Aboveground production and nutrient circulation along a flooding gradient in a South Carolina Coastal Plain forest[1]

Marianne K. Burke, B. Graeme Lockaby, and William H. Conner

Abstract: Relative to effects of flooding, little is known about the influence of hydrology–nutrient interactions on aboveground net primary production (NPP) in forested wetlands. We found that nutrient circulation and NPP were closely related along a complex physical, chemical, and hydrologic gradient in a bottomland hardwood forest with four distinct communities. Aboveground biomass, NPP, biomass partitioning to stem production, growth efficiency, and soil macronutrient availability were greatest in the flooded zone, possibly because of the stable hydrologic regime. In the wet transition zone, trees were least productive, nutrient use efficiency was highest, and N retranslocation from foliage before abscission was "complete." Wet and dry transition zones had the lowest litterfall quality. Soil organic matter was negatively correlated with extractable NH_4-N plus NO_3-N before in situ incubations and positively correlated with litterfall lignin/N ratios. Lignin/P and C/N ratios were positively correlated with exchangeable soil Ca and Mg, cation exchange capacity, and clay content and negatively correlated with extractable soil P. We concluded that periodic flooding and associated widely fluctuating soil chemistry resulted in disequilibrium between the plant community and environmental conditions, which led to nutrient deficiency and low NPP in the transition zones compared with the continuously flooded and mesic zones.

Résumé : En relation avec les effets des inondations, on connaît peu de choses de l'influence des interactions entre l'hydrologie et les nutriments sur la production primaire nette aérienne (PPN) des terres humides boisées. Nous avons observé que la circulation des nutriments et la PPN étaient étroitement reliées le long d'un gradient physique, chimique et hydrologique complexe dans une forêt feuillue des basses terres comportant quatre communautés distinctes. La biomasse épigée, la PPN, la répartition de la biomasse dans la production de tiges, l'efficacité de croissance et la disponibilité du sol en macronutriments étaient plus élevées dans la zone inondée, probablement à cause du régime hydrologique stable. Dans la zone de transition humide, les arbres étaient moins productifs, l'efficacité d'utilisation des nutriments était la plus élevée et la retranslocation de N du feuillage avant l'abcission était « totale ». Les zones de transition humide et sèche avaient la plus faible qualité de litière. La matière organique du sol était négativement corrélée à $N\text{-}NH_4$ plus $N\text{-}NO_3$ extractibles avant les incubations in situ et positivement corrélée aux rapports lignine/N de la litière. Les rapports lignine/P et C/N étaient positivement corrélés à Ca et Mg échangeables du sol, à la capacité d'échange des cations et au contenu en argile, et négativement corrélés au P extractible du sol. Nous en concluons que les inondations périodiques et la grande fluctuation de la chimie du sol associée aux inondations se traduisent par un déséquilibre entre la communauté floristique et les conditions environnementales, résultant en une déficience nutritionnelle et une faible PPN dans les zones de transition comparativement aux zones continuellement inondées et aux zones mésiques.

[Traduit par la Rédaction]

Introduction

Annual aboveground net primary production (NPP) ranges from 300 to 2000 g/m^2 in forested wetlands of the South Atlantic Coastal Plain (Conner 1994). This range has been attributed to differences in hydroperiod (Megonigal et al. 1997), salinity of groundwater (Brinson et al. 1985), and successional stage (Muzika et al. 1987). There has been little published on the influence of biogeochemistry on NPP in these forests, although hydroperiod and biogeochemistry interact and can have an integrated influence on NPP.

To date, comparisons of aboveground NPP in forested wetlands are based on hydroperiod (e.g., Megonigal et al. 1997), and conceptual models developed from such comparisons indicate that flooding can have positive or negative effects on production depending on timing, duration, and hydrologic energy (Odum 1978; Mitsch and Ewel 1979; Brinson et al. 1981; Taylor et al. 1990; Odum et al. 1995). The "subsidy-stress" model introduced by Odum (1974) and adapted by Lugo (1978) proposed that greatest NPP should occur where floods are periodic and of short duration, resulting from the subsidy of water and nutrients. Also, the model

Received September 25, 1998. Accepted April 22, 1999.

M.K. Burke.[2] USDA Forest Service, Center for Forested Wetlands Research, Charleston, SC 29414, U.S.A.
B.G. Lockaby. School of Forestry, Auburn University, Auburn, AL 36849, U.S.A.
W.H. Conner. Belle W. Baruch Forest Science Institute, Clemson University, Georgetown, SC 29442, U.S.A.

[1]Technical Contribution No. 99-02 of the Belle W. Baruch Forest Science Institute, Clemson University, Georgetown, S.C.

[2]Corresponding author. e-mail: burkem@cofc.edu

© 1999 NRC Canada

proposed that low NPP at hydrologic extremes was caused by physiological stress where floods endured and the lack of nutrient and moisture subsidies in unflooded zones. Studies of shallow-water impoundments support this hypothesis (Broadfoot 1967). A contrasting hypothesis offered by Mitsch and Rust (1984) suggested that potential subsidies of periodic flooding could be negated by the physiological stresses to trees produced by anaerobic soil during the growing season. A recent test of these hypotheses showed that, in the southeastern United States, a more complex interaction between subsidy and stress factors exist (Megonigal et al. 1997). "Subsidy stress," therefore, did not totally explain the variation in NPP in wetland forests, although published data generally supported that hypothesis.

Brinson (1993) pointed out that focusing only on "wetness" limits our ability to explain variation in the functioning of wetlands along hydrologic gradients. Forested wetlands are linked biogeochemically with uplands, which in conjunction with the complex chemical changes associated with anaerobic conditions, create complex chemical changes along wetness gradients.

Nutrient cycling processes have been all but ignored in watersheds containing forested wetlands in the southern United States, although such wetlands can be sources, sinks, and transformers of nutrients (e.g., Richardson 1994). The influence of nutrient availability on NPP and organic matter decomposition is well known, but many of the biochemical processes that regulate responses to nutrient availability are poorly understood. It follows that nutrient cycling is the process that integrates many other functions of an ecosystem. One particularly important process is the retranslocation of nutrients into perennial tissue before litterfall, which conserves nutrients and influences NPP. The contribution of internal retranslocation to the annual nutrient requirements of perennial vegetation may be considerable (Switzer and Nelson 1972; Kimmins 1987). While the relative magnitude of nutrient retranslocation has generated appreciation for its importance in plant nutrition, a thorough understanding of the process of internal retranslocation remains elusive. Much of the fundamental interest in internal translocation has focused on its possible role as an adaptation to low nutrient availability, and some evidence suggests that internal retranslocation efficiency, i.e., the proportion of the annual maximum foliar content retranslocated prior to senescence, increases as nutrient availability decreases (Ostman and Weaver 1982; Boerner 1984; Kimmins 1987).

Other reports indicate that relationships between nutrient availability and internal retranslocation efficiency are uncertain. Results from controlled studies have shown increases (Nambiar and Fife 1987), decreases (Dalla-Tea and Jokela 1994), and no change (Crawford et al. 1991) in the internal retranslocation efficiency of fertilized pine. There are indications that increased internal retranslocation efficiency for N is related to increases in ratios of soluble to insoluble proteins, but it is uncertain whether soluble proteins are elevated or reduced by low nutrient availability (Lajtha 1987; Pugnaire and Chapin 1993). Small (1972) and Pugnaire and Chapin (1993) have suggested that N retranslocation varies with fertility more than P does, but this may merely reflect a greater tendency for N to be limiting in some systems.

While it is acknowledged that internal retranslocation is a critical process in plant nutrition, the biotic and abiotic controls over that process are uncertain (Pugnaire and Chapin 1993). Our lack of understanding is particularly acute in forested wetlands because hydroperiod exerts a strong influence on nutrient availability, vegetation composition, and NPP. A limited number of internal translocation efficiency investigations in wetlands support the nutrient conservation strategy (Small 1972; Walbridge 1991) and document that retranslocation of both N and P occur (Schlesinger 1978; DeLucia and Schlesinger 1995). However, no comparisons of internal retranslocation efficiency and related indices of nutrient cycling efficiency have been made of different community–hydroperiod complexes. Trees that retranslocate large amounts of nutrients before leaves abscise have high nutrient use efficiencies (NUE) in biomass production and return a smaller quantity of nutrients to the forest floor with litterfall. Estimated as the ratio of litterfall mass to nutrient content, NUE is sometimes used as a surrogate for nutrient availability (Barnes et al. 1998, p. 554). Generally, limited N or P availability results in greater retranslocation before leaf abscission, which increases NUE. Trees that can conserve nutrients through high NUE have a competitive advantage on nutrient-poor sites (Pastor et al. 1984), and trees that can respond to differences in nutrient availability through adjustment in NUE can increase their ecological range of sites (Zak et al. 1986). It is still unknown how differences in hydroperiod, and the resulting differences in vegetative community structure and function, influence the manner by which nutrients are cycled.

We attempted to resolve some of these questions and quantify differences in woody plant community structure, aboveground NPP, biomass partitioning, and nutrient circulation in aboveground tissue in four vegetation zones on a flooding gradient. Compared with other forested wetland sites in the southeastern United States, the study site has low N availability relative to P (Lockaby and Walbridge 1998). We tested hypotheses relating aboveground NPP to hydroperiod and nutrient circulation: (*i*) production should be greatest where floods are periodic and of short duration and lowest where continuous flooding occurs (subsidy stress), (*ii*) NUE should be lower for either excessively flooded or drained conditions, and (*iii*) soil N availability should be positively related to aboveground NPP and inversely related to NUE.

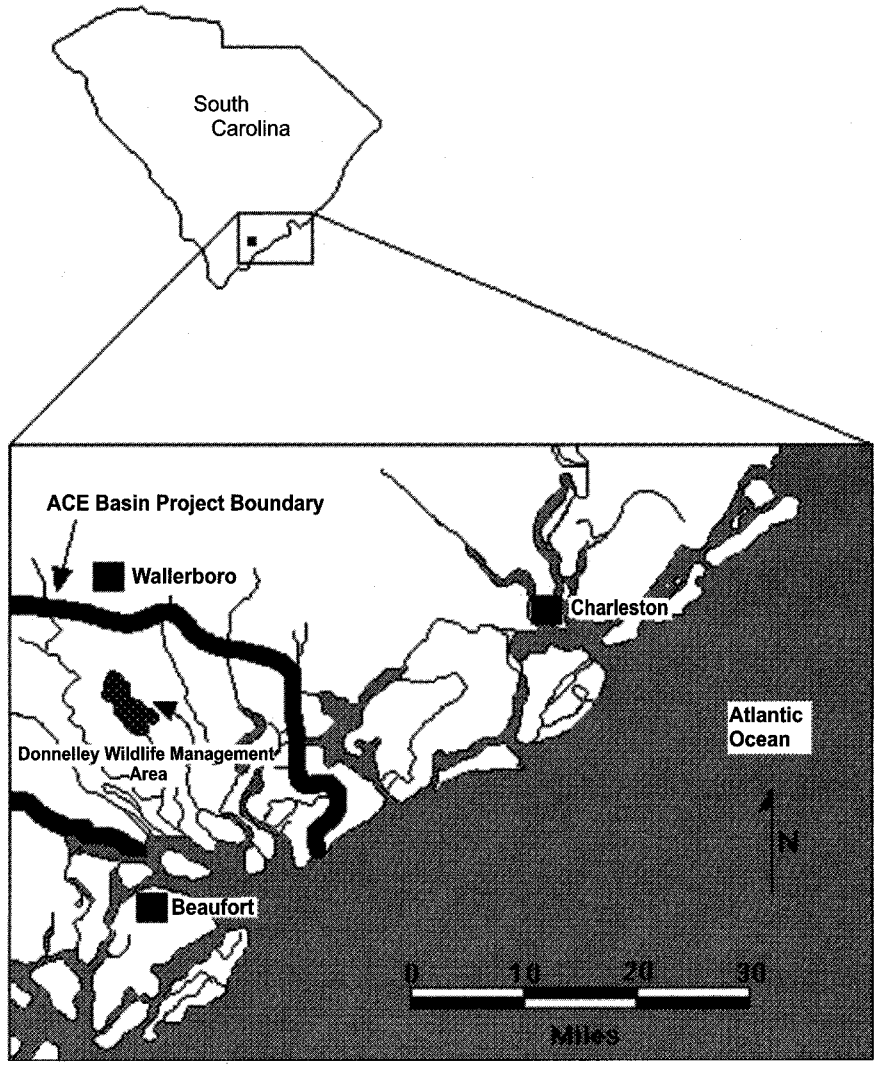
Methods

Study area

The study site is within the Donnelley Wildlife Management Area near Green Pond, S.C. (32°40′N, 80°40′W), in Colleton County (Fig. 1). Before 1700 the study site was probably under freshwater tidal influence flooded by the Chehaw River, a tributary of the Combahee River. During the early 1700s, dikes were built that excluded the site from the river and the tidal influence of the Helena Sound Estuary. Rice cultivation along the Chehaw River floodplain followed, and the site was used as a freshwater reservoir for summer flooding of the rice fields. Rice cultivation ended in the early 1900s, following a hurricane that damaged the dikes. Today, the former rice fields, freshwater swamps, and surrounding uplands are managed for wildlife habitat by Ducks Unlimited and the South Carolina Department of Natural Resources and Marine Fisheries (D. Gordon, USDI Fish and Wildlife Service, personal communication).

© 1999 NRC Canada

Fig. 1. Location of the Donnelly Wildlife Management Area within the ACE Basin Project in South Carolina. (1 mile = 1.609 344 km.)

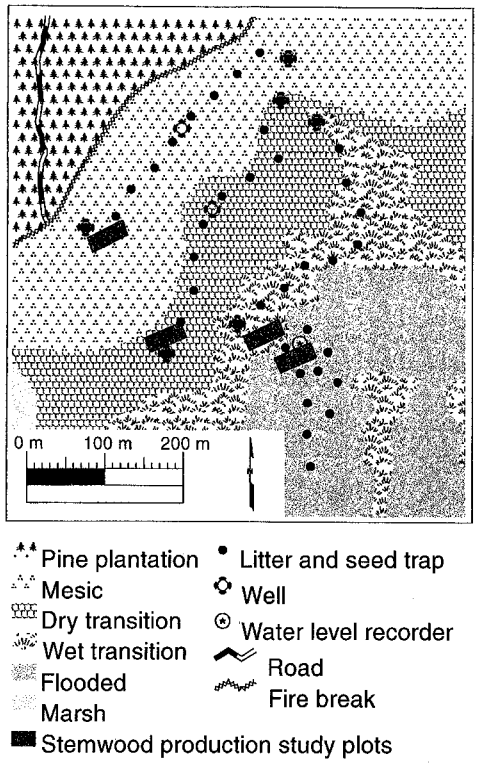


Four hydrologic regimes were determined from site inspection: permanently flooded (flooded), seasonally and intermittently flooded (wet transition), seasonally ponded (dry transition), and not flooded (mesic) zones (Fig. 2). Soils in the flooded and wet transition zones are classified as a Cape Fear loam, a loamy, siliceous, thermic Typic Umbraquult (Stuck 1982). This soil is very poorly drained and nearly level, the type typically found in low depressional areas and in the drainages of lower marine terraces. The surface is black loam about 7 cm thick, and the subsoil (B horizon) is dark-gray clay to a depth of 90 cm. Clay content is 5–60%, pH ranges from 4.5 to 6.5, and permeability is 0.2–0.5 cm/h. Underlying material is gray sand to 210 cm. Soils in the dry transition and mesic zones are classified as Argent loam, fine, mixed, thermic Typic Ochraqualf (Stuck 1982). This nearly level soil also is poorly drained with a permeability of 0.2–1.5 cm/h. There is a 12 cm deep surface of dark gray loam with a grayish clay and grayish clay loam subsoil to about 40 cm. Soil pH ranges from 3.6 to 6.0 above the 130 cm depth and 5.6 to 8.4 in the underlying material.

The mesic site is a mixed pine–hardwood community with a well-developed canopy dominated by cherrybark oak (*Quercus falcata* Michx. var. *pagodifolia* Ell.), swamp chestnut oak (*Quercus michauxii* Nutt.), white oak (*Quercus alba* L.), water oak (*Quercus nigra* L.), longleaf pine (*Pinus palustris* Mill.), loblolly pine (*Pinus taeda* L.), spruce pine (*Pinus glabra* Walt.), shortleaf pine (*Pinus echinata* Mill.), sweetgum (*Liquidambar styraciflua* L.), and mockernut hickory (*Carya tomentosa* (Poir.) Nutt.). The dry transition community is diverse with the canopy dominated by cherrybark oak, swamp chestnut oak, willow oak, water oak, and laurel oak (*Quercus laurifolia* Michx.), loblolly pine, spruce pine, and shortleaf pine with sweetgum, mockernut hickory, American elm (*Ulmus americana* L.), yellow-poplar (*Liriodendron tulipifera* L.), and black cherry (*Prunus serotina* Ehrh.). The understory is sparse and composed of scattered red maple (*Acer rubrum* L.) and ironwood (*Carpinus caroliniana* Walt.). The canopy of the wet transition site is dominated by swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) with water tupelo (*Nyssa aquatica* L.), red maple, green ash (*Fraxinus pennsylvanica* Marsh.), laurel oak, sweetgum, water oak, willow oak (*Quercus phellos* L.), and American elm. There is very little understory in this zone. Flooded year round, the number of species in the flooded site is small, with water tupelo the dominant canopy species with some swamp tupelo and green ash. Scattered red maple occur in the understory. No known forest management history is available for the study site, although surrounding forests were managed for agriculture and pine plantations (D. Harrigal, South Carolina Department of Natural Resources and Marine Fisheries, personal communication). Records or personal recollections of when logging occurred on the

© 1999 NRC Canada

Fig. 2. Map of the study site within the Donnelly Wildlife Management Area showing the location of plots, traps, wells, water level recorder, and vegetation zones.



study site have not been found. Based on the lack of stumps, large size of trees, and species composition generally found in the later stages of stand development (Sharitz and Mitsch 1993; Meadows and Nowacki 1996), we assumed that there has been no logging on the study site during the past 50–75 years and that the stands were similar in age.

Field procedures

In September 1993, a 200 m long transect was established in each of the four zones (Fig. 2). The transects, placed along contours in each hydrologic zone, ranged from approximately 75 to 200 m apart, and reference points were located every 20 m. Two 20 × 25 m plots were located with the long axis on the contour on each transect. Within each plot, all trees ≥10 cm diameter at breast height (DBH) were identified to species, tagged, and measured for DBH at marked locations on each stem. Diameters were measured on November 11, 1993; January 10, 1995; and January 5, 1996 at the marked locations and changes in diameter were used to estimate annual basal area.

Production of foliage and reproductive tissue was estimated by collecting litter at each reference point in 0.5-m^2 litter–seed traps (Phillips et al. 1995), which were installed on September 23, 1993. Traps were emptied every 10–32 days, depending on the amount of litterfall, from September 1993 to September 1995. Litterfall associated with the nutrient-cycling portion of this study was collected from the littertraps September 1994 to August 1995. Live foliage was collected from 37 trees from 9 species during midsummer by shooting foliage in the upper third of crowns on the southern side of codominant trees.

In April 1995, three wells were installed in each of the mesic and in the dry transition zones, and two wells were installed in the wet transition zone, one at each end of the transect. Depth to water table was measured monthly from April to November 1995. Water level in the flooded zone was continuously recorded using one Stephens water level recorder (Leopold and Stevens, Inc., Beaverton, Oreg.). Relative elevations for each well and reference point were estimated from a topographic survey.

Four soil samples per transect were collected on November 28, 1996, using a 2.5 cm push probe for analysis of nutrient and physical characteristics. Each sample was a bulked composite of five subsamples collected from one corner of the 4-m^2 plots with centers at littertraps 2, 4, 6, 8, and 10 in each transect. Cores were taken from the surface 15 cm of soil after the leaf litter layer was removed.

Nitrogen plant availability was indexed using in situ soil incubations. At three randomly chosen points on each transect, approximately 200 g of soil was collected from the surface 15 cm of soil below the forest floor and thoroughly mixed on June 6, July 7, August 8, September 9, and October 10, 1997. One half of each sample was incubated in situ in sealed plastic bags for 1 month before being processed, and the other half was processed immediately as described below.

Laboratory procedures

Soil samples for nutrient and physical parameter measurements were air-dried and ground twice to pass through a 2-mm screen. The samples were analyzed at Waters Laboratory in Camilla, Ga., for pH, soil organic matter using the Walkley and Black (1934) method, total calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), manganese (Mn), and zinc (Zn) with an inductively coupled plasma emission spectrometer (ICP) after double acid extraction (Soltanpour et al. 1982). Soil texture was analyzed by the hydrometer method (Day 1965) at the Center for Forested Wetlands Research.

Fresh soil from in situ incubations was refrigerated at 4°C, extracted using 2 M KCl within 48 h as in Burke et al. (1992), and analyzed for nitrate using a Technicon autoanalyzer I and for ammonium using a Wescan ammonium analyzer by Waters Laboratory.

For each of the nine tree species studied (n = 1 – 6), surface area and mass of individual leaves were measured for green and abscised foliage. An average of four green leaves per subsample (three to five subsamples) per trap location were collected for leaf area determination and nutrient analysis. Mass per square centimetre of leaf area was estimated for each subsample.

Materials collected from litterfall traps was sorted into foliage, seeds, woody components, and miscellaneous reproductive material. All biomass intended for chemical analysis was dried at 70°C for 48 h and then ground to pass through a 20-mesh (0.85 mm) sieve. The laboratory procedure for determination of nutrient reabsorption followed those outlined in Crawford et al. (1991).

Bulk litterfall samples and the leaves of individual tree species were analyzed for C, N, P, and lignin, while live foliage was analyzed for N and P. Thermal combustion was used for C and N determination (Perkin-Elmer 2400 CN analyzer, Norwalk, Conn.). Phosphorus was determined colorimetrically using a HCl color indicator solution, and lignin was analyzed using a forage fiber analysis method (Van Soest and Wine 1986). Individual leaf dry masses and dimensions were used to calculate retranslocation based on surface area, individual leaf mass, and percent foliar content.

Data analyses

The mean, maximum, and minimum growing-season water levels were calculated for the three driest zones, while water level in the flooded zone was averaged on a daily basis. Annual litter- and seed- fall were estimated for each trap. When data were missing, they were replaced by the average of other litter traps in that community during the same time period. We assumed that the error terms for each trap were uncorrelated across time. Because all traps were collected simultaneously, variance in the average annual total was calculated by summing the variance for each time period.

© 1999 NRC Canada

Fig. 3. Relative locations of soil surface, seasonal maximum and minimum water levels for each vegetation zone, and the bottom of the well in the dry transition zone. The datum is the soil surface at the water level recorder in the flooded zone. The hydrologic gradient between flooded and dry transition is negligible (0.003%).

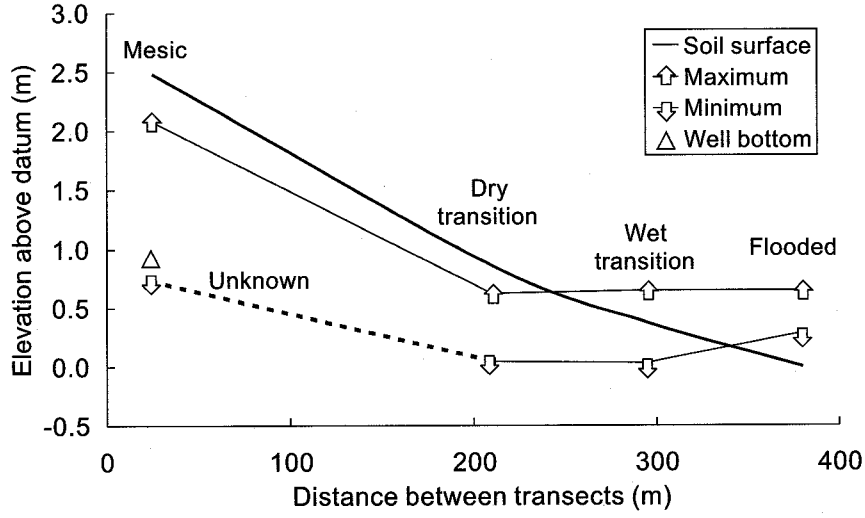


Table 1. Hydrologic characteristics, tree density, and basal area in the four vegetation zones.

	Vegetation zone			
Parameter	Flooded	Wet transition	Dry transition	Mesic
Mean annual water depth (cm)	47	–4	–57	–128
Minimum water depth (cm)	>0	–30	–80	<–150
Maximum water depth (cm)	86	30	–20	–40
Relative elevation (m)	0	0.4	0.9	2.5
Tree density (trees/ha)*	520 (80.1)*ab*	700 (40.4)*a*	430 (9.9)*ab*	330 (9.9)*b*
Basal area (m^2/ha)	39.4 (1.7)*a*	27.1 (2.1)*b*	32.6 (2.3)*ab*	27.3 (2.3)*b*

Note: Values for density and basal area are means with SE given in parentheses. Values within rows followed by the same letter are not significantly different (p = 0.05).

*Variance of tree density was heterogeneous according to Hartley's test, so the ANOVA was performed after natural log transformation.

The standard error of the mean was calculated using this total variance and assuming that the sample size was actually 10.

Stemwood production was calculated using DBH measurements and regression equations for each species from Clark et al. (1985) to estimate changes in biomass. Aboveground NPP for each zone was determined by summing the annual estimates of litterfall, seedfall, and stemwood production.

Internal retranslocation efficiencies were calculated according to Ostman and Weaver (1982), Boerner (1984), and Kimmins (1987) as [(midsummer N or P content – abscised content)/midsummer content] × 100. Nutrient reabsorption proficiencies were made using N and P concentrations and content per square centimetre of abscised leaf material, according to Killingbeck (1996). Reabsorption proficiency was graded by Killingbeck as "complete" when nutrients in senesced leaves were <0.7% N or <0.05% P or their content based on leaf surface area was <50 μg N/cm^2 or <3 μg P/cm^2, "incomplete" when nutrients in senesced leaves were >1% N or >0.08% P or >75 μg N/cm^2 or >8 μg P/cm^2, and otherwise, reabsorption proficiency was "intermediate."

Soil N availability was indexed as the KCl-extractable nitrate plus ammonium before incubation. Increases in nitrate and ammonium during incubation suggested nitrification and N mineralization, and decreases suggested N immobilization or denitrification.

Statistical analyses were used to judge differences between the zones, but because the zones were not replicated the presence or absence of a difference cannot be interpreted as unequivocal support for hydrologic or nutrient effects. Linear correlations among soil properties, soil nutrient availability indices, foliar nutrient and litter quality characteristics, and primary production estimates were estimated using Pearson correlation analysis procedure of SAS (SAS Institute Inc.1985). To ensure homogeneity of variance we used Hartley's test (Winer 1971), and if variance was not homogeneous, we used natural logarithms to transform data before analyzing them with ANOVA, Tukey's HSD test, and the general linear model procedure of SAS (SAS Institute Inc. 1985). Probability levels for mean separation tests were set at 0.05 unless otherwise specified. When the interaction of month and zone were contrasted for soil N availability, a Bonferroni alpha level of 0.0004 (0.05/120) was used. As was the case with laboratory methods, statistical analyses of reabsorption data were guided by those used in Crawford et al. (1991) where a 0.10 probability level was used. This significance level was selected based on the comparisons of a relative index for reabsorption rather than estimates of absolute nutrient contents involved in this process.

Results

Hydrologic gradient

There was a distinct hydrologic gradient perpendicular to the transects (Fig. 3, Table 1). There was continuous

© 1999 NRC Canada

Fig. 4. Water level in the flooded zone during the study. The mean elevation of the wet transition and dry transition zones are given to illustrate the differences in hydroperiod among the three vegetation zones.

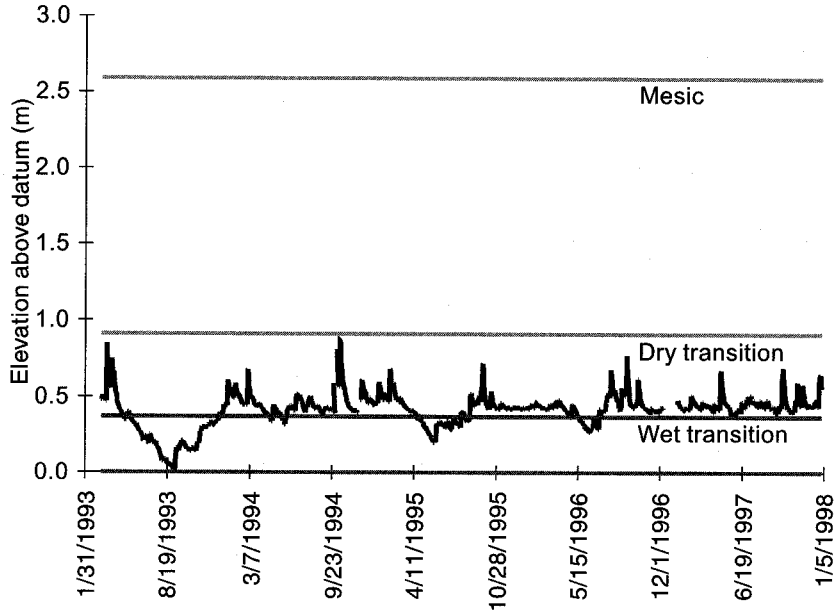


Table 2. Soil characteristics in the four vegetation zones.

	Vegetation zone			
Soil characteristic	Flooded	Wet transition	Dry transition	Mesic
Calcium (μg/g)*	2042 (423)*a*	1908 (109)*a*	1048 (75)*a*	328 (76)*b*
Potassium (μg/g)	11 (1)*c*	33 (1)*b*	36 (2)*b*	48 (4)*a*
Magnesium (μg/g)	323 (14)*a*	258 (16)*b*	157 (8)*c*	67 (9)*d*
Phosphorus (μg/g)	1.1 (0.1)*b*	1.5 (0.7)*b*	3.5 (0.4)*a*	4.2 (0.4)*a*
Manganese (μg/g)	3.2 (0.1)*b*	3.2 (0.3)*b*	2.8 (0.8)*b*	19.2 (2.0)*a*
Zinc (μg/g)	0.8 (0.2)*ab*	0.8 (0.1)*ab*	1.5 (0.2)*a*	0.7 (0.1)*b*
pH	4.8 (0.1)*ab*	5.0 (0.1)*a*	4.1 (0.1)*c*	4.5 (0.1)*b*
Soil organic matter (%)	5.5 (0.2)*a*	3.6 (0.5)*b*	5.7 (0.2)*a*	6.0 (0.3)*a*
CEC (cmol/kg)	18.5 (2.1)*a*	15.6 (1.0)*ab*	12.4 (0.2)*bc*	8.2 (0.4)*c*
BS (%)	68.0 (6.6)*ab*	75.8 (0.9)*a*	53.2 (2.4)*bc*	27.8 (4.5)*c*
BS Ca (%)	52.9 (7.5)*ab*	61.3 (0.7)*a*	41.9 (2.1)*b*	19.6 (3.9)*c*
BS K (%)	0.2 (0.02)*c*	0.6 (0.05)*b*	0.8 (0.03)*b*	1.5 (0.1)*a*
BS Mg (%)	14.9 (1.2)*a*	13.9 (0.4)*a*	10.5 (0.4)*b*	6.7 (0.7)*c*
BS H (%)	32.0 (6.4)*bc*	24.3 (0.9)*c*	46.8 (2.4)*b*	72.2 (4.5)*a*
Clay (%)	49.5 (0.5)*a*	37.6 (0.7)*b*	21.9 (1.2)*c*	10.6 (0.9)*d*
Sand (%)	31.0 (0.4)*a*	35.5 (1.2)*a*	58.6 (1.5)*b*	79.1 (1.0)*c*

Note: Values are means with SE given in parentheses. Values within rows followed by the same letter are not significantly different at $p = 0.05$.

*Variance was heterogeneous according to Hartley's test, so the ANOVA was performed on natural log transformed data.

standing water in the flooded zone, but the water level fluctuation resulted in extended episodes of flooding in the wet transition zone during the growing seasons (Fig. 4). Although never flooded, surface ponding occurred during the autumn, winter, and spring in the dry transition zone. Ponding was not observed in the mesic zone.

Soil characterization

In addition to a flooding gradient, there was a complex soil chemical and physical gradient. Soil organic matter (SOM) was lower in the wet transition zone than in all other zones (Table 2), and there was a decline in the cation exchange capacity (CEC) up the flooding gradient. Extractable Ca and percent base saturation (BS) by Ca was lower in the mesic (<0.5) than in the other zones, extractable K increased up the elevational gradient, and there was a strong decline in extractable Mg up the gradient. Percent BS and percent clay decreased up the gradient while percent sand increased. High clay content in the two wettest zones, neutral to basic subsoil, and low position of these zones in the watershed

© 1999 NRC Canada

Fig. 5. Mean (±1SE) of extractable ammonium (△) and nitrate (○) before incubation and the change in extractable ammonium (shaded bars) and nitrate (open bars) during incubation for monthly in situ incubations initiated June 6, July 7, August 8, September 9, and October 10, 1997 (n = 3).

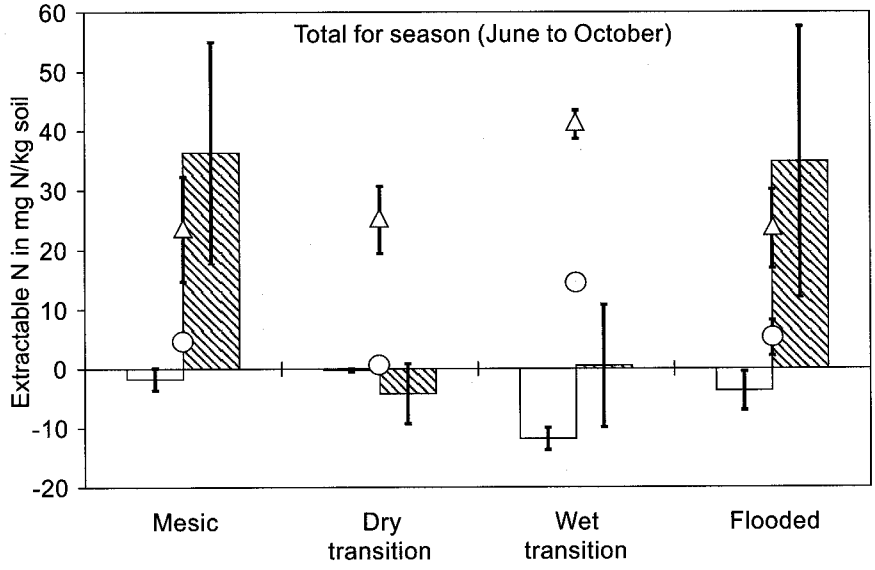


Table 3. Aboveground production in four hydrologic zones during two consecutive years.

Year	Hydrologic zone	Litterfall (g/m^2)	Seedfall (g/m^2)	Stemwood (g/m^2)	Total (g/m^2)
1993–1994	Mesic	634.3 (41.2)	20.2 (8.7)	607 (23)	1262
	Dry transition	625.0 (25.6)	13.9 (5.8)	505 (28)	1144
	Wet transition	489.4 (36.9)	22.4 (11.4)	570 (92)	1082
	Flooded	530.2 (16.5)	40.7 (12.0)	908 (94)	1479
1994–1995	Mesic	544.2 (32.2)	16.8 (7.0)	566 (57)	1127
	Dry transition	524.8 (24.7)	24.0 (8.6)	420 (62)	969
	Wet transition	335.6 (30.0)	20.0 (9.9)	448 (1)	804
	Flooded	300.2 (17.3)	69.6 (25.5)	854 (58)	1224

Note: Values are means with SE given in parentheses.

certainly contributed to the high soil extractable Ca and Mg concentrations, percent BS, and CEC in the flooded zones. In contrast, the low Ca and Mg concentrations, percent BS, and CEC in the dry transition and mesic zones was probably related to the high sand content and acidic subsoil. Soil P was lower in the flooded (<0.5) than in the drained zones.

Generally, N availability (indexed by KCl-extractable nitrate plus ammonium before incubation) was similar among the zones and ammonium was greater than nitrate (Fig. 5). The exception was the wet transition zone, where this index of N availability was greater than in the other zones during July and August, and extractable nitrate was greater than ammonium in July before incubation. Accumulation of ammonium during incubation (N mineralization) was greater than accumulation of nitrate (nitrification) in all zones for all months, and nitrate loss during incubation (immobilization or denitrification) was significant in the wet transition in July.

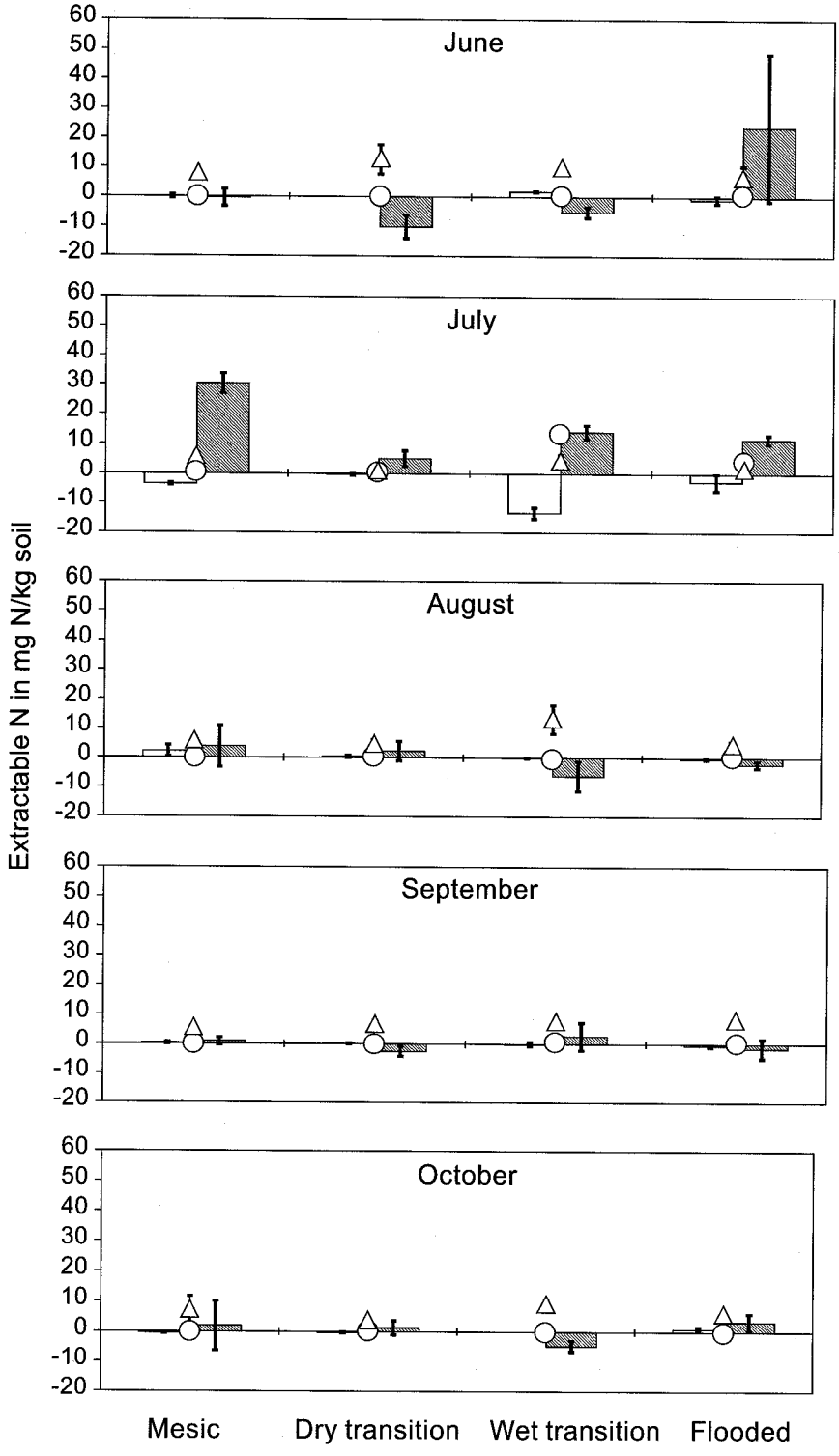
Seasonal mean N availability (indexed by the average of KCl extractable nitrate plus ammonium before all incubations for all months) was greater in the wet transition zone (56 mg N/kg soil) than in the other zones (26–29 mg N/kg soil) because of high initial NO_3-N concentrations (Fig. 6). Seasonal mean accumulation of ammonium during incubation was greater in the mesic and flooded zones (36 and 35 mg N/kg soil) than in the dry transition (–4.2 mg N/kg soil) and wet transition (0.5 mg N/kg soil) zones. There was a mean net loss of nitrate during incubation in all zones, but losses in the flooded and wet transition zones (–3.8 and –12.0 mg N/kg soil) were significantly greater than in the other zones (–0.2 to –1.8 mg N/kg soil).

Aboveground production

Tree densities in the wet transition zone were 89% greater than in the mesic zone and basal area was 45% greater in the flooded zone than in the wet transition and mesic zones (Table 1). During both years of the study, total aboveground NPP was greatest in the flooded zone and least in the wet transition zone (Table 3). Using years as replicates (n = 2), the mean annual aboveground NPP in the flooded zone (1352 g/m^2) was greater than in the dry transition (1056 g/m^2) and wet transition zones (943 g/m^2) (p = 0.009). Production in the mesic zone (1194 g/m^2 per year) was not significantly different from production in the flooded zone.

© 1999 NRC Canada

Fig. 6. Mean (±1SE) of total (seasonal sum at each sample location) extractable ammonium and nitrate before incubation and the change in extractable ammonium and nitrate during incubation for monthly in situ incubations (n = 3). Symbols, shading, and dates of initiation are the same as in Fig. 5.



Annual stemwood production was greater in the flooded zone (881 g/m^2) than in the other zones, and greater in the dry zone (586 g/m^2) than in the wet transition (509 g/m^2) and dry transition (462 g/m^2) zones (p = 0.002). Stemwood production in sweetgum and red maple comprised 43 and 18% of total stemwood production, respectively, in the wet transition zone but an insignificant amount (<5%) in the other zones.

Mean annual foliar litterfall was not significantly greater (p = 0.1) in the mesic zone (589 g/m^2) than in the flooded (415 g/m^2) and wet transition (412 g/m^2) zones. Greater biomass partitioning to stemwood in the flooded zone resulted

© 1999 NRC Canada

in more than two thirds of the aboveground biomass production occurring in the bole. By contrast, partitioning to stemwood production was between 44 and 53% in the other three zones. In all zones, NPP was lower the second year than the first, and in all zones, litterfall constituted most of the differences. The largest difference in litterfall (230 g/m^2 per year) was in the flooded zone, which also had the least difference in stemwood production.

Mean annual seedfall was greater in the flooded zone (55.1 g/m^2) than in the mesic (18.5 g/m^2), dry transition (19.0 g/m^2), or wet transition (21.2 g/m^2) zones (p = 0.09). The timing of seedfall was quite different among zones; seedfall was limited to autumn in the flooded zone, spring and autumn in the wet transition zone, and autumn and winter in the mesic zone.

Nutrient circulation

Litterfall N (Fig. 7) and P (Fig. 8) concentrations were least from September through December in all zones. Nitorgen concentrations of litterfall were least variable (50% difference) in the mesic zone. The largest temporal differences in litterfall N concentrations were in the wet and dry transition zones (240% differences). Trees in the wet transition zone were most proficient in N retranslocation, and this was the only zone where complete reabsorption values (<0.7%) were observed (in January). Reabsorption was intermediate in the dry transition and mesic zone, and incomplete (>1.0%) in the flooded zone. As with N, the mesic zone was least variable in litterfall P concentrations (80% difference) and fluctuations in litterfall P concentrations were greater in other zones as follows: 240% in the flooded, 190% in the wet transition, and 170% in the dry transition zones. Reabsorption proficiency of P was incomplete (>0.08%) at all times in all zones.

Given differences among communities in terms of the magnitude and efficiency of retranslocation (Table 4), we questioned whether differences in nutrient circulation can be attributed to differences among zones within species or differences in species composition among zones. Retranslocation data for a single species across three of the zones (Table 5) showed that the magnitude of internal cycling of both N and P tended to be highest (p < 0.10) for sweetgum in the mesic zone. There were no statistical differences in N or P internal retranslocation efficiencies, although sweetgum leaves in the upland community tended to retranslocate a greater proportion of each element. Across all zones, N reabsorption in sweetgum led to some of the lowest litterfall concentration and content levels for deciduous species (Killingbeck 1996). By contrast, P retranslocation was intermediate in this species and was just below average for deciduous trees. Of the other tree species studied, most were completely proficient in N absorption (Table 6). Exceptions included white oak with high initial foliar N concentrations and swamp chestnut oak, with intermediate retranslocation efficiency. Both internally and externally, oaks cycled N in a manner distinctly different from each other and from other species.

Most N (Fig. 7) and P (Fig. 8) was added to the forest floor via litterfall in December and January for the dry transition and mesic zones and in October to December in the two wettest zones. In all zones, the time when most nutrients were added to the forest floor with litterfall coincided with lowest litterfall nutrient concentrations.

Litter quality was lower in the wetter zones regardless of the metric used (Table 7). Litterfall lignin/N ratios in the wet transition zone were 25–50% greater than in the three other zones, lignin/P ratios were 50% lower in the mesic zone than in the flooded and wet transition zones, and the C/N ratio of leaf litter in the wetter zones was 60% greater than in the better drained zones. In addition, the amount of N and P retranslocated per leaf was 80–120% greater in the mesic zone than in the two transition zones (Table 4). Retranslocation efficiencies were not significantly different among zones.

For most of the species considered, there was no consistent tendency towards change in litterfall N or P concentrations, nor in reabsorption efficiencies or proficiencies along the flooding gradient (Table 6). The exception was sweetgum, in which both green foliage and litterfall N and P concentrations tended to be higher than the mean on the drier sites and lower in the wet transition zone and more N was retranslocated in the mesic and dry transition zone. Reabsorption of P in sweetgum was not significantly greater (p = 0.1) than the mean in those zones.

Generally, trees were more or similarly efficient in retranslocating N and P, although exceptions were observed: water oak in the mesic zone and swamp tupelo in the flooded zone were more efficient in retranslocating P. The most proficient species were swamp tupelo and laurel oak. The least proficient were swamp chestnut oak, white oak, and water tupelo.

NUE for N (g/g N) was greater in the wet transition zone (120 g) than in the flooded (92 g), dry transition (100 g), and mesic (109 g) zones. By contrast, NUE for P (g/g P) was lower in the dry transition (639 g) and the mesic (676 g) zones than in the wet transition (785 g) and flooded (748 g) zones. Growth efficiency (stemwood produced per unit foliage mass, g/g) was greater in the flooded zone (2.8 g) than in the wet transition (2.2 g), mesic (2.0 g), and dry transitions (1.8 g) zones. Retranslocation efficiency of N and P were similar among zones, suggesting that these processes are related and not completely dependent on nutrient availability.

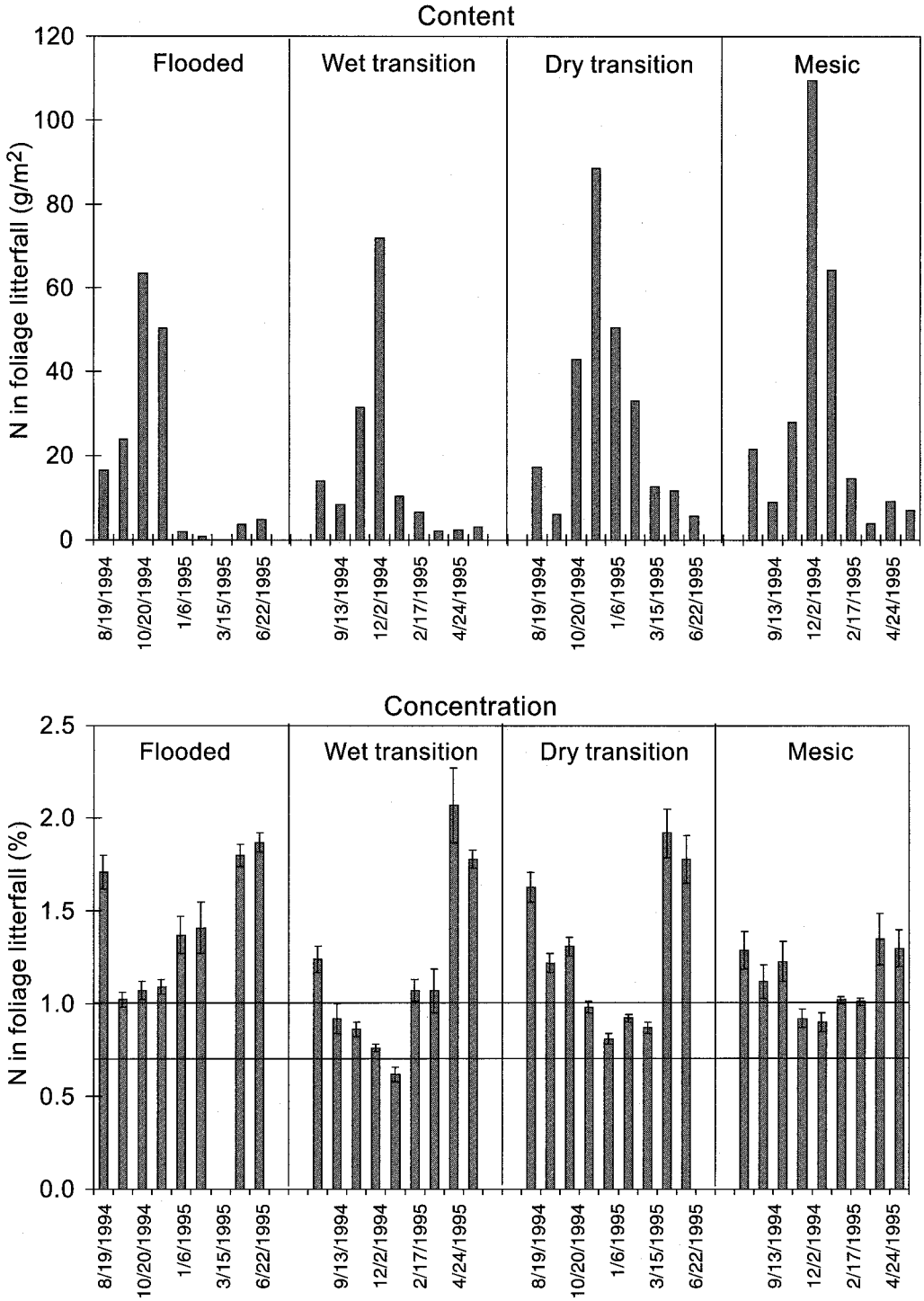
Production and nutrient relationships

Although there was no difference in foliar litter production, there were negative correlations (p = 0.05 unless otherwise noted) between this component of primary production and soil clay content, soil clay plus silt content, CEC, and extractable soil Ca and Mg contents (Table 8). Positive correlations exist between foliar mass and P content and between litterfall P content and N content (p = 0.1). Foliar N content was negatively correlated with NUE for P.

Soil N availability, indexed as KCl extractable ammonium plus nitrate before incubation was not correlated with either foliar production or total aboveground NPP, was negatively correlated with SOM content, and was positively related to litterfall lignin/N ratios (p < 0.1). Nitrogen mineralization (sum of extractable soil nitrate and ammonium gains during five in situ incubations) was (not significantly) related to

© 1999 NRC Canada

Fig. 7. Amount of N returned to the forest floor with leaf litter in each zone by litter collection date (upper panel) and N concentrations (mean ± SE) in foliage from each zone by sampling date (lower panel). The horizontal lines show the upper and lower level of intermediate resorption proficiency (according to Killingbeck 1996). Values above the upper line indicate incomplete resorption, or low proficiency in resorption. Values below the lower line indicate complete resorption, or high proficiency in resorption.



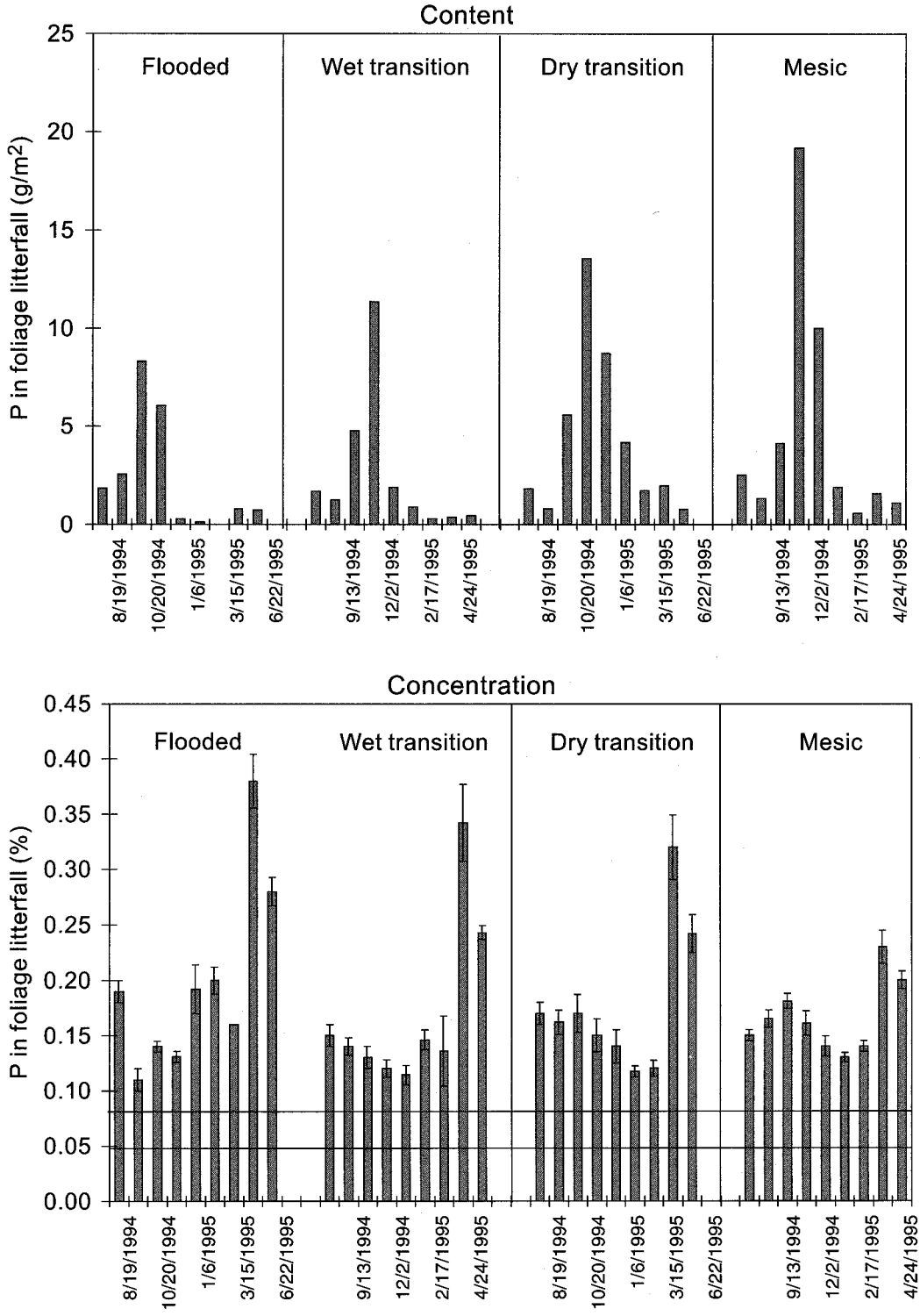
NPP. The lignin to N ratio was negatively correlated with SOM and positively correlated with tree density. Lignin/P and C/N ratios were positively correlated with a number of soils characteristics (Table 8), including exchangeable Ca and Mg, CEC, and clay content. These ratios were negatively correlated with soil P.

Discussion

Net primary productivity along this hydrologic gradient did not support the subsidy-stress hypothesis because the lowest rather than the highest NPP occurred with intermittent flooding (wet transition zone). The alternative hypothesis

© 1999 NRC Canada

Fig. 8. Amount of P returned to the forest floor with leaf litter in each zone by litter collection date (upper panel) and P concentrations (mean ± SE) in foliage from each zone by sampling date (lower panel). The horizontal lines show the upper and lower level of intermediate resorption proficiency (according to Killingbeck 1996). Values above the upper line indicate incomplete resorption, or low proficiency in resorption. Values below the lower line indicate complete resorption, or high proficiency in resorption.



offered by Mitsch and Rust (1984) was supported suggesting that physiological stresses produced by saturated soil were more important than potential subsidies of nutrients and water with flooding. In the wet transition zone, the water level oscillated above and below the soil surface during the growing season, so it is likely that the redox potential and associated chemistry fluctuated widely. In fact, this zone exhibited the greatest fluctuation in ammonium and nitrate availability.

© 1999 NRC Canada

Table 4. Retranslocation indices for litterfall from the four hydrologic zones.

	Magnitude (mg/leaf)		Efficiency (% of foliar content)	
Community	N	P	N	P
Mesic	3.91 (1.1)*a*	0.77 (0.2)*a*	53 (5.5)*a*	56 (7.8)*a*
Dry transition	2.19 (1.0)*b*	0.37 (0.1)*b*	36 (14.3)*a*	30 (18.3)*a*
Wet transition	1.77 (0.3)*b*	0.24 (0.1)*b*	56 (5.9)*a*	55 (7.9)*a*
Flooded	3.82 (1.5)*ab*	0.49 (0.2)*ab*	62 (9.2)*a*	65 (9.6)*a*

Note: Values are means with SE given in parentheses. Values within columns followed by the same letter are not significantly different at $p = 0.05$. Variances were heterogeneous according to Hartley's test, so the ANOVA was performed on natural log transformed data.

Table 5. Retranslocation indices for sweetgum in the three hydrologic zones in which it occurs.

	Retranslocation (mg/leaf)		Proficiency (μg/cm^2)*		Efficiency (% of foliar content)	
Zone	N	P	N	P	N	P
Mesic	7.60 (1.8)*a*	1.60 (0.5)*a*	15.3	5.22	76 (10.8)*a*	65 (11.4)*a*
Dry transition	2.65 (1.7)*b*	0.22 (0.2)*b*	11.2	2.24	60 (21.4)*a*	34 (26.3)*a*
Wet transition	2.28 (0.6)*b*	0.28 (0.1)*b*	14.9	3.36	54 (9.4)*a*	43 (10.2)*a*

Note: Values for retranslocation and efficiency are means with SE given in parentheses. Values within columns followed by the same letter are not significantly different ($p = 0.10$). Variances were heterogeneous according to Hartley's test, so the ANOVA was performed on the natural log transformed data.

*Statistics were not performed on proficiency values, which were calculated using μg/g × g/cm.

Table 6. Mean foliage nutrient concentrations and retranslocation efficiency ratings for individual tree species.

		Nitrogen				Phosphorus			
Species (*n*)	Zone	Green	Abscised	Efficiency (%)	Proficiency (μg/cm^2)	Green	Abscised	Efficiency (%)	Proficiency (μg/cm^2)
Sweetgum (6)	WT	1.20 (0.6)	0.62 (0.1)	48	14.9	0.19 (0.02)	0.14 (0.02)	26	3.36
Sweetgum (2)	DT	1.49 (0.4)	0.80 (0.2)	46	11.2	0.24 (0.05)	0.16 (0.02)	33	2.24
Sweetgum (3)	M	1.53 (0.1)	0.85 (0.3)	44	15.3	0.36 (0.01)	0.29 (0.04)	19	5.22
Red maple (2)	F	1.51 (0.0)	0.78 (0.3)	48	9.4	0.19 (0.01)	0.10(0.03)	47	1.20
Red maple (4)	WT	1.46 (0.1)	0.64 (0.1)	56	10.9	0.21 (0.00)	0.12 (0.01)	43	2.04
Water oak (2)	DT	2.24 (0.0)	0.92 (0.2)	59	14.7	0.22 (0)	0.12 (0.02)	45	1.92
Water oak (3)	M	1.75 (0.0)	0.90 (0.1)	49	12.6	0.26 (0.02)	0.11 (0.01)	58	1.54
Chestnut oak (1)	M	1.91	1.60	16	48.0	0.26	0.29	–12*	8.70
Hickory (2)	M	2.05 (0.1)	1.36 (0.0)	34	16.3	0.26 (0.02)	0.26 (0.03)	0	3.10
White oak (1)	M	2.35	1.45	38	37.7	0.28	0.24	14	6.20
Swamp tupelo (3)	F	1.51 (0.0)	0.49 (0.1)	43	4.4	0.17 (0.01)	0.07 (0.01)	59	0.60
Water tupelo (3)	F	1.70 (0.0)	0.96 (0.1)	44	39.4	0.22 (0.00)	0.14 (0.02)	36	5.70
Laurel oak (5)	WT	1.28 (0.1)	0.83 (0.1)	35	8.4	0.19 (0.01)	0.12 (0.01)	37	1.20

Note: Values for green and abscised leaves are means with SE given in parentheses. Positive efficiency values indicate a decline in nutrient concentration between midsummer and leaf abscission. Zone code: F, flooded; WT, wet transition; DT, dry transition; M, mesic.

*Negative efficiency values result from an increase in foliar nutrient concentration between midsummer and abscission.

Table 7. Annual litterfall mass, nutrient content, and litter quality indices for the four hydrologic zones.

Zone	Litterfall (g/m^2)	N (g/m^2)	P (g/m^2)	Lignin/N	Lignin/P	C/N
Mesic	537.2 (36.2)*a*	5.2 (0.24)*a*	0.84 (0.06)*a*	18.1 (3.5)*a*	119.9 (17.5)*b*	48.8 (5.4)*a*
Dry transition	499.8 (26.8)*a*	5.0 (0.26)*a*	0.74 (0.06)*a*	19.6 (3.4)*a*	143.2 (35.5)*ab*	51.0 (5.4)*a*
Wet transition	361.0 (32.4)*b*	3.0 (0.28)*b*	0.46 (0.04)*b*	27.3 (4.8)*b*	177.5 (37.5)*a*	80.4 (6.7)*b*
Flooded	329.6 (21.8)*b*	3.6 (0.28)*b*	0.44 (0.04)*b*	21.8 (4.2)*a*	175.7 (36.7)*a*	85.5 (12.2)*b*

Note: Values are means with SE given in parentheses. Values within columns followed by the same letter are not significantly different at $p = 0.05$. Litterfall values differ from those reported in Table 1 because a different period of production was used in the nutrient analysis component of the study (August 1994 to July 1995) than for the biomass production component of the study (September 1993 to September 1995).

© 1999 NRC Canada

Table 8. Linear correlations among soil properties, foliar chemical composition, and productivity estimates.

	N-min	N-avail	NPP	Litter	N	P	Lignin/N	Lignin/P	C/N	Ca-soil	K-soil
N-avail	–0.603										
NPP	0.870	–0.669									
Litter mass	0.182	–0.504	–0.142								
N	0.376	–0.778	0.169	0.935*							
P	0.278	–0.564	–0.046	0.995**	0.956**						
Lignin/N	–0.632	0.933*	–0.515	–0.754	–0.931*	–0.807					
Lignin/P	–0.413	0.587	–0.066	–0.970**	–0.946**	–0.988**	0.836				
C/N	–0.124	0.531	0.160	–0.995**	–0.942*	–0.985**	0.757	0.947**			
Ca-soil	–0.364	0.500	0.016	–0.973**	–0.913*	–0.985**	0.775	0.995**	0.946**		
K-soil	–0.060	0.009	–0.504	0.854	0.617	0.820	–0.335	–0.794	–0.821	–0.851	
Mg-soil	–0.216	0.365	0.186	–0.976**	–0.859	–0.971**	0.666	0.965**	0.950**	0.985**	–0.926*
P-soil	0.220	–0.511	–0.114	0.999	0.937	0.998	–0.765	–0.979	–0.990	–0.982	0.854
SOM	0.694	–0.979**	0.660	0.606	0.842	0.670	–0.979**	–0.709	–0.614	–0.634	0.137
CEC	–0.231	0.315	0.194	–0.956**	–0.824	–0.953**	0.630	0.953**	0.923*	0.979**	–0.939*
% BS	–0.591	0.619	–0.236	–0.896*	–0.905*	–0.933*	0.859	0.977**	0.859	0.966**	–0.710
% Clay	–0.144	0.334	0.250	–0.978**	–0.849	–0.967**	0.634	0.949**	0.957**	0.972**	–0.940*
% Sand	0.359	–0.486	–0.026	0.972**	0.906*	0.983**	–0.765	–0.993**	–0.943*	–1.000**	0.858
Tree density	–0.650	0.873	–0.463	–0.809	–0.947**	–0.860	0.990**	0.896*	0.801	0.847	–0.443
Basal area	0.291	–0.496	0.725	–0.486	–0.149	–0.433	–0.158	0.410	0.438	0.502	–0.870
Ret. Eff.-N	0.460	0.338	0.461	–0.672	–0.631	–0.617	0.396	0.491	0.740	0.483	–0.492
NUE-N	–0.473	0.780	–0.812	0.140	–0.219	0.075	0.508	–0.047	–0.095	–0.150	0.632
NUE-P	–0.160	0.782	–0.073	–0.867	–0.954**	–0.871	0.865	0.821	0.905	0.780	–0.504

Note: N-min, sum of extractable soil NO_3-N and NH_4-N gains during five (May to October) in situ incubations; N-avail, sum of extractable soil NO_3-N plus NH_4-N at the beginning of five in situ incubations; Ret. Eff.-N, retranslocation efficiency for N.

*$p < 0.1$.

**$p < 0.05$.

Anoxic and reduced soil conditions produced by flooding events can be persistent and may last for several weeks after a flooding episode during the growing season (Megonigal et al. 1993; Faulkner and Patrick 1992). Even shallow and short flooding events can decrease stomatal conductance and photosynthetic rates (Peterson and Bazzaz 1984; Will et al. 1995), although bottomland hardwood trees in general can tolerate short periods of soil saturation. In addition, changes from an anoxic to an aerated rhizosphere can cause post-anoxic injury to roots, so an incidence of high root mortality may follow flooding events (Crawford 1993). If root mortality and turnover are stimulated by flooding, plant energy resources can be depleted, resulting in depressed aboveground production. These mechanisms could contribute to the reduced aboveground NPP in the wet transition in this site and in the wet sites identified by Megonigal et al. (1997).

If leaf litterfall is used as an index of photosynthetic capacity, and it is the most unambiguous measure of stress since root production is unknown, trees in both the wet transition and flooded zones were stressed relative to the other zones. However, it appears that continuous flooding may be less "stressful" to flood-adapted plants than intermittent flooding. Some wetland tree species develop morphologically and physiologically different root systems under continually flooded or intermittently flooded conditions (Hook et al. 1971; Megonigal and Day 1992). Water roots, which develop under continuously flooded conditions, have a higher tolerance for anaerobic respiration and a greater capacity for oxygenating the rhizosphere than do roots developed during intermittent flooding (Keeley 1979). Flexibility in the development of one or the other type of root system appears to be limited to the seedling stage (Hook and Brown 1973; Keeley 1979; Megonigal and Day 1992), so changes in hydroperiod can increase mortality even in flood-tolerant tree species (Harms et al. 1980).

When plants are neither physiologically nor morphologically adapted to flooding, fluctuating water levels can prevent them from acclimating to the extremes of either flooded or drained conditions. We attribute low NPP in the wet transition zone to physiological stresses produced by alternating saturated to unsaturated soil. This supports the suggestion by Megonigal et al. (1997) that low NPP can result from disequilibrium between plant community composition and hydrologic regime.

High aboveground NPP in the flooded zone was consistent with higher biomass partitioning to aboveground tissue in wetter zones (Megonigal and Day 1992; Day and Megonigal 1993; M.K. Burke, unpublished data), possibly conferring a competitive advantage in flooded soils (Tilman 1988). Also, we attribute higher aboveground NPP to greater soil nutrient capital and turnover in the flooded zone, suggested by the relatively nutrient rich foliage, low nutrient use efficiency, high soil macronutrient content, and high growth efficiency in the flooded zone. However, lower photosynthetic rates in this zone could be masked by swelling of the stem due to greater water storage.

Although physiological stress from flooding or postanoxic injury to roots may help explain low production in the wet transition zone, a second likely factor is N deficiency.

© 1999 NRC Canada

	Mg-soil	P-soil	SOM	CEC	% BS	% Clay	% Sand	Tree density	Basal area	Ret. Eff.-N	NUE-N
N-avail											
NPP											
Litter mass											
N											
P											
Lignin/N											
Lignin/P											
C/N											
Ca-soil											
K-soil											
Mg-soil											
P-soil	–0.981**										
SOM	–0.501	0.618									
CEC	0.997**	–0.963**	–0.462								
% BS	0.910*	–0.914*	–0.756	0.907*							
% Clay	0.997**	–0.980**	–0.464	0.992**	0.879						
% Sand	–0.987**	0.981**	0.621	–0.982**	–0.964**	–0.974					
Tree density	0.748	–0.823	–0.947**	0.721	0.923*	0.715	–0.839				
Basal area	0.628	–0.486	0.350	0.668	0.335	0.649	–0.516	–0.030			
Ret. Eff.-N	0.536	–0.639	–0.292	0.480	0.306	0.586	–0.477	0.370	0.205		
NUE-N	–0.299	0.136	–0.667	–0.348	0.023	–0.328	0.166	0.392	–0.930*	–0.015	
NUE-P	0.739	–0.856	–0.791	0.686	0.735	0.746	–0.770	0.847	0.030	0.803	0.304

Litterfall N concentrations in the wet transition zone were near the lowest possible biological limit (Killingbeck 1996), indicating N was tightly conserved within the trees. By contrast, N reabsorption was incomplete in trees of the mesic and flooded zones. Compared with Vitousek's analysis of a range of forest types, plant communities in this study were average in NUE for N, and efficiency in the wet transition site was characteristic of sites with low N availability (Vitousek 1982; Bridgham et al. 1995). By contrast, P efficiencies were near the lowest documented by Vitousek, suggesting that P was abundant on this site relative to N.

Nutrient circulation in litterfall is considered a reliable indicator of nutrient availability (Vitousek 1982) so based on foliar values, low soil N availability in the wet transition zone and high availability in the flooded zone was expected. Indeed, the amount of N mineralized during incubation, a better indicator than initially extractable N of plant available soil N, was least in the wet transition zone and was positively related to NPP. Because uptake of N by plants was restricted during in situ incubation, microbes appear to be strong competitors for N in the wet transition zone and weaker competitors in the mesic and flooded zones.

Efficiency in retranslocation differed among zones by 70% for N and 220% for P, although values were not significantly different. Nutrient retranslocation efficiency was least in the dry transition zone, and differences among species in retranslocation efficiency likely contributed to the differences among zones. The two wettest zones contained some of the most efficient and proficient nutrient retranslocators (laurel oak and swamp tupelo) as well as the highly efficient but intermediately proficient species (sweetgum and red maple). In contrast, the two more drained zones contained more of the low efficiency and low proficiency species (swamp chestnut oak) and moderately efficient and low proficiency species (white oak). Therefore, differences in nutrient circulation among zones can be attributed to species differences and nutrient availability, but the within-species response to gradient was less than the zone-level response, which includes the effect of changing species composition. This conclusion confirms the results of Chapin and Molilanen (1991) and Crawford et al. (1991), who found that resource availability influenced internal translocation efficiencies less than absolute quantities of retranslocated elements. We suggest that community differences in internal retranslocation efficiencies are primarily a function of changing species composition across the gradient but that the magnitude of differences may reflect both species and resource availability shifts. These findings are in agreement with Vitousek (1982) who asserted that N availability can influence N circulation.

The N and P reabsorption proficiencies of tree species were positively correlated (r = 0.93), supporting the suggestion by Killingbeck (1996) that reabsorption intensity is similar among species on a given site. Also, estimates of N and P retranslocation on a stand level were not significantly related when using content per leaf (r = 0.87) but were correlated when using percent of foliar content (r = 0.99). It follows then that, regardless of the method used to measure it, retranslocation of N and P are closely related. In addition,

© 1999 NRC Canada

NPP was (not significantly) related to retranslocation indexed using milligrams per leaf ($r = 0.91$), which suggested that the amount of N retranslocated and aboveground NPP were related, although there was no relationship between NUE and aboveground NPP.

Because there were no differences in susceptibility to foliage leaching among tree species (B.G. Lockaby, unpublished data), we concluded that retranslocation results were not affected by differences in throughfall leaching. Differences were assumed to represent internal retranslocation and were calculated to range from 36 to 62% for N and from 30 to 65% for P. These ranges are similar to those reported in a number of previous retranslocation investigations (Switzer and Nelson 1972; Ostman and Weaver 1982; Boerner 1984; Crawford et al. 1991).

Litter quality, indexed with lignin/N, lignin/P, and C/N ratios, was positively related to productivity and inversely related to wetness. This suggested that, apart from obvious differences in microenvironment, organic matter mineralization should have been slower in the wetter communities. It follows that soil N availability should be lower in the wet zones and a negative feedback of low N availability and low N return via litter should occur because annual N demand is supplied by internal recycling rather than atmospheric or flooding sources, and N mineralization was expected to be slower in low quality litter.

Counter to what was expected, when N availability was indexed as KCl-extractable nitrate plus ammonium before incubation, N availability was high in both wet zones, although soil N dynamics differed between the wet zones. Based on results from the in situ incubations, N mineralization was quite high in the flooded zone, supporting the suggestion that microbial competition for N is low in saturated soil (Stevenson 1986). In comparison, the wet transition zone was similar to the flooded zone in chemical and physical soil characteristics, and mineral N was highly available prior to soil incubation; however, there was a dramatic net loss of mineral nitrogen, particularly nitrate, during incubation. This loss could not have been the result of plant uptake. The polyethylene bags, although permeable to O_2 and CO_2 (Westerman and Crothers 1980) are impermeable to plant roots and water so that no NO_3-N or NH_4-N should enter or leave the bags (Pastor et al. 1982). Although not measured, denitrification is a dominant mechanism of N removal in southern forested wetlands (Lockaby and Walbridge 1998), although high N immobilization could contribute to the net loss. Both processes can help explain the low NPP, low litter quality, high NUE, and high retranslocation proficiency of trees in the wet transition zone.

In this study, intermittent flooding appeared to be more a stress than a subsidy for trees, perhaps because of induced physiological disequilibrium or enhanced denitrification in the alternating wet and drained sediment. We conclude that NPP and nutrient circulation are closely related along the complex physical, chemical, and hydrologic gradients in this watershed.

Acknowledgments

We thank Dave Gordon and Ducks Unlimited for permission to work on the site and Dean Harrigal and the South Carolina Department of Natural Resources and Marine Fisheries who manage the site. We thank L. Wayne Inabinnett, Carl Phillips, Tom Hunnicutt, Andrew Hulin, Mark Eisenbies, Laura Murray, Cindy Bunton, Dave Gartner, and Andy Harrison for technical assistance; Paul Smith and Susan O'Ney for editorial assistance; and G.C.G. Goelz, Hal Liechty, Bernie Parresol, and three anonymous reviewers for helpful comments on an earlier version of this manuscript.

References

Barnes, B.V., Zak, D.R., Denton, S.R., and Spurr, S.H. 1998. Forest ecology. 4th ed. John Wiley & Sons, Inc., New York.

Boerner, R.E.J. 1984. Foliar nutrient dynamics and nutrient use efficiency of four deciduous tree species in relation to site fertility. J. Appl. Ecol. **21**: 1029–1040.

Bridgham, S.D., Pastor, J., McClaugherty, C.C., and Richardson, C.J. 1995. Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient availability gradient in North Carolina peatlands. Am. Midl. Nat. **145**: 1–21.

Brinson, M.M. 1993. Changes in the functioning of wetlands along environmental gradients. Wetlands, **13**: 65–74.

Brinson, M.M, Lugo, A.E., and Brown, S. 1981. Primary productivity, consumer activity, and decomposition in freshwater wetlands. Annu. Rev. Ecol. Syst. **12**: 123–161.

Brinson, M.M., Bradshaw, H.D., and Jones, M.N. 1985. Transitions in forested wetlands in North Carolina along gradients of salinity and hydroperiod. J. Elisha Mitchell Sci. Soc. **102**: 76–94.

Broadfoot, W.M. 1967. Shallow-water impoundment increases soil moisture and growth of hardwoods. Soil Sci. Soc. Am. Proc. **31**: 562–564.

Burke, M.K., Raynal, D.J., and Mitchell, M.J. 1992. Soil nitrogen availability influences seasonal carbon allocation patterns in sugar maple (*Acer saccharum*). Can. J. For. Res. **22**: 447–456.

Chapin, F.S., and Moilanen, L. 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. Ecology, **72**: 709–715.

Clark, A., Phillips, D.R., and Fredrick, D.J. 1985. Weight, volume, and physical properties of major hardwood species in the Gulf and Atlantic Coastal Plains. USDA For. Serv. Res. Pap. SE-250.

Conner, W.H. 1994. Effects of forest management practices on southern forested wetland productivity. Wetlands, **14**: 27–40.

Crawford, D.T., Lockaby, B.G., and Somers, G.L. 1991. Genotype–nutrition interactions in field-planted loblolly pine. Can. J. For. Res. **21**: 1523–1532.

Crawford, R.M.M. 1993. Plant survival without oxygen. Biologist, **40**: 110–114.

Dalla-Tea, F., and Jokela, E.J. 1994. Needlefall returns and resorption rates of nutrients in young intensively managed slash and loblolly pine stands. For. Sci. **40**: 650–662.

Day, F.P., and Megonigal, J.P. 1993. The relationship between variable hydroperiod, production allocation, and belowground organic turnover in forested wetlands. Wetlands, **13**: 115–121.

Day, P.R. 1965. Particle fractionation and particle-size analysis. *In* Methods of soil analysis. Part 1. *Edited by* C.A. Black, D.D. Evans, J.L. White, L.E. Ensminger, F.E. Clark, R.C. Dinauer. American Society of Agronomy, Inc. Madison, Wis. pp. 545–567.

DeLucia, E.H., and Schlesinger, W.H. 1995. Photosynthetic rates and nutrient-use efficiency among evergreen and deciduous shrubs in Okefenokee swamp. Int. J. Plant Sci. **156**: 19–28.

© 1999 NRC Canada

Faulkner, S.P., and Patrick, W.H., Jr. 1992. Redox processes and diagnostic wetland soil indicators in bottomland hardwood forests. Soil Sci. Soc. Am. J. **56**: 856–865.

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

Hook, D.D., and Brown, C.L. 1973. Root adaptations and relative flood tolerance of five hardwood species. For. Sci. **19**: 225–229.

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

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

Killingbeck, K.T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology, **77**: 1716–1727.

Kimmins, J.P. 1987. Forest ecology. MacMillian, New York.

Lajtha, K. 1987. Nutrient resorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata* (DC) Cov. Biogeochemistry, **4**: 265–276.

Lockaby B.G., and Walbridge, M.R. 1998. Biogeochemistry. *In* Ecology and management of forested wetlands in the southeastern US. *Edited by* M.G. Messina and W.H. Conner. CRC Press, Boca Raton, Fla. 149–172.

Lugo, A.E. 1978. Stress and ecosystems. *In* Energy and environmental stress. *Edited by* J.H. Thorp and J.W. Gibbons. Department of Energy, Washington, D.C. DOE No. 771114. pp. 62–101.

Meadows, J.S., and Nowacki, G.J. 1996. An old-growth definition for eastern riverfront forests. USDA For. Serv. Gen. Tech. Rep. SRS-4.

Megonigal, J.P., and Day, F.P., Jr. 1992. Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. Ecology, **73**: 1182–1193.

Megonigal, J.P., Patrick, W.H., and Faulkner, S.P. 1993. Wetland identification in seasonally flooded forest soils: soil morphology and redox dynamics. Soil Sci. Soc. Am. J. **57**: 140–149.

Megonigal, J.P., Conner, W.H., Kroeger, S., and Sharitz, R.R. 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy-stress hypothesis. Ecology, **78**: 370–384.

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

Mitsch, W.J., and Rust, W.G. 1984. Tree growth response to flooding in a bottomland forest in northeastern Illinois. For. Sci. **30**: 499–510.

Muzika, R.M., Gladden, J.B., and Haddock, J.D. 1987. Structural and functional aspects of succession in southeastern floodplain forests following a major disturbance. Am. Midl. Nat. **117**: 1–9.

Nambiar, E.K.S., and Fife, D.N. 1987. Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. Ann. Bot. (London), **60**: 147–156.

Odum, E.P. 1978. Ecological importance of the riparian zone. *In* Strategies for protection of floodplain wetlands and other riparian ecosystem. *Edited by* B.R. Johnson and J.F. McCormick. U.S. Forest Service, Washington, D.C. pp. 2–4.

Odum, H.T. 1974. Energy cost–benefit models for evaluating thermal plumes. *In* Thermal Ecology Conference. *Edited by* J.W. Gibbons and R.R. Sharitz. National Technical Information Service, U.S. Department of Commerce, Springfield, Va. Publ. No. 730505. pp. 628–649.

Odum, W.E., Odum, E.P., and Odum, H.T. 1995. Nature's pulsing paradigm. Estuaries, **18**: 547–555.

Ostman, N.L., and Weaver, G.T. 1982. Autumnal nutrient transfers by retranslocation, leaching, and litterfall in a chestnut oak forest in southern Illinois. Can. J. For. Res. **12**: 40–51.

Pastor, J., Aber, J.D., McClaugherty, C.A., and Melillo, J.M. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology, **65**: 256–268.

Peterson, D.L., and Bazzaz, F.A. 1984. Photosynthetic and growth responses of silver maple (*Acer saccharinum* L.) seedlings to flooding. Am. Midl. Nat. **112**: 261–272.

Phillips, C.N., Burke, M.K., and Hunnicutt, T.B., Jr. 1995. Improvements on a reliable oak seed trap. USDA For. Serv. Res. Note No. SE-371.

Pugnaire, F.I., and Chapin, F.S. 1993. Controls over nutrient resorption from leaves of evergreen Mediterranean species. Ecology, **74**(1):124–129.

Richardson, C.J. 1994. Ecological functions and human values in wetlands: a framework for assessing forestry impacts. Wetlands, **14**: 1–9.

SAS Institute Inc. 1985. SAS user's guide, version 5 edition. SAS Institute Inc., Cary, N.C.

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

Sharitz, R.R., and Mitsch, W.J. 1993. Southern floodplain forests. *In* Biodiversity of the southeastern United States: lowland terrestrial communities. *Edited by* W.H. Martin, S.G. Boyce, and A.C. Echternacht. Wiley & Sons, New York. pp. 311–372.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Can. J. Bot. **50**: 2227–2233.

Soltanpour, P.N., Jones, J.B., Jr., and Workman, S.M. 1982. Optical emission spectrometery. *In* Methods of soil analysis. Part 2. Chemical and microbiological properties. *Edited by* A.L. Page, R.H. Miller, and D.R. Keeney. Soil Science Society of America, Inc., Madison, Wis. pp. 29–66.

Stevenson, F.J. 1986. Cycles of soil. John Wiley & Sons, New York.

Stuck, W.M. 1982. Soil survey of Colleton County, South Carolina. USDA Soil Conservation Service, Washington, D.C.

Switzer, G.L., and Nelson, L.E. 1972. Nutrient accumulation and cycling in loblolly pine plantation ecosystems: the first twenty years. Soil Sci. Soc. Am. J. **36**: 143–147.

Taylor, J.R., Cardamone, M.A., and Mitsch, W.H. 1990. Bottomland hardwood forests: their functions and values. *In* Ecological processes and cumulative impacts: illustrated by bottomland hardwood wetland ecosystems. *Edited by* J.G. Gosselink, L.C. Lee, and T.A. Muir. Lewis Publishers, Inc., Chelsea, Mich. pp. 13–86.

Tilman, D. 1988. Plant strategies and the dynamics and structure of pant communities. Princeton University Press, Princeton, N.J.

Van Soest, P.J., and Wine, R.H. 1986. Determination of lignin and cellulose in acid-determent fiber with permanganate. J. Assoc. Anal. Chem. **51**: 780–785.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. Am. Mid. Nat. **119**: 553–572.

Walbridge, M. 1991. Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. Ecology, **72**: 2083–2100.

Walkley, A., and Black, I.A. 1934. An examination of the Degtjareff method for determining soil organic matter and a

© 1999 NRC Canada

proposed modification of the chromic acid titration method. Soil Sci. **37**: 29–38.

Westerman, D.T., and Crothers, S.E. 1980. Measuring soil nitrogen mineralization under field conditions. Agron. J. **72**: 1009–1012.

Will, E.W., Seiler, J.R., Feret, P.P., and Aust, M. 1995. Effects of rhizosphere inundation on the growth and physiology of wet and dry-site *Acer rubrum* (red maple) populations. Am. Midl. Nat. **134**: 127–139.

Winer, B.J. 1971. Statistical principles in experimental design. 2nd ed. McGraw Hill Book Company, New York.

Zak, D.R., Pregitzer, K.S., and Host, G.E. 1986. Landscape variation in nitrogen mineralization and nitrification. Can. J. For. Res. **16**: 1258–1263.

© 1999 NRC Canada