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The role of floods in particulate organic matter dynamics of a southern Appalachian river–floodplain ecosystem

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Abstract. We investigated the effect of a flood on particulate organic matter (POM) dynamics in the floodplain and active channel of the Little Tennessee River in western North Carolina. We measured litterfall, leaf breakdown, and floodplain litter (before and after the flood) at 12 sites. Annual litterfall (256–562 g m^{-2} y^{-1}) was typical of a temperate deciduous forest but lower than lowland floodplain forests in the eastern US. Leaf breakdown rates of 4 tree species (*Acer rubrum*, *Carpinus caroliniana*, *Juglans nigra*, and *Platanus occidentalis*) ranged from 0.001 to 0.010/d. We separated the 12 sites into 2 groups (inundated and non-inundated) based on the degree of flooding after a flood on 8 January 1998 and determined POM exchange between the active channel and floodplain. Significant transport of leaves from the floodplain to the river occurred at inundated sites, but transport of herbaceous or woody material did not occur. The flood increased leaf breakdown rates of all 4 tree species. Our measurements of litterfall, leaf breakdown, and floodplain litter standing crop suggest that leaves entrained from the floodplain of Little Tennessee River during floods are a source of POM to the active channel. However, flood input of leaves to the river were a small source of POM compared to direct leaffall.

Key words: organic matter dynamics, litterfall, leaf breakdown, particulate organic matter, river, floodplain.

Allochthonous particulate organic matter (POM) is an important source of C for many streams and forms a link between streams and their adjacent riparian areas. Small headwater streams in temperate forests are often heterotrophic because they are dependent on POM as their primary source of C (Fisher and Likens 1973, Cummins 1974), but a shift from heterotrophy to autotrophy is predicted in mid-order reaches of streams adjacent to deciduous or coniferous forest (Vannote et al. 1980). Determining the importance of allochthonous POM inputs in rivers is complicated by POM dynamics in associated floodplains (e.g., Webster et al. 1995). Rivers often are strongly coupled to their floodplains, and lateral exchange of POM between rivers and their floodplains can be extensive. This exchange of POM usually occurs via surface flow during floods when the net movement of organic materials can be from floodplain to river or from river to floodplain. Cuffney (1988) proposed that a particular floodplain may be a sink or source of POM depending on the flood regime, floodplain topography, and sediment load of the river.

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Lateral exchange of POM between rivers and their floodplains is potentially important in river organic matter budgets (e.g., Minshall et al. 1985, Junk et al. 1989). Most studies have measured lateral exchange processes in large rivers or coastal plain streams (Mulholland 1981, Grubaugh and Anderson 1989, Junk et al. 1989, Smock 1990, Jones and Smock 1991, Tockner et al. 1999). These streams generally are low gradient, flood regularly, and have extensive floodplains. For example, the floodplain of the 6th-order Ogeechee River in eastern Georgia is ~1.2 km wide, and 50% of the floodplain is inundated annually for 2 mo (Benke et al. 2000). Subsidies of organic matter from the floodplain are often a large source of allochthonous POM to the river in large rivers and coastal plain streams (e.g., Cuffney 1988).

Few studies have focused on the effects of floods on POM dynamics of smaller, higher-gradient rivers (4th- through 6th-order). Small, high-gradient rivers occur at or near the inflection point between heterotrophy and autotrophy and, therefore, they may share characteristics with both small streams and large rivers. Typically, floodplains of small rivers are much smaller and floods more infrequent than in large rivers or coastal plain streams. For exam-

ple, the floodplain of the 6th-order New River in Virginia averages 20 m wide, and records from 1950 to 1980 show that the floodplain was inundated annually for an average of 6 d (Hill 1981). However, lateral exchange of POM between the river and floodplain may still be important in these rivers. Hill (1981) suggested that the floodplain contribution of POM to the New River could, at maximum, be 1.5x that of direct litterfall, assuming no terrestrial decomposition, complete removal of litter from the floodplain, and no redeposition when flood waters recede.

Anthropogenic disturbances, such as water pollution, foodweb manipulation, or hydrologic control, can complicate studies in rivers (e.g., Stanford et al. 1996). Up to 90% of river ecosystems in the United States and Europe have been affected by changes in land use (Tockner and Stanford 2002). Changes in land use may seriously disrupt the dynamics of organic matter in rivers by reducing the quantity and changing the quality of POM inputs. The effects of reducing POM inputs to headwater streams have been well documented (e.g., Wallace et al. 1999). However, in rivers, reduction of sources of POM (e.g., trees) may affect direct litterfall and alter the pool of organic material available for lateral exchange between river and floodplain.

We measured floodplain litterfall, leaf breakdown, and POM standing crop before and after a flood to assess its effect on the dynamics of POM in a river–floodplain ecosystem in the southern Appalachian Mountains. The river is mid-sized (4th–6th order) and floods approximately biennially. Its floodplain has experienced varying degrees of change in land use. Specifically, we addressed 3 research questions: 1) Is the floodplain a source of stored POM to the river during a flood? 2) If so, how important is the subsidy of POM compared to direct leaffall to the river? 3) How does the width of riparian forest affect POM dynamics on floodplains?

Methods

Site Description

We conducted this study on the floodplain of the Little Tennessee River (LTR), Macon and Swain counties, North Carolina. Twelve sites were established along a 65-km reach of river beginning at the confluence with Coweeta Creek and ending near Fontana Reservoir (Fig. 1). Five sites (U1–5) were 4th-order, 3 sites (M1–3) were 5th-order and 4 sites (L1–4) were 6th-order. In July 1997, we surveyed the study reach by canoe. We measured the width of the active channel, floodplain, and riparian forest on the floodplain every 500 m. The floodplain was broad (>50 m) in the upper 25 km of the reach. Gradient increased in the lower 40 km of river, constricting the floodplain in some areas to 10 m. Width of the active channel ranged from 21 to 91 m (Table 1). Much of the floodplain has been converted to agriculture, often restricting trees to a small corridor immediately adjacent to the river. About 80% of the first 5 m of floodplain immediately adjacent to river bank consisted of riparian forest, whereas only 40% of the second 5 m was forested. We classified sites into 3 types based on the width of riparian forest (<5 m, 5–15 m, and >15 m), and we selected sites in proportion to the relative abundance of each type. The width of the floodplain at all of our sites was >20 m.

Discharge of the LTR has been monitored since 1945 at 2 USGS gauging stations, Prentiss and Needmore (US Geological Survey, Raleigh, North Carolina). Floods have occurred approximately biennially since 1945 and have lasted 1 to 2 d. On 8 January 1998, the river experienced an overbank flood that receded within 2 d. For the years on record (1945–1998), 7 annual peakflows exceeded this flood at Prentiss and 5 annual peakflows exceeded this flood at Needmore (Fig. 2). The flood recurrence interval, calculated according to Dunne and Leopold (1978), was 7.4 y at Prentiss and 8.4 y at Needmore.

Forest structure

We established a 20 × 100 m plot parallel to the river bank at each site in October 1998. We identified each tree and measured the diameter at breast height (DBH = stem diameter 1.4 m above the ground) of stems ≥2 cm DBH within each plot. We used these measurements to calculate basal area, tree density, and importance values (IV, modified from Brower and Zar 1984):

$$\mathrm{IV} = \frac{\text{relative basal area} + \text{relative density}}{2} \quad [1]$$

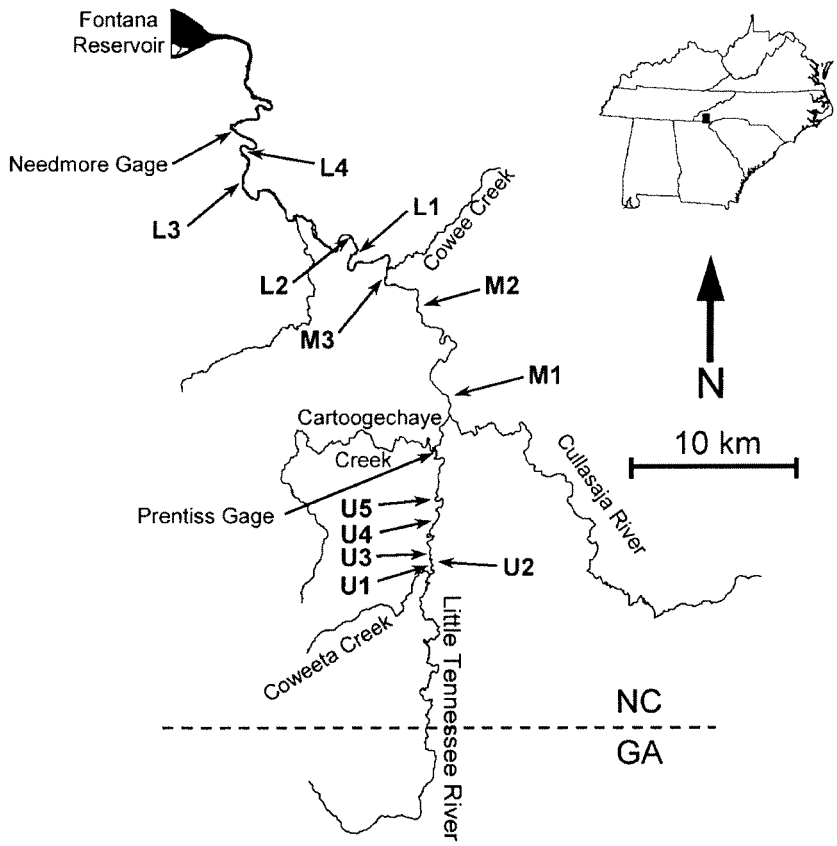

FIG. 1. Locations of study sites along the Little Tennessee River, North Carolina, USA. U = 4th-order, M = 5th-order, L = 6th-order sites.

TABLE 1. Characteristics of the 12 floodplain sites along the Little Tennessee River. River km is the distance downstream from the confluence with Coweeta Creek. U = 4th-order, M = 5th-order, L = 6th-order sites.

Site	River km	Channel width (m)	Riparian forest width (m)
U1	1.2	31	5–15
U2	1.7	22	<5
U3	3.5	25	<5
U4	6.1	25	>15
U5	9.1	21	<5
M1	18.0	38	>15
M2	28.8	80	>15
M3	33.3	44	5–15
L1	38.4	44	5–15
L2	40.4	55	>15
L3	51.5	91	>15
L4	53.3	78	5–15

Litter inputs to the floodplain

We estimated litter inputs to the floodplain using litter traps that consisted of a 0.25-m^2 frame fitted with 1-mm mesh fiberglass screen supported by three 61-cm wooden stakes. We placed 10 traps at 2- to 5-m intervals along a transect parallel to the river channel at each site ~1 to 3 m from the river bank to emphasize direct leaffall to the river. We removed litter from the traps twice monthly during peak leaffall (October–November) and monthly at other times (September 1997, December 1997–September 1998). We dried litter at 50°C for 2 d and sorted it as leaves, wood, or miscellaneous material (flowers, fruits, or seeds from trees). We sorted leaves by tree species and weighed them before combining sorted leaves by site. We weighed wood and miscellaneous material separately. We ground and subsampled leaves, wood, and miscellaneous material. We weighed,

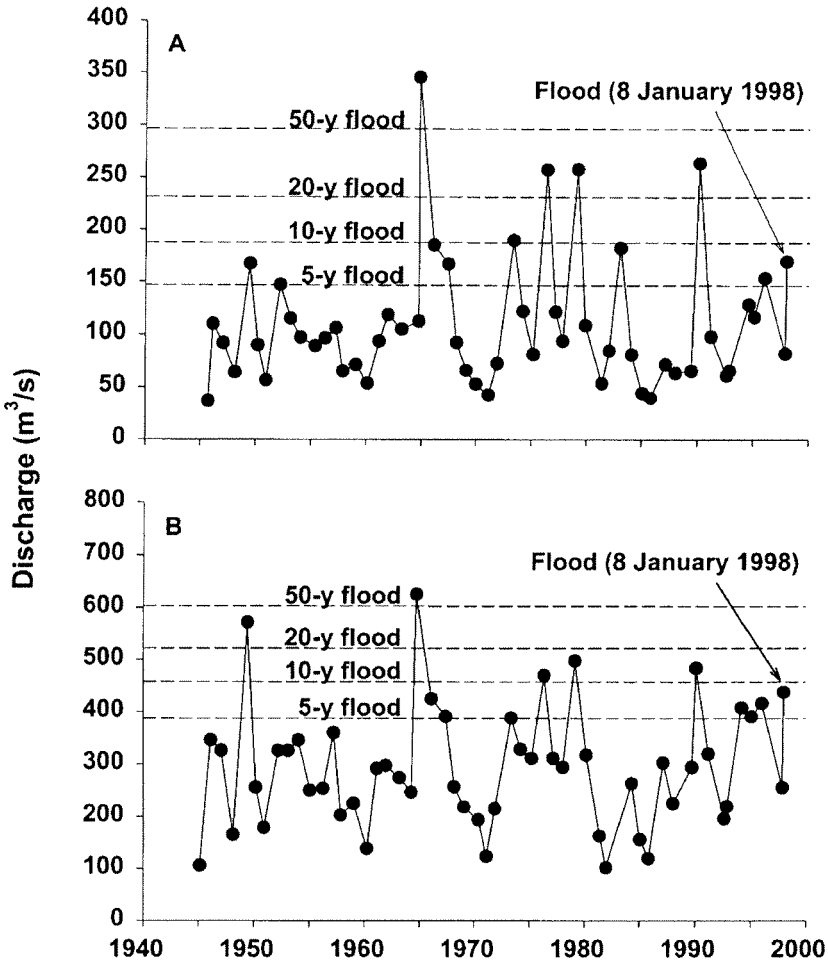

FIG. 2. Annual peakflow discharge at Prentiss (A) and Needmore (B) USGS gauges. Arrows show peak discharge of the flood on 8 January 1998. Lines indicate flood recurrence intervals for 5-, 10-, 20-, and 50-y floods.

ashed (550°C, 45 min), and reweighed subsamples to determine ash-free dry mass (AFDM).

The flood affected litter traps at 8 of 12 sites. All traps were missing at U2 and L4, and we did not replace them. We discarded litter collected from the remaining 6 sites in January 1998 because it was impossible to determine whether the litter originated from litterfall or flood transport. We also lost litter traps from L2 in March 1998 because of vandalism, and we did not replace them.

We estimated leaffall for sites missing only the January collection period (18 or 19 December–18 January) using linear interpolation of log transformed leaffall rates of previous (23 November–18 or 19 December) and following (18 January–14 or 15 February) collection periods. We estimated wood and miscellaneous material similarly, except we used linear interpolation of non-log transformed data.

Leaf breakdown

We measured leaf breakdown on the floodplain using litter bags made of 2-mm^2 mesh polypropylene fabric (Cady Bag Company, Pearson, Georgia). We collected freshly senesced leaves of *Platanus occidentalis* (sycamore), *Carpinus caroliniana* (American hornbeam), *Juglans nigra* (black walnut), and *Acer rubrum* (red maple) from the LTR floodplain in October 1997. We filled each litter bag with 8 g of air-dried leaves

from a single tree species. McArthur et al. (1994) showed that leaf breakdown rates of a single species may change when placed in combination with other species, but we used single-species litter bags to facilitate comparisons of breakdown rates in our study with those from other studies conducted in floodplains and streams. We covered litter bags with existing litter at a site to minimize the single-species effect.

We placed litter bags containing the 2 most important floodplain species, *P. occidentalis* and *C. caroliniana*, at 8 of the 12 sites, and litter bags containing 2 other important floodplain species, *A. rubrum* and *J. nigra*, at 3 sites. Litter bags containing a given species were placed only at sites where that species was common because we were interested in estimating leaf breakdown rates across the entire river reach rather than comparing leaf breakdown rates among sites. At each site, we placed 15 litterbags of each species randomly within one plot that extended 10 m inland from the river bank and 30 m longitudinally along the river. We retrieved 3 randomly selected replicate litter bags of *C. caroliniana*, *J. nigra*, and *A. rubrum* from each site after 1, 2, 4, 6, and 7 mo. We did not collect *A. rubrum* litter bags from L3 at 7 mo because of vandalism. We retrieved *P. occidentalis* litter bags at slightly different intervals (1, 2, 4, 7, and 9 mo) because breakdown of this species was slow. We classified litter bags collected following the flood of January 1998 as inundated or non-inundated based on whether the litter bags from a site had been buried in sediment by the flood.

We washed all leaves, dried them at 50°C, and weighed, ground, and subsampled them. We weighed, ashed, and reweighed subsamples to determine AFDM. We calculated species-specific breakdown rates of all 4 species using an exponential decay model (e.g., Benfield 1996).

FPL standing crop

We measured floodplain litter (FPL) standing crop by removing all coarse litter from twenty 0.06-m^2 plots at each site on 18 or 19 December 1997 (pre-flood) and 30 or 31 January 1998 (post-flood). We washed, dried, and separated the litter into leaves, wood, or herbaceous plant material. We weighed, ground, and subsampled sorted materials to determine AFDM. FPL was unevenly distributed in debris piles at U1, U4, U5, M2, and L4 after the flood. We measured the length and width of the debris piles within a 10 × 100 m plot at each site and removed a 0.06-m^2 subsample from the middle of each pile. We adjusted mean FPL of each litter type to include litter in debris piles at these sites. We categorized sites as inundated, partially inundated, or non-inundated based on the degree of flooding in the sample collection area. Only a small part of the sampling area was inundated at partially inundated sites, and replication of partially inundated (n = 2) and non-inundated (n = 2) groups was low, so we reclassified these groups as non-inundated (n = 4) for all types of litter. We feel this treatment is conservative because POM dynamics at partially inundated sites were somewhat affected by the flood.

We estimated transport of leaves from the floodplain by the flood. We could not assume the difference between pre- and post-flood leaf FPL was a consequence of flood transport alone because of inputs from leaffall and losses associated with leaf breakdown during the 42- to 44-d gap between pre- and post-flood sampling. Therefore, we used pre- and post-flood leaf FPL, leaffall, and leaf breakdown rates to calculate flood transport at each site:

$$T_L = L_B - L_C - L_A \qquad [2]$$

where T_L = flood transport of leaves from the flood plain, L_B = pre-flood leaf FPL, L_C = change in standing crop because of leaffall and leaf breakdown, and L_A = post-flood leaf FPL.

We estimated L_C by integrating the difference between leaffall and leaf breakdown during the gap between pre- and post-flood sampling:

$$\frac{dL}{dt} = F_L - k_C L \qquad [3]$$

where F_L = leaffall, k_C = leaf breakdown rate, and L = instantaneous standing crop of leaf FPL at time t. L_B was the initial condition for L. We estimated a breakdown rate for each site using weighted averages based on the species composition of leaffall through December 1997. We determined a winter (December–February) breakdown rate for each species contributing litter to a site. We classified breakdown rates of species not measured in the field as fast or slow according to rates listed by Webster and Benfield (1986). We assigned leaves with relatively fast breakdown rates the mean breakdown rate of *C. caroliniana*, *J. nigra*, and *A. rubrum*, and

leaves with relatively slow breakdown rates the breakdown rate of *P. occidentalis*. We estimated leaf inputs in the model using a linear interpolation of leaffall rates. We did not include leaf inputs for U2 and L4 because all litter traps were removed by the flood.

We did not correct flood transport of woody and herbaceous material for litterfall or breakdown because we did not measure breakdown rates, and 0.25-m^2 litter traps are not large enough to adequately sample inputs of large wood.

Leaf inputs to the river

Direct leaffall to the LTR was estimated using a modified version of an empirically derived model for lakes (Gassith and Hasler 1976, Sebetich and Horner-Neufeld 2000). The model assumes a linear decline in litterfall with increasing distance from the shore. Our model predicted that leaffall should be zero 10 m from the river bank:

$$F_W = F_B - \left(\frac{F_B w}{10}\right) \quad [4]$$

where F_B is bank leaffall, w is distance from the bank, and F_W is leaffall at some distance w from the bank. We placed litter traps near the banks (1–3 m), so our leaffall values were equivalent to bank leaffall. We estimated annual leaffall to the river by integrating the model from 0 to 10 m. We converted the result to g AFDM/m^2 of river surface by multiplying by 2, assuming that leaffall is equal on both sides of the river, and dividing by river width.

We estimated floodplain leaffall at U2, L2, and L4 to obtain direct leaffall to the LTR at these sites. We made pairwise Pearson correlations of leaffall by date between each missing site and all sites with complete leaffall data before traps were lost (reference sites). We selected the reference site with the highest *r* with a given missing site and used the regression equation from this relationship to predict leaffall at each missing site for each date after the traps were lost. Correlation coefficients of missing and reference sites were >0.97. We calculated annual leaffall at each missing site by summing leaffall for all dates. We validated this technique by estimating leaffall of sites with complete annual leaffall and found that predicted leaffall was ±15% of measured leaffall at all sites except M1, where leaffall was not highly correlated ($r < 0.73$) with any other site.

We had difficulty determining how much of the floodplain had been inundated at several sites, but ≤10 m of floodplain on both sides of the river were inundated at sites where we could determine the extent of inundation. Therefore, we assumed that 10 m on both sides of the river had been inundated for all sites when estimating flood input of leaves to the river. This assumption probably led us to overestimate the amount of inundated floodplain, but it provided a maximum estimate of flood inputs for this flood. We converted T_L (g AFDM/m^2 of floodplain) to flood input of leaves to the river (g AFDM/m^2 of river) by:

$$T_R = (T_L)(W_F)/(W_R) \quad [5]$$

where T_R = flood input of leaves to the river, W_F = width of the inundated floodplain, and W_R = width of the river.

Statistical analysis

We conducted all statistical analyses using Statistical Analysis System (version 8.01, SAS Institute, Cary, North Carolina). We used a general linear model with a dummy variable (GLM) to make pairwise comparisons of leaf breakdown rates between species or between inundated and non-inundated leaves. We adjusted α according to a standard Bonferroni technique based on the number of pairwise comparisons (Sokal and Rohlf 1995).

We used analysis of variance (ANOVA) to compare tree basal area and density among site types and to evaluate the effect of riparian forest width on floodplain litterfall through December 18 only. Replication of the <5 m group was too low (n = 2) to conduct an ANOVA on annual litterfall data.

We compared T_L among inundation groups with analysis of covariance (ANCOVA) using L_B as a covariate because flood transport was potentially dependent on the pool of leaves available for transport. We analyzed the effect of the flood on woody material and herbaceous material similarly except we compared the net difference between pre- and post-flood standing crop. We recognize that the net difference is not equivalent to flood transport, and any significant results should be interpreted with caution.

TABLE 2. Forest structure of the 12 sites along the Little Tennessee River. Means were calculated across site types with standard deviation in parentheses. Importance values (IV) are presented for trees with stems ≥2 cm diameter at breast height (DBH) and IV ≥20 at each site. All species were identified using the keys of Radford et al. (1968). Values with different lower-case letters are significantly different ($p < 0.05$).

Site type	Site	Total tree basal area (m^2/ha)	Total tree density (no. trees/ha)	Important tree species (IV)
<5 m	U2	2.3	105	*Juglans nigra* (45), *Carpinus caroliniana* (35), *Prunus serotina* (21)
	U3	0.8	45	*Carpinus caroliniana* (41), *Juglans nigra* (38), *Prunus serotina* (31)
	U5	3.4	90	*Juglans nigra* (113), *Prunus serotina* (26)
	Mean	2.2 (1.3)[a]	80 (31)[a]	
5–15 m	U1	43.5	180	*Platanus occidentalis* (38), *Prunus serotina* (16), *Juglans nigra* (11)
	M3	4.1	105	*Lindera benzoin* (33), *Platanus occidentalis* (18), *Halesia carolina* (13), *Juglans nigra* (12)
	L1	5.4	170	*Juglans nigra* (91)
	L4	23.4	335	*Acer rubrum* (34), *Halesia carolina* (16)
	Mean	19.1 (18.5)[a]	198 (98)[b]	
>15 m	U4	42.1	405	*Platanus occidentalis* (29), *Carpinus caroliniana* (29), *Asimina triloba* (17), *Acer rubrum* (13)
	M1	24.1	600	*Platanus occidentalis* (44), *Salix nigra* (17), *Robinia pseudoacacia* (15), *Cornus* sp. (12)
	M2	32.7	415	*Liriodendron tulipifera* (23), *Acer rubrum* (20), *Carpinus caroliniana* (18)
	L2	14.3	905	*Carya glabra* (29), *Carpinus caroliniana* (29), *Calycanthus florida* (19)
	L3	21.7	490	*Liriodendron tulipifera* (25), *Carpinus caroliniana* (23), *Halesia carolina* (13), *Acer rubrum* (11)
	Mean	27.0 (10.7)[a]	563 (206)[b]	

Results

Forest structure

Total basal area of trees in the sites ranged from 0.8 to 43.5 m^2/ha, and tree density ranged from 45 to 905 trees/ha. Tree density at sites with <5 m of riparian forest was significantly lower than at the other 2 site types (Table 2, Tukey's test, $p < 0.05$). Basal area did not significantly differ among site types, but mean basal area was lowest at sites with <5 m of riparian forest.

Juglans nigra and *Prunus serotina* (black cherry) were the most important species at sites with <5 m of riparian forest (Table 2). In contrast, *P. occidentalis*, *Liriodendron tulipifera* (yellow-poplar), and *A. rubrum* were important at sites with >15 m of riparian forest. Sites with 5–15 m of riparian forest generally contained a mix of the species found at the other 2 types. *Carpinus caroliniana* was an important forest species at most sites, regardless of type.

Litter inputs to the floodplain

Litter inputs ranged from 256 to 562 g AFDM m^{-2} y^{-1} with a mean of 481 g AFDM m^{-2} y^{-1} across all site types (Table 3). Leaves constituted 403 g AFDM m^{-2} y^{-1} (84%), wood 56 g AFDM m^{-2} y^{-1} (11%), and miscellaneous material 22 g AFDM m^{-2} y^{-1} (5%) of the total inputs. Most leaves fell in autumn (Fig. 3). Leaffall was low in the winter and spring but increased in mid-August. In contrast, wood inputs were low during the autumn and summer and highest during the winter; 55% of wood inputs occurred from January to April. Miscellaneous material inputs were high during autumn because of large inputs of nuts at a few sites, especially from *J. nigra* and *Carya glabra* (pignut hickory), but de-

TABLE 3. Litterfall estimates for 3 site types along the Little Tennessee River. Types were defined by the width of wooded riparian vegetation (<5 m, 5–15 m, and >15 m). Values are in g ash-free dry mass/m^2. Means were calculated across site types with standard deviation in parentheses. Data from U2 (<5 m), L4 (5–15 m), and L2 (>15 m) were omitted from annual litterfall estimates. Values with different lower-case letters are significantly different ($p < 0.05$). Misc. = miscellaneous material (see Methods for details).

Site type	Litterfall to 18 December 1997				Annual litterfall			
	Leaves	Wood	Misc.	Total	Leaves	Wood	Misc.	Total
<5 m	156 (30)[a]	1 (1)[a]	5 (4)[a]	162 (30)[a]	239 (42)	7 (1)	11 (9)	256 (32)
5–15 m	284 (46)[ab]	13 (9)[a]	9 (5)[a]	307 (45)[b]	428 (50)	59 (47)	38 (15)	524 (49)
>15 m	326 (82)[b]	13 (7)[a]	8 (4)[a]	347 (83)[b]	467 (78)	67 (79)	10 (16)	562 (45)
Mean	270 (91)	10 (8)	8 (5)	287 (96)	403 (110)	56 (46)	22 (16)	481 (135)

creased during winter. Miscellaneous material inputs were also high in the spring and early summer mainly from fruit of *P. serotina* at U1 and flowers of *C. caroliniana* at all sites.

Litterfall differed significantly among site types (ANOVA, $p < 0.01$; Table 3). This difference was a consequence of leaffall; site types did not differ with respect to wood or miscellaneous material. Leaffall was significantly lower at sites with <5 m of wooded riparian vegetation than at sites with >15 m of wooded vegetation (Tukey's test, $p < 0.05$), but leaffall at sites with 5–15 m of wooded vegetation was not significantly different than at the other 2 site types ($p > 0.05$).

Thirty-seven species contributed leaves to the floodplain of the LTR, although only 11 contributed ≥2% of the total mass through 18 December (Table 4). *Platanus occidentalis* and *C. caroliniana* contributed 33% of total leaffall during this period. At a few sites, leaf inputs from *J. nigra* and *A. rubrum* and, to a lesser extent, *Halesia carolina* (Carolina silverbell), *L. tulipifera*, and *P. serotina* were substantial. Leaf inputs

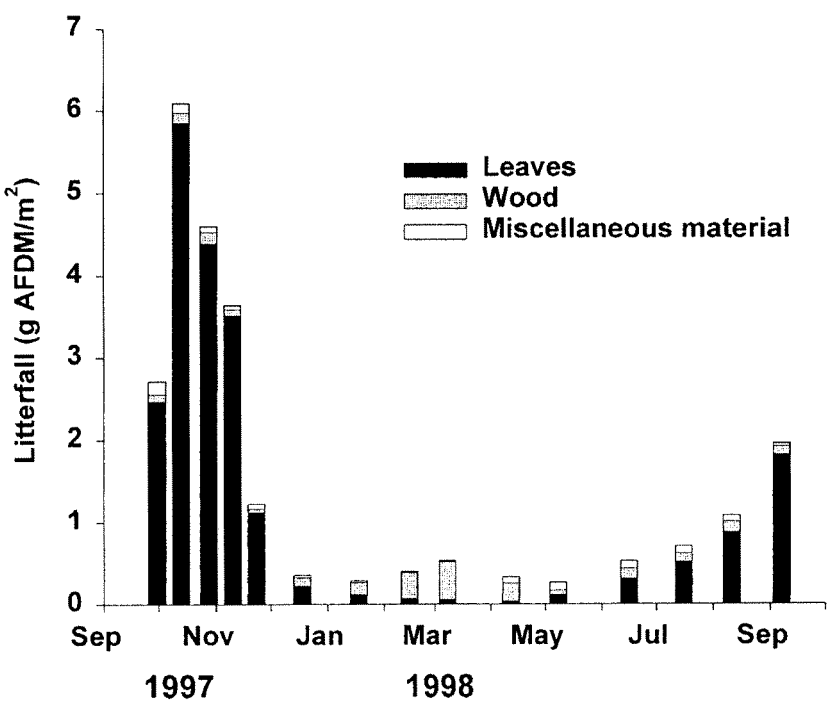

FIG. 3. Litter inputs of leaves, wood, and miscellaneous material to the floodplain of the Little Tennessee River, North Carolina, from September 1997 to September 1998. Values are means of sites combined. AFDM = ash-free dry mass.

TABLE 4. Species composition of leaffall (g ash-free dry mass/m²) to the Little Tennessee River floodplain from September 1997 to December 1997. Species are ordered by % of total leaffall. Values are site means and are presented for species that contributed ≥2% of total leaffall. Miscellaneous leaves = unidentified leaf fragments.

Tree species	Site												Mean	% of total
	U1	U2	U3	U4	U5	M1	M2	M3	L1	L2	L3	L4		
Platanus occidentalis	46	25	1	53	31	153	19	73	45	1	14	88	46	17
Carpinus caroliniana	47	57	91	102	0	3	55	81	0	4	66	11	43	16
Juglans nigra	26	43	8	5	72	0	2	7	205	0	0	41	34	12
Miscellaneous leaves	37	17	13	19	33	45	47	36	16	18	25	56	30	11
Acer rubrum	3	0	1	89	8	0	61	88	0	2	98	1	29	11
Carya glabra	0	0	0	0	8	0	61	0	0	142	0	0	18	6
Halesia caroliniana	31	0	0	6	0	0	66	5	0	5	8	63	15	6
Liriodendron tulipifera	2	0	1	25	0	0	62	0	0	0	46	0	11	4
Prunus serotina	23	2	4	0	19	0	21	15	1	0	0	20	9	3
Quercus alba	0	0	0	0	0	0	0	0	0	1	81	0	7	2
Nyssa sylvatica	39	1	0	1	0	0	0	0	0	0	31	0	6	2

from *C. glabra*, *Nyssa sylvatica* (black gum), and *Quercus alba* (white oak) were confined to 1 or 2 sites. We found sizable inputs of unidentifiable leaf fragments at all sites.

Leaf breakdown

The breakdown rate of *P. occidentalis* leaves was significantly slower than the other 3 species ($p < 0.001$; Fig. 4). More than 65% of the original *P. occidentalis* leaf mass remained after 9 mo. The breakdown rate of *A. rubrum* leaves was significantly slower than *J. nigra* ($p < 0.001$). In contrast, the breakdown rates of *J. nigra* and *C. caroliniana* leaves were similar, as were the rates of *A. rubrum* and *C. caroliniana* leaves.

The flood of January 1998 had a similar effect on all 4 species (Fig. 5). Leaves inundated by the flood had significantly faster breakdown rates than non-inundated leaves. The difference in breakdown rates between inundated and non-inundated *P. occidentalis* leaves, however, was not apparent until the last collection date (8 September 1998). It is not clear whether this divergence would have remained consistent through time.

FPL standing crop

L_B ranged from 165 to 423 g AFDM/m² before the flood (Table 5). L_A, corrected for debris piles, ranged from 51 to 385 g AFDM/m². T_L was significantly greater at inundated than non-inundated sites (ANCOVA, $p < 0.05$). Mean T_L was 114 g AFDM/m² for inundated sites, all of which lost leaves. In contrast, T_L was only 19 g AFDM/m² for non-inundated sites.

Pre-flood herbaceous FPL ranged from 30 to 142 g AFDM/m², and post-flood herbaceous FPL ranged from 26 to 184 g AFDM/m² (Table 6). Floodplain wood FPL ranged from 24 to 294 g AFDM/m² before the flood and from 11 to 299 g AFDM/m² after the flood. The net difference between pre- and post-flood herbaceous or wood FPL did not differ between inundation groups ($p > 0.05$). Some inundated sites showed an increase in standing crop, whereas others showed a decrease.

Leaf inputs to the river

Average direct leaffall to the LTR was 94 g AFDM m^{-2} y^{-1} for our entire study reach (Table 7). When separated, the 4th-, 5th-, and 6th-order stream segments received 121, 97, and 59 g AFDM m^{-2} y^{-1}, respectively. T_R at inundated sites was 59 g AFDM/m². T_R at non-inundated sites was assumed to be 0. Mean T_R decreased to 40 g AFDM/m² when non-inundated sites were included with inundated sites in the calculation. T_R was lower than direct leaffall, except at L4, and constituted 30% of total leaf inputs to the river.

Discussion

Litter inputs to the floodplain were controlled more by the restriction of riparian forest by an-

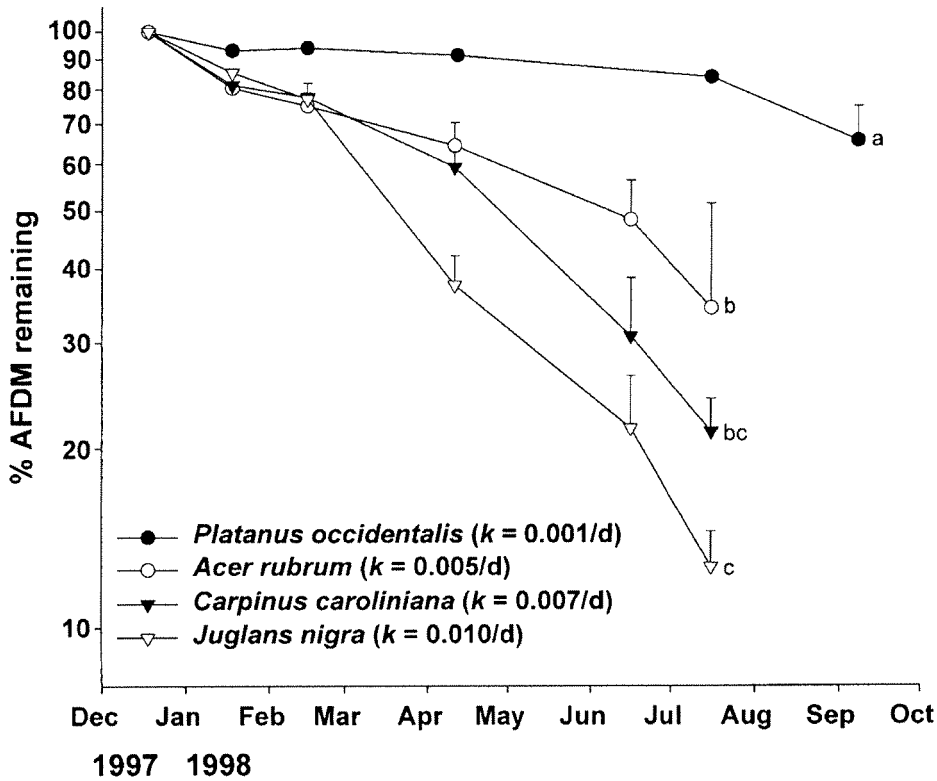

FIG. 4. Leaf breakdown of the 4 common floodplain tree species as % ash-free dry mass (AFDM) remaining (+1 SE) based on mean breakdown of all litter bags. Species with different lower-case letters are significantly different (dummy variable analysis, $p < 0.05$). Values in parentheses are mean species breakdown rates (k). Note the log scale on the y-axis.

thropogenic changes in land use than by the flood. The floodplain was a net exporter of POM, but flood input of leaves to the river was smaller than estimated direct leaffall, even though flood inputs were calculated based on the maximum potential export of POM from the floodplain. We conclude that flood POM inputs probably have a small influence on the energetics of the LTR, especially because floods are rather infrequent (1 in 2 y) and of short duration (1–2 d). However, the flood had 2 effects on floodplain POM dynamics. First, the flood increased the leaf breakdown rates of all species measured in our study. Second, the flood caused a lateral movement of leaves from the floodplain to the river via entrainment.

Litter inputs to the floodplain

Litter inputs to the floodplain of the LTR were within the range of 240 to 810 g AFDM m^{-2} y^{-1} reported for warm temperate angiosperm forests (Bray and Gorham 1964), but they were lower than values reported for other floodplain forests (Table 8). We see 3 possible explanations for this result. First, we may have underestimated litter inputs to the floodplain because we placed our litter traps near the banks of the river. Thus, the traps received minimal litter inputs from the river side. Second, most litterfall studies on floodplains have been conducted in large river systems or coastal plain streams with extensive floodplains and long periods of inundation, whereas inundation of the LTR floodplain is relatively infrequent, and flood duration is short. Floodplain forests typically have higher litterfall than adjacent upland forests (Conner and Day 1976, Bell et al. 1978, Gomez and Day 1982, Shure and Gottschalk 1985, but see Megonigal et al. 1997) because of subsidies of nutrients and water from floods. However, the LTR did not flood in 1997 and, therefore, the LTR floodplain received no subsidies of nutrients and water

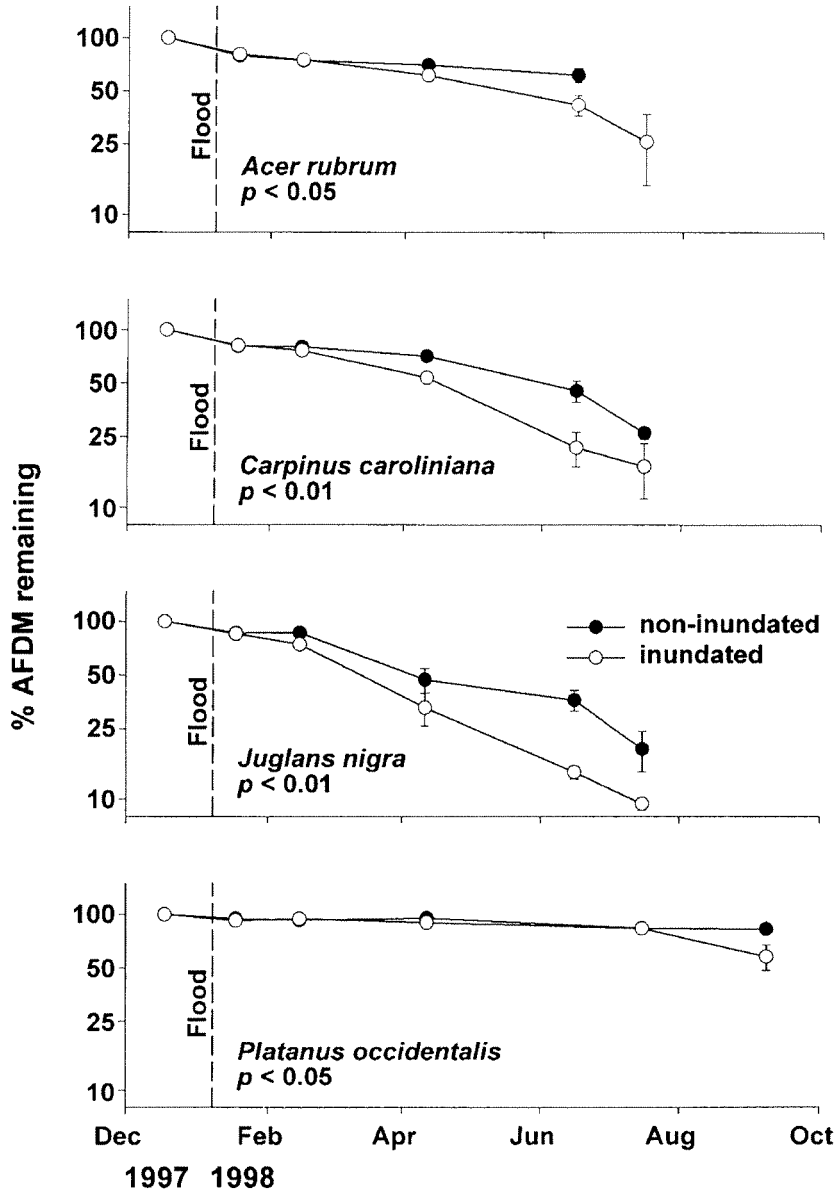

FIG. 5. Leaf breakdown (±1 SE) of inundated and non-inundated litter bags. Litter bags for a given species were compared using a general linear model with a dummy variable (see Methods for details). The flood occurred on day 21. Note the log scale on the y-axis. AFDM = ash-free dry mass.

from floods before or during the growing season in 1997. Third, litter inputs to the floodplain of the LTR may be affected by anthropogenic land use. Many southern Appalachian catchments consist of headwater regions that are high gradient and typically forested and low-gradient regions dominated by active agriculture (Wear and Bolstad 1998). Ninety percent of the LTR watershed was forested in 1990 (Wear and Bolstad 1998), but only 57% of the riparian area within 30 m of the river was forested (M. E. McTammany, Virginia Polytechnic Institute and State University, personal communication). In our study, sites with <5 m of forested vegetation had significantly less litterfall than sites with 5–15 m or >15 m of riparian forest. The decline in litterfall associated with decreasing forest width may be attributed to differences in both basal area and tree density among site types.

TABLE 5. Standing crop of leaf floodplain litter (FPL) before (18–19 December 1997) and after (30–31 January 1998) the flood and estimated flood transport of FPL. Values are in g ash-free dry mass/m². Means were calculated across sites within types with standard deviation in parentheses. Flood transport of leaves (T_L) is the difference between pre- (L_B) and post-flood (L_A) leaf FPL after correcting for leaffall and leaf breakdown. Calculations for determining leaffall and leaf breakdown are described in the text.

Site	Pre-flood (L_B)	Post-flood with debris (L_A)	Leaffall	Leaf breakdown	Flood transport (T_L)
Inundated					
U1	220	92	3	35	96
U2	204	64	–	31	109
U4	358	222	3	55	83
M1	260	107	12	30	136
M2	339	268	11	58	24
M3	277	86	6	38	159
L1	265	125	4	42	102
L4	296	51	–	42	203
Mean	277 (53)	127 (77)	6 (4)	41 (10)	114 (53)
Non-inundated					
U3	165	89	2	28	49
U5	168	126	2	26	18
L2	296	222	2	47	29
L3	423	385	4	61	−19
Mean	263 (123)	206 (132)	3 (1)	41 (17)	19 (29)

TABLE 6. Standing crops of herbaceous and wood floodplain litter before (18–19 December 1997) and after (30–31 January 1998) the flood. Values are in g ash-free dry mass/m². Means were calculated across sites within types with standard deviation given in parentheses.

	Herbaceous material			Wood		
Site	Pre-flood	Post-flood	Net difference	Pre-flood	Post-flood	Net difference
Inundated						
U1	137	112	25	271	148	123
U2	53	31	22	294	119	175
U4	32	110	−78	111	107	4
M1	93	35	58	141	89	52
M2	35	111	−76	246	299	−53
M3	74	20	54	113	47	66
L1	142	184	−42	140	65	75
L4	85	41	44	148	73	75
Mean	82 (42)	81 (60)	1 (57)	183 (74)	118 (80)	65 (69)
Non-inundated						
U3	30	28	2	24	11	13
U5	81	127	−46	49	23	26
L2	61	71	−10	38	28	10
L4	33	26	7	161	161	0
Mean	51 (24)	63 (47)	−12 (24)	68 (63)	56 (71)	12 (11)

TABLE 7. Comparison of flood input of leaves (T_R) and direct leaffall to the Little Tennessee River. Direct leaffall was calculated assuming all littertraps were placed at the river bank. T_R was calculated assuming that a 10-m area on both sides of the river had been inundated. Leaffall to the floodplain for sites U2, L2, and L4 were predicted by regression. Values are g ash-free dry mass/m^2.

	Litter inputs to flood-plain	Leaf inputs to river		
	Leaffall	T_R	Direct leaffall	Total
Inundated				
U1	392	62	126	188
U2	217	99	99	198
U4	422	66	169	235
M1	411	72	108	180
M2	581	6	73	79
M3	485	72	110	182
L1	406	46	92	138
L4	327	52	42	94
Mean	405	59	102	161
Non-inundated				
U3	209	0	84	84
U5	269	0	128	128
L2	326	0	50	50
L3	455	0	50	50
Mean	315	0	78	78
All sites	375	40	94	134

Leaf breakdown

Leaf breakdown rates are usually faster in floodplains than in adjacent upland forests (Peterson and Rolfe 1982, Shure et al. 1986), although they are slower than in aquatic ecosystems (Webster and Benfield 1986, Cuffney and Wallace 1987). Leaf breakdown rates of all species in our study except *P. occidentalis* were at the high end of the range of rates reported for other floodplain forests in the eastern United States (Brinson 1977, Peterson and Rolfe 1982, Shure et al. 1986, Cuffney and Wallace 1987, McArthur et al. 1994). These studies were conducted on floodplains where inundation is long and soils are anoxic. Brief, aerobic inundations have been associated with faster breakdown rates than longer inundations in which soils become anoxic (Lockaby et al. 1996), and our litter bags were either inundated briefly or not inundated.

The flood of January 1998 influenced rates of leaf breakdown. Breakdown of inundated leaves was faster than breakdown of non-inundated leaves for all species used in our study. The flood could have affected breakdown rates in several different ways. First, nutrient subsidies from the river may have increased the availability of soil nutrients in the floodplain, resulting in greater heterotrophic activity. Second, the flood may have increased mechanical breakdown, which is unlikely because we did not find a large decrease in litter bag AFDM for any species immediately following the flood. Inundated and non-inundated litter bags collected in January 1998 had nearly the same % AFDM remaining. Third, the flood covered most of the litter bags with a layer of sediment from the river. Chauvet (1988) found that burial of leaves by sediments may slow breakdown. However, we feel that the layer of sediment kept the litter bags moist and probably increased breakdown

TABLE 8. Litter inputs to river–floodplain ecosystems of the eastern United States.

River–floodplain ecosystem	Input (g m^{-2} y^{-1})			Reference
	Litterfall	Leaves[a]	Wood	
Little Tennessee River, North Carolina	481	425	56	This study
Buzzards Branch, Virginia	527	489	38	Smock 1990
Sangamon River, Illinois	575	506	69	Bell et al. 1978
Prairie Creek, Florida	597	536	61	Brown 1981
Creeping Swamp, North Carolina	605	472	178	Mulholland 1981
Lower Three Runs Creek, South Carolina	635	524	111	Shure and Gottschalk 1985
Sangamon River, Illinois	797	491	306	Peterson and Rolfe 1982
Ogeechee River, Georgia	901	839	62	Cuffney 1988
Colliers Creek, Virginia	963	538	425	Smock 1990

[a] Includes leaves and reproductive material (flowers, fruits, and seeds)

rates, whereas non-inundated leaf bags were often dry, limiting breakdown.

FPL standing crop

FPL standing crop decreased following the flood. The flood of January 1998 was brief, so the mechanism of FPL removal from the floodplain was most likely direct lateral transport of intact leaves to the river via entrainment in the water column. Therefore, the floodplain was a source of POM to the river during the flood. The flood also could have transported leaf FPL longitudinally, resulting in redistribution of FPL on the floodplain. However, were this the case, some of the inundated sites would have shown an increase in leaf FPL, and all inundated sites lost leaves. Our results are consistent with those reported in other studies (Mulholland 1981, Cuffney 1988, Grubaugh and Anderson 1989, Jones and Smock 1991, Tockner et al. 1999), although the transport mechanism may be different. In other studies, leaf litter was fragmented on the floodplain during floods and transported to the river as fine particulate organic matter or dissolved organic matter (Mulholland 1981, Grubaugh and Anderson 1989, Junk et al. 1989, Smock 1990, Jones and Smock 1991).

Wood was less mobile than leaves, but all inundated sites except M2 lost wood during the flood. In contrast, the standing crops of herbaceous material were variable before and after the flood, but the floodplain generally retained herbaceous litter. In January, we observed that most herbaceous material was standing dead, still firmly rooted in the ground, and not easily dislodged. In addition, herbaceous material constituted ~44% of debris piles, suggesting that herbaceous material may not be an important source of POM to the river.

Leaf inputs to the river

Direct leaffall to the LTR was much lower than the average for eastern streams in deciduous forests, where values ranged from 202 to 538 g AFDM m^{-2} y^{-1} (Webster et al. 1995). These streams, however, are mostly 1st- and 2nd-order. Allochthonous inputs to 1st- through 3rd-order streams at Coweeta Hydrologic Laboratory, which are in the LTR drainage, ranged from 460 to 600 g AFDM m^{-2} y^{-1} (Benfield et al. 2000). However, low-order streams within Coweeta Hydrologic Lab have riparian areas that are primarily forested, and the riparian zone of the LTR often consists of only a thin strip of forest. Thus, direct allochthonous inputs in the 4th- through 6th-order sections of the LTR may be low relative to Coweeta streams because of stream size as predicted by Vannote et al. (1980) and because of the narrow width of the riparian forest.

In our study, nearly 50% of leaf litter standing crop remained on the floodplain after the flood. Direct leaffall to the LTR was >2x higher than flood input of leaves to the river. In contrast, flood inputs in the Ogeechee River were ~5x annual direct litterfall (Cuffney 1988), and flood inputs to the New River were predicted to be 1.5x direct litterfall (Hill 1981). We estimate that 30 m of forested floodplain on both sides of the LTR would have had to be inundated for flood input of leaves to equal direct leaffall.

Flood input of leaves to the river probably was close to a maximum for 2 reasons in our study. First, we probably overestimated flood inputs. The flood of January 1998 was the 7th largest flood of 27 floods that have occurred on this river since 1945, but it is unlikely that 10 m on both sides was inundated. Second, the flood occurred in early winter, near the peak of leaf FPL standing crop when a large store of litter was available for flood transport, and flood inputs still were smaller than direct leaffall. This result suggests that flood input of leaves is a small source of POM compared to direct leaffall. Furthermore, autochthonous sources of C are probably more important than allochthonous sources. Instream production (gross primary production) in the LTR was 3x greater than allochthonous POM inputs (direct leaffall + flood leaf inputs) (McTammany et al. 2003).

Implications for stream ecology

Floodplains are often strongly connected to rivers through periodic and predictable flooding. Floods are natural occurrences that maintain biological diversity and production in many large rivers and coastal plain streams (Junk et al. 1989, Bayley 1995). In such systems, the absence of floods is a disturbance. In contrast, floods in high-gradient streams are disturbances that may cause severe mechanical damage to the stream channel and riparian vegetation (e.g., Swanson et al. 1998). Flooding of the LTR, how-

ever, probably cannot be classified as either an important natural occurrence or a disturbance. Floods are too infrequent and short to establish a great degree of connectivity between floodplain and river, and the floodplain is large enough to displace potential catastrophic effects. However, alteration or removal of riparian vegetation by humans may have a substantial effect on river energetics by decreasing POM inputs from leaffall.

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