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Leaf Litter Decomposition and Nutrient Dynamics in Four Southern Forested Floodplain Communities

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ABSTRACT

Decomposition of site-specific litter mixtures was monitored for 100 wk in four floodplain communities: (i) a mixed oak community along the Cache River in central Arkansas, (ii) a sweetgum (*Liquidambar styracijlua* L.)–cherrybark oak (*Quercus falcata* var. *pagodaefolia* ELI.) community along Iatt Creek in central Louisiana, (iii) a sweetgum-swamp tupelo [*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.] community, and (iv) a laurel oak (*Quercus laurifolia* Michx.) community along the Coosawhatchie River in southeastern South Carolina. Soil temperature, hydroperiod, and litter quality (C:N, C:P, N:P, lignin:N) were used to interpret differences in the rates of mass loss and nutrient dynamics. After 100 wk, litter mixtures retained 33, 18, 8, and 5% of original mass on the Cache, Coosawhatchie (laurel oak community), Coosawhatchie (sweetgum-swamp tupelo community), and Iatt floodplains, respectively, and these differences appeared related to hydroperiod. Decay rates were comparable to rates reported in similar floodplain environments. Net mineralization of both N and P was observed after 100 wk, but both elements accumulated in litter mixtures periodically. Differences in hydroperiod were observed among the four floodplain communities and decomposition of and nutrient mineralization from litter among them appeared to be inversely related to the number and duration of flood events. Litterbags containing leaf litter of a single-species (i.e., cherrybark oak) were also monitored on three of the four sites to compare decay rates and nutrient dynamics with the litter mixtures. On the Cache River floodplain, slower decay of poorer quality cherrybark oak litter suggested that titter quality drove decomposition under similar edaphic conditions.

ABOVEGROUND NET PRIMARY PRODUCTION (AGNPP) in southeastern floodplain and wetland forests ranges from 2000 to 20 000 kg ha^{-1} yr^{-1} (Conner, 1994; Megonigal et al., 1997). Leaf material comprises approximately 43% of this production (Conner, 1994) which annually returns to the forest floor in the form of litterfall. Given these quantities, decomposition of leaf litter is an integral and significant part of biochemical (i.e., intrasystem) nutrient cycling and food webs of floodplain forests. As used here, decomposition refers to both the physical and chemical breakdown of litter and the mineralization of nutrients (Boulton and Boon, 1991). The micro and macro invertebrate, bacterial, and fungal communities depend on these organic resources for food. Through decomposition the nutrients within leaf litter are converted into a form available for uptake by vegetation, thereby exercising a critical control on vegetation productivity (Mitsch and Gosselink, 1993; Groffman et al., 1996).

Decomposition processes in wetland and floodplain environments have also received considerable attention with regard to biogeochemical (i.e., intersystem) nutrient cycling (Brinson, 1977; Brinson, 1981; Elder, 1985; Brinson, 1993; Lockaby and Walbridge, 1998). Particularly in floodplain systems, significant quantities of nutrients may be imported from upslope and/or upstream ecosystems through riparian transport or in floodwaters. Also, aquatic systems rely on the decomposition of foliar litter and coarse woody debris (CWD) as a source of dissolved organic carbon (DOC), the foundation of aquatic food webs (Brinson, 1981; Schlesinger, 1991). Although the degree to which organisms in aquatic systems are dependent upon allochthonous inputs of DOC has been the source of much debate (Vannote et al., 1980; Junk et al., 1989, as cited in Thorp and Delong, 1994), it is clear that the riparian system (i.e., floodplain) plays a vital role in contributing those inputs (Meyer, 1990). A great deal of effort also has been devoted to determining the extent to which individual floodplain systems or communities within those systems serve as nutrient sinks, sources, or transformers (Mitsch and Gosselink, 1993). In most cases, wetlands, floodplains included, act as storage reservoirs for nitrogen (N) and phosphorus (P) through microbial immobilization and plant uptake, thereby accomplishing a biochemical filtering function and improving water quality (Walbridge, 1993). By converting or transforming inorganic forms of these elements to organic forms, wetlands and floodplains effectively reduce the risk of eutrophication of downstream environments (Lockaby and Walbridge, 1998).

Because of the highly dynamic nature of floodplain

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Abbreviations: AR, Cache River; SCdry, Coosawhatchie River—laurel oak; SCwet, Coosawhatchie River-sweetgum/swamp tupelo; LA, Iatt Creek.

systems, estimating the absolute quantity of nutrients that are retained, exported, or transformed within even a single floodplain is difficult. However, decomposition studies that monitor the nature and extent of nutrient mineralization or immobilization during leaf litter decay provide an understanding of whether certain nutrients are being biologically immobilized within a community, released to downstream systems, or mineralized. Similarly, the extent of nutrient immobilization or mineralization within a forested floodplain community can suggest the degree to which community productivity may be limited by certain nutrients. Immobilization of P by soil organisms during decomposition, for instance, may suggest that this element is in short supply, leading to competition for P between soil flora and fauna and vegetation.

On a global or broad regional scale, temperature and precipitation are largely responsible for determining the rate and extent of decomposition (Swift et al., 1979; Meentemeyer, 1978). Generally, warmer temperatures and higher precipitation result in higher rates of decomposition, faster litter turnover, and less organic matter accumulation. However, these climatic factors interact with forest type, substrate quality, and nutrient availability, obscuring patterns within similar climatic and regional zones (Vogt et al., 1986).

At a local scale, the rate of decomposition and quantity of nutrients cycled through the decomposition mechanism are influenced primarily by (i) the quality of the resource being decomposed (McClaugherty et al., 1985; Meentemeyer and Berg, 1986; Blair, 1988; Lockaby et al., 1995; Belyea, 1996; Cornelissen, 1996; Hobbie, 1996; Heal et al., 1997), (ii) physicochemical properties (i.e., temperature and moisture regime, pH, oxygen) that affect decomposer organisms in situ (Swift et al., 1979; Moore, 1986; Donnelly et al., 1990; Berg et al., 1993), and (iii) the length of time the resource is in contact with the soil microenvironment (Lockaby and Walbridge, 1998). However, the relative importance of these factors appears to shift in response to spatial, temporal, and site-specific variations. Among four distinct communities subject to variable hydrologic regimes in the Great Dismal Swamp of Virginia and North Carolina, Day (1982) reported that litter quality was more important than site factors in determining the rate of decomposition, although litter mixtures decayed more rapidly on sites that experienced more flooding.

In forested floodplain ecosystems, the factors governing decomposition are particularly complex as a result of hydrologic processes that create a mosaic of vegetation communities (leading to differences in litter quality) and physicochemical environments. Hydroperiod (i.e., inundation frequency and duration) is the single most important factor governing ecological processes in wetland and floodplain environments (Mitsch and Gosselink, 1993), and its significance with respect to decomposition processes should not be overlooked. Not only does hydrologic regime determine vegetation community type (Wharton, 1978; Hardin and Wistendahl, 1983; Dollar et al., 1992), but the frequency and duration of floodwater inundation determines the suitability of the soil environment for decomposer organisms to process organic materials (Tate, 1980; Paul and Clark, 1989; Groffman et al., 1996). While adequate moisture is required for decomposer organisms to operate efficiently, excessive moisture or anaerobic conditions resulting from prolonged inundation may impede the activity of soil flora and fauna and the decomposition process (Tate, 1980; Paul and Clark, 1989; Groffman et al., 1996). Brinson (1981) has suggested that decomposition is optimized at a point along the soil moisture continuum where cycles of wetting and drying prevail. Rates are lower where permanently flooded, permanently dry, or even alternating aerobic and anaerobic conditions prevail. Lockaby et al. (1996) suggested that brief flooding regimes, followed by moist but well aerated conditions, maximized mass and carbon (C) loss.

Brinson (1981) also has suggested that, where decomposition is not limited by either oxygen availability or moisture, temperature is the "single most important variable" governing mass loss. However, decomposition is not strongly limited by low temperatures in bottomlands of the southern United States (Megonigal et al., 1996), yet flooding is common in these systems and may create periods of anaerobic or oxygen limited conditions.

Even within a single forested floodplain, differences in litter quality, soil properties, and other microenvironment factors may result in marked differences in decomposition rates, extents, and nutrient mineralization/immobilization patterns. The question remains as to which of these is the most important driving variable. Also, as Lockaby and Walbridge (1998) suggest, the timing of litter input to the soil microenvironment may have a substantial influence on decomposition processes. For example, two different vegetative assemblages on the Flint River, Georgia produced different quantities of litter at different times (Lockaby and Walbridge, 1998), resulting in distinctly different decomposition environments. Most decomposition studies do not account for these differences.

The objectives of this study were (i) to quantify and compare mass loss of leaf litter mixtures representative of the species composition of litterfall in four bottomland hardwood forests, (ii) to quantify and compare mass loss of a single species' litter among forests, and (iii) to compare nutrient mineralization and immobilization patterns for mixed-species litter combinations and a single species litter in each forest as a function of time of contact with the forest floor, litter quality, hydroperiod, and soil temperature.

It was hypothesized that (i) higher quality leaf litter (i.e., litter with narrow litter quality ratios such as C:N, C:P, N:P, lignin, and lignin:N) would decompose faster than low quality litter (i.e., litter with wider ratios); (ii) decomposition of the common substrate (i.e., single-species litter) would occur more rapidly in communities that experienced frequent, pulsing flood events as opposed to no flooding or long periods of inundation; (iii) litter would exhibit net N and P mineralization; and (iv)

patterns of N and P accumulation would be inversely related to litter quality.

MATERIALS AND METHODS

Study Sites

Three floodplain sites within the southeastern USA were chosen: the Cache River in Arkansas, the Coosawhatchie River in South Carolina, and Iatt Creek in Louisiana (Fig. 1). These floodplains forests are located within the Southern Forest zone as described by Brinson (1990) and are considered bottomland hardwood forests (Sharitz and Mitsch, 1993). However, each floodplain differs in terms of local climate, river origin (i.e., Piedmont versus Coastal Plain), and vegetation.

The Cache River study site is located in the Rex Hancock/Black Swamp State Wildlife Management Area, Woodruff County, in east central Arkansas (approximately 35°N, 91°W). The Cache is a redwater (or alluvial) river according to the classification used by Wharton et al. (1982) (also see Stanturf and Schoenholtz, 1998). Stage may fluctuate as much as 3 m vertically, flows range between 0 and 280 $m^3 s^{-1}$ (King, 1996), and flooding occurs seasonally with long periods of inundation. The Cache River watershed is subjected to a variety of agricultural uses but approximately 20%, including the study site, remains as bottomland hardwood forests (King, 1996). The Cache River typically transports large quantities of sediment (Kleiss, 1996). Soils on the study site were classified in the Mhoon Series as fine-silty, mixed, thermic Fluventic Haplaquepts (Richard Day, personal communication, 1998). These soils have been described as alluvial soils with dark gray, fine sandy loam surface layers typically grading to silty clay loam in subsurface strata. While bottomland hardwood forests on the Cache River floodplain are composed of a variety of vegetative communities, this study was conducted in a mixed oak community with overcup oak Walter) and nuttall oak (*Quercus nuttalli* Palmer) as the dominant components.

The Coosawhatchie River study site, owned by Westvaco Timberlands, Inc., is located in Jasper County, southeastern South Carolina (approximately 31°N, 81°W). The Coosawhatchie originates in the Coastal Plain. Annual mean flow on the Coosawhatchie River is 360 $m^3 s^{-1}$ and flooding can occur several times per year and last between 0 to 48% of the year (Eisenbies and Hughes, 2000). The Coosawhatchie appears unusual among streams originating in the Coastal Plain in that AGNPP is among the highest reported for floodplain forests in the southeastern USA (Burke et al., 1999). It has been suggested that underlying marl stratigraphy deposited during interglacial periods contributes to relatively high P and Ca economy on the site (Murray et al., 2000) resulting in a Coastal Plain system that is apparently not P deficient.

The Coosawhatchie River study site supported two distinct study areas for this investigation: a frequently inundated, low lying sweetgum-swamp tupelo community and a higher elevation, less frequently inundated, laurel oak (*Quercus laurifolia* Michx.) community. Soils in both communities were classified in the Brookman series, and have been described as fine, mixed, thermic Typic Umbraqualfs (Murray et al., 2000). These soils have thick, black loamy surface layers and dark gray clayey subsoils. More detailed descriptions of soils and vegetation on this site are reported in Murray et al. (2000) and Burke et al. (2000), respectively. These two adjacent communities were within the same floodplain and on similar soils. Thus, decomposition could be compared between distinct communities while holding constant those variables that otherwise differed among floodplains (i.e., climate, nutrient status of floodwaters, soil types).

The Iatt Creek study site is located on the Kisatchie Na-

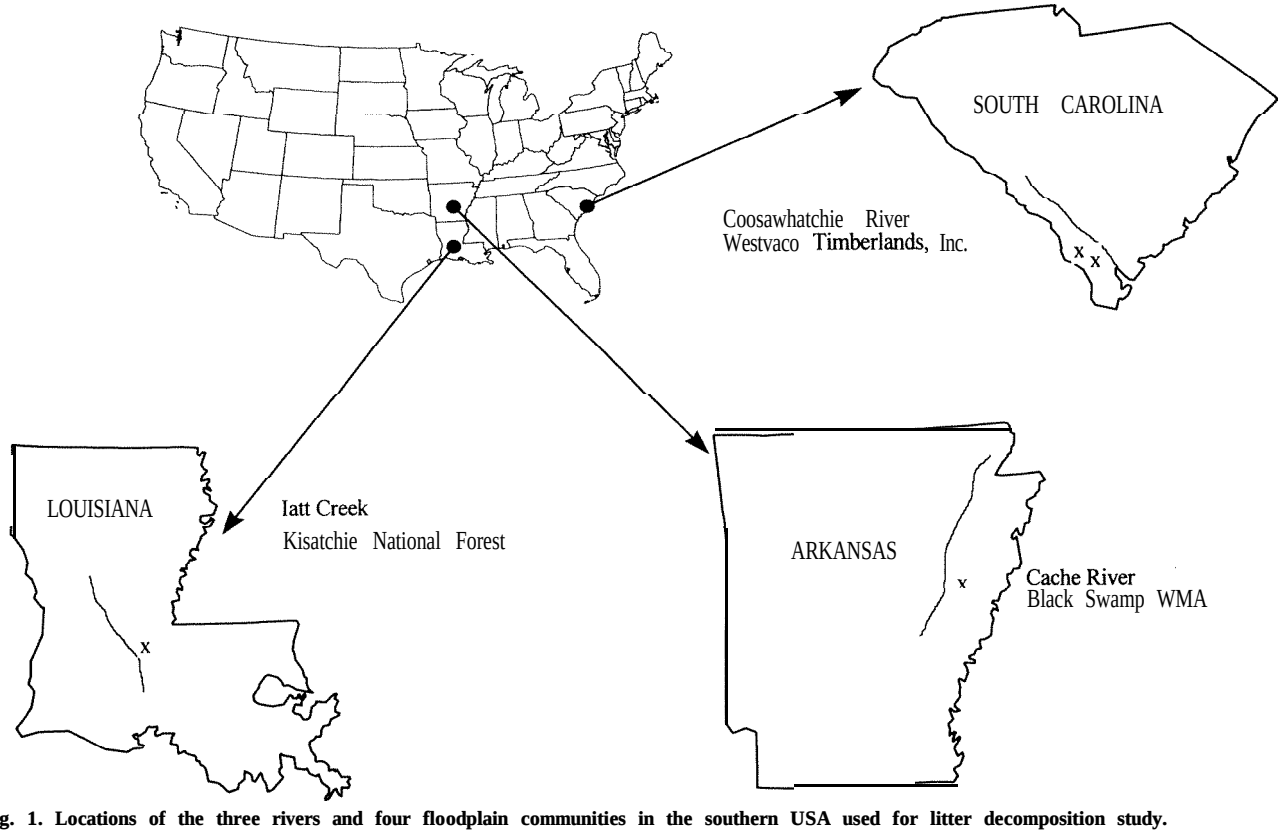

Fig. 1. Locations of the three rivers and four floodplain communities in the southern USA used for litter decomposition study.

tional Forest in Winn Parish, LA (approximately 31°N, 92°W). Iatt Creek originates in the Hilly Coastal Plain. The watershed is subjected to various types of land use but is mostly forested. Iatt Creek and its tributaries are deeply incised (commonly 5 m and 2 m, respectively). Streamflow in Iatt Creek ranges from virtually zero in the dry summer months to flashy overbank flooding during the winter and spring months that typically recedes within two or three days (C.E. Meier, personal communication, 1998). Soils are classified in the Guyton series and have been described as fine-silty, siliceous, thermic Typic Glossaqualfs (C.E. Meier, personal communication, 1998). The Iatt Creek floodplain supports a variety of vegetative communities ranging from cypress (*Taxodium* communities in the low lying sloughs to mixed bottomland hardwood and pine communities (*Pinus taeda* L.) on higher areas within the floodplain. This study was conducted in a community composed of primarily sweetgum and cherrybark oak (*Quercus falcata* var. *pagodaefolia* Ell.).

Temperature and Flooding

Soil temperature was monitored with two portable temperature recorders (Onset Computer Corporation, Pocasset, MA) placed in the litter layer at each site. Because launch failures, water contamination, and long flooding events prevented consistent temperature recording at the Cache River site, surface soil temperature data from a nearby meteorological station (MET Station, Data Loggers, Ogden, UT) was used. Depth and duration of flooding above the soil surface was determined with capacitance based water level recorders (WL-80, Remote Data Systems, Wilmington, NC) installed adjacent to decomposition sites. Using data from WL-80 wells and their elevation relative to that of litterbag sites, the depth and duration of flooding at the litterbags were estimated.

Leaf Litter Collection and Preparation

Leaf litter collection began on the three floodplains in October, 1995 when substantial annual litterfall was first observed. On sites where floodwaters threatened to disturb litter collection traps, heavy plastic tarpaulins were suspended from poles approximately 2 m above the ground to intercept falling leaf litter. On drier sites, similar tarpaulins were placed on the ground and anchored with stakes to collect leaf litter. It is important to collect litter from the same community in which decomposition processes will be monitored, particularly on floodplain sites where microtopographical variation contributes to community and litter quality variability over short distances (Hardin and Wistendahl, 1983; Dollar et al., 1992; Brinson, 1993; Johnston, 1993). Otherwise, litter quality and microsite variation can lead to erroneous conclusions about nutrient cycling dynamics within a particular community. Every effort was made to collect mixed-species litter specifically from the plant community in which litterbags were to be placed.

Litter from each of the five major species of each site was composited by community to form weighted average mixtures for inclusion in litterbags (Table 1). Litterbags (30.5 by 45.7 cm with 6- and 2-mm openings on the upper and lower sides, respectively) were sealed at the open end with stainless steel staples. A second set of litterbags containing only cherrybark oak leaf litter, collected from the Iatt Creek site, were placed adjacent to mixed-species litterbags to test for edaphic influences on decomposition processes (i.e., litter quality remained constant). All litterbags were placed on the soil surface and anchored with pin flags to prevent them from being washed away during flooding. Because of a limited quantity of available litter, single-species litterbags were not used in the sweetgum-swamp tupelo community on the Coosawhatchie River site. All litterbags contained approximately 20 g of air dried leaf litter. Three replicates of each litterbag type were oven dried to a constant weight at 70°C and compared with their air dried weight to obtain a correction factor for the difference between air and oven dried weight. Three replicates of each litterbag type were taken to all sites at the time of placement and immediately returned to the lab and weighed to obtain correction factors for handling loss during placement. For each floodplain community, three replicates of 14 bags each were installed for both the single-species litter and the mixed-species litter.

Popsicle Sticks

Wooden (*Betula papyrifera* Marsh.) popsicle sticks (Solon Manufacturing, Solon, ME) were placed on all study sites to assess the effects of decomposition microenvironment on a relatively homogenous substrate. Three popsicle sticks (with a hole drilled in one end) were attached with plastic rings to each mixed-species litterbag and collected at the same time litterbags were removed. Popsicle sticks were used to track mass loss patterns among floodplain sites but were not used to assess nutrient mineralization/immobilization dynamics. Popsicle sticks were returned to the laboratory with each litterbag collection, washed free of sediment, oven dried to a constant, weight at 70°C, and weighed.

Litterbag Collection and Nutrient Analyses

Litterbags were placed in the field in April, 1996 and samples were collected after o-2-4-6-8-12-16-22-28-38-48-64-80 and 100-wk. On several occasions, litterbags could not be

Table 1. Representative mixtures of leaf fitter (20 g total) used in litterbags. The quantity of litter from each species was determined as a relative proportion of all litter collected from each floodplain community thereby reflecting the importance of each species' litter present on the forest floor. Numbers indicate percentage of each species contained in litterbags in each community.

Cache River (Arkansas) Mixed oak Community (AR)	Coosawhstchie River (South Carolina) Laurel Oak Community (SCdry)	Coosawhatchie River (South Carolina) Sweetgum/Swamp Tupelo Community (SCwet)	Iatt Creek (Louisiana) Sweetgum/Cherrybark Oak Community (LA)
Nyssa spp. 39%	Quercus spp. small, entire-leaved *31%*	*Liquidambar styraciflua 48%*	*Quercus* spp. large, lobed-leaved 60%
Quercus spp. small, entire-leaved 34%	*Liquidambar styraciflua 29%*	*Quercus* spp. large, lobed-leaved 21%	*Liquidambar styraciflua* 19%
Quercus spp. large, lobe-leaved 11%	Quercus spp. large, lobed-leaved 26%	*Nyssa aquatica* 16%	*Carya aquatica 8%*
Acer spp. 9%	*Acer rubrum 8%*	Quercus spp. small, entire-leaved 12%	*Fagus grandifolia 7%*
Ulmus spp. 7%	not applicable?	*Acer* spp. *3%*	Quercus spp. small, entire-leaved 6%
89%‡	not available	not available	*92%*

† A fifth species was excluded from these litterbags because the remaining litter collected from this community was composed of many species, none of which occupied a dominant proportion.

‡ The proportion that the five species represents with respect to total litterfall collected.

collected at the precise time interval due to extreme flood events and deep water. Samples were returned to the laboratory within two days (or placed under refrigeration until shipment). All material was removed from litterbags and foreign materials (e.g., sediment, woody materials, reproductive parts) were sorted out and removed. Litter was oven dried to constant weight at 70°C, weighed, ground to pass a 20-mesh sieve, and analyzed for N, P, and C. Leaf litter N and C concentration were determined by thermal combustion using a Perkin-Elmer 2400 CHN Analyzer (Perkin Elmer Corp., Norwalk, CT) on subsamples taken from leaf mixed-species litter from each sample period. Leaf litter total P concentration was determined colorimetrically using an ammonium vanadate solution on an HCl extract following dry ashing at 400°C for 4 h (Jackson, 19.58). Leaf litter N, C, and P concentrations were multiplied by the oven dried weight of leaf litter remaining at each sample period to determine N, C, and P content of litter. Mass loss and decay coefficients were expressed on an ash free basis. Lignin and cellulose were determined using the acid detergent fiber method (Van Soest and Wine, 1968), and lignocellulose indices (LCI) (Mellilo et al., 1989; Aber et al., 1990) were calculated as % lignin/(% lignin + % cellulose).

Statistical Analyses

Sites were selected on the basis of the plant communities from which litter was collected and their proximity to existing vegetation productivity plots. There were three replicates of each litter type on the four sites and all litterbags were randomly selected for collection. All data were analyzed by SAS (SAS Institute, 1991). The Non-Linear (NLIN) procedure was used to calculate rates of mass loss (k) [$(XIX,) = e^{-kt}$] (Olson, 1963) for each litterbag type and popsicle sticks. Analyses were conducted separately for mixed- and single-species litter (e.g., k, % mass remaining, N, and P) and popsicle sticks (e.g., k, % mass remaining) by the General Linear Model (GLM) procedure. ANOVA was conducted in a randomized complete block design with site as the primary treatment variable. The single-species litter was also compared with the mixed-species litter combinations within each floodplain, and these ANOVAs utilized litter type as the primary treatment variable. Duncan's multiple range procedure was used to test for significant differences among means at the 0.05 probability level. Comparisons of N and P remaining in litter within each community at every sampling date were conducted at the 0.05 probability level.

RESULTS

Temperature and Flooding

Although average daily temperature was not identical among the four communities, differences were of short duration and were not dramatic. We make the assumption here that temperature differences did not drive differences in decomposition. Depth and duration of flooding among the communities were markedly variable (Fig. 2 and Table 2). Flooding at AR occurred five separate times, and litterbags were inundated for nearly 6 mo during winter 1996 and 1997—the longest continuous period of flooding among the four floodplain communities. LA experienced three very short duration flooding events (2-3 d each) suggesting that litterbags at this site were inundated for only the short period during which floodwaters rose and receded. Litterbags

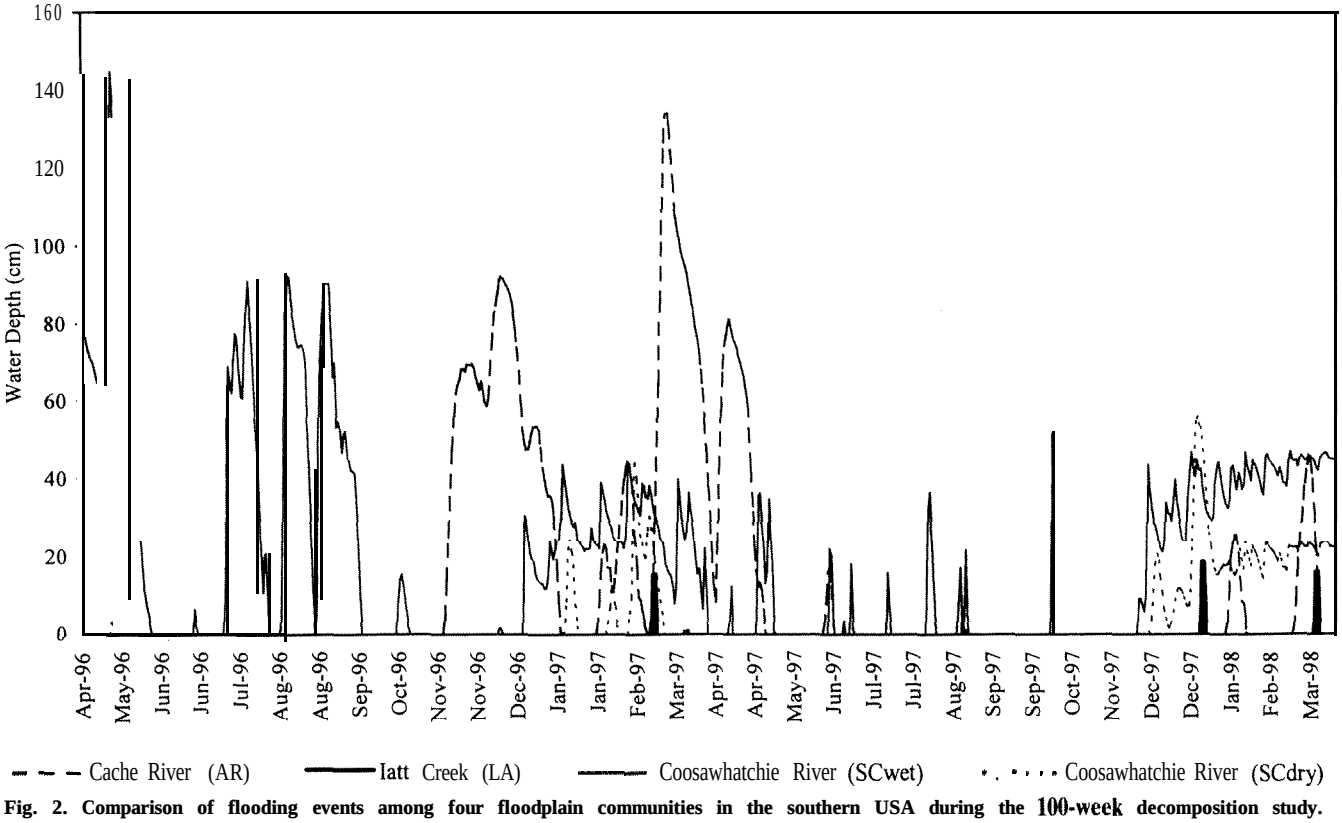

Fig. 2. Comparison of flooding events among four floodplain communities in the southern USA during the 100-week decomposition study. x-Axis depicts continuous time flooded over 100 wk, not discrete periods of' time. Months that are repeated do not represent additional flood events or longer flooding periods.

at SCdry experienced eight separate periods of inundation, most of which were brief (1-21 d) except for one event that lasted for several months. Litterbags at SCwet were inundated more frequently (approximately 17 events) than litterbags at other sites. Table 2 provides a ranking of the floodplain sites in terms of the proportion of total time inundated and number of wetting/drying cycles.

Mass Dynamics

Decomposition rates for the mixed-species litter combinations varied significantly among floodplain sites (Tables 2 and 3). A similar statistically significant pattern was observed for single-species litter (Tables 2 and 3). Comparisons made between each litterbag type (i.e., mixed- versus single-species) within each floodplain site revealed that the single-species litter decayed significantly slower at AR (Table 3).

Comparisons of the percentage of original mass remaining of mixed- and single-species litter at the final collection (approximately 100 wk) revealed similar rankings to decay rates (Table 2) among the four floodplain communities, although there was no statistical difference between LA and SCwet (Table 3). Mixed-species litter at LA and SCwet contained significantly lower percentages of original mass than AR and SCdry, and SCdry contained significantly less than AR. The same pattern was observed for single-species litter (excluding SCwet where no single-species litterbags were installed) (Tables 2 and 3). The percent of original mass remaining for single-species litter differed dramatically among the three sites, and all of these values differed statistically. Within each floodplain community, litter types (mixed- versus single-species litter) were not statistically different in the percentage of original mass remaining (Table 3).

Popsicle Sticks

Because of incomplete collection of popsicle sticks during the final sample on three of the floodplain sites, analyses were conducted on the previous (approximately 80 wk) sample. Although no statistical separation was observed between SCwet and LA, the average decay rate for popsicle sticks on SCwet was significantly greater than the average decay rates on SCdry or AR (Table 3). Comparisons of the percentage of original popsicle stick mass remaining after 80 wk among floodplain sites exhibited a pattern similar to decay rates (Table 2), but no statistical separation was detected.

Table 2. Simple ranking among floodplain sites for variables examined. Table is desigued as a quick reference for discussion in text. Refer to Tables 3 and 4 for detailed statistical comparisons.

Variable	Ranking Among Sites‡
Days Inundated	SCwet>AR>SCdry>LA
Wetting/Drying Cycles	SCwet>SCdry>AR>LA
Mixed-Species Litter	
Decomposition Rate (k)	LA>SCwet>SCdry>AR
Mass Lost after 100 wkt	LA=SCwet>SCdry>AR
C Lost after 100 wk	LA=SCwet>SCdry>AR
N Lost after 100 wk	LA=SCwet>SCdry>AR
P Lost after 100 wk	LA=SCwet=SCdry>AR
Single-Species Litter	
Decomposition Rate (k)	LA>SCdry>AR
Mass Lost after 100 wk	LA>SCdry>AR
C Lost after 100 wk	LA=SCdry>AR
N Lest after 100 wk	LA>SCdry>AR
P Lost after 100 wk	LA=SCdry>AR
Popsicle Sticks	
Decomposition Rate (k)	SCwet=LA=SCdry=AR
Mass Lost after 80 wk	SCwet=LA=SCdry=AR

† The variable mass lost is used here, rather than mass remaining, to allow ranking to be consistent.
‡ An equal sign indicates no statistically significant difference was observed between the two adjacently ranked sites.

Carbon, Phosphorus, and Nitrogen Dynamics

Net changes in C remaining after 100 wk (Table 4) exhibited a pattern nearly identical to percent mass remaining among floodplain sites. Temporal patterns in C remaining through the 100-week period also closely resembled those of mass loss. Because a steady trend of C mineralization was observed for both mixed- and single-species litter within each floodplain community, and because the patterns so closely resembled those of mass loss, the temporal C data are not presented.

The net percentage of P remaining in mixed-species litter after 100 wk among the four floodplain communities exhibited a ranking similar to C (Tables 2 and 4). Once again, no significant differences were observed between LA and SCwet nor between SCwet and SCdry mixed-species litter, but mixtures at AR showed significantly lower net P loss than mixtures in the other communities. The percentage of P remaining in single-

Table 3. Decomposition rates and percentage of mass remaining in leaf litterbags (after 100 wks) aud popsicle sticks (after 80 wks) in four floodolain communities of the southern USA. Standard errors of the means are in parentheses.

	Decay Coefficient (k) (yr^{-1})			Mass Remaining (%)		
	Mixed Species	Single Species	Popsicle Sticks	Mixed Species	Single Species	Popsicle Sticks
Cache River, AR (AR)	0.686A‡ (0.05)a§	0.416A (0.02)b	0.445A (0.10)	32.9A (6.65)a	53.5A (1.90)a	44.9A (18.36)
Coosawhatchie River, SC Laurel Oak (SCdry)	0.841 B (0.04)a	0.788B (0.04)a	0.564A (0.08)	17.8B (1.87)a	15.8B (2.72)a	38.7A (4.65)
Coosawhatchie River, SC Sweetgum/Swamp Tupelo (SCwet)	0.995C (0.03)	not applicable	0.906B (0.02)	8.1C (0.88)	not applicable	9.4A (1.50)
Iatt Creek, LA (LA)	1.2681) (0.05)a	1.330C (0.08)s	0.646AB (0.07)	5.2C (1.36)a	6.9C (1.65)a	32.7A (8.68)

† calculated as $(X/X,) = e^{kt}$.
‡ Means within each littertype with the same uppercase letter are not significantly different at the alpha = 0.05 level.
§ Lowercase letters compare decay coefficient or mass between littertypes within a single community: means with same lowercase letter are not significantly different at the alpha = 0.05 level.

Table 4. Percentage of C, N, and P remaining in leaf litter in four floodplain communities of the southern region of the USA after 100 wks. Standard errors of the means are in parentheses.

	Carbon Remaining %		Nitrogen Remaining %		Phosphorus Remaining %	
	Mixed Species	Single Species	Mixed Species	Single Species	Mixed Species	Single Species
Cache River, AR (AR)	29.6A‡ (9.2)a‡‡	50.8A (3.9)b	68.8A (5.5)a	94.6A (3.5)a	53.6A (7.4)a	107.1A (13.6)b
Coosawhatchie River, SC Laurel Oak (SCdry)	15.7B (4.2)a	14.7B (4.7)a	35.8B (1.1)a	31.0B (2.4)a	24.4B (1.4)a	27.3B (5.0)a
Coosawhatchie River, SC Sweetgum/Swamp Tupelo (SCwet)	7.0BC (1.9)	n/a	16.6C (0.6)	n/a	16.7BC (2.2)	n/a
Iatt Creek, LA (LA)	4.4C (1.2)a	6.0B (3.4)a	8.2C (0.8)a	10.1C (1.7)a	8.2C (1.6)a	11.1B (3.0)a

‡ Means within each littertype with the same uppercase letter are not significantly different at the alpha = 0.05 level.
‡‡ Lowercase letters compare C, N, or P between littertypes; means with same lowercase letter within a single community are not significantly different at the alpha = 0.05 level.

species litter was not significantly different between LA and SCdry, but AR retained nine and four times the amount of original P as was retained in the same litter at LA and SCdry, respectively. As we observed with C, single-species litter retained a significantly higher percentage of P than mixed-species litter at AR after 100 wk.

Temporal analyses of percent P remaining in mixed-species litter combinations over the 100-wk period suggested variable patterns of mineralization and accumulation among the four floodplain sites (Fig. 3). Significant P mineralization occurred between sampling dates on all sites several times throughout the study, particularly in the later sample dates. Although there was evidence of accumulation or immobilization between several intervals, only AR (Week 64, Fig. 3) and SCwet (Week 4 and 6, Fig. 3) exhibited statistically significant net P accumulation for mixed-species litter, and this occurred over relatively short periods. For the single-species litter, mineralization was also significant between a number of sampling intervals on all sites, except at AR, where P immobilization occurred (week 64, Fig. 4). There was no significant difference in P content of single-species litter at the time of final collection (100 wk) compared to fresh single-species litter. This would suggest that P accumulated in the litter that remained at AR even after it had lost approximately 50% of its original mass (Tables 3 and 4).

The net percentage of N remaining in mixed-species litter after 100 wk exhibited a ranking similar to C and P (Tables 2 and 4). Although significant differences were not detected between LA and SCwet, these two communities retained significantly less original N than

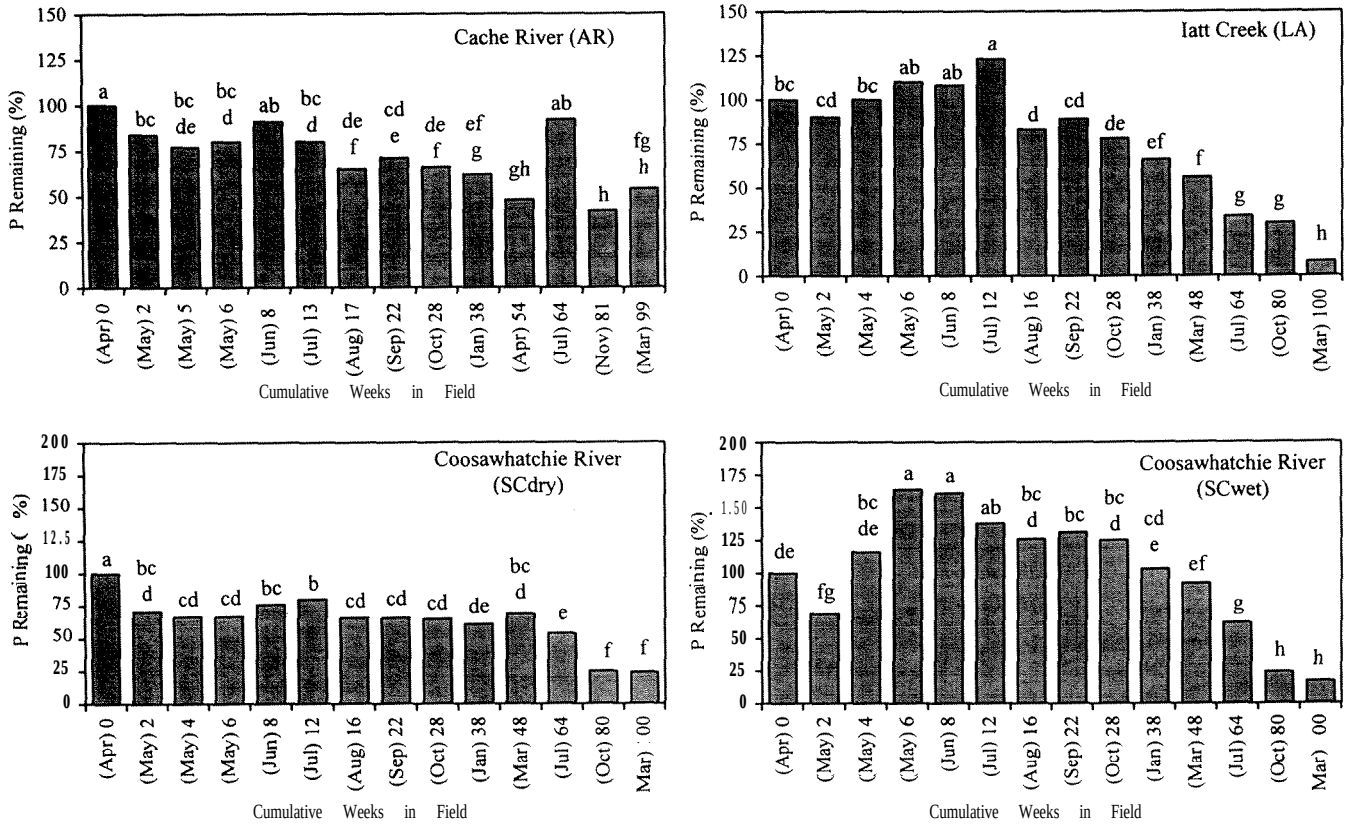

Fig. 3. Percent P remaining for mixed-species leaf litter combinations in four forested floodplain communities in the southern USA. Means with the same lowercase letter are not significantly different (alpha = 0.05). Scale on x-axis is not linear.

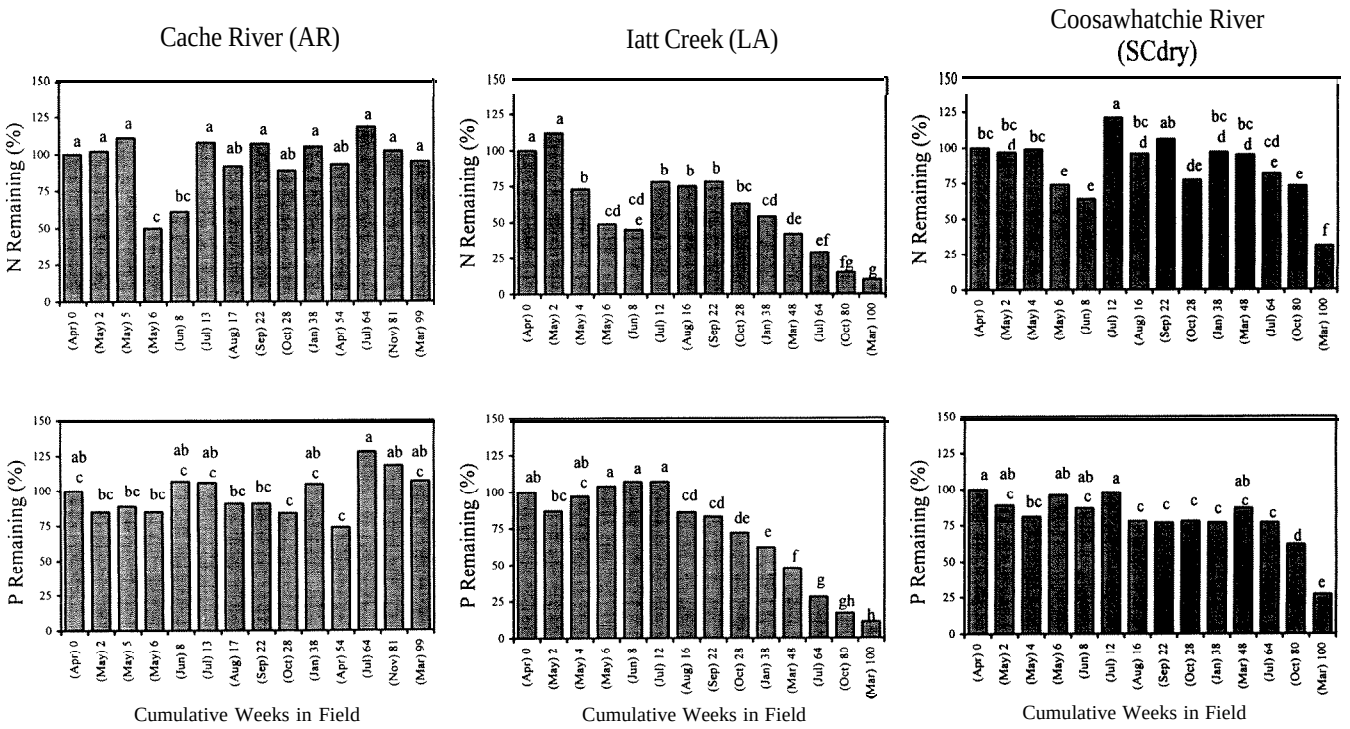

Fig. 4. Percent N and P remaining in cherrybark oak leaf litter in three forested floodplain communities in the southern USA. Means with the same lowercase letter are not significantly different (alpha = 0.05). Scale on x-axis is not linear.

SCdry and AR (Table 4). The net percentage of N remaining in single-species litter was significantly different among each floodplain community in which this litter was installed (Table 4). The single-species litter at AR retained approximately nine times more N than the single-species litter at LA and three times the amount that was retained at SCdry. There were no significant differences between single- and mixed-species litter N remaining after 100 wk at any of the sites.

Temporal analyses of percent N remaining in mixed-species litter combinations suggested net mineralization after 100 wk but patterns of mineralization and accumulation varied among the four floodplain sites (Fig. 5). Accumulation of N was observed in mixed-species litter between sampling intervals at least once in each floodplain community except SCwet. As in the case of P, N accumulation could occur over fairly short intervals and roughly at the same time in all communities (between Weeks 6 and 8 at AR and Weeks 8 and 12 at LA and SCdry). Unique among the floodplain sites, N accumulation was observed in mixed-species litter within 2 wk of placement at LA and at Week 64 at AR. Although significant N accumulation occurred in single-species litter on all floodplain sites, only LA and SCdry exhibited net N mineralization (Fig. 4). Similar to P, single-species litter at AR had accumulated N such that there was no significant difference in N content between the time it was installed and at the final collection.

Litter Quality

Initial C:N ratios ranged from 46 to 68 for mixed-species litter combinations in the four floodplain communities (Table 5). The C:N ratio for the SCdry mixture was significantly wider than any of the other floodplain species mixtures, and the C:N ratio for the SCwet mixture was significantly wider than the LA mixture. After 100 wk in contact with the forest floor, these ratios narrowed, but the SCdry mixture narrowed significantly less. No significant differences were detected in C:N ratios of the single-species litter after 100 wk among the three floodplain communities.

Initial C:P ratios ranged between 242 and 358 for mixed-species litter on the four floodplain sites (Table 5). Although no significant differences in C:P ratios were detected among SCdry, SCwet, and LA mixed-species litter combinations, the ratio for mixed litter from AR was significantly narrower than any of these other three mixtures. After approximately 100 wk in contact with forest floor, these indices had narrowed on all sites to between 123 and 194. At this time, both AR and SCwet exhibited significantly narrower C:P ratios than either SCdry or LA. After 100 wk, C:P ratios for the single-species litter had also narrowed, but remained wider on SCdry as compared to the other communities (Table 5).

Initial N:P ratios for the mixed-species litter, ranging from 5 to 8 among the four communities, were significantly wider on LA than any of the other floodplain communities (Table 5). SCwet also exhibited significantly wider N:P ratios than AR. After 100 wk in the field, the LA mixture retained the widest N:P ratios and these were significant in comparison to both AR and SCwet. No significant differences were detected among N:P ratios in the single-species litter after 100 wk.

No statistically significant differences were detected among lignin, cellulose, and LCI estimates for mixed-species litter from the four floodplain communities (Table 6). However, lignin:N ratios for mixed-species litter

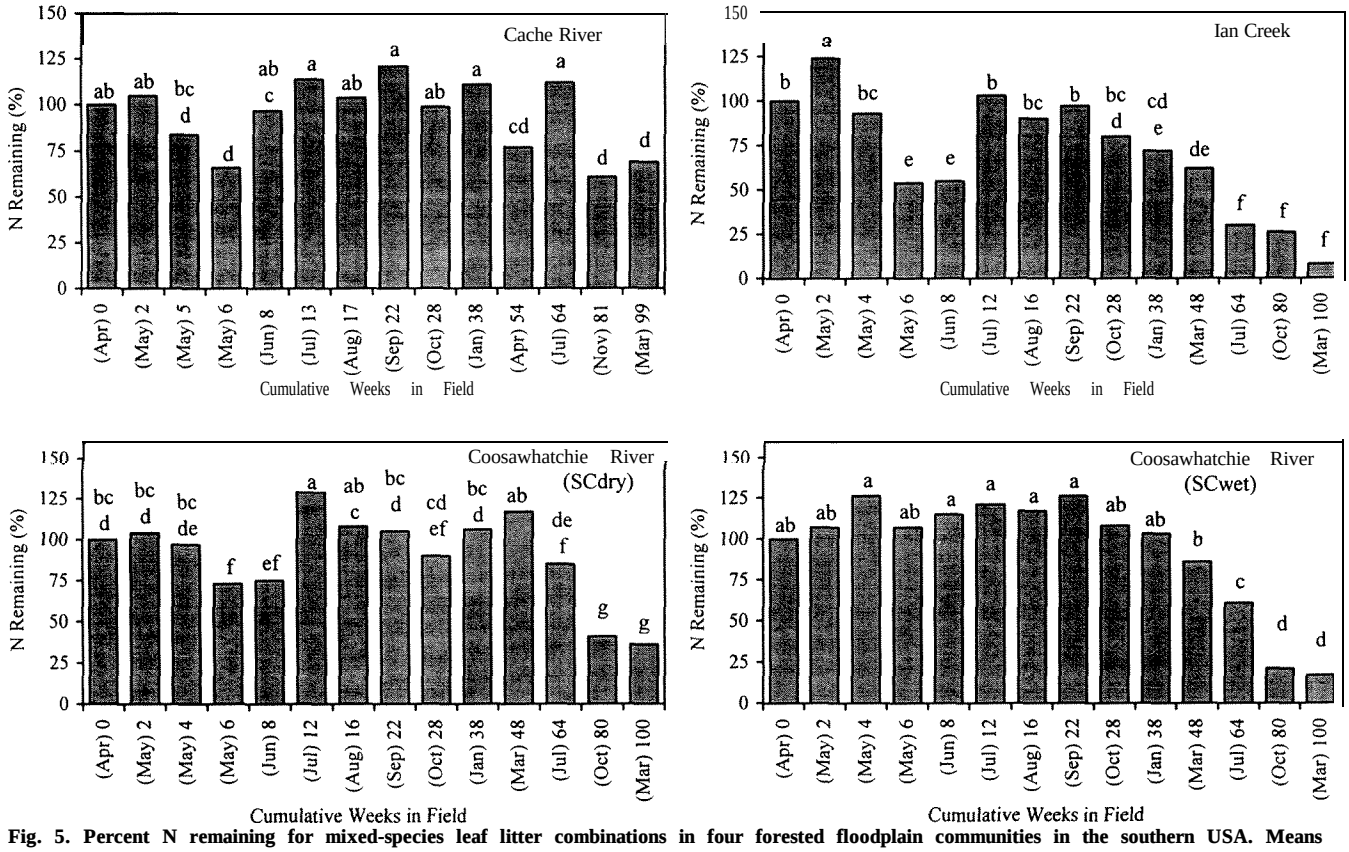

Fig. 5. Percent N remaining for mixed-species leaf litter combinations in four forested floodplain communities in the southern USA. Means with the same lowercase letter are not significantly different (alpha = 0.05). Scale on x-axis is not linear.

at SCdry were significantly wider than mixtures from the other three floodplain communities.

Mixed-species litter at AR exhibited significantly narrower N:P and C:P ratios than single-species litter at this site at the time of installation but no significant differences were observed after 100 wk (Table 5). Mixed-species litter at SCdry and LA both exhibited significantly narrower N:P ratios than single-species litter at these sites at the time of installation but no significant differences were detected after 100 wk. At the time

Table 5. Elemental ratios describing substrate quality differences among leaf litter combinations at installation and after 100 weeks among four floodplain communities of the southern region of the United States. Standard errors of the means are in parentheses.

	At time of installation					
	N/P		C/N		C/P	
	Mixed Species	Single Species	Mixed Species	Single Species	Mixed Species	Single Species
Cache River, AR (AR)	4.7A† (0.38)a‡	7.8§ (0.31)b	52.4AB (2.71)a	47.2 (3.13)a	241.9A (8.64)a	366.7 (20.52)b
Coosawhatchie River, SC Laurel Oak (SCdry)	4.8AB (0.17)a	7.3 (0.27)b	68.1C (3.44)a	54.0 (4.91)a	325.1B (25.03)a	390.9 (20.47)a
Coosawhatchie River, SC Sweetgum/Swamp Tupelo (SCwet)	6.1B (0.60)	n/a	57.3A (3.31)	n/a	329.9B (16.51)	a la
Iatt Creek, LA (LA)	7.8C (0.33)a	9.2 (0.35)b	46.0B (2.99)a	37.6 (1.65)a	358.0B (11.67)a	346.0 (3.65)a
	After 100 weeks					
Cache River, AR (AR)	5.6A (0.27)a	6.6A (0.57)a	22.1A (1.60)a	25.6A (1.24)a	123.3A (8.02)a	164.4A (8.93)b
Coosawhatchie River, SC Laurel Oak (SCdry)	6.5AB (0.45)a	7.9A (0.38)a	29.9B (1.38)a	25.2A (0.58)b	193.78 (9.33)s	203.7B (5.94)a
Coosawhatcbie River, SC Sweetgum/Swamp Tupelo (SCwet)	5.6A (0.07)	n/a	23.3A (0.68)	n/a	130.0A (5.15)	n/a
Iatt Creek, LA (LA)	7.6B (0.53)a	7.5A (1.02)a	24.5A (1.36)a	23.8A (2.89)a	186.4B (18.70)a	172.6A (3.72)a

† Means for each floodplain community within each littertype with the same uppercase letter are not significantly different at the alpha = 0.05 level.
‡ Means for each littertype within each floodplain community with the same lowercase letter are not significantly different at the alpha = 0.05 level.
§ No statistical separation was conducted for the single-species litter as this material was assumed to be homogenous.

Table 6. Indices describing quality of leaf liter combinations at installation among four floodplain communities of the southern region of the United States. Standard errors of the means are in parentheses.

	Lignin (%)		Cellulose (%)		Lignocellulose Index (LCI)		Lignin/N	
	Mixed Species	Single Species	Mixed Species	Single Species	Mixed Species	Single Species	Mixed Species	Single species
Cache River, AR (AR)	22.0A (0.48)a‡	22.71 (0.42)a	27.2A (0.48)a	27.3 (0.42)a	0.447A (0.01)a	0.455 (0.01)a	23.7A (0.05)a	21.6 (0.08)a
Coosawhatchie River, SC Laurel Oak (SCdry)	24.3A (0.54)a	24.9 (0.55)a	25.3A (0.45)s	25.2 (0.52)a	0.490A (0.01)s	0.500 (0.01)a	33.6B (0.04)a	27.6 (0.08)a
Coosawhatchie River, SC Sweetgum/Swamp Tupelo (SCwet)	21.5A (2.77)	n/a	27.9A (2.73)	n/a	0.435A (0.06)	n/a	24.2A (0.05)	n/a
Iatt Creek, LA (LA)	21.4A (0.84)a	20.6 (0.33)a	28.3A (1.04)a	29.4 (1.33)a	0.431A (0.02)a	0.411 (0.01)a	20.2A (0.10)a	15.3 (0.19)b

† Means for each floodplain community within each littertype with the same uppercase letter are not significantly different at the alpha = 0.05 level.
‡ Means for each littertype within each floodplain community with the same lowercase letter are not significantly different at the alpha = 0.05 level.
§ No statistical separation was conducted for the single-species litter as this material was assumed to be homogenous.

of installation, mixed-species litter at LA did exhibit significantly wider lignin:N ratios than single-species litter at this site (Table 6).

No statistical separation was conducted for fresh single-species litter quality as this material was assumed to be homogenous. However, numerical differences in litter quality indices for single-species litter were observed, particularly in C:N, C:P, and lignin:N ratios, as well as LCI indices (Tables 5 and 6). Variation in litter quality even within the single-species litter may have been a result of site-specific variation in litter quality from collection sites and/or differences in storage time and conditions before litter was collected and processed. After 100 wk, there were no significant differences among litter quality indices for the single-species litter with the exception of C:P ratios. Single-species litter at SCdry exhibited significantly higher C:P ratios after 100 wk than the same litter at other sites.

DISCUSSION

Mass Dynamics

Brinson (1981, 1990) has conducted thorough reviews of decomposition rates from other studies. As calculated by Lockaby and Walbridge (1998), the average decay rate (k) for temperate riverine forests from the range of studies compiled by Brinson (1990) was 1.01. That average is only slightly higher than the average decay rate for the four floodplain communities (k = 0.95) in this study. While decay coefficients at AR were lower than those reported by Conner and Day (1991) for a natural, an impounded, and a crayfish pond site, decay coefficients from the other three communities in our study were higher than Conner and Day's (1991) natural (0.832) and impounded (0.769) sites, but less than those reported for the crayfish pond (2.081). Annual decay rates for litter mixtures were greater in each community than those observed by Day (1982) (0.341-0.667) for litter mixtures in the Great Dismal Swamp. Also, in all of the floodplain communities in this study, the percentage of original mass remaining in litter mixtures after 100 wk was less than the fraction remaining in Day's (1982) litter mixtures after two years in the Great Dismal Swamp. Probably, differences in litter quality, hydroperiod, and soil microenvironment contributed to differences between our study and Day's (1982).

Other investigations have implicated litter quality as the primary factor governing decomposition (Day, 1982; Elliot et al., 1993; Hobbie, 1996). Our results suggest that the importance of litter quality can be diminished when compared across a wide range of flooding regimes. Depending on its duration, flooding may either stimulate (i.e., LA and SCwet) or inhibit (i.e., AR) decomposition as it affects the decomposition microenvironment.

Results from the single-species litterbags support this contention. Although the single-species litter quality varied somewhat among the three floodplain communities at the start of the study, other influences (i.e., flooding, decomposer communities) may be partly responsible for the dramatically divergent rates and extents of decay. Decay was more rapid on sites experiencing brief, pulsed flood events as opposed to prolonged flooding.

Results from our study agree with those of Lockaby et al. (1996) who concluded that brief flooding events stimulate mass loss to the greatest extent. Among the four floodplain communities, LA (where there were only three, very brief flood events, Fig. 2) retained the lowest percentage of original mass. However, the first flooding event at LA occurred 11 mo after installation of litterbags-well after LA had exhibited the fastest rate of decay among the four floodplain communities. This suggests that other factors, such as soil microenvironment and the microbial community, were also important in determining the rapid decay observed at LA.

LA was characterized by flashy, short duration flood events that typically fluctuated more than floodwaters on the other floodplain sites (Fig. 2). Such conditions were probably responsible for greater physical fragmentation of leaf litter and export of coarse and fine particulate organic matter from litterbags (Peterson and Rolfe, 1982; Yates and Day, 1983), which would elevate estimates of mass loss from litterbags. Also, the brief wetting and drying cycles observed at LA versus the longer periods of inundation observed at other sites may have accelerated decomposition (Brinson, 1981; Mitsch and Gosselink, 1993).

The proportion of time each community was flooded over the 100-wk period was LA (<1%) < SCdry (21%) < AR (28%) < SCwet (52%). With the exception of SCwet, this is identical to the ranking for decay rate and extent. Although SCwet remained inundated for a much greater proportion of total time, litterbags in this community experienced many cycles of wetting and drying, which probably stimulated decomposition.

The dramatically greater percentage of original mass remaining in mixed-species litter at AR was probably a result of a single, long period during which this community remained flooded (Fig. 2), creating an unfavorable (i.e., anaerobic) decomposition environment. In addition, heavy loads of sediment (carried in the floodwaters on this site) were observed coating litterbags at AR. Despite efforts to remove sediment and correct using an ash free basis, these sediment loads could have complicated mass loss estimations or it is possible that this coating of sediment might have created an unfavorable environment for decomposing organisms.

In this study, all litterbags were exposed to the decomposition microenvironment for approximately the same time period. Therefore, time can be eliminated as a variable in explaining differences in rate and extent of decomposition. Microbial activity was not measured directly but wider litter quality indices (i.e., C:P and N:P, Table 5) at LA suggested that leaf litter there might be less decomposable (a deficit of P relative to C). In fact, C:P ratios of 358 for mixed-species litter at LA were well above the threshold value of 200 required for complete decay of organic matter by decomposer organisms (Brinson, 1977), although N:P ratios for the same litter were below the threshold values of 15 reported in other studies (Vogt et al., 1986; Lockaby and Walbridge, 1998). The very narrow N:P ratios observed for litter mixtures in this study may indicate a shortage of N relative to P.

Slower decomposition rates for the mixed-species litter at AR, as compared to the other communities, was unexpected (Table 3). High sedimentation at the Cache River site (Kleiss, 1996) may have masked actual mass loss despite efforts to remove sediment and express values on an ash free basis. Personal observation of high sediment loads on litter supports this notion. Brinson (1977) reported similar difficulties in an environment prone to flooding. C:P indices at the time of installation for this litter mixture were significantly narrower than the mixtures at other sites (Table 5), suggesting that decay might not be as P limited and may proceed more rapidly or completely. Although not all litter quality indices agreed (Tables 5 and 6), two of the more widely used indices (e.g., N:P, C:P) indicated that LA exhibited the widest and AR exhibited the most narrow litter quality indices. However, comparisons of decay rate and extent among these two communities exhibited the exact opposite pattern of the litter quality indices, with the poorest quality litter showing the highest decay rate. Thus, either decay rates were controlled by factors other than litter quality alone or our indices did not fully encompass differences in litter quality.

Both decay rate and decay extent differed significantly between the two communities on the Coosawhatchie River. Although SCdry exhibited significantly wider C:N and lignin:N ratios, other indices for mixed-species litter did not differ (Tables 5 and 6). Therefore, we might speculate that SCdry was more N limited than SCwet. Although not statistically significant, wider C:P and N:P ratios at SCwet suggest that this community might be more P limited. Soil temperature differences were probably insufficient to measurably affect decomposition rates but hydrologic regime also differed between the two communities (Fig. 2) and may explain the faster rate and greater extent of decay at SCwet. However, the inundated conditions at SCwet were probably not prolonged enough to impede decomposition as was the case at AR. It appears, therefore, that both litter quality and edaphic considerations interacted to promote differences in decomposition between the two Coosawhatchie River communities.

Comparisons of decay rates and final percent mass remaining between mixed-species litter combinations and single-species litter within each site revealed interesting patterns. Both mixed- and single-species litterbags were exposed to similar microenvironmental and edaphic conditions on each site. However, the single-species litter decayed significantly more slowly and retained a greater percent of original mass on the Cache River floodplain as compared to the other sites (Table 3). The differences in decay rate between mixed- and single-species litter on the same site would obviously be a result of differences in litter quality. C:P and N:P ratios suggested that the single-species litter exhibited significantly wider ratios than the litter mixture, implying that decomposition of the single-species litter may be P limited (Table 5).

Other studies also have observed different decay patterns and nutrient dynamics for mixed-species litter as compared to a single-species litter under similar environmental conditions. Blair et al. (1990) observed lower N mineralization from single-species litterbags as compared to mixed-species litterbags and concluded this resulted from different microbial and microarthropod densities within the two littertypes. It is also probable that mixed-species litters can support a more diverse decomposer community than single-species litter, thereby resulting in more complete decay. Comparing four communities subject to different hydrologic regimes, Day (1982) observed that mixed-species litter decomposed more rapidly than a single-species litter in two wetter communities whereas this pattern was reversed in two drier communities. In the same study, Day (1982) observed that mixed-species litter decayed more rapidly than single-species litter comprised of the dominant species from that community (with one exception). Although results from our study suggested that hydroperiod may have superseded litter quality in governing decomposition among the four floodplain communities, litter quality differences between the mixed- and single-species litter appeared to be a more significant regulator of decomposition within a single community.

Popsicle Sticks

Contrary to the results of leaf litter decomposition, popsicle stick decay rates and extent after 80 wk were greatest at SCwet, although not significantly greater than those at LA (Table 2). The resilient nature of popsicle sticks prevented rapid fragmentation and loss of popsicle sticks until late in the study and only after extensive decay. Therefore, differences in popsicle stick decay can be attributed to edaphic factors which con-

trolled decomposition, as substrate quality remained constant among the popsicle sticks. Particularly in the case of the two Coosawhatchie River communities where temperature and nutrient status may have been more similar than among the four floodplain communities, hydroperiod (wetting and drying cycles) appears to be the primary difference explaining divergent rates of decay.

Phosphorus and Nitrogen Dynamics

Differences in the percentage of original P remaining after 100 wk for both mixed- and single-species litter among the floodplain communities resembled differences in mass (Table 4). C:P indices for mixed- and single-species litter at the time of installation (Table 5) suggested that P may limit complete decomposition of leaf litter (i.e., C:P > 200). However, N:P ratios of mixed- and single-species litter were below the threshold values considered necessary for P limitation (i.e., 10–15) (Vogt et al., 1986; Lockaby and Walbridge, 1998). It was unexpected that the litter mixture that exhibited the most narrow C:P and N:P ratios (Table 4, AR-C:P = 242, N:P = 4.7) decomposed most slowly and to the least extent as compared to the litter mixture that exhibited the widest C:P and N:P ratios and decomposed most rapidly (Table 4, LA-C:P = 358, N:P = 7.8). We would expect that the greater abundance of P relative to C and N at AR as compared to the other floodplains would have encouraged more rapid and greater decomposition. The relative abundance of P at AR was not surprising given the high sedimentation on this floodplain and the probable P influx (from agricultural sources) associated with this sediment (Kleiss, 1996).

Accumulation of nutrients in decomposing leaf litter has been shown in several wetland systems (Brinson, 1977; Day, 1982; Conner and Day, 1991; Lockaby et al., 1996) and may come from several exogenous sources or through immobilization by soil flora and fauna inhabiting the leaf litter. Mixed-species litter at LA and SCwet exhibited the widest C:P and N:P ratios and also retained a higher P content for a longer period throughout the study than litter mixtures at other floodplains (Fig. 3). In fact, litter mixtures in both communities contained greater than 100% of original P on several occasions and at SCwet for the majority of the study (Fig. 3). Peaks in immobilization occurred in mixed-species litter (AR at Week 64 and SCwet at wk 4 and 6) during the warm summer months (Fig. 3). Although Megonigal et al. (1996) concluded that microbial activity in southeastern hydric soils is never temperature limited, microbial activity does increase as temperature increases (Paul and Clark, 1989). Although it cannot be conclusively stated that the observed accumulation resulted from increased microbial activity and demand, it is likely that the population of decomposers may have been expanding rapidly at this time, accounting for at least some of the immobilization observed. P associated with deposited sediment may also have been partly responsible because the immobilization peak during week 64 at AR was preceded by a long period of inundation. Field observations also indicated that the SCwet site was frequented by numerous wading birds, perhaps in search of insects and other invertebrates (Don Stoeckel, personal communication, 1998). High inputs of animal excreta may have been responsible, to some degree, for the accumulation of P observed at this time.

Significant P immobilization at SCwet might be expected because this river originates in the Coastal Plain and such systems are often P limited (Lockaby and Walbridge, 1998). However, recent evidence suggests that the Coosawhatchie River represents a departure from typical Coastal Plain systems as a result of underlying marl deposits and higher soil P (Murray et al., 2000). Nonetheless, P immobilization in mixed-species litter from this community suggests that the element may be limited relative to demand at certain times of the year. The only significant P immobilization that occurred in the single-species litter was at AR. Comparisons of N:P and C:P ratios at the time of installation revealed that these indices were significantly wider for the single-species litter than for the litter mixture obtained from AR (Table 5). The lower resource quality suggested by the N:P and C:P ratios in the single-species litter may have been responsible for the observed immobilization as well as the significantly lower rate and extent of decomposition (Table 3). The immobilization peak at AR in single-species litter occurred at the same time it was observed in mixed-species litter. This suggests the same factors (i.e., sediment deposition, increased microbial activity) contributed to P accumulation in both litter types.

Differences in the percentage of original N remaining after 100 wk for both mixed- and single-species litter among the floodplain communities resembled differences in C remaining (Table 4). Paul and Clark (1989) reported that detritus with C:N ratios above a threshold value of 50 (for forested systems) would exhibit immobilization during decomposition; below this value, mineralization could be expected. On the basis of this threshold value, all litter mixtures, except the LA mixture, were N limited, but not by a wide margin. Litter mixtures at LA also exhibited the most narrow lignin:N ratio among the four floodplain communities, although this was not statistically significant. Therefore, Nitrogen was less limiting to decomposition at LA than at the other floodplain communities. It is interesting to note that the AR litter mixture exhibited C:N and lignin:N ratios most similar to the LA mixture, yet decay rates and extents and N mineralized at AR were significantly less than those at LA. This provides further evidence that decomposition and nutrient mineralization were largely affected by environmental variables (e.g., frequency and duration of flooding, edaphic factors). Once again, this is supported by the divergent results in terms of N remaining in the single-species litter after 100 wk at both of these sites.

With the exception of N and P in single-species litter on the Cache River floodplain, both mixed- and single-species litter exhibited net N mineralization over the 100-week study (Fig. 4 and 5). However, there were several instances when significant N accumulation was observed. Only mixed-species litter at SCwet lacked significant N accumulation between sampling intervals,

although they retained greater than 100% N for some time. As with P accumulation, N accumulation occurred over short intervals and to the largest extent during the growing season. At least some of the accumulation may be attributable to immobilization by decomposers, although exogenous sources such as sediment must also be considered. It is interesting that SCwet exhibited the least tendency to accumulate N but the strongest tendency to accumulate P. However, SCdry showed one of the strongest tendencies to accumulate N, but minimal accumulation of P. If such accumulations are indicative of nutrient limitations (MacLean and Wein, 1978), then these two communities exhibited completely different nutrient limitations within a short distance of one another on a single floodplain. The significantly wider C:N ratios for mixed-species litter at SCdry (e.g., 68) as compared to SCwet (e.g., 57) may explain the tendency for N to accumulate in the former. However, no such relationship existed to explain the tendency for mixed-species litter at SCwet to accumulate P. It is possible that accumulation of P at SCwet is a result of that element being deposited from exogenous sources (perhaps in association with sediment in floodwaters or through the reduction of iron and aluminum phosphates) and may represent luxury consumption by decomposing organisms.

CONCLUSIONS

The rate and extent of decay for both mixed- and single-species litter among the four floodplain communities appeared to be most strongly affected by hydroperiod. Flood events at Iatt Creek were infrequent and brief, which stimulated mass loss and nutrient release from both mixed- and single-species litter. Long periods of inundation appeared to inhibit decomposition of and nutrient release from mixed- and single-species litter on the Cache River site, although burial by sediment might also be a factor. Although litter quality may determine the rate and extent of decomposition under similar edaphic conditions, its significance appears to be diminished when making comparisons among sites that experience dramatically different flooding regimes. Litter quality was a more significant factor when comparing decomposition dynamics between the two communities on the Coosawhatchie River floodplain. Decomposition of mixed-species litter in the drier laurel oak community was probably N limited whereas decomposition was P limited in the more hydric sweetgum/swamp tupelo community. Litter quality differences also explained differences in decay rates between mixed- and single-species litter subjected to the same flooding regime on the Cache River floodplain.

Both mixed- and single-species litter exhibited net mineralization over the 1 OO-week study. However, brief periods of N and P accumulation were observed and suggested that these nutrients accumulate in decomposing leaf litter at least briefly during the early to mid growing season. The accumulation of P also coincided with floodwater recession and some fraction of the accumulation may be the result of P association with sediment being deposited on decomposing litter. However, the bulk of the accumulation of both N and P is probably attributable to immobilization by decomposers, particularly as this coincided with periods of peak biological activity and floodwater recession. As other studies have indicated, the tendency for N and P to accumulate in decomposing leaf litter was greater in leaf litter with relatively wide litter quality indices. This may suggest that decomposer organisms exhibit a greater tendency to immobilize nutrients from exogenous sources during decomposition of less palatable substrates.

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