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ECOSYSTEMS

Changes in Production and Nutrient Cycling across a Wetness Gradient within a Floodplain Forest

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Abstract

Floodplain forest ecosystems are highly valuable to society because of their potential for water quality improvement and vegetation productivity, among many other functions. Previous studies have indicated that hydrology influences productivity but that the relationship between hydroperiod and productivity is a complex one. Consequently, we compared multiple indexes of productivity, nutrient circulation, and hydroperiod among three communities on the Flint River floodplain, Georgia, that differed in terms of inundation frequency. We hypothesized that (a) the wettest community would have the lowest total net primary production (NPP) values because of saturated soil conditions; (b) as wetness increases, nutrient circulation in litterfall would decrease because of the hypothesized lower productivity in the wetter community; and (c) as wetness increases, internal translocation would become more efficient. The study site was partitioned into three wetness types-somewhat poorly drained (SPD), intermediate (I) and poorly drained (PD). We found that belowground biomass was greatest on the SPD, litterfall was similar for all three sites, and that woody biomass current annual increment (CAI) was greatest in the PD community. However, when the three variables were totaled for each site, the PD had the greatest NPP, thus disproving hypothesis (a). For hypothesis (b), we observed that P content in litterfall, although not significant, followed the predicted trend; nitrogen (N) content displayed the opposite pattern (PD > I > SPD). As wetness increased, internal translocation became more efficient for phosphorus (support for hypothesis [c]), but the SPD community was more efficient at retranslocating N (contradiction of hypothesis [c]).

Key **words:** carbon; forested floodplain; nitrogen; nutrient cycling; phosphorus; productivity.

Forested floodplains are highly valued for their wildlife, timber, and recreation uses (Walbridge 1993). Riverine forests are reputed to be dynamic systems that have high primary productivity and biomass (Brinson 1990). Litterfall production in wetlands frequently exceeds that in many other community types (Bray and Gorham 1964; Shure and Gottschalk 1985; Vogt and others 1986; Conner and Day 1992) and has been reported to reach 734 g m^{-2} y^{-1} in the southeastern United States (Conner 1994). The productivity function is strongly influenced by hydrology, so that seasonally flooded sites have greater production than continuously flooded swamps (Conner and Day 1976).

Both litterfall and fine root turnover play a vital role in nutrient cycles and energy flux within a forested ecosystem (Persson 1983; Fahey and others 1988; Lonsdale 1988; Hendrick and Pregitzer 1993; Fahey and Hughes 1994). However, belowground production studies are known to be difficult and problematic (Hendrick and Pregitzer 1992; Megonigal and Day 1992; Nadelhoffer and Raich 1992; Fahey and Hughes 1994). The role of fine

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roots in net primary production is not well understood (McClaugherty and others 1982), especially in riverine forests, where little attention has been paid to belowground production (Symbula and Day 1988; Brinson 1990; Powell and Day 1991). As a result of the numerous challenges associated with fine root studies, many researchers have relied upon mean annual increment, site index, and litterfall as indicators of site productivity (Bray and Gorham 1964). However, reliance upon litterfall estimates alone may lead to inaccurate assessments of NPP (Megonigal and others 1997).

It has been proposed that there is a positive relationship between litterfall production and fine root production (Raich and Nadelhoffer 1989; Nadelhoffer and Raich 1992; Jones and others 1996). However, research in the Great Dismal Swamp suggests that in some forested floodplains, the relationship between litterfall and fine root production may vary due to differential flooding (Megonigal and Day 1988; Powell and Day 1991; Day and Megonigai 1993). Therefore, productivity studies should examine belowground biomass because use of the aboveground data alone could generate misleading conclusions (Day and Megonigal 1993).

The specific objectives of this study were to compare three primarily deciduous communities along a wetness gradient in terms of above- and belowground productivity and nutrient circulation in litterfall and roots. We hypothesized that (a) the wettest community would have the lowest total NPP values because of saturated soil conditions; (b) as wetness increases, nutrient circulation in litterfall would decrease because of the hypothesized lower productivity in the wetter community; and (c) as wetness increases, internal translocation would become more efficient.

STUDY SITE

This research was conducted on the Flint River floodplain, near Reynolds, Georgia (32°28'N, 84°1'W). The Flint River is an alluvial redwater river (Wharton 1978); consequently, its floodplain soils may be expected to be relatively fertile (Lockaby and Walbridge 1998; Lockaby and Conner 1999). The study site was partitioned into three wetness types, somewhat poorly drained (SPD), intermediate (I), and poorly drained (PD), based upon water well measurements, vegetation, and soil data collected on site prior to initiation of the project. Four transects (200 m long and 50 m apart) were installed across this wetness gradient. Each transect consisted of six subplots (0.025 ha) spaced at 30-m intervals. The first two subplots were located in the SPD portion of the gradient, the next two were in the I zone, and the last two subplots along each transect were situated in the PD zone. Thus, there were a total of 24 subplots; eight subplots per community type.

The overstory vegetation consisted of red maple (*Acer rubrum* L.), sweetgum ***(Liquidambar** styraciflua* L.), laurel oak ***(Quercus** laurifolia* Michx.), water oak ***(Quercus nigra*** L.), and willow oak ***(Quercus** phellos* L.), which were found in all three communities: Loblolly pine (*Pinus raeda* L.) also grew on SPD and ***I:*** Sweet bay ***(Magnolia virginiana*** L.) was located in I and PD communities, and blackgum (*Nyssa sylvatica* Marshall) grew only on the PD sites.

Precipitation during the study period reflected that of the 30-year normal precipitation (1961-90) (K. S. Harker, personal communication), except for greater rainfall during March and August 1996 and lower precipitation in March 1997 (Figure 1).

METHODS

Water

One 2.4-m groundwater well was installed on each subplot to monitor groundwater table depth on a monthly basis when the sites were not flooded above the soil surface. During flood events, access to the sites was denied. Depth to groundwater was recorded from November 1995 through April 1997 (Figure 1). Stream stage levels were recorded by the United States Geological Survey (USGS) streamgauging station in Montezuma, Georgia:

Soil

Soil taxonomy for the SPD, I, and PD zones, respectively, was as follows: Chewacia series-Fluvaquentic Dystrochrept; Transition; Chastain series-Typic Fluvaquent. Depth to 10 YR 7/2 mottles (that is, Munsell soil chart color composed of hue, value, and chroma, which are related to the physical and chemical properties of the soil) was recorded in the field at 36 cm for the SPD zone, 15 to 20 cm for the I zone, and at the surface of the mineral soil for the PD zone. Drainage classes (according to frequency and duration of saturation) ranged from somewhat poorly drained on the drier end of the gradient to poorly drained on the wetter end (Woods and Smith 1983). In major floodplains of the southern United States, such changes in soil oxidation arc ample to induce major changes in abiotic factors that control vegetation community composition and productivity (Sharitz and Mitsch 1993; Kellison and others 1998).

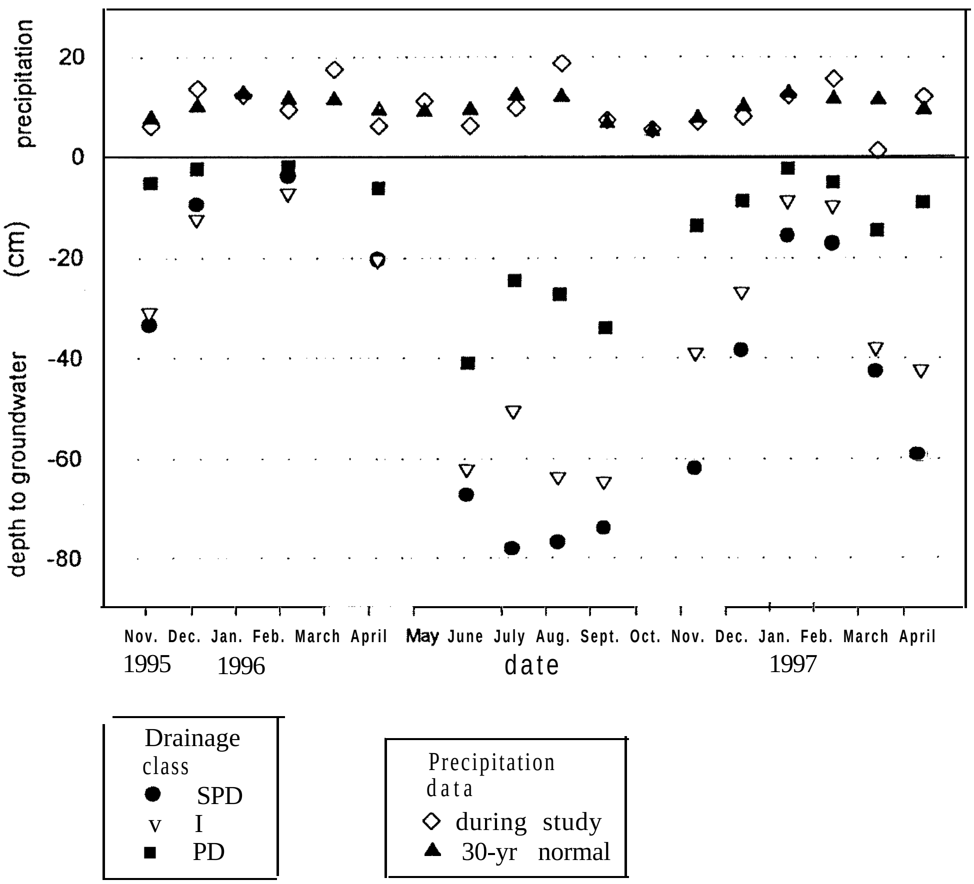

Figure 1. Total monthly and 30-year normal precipitation and depth to water table across a wetness gradient on the Flint River floodplain, Reynolds, Georgia.

Aboveground Productivity

Litterfall samplers, 0.5-m’ screen baskets (mesh 10 X 10 holes per inch) elevated 0.9 m, were installed, one per subplot, in November 1995. Litterfall samples were collected monthly from December 1995 through March 1997 except when flooding made sampling unsafe. We did not collect litterfall from herbaceous and shrub vegetation because these types of cover occurred infrequently under the closed canopies of the three communities. Litterfall was dried at 70°C for at least 48 h or until constant mass was attained prior to separation into components. Biomass (g) for total litterfall, reproduction, branches, miscellaneous pieces, and individual species was recorded for each trap. Samples were ground in a Wiley mill to pass a 20 mesh sieve and analyzed for N, phosphorus (P), and carbon (C).

To calculate the annual increment, the overstory was inventoried on each subplot using a prism system (Husch and others 1972). Diameter at breast height (DBH) was measured at 1.4 m in November 1995 and March 1997 on stems larger than 7.6 cm counted in the prism inventory. Tree height also was recorded in 1997. Based upon tree height-DBH relationships, a regression equation was developed to predict height for trees in 1995 and those not recorded in 1997. Aboveground wood and bark dry weights were calculated for hardwood species using the regression equations of Clark and others (1985); for loblolly pine, we used Taras and Clark (1974). Basal area was calculated using the volume equations of Avery and Burkhart (1994). Then we took the difference in the calculated weight of trees between 1997 from 1995. This value was multiplied by a conversion factor, divided by the number of plots per drainage class type, and converted to kg/ha.

To assess nutrient retranslocation for N and P (Burke and others 1999) prior to foliage senescence, we collected live foliage in August 1996 from red maple located in each community type. Live foliage and abscised litter were collected from the same overstory trees. Leaf areas were measured on approximately 270 leaves; the leaves were then dried at 70°C for 48 h, weighed, and ground. Freshly abscised foliage was collected in December 1996 and prepared in the same manner as the live leaves. The amount of nutrients in the live leaves were compared to that of the abscised leaves to determine reabsorption values.

Fine Root Productivity

To determine the most feasible depth to study fine root dynamics on this site, preliminary soil cores (13 cm in diameter) were collected on 12 subplots at two depths (0 to 15 cm and 15 to 30 cm) in January 1996 across the entire moisture gradient. Soil cores to a depth of 30 cm were examined initially because Montague and Day (1980) reported that fine root biomass within the top 30 cm encompassed 90% of their total on the mixed hardwood sites and 80% on the maple-gum sites. On the Flint floodplain, root weight in the soil cores was three times greater in the upper 0 to 15 cm than in the 15 to 30 cm depth. Root length was 3.3 and five times greater in the upper 0 to 15 cm on the PD and SPD sites, respectively. This depth distribution is similar to that reported by Powell and Day (199 1), who examined root production to a depth of 40 cm and found that significantly more fine root biomass was located within the top 10 cm. Similarly, Baker (1998) reported that 74% of the fine roots on the Coosawhatchie floodplain were restricted to the top 15 cm. Therefore, based upon these results, the difficulty of extracting an intact soil core of a given volume from the saturated soils, and our desire to compare the Flint River data with those from the Pearl River floodplain (Schilling et al. 1999), we chose to sample fine roots to a depth of 11 cm.

In February 1996, eight fiberglass screens (7.62 cm width, 15.24 cm length, 10 X 10 holes per inch) were inserted at a 45” angle into the soil to a vertical depth of 11 cm on each subplot (Baker 1998; Melhuish and Lang 1968, 197 1; Schilling and others 1999). Soil cores containing screens were collected in April, June, September, November 1996, and January 1997. Soil cores (13 cm X 16 cm) containing in situ screens were processed as follows: (a) Cores were collected and transported to Auburn; (b) the number of roots growing through the screen were counted by diameter class to calculate root length (Melhuish and Lang 1968, 1971); (c) live fine roots were removed from the soil core, nonroot organic matter was removed, and roots were separated into diameter class (0. l-l .O mm, 1.1-2.0 mm, 2.1-3.0 mm); (d) number of roots intersecting a grid were counted, and length was calculated for each diameter class using Böhm's (1979) methodology; (e) three l-cm root pieces were cut from each diameter class within each sample to calculate a weight per root length; (f) the roots were dried in an oven at 70°C, and actual oven-dried weight cf all fine roots within each diameter class per sample were recorded; (g) samples were ground in a Wiley mill to pass a 20 mesh screen; (h) samples were analyzed for N, P, and C.

Root length was calculated (Böhm 1979; Melhuish and Lang 1968, 197 1) and then multiplied by an expansion factor to compute root length in an m^2 plot to a depth of 0.11 m (m m^{-2}). This length was multiplied by the dry weight of the 0.01-m piece of root from the corresponding size class to get a root weight (g m^{-2}). For statistical analysis, the size classes 0. l-l .O and 1.1-2.0 mm were combined in order to facilitate comparisons with other belowground biomass studies performed in the southeastern United States.

Laboratory Analysis

Litterfall and root samples were analyzed for total C and N using thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin Elmer Corp., Norwalk, CT, USA). Total P samples were dry-ashed, extracted, and determined using the vanadomolybdate procedure (Jackson 1958). The total P samples were read on a Spectronic 501 spectrophotometer (Milton Roy Co., Rochester, NY, USA). Foliar litter samples for lignin arid cellulose analysis were analyzed according to Van Soest and Wine’s (1986) methodology.

Soil samples were air-dried. Extractable P, exchangeable K, Mg, and Ca were determined after extraction with the Mehlich 1 (0.05 N HCl and 0.025 N H_2SO_4) reagent. For 5 min, 5 g of soil in a 1:4 soil to solution ratio was shaken and then filtered. Phosphorus was determined colorimetrically using a Bausch **and** Lomb Spectronic 100. Potassium, Ca, and Mg were determined using atomic absorption spectroscopy; the latter two elements were measured in the presence of lanthanum (Hue and Evans 1986).

Statistical Analysis

Wetness types were compared using the t statistic (SAS 1985) to test the hypothesis that the means for two wetness types were equal ($P > 0.05$). The following comparisons were analyzed: SPD vs I; SPD vs PD; and I vs P,D.

Results and Discussion

Water

Relatively few studies have reported data for both above- and belowground productivity in relation to groundwater depths (Megonigal and others 1997). Yet hydrology is the most important controlling factor in a wetland (Mitsch and Gosselink 1986). Thus, data on flood events, groundwater depths, and precipitation are needed in combination with productivity estimates to gain a better understanding of system responses. Major flood events (and corresponding maximum river stage level for flood events) occurred from 28 January to 11 February (5.7 m), 7 to 25 March (6.4 m), and 28 March to 3 April 1996 (3.1 m).

Depth to groundwater differed by wetness class throughout the year, although a more pronounced difference was observed during June through November (Figure 1). On the SPD, I, and PD floodplain sites, respectively, depth to groundwater (m) ranged from -0.16, -0.08, and -0.02 in January to -0.74, -0.66, and -0.34 in September. Depth to groundwater was statistically deeper on the SPD and I portions when compared to the PD end of the gradient during every collection except for February 1996 in the case of the SPD. The SPD community was statistically deeper than the I during November and December 1996 and during January, February, and April 1997.

It is interesting to note that groundwater was within the top 0.3 m on the PD community throughout the entire year with the exception of June and September 1996, whereas on the SPD and I communities groundwater was only within the top 0.3 m during the winter months (Figure 1). Water tables remained high during the winter months even after flood events had subsided. Mean groundwater table during March through November 1996 was-O.63 m for the SPD community, -0.5-m for the I community, and -0.24 m for the PD community. These depths were comparable to depths recorded on other wetland sites in the Southeast (Jones and others 1994; Megonigal and others 1997).

Soil Chemistry

Soils on the SPD and I sites consisted of loams and light clays with a cation exchange capacity (CEC) less than 4.6-9.0 $cmol_c kg^{-1}$. The PD portion of the gradient had a larger component of organic matter and clay with a CEC greater than 9.0 $cmol_c kg^{-1}$. The soil in the SPD portion of the gradient was significantly lower in Ca and Mg than the PD portion. Total N was significantly higher in the PD community soil when compared to the soil in the I zone (Table 1). The PD community had more organic matter in the soil than the SPD community, probably due to slower decomposition rates in the former. Similar findings were observed in the Great Dismal swamp, where more soil organic matter was observed on wetland sites than on upland sites (Megonigal and Day 1988).

Table 1. Soil Chemistry to a Depth of 15 cm

	Community Type		
Variable	SPD	I	PD
Total C	3.48	3.33	5.16
Total N	0.25	0.23	0.37
pH	4.60	4.64	4.78
Extractable P (mg kg-‘)	2.88	3.25	3.00
Exchangeable K (mg kg-‘)	74.0	67.0	63.6
Exchangeable Mg (mg kg-‘)	65.6	81.0	107.6
Exchangeable Ca (mg kg-‘)	136.9	216.3	423.8

Aboveground Productivity and Related Nutrient Cycling

No statistical differences were observed in foliar litterfall biomass or nutrient content, although the SPD zones had numerically higher P content whereas the PD community had higher N content in the litterfall (Table 2). N:P ratios in litterfall for the SPD, I, and PD sites, respectively, were 7.2, 8.0, and 8.8. These N:P ratios are similar to those observed on the ACE Basin in South Carolina, the Ogeechee River in Georgia, and other forested tracts along the Flint River (Lockaby and Walbridge 1998; Lockaby and Conner 1999). Lockaby and Walbridge (1998) have suggested that N:P ratios less than 12 may indicate that the system is primarily N-deficient. Based upon their N:P ratio hypothesis, it would appear that the Flint SPD community is slightly more N-deficient than the PD community.

Although annual total litterfall biomass was not statistically different among wetness types, temporal variations in total litterfall patterns were observed between soil wetness communities (Figure 2). Litterfall in the PD portion of the gradient began in August and continued through November; relatively consistent amounts were deposited each month during autumn. The SPD portion began litterfall in September and continued through December, peaking in November. The latter pattern also was observed on the I zone. The nutrient content of

Table 2. Trends in Productivity, Nutrient Circulation, and Retranslocation Efficiency

Variable	Wetness Type		
	SPD	I	PD
Productivity			
Litterfall	583.1	617.7	564.4 g m^{-2} y^{-1}
woody	875.9	775.2	1108.3 g m^{-2} y^{-1}
Belowground	211.1	130.5	56.2 g m^{-2} y^{-1}
Nutrient circulation			
Amount of nitrogen in litterfall	31.4	32.8	35.2 g m^{-2} y^{-1}
Amount of phosphorus in litterfall	4.4	4.1	4.0 g m^{-2} y^{-1}
Amount of carbon in litterfall	1524.9	1605.2	1493.3 g m^{-2} y^{-1}
Amount of nitrogen in roots	2.2	1.1	0.6 g m^{-2} y^{-1}
Amount of phosphorus in roots	0.365	0.207	0.104 g m^{-2} y^{-1}
Amount of carbon in roots	97.6	58.8	23.2 g m^{-2} y^{-1}
Retranslocation efficiency			
Nitrogen	49	21	14%
Phosphorus	51	51	40%

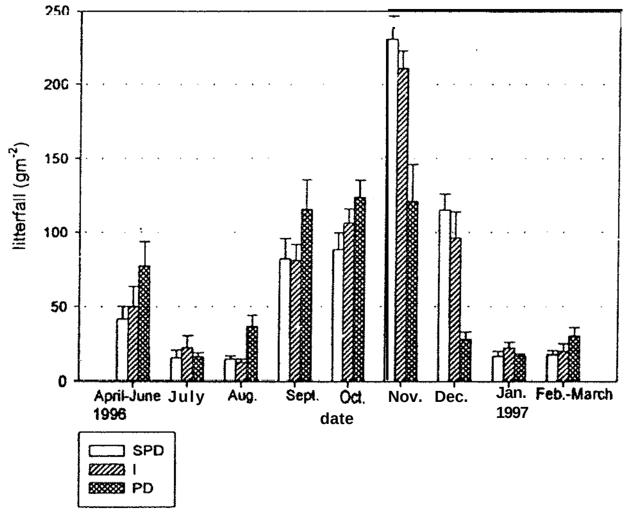

Figure 2. Litterfall mass by month along a wetness gradient on the Flint River floodplain, Reynolds, Georgia.

litterfall by month followed the same trend as biomass within each wetness type. Brinson and others (1980) also reported that elemental flux in litterfall followed litterfall biomass.

Mean N concentrations for litterfall on the SPD, I, and PD communities, respectively, were 10,900, 10,700, and 12,400 mg kg^{-1} (average of three communities = 11,333). Brinson and others (1980) also reported a mean N value of 11,300 mg kg^{-1} for litterfall from an alluvial swamp in North Carolina. In all wetness zones, litterfall phosphorus values were higher during the spring and early summer months (February-June).

Higher N and P concentrations were also observed in the spring (April) than in the latter part of the growing season (August and October) on Meyers Branch, South Carolina (Moorhead and McArthur 1996) and on the Tar River, North Carolina (Brinson and others 1980). However, we did not notice the autumn pulse in nutrient concentrations that Brinson and others (1980) observed. Carbon concentrations did not exhibit strong seasonal fluctuations as did N and P. Carbon:N ratio in the Flint litterfall was 48.63 for the SPD community, 49.02 for the **I** community, and 42.43 for the PD community.

Total litterfall on the SPD, I, and PD sites, respectively, consisted of leaves 79.5%, 81.3%, and 86.5%; branches 6.0%, 8.7%, and 10.4%; and reproductive parts 14.4%, 10.0%, and 3.0%. Shure and Gottschalk (1985) reported similar total leaf values of 73%–84% in a floodplain forest in South Carolina. In comparison with Brinson's and others (1980) value of 65.7% on a North Carolina alluvial swamp, the percent of leaves in litterfall was higher on the Flint River floodplain in all wetness types. However, branch values on the Flint were lower than the 14.1% reported by Brinson and others (1980). Shure and Gottschalk (1985) observed a decrease in branch input from floodplain to upland site. This corresponds to the decrease in percent branch input as soil wetness decreased on the Flint, Georgia, floodplain. Percent of reproductive parts in litterfall was similar on both Brinson and others (1980) site (15.6%) and for the Flint SPD community (14.4%), but the Flint PD community was much lower.

Leaf fall tracked litterfall patterns on all three wetness types. Although the SPD was statistically

Table 3. Comparison of Litterfall Estimates from the Southeastern United States

Location	Type	Biomass ($g\ m^{-2}\ y^{-1}$)	Source (yr)
GA	FF, SPD	583.1	Present study
GA	FF, I	617.7	Present study
GA	FF, PD	564.4	Present study
GA	Hardwood	335.7	Vogt and others (1986)
GA	FF, east	902.0	Cuffney (1988)
GA	FF, west	784.0	Cuffney (1988)
LA	Natural swamp	405.0	Conner and Day (1992)
LA	Hardwood	574.0	Conner and Day (1976)
LA	Tupelo	379.0	Conner and Day (1982)
LA	Cypress/tupelo	417.4	Conner and others (198 1)
SC	Hickory	459.9	Vogt and others (1986)
SC	Yellow poplar	414.4	Vogt and others (1986)
SC	oak	399.7	Vogt and others (1986)
SC	FF-bank	414.7	Shure and Gottschalk (1985)
SC	FF-30 m	455.4	Shure and Gottschalk (1985)
SC	FF-60 m	538.6	Shure and Gottschalk (I 985)
SC	FF-upland	510.6	Shure and Gottschalk (1985)
VA	Cypress	678.0	Megonigal and Day (1988)
VA	Cedar	758.0	Megonigal and Day (1 388)
VA	Maple–gum	659.0	Megonigal and Day (1988)
VA	Hardwood	652.0	Megonigal and Day (1388)

FF, floodplain; GA. Georgia; LA, Louisiana: SC, South Carolina; VA, Virginia.

lower than the PD from April to October 1996 and February to March 1997, the SPD was statistically higher than the PD in November and December 1996. Even though the SPD and I did not differ statistically throughout the study, the I was statistically lower than the PD in July and August 1996, and it was higher in November and December 1996.

The reproductive component of total litterfall followed a similar pattern on both the SPD and I wetness communities. A pulse in reproductive material was observed in September, followed by a slight dip; both the SPD and I sites, respectively, had peak reproduction values in November (44.4 $g\ m^{-2}$ and 26.7 $g\ m^{-2}$). The PD communities had relatively low stable values throughout the year ranging from 0 to 3.9 $g\ m^{-2}$ when compared to the other two communities but displayed a small peak in August (3.9 $g\ m^{-2}$) and then in November (3.6 $g\ m^{-2}$). Statistical differences between the SPD and PD communities were observed for the September and November 1996 collections and between the I and PD communities in September, November, and December 1996.

In an alluvial swamp in North Carolina, Brinson and others (1980) documented leaf fall beginning to increase in September, peaking in October, and subsiding by November. Conner and Day (1992) documented leaf fall beginning in September and ending by January in forested wetlands in Louisiana. Shure and Gottschalk (1985) reported that leaf fall on their upland (drier) sites extended later than the floodplain sites, which reflects the temporal pattern observed on the Flint floodplain.

Because initiation of leaf fall may be different for various species, this may have contributed to the early leaf fall observed on the Flint's PD site. Conner and Day (1992) reported that Nyssa sp. fell early and that the PD site overstory contained a majority of *Nyssa* sp. Lower productivity has been attributed to long periods of flooding (Conner and Day 1992), so moisture stress may have contributed to the low litterfall value observed on the Flint's PD site as well as inducing early litterfall. It is possible that more litterfall was dropped in the I zone because it was less stressed by hydrologic extremes.

The litterfall values observed on the Flint floodplain fell within the range of values reported throughout the southeastern United States (Table 3). The litterfall value for the Flint PD community (564.4 $g\ m^{-2}\ y^{-1}$) was similar to the average values reported by Shure and Gottschalk (1985) (538.6 $g\ m^{-2}\ y^{-1}$) for their site, which had (*Nyssa/Acer/Liquidambar)* overstory composition, and to the 574 $g\ m^{-2}\ y^{-1}$ reported by Conner and Day (1976) in a

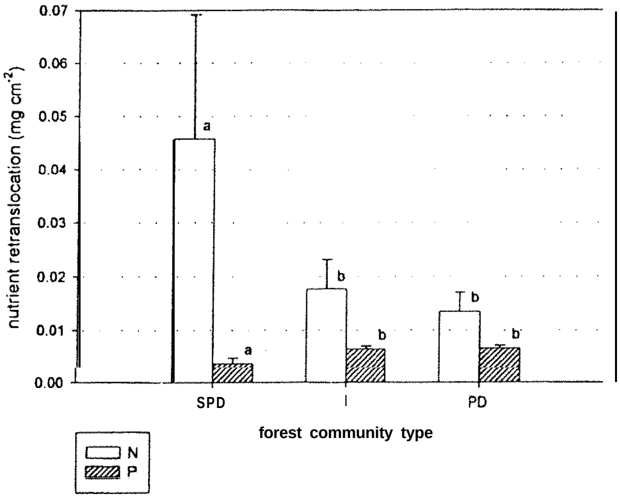

Figure 3. Retranslocation for red maple across a wetness gradient on the Flint River floodplain, Reynolds, Georgia.

Louisiana bottomland hardwood swamp. However, although overstory composition (*Nyssa/Acer*) and litterfall biomass were very similar on both our site and Conner and Day's (1976) site, the timing of leaf drop was different (in Louisiana, it peaked in November and in Georgia it remained stable from September through November).

August litterfall was analyzed for lignin and cellulose. The lignin-cellulose index (LCI) was calculated as the %lignin/(%lignin + %cellulose) (Melillo and others 1989). LCI values for the SPD, I, and PD communities, respectively, were 0.40, 0.43, and 0.48. These values suggest that on this site as the soil becomes better drained, leaf quality is improved. The LCI values were statistically significant between the SPD and PD communities as well as between the I and PD communities.

Retranslocation

Red maple was analyzed for nutrient retranslocation in an effort to eliminate differences due to species. The amount of phosphorus retranslocated was statistically lower in the SPD community *(0.0038 < 0.0065 < 0.0067* [mg cm^{-2}]) when compared to the I and PD community at the 10% probability level (Figure 3). No significant difference was found for P between the I and PD sites. The amount of N retranslocated was statistically higher in the SPD community (0.0457 > 0.0177 > 0.0135 [mg cm^{-2}]) compared to the I at the 10% level. The SPD community was statistically less efficient at retranslocating P and more efficient at retranslocating N than the I community (Table 2).

When Day (1987) studied the response of red maple seedlings to N and P enrichment, he found that the nutrient use efficiency was lower for fertilized plants than in nonfertilized seedlings. Day (1987) also observed higher concentrations of N and P in seedlings fertilized with those nutrients. Therefore, if more than enough nutrient is available for the plant to utilize, translocation efficiency is less critical and accumulation may occur. On the Flint floodplain, these data suggest that phosphorus availability is more limited on the PD site, whereas an inadequate N supply is a greater constraint in the SPD community.

Aboveground Total Tree and Bark Estimates

Current annual increment (CAI) of tree wood and bark production was numerically lower in the SPD community, with the largest CAI occurring in the wettest community (875.9 vs 1108.3 g m^{-2}, respectively) (Table 2). The high CAI in the PD community was probably due to the larger trees, which were found there as well as in the higher basal area (Table 4). Small growth increments in DBH for large trees wouid represent larger biomass estimates than in smaller trees. In contrast, Conner and Day (1976) suggested that the 800 g m^{-2} y^{-1} woody biomass increase observed on their bottomland hardwood swamp in LA was due to young trees (less than 30 years old) growing on the site. Because both studies document high aboveground productivity in a *Nyssa/Acer* community, it is probable that this community type contributes a greater woody biomass component to NPP. Megonigal and Day (1988) also noted that wood production was significantly greater on flooded sites.

The sum of litterfall and wood production was used to approximate aboveground net primary production. The aboveground NPP values for the Flint site ranged from 1392 to 1672 g m^{-2} y^{-1} and were higher than the aboveground NPP values (1050–1 176 g m^{-2} y^{-1}) for the Great Dismal Swamp in Virginia (Megonigal and Day 1988), as well as the intermediately flooded plots located on the Savannah River in South Carolina (1047-1055 g m^{-2} y^{-1}), on Upper Three Runs, South Carolina (825-1066 g m^{-2} y^{-1}), and on Meyers Branch, South Carolina (851-1175 g m^{-2} y^{-1}) (Megonigal and others 1997). The Flint aboveground NPP values were similar to the bottomland hardwood sites on the Pearl River, Louisiana (974-1608 g m^{-2} y^{-1}) (Megonigal and others 1997). These results are in line with the productivity pattern suggested by Lockaby and Walbridge (1998), who found that NPP is higher on redwater (such as the Flint and Pearl rivers) than on blackwater rivers floodplains (such as, Meyers Branch and Upper Three Runs).

Table 4. Basal Area and Average Diameter at Breast Height (DBH) by Species

Community	Species[a]	Basal area (m^2 ha^{-1})	DBH (m)	DBH (standard error)
SPD	Laurel oak	0.57	0.31	—
	Loblolly pine	0.57	0.51	8.3
	Sweetgum	4.89	0.25	3.1
	Water oak	1.45	0.21	4.9
	Willow oak	9.47	0.39	2.5 Total . . . 17.0
	Laurel oak	2.29	0.29	7.1
	Red maple	2.02	0.26	2.9
	Sweetbay	2.02	0.25	3.3
	Sweetgum	6.03	0.29	2.9
	Water oak	1.45	0.18	—
	Willow oak	6.88	0.35	2.6 Total . . . 20.7
PD	Blackgum	4.89	0.31	2.9
	Laurel oak	0.87	0.37	12.4
	Red maple	3.44	0.30	3.9
	Sweetbay	6.61	0.24	1.9
	Sweetgum	5.73	0.44	3.9
	Willow oak	0.29	0.46	— Total . . . 21.8

SPD, somewhat poorly drained: I, intermediate; PD, poorly drained
[a]Red maple fell outside prism plots on SPD community.

Fine Root Production

Belowground fine root production ($g\ m^{-2}\ y^{-1}$) as determined by Melhuish and Lang's (1968, 1971) and Böhm's (1979) methodologies, respectively, was 211.1, 206.2 for the SPD zone; 130.5, 131.1 for the I zone; and 56.2, 68.9 for the PD zone. These two methods used to estimate belowground production were not statistically significant. However, when annual fine root production to a depth of 11 cm was compared among wetness types, a statistical difference was observed between the SPD vs PD and I vs PD sites. Fine root production decreased as wetness increased (211.1 > 130.5 > 56.2 $g\ m^{-2}\ y^{-1}$) (Table 2). The PD community allocated a smaller percentage of net primary production belowground. This trend was also observed by Powell and Day (1991) in their flooded stand. Megonigal and Day (1988) reported that fine root production on flooded stands was lower than on the unflooded stand. *Nyssa sylvatica* seedlings grown under flooded conditions were found to allocate less biomass to roots than to shoots (Keeley 1979). These data suggest that the amount of belowground biomass allocation by vegetation may be both wetness and species dependent.

Fine root biomass values are similar to those reported on other floodplain sites in the southeastern United States (Table 5). Belowground biomass of the Flint communities (SPD-hardwoods > PD–maple/gum) followed the same pattern of mixed hardwoods > cedar > cypress > maple/gum noticed by Powell and Day (1991). Although Montague and Day (1980) examined a larger root size class than Powell and Day (1991), they also documented the same belowground trend among vegetative types. Powell and Day (1991) suggested that soil type as well as the frequency and duration of flooding influenced belowground production because their hardwood site, which was not flooded, had the highest production rate. As proposed by Montague and Day (1980), anaerobic soil conditions probably have contributed to lower fine root production on the Flint PD communities. Baker (1998) also observed lower fine root production on a poorly drained community type on the Coosawhatchie floodplain in South Carolina.

We examined fine root standing crop for each belowground collection. Seasonal fluctuations in standing crop biomass were observed in the SPD and I communities, whereas the PD community maintained a relatively constant standing crop throughout the year (Figure 4). The SPD community peaked in April, September, and January; whereas the I community showed progressive accumulation of biomass, which peaked in September. This autumn peak was also observed by Schilling and others (1999). Symbula and Day (1988), and Powell and Day (1991). Schilling and others

Table 5. Comparison of Belowground Biomass Production Estimates from Floodplains in the Southeastern United States

ST Type	Depth (cm)	Size Class	Method	Biomass ($g\ m^{-2}\ y^{-1}$)	Source (yr)
GA FF, SPD	11	<2 mm	Screen	211.1	Present study
GA FF, I	11	<2 mm	Screen	130.5	Present study
GA FF, PD	11	<2 mm	Screen	56.2	Present study
MS FF, mxd.hdw.	11	<2 mm	Screen	171.9	Schilling (1998)
MS FF, mxd.hdw.	11	<2 mm	Core	123.7	Schiliing (1998)
NC TS	10	<2 mm	Pit	137.0	Brinson and others (1981)
NC CS	10	<2 mm	Pit	365.2	Brinson and others (1981)
SC FF, dry	15	≤3 mm	Screen	153.9	Baker (1998)
SC FF, int	15	≤3 mm	Screen	180.9	Baker (1998)
SC FF, wet	15	≤3 mm	Screen	93.7	Baker (1998)
VA GDS, mxd.hdw.	10	<1 cm	Pit	828.8	Montague and Day (1980)
VA GDS, mxd.hdw	10	<2 mm	Core	490.0	Powell and Day (1991)
VA GDS, cedar	10	<1 cm	Pit	691.3	Montague and Day (1980)
VA GDS, cedar	10	<2 mm	Core	345.0	Powell and Day (1991)
VA GDS, cypress	10	<1 cm	Pit	369.1	Montague and Day (1980)
VA GDS, cypress	10	<2 mm	Core	139.0	Powell and Day (1991)
VA GDS, map/gum	10	<1 mm	Pit	333.3	Montague and Day (1980)
VA GDS, map/gum	10	<2 mm	Core	117.0	Symbula and Day (1988)
VA GDS, map/gum	10	<2 mm	Core	135.0	Powell and Day (1991)

SPD, somewhat poorly drained: I, intermediate: PD. poorly drained: CS, Creeping Swamp: FF. forested floodplain; GDS, Great Dismal Swamp: TS, Tar Swamp; mxd. hdw., mixed hardwood; map/gum, maple/gum; GA, Georgia; MS, Mississippi; NC, North Carolina; SC, South Carolina; VA, Virginia.

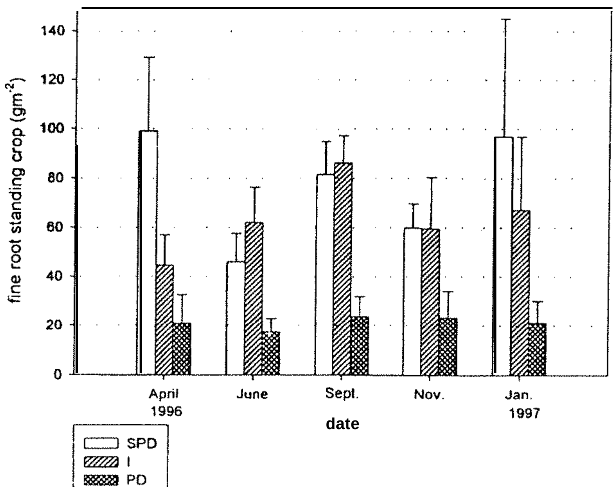

Figure 4. Fine root standing crop biomass (0.1-2.0 mm) to a depth of 11 cm along a wetness gradient on the Flint River floodplain, Reynolds, Georgia.

(1999) noted that fine root biomass on a Mississippi floodplain peaked in May and September. The data of Schilling and others (1999) reflected the bimodal belowground growth curve proposed by Symbula and Day (1988) based upon fine root biomass peaking in June and September. Powell and Day (1991) recorded a peak in belowground production in summer and late fall-winter in mixed hardwood and cedar stands, which were their most productive belowground sites. Although the SPD community displayed both a spring and autumn-winter peak, the PD community did not follow this pattern but instead functioned similar to Powell and Day's (1991) maple-gum and cypress sites, which displayed little seasonal variation.

Potential differences between wetness communities for standing crops of root biomass and nutrient contents were tested. During each collection, except for January 1997, the SPD community had statistically more standing crop biomass throughout the year than the PD community. This trend was also observed for P, N, and C contents. The I zone was also statistically higher in biomass and nutrient contents than the PD zone during the June and September 1996 collections. Schilling and others (1999) also observed that P, N, and C in fine roots mirrored biomass estimates on their site. Nitrogen concentrations for the Flint SPD community (Table 2) fell within the N range reported by Brinson and others (1981) for fine roots less than 2 mm to 10 cm in the Tar River Swamp (1.35 $g\ m^{-2}$) and the Creeping Swamp (3.72 $g\ m^{-2}$). Phosphorus values for all three research sites were almost the same:

Tar River Swamp, 0.34 g m^{-2}); Creeping Swamp, 0.37 g m^{-2}; and Flint SPD community, 0.36 g m^{-2} y^{-1}.

CONCLUSIONS

Prior to conducting this research, we hypothesized that the PD community would have the lowest total net primary production values (NPP = litterfall + woody biomass increment + fine root production) when compared across the wetness gradient because of longer duration of soil saturation. Actually, total NPP was highest in the PD community (PD 1728.9 > SPD 1670.1 > I 1523.4), due to the woody biomass CAI. The belowground component of total NPP (that is, fine root production) was higher in the SPD community, and the litterfall components were similar among the three sites (Table 2). These results support the conclusions by Megonigal and Day (1988) and Powell and Day (1991), as well as Day and Megonigal (1993) that biomass allocation will be strongly influenced by flooding gradient. These researchers also observed that flooded sites in the Great Dismal Swamp allocated more production aboveground whereas the SPD sites allocated more belowground. Day and Megonigal (1993) reported that the unflooded site in the Great Dismal Swamp appeared least productive based upon aboveground production data, but that site was actually the most productive when belowground data were added. Because fine root biomass was greater on the Flint SPD community, NPP values may have been closer had we been able to sample coarse lateral roots to a greater depth or whole root systems to estimate a total belowground biomass for each community.

The question arises as to whether nutrients or the availability of water may be more limiting to productivity in these gradient stands. Although it is not possible to state with certainty which is the dominant growth-limiting factor based on our data, we believe that a greater potential for soil water deficits to develop during late summer on the drier end of the gradient may be a contributing factor. However, further research would be needed to clarify this point.

Second, we hypothesized that as wetness increased, nutrient circulation would become slower. Although it was not statistically significant, phosphorus content in the litterfall followed this predicted trend (SPD > I > PD); however, N content displayed the opposite pattern (PD > I > SPD). Nitrogen and P concentration values were high in February-June, decreased as the growing season progressed, then gradually started rising in January. Relationships between fine root biomass vs fine root production have been suggested to be a function of nutrient availability in forest ecosystems. Sites with higher N availability would have greater fine root production, whereas sites with lower available N would have greater biomass. Because fine root production was lower in the PD site and the N status of vegetation was higher there, the PD site may fit the above-mentioned scenario.

Third, we proposed that as wetness increased, internal translocation would become more efficient. This hypothesis held true for phosphorus retranslocation, but the SPD community was most efficient at retranslocating N. The N/P ratio in litterfall for the SPD community was 7.21; for the PD, it was 8.77. Based upon N:P ratios, N was slightly more limiting in the SPD than in the PD. Similarly, the wider N:P ratio of the PD suggests a slight tendency toward more P imbalances there compared to the SPD. Suggestions of subtle shifts in the N or P balance between the SPD and PD communities may reflect differences in mineralization rates and/or seasonality of root uptake. It is likely that the hydric conditions of the PD alter N and P immobilization/mineralization patterns in litter as well as the proportion of each year during which the rooting zone is well oxidized. The integration of these differences is critically linked to nutrient balance and production at the community level but they are still poorly understood.

The results of this study suggest that although litterfall usually tracks productivity, measurements of both aboveground woody biomass increment (that is, wood production) and belowground production should also be considered when estimating stand productivity. The allocation of belowground production did not increase with aboveground production in this riparian floodplain system; instead, an inverse relationship was observed. Above- and belowground production within the SPD and I communities showed definitive pulses whereas the PD community remained relatively stable throughout the year. Trees growing on the same floodplain will allocate nutrient and biomass resources differently depending upon hydroperiod and related edaphic factors.

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