CYPRESS ROOT DECOMPOSITION IN EXPERIMENTAL WETLAND MESOCOSMS

Frank P. Day, Jr.
Department of Biological Sciences, Old Dominion University
Norfolk, Virginia 23529

J. Patrick Megonigal
Savannah River Ecology Laboratory
Drawer E, Aiken, South Carolina 29801

Lyndon C. Lee
Office of Wetlands Protection
U.S. Environmental Protection Agency and University of Georgia
401 M Street SW, Washington, DC 20460

Abstract: Two forested wetland mesocosms containing organic soil (a sapric histosol) and cypress seedlings were constructed in the rhizotron facility at the University of Georgia's Savannah River Ecology Laboratory. A different hydroperiod (continuous versus periodic) was designed and implemented for each mesocosm. A vertical litter bag technique was used to measure cypress root decomposition rates in the mesocosms. Rapid leaching losses followed by 6 months of no mass loss occurred in both mesocosms. During the final 9 months of the study, roots in the periodically flooded mesocosm began to significantly decompose while those in the continuously flooded mesocosm remained unchanged. Inhibited decay was correlated with reduced redox potential, oxygen, and pH, but the delayed response to changes in these factors suggests that the coupling between root decomposition and the abiotic environment is not tight. The presence of living cypress roots could explain more rapid decay near the surface of the periodically flooded mesocosm. In general, nutrients were higher in concentration and amount in the periodically flooded decomposing roots but lower in the soil water. Net accumulations of N occurred in the periodically flooded roots. These patterns indicate that periodically flooded ecosystems should have more conservative nutrient cycles than continuously flooded systems. In general, mesocosms appear to provide a useful experimental approach to the study of belowground ecosystem processes.

Key Words: anoxia, cypress, decomposition, forested wetland, hydroperiod, mesocosm, root.

INTRODUCTION

Fine roots represent a large and dynamic portion of belowground biomass, soil detritus, and nutrient capital; however, there have been few studies in which root

decomposition or turnover have been measured (Waid 1974, McGinty 1976, Hackney and de la Cruz 1980, Harris *et al.* 1980, Brinson *et al.* 1981, McClaugherty *et al.* 1982, Ellison *et al.* 1986, Hackney 1987, Tupacz 1988, Gallagher 1988). In a periodically flooded wetland, fluctuating water levels are likely to have significant effects on belowground ecosystem dynamics (Dickson and Broyer 1972, Reddy and Patrick 1975). The waterlogged portion of the soil profile is expected to be quite different chemically and physically from the non-waterlogged portion, and these differences, in turn, should produce varied root decomposition rates.

Brinson *et al.* (1981) stated that "... detritus produced by root mortality is almost universally excluded (from wetland studies)." This paucity of knowledge is directly related to the difficulty of obtaining belowground measurements without severely disturbing the soil (Bohm 1979), and these problems are especially severe in flooded soils. It is also difficult to test hypotheses regarding the effects of flooding using conventional approaches. Field measurements are subject to the vagaries of the natural environment, and highly controlled microcosm experiments lack realism. There is a need for new approaches for studying belowground dynamics.

The rhizotron facility at the University of Georgia's Savannah River Ecology Laboratory (SREL) provided a unique opportunity for a mesocosm approach to the study of belowground processes. Mesocosms are experimental units that hold much promise for manipulative ecological studies (Odum 1984). A mesocosm fills the gap between the difficult-to-manipulate natural field plot and the unrealistic microcosm. A mesocosm approach allows for a significant amount of realism because of the large size of the experimental unit, but it also provides a high degree of control so that hypotheses can be tested. These units still have some oversimplified and artificial characteristics, but they are more realistic than smaller units.

In this study, two forested wetland mesocosms containing an organic soil and cypress (*Taxodium distichum*) seedlings were constructed in the rhizotron facility at the Savannah River Ecology Lab. A different hydroperiod treatment (continuous flooding versus periodic flooding) was incorporated into each mesocosm to evaluate the effects of varied flood patterns on several system processes. Since treatment effects could not be directly tested because of the lack of mesocosm cell replication, the pretreatment conditions were carefully monitored in both cells to establish their initial states. This paper presents the results of the hydroperiod manipulations on cypress root decomposition and offers an interpretation of the results as they relate to ecosystem processes. Environmental conditions in the mesocosms were monitored throughout the soil profile for the duration of the study. Results from a greenhouse study of root decay in pots exposed to different hydroperiods are also reported and related to the mesocosm study.

METHODS

The Mesocosms

Two mesocosms were constructed during the winter and spring of 1985-86 in the rhizotron facility at the Savannah River Ecology Laboratory. The soil profiles consisted of about 1 m of a sapric histosol underlain by layers of sand and gravel (Figure 1). The soil was obtained by a commercial peat mining company from a former cypress wetland near Jacksonboro, S.C. Oxygen chambers (Carter *et al.* 1984), redox probes, and thermisters were installed, and rain collectors were attached to the rhizotron walls. Twenty-five cypress seedlings were planted with even spacing in each mesocosm. Vertical movement of water through the mesocosms was allowed to prevent complete stagnation. For the duration of the experiment, the valves from the sumps were adjusted to allow an output flow of

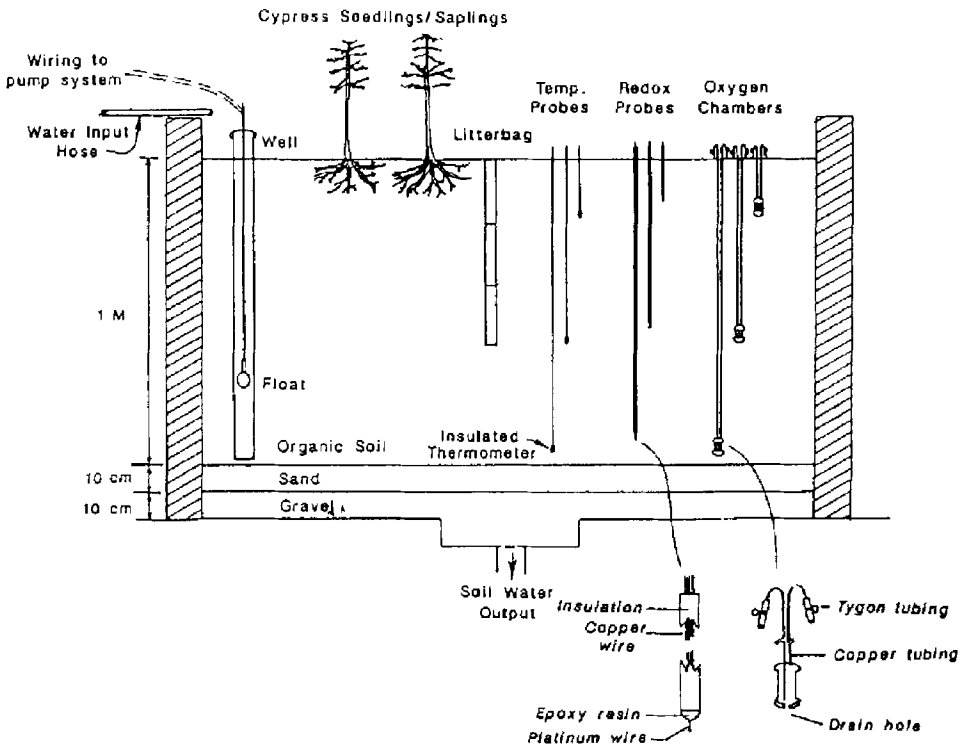

Figure 1. Cross sectional diagram of a cypress wetland mesocosm. The dimensions of each unit are 2.83 m wide, 2.83 m long, and 1.5 m deep (1 m of soil).

about 114 L per day into calibrated storage tanks. A system of floats, solenoid switches, and pumps delivered water (collected from Upper Three Runs Creek) from a storage tank into the cells through a sprinkler hose on the soil surface so that prescribed water levels were maintained. Flow meters were used to measure the volume of input.

Since structure and function in wetland systems are highly dependent on the timing and extent of flood events (Brinson *et al.* 1981, Wharton *et al.* 1982, Day *et al.* 1988), a different hydroperiod was initiated in each mesocosm on May 23, 1986 and maintained for the duration of the study. One mesocosm was continuously flooded and the other simulated a periodic flood cycle typical of many southeastern forested wetlands (Figure 2). Seasonally flooded forested wetlands commonly exhibit minimal surface flooding but extensive saturation of the rooting zone.

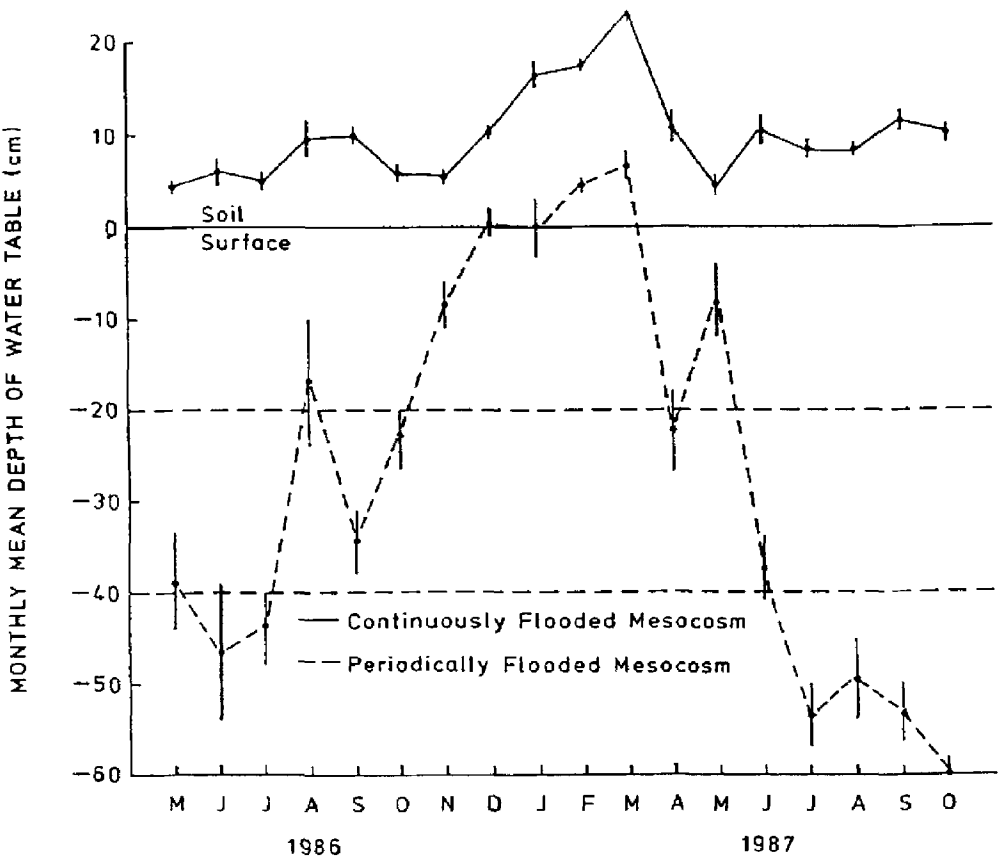

Figure 2. Hydroperiods of the two mesocosms during the root decomposition study. Vertical bars represent ± 1 SE.

Soil oxygen content, pH, redox potential (Eh), and temperatures were determined at 20 cm depth intervals prior to the initiation of hydroperiod treatments and every two weeks thereafter. Gas-water sample chambers were used to determine oxygen content and take soil water samples (Carter *et al.* 1984). Each chamber consisted of a 6 cm diameter, 20 cm length of PVC pipe capped on each end (Figure 1). The sides of the pipe were slotted and covered with a fine mesh stainless steel screen to allow movement of soil water into the chamber. A copper tube that perforated the top cap, but did not extend below it, allowed us to sample the gas trapped under the cap (Patrick 1977). Another tube that extended to the bottom of the chamber allowed us to sample the soil pore water. Oxygen was measured as a percentage of atmospheric concentration with an oxygen meter from paired chambers at each depth.

Redox probes were constructed by fusing a 1 cm length of pure 22 gauge platinum wire to a length of 12 gauge insulated copper wire (Figure 1). The junction of the wires was sealed with epoxy so that only the platinum tip was exposed. The probes were checked for accuracy with a saturated solution of guinhydrone in pH 7 buffer and rejected if they deviated 10 mV (the accuracy of our meter). Potentials were measured against a calomel reference probe with a pH meter and corrected for the reference potential by adding 244 mV. There were three replicate probes at each depth. Temperature was determined with a thermistor.

Soil water was collected once a month at five depths in duplicate from each mesocosm for determinations of total NH_4-N, PO_4-P, Ca, Mg, K, Mn, and Fe. Water in the sample chambers was emptied 24 h before collection to ensure a fresh sample. The pH of each sample was determined within 4 h of collection. The samples were then passed through 0.45 µm filters using acid-washed filter flasks and preserved with concentrated HCL. Filter blanks were substracted from each sample. An unpreserved subsample was used to determine total NH_4-N on a LaChat autoanalyzer within 48 h of collection (Crooke and Simpson 1971). Total PO -P, Ca, Mg, K, Mn, and Fe were determined on a Jarrell-Ash Model 965 inductively coupled Plasma Emission Spectrograph (PES) (Method 200.7, U.S. Environmental Protection Agency 1983). Quality control for PES samples was achieved with spikes and splits of 10% of the samples. Percent recovery on the spikes averaged 86% (PO_4-P), 99% (K), 93% (Ca), 87% (Mg), 80% (Fe), and 98% (Mn). The split samples showed equal precision. The same elements were analyzed in soil samples. Microenvironmental variation between mesocosms and among sample dates and depths was tested by ANOVA and Duncan's Range Test ($p < 0.01$). Treatment effects could not be directly tested because hydroperiod treatments were not replicated. However, we can infer that differences between mesocosms were due to hydroperiod effects if the cells were the same prior to treatment and the only difference afterward was in hydroperiod. Both mesocosms were almost identical at the start of the study (Table 1), and they were treated the same for the duration of the study except for the hydroperiod.

Table 1. Initial conditions in the soils of the two mesocosms.

	Continuously Flooded Mesocosm					Periodically Flooded Mesocosm				
	20cm	40cm	60cm	80cm	100cm	20cm	40cm	60cm	80cm	100cm
Redox Potential (mv)	192	171	172	191	161	221	151	77	161	171
Oxygen (mg/1)	1.6	1.4	0.4	0.5	0.4	0.5	0.8	1.0	0.6	1.2
Soil Organic Matter (%)	84.0					80.5				
Soil pH	5.8					5.7				
Water pH	4.0					4.2				
Soil Bulk Density (g/cm^3)	0.27					0.27				
Temperature (C)	27	28	25	26	25	27	28	28	25	28
Total PO_4-P (ppm)	2	5	6	5	6	2	5	6	9	9
Total NH_4-N (ppm)	3	8	10	8	19	3	6	8	13	13
Total N (%)	0.7					0.7				
Ca (ppm)	747					670				
Mg (ppm)	666					690				

Root Decomposition Measurements

Just prior to the start of the hydroperiod treatments, vertical 1 mm mesh bags (60 cm long with 20 cm segments) filled with preweighed cypress roots were inserted into the soil in the mesocosms (30 bags each). Vertical bags were used so decomposition could be integrated over a depth range with which detailed micro-environmental conditions could be associated (Tupacz 1988). The cypress roots were collected from a forested wetland located at the Savannah River Plant. These were washed and air dried. Approximately 6 - 8 g of 2 - 5 mm diameter roots were placed in each bag segment. Air dry mass/oven dry mass conversion factors were determined from subsamples. Five bags were retrieved from each mesocosm approximately every 2 months; the final collection intervals were extended. The roots were washed, oven dried for 48 h at 60 C, and weighed. Decomposition was estimated by the percentage of the original mass remaining. The roots were also analyzed for total N, total P, Ca, Mg, K, Mn, and Fe by previously described methods. Differences between mesocosms and among sample dates and depths were tested by ANOVA and Duncan's Range Test ($p < 0.01$). Cross correlations (Pearson's) were computed among all environmental parameters and mass loss rates to identify significant relationships.

Greenhouse Study

The effects of hydroperiod on root decomposition rates were also examined in a greenhouse experiment at Old Dominion University. The experiment had a complicating factor (*Acer rubrum* seedlings in the pots), but the results provide some insight into the patterns observed in the mesocosms. Tree roots were obtained in March, 1985 at a single site in the Great Dismal Swamp, Virginia. No attempt was made to separate the roots by species, but the dominants on the site were *Acer rubrum, Nyssa aquatica,* and *Nyssa sylvatica* var. *biflora.* Preweighed (1 - 2 g), unconfined root bundles were prepared by tying together three root segments, 7 cm long and 2-5 mm diameter. Care was taken to make the bundles as uniform as possible in root type, size and general appearance. Air dry mass/oven dry mass conversion factors were determined.

The experimental design involved 192 clay pots (15 cm diameter) that contained 1-yr old *Acer rubrum* seedlings and soil from the maple-gum site where the roots were obtained. The pots were placed in 33 cm x 33 cm x 20.3 cm deep watertight plastic boxes (4 pots per box). Sixteen boxes were assigned to each of three flood treatments (no flooding, continuous flooding, and periodic flooding). One root bundle was inserted vertically into the soil in each pot. The treatments were initiated in April, 1985 (Day 1987). The flooded pots were inundated to 5 cm above the soil surface with deionized water. The periodically flooded pots were alternately drained and reflooded to 5 cm above the soil every 2 weeks. The unflooded pots were watered two to three times a week with equal volumes of deionized water.

In June, August, and October, 1985, root bundles were extracted from five randomly chosen pots from each treatment, washed, oven dried at 70 C for 48 h, and weighed. Disappearance of mass was used as a quantitative indicator of decomposition. ANOVA and Duncan's Multiple Range Test ($p < 0.01$) were used to test for significant flooding effects.

RESULTS

Cypress Root Decomposition in Mesocosms

Three distinct phases of root decay were apparent (Figure 3). A rapid 12 - 19% mass loss occurred during the first 2 months of the study in both mesocosms and at all depths. During the following 6 months, little or no decomposition was observed in either mesocosm. No significant differences (ANOVA, $p < 0.05$) between mesocosms or among depths were detected during these first two phases. In the 15th month (all depths) and 17th month (top 20 cm only) of the study, the cypress roots in the periodically flooded mesocosm had significantly (ANOVA, $p < 0.05$) less mass remaining than the roots in the continuously flooded mesocosm. During the final 9 months of the study, roots in the top 20 cm of the periodically flooded mesocosm began to decompose rapidly while those in the continuously flooded mesocosm still showed essentially no mass loss (Figure 3). A slight trend of slower decay with increasing depth was observed, but the only statistically significant relationship was detected in the periodically flooded mesocosm on the final sample date (ANOVA, $p = 0.022$).

Nutrient Dynamics in Decomposing Roots

In general, nutrients were found in higher concentrations (ANOVA, $p < 0.05$) and higher absolute amounts in the periodically flooded roots compared to the continuously flooded ones (Figure 4). Nitrogen was accumulated in amounts greater than the initial content in the periodically flooded roots but generally showed a net loss from the continuously flooded roots (Figure 4). Phosphorous (Figure 4), Ca, and K (not shown here) all decreased in content in both mesocosms as decomposition progressed. Iron was usually above our detection limits, and Mn behaved similar to P. Magnesium showed little loss from the decomposing roots and no temporal dynamics. There were no consistent differences in nutrient dynamics among depths.

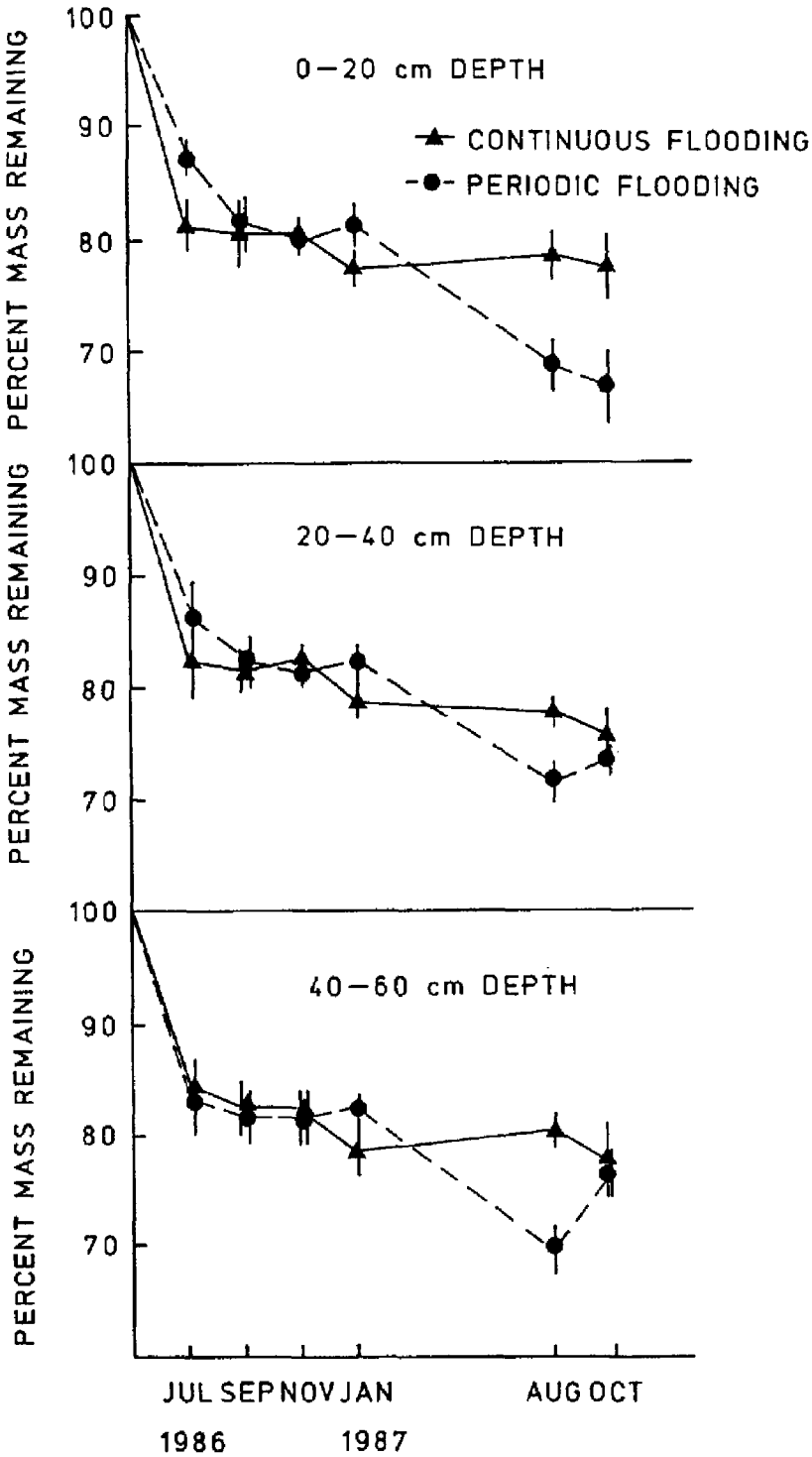

Figure 3. Mass loss from cypress roots in vertical litter bags in the two mesocosms. Bags were implanted on May 24, 1986. Vertical bars are ± 1 SE; N=5.

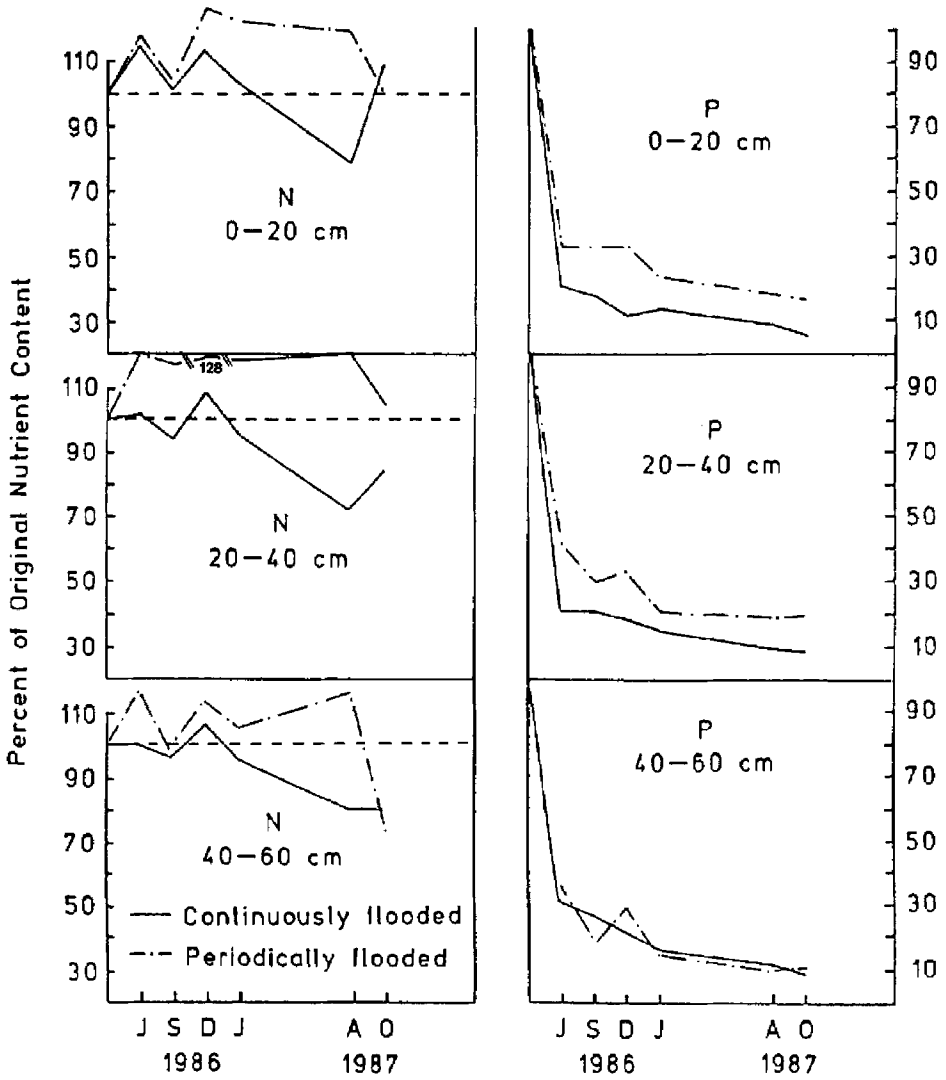

Figure 4. Total nitrogen and phosphorous content (expressed as percent of original content) in decomposing roots.

Microenvironment of Mesocosms

The continuously flooded mesocosm had redox potentials in the anoxic range throughout the study at all depths, and the oxygen measurements reflected this pattern (Figure 5). There were no significant differences (ANOVA, $p < 0.05$) in

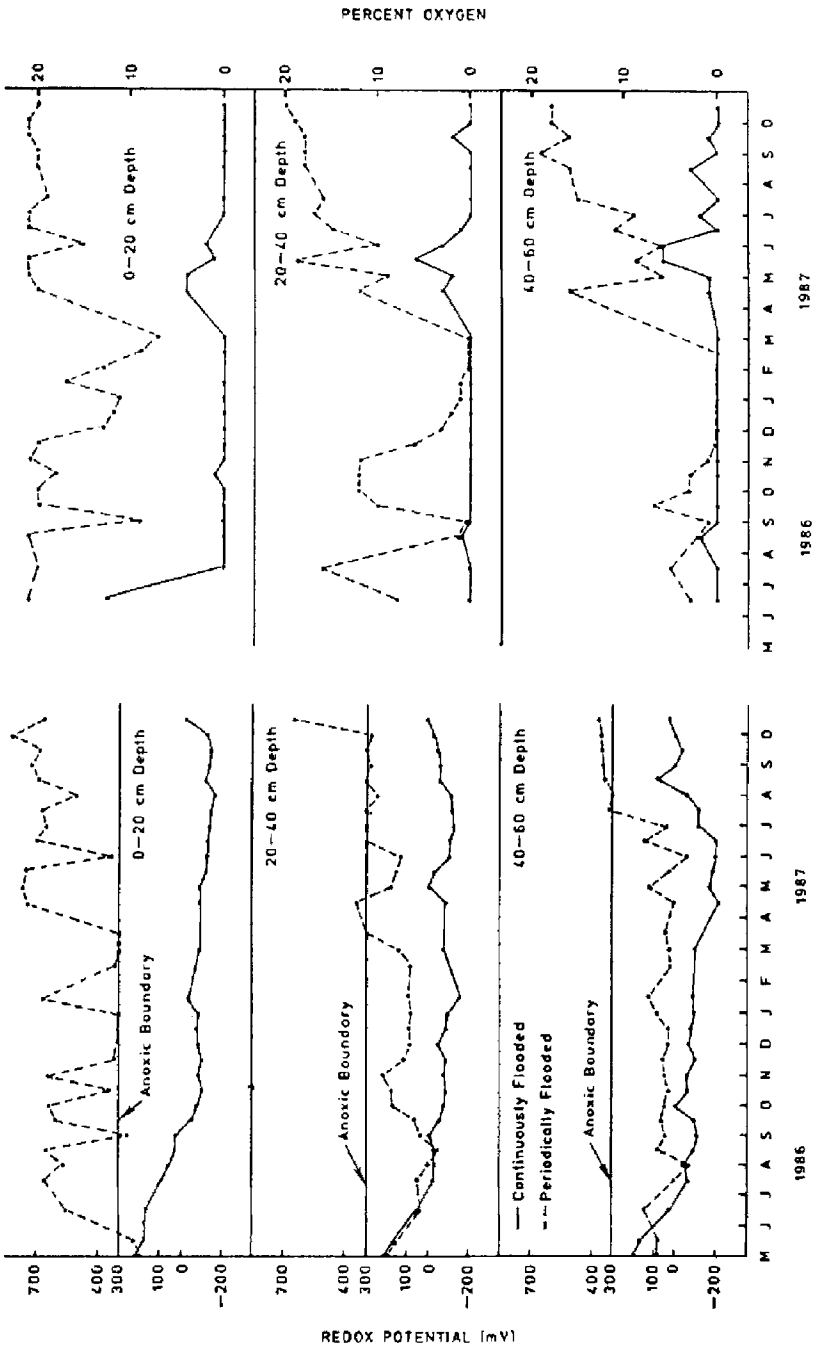

Figure 5. Redox potential (Eh) and percent oxygen at three depths in the two mesocosms. The anoxic boundary is not a constant but only approximates the level at which anaerobic conditions develop.

redox or oxygen among depths in the continuously flooded mesocosm. The periodically flooded mesocosm remained aerobic in the top 20 cm of soil throughout the study (Figure 5), but had progressively lower redox and oxygen levels with increasing depth (Duncan's, $p < 0.01$). The duration of oxygen deficit, which occurred during the peak flood period (Figure 2), increased with increasing depth (Figure 5). The periodically flooded mesocosm had significantly higher redox potentials and oxygen levels than the continuously flooded mesocosm at all depths.

The pH of the top 40 cm of soil was significantly (ANOVA, $p < 0.05$) greater in the periodically flooded mesocosm (4.4 - 5.6) than the continuously flooded mesocosm (4.2 - 5.2) (Table 2). In both mesocosms, pH decreased with increasing depth. There were no significant (ANOVA, $p < 0.05$) differences in soil temperatures between mesocosms or among depths.

Concentrations of nutrients in the soil water were generally greater in the continuously flooded mesocosm (ANOVA, $p < 0.05$) (Table 2). In the continuously flooded mesocosm, all elements increased in concentration with increasing depth (ANOVA, $p < 0.01$) (Table 2). This pattern was significant only for Fe in the periodically flooded mesocosm. Seasonal patterns were apparent in the concentration data. Nutrient concentrations peaked during late summer and early fall and declined to lows in the spring. Peak concentrations in the water were considerably lower in the second year of the study compared to the first.

Environmental Correlations

The data from the two mesocosms were combined for correlation analysis because some data were missing from the periodically flooded cell when water was not present, and the continuously flooded cell exhibited reduced variation because it was flooded all of the time. Since the greatest variation in nutrient concentrations was seasonal and all nutrients showed similar seasonal patterns, all nutrients correlated significantly ($p < 0.01$) with each other (Table 3). Temperature is, of course, also seasonal, and it correlated positively with all nutrients. Decreases in Eh were highly related to decreases in O_2 ($r = 0.86$, $p < 0.01$). Redox potential and O_2 were, in turn, positively correlated with pH and negatively correlated with the duration of flooding or soil saturation and concentrations of NH_4-N, PO_4-P, and Fe (Table 3). Reduced root decomposition, as indicated by higher mass remaining or lower decay rates, was associated with increased NH_4-N, PO_4-P, duration of flooding and temperature, and decreased Eh, O_2, and pH (Table 3). However, most of the relationships between environment and decay rates only became apparent near the end of the study when significant variation in decay was observed.

Table 2. Ranges of mean environmental parameters during the course of the study. WL= water table level, %F= percent of the period a given depth was flooded or saturated.

	Continuously Flooded Cell			Periodically Flooded Cell		
	0 - 20cm	20 - 40cm	40 - 60cm	0 - 20cm	20 - 40cm	40 - 60cm
Total NH_4-N (ppm)	0.7-12.0	1.8-45.5	3.0-39.5	0.3-2.0	1.3-8.6	0.6-19.5
Total PO_4-P (ppm)	0- 3.6	0.2- 7.7	0.5- 9.2	0.3-0.8	0.4-1.4	0.1- 4.2
K (ppm)	0- 8.9	0-53.4	1.2-16.5	0-5.2	0.7-10.1	0-11.6
Ca (ppm)	0.3- 3.3	0.7-11.7	1.2-16.6	0.3-4.9	1.0- 6.7	0.7- 9.1
Mg (ppm)	0.5- 4.7	0.6-15.0	1.4-20.6	0.4-10.2	1.2-14.0	0.8-21.3
Fe (ppm)	0.3- 2.1	0.6- 7.6	1.2- 7.6	0.2- 0.8	0.8- 2.1	0.6- 1.9
Mn (ppm)	0- 0.02	0.01-0.06	0.01-0.08	0-0.02	0.01-0.03	0- 0.06
Eh (mV)	-163-194	-161-47	-216-67	294-747	-46-651	-16-364
pH	4.4-5.2	4.2-5.1	3.8-4.9	4.9-5.6	4.5-5.3	3.9-4.9
O_2 (%)	0-14	0-6	0-6	7-21	0-20	0-18
T (C)	9-30	10-30	12-27	9-33	10-29	11-28
WL (cm)	5-23	5-23	5-23	-60-7	-60-7	-60-7
%F (%)	100	100	100	0-100	0-100	58-100

Table 3. Pearson correlation coefficients for environmental and root mass loss data. Only statistically significant values are reported; all values are significant at $p < 0.01$ except where noted. T = soil temperature, WL = water table level, %F = percent of period given depth is flooded or saturated, RMR = root mass remaining, DRATE = root decomposition rate for previous period. N is in parentheses.

	Total NH_4-N	Total PO_4-P	K	Ca	Mg	Fe	Mn	Eh	pH	O_2	T	WL	%F	RMR
Total PO_4-P	0.81 (82)													
K	0.77 (81)	0.62 (81)												
Ca	0.70 (81)	0.76 (81)	0.61 (81)											
Mg	0.57 (81)	0.63 (81)	0.62 (81)	0.91 (81)										
Fe	0.64 (81)	0.68 (81)	0.43 (81)	0.84 (81)	0.58 (81)									
Mn	0.70 (81)	0.76 (81)	0.59 (81)	0.97 (81)	0.91 (81)	0.80 (81)								
Eh	-.25[a] (76)	-0.23[a] (76)				-0.33 (75)								
pH	-0.59 (80)	-0.59 (80)	-0.46 (79)	-0.65 (79)	-0.59 (79)	-0.56 (79)	-0.63 (79)	0.41 (76)						
O_2	-0.28[a] (79)	-0.28[a] (79)				-0.32 (78)		0.86 (94)	0.43 (79)					
T	0.46 (82)	0.43 (82)	0.46 (81)	0.46 (81)	0.42 (81)	0.41 (81)	0.43 (81)		-0.47 (82)	0.23[a] (99)				
WL					-0.32 (81)			-0.68 (96)		-0.78 (99)	-0.42 (102)			
%F								-0.76 (96)		-0.78 (99)	-0.32 (102)	0.73 (102)		
RMR	0.53 (28)	0.49 (28)						-0.39[a] (36)		-0.35[a] (36)		0.36[a] (36)	0.42[a] (36)	
DRATE	-0.75 (28)	-0.55 (28)	-0.50 (28)						0.51 (29)		-0.55 (36)			-0.36[a] (36)

[a] Significant at $p < 0.05$.

Root Decomposition in Greenhouse

Root mass decreased significantly during the study in all treatments (Figure 6). The analysis showed a significant (ANOVA, $p = 0.0002$) flooding effect on decomposition by the end of the study, as the non-flooded roots showed greater mass loss than the continuously flooded and periodically flooded roots. The continuously flooded and periodically flooded roots had 70% (±1.4) and 68% (±2.5) of their original mass remaining after 6 months, while the non-flooded roots had 54% (±4) mass remaining. Visual inspection revealed substantially more fragmentation of the root bundles by actively growing roots of the red maple seedlings in the non-flooded pots.

DISCUSSION

Decomposition of Roots

The decay of belowground roots is similar in some ways but dissimilar in others to the process of aboveground litter decay. The initial, relatively rapid loss of mass in the first few weeks or months is likely a result of leaching (Tupacz 1988). This first stage of root decay is quite comparable to what occurs in aboveground leaf litter (Day 1983). The differences in hydroperiod in the present study seemed to have no effect on initial leaching rates. Following the initial leaching loss, decomposition was arrested for the duration of the study in the continuously flooded mesocosm and for at least 6 months in the periodically flooded mesocosm. The late initiation of decay in the periodically flooded cell at 20 cm depth and the results of the correlation analysis suggest that the abiotic environment is influencing root decomposition but the coupling between the two is not tight. Divergence of the two major treatments is not apparent until the fifteenth month of the study. Just as aboveground litter decomposition is strongly influenced by the chemical and structural nature of the litter (Day 1982), our results support Tupacz's (1988) suggestion that the highly lignaceous property of roots accentuates this influence belowground. However, near the end of the study, abiotic and/or biotic environmental differences in the two mesocosms were beginning to have an effect on root decomposition.

Abiotic Environment

The correlation results indicate that reduced root decomposition is associated with increased duration of flooding or soil saturation and decreased redox potential, oxygen levels, and pH. Chronic anoxic conditions in the continuously flooded mesocosm could explain greater inhibition in the constantly flooded unit.

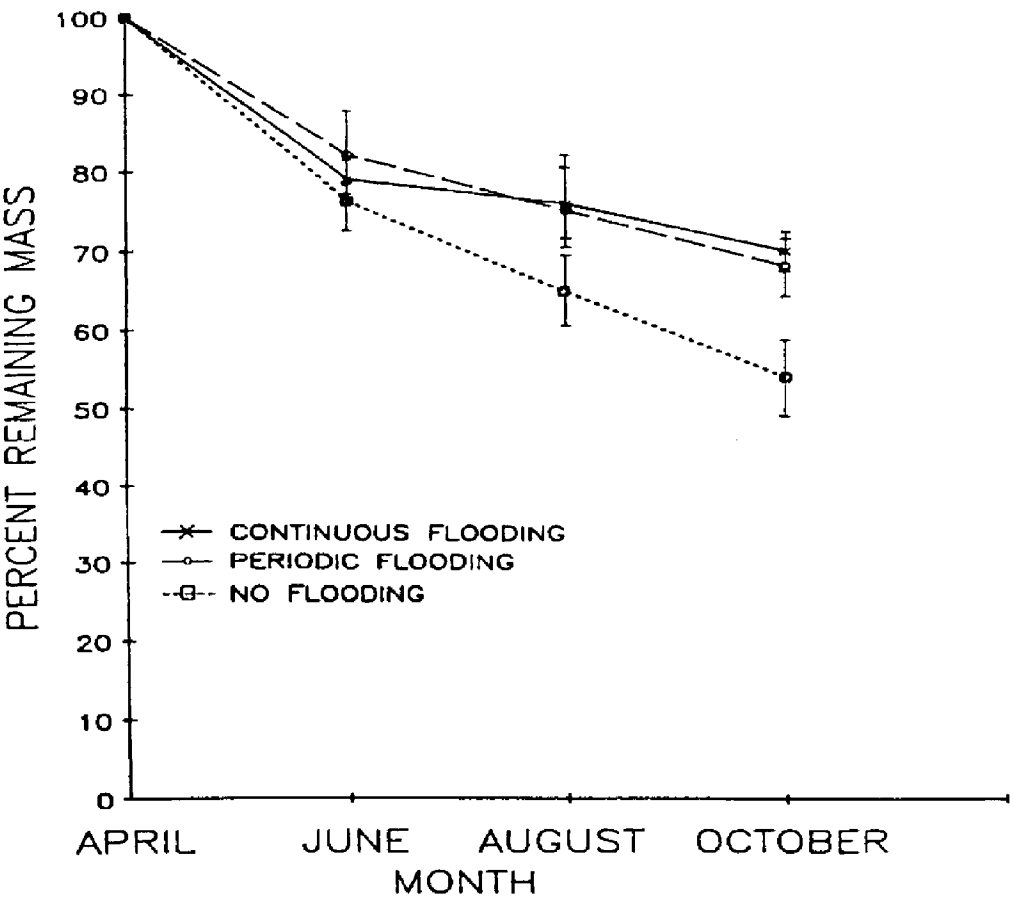

Figure 6. Mass loss from root bundles in greenhouse study. Vertical bars are ± 1 SE; N= 20.

The periodically flooded mesocosm, which did show accelerated decay later in the study, remained aerobic in the top 20 cm of soil throughout the study. In wetland ecosystems, anoxia is a commonly identified inhibitor of decay (Reddy and Patrick 1975, Swift *et al.* 1979, Kuhlman 1980, Brinson *et al.* 1981.) However, the unexpected relationships between reduced decomposition and increased NH_4-N, PO_4-P, and temperature and the slowness of response to changes in the abiotic environment still suggest that decomposition is not tightly coupled to abiotic factors.

The different hydroperiods created in this study certainly generated different microenvironmental conditions in the two mesocosms. Increased duration of flooding resulted in decreased redox potential and oxygen, which were strongly correlated with each other. Reduced redox and oxygen were associated with lower

pH and increased concentrations of NH_4-N, PO_4-P, and Fe. Nutrient levels in the soil water were generally higher in the constantly flooded mesocosm. This suggests that under reduced conditions in constantly flooded ecosystems, nutrients remain or are released into the soil water where they are subject to loss from the system. The availability of nutrients in continuously flooded forested wetlands might, therefore, be expected to decline over the long-term.

Biotic Environment

The lack of a high degree of association between root decomposition and the abiotic environment might point to biotic factors to explain the delayed acceleration of decay in the top 20 cm of the periodically flooded mesocosm. It may have taken 6 months for significant invasion of decomposer organisms to occur; this process is expected to be slower in woody detritus (Harmon *et al.* 1986). The prescence of living roots may also have had an effect on root decay in the periodically flooded treatment. Hackney (1987) suggested that living roots alter the chemical environment of the soil and may, therefore, accelerate decay of soil organic matter. In the mesocosms, the litter bags were buried at least 0.5 m from the nearest cypress seedlings, so roots in the litter bags were not initially in contact with living roots. Acceleration of decay in the periodically flooded mesocosm occurred at a time when living cypress roots from the seedlings had begun to penetrate the area around the litter bags. Living roots were found inside the bags from the periodically flooded treatment on the last two collections but not in bags from the continuously flooded treatment. Physical fragmentation of detritus by growing roots may play a role in accelerating root decomposition. In the greenhouse study, the most rapid root decay occurred in the non-flooded pots, and root production by the red maple seedlings was greatest in those pots (Day 1987). Penetration and fragmentation of the dead roots by live roots was observed. Fragmentation of soil detritus by growing roots may be an unappreciated force in organic turnover belowground.

Nutrient Dynamics in Decomposing Roots

Even though nutrient concentrations in soil water were higher in the continuously flooded mesocosm, the amounts of nutrients remaining in the continuously flooded roots were smaller. These mesocosm differences are probably a result of more extensive leaching losses from the roots in the constantly flooded cell due to continuous soaking (Day 1983) and net nitrogen accumulation in the more rapidly decomposing roots in the periodically flooded mesocosm due to more active microbial immobilization of N (Vogt *et al.* 1986). The accumulation of N in the periodically flooded roots is very similar to N accumulation observed in decomposing leaf litter (Day 1982). As suggested in reference to potentially greater nutrient

losses from constantly flooded systems, these data indicate that N is conserved in the belowground detritus of periodically flooded systems and these systems should, therefore, exhibit more conservative nutrient cycles.

Conclusions

Mesocosms allow quantitative measurements in controlled, yet reasonably realistic environments. We believe they represent a useful experimental approach to the study of belowground ecosystem processes. Departures from reality must be noted, however, and interpretations tempered accordingly. There were a couple of anomalies in the present study that we could not explain. Soil water pH decreased with increasing depth and decreasing redox potential, although increased pH is usually associated with declining redox. Also, soil water nutrient concentrations were significantly lower in the second year of the study compared to the first. This indicates a progressive loss of nutrients from both mesocosms. Regardless, we believe our study generated meaningful results.

The belowground environment, particularly in wetlands, produces a different abiotic and biotic regulatory complex than exists aboveground. Decomposition processes aboveground occur in essentially a horizontal plane, whereas belowground processes are more three dimensional. This necessitates a different approach to measurement (e.g., vertical litter bags) and a vertical characterization of the variation in microenvironment. Mesocosms provide a means to do this with a relatively high degree of precision.

The results of our study seem to demonstrate a very weak coupling between belowground root decompositon and the abiotic environment. Decomposition during the first year was apparently determined primarily by the leachable and recalcitrant fractions of the roots. The divergence of decay rates in the different hydroperiod treatments near the end of the study may be attributed to biotic factors, in particular the influence of living roots on decomposition. Regardless of what the controlling mechanisms are, root decomposition is quite slow, and this supports the contention that dead roots are the major contributor to the belowground organic matter pool.

The results of this study have several implications with regard to responses of restored or created wetlands to perturbation and to wetland management. If periodically flooded systems have more conservative nutrient cycles, they should retain nutrients more efficiently than continuously flooded systems. A system that is always flooded would not be expected to assimilate nutrient loadings as effectively. Natural wetland hydroperiods generally involve periodic flooding, and the hydrology of restored wetlands should consequently be managed for fluctuation.

The demonstrated importance of roots in ecosystem processes suggests that created wetlands will initially have impaired functions until the root systems have fully developed. Organics may significantly accumulate prior to full restora-

tion of belowground function. Regulation of wetlands is strongly tied to aboveground structure. We suggest that belowground processes are the key to a functional wetland.

ACKNOWLEDGMENTS

This research was supported by the National Environmental Research Park (NERP) program of the Savannah River Ecology Laboratory (SREL) and the Division of Wetlands Ecology under contract DE-AC09-76SR00-819 between the United States Department of Energy and the University of Georgia. The first author's travel to SREL was partially funded by an Oak Ridge Associated Universities Faculty Research Participation Travel Contract (S-3221). The greenhouse study was supported by National Science Foundation grant number BSR-8405222. We thank the following individuals for their assistance in various stages of the research: John Bailey, Claudia Mitchell, Jeff Owens, Rebecca Sharitz, Gary Wein, Jerry Garvin, Fred Stone, and Mike Scott. Revision of the manuscript was aided by helpful comments from Mark Brinson and an anonymous reviewer.

LITERATURE CITED

Bohm, W. 1979. Methods of Studying Root Systems. Springer-Verlag, New York, NY, USA.

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.

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.

Crooke, W.M. and W.E. Simpson. 1971. Determination of ammonium in Kjeldahl digests of crops by an automated procedure. Journal of Science of Food and Agriculture 22:9-10.

Day, F.P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63:670-678.

Day, F.P. 1983. Effects of flooding on leaf litter decomposition in microcosms. Oecologia (Berlin) 56:180-184.

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., S.K. West, and E.G. Tupacz. 1988. The influence of ground-water dynamics in a periodically flooded ecosystem, the Great Dismal Swamp. Wetlands 8:1-13.

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.

Ellison, A.M., M.D. Bertness, and T. Miller. 1986. Seasonal patterns in the belowground biomass of *Spartina alterniflora* across a tidal gradient. American Journal of Botany 73:1548-1554.

Gallagher, J.L. 1978. Decomposition processes: summary and recommendations. p. 145-151. *In* R.E. Good, D.F. Whigham, and R.L. Simpson (eds.) Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, NY, USA.

Hackney, C.T. 1987. Factors affecting accumulation or loss of macroorganic matter in salt marsh sediments. Ecology 68:1109-1113.

Hackney, C.T., and A.A. de la Cruz. 1980. *In situ* decomposition of roots and rhizomes of two tidal marsh plants. Ecology 61:226-231.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Harris, W.F., D. Santantonio, and D. McGinty. 1980. The dynamic belowground ecosystem. p. 119-129. *In* R.H. Waring (ed.) Forests: Fresh Perspectives from Ecosystem Analysis. Oregon State Univ. Press, Corvallis, OR, USA.

Kuhlman, E.G. 1980. Influence of moisture on rate of decay of loblolly pine root wood by *Heterobasidium annosum*. Canadian Journal of Botany 58:36.

McClaugherty, C.A., J.D. Aber, and J.M. Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481-1490.

McGinty, D.T. 1976. Comparative root and soil dynamics on a white pine watershed and in the hardwood forest in the Coweeta Basin. Ph.D. Dissertation. University of Georgia, Athens, GA, USA.

Odum, E.P. 1984. The mesocosm. Bioscience 34:558-562.

Patrick, W.H. 1977. Oxygen content of soil air by a field method. Soil Science Society of America Proceedings 41:651-652.

Reddy, K.R. and W.H. Patrick. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition, and nitrogen loss in a flooded soil. Soil Biology and Biochemistry 7:87-94.

Swift, M.J., O.W. Heal, and J.M. Anderson. 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publishers, London, England.

Tupacz, E.G. 1988. Decomposition of roots in the Great Dismal Swamp. M.S. Thesis. Old Dominion University, Norfolk, VA, USA.

U.S. Environmental Protection Agency. 1983. Methods for chemical analysis of water and wastes. Environmental Monitoring and Support Laboratory. Office of Research and Development, U.S. EPA, Cincinnati, Ohio, USA.

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.

Waid, J.S. 1974. Decomposition of roots. p. 175-211. *In* C.H. Dickinson and G.J.F. Pugh (eds.) Biology of Plant Litter Decomposition. Academic Press, New York, N.Y., USA.

Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: a community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, DC, USA FWS/0BS-81/37.