in the surface 30 cm was estimated from 20 random soil cores (9.6 cm diameter). Random sampling coordinates were chosen with a pseudo-random number generator.

Statistical analyses

A limited number of treatment means were compared with *t* tests (SAS 1985). Analysis of covariance (ANCOVA) and Type I sums of squares were used to test for homogeneity of slopes and differences in the *Y* intercept. Differences in rates of production and relative growth are based on the time × treatment interaction term in an Analysis of Variance (ANOVA) as described by Poorter and Lewis (1986).

RESULTS

Environmental conditions

The water level was consistently 10–20 cm above the soil surface in the continuously flooded (CF) treatment. The water table varied in the periodically flooded (PF) treatment according to the schedule of maximum water-table depth and rain events (Fig. 1). Redox potential in the CF treatment fell to an average of −18 mV at 20 cm depth for the entire study. The PF treatment had an average redox potential of 511 mV at 20 cm (Fig. 2). Redox potentials lower than 200–400 mV generally reflect aerobic conditions (Bohn 1971). Oxygen concentrations at 20 cm averaged 1% in the CF cell and 16% in the PF cell. Thus, the CF treatment was nearly always anaerobic and reduced near the surface, while the PF treatment was nearly always aerobic (or hypoxic) and oxidized.

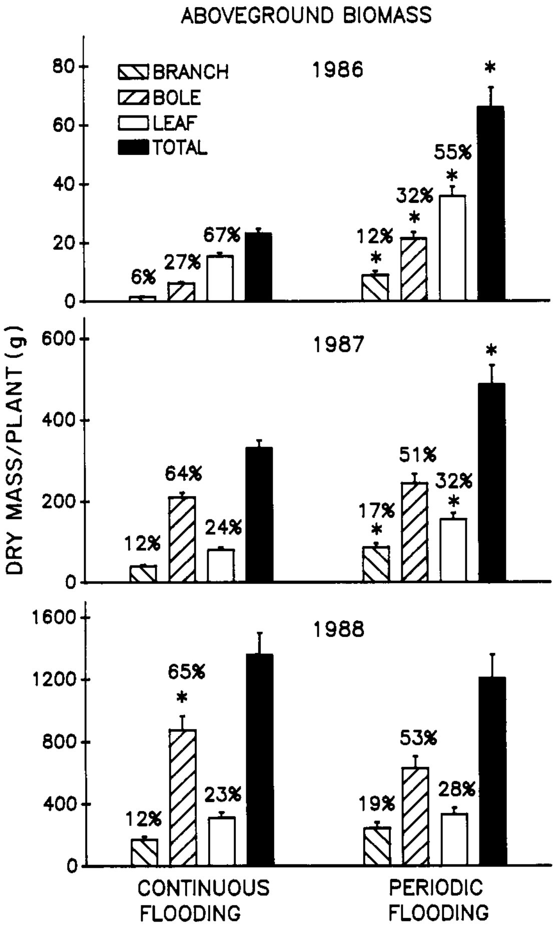

FIG. 3. Aboveground biomass (means and 1 SE) of continuously flooded and periodically flooded bald cypress seedlings for three growing seasons. Percentages are the component biomass relative to total biomass within a treatment. Significant differences ($P \leq .05$) in component biomass between flooding treatments are marked with an asterisk (*) placed above the bar with the higher mean.

Over the course of the study, the CF cell received ≈ 2.5 m^3 more creek water than the PF cell; water output from the CF cell was ≈ 0.2 m^3 less (Table 2). Total inputs and outputs of nutrients were similar. The generally greater pool of soil solution nutrients in the CF cell suggests greater leaching or mineralization in the continuously flooded soil.

Shoot biomass

Shoot growth of bald cypress was very rapid in both cells. Three-yr-old saplings were 2 m tall and up to 8.4 cm in diameter (measured at 20 cm above the soil surface). After one growing season the shoot biomass of PF seedlings was approximately three times that of CF seedlings ($P \leq .0001$). However, the difference in aboveground biomass narrowed during subsequent growing seasons (Fig. 3). At the end of the second growing season, average shoot biomass of the PF cypress was 0.5 times greater than the CF cypress ($P = .008$). At the end of the third growing season there was no significant difference in shoot biomass between treatments.

Biomass allocation to leaves, branches, and boles differed between years and treatments. During the first growing season, continuously flooded plants allocated more shoot biomass to leaves than periodically flooded plants (67% vs. 55%, $P \leq .0001$, Fig. 3). Periodically flooded plants allocated more to wood ($P \leq .0007$). This pattern did not persist in subsequent growing seasons, when CF plants allocated less biomass to leaves and branches and more biomass to boles than PF plants ($P \leq .0005$ for each comparison).

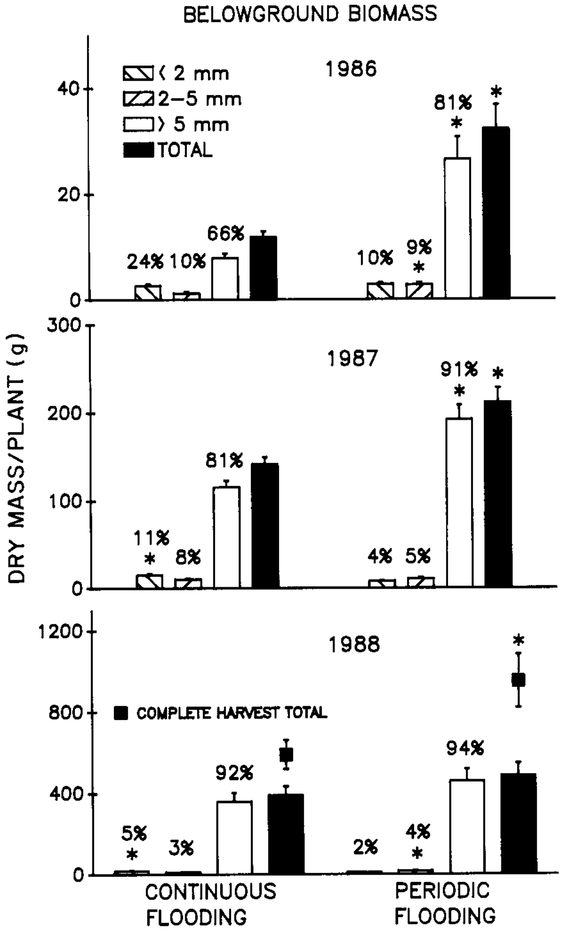

FIG. 4. Belowground biomass (means and 1 SE) of the continuously flooded bald cypress seedlings. Bars give totals from 30 × 30 × 30 cm excavations following each growing season. Square symbols (■) in the 1988 frame are total belowground biomass inclusive of roots recovered in a complete excavation of each rhizotron cell. Asterisks (*) mark significant differences at $P \leq .02$ in between-treatment comparisons.

TABLE 3. Annual biomass increment of bald cypress grown in large rhizotron cells. Estimates are based on annual differences in mean biomass.† CF = continuously flooded, PF = periodically flooded.

Annual production (g·plant^{-1}·yr^{-1})	1986		1987		1988	
	CF	PF	CF	PF	CF	PF
Shoot total‡	22.0	64.7***	308.4	420.9*	1,026.8	718.7 NS
Root total	11.4	31.7***	129.6	179.0*	448.8	739.8*
Grand total	33.4	96.4***	438.0	599.9*	1,475.6	1,458.5 NS
RGR§	3.11	4.00***	2.60	1.96*	1.42	1.13 NS

† Statistical comparisons were made between treatments within years for each measurement of growth. Significant differences are indicated with asterisks (* = ≤.05, *** = ≤.001, NS = not significant).

‡ The 1986 estimate accounts for the biomass of the seedling stock (leaf = 0.54, bole = 0.62, branch = 0, root = 0.52 g/plant).

§ Relative growth rate = $\log_e$(final mass) − $\log_e$(initial mass).

Root biomass

Root biomass estimates based on 30 × 30 × 30 cm excavations show a temporal pattern similar to that of shoot biomass (Fig. 4). The average total root biomass was 2.5 times as large in the PF treatment as the CF treatment after one growing season, and 1.5 times as large after two growing seasons ($P \leq .003$, Fig. 4). At the end of the third growing season, there was no significant difference in root biomass between the treatments.

Although useful for making comparisons, the 30 × 30 × 30 cm plot samples underestimated root biomass for 2- and 3-yr-old plants. The complete excavation at the end of the study showed that average total root mass was considerably higher under periodic flooding (mean ± SE = 951 ± 133 vs. 590 ± 72 g/plant, $P = .04$, Fig. 4).

The 1987 harvest (2-yr-old plants) excluded roots outside the sample plots. These roots were recovered in a single batch sample during the 1988 destructive harvest (root size classes ≥2 mm diameter). Their average biomass was 17 g/plant (CF) and 100 g/plant (PF). Random cores of the upper 30 cm taken in 1988 showed more fine root biomass (<2 mm diameter) in the PF treatment than in the CF treatment (mean ± 1 SE = 33 ± 2 g/m^2 and 21 ± 4 g/m^2, $P = .01$).

Root and shoot increment

Estimates of the annual biomass increment to shoots and roots were calculated as the difference between the mean biomass of each component in successive years (Table 3). In 1986 and 1987 the biomass increment of PF cypress was greater than that of CF cypress ($P = .0001$ and .03, respectively). In 1988 the total production was nearly the same under continuous and periodic flooding (CF = 1,476 g/plant and PF = 1,459 g/plant; $P = .96$), but there was a difference in biomass allocation. Average root increment in the PF cell was greater by 291 g/plant ($P = .05$), while average shoot increment was lower by 308 g/plant ($P = .14$). In the second year, relative growth rates of CF plants were greater than PF plants ($P = .001$). There was no significant difference in relative growth rates in the third growing season ($P = .34$).

Root size class and depth distributions

Based on the 30 × 30 × 30 cm excavations, CF plants allocated a greater proportion of belowground mass to fine roots (<2 mm diameter) than PF plants during each year of the study (Fig. 4, $P \leq .003$). PF plants allocated more mass to structural roots (>5 mm diameter) in 1986 and 1987 ($P \leq .0001$).

A complete excavation of the cells after 3 yr of treatment revealed that PF cypress saplings had deeper root systems than CF saplings. The proportion of total root mass below 30 cm was 30% in the PF cell and 6% in the CF cell. Some roots in the PF cell reached to the bottom of the 100-cm soil profile.

Soil water roots (sensu Hook 1984) emerged from the soil surface of the CF cell early in the second growing season. They were initiated on the lateral roots and grew upward into the water column. Some eventually reentered the soil. They began secondary thickening during the second growing season. After three growing seasons the soil water roots accounted for 37% of the fine root (<2 mm diameter) biomass and 19% of the medium root (2–5 mm diameter) biomass of CF plants. Primary soil water roots were ≈2 mm in diameter, white, and succulent, with many fibrous secondary roots. Roots >5 mm diameter comprised roughly 3% of the water root biomass after 3 yr.

Root-to-shoot ratios

Regressions of root biomass on shoot biomass were significant for the CF cell after 1 yr and for both cells after 3 yr ($P < .002$; Fig. 5). There was no difference in slope or Y intercept for 1-yr-old seedlings ($P \geq .21$). Regression lines for 3-yr-old saplings had a common slope but different Y intercepts ($P = .01$). Thus, for a given amount of shoot biomass, PF plants had more root biomass than CF plants. The CF plants allocated 28% of total dry mass increment belowground while PF plants allocated 46% belowground (Table 3). There

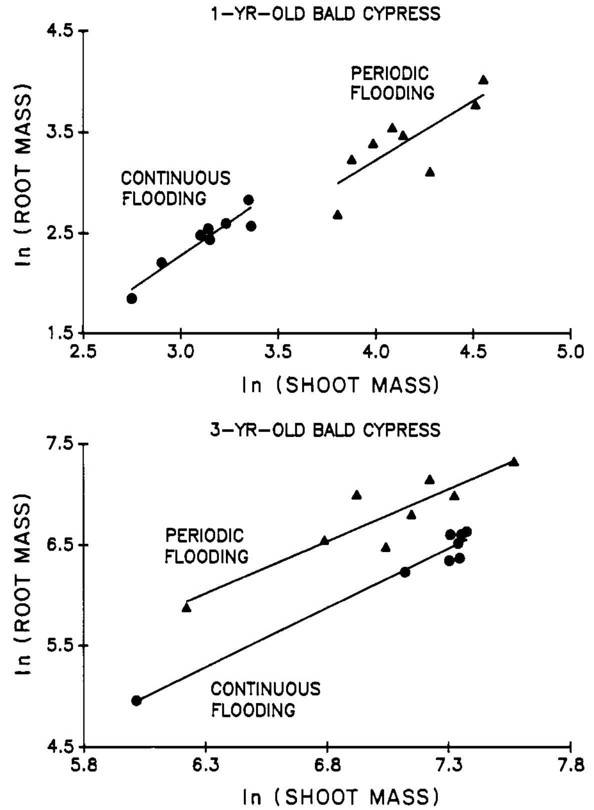

FIG. 5. Plots of ln(root mass) vs. ln(shoot mass) for the first and third growing-season harvests. Regression models were significant for the continuously flooded treatment in the first year ($P = .0004$) and for both treatments in the third year ($P \leq .002$).

was surprisingly little variation in the biomass of 3-yr-old CF plants (Fig. 5). Variability in the water table may have promoted the expression of genotypic variation in PF plants (Lewontin 1974).

Stem and root anatomy

Hand-cut sections of root and stem tissue were stained with toluidine blue and studied with light microscopy. Intercellular spaces were apparent in the secondary phloem of both the continuously and periodically flooded plants. However, the air spaces were consistently much larger, far more numerous and more continuous in the phloem of CF plants. A layer of spongy tissue characterized by loosely packed parenchyma cells and schizogenic intercellular spaces occurred in the outer ¼ of the phloem of PF plants but often extended to near the cambial layer in the phloem of CF plants. Air spaces occurred both within the rays and in the phloem tissue between the rays. In radial section the air spaces were longitudinally continuous in the tissue of CF plants. There was a total absence of air space in the xylem. Intercellular spaces cannot account for the relatively large, buttressed bases of the CF stems.

Root system structure

Root system morphology after three growing seasons was studied by removing the top 30 cm of soil while leaving roots ≥2 mm diameter in place. The two flooding regimes resulted in strikingly different root systems (Fig. 6). Continuously flooded roots were diageotropic or negatively geotropic, highly tapered, succulent, and restricted to a relatively confined area around the stem. The root systems of individual stems showed relatively little overlap. Periodically flooded roots were positively geotropic (disappearing below the 30 cm soil plane in a short distance), longer, and less tapered. The root systems of PF stems tended to overlap.

DISCUSSION

In this 3-yr study we found striking differences in growth and allocation by bald cypress exposed to continuous and periodic flooding. Because each flooding regime was represented by a single experimental unit, caution in interpretation is warranted due to the lack of true replicates (Hurlbert 1984, but see Hawkins 1986). We suggest, however, that the observed differences in plant response are most parsimoniously interpreted as the effects of differential flooding patterns.

Biomass production

Biomass production by bald cypress was greater with periodic flooding than with continuous flooding during the first growing season. Similar flooding effects have been reported for the seedlings of a variety of woody, hydrophytic species in short-term microcosm studies (Keeley 1979, Sena Gomes and Kozlowski 1980*a*, 1988, Newsome et al. 1982, Norby and Kozlowski 1983, Peterson and Bazzaz 1984, Day 1987, Donovan et al. 1988). Studies of bald cypress seedlings, however, have reported variable growth responses to continuous inundation (Table 1). In the present study, treatment effects on growth rate varied with age. Rates of relative growth in the continuously flooded (CF) cell were greater than or equal to the periodically flooded (PF) cell in the second and third growing seasons.

The relative difference between cells in total biomass and biomass increment decreased over the three years of the study (Figs. 3 and 4, Table 3). Increased relative growth rate in the CF cell during the second growing season suggests that the plants had acclimated to the flooding through morphological and physiological adaptations (e.g., water roots and intercellular spaces). Because plants generally meet the demands of leaf and root production before investing in wood (Waring and Schlesinger 1985: 34), relatively little allocation to stems in the first (1986) growing season suggests that the CF plants were stressed. Increased allocation to wood in the CF cell coincided with improvements in growth rate in 1987 and 1988.

It is likely that relatively slow growth in the CF cell during the first growing season was due to transplant

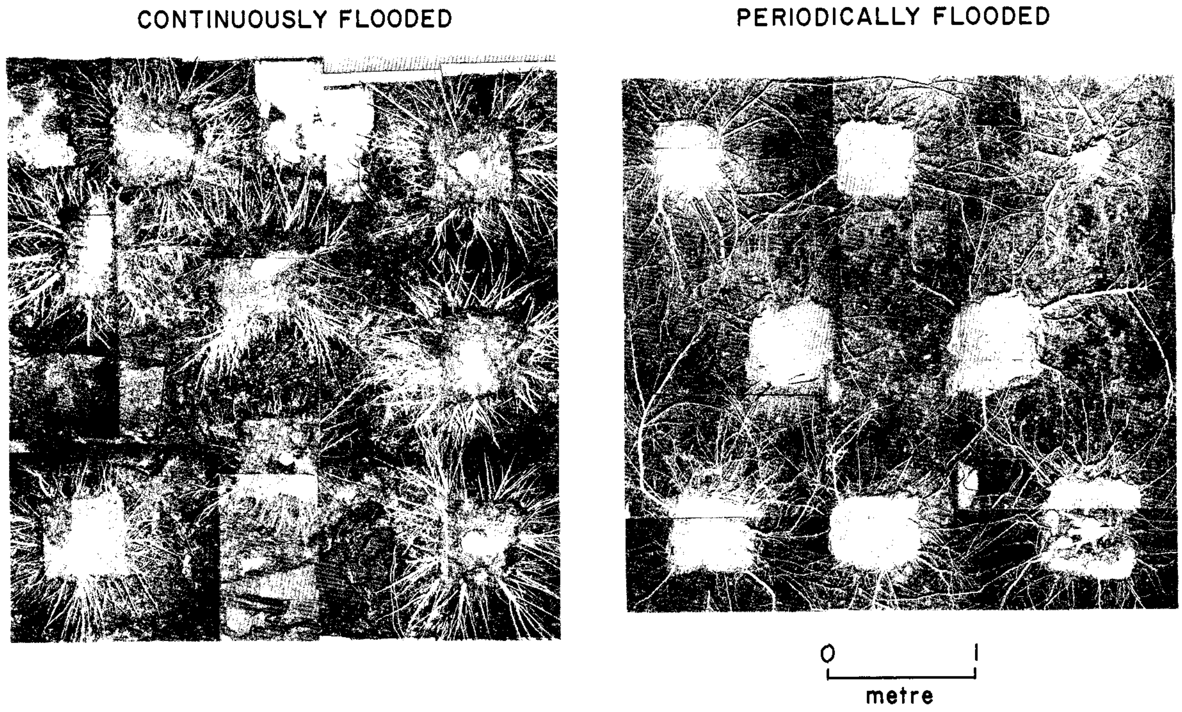

FIG. 6. Composite photographs of the root systems of the two treatments. The top 30 cm of soil was removed, leaving all roots ≥2 mm in diameter in place. The rhizotron cells are 2.83 m long, 2.83 m wide, and 1.5 m deep.

shock. Despite a continuous turnover of soil water, the CF cell was always anoxic and reduced (study mean = −18 mV at 20 cm, Fig. 2). Although few microcosm studies report soil redox potential or oxygen status, it is possible that flooded microcosms remain in a partially aerated condition. Jones et al. (1989) reported an average redox potential of 178 mV in the center of waterlogged flower pots, a value that suggests an anaerobic but relatively oxidized environment compared to our cells. Flood-conditioning our seedlings in microcosms may not have been sufficient to acclimate them to the relatively reduced environment of the rhizotron cells. Relatively slow growth of CF plants in 1986 may have been the result of direct injury to the root system. Another factor contributing to transplant shock and subsequent recovery is flooding depth relative to plant height. At 40 cm in height, newly planted CF seedlings were 50% submerged, while 3-yr-old saplings were only 5% submerged.

As an alternative explanation, rapid early growth in the PF treatment may have led to competition for light, nutrients, and water. Competition may have been less important in limiting the growth of the CF plants, which were relatively small. However, we believe that competition is an unlikely explanation for the change in relative growth rates after one growing season. The fall harvests removed ⅓ of the individuals (roots and shoots) in 1986 and ½ of the individuals in 1987. Under the competition scenario, thinning should have caused a burst of growth in the PF treatment at the beginning of the 1987 and 1988 growing seasons. Diameter measurements taken regularly during the 1988 growing season demonstrate that this was not the case. Following thinning, both treatments grew at the same relative rate for the first 3 mo of the growing season ($P = .69$; mean [± 1 SE] increment in relative basal area = 0.92 ± 0.06 [CF] and 0.86 ± .08 [PF]).

Stem and root anatomy

Production of adventitious roots and intercellular spaces are common responses to waterlogged soils and are frequently associated with flooding tolerance (Crawford 1983, Hook 1984). Adventitious roots are believed to confer tolerance to flooding (Sena Gomes and Kozlowski 1980*a*, Tsukahara and Kozlowski 1985, Kozlowski et al. 1991). Initiation of adventitious roots has been correlated with stomatal reopening in *Fraxinus pennsylvanica* and with improved growth in *Eucalyptus camaldulensis* (Sena Gomes and Kozlowski 1980*a*, *b*). In the present study, the appearance of soil water roots on CF plants coincided with increased growth in the second growing season. These roots comprised a significant fraction of fine and medium root biomass in 1988 (37% and 19%, respectively).

A number of potential functions have been suggested for adventitious roots: they (1) allow water absorption upon loss of the original root system (Sena Gomes and Kozlowski 1980*a*); (2) allow rapid uptake of dissolved oxygen and nutrients from the relatively oxic water column; (3) are sites of accelerated alcoholic fermentation and provide a compensatory energy source during periods of anaerobiosis (Hook et al. 1971, Keeley and Franz 1979); and (4) release toxins such as CO_2, ethanol, and ethylene (Crawford 1983). Soil water roots may have contributed to the recovery of normal physiological function in the CF plants.

In trees the ability to transport oxygen from above the water surface to the root system is key to long-term success in flooded environments. Hook et al. (1971) demonstrated that there was oxygen transport through the stem to the root system of flooded *Nyssa sylvatica* var. *biflora*. Histological studies of the roots revealed intercellular spaces in the phloem and cortex (Hook et al. 1970*a, b*). Schizogenous formation of intercellular spaces and oxygen transport through the stem was demonstrated in *Pinus serotina,* a moderately flood-tolerant gymnosperm (Topa and McLeod 1986). Fisher and Stone (1990) measured high values of air permeability in the roots of *Taxodium ascendans.* It is likely that well-developed intercellular spaces in the phloem of CF bald cypress saplings permitted oxygen transport to the root system and contributed to high production rates in the second and third years of the present study. The fact that schizogenous intercellular spaces were less developed in the PF plants is consistent with the relatively short flooding treatment.

Root system structure

Several microcosm studies have shown that upon flooding hydrophytic plant species replace much of the original root system with a new, morphologically distinct root system (Hook 1984). The adventitious roots and soil water roots of continuously flooded seedlings are typically larger in diameter, less branched, and more succulent than those grown in the absence of flooding. Flooded roots often exhibit diageotropism. Continuously flooded roots in the present study had these characteristics. Keeley (1979) observed that soil water roots on continuously flooded swamp tupelo (*Nyssa sylvatica* var. *biflora*) seedlings were replaced within 1 yr by roots resembling those from a "drained" treatment. Our data suggest that soil water roots become the primary root system of flood-tolerant tree species as proposed by Hook (1984). Indeed, Harms et al. (1980) observed water roots on mature bald cypress and swamp tupelo 3 yr after the construction of a reservoir caused an increase in the depth and duration of flooding.

Carbon allocation

Root-to-shoot ratios commonly decrease in response to prolonged flooding in microcosms (Dickson and Broyer 1972, Keeley 1979, Sena Gomes and Kozlowski 1980*a*, Kane 1981, Newsome et al. 1982, Norby and Kozlowski 1983, Peterson and Bazzaz 1984, Tang and Kozlowski 1984, Topa and McLeod 1986, Day 1987, but see Shanklin and Kozlowski [1985] for an exception). Similar observations have been made in the field (Megonigal and Day 1988). At least three possibilities explain this phenomenon: (1) ample water and nutrients in the rooting zone permit a shift in carbon allocation from roots to shoots (Tilman 1988); (2) flooding causes extensive root mortality, restricts translocation of carbon to roots, or limits root cambial activity; or (3) flooding decreases root biomass but increases root turnover, and root production is relatively unaffected (Nadelhoffer et al. 1985). It is likely that transplant shock caused root-system mortality in the CF treatment at the beginning of the study. By the end of the first growing season, however, CF plants had root to shoot ratios comparable to those of PF plants. Apparently, the CF plants had made morphological adjustments to flooding stress by the end of the first growing season (Fig. 5).

Root-to-shoot ratios for 3-yr-old cypress saplings were clearly lower in the CF treatment than the PF treatment (Fig. 5). The high growth rates of the CF plants make it appear unlikely that reduced root biomass was due to toxic soil effects. Higher root turnover is unlikely because there were few dead roots, and decomposition rates were relatively slow in the CF treatment (Day et al. 1989). Rather, the data suggest a difference in carbon allocation. Abundant water and dissolved nutrients in the rooting zone of the CF treatment afforded these plants adequate belowground resources at a minimum investment in root biomass. They were essentially growing in a hydroponic solution. A high relative proportion of fine roots provided increased water- and nutrient-absorbing area. In continuously flooded environments, low root-to-shoot ratios may confer a competitive advantage by allowing an increase in leaf biomass (Tilman 1988).

The PF plants had high root-to-shoot ratios and deep root systems (to 100 cm). A relatively deep rooting zone may have provided the PF saplings access to water and dissolved nutrients within the water table (50–60 cm below the soil surface during summer; Fig. 1).

A common observation is that rooting depth is related to flooding frequency in swamp forests. Lieffers and Rothwell (1987) found a strong relationship between rooting depth and the depth to water table for *Larix laricina* and *Picea mariana* on a peat soil. Armstrong et al. (1976) found a strong correlation between soil oxygen flux and root mass for *Picea sitchensis.* Root mass was positively correlated with the force required to topple the tree. Our data (present study) contribute experimental evidence for a positive relationship among rooting depth, root biomass, and the depth to water table.

Flood and drought tolerance

Although highly tolerant of flooding, bald cypress exhibits adaptations characteristic of less tolerant tree species, such as buttressed bases, soil water roots, and intercellular air spaces. These adaptations promote gas transport to the root system and oxidation of the rhizosphere, allowing the plant to carry on aerobic respiration (Armstrong 1964, Hook et al. 1971, Keeley and Franz 1979, Topa and McLeod 1988). Thus, the optimum environment for cypress is probably an aerobic one. Why then can bald cypress grow equally well in continuously flooded (but not stagnant) and periodically flooded environments?

Highly flood-tolerant trees are generally drought sensitive. Dickson and Broyer (1972) showed that low soil moisture caused internal moisture stress and reduced growth in bald cypress. Under drought stress, cypress shoots were irreparably damaged in 3–4 hr. The periodically flooded plants in the present study showed signs of water stress (e.g., red and yellow colored foliage), especially in the third year of growth. Optimum growth probably could have been achieved by holding the water table close to the surface during the summer (at −20 cm rather than at −50 cm), thereby permitting both adequate aeration and soil moisture.

Field studies have usually found continuous or excessive flooding associated with reduced aboveground production in bottomland forests (Conner and Day 1982, Malecki et al. 1983) and cypress swamps (Schlesinger 1978, Mitsch and Ewel 1979, Brown 1981). Natural and human-made impoundments have been linked to decreased growth (Mitsch et al. 1979) and increased mortality (Harms et al. 1980) in mature cypress swamps. Likewise, field studies have found that periodic flooding is associated with improved aboveground production in bottomland forests (Mitsch and Ewel 1979, Brown 1981, Conner and Day 1982, Megonigal and Day 1988, but see Brown and Peterson [1983] for an exception). Stem growth in cypress domes was best on sites that were neither extremely wet nor extremely dry (Mitsch and Ewel 1979, Marois and Ewel 1983). Bald cypress may be more sensitive to inadequate moisture than excessive moisture. Indeed, sensitivity to drought stress may help explain why they occur only in the most flooded habitats.

Conclusions

Continuous flooding is usually considered more physiologically stressful to hydrophytes than periodic flooding, but for bald cypress and other extreme hydrophytes there is a trade-off between flood tolerance and drought tolerance (Keeley 1979). If dominated by hydrophytes, a soil that is continuously flooded with shallow water may support higher productivity than a periodically flooded soil that frequently dries to the wilting point. Donovan et al. (1988) noted that growth of water tupelo is not consistently affected by saturation or flooding. This is also the case with bald cypress (Table 1). Bald cypress and water tupelo may have a narrow range of tolerance for wet and dry extremes. The varied responses of these species to flooding treatments in microcosm studies may reflect the wide variety of conditions that researchers consider "flooded" or "drained" (Table 1). The relatively short duration of these studies may also have contributed to variations in the growth response.

Most field studies concerning the effects of hydrology on primary production are based solely on aboveground estimates (Schlesinger 1978, Brown 1981, Conner and Day 1982). Yet plants are generally plastic in partitioning carbohydrates to roots or shoots (Tilman 1988). Although aboveground productivity is related to total productivity on a broad scale, our data demonstrate the importance of measuring root production when relating production to environmental variables. For example, without the belowground production estimates we would have concluded that continuously flooded plants tended to be more productive than periodically flooded plants in the third growing season.

There are an estimated 13 million ha of palustrine forested wetlands in 10 states of the southeastern United States (Hefner and Brown 1985). Many of these forests are dominated by bald cypress and water tupelo. Palustrine forests are an important source of organic carbon for southeastern aquatic ecosystems. Leaf litter and other forms of allochthonous carbon are the primary source of energy for coastal plain rivers in the region (Mulholland 1981, Meyer and Edwards 1990). Changes in hydroperiod—e.g., with global sea-level rise—that affect either forest productivity or carbon allocation to roots and shoots can potentially reduce leaf litter export. A better understanding of the role of wetland forests in linking upland and aquatic ecosystems will require increased attention to root production and other belowground processes.

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LITERATURE CITED

Armstrong, W. 1964. Oxygen diffusion from the roots of some British bog plants. Nature **204**:801–802.

Armstrong, W., T. C. Booth, P. Priestley, and D. J. Read. 1976. The relationship between soil aeration, stability and growth of sitka spruce (*Picea sitchensis* (Bong.) Carr.) on upland peaty gleys. Journal of Applied Ecology **13**:585–591.

Bohm, W. 1979. Methods of studying root systems. Springer-Verlag, New York, New York, USA.

Bohn, H. L. 1971. Redox potentials. Soil Science **112**:39–45.

Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics **12**:123–161.

Brown, S. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecological Monographs **51**:403–427.

Brown, S., and D. L. Peterson. 1983. Structural characteristics and biomass production of two Illinois bottomland forests. American Midland Naturalist **110**:107–117.

Carter, V., D. Shultz, M. K. Garrett, and W. E. Webb. 1984. A technique to measure oxygen in the root zone of saturated and unsaturated soils. Selected Papers in Hydrologic Science **1-5.**

Conner, W. H., and J. W. Day. 1982. The ecology of forested wetlands in the southeastern United States. Pages 69–87 *in* B. Gopal, R. E. Turner, R. G. Wetzel, and D. F. Whigham, editors. Wetlands: ecology and management. International Scientific Publications, Jaipur, India.

Crawford, R. M. M. 1983. Root survival in flooded soils. Pages 257–283 *in* A. J. P. Gore, editor. Ecosystems of the world. Elsevier Scientific, Amsterdam, The Netherlands.

Day, F. P. 1987. Effects of flooding and nutrient enrichment on biomass allocation in *Acer rubrum* seedlings. American Journal of Botany **74**:1541–1554.

Day, F. P., J. P. Megonigal, and L. C. Lee. 1989. Cypress root decomposition in experimental wetland mesocosms. Wetlands **9**:263–282.

Dickson, R. E., and T. C. Broyer. 1972. Effects of aeration, water supply, and nitrogen source on growth and development of tupelo gum and bald cypress. Ecology **53**:626–634.

Donovan, L. A., K. W. McLeod, K. C. Sherrod, and N. J. Stumpff. 1988. Response of woody swamp seedlings to flooding and increased water temperatures. I. Growth, biomass, and survivorship. American Journal of Botany **75**:1181–1190.

Donovan, L. A., N. J. Stumpff, and K. W. McLeod. 1989. Thermal flooding injury of woody swamp seedlings. Journal of Thermal Biology **14**:147–154.

Faulkner, S. P., W. H. Patrick, and R. P. Gambrell. 1989. Field techniques for measuring wetland soil parameters. Soil Science Society of America Journal **53**:883–890.

Fisher, H. M., and E. L. Stone. 1990. Air-conducting porosity in slash pine roots from saturated soils. Forest Science **36**:18–33.

Harms, W. R., H. T. Schreuder, D. D. Hook, and C. L. Brown. 1980. The effects of flooding on the swamp forest in Lake Ocklawaha, Florida. Ecology **61**:1412–1421.

Harris, W. F., D. Santantonio, and D. McGinty. 1980. The dynamic belowground ecosystem. Pages 119–129 *in* R. H. Waring, editor. Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon, USA.

Hawkins, C. P. 1986. Pseudo-understanding of pseudoreplication: a cautionary note. Bulletin of the Ecological Society of America **67**:184–185.

Hefner, J. M., and J. D. Brown. 1985. Wetland trends in the southeastern United States. Wetlands **4**:1–11.

Hook, D. D. 1984. Adaptations to flooding with fresh water. Pages 265–294 *in* T. T. Kozlowski, editor. Flooding and plant growth. Academic Press, Orlando, Florida, USA.

Hook, D. D., C. L. Brown, and P. P. Kormanik. 1970*a*. Lenticel and water root development of swamp tupelo under various flooding conditions. Botanical Gazette **131**:217–224.

Hook, D. D., C. L. Brown, and P. P. Kormanik. 1971. Inductive flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.). Journal of Experimental Botany **22**:78–89.

Hook, D. D., O. G. Langdon, J. Stubbs, and C. L. Brown. 1970*b*. Effect of water regimes on the survival, growth, and morphology of tupelo seedlings. Forest Science **16**:304–311.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187–211.

Jones, R. H., R. R. Sharitz, and K. W. McLeod. 1989. Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. American Midland Naturalist **121**:165–175.

Kane, E. 1981. Swamp forest root systems: biomass distribution, nutrient content, and aspects of growth and mortality. Thesis. East Carolina University, Greenville, North Carolina, USA.

Keeley, J. E. 1979. Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica.* Ecological Monographs **49**:89–108.

Keeley, J. E., and E. H. Franz. 1979. Alcoholic fermentation in swamp and upland populations of *Nyssa sylvatica*: temporal changes in adaptive strategy. American Naturalist **113**:587–592.

Kozlowski, T. T. 1984. Responses of woody plants to flooding. Pages 129–162 *in* T. T. Kozlowski, editor. Flooding and plant growth. Academic Press, New York, New York, USA.

Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, New York, New York, USA.

Lewontin, R. C. 1974. The analysis of variance and the analysis of causes. American Journal of Human Genetics **26**:400–411.

Lieffers, V. J., and R. L. Rothwell. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Canadian Journal of Botany **765**:817–821.

Malecki, R. A., J. R. Lassoie, E. Rieger, and T. Seamans. 1983. Effects of long-term artificial flooding on a northern bottomland hardwood forest community. Forest Science **29**:535–544.

Marois, K. C., and K. C. Ewel. 1983. Natural and management-related variation in cypress domes. Forest Science **29**:627–640.

McLeod, K. W., L. A. Donovan, N. J. Stumpff, and K. C. Sherrod. 1986. Biomass, photosynthesis and water use efficiency of woody swamp species subjected to flooding and elevated water temperatures. Tree Physiology **2**:341–346.

McLeod, K. W., and K. C. Sherrod. 1981. Bald cypress seedling growth in thermally altered habitats. American Journal of Botany **68**:918–923.

Megonigal, J. P., and F. P. Day. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Great Dismal Swamp. American Journal of Botany **75**:1334–1343.

Meyer, J. L., and R. T. Edwards. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. Ecology **71**:668–677.

Mitsch, W. J., and K. C. Ewel. 1979. Comparative biomass and growth of cypress in Florida wetlands. American Midland Naturalist **101**:417–426.

Mitsch, W. J., C. L. Dorge, and J. R. Wiemhoff. 1979. Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. Ecology **60**:1116–1124.

Mooney, H. A. 1972. The carbon balance of plants. Annual Review of Ecology and Systematics **3**:315–346.

Mulholland, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecological Monographs **51**:307–322.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology **66**:1377–1390.

Newsome, R. D., T. T. Kozlowski, and Z. C. Tang. 1982. Responses of *Ulmus americana* seedlings to flooding of soil. Canadian Journal of Botany **60**:1688–1695.

Norby, R. J., and T. T. Kozlowski. 1983. Flooding and SO_2 stress interaction in *Betula papyrifera* and *B. nigra* seedlings. Forest Science **29**:739–750.

Peterson, D. L., and F. A. Bazzaz. 1984. Photosynthetic and growth responses of silver maple (*Acer saccharinum* L.) seedlings to flooding. American Midland Naturalist **112**: 262–272.

Poorter, H., and C. L. Lewis. 1986. Testing differences in relative growth rate: a method avoiding curve fitting and pairing. Physiologia Plantarum **67**:223–226.

Raich, J. W., and K. J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology **70**:1346–1354.

SAS. 1985. SAS procedures guide for personal computers, Version 6 edition. SAS Institute, Cary, North Carolina, USA.

Schlesinger, W. H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee cypress swamp-forest. Ecological Monographs **48**:43–65.

Sena Gomes, A. R., and T. T. Kozlowski. 1980*a*. Growth responses and adaptation of *Fraxinus pennsylvanica* seedlings to flooding. Plant Physiology **66**:267–271.

Sena Gomes, A. R., and T. T. Kozlowski. 1980*b*. Effects of flooding on *Eucalyptus camaldulensis* and *Eucalyptus globulus* seedlings. Oecologia (Berlin) **46**:139–142.

Sena Gomes, A. R., and T. T. Kozlowski. 1988. Physiological and growth responses to flooding of seedlings of *Hevea brasiliensis*. Biotropica **20**:286–293.

Shanklin, J., and T. T. Kozlowski. 1985. Effect of flooding of soil on growth and subsequent responses of *Taxodium distichum* seedlings to SO_2. Environmental Pollution **38**: 199–212.

Tang, Z. C., and T. T. Kozlowski. 1984. Water relations, ethylene production, and morphological adaptation of *Fraxinus pennsylvanica* seedlings to flooding. Plant and Soil **77**:183–192.

Tilman, D. 1988. Plant strategies and the dynamics and structures of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Topa, M. A., and K. W. McLeod. 1986. Responses of *Pinus clausa, Pinus serotina* and *Pinus taeda* seedlings to anaerobic solution culture. I. Changes in growth and root morphology. Physiologia Plantarum **68**:523–531.

Topa, M. A., and K. W. McLeod. 1988. Promotion of aerenchyma formation in *Pinus serotina* seedlings by ethylene. Canadian Journal of Forest Research **18**:276–280.

Tsukahara, J., and T. T. Kozlowski. 1985. Importance of adventitious roots to growth of flooded *Platanus occidentalis* seedlings. Plant and Soil **88**:123–132.

Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecological Research **15**:303–377.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems. Academic Press, New York, New York, USA.