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Abstract: Many North American blackwater rivers exhibit low dissolved O_2 (DO) that may be the result of benthic respiration. We examined how tree species affected O_2 demand via the quantity and quality of litter produced. In addition, we compared areal estimates of surface leaf-litter microbial respiration to sediment O_2 demand (SOD) and ecosystem respiration (ER) in stream and swamp reaches of a blackwater river to quantify contributions of surface litter decomposition to O_2 demand. Litter inputs averaged 917 and 678 g m^{-2} y^{-1} in the swamp and stream, respectively. Tree species differentially affected O_2 demand via the quantity and quality of litter produced. Bald cypress (*Taxodium distichum*) contributed most litter inputs because of its dominance and because it produced more litter per tree, thereby making greater relative contributions to O_2 demand in the swamp. In the stream, water oak (*Quercus nigra*) produced litter supporting lower fungal biomass and O_2 uptake rates, but produced more litter than red maple (*Acer rubrum*). Breakdown rates in the swamp were faster, whereas standing stock decreases were lower than in the stream, indicating greater organic matter retention. Surface litter microbial respiration accounted for 89% of SOD (6.37 g O_2 m^{-2} d^{-1}), and 57 to 89% of ER in the swamp. Our findings suggest that surface litter drives the majority of O_2 demand in some blackwater swamps, and tree species with higher rates of litterfall may make larger contributions to ER. Forested swamps may be hotspots of O_2 demand in blackwater rivers because low water velocities enhance retention.

Key words: hypoxia, SOD, swamp, litterfall, intermittent, fungi, *Taxodium*, *Nyssa*, *Acer*, *Quercus*, Suwannee

Dissolved O_2 (DO) availability is a critical factor affecting the structure and function of aquatic ecosystems. Isolated areas of hypoxia may develop in freshwater ecosystems, such as in the bottom waters of stratified lakes (Wetzel 2001) or in hyporheic zones of streams and rivers (Malard and Hervant 1999), but system-wide hypoxia is widely regarded as rare except in cases of anthropogenic nutrient loading (Mallin et al. 2006). However, some streams and rivers can experience hypoxia throughout the water column for extended periods, apparently in the absence of substantial anthropogenic nutrient loading. For example, blackwater rivers experience low DO during summer months, which may be caused in part by seasonally high temperatures (Sinsabaugh 1997), low discharge (Meyer 1992), and large inputs of floodplain-derived organic mat-

ter (Mulholland 1981, Edwards and Meyer 1987). Eutrophication can cause hypoxia in blackwater rivers by enhancing algal blooms or microbial growth and respiration (McCormick and Laing 2003, Mallin et al. 2004), but many that are low in DO do not show obvious signs of anthropogenic nutrient loading (Meyer 1992, Carey et al. 2007, Todd et al. 2009). Until recently, most state water-quality standards did not allow for seasonal variation in minimum allowable DO concentrations, nor did they fully consider the potential role of natural factors (i.e., low gradient, large inputs of organic C, high temperatures) in DO depletion. Thus, many water bodies in the southeastern US routinely fail to meet regulatory criteria for DO concentrations. For example, in Georgia, 86% of all impaired blackwater stream and river segments on the Environmental Protection Agen-

cy's 2004 303(d) list were designated as being impaired for DO.

Low DO dynamics in blackwater rivers may be a result, in part, of natural causes (Meyer 1992). Large stocks of dissolved and particulate organic C, which are characteristic of many blackwater rivers (Meyer et al. 1997, Smock 1997), have the potential to increase DO demand via the respiratory activities of microbial decomposers. Todd et al. (2009) examined sediment (benthic) O_2 demand (SOD) in a seasonally hypoxic blackwater tributary of the Suwannee River in southeastern Georgia and measured SOD rates that were among the highest reported for blackwater rivers. Variability in SOD was best explained by concentration of benthic organic C, but the various sources and contribution of specific organic C substrates (e.g., surface leaf litter, wood, buried detritus) to SOD were not quantified. Our goal was to quantify the contribution of surface (unburied) leaf-litter decomposition to total O_2 demand and ecosystem respiration.

Shifts in forest composition have the potential to alter benthic O_2 demand in rivers because tree species may differ in the timing, quality, or quantity of litter produced. Forest composition in blackwater rivers may differ spatially because of nutrients and O_2 availability in soils (Neatrour et al. 2007) and hydrological differences among river reaches (Burke et al. 2003) or temporally because of natural succession (Penfound 1952) and human impacts, such as logging, but the resulting effects on ecosystem function are poorly understood. The bald cypress (*Taxodium distichum* [L.] Rich), which is dominant in many coastal plain blackwater rivers, is listed as one of the world's "foundation species" that is being lost because of intensive logging and removal (Ellison et al. 2005). For example, mature stands of *T. distichum* in the Okefenokee Swamp were extensively harvested during the early 1900s, and nearly 950,000 m^3 (400 million board feet) of bald cypress lumber were selectively removed before 1926 (Lehrbas and Eldredge 1941, Hopkins 1947). Most of the harvested areas show no sign of returning to their prelogging species composition (Hamilton 1984) and are now dominated by swamp tupelo (*Nyssa sylvatica* var. *biflora* Walter) or bay magnolia (*Magnolia virginiana*). Other investigators have reported postlogging shifts to other species, such as mixed hardwoods or willow (*Salix* spp.) (Gunderson 1984).

The role and effect of *T. distichum* on ecosystem function in blackwater systems are poorly understood. In controlled growth experiments, *T. distichum* produced more leaf litter than other tree species in flooded conditions (McLeod and Ciravolo 2003) and, thus, might contribute more to organic matter standing stocks and subsequent O_2 demand than other tree species that replace it. However, differences in litter production among individual tree species are rarely quantified in a field setting. We quantified organic matter inputs by riparian tree species and the

role of surface litter-associated microbial respiration in O_2 demand in 2 reaches of a blackwater river in southeastern USA. Our objectives were to: 1) quantify the contribution of surface leaf litter and associated microbial activity to SOD and ecosystem respiration (ER) and 2) compare quality and relative quantities of leaf litter and its contribution to total organic matter inputs among tree species.

METHODS

Study sites

This study was done in 3rd- and 5th-order reaches of the Little River, a blackwater river situated in Georgia's coastal plain and contained within the Little River Experimental Watershed (LREW). Both reaches are intermittent and dry completely during summer and autumn in most years. Wet seasons typically begin in late autumn or winter (October–January) and end in late spring or early summer (April–June), when the channel dries completely. In some years, short periods of inundation may occur during the summer, if large storms move through the watershed. The 33,400-ha watershed is in the headwaters of the upper Suwannee River basin and has been monitored intensively since 1967 by the US Department of Agriculture (USDA)-Agriculture Research Station (ARS) Southeast Watershed Research Laboratory. The watershed has 8 nested, gauged subwatersheds ranging from 260 to 11,500 ha where rainfall, discharge, nutrient concentrations, and DO concentrations are monitored regularly (Feyereisen et al. 2007).

The 3rd-order reach (stream; lat 31°41′32″N, long 83°42′09″W) drains a 2200-ha watershed and meanders through a 2nd-growth forested floodplain with moderate water velocities. Low-O_2 events occur during spring and summer, but O_2 concentrations rarely approach 0, and infrequently are <4 mg/L. The 5th-order reach (swamp; lat 31°28′54″N, long 83°35′03″W) drains the entire 33,400-ha watershed, which contains a large swamp where the channel widens to ~300 m and water velocities decrease substantially compared to the stream. Low DO events are frequent, with concentrations <1 mg/L from early April until flow stops and the channel dries completely between late spring and summer. The swamp is bordered on the east by sand hills and pine forest and on the west by low-intensity livestock operations with an intact forested riparian buffer strip. Temporal changes in discharge and DO concentration in both sites are shown in Fig. 1A, B.

Chemical analyses

Flow-proportional 7-d composite water samples were collected using an automated ISCO model 3710 sampler (Teledyne Isco, Inc., Lincoln, Nebraska), immediately deposited in a refrigerated (4°C) housing (Feyereisen et al. 2007), and returned to the laboratory for chemical analysis. In the laboratory, water samples were filtered through
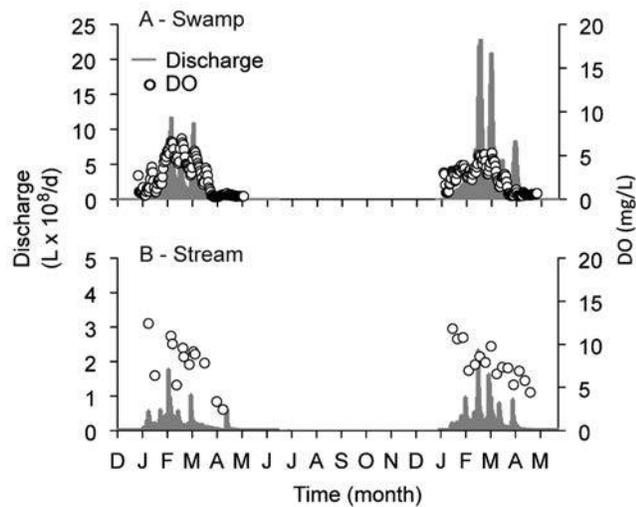
Figure 1. Discharge and dissolved O$_2$ (DO) at the swamp (A) and the stream (B) sites. Note axis scales in A and B.

glass-fiber filters (934-AH, nominal pore size 1 µm; Whatman, Maidstone, UK) and immediately frozen (−202C). Dissolved organic C (DOC) was analyzed with a 5050A Total Organic Carbon Analyzer (Shimadzu Scientific Instruments, Inc., Columbia, Maryland; method 5310B; APHA 1999). Dissolved NO$_3^-$ + NO$_2^-$–N, NH$_4^+$–N, soluble reactive P (SRP), total Kjeldahl N (TKN), and total P were analyzed using a Lachat 8000 flow injection analyzer (Lachat Instruments, Milwaukee, Wisconsin), with methods described by APHA (1999) and modified according to Lachat Instruments (1998). Summary chemical variables are shown in Table 1.

Litterfall sampling and forest composition

Litterfall collectors were installed in the stream and swamp to quantify seasonal litter inputs. In the swamp, litterfall collectors (49 total) were placed every 25 m along 5 transects running laterally across the channel, spaced ~150 m apart longitudinally, to the wetted perimeter of the channel during the wet season. In the stream, litterfall collectors (56 total) were placed along 5 transects spaced ~70 m apart longitudinally. One litterfall collector was placed in the center of the stream channel followed by collectors placed 5 m on either side. Additional collectors were spaced 10 m apart to the farthest wetted perimeter of the floodplain. Litterfall collectors were constructed from round plastic laundry baskets equipped with drain holes and lined with 1-mm mesh. Baskets were mounted on metal poles 1 m from the ground surface to prevent submergence during high flows. Leaf litter was collected monthly, except during periods of heavy leaf fall, when litter was collected biweekly. The point-centered-quarter method (Cottam and Curtis 1956) was used at each litterfall sampling point to estimate (for each tree species)

density, basal area, relative dominance, and importance value. Diameter at breast height (dbh; 1.3 m height) and distance to the nearest tree >2.5 cm dbh in the northeast, northwest, southeast, and southwest quarters were measured. Tree species importance values were calculated according to Cottam and Curtis (1956), as relative density + relative dominance + relative frequency. Data collected on the 4 trees closest to each collector also were used in models comparing quantity of leaf-litter inputs among tree species. To account for potential effects of litter from additional trees farther from the litterfall collector (in addition to the 4 closest), % abundance within a larger radius was recorded for ½ of all sampling points (density/tree species within a 5-m radius).

Litter standing stocks

Standing stocks of leaf litter and small woody debris (≤5 cm diameter), and leaf-associated fungal biomass were estimated in the swamp in February, March, and December 2007 and in April and August 2008 according to methods described by Suberkropp et al. (2010) and Pozo and Elosegi (2005). For comparison, standing stock and leaf-associated fungal biomass in the stream were estimated in December 2007 and April and August 2008. Five intervals were established in the stream and swamp, with 1 immediately upstream of each litterfall transect described earlier. On each sampling date, standing stock was collected at points ¼, ½, and ¾ of the way across 1 random transect within the central interval and the interval farthest upstream and downstream (3 transects/site on each date).

A modified Surber sampler (0.45-m-diameter, square polyvinyl chloride [PVC] frame with a 500-µm mesh net) was used to collect all coarse particulate organic matter (CPOM; except for wood >5 cm diameter) from the streambed surface. All material within the PVC frame was collected

Table 1. Mean (±1 SE) physical and chemical data for 2 study reaches in the Little River Experimental Watershed (LREW) during 2007–2008. DOC = dissolved organic C, SRP = soluble reactive P.

Variable	3rd-order reach (stream)	5th-order reach (swamp)
DOC (mg/L)	11.25 ± 0.68	22.89 ± 1.47
SRP (µg/L)	9.83 ± 4.09	22.67 ± 1.47
Total P (µg/L)	46.50 ± 10.38	79.59 ± 28.38
NO$_3^-$–N (µg/L)	27.27 ± 8.30	33.07 ± 10.58
NH$_4^+$–N (µg/L)	28.13 ± 7.27	36.54 ± 9.00
Total Kjeldahl N (µg/L)	1199.47 ± 255.13	969.63 ± 249.00
pH	5.76 ± 0.08	6.11 ± 0.04
Discharge (L/s)	353.29 ± 40.34	3343.06 ± 445.66
Velocity (m/s)	0.19 ± 0.02	0.028 ± 0.0028

≤1 cm below the water–sediment interface, following methods described by Suberkropp et al. (2010). Wood <5 cm diameter was broken or cut where it met the edges of the PVC frame. Standing stock samples were put in clean, individually labeled resealable plastic bags, placed on ice, transported to the laboratory, and immediately frozen at −20°C until analyzed. During processing, litter was thawed and gently rinsed with tap water over a 1-mm sieve to remove macroinvertebrates, fine particulate organic matter (FPOM), and inorganic sediment. Litter was sorted by species and type (wood, leaves, fruit, flowers), dried at 60°C, weighed, and subsamples were combusted at 500°C and reweighed to determine ash-free dry mass (AFDM). Litterfall samples and standing stock collected during dry periods were not initially rinsed.

Litter microbial respiration

In situ rates of microbial respiration from the 3 or 4 most common leaf-litter species were measured at 1 randomly selected point/transect (5 points/date) with methods described by Suberkropp et al. (2010). Briefly, ten 17-mm-diameter leaf disks (~fifteen 20-cm lengths for *T. distichum* and *Pinus* spp.) were cut from a single species and immediately enclosed in a 26-mL respiration chamber containing unfiltered stream water. Uniform disks and lengths of leaves were used to roughly standardize the mass of organic matter among samples. Changes in DO concentrations in chambers were measured every 5 min for 30 min with a YSI 5100 dissolved oxygen meter (Yellow Springs Instruments, Yellow Springs, Ohio). All measurements were conducted at ambient stream water temperatures in darkness. O_2 uptake rate was estimated as the slope of the regression of DO concentrations vs time minus a control slope measured with stream water alone. Following respiration measurements, leaf discs were put in labeled foil packets, placed on ice, and transported to the laboratory where they were dried at 60°C to constant mass.

SOD

Total SOD reported by Todd et al. (2009) was measured in 65-L recirculating Al respiration chambers originally designed by Murphy and Hicks (1986) and modified by Utley et al. (2008). SOD measurements incorporate all benthic O_2-consuming processes (e.g., sediment- and leaf-litter-associated microbial respiration, animal respiration). Each chamber covered 0.27 m^2 of sediment, and measured O_2 depletion generated by all material (i.e., sediment, leaf litter, wood, biota, etc.) in the benthos. Four chambers, one of which served as a control in which only respiration in the water column was measured, were deployed for 3 h on each sampling date. Care was taken to minimize disruption of sediments while installing chambers. SOD was calculated by subtracting the change in DO

in the control chamber from that in each chamber measuring total benthic O_2 demand.

Hydrologic measurements

Streamflow data were collected at 15-min intervals at both sites with methods described by Bosch and Sheridan (2007) and Bosch et al. (2007). Average swamp and stream depths were estimated by measuring water depth throughout the wet season at each litterfall sampling point, along the same 5 transects described earlier. Discharge was measured continuously at the weir at each site, so a power equation was used to extrapolate depth based on river discharge on any date in the stream and swamp:

$$H_{stream} = 2.98Q^{0.35} \qquad \text{(Eq. 1)}$$

$$H_{swamp} = 2.49Q^{0.39} \qquad \text{(Eq. 2)}$$

where H_{stream} and H_{swamp} = water depth (cm) in the stream and swamp, respectively, and Q = discharge (L/s). Water velocity was extrapolated from Q by fitting a power equation to depth and velocity measured directly by Cathey (2005) in the stream and swamp:

$$u_{stream} = 0.0011Q^{0.89} \qquad \text{(Eq. 3)}$$

$$u_{swamp} = 0.0001Q^{0.72} \qquad \text{(Eq. 4)}$$

where u_{stream} and u_{swamp} = water velocity (m/s) in the stream and swamp, respectively.

Swamp ecosystem respiration

Ecosystem respiration (ER) was calculated for time periods overlapping (beginning 1 d before and ending 1 d after) measurement of leaf-litter microbial respiration and SOD in the swamp. DO and temperature were recorded at 15-min intervals in the swamp with submersible DO (Sensorex DO6000; Campbell Scientific Inc., Logan, Utah) and temperature sensors (CS107; Campbell Scientific Inc.) and at a v-notch weir with an optode recording DO and temperature at 10-min intervals on specific dates (described below) in the middle of the stream channel and at mid-depth.

To calculate reaeration, we used the O'Connor Dobbins equation:

$$k_r = \frac{3.9u^{0.5}}{H^{1.5}} \qquad \text{(Eq. 5)}$$

where k_r = reaeration coefficient at 20°C (d^{-1}), u = average stream velocity (m/s), and H = average stream depth (m). Temperature adjustments were made using the equation

$$k_T = k_r\theta^{(T-20)} \qquad \text{(Eq. 6)}$$

where T = target temperature and θ = a temperature-dependence factor (1.024). ER was calculated (g O_2 m^{-2} d^{-2}) by the single-station method (Owens 1974, Bott 1996) as the average reaeration-corrected O_2 (O_2) flux from midnight (0000 h) until ≤15 min before sunrise.

Stream ER

DO and temperature were measured on a weekly basis at the stream site with a handheld YSI 6600 V2 Sonde (Yellow Springs Instruments). To calculate ER, DO and temperature also were measured on 7–8 and 15–16 February with an O_2 optode (Oxygen Optode 3975; Aanderaa Instruments, Bergen, Norway) logging to a handheld computer (Axim X50; Dell, Round Rock, Texas) every 10 min (MJT, unpublished data). Solar flux density (incoming solar radiation) was measured at a weather station in the LREW (lat 31°38'35.73"N, long 83°24'40.80"W). A daytime regression method based on the study by Kosinski (1984) and modified and presented in full by Atkinson et al. (2008) was used to calculate reaeration (k). Model Maker 4.0 (AP Benson, Wallingford, UK), was used to estimate k with an iterative model to minimize the difference between measured and modeled data ($r^2 \geq 0.95$). ER was calculated as the average reaeration-corrected O_2 flux from midnight (0000 h) until ≤15 min before sunrise. Rates were temperature-corrected to 15°C for comparisons among leaf-litter respiration, ER, and SOD.

Fungal biomass

Leaf litter from each of the most common tree species (five 12-mm diameter discs, or ten 1-cm lengths for conifers) were collected in the field at all 15 sampling points to estimate litter-associated fungal biomass. Discs were put in clean 20-mL plastic scintillation vials, preserved with 5 mL of high-performance liquid chromatography (HPLC)-grade methanol, placed on ice, and transported to the laboratory where they were stored in the dark at −20°C until analyzed. Fungal biomass was estimated from ergosterol concentrations in freeze-dried, preweighed leaf litter after extraction in alcoholic KOH (0.8% KOH in methanol, total extraction volume = 10 mL) for 30 min at 80°C in tightly capped tubes with constant stirring. The crude extract was partially cleaned by solid-phase extraction, and ergosterol was quantified by HPLC (Gessner 2005).

Statistical analysis

Statistical analyses were done in SAS (version 9.2; SAS Institute, Cary, North Carolina). Most data sets were analyzed with analysis of variance (ANOVA) or simple or multiple linear regression. To evaluate the factors affect-ing litter production among dominant tree species in the swamp and stream sites, candidate multiple regression models were compared with Akaike's Information Criterion for small samples (AIC_c) (Burnham and Anderson 2002). Only tree species occurring at >50% of litterfall collectors at a site were included. The response variable was annual litterfall/tree species in a litterfall collector, with the independent variables mean distance from trees of a given species to the litterfall collector, summed basal area of trees of a given species adjacent to the collector, and % abundance of trees (out of 4 trees) of a given species at the litterfall collector. Tree species were coded with binary categorical variables (0 or 1). Differences between a candidate model's AIC_c and that of the top model (Δ_i) and Akaike weights (w_i) were calculated for all candidate models with $\Delta_i \leq 10$. Parameter importance weights were calculated as the sum of the values of w_i for all models containing the parameter of interest. When necessary, data were transformed to meet assumptions of normality and homoscedasticity.

RESULTS

Forest composition and litterfall

The swamp was dominated by bald cypress, swamp tupelo, Ogeechee tupelo (*Nyssa ogeche* Bartram ex Marsh.), and red maple (*Acer rubrum* L. var. *trilobum* Torr. & A. Gray ex K. Koch), whereas the stream was dominated by water oak (*Quercus nigra* L.), swamp tupelo, loblolly and slash pines (*Pinus* spp.), red maple, and Ogeechee tupelo (Table 2). Total annual litter inputs to the swamp averaged ~917 ± 31 g m^{-2} y^{-1}, and were dominated by *T. distichum* (mean ± SE; ~490 ± 44 g m^{-2} y^{-1}), *N. ogeche* (~79 ± 7 g m^{-2} y^{-1}), and *N. sylvatica* (~73 ± 4 g m^{-2} y^{-1}) (Table 2). In the interior, deeper portions of the swamp, litterfall was as high as 1346 g m^{-2} y^{-1}, whereas in shallower marginal zones it was as low as 506 g m^{-2} y^{-1}. Total annual litter inputs to the stream averaged ~678 ± 40 g m^{-2} y^{-1} and ~823 ± 26 g m^{-2} y^{-1} in the main channel and floodplain, respectively. Channel inputs were dominated by *Q. nigra* (~238 ± 35 g/m^2), *N. sylvatica* (~111 ± 27 g/m^2), *Pinus* spp. (~78 ± 52 g/m^2), *A. rubrum* (~64 ± 25 g/m^2), and *N. ogeche* (~42 ± 14 g/m^2) (Table 2). Litterfall in the stream also varied spatially, with values as low as 510 g m^{-2} y^{-1} entering the main channel directly, and up to 1183 g m^{-2} y^{-1} in the floodplain, specifically in areas where *Q. nigra* and *A. rubrum* dominated.

Litter inputs differed significantly among tree species, and multiple factors were significantly related to annual litterfall (Tables 2, 3, Fig. 2). In the swamp, *T. distichum* produced significantly more litter annually than *N. sylvatica* ($t_{1,52}$ = 21.61, $p < 0.0001$; Tables 2, 3), regardless of how input was calculated; i.e., controlling for basal area (Fig. 2A), % abundance (Fig. 2B), or distance from the litterfall collector (Fig. 2C). In the stream, *Q. nigra*

Table 2. Forest composition metrics including the total number of trees of a given species per site survey (n), density, median basal area, relative dominance, and importance value (I.V.). Litterfall values are provided for the swamp, stream floodplain, and stream main channel. Total litterfall is the sum of all litter inputs, whereas individual tree species values include only leaf and flower/pollen cone litter. – indicates a tree species not detected in field surveys.

Taxon	n	Density (no./ha)	Median basal area (m² × 10²)	Relative dominance (%)	Importance value	Litter (g m⁻² y⁻¹)	Floodplain litter (g m⁻² y⁻¹)	Channel litter (g m⁻² y⁻¹)
Swamp								
Total (including wood)		1554.43	4.06 (0.73)			916.53 (30.95)		
Taxodium distichum	61	483.78	8.56 (1.02)	48.20	105.04	489.57 (44.29)		
Nyssa sylvatica v. biflora	58	459.99	3.49 (0.57)	20.66	80.72	73.40 (3.68)		
Acer rubrum v. trilobum	34	269.65	0.18 (0.52)	3.14	34.77	39.64 (10.35)		
Nyssa ogeche	25	198.27	3.84 (4.22)	18.31	47.25	79.30 (6.89)		
Fraxinus caroliniana	8	63.45	0.68 (3.07)	2.12	10.97	4.60 (2.08)		
Pinus spp.	4	31.72	11.65 (4.19)	3.79	8.68	33.13 (15.02)		
Quercus nigra	3	23.79	3.41 (12.74)	3.24	7.62	25.23 (8.80)		
Salix nigra	2	15.86	3.66 (3.51)	0.54	3.47	5.11 (2.34)		
Liquidambar styraciflua	1	7.93	0.09	0.01	1.47	8.47 (4.36)		
Magnolia virginiana	–	–	–	–	–	7.43 (2.66)		
Stream								
Total (including wood)		1638.11	0.96 (0.72)				822.68 (25.91)	677.97 (39.95)
Nyssa sylvatica v. biflora	66	491.43	1.83 (1.05)	27.00	77.61		105.15 (8.34)	111.01 (26.69)
Acer rubrum v. trilobum	57	417.72	0.32 (0.51)	9.22	60.11		71.63 (9.62)	64.29 (25.03)
Quercus nigra	48	376.76	2.89 (2.53)	45.08	95.36		321.80 (19.31)	237.55 (34.66)
Nyssa ogeche	18	106.48	2.08 (1.07)	5.31	19.56		25.15 (3.64)	41.72 (13.62)
Cyrilla racemiflora	11	90.10	0.10 (0.02)	0.12	12.30		2.23 (0.92)	0.01 (0.01)
Pinus spp.	9	65.52	7.30 (5.02)	12.76	20.85		87.94 (13.37)	78.10 (51.74)
Magnolia virginiana	7	57.33	0.15 (0.09)	0.19	8.89		0.67 (0.24)	0
Symplocos tinctoria	2	16.38	0.11 (0.01)	0.02	2.50		0.61 (0.43)	0
Taxodium distichum	1	8.19	2.55	0.28	1.54		9.70 (2.47)	4.20 (3.52)
Prunus serotina	1	8.19	0.13	0.01	1.26		0.11 (0.07)	0
Liriodendron tulipifera	–	–	–	–	–		0.71 (0.31)	0.10 (0.07)

Table 3. Comparison of candidate models explaining variation in litterfall among dominant tree species at swamp and stream sites in the Little River Experimental Watershed. K is the number of model parameters, C_p is Mallow's C_p, R^2_{adj} is adjusted R^2, AICc is Akaike's Information Criterion corrected for small sample size, Δ_i is the difference between the candidate and best model's AICc, L is likelihood, and w_i is the relative strength of evidence for each model (0–1). Species names are categorical variables (0 or 1). Abundance is the percentage (of 4 trees) of *Nyssa sylvatica* or *Taxodium distichum* (swamp), or *Acer rubrum*, *N. sylvatica*, or *Quercus nigra* (stream) around a litterfall collector. Distance is the average distance from trees of a given species to the litterfall collector. Basal area is the total basal area of all trees of a given species around a litterfall collector. Parameter importance weights are calculated as the sum of the values of w_i for all models containing the parameter of interest. All parameters included in models are statistically significant (α = 0.05).

Model	K	C_p	R^2_{adj}	AICc	Δ_i	L	w_i	Parameter Importance weight	Parameter estimate
Swamp									
T. distichum, abundance, distance, basal area	6	4.55	0.93	−124.39	0	1	0.46		
T. distichum, abundance, distance	5	6.92	0.92	−122.26	2.13	0.34	0.16		
T. distichum, abundance, basal area	5	7.99	0.92	−121.18	3.21	0.20	0.09		
T. distichum, distance, basal area	5	8.40	0.92	−120.77	3.61	0.16	0.08		
T. distichum, abundance	4	10.62	0.92	−119.14	5.24	0.07	0.03		
Parameter									
T. distichum								0.98	+2.04
Abundance								0.89	+0.49
Basal area								0.68	+0.13
Distance								0.83	−0.11
Stream									
A. rubrum, *N. sylvatica*, abundance, basal area	6	4.48	0.70	−110.01	0.00	1	0.89		
A. rubrum, *N. sylvatica*, basal area	5	8.73	0.69	−105.87	4.14	0.13	0.11		
Parameter									
A. rubrum								1	−1.33
N. sylvatica								1	−1.21
Abundance								0.89	+0.77
Basal area								1	+0.26

produced significantly more litter than either *A. rubrum* ($t_{1,104} = -8.25$, $p < 0.0001$; Tables 2, 3) or *N. sylvatica* ($t_{1,104} = -8.42$, $p < 0.0001$; Tables 2, 3), and like in the swamp, litterfall was positively related to trunk basal area ($t_{1,104} = 6.62$, $p < 0.0001$; Fig. 2D) and % abundance ($t_{1,104} = 2.51$, $p < 0.05$; Fig. 2E). However, distance from the litterfall collector was not significantly related to litterfall in the stream ($t_{1,104} = -0.25$, $p > 0.80$; Fig. 2F).

Standing stock

Detrital standing stock at both sites consisted primarily of leaf litter (~65% of total in December 2007; Fig. 3A, B). In the swamp, the largest decrease in leaf-litter standing stock occurred between December 2007 and April 2008 (from 1080 ± 77 to 674 ± 56 g/m²), with a further decrease to 587 ± 71 g/m² by August 2008 (Fig. 3A). In the stream, leaf-litter standing stocks also decreased most during the wet season (Fig. 3B) (from 867 ± 227 to 112 ± 43 g/m²) between December and April. Greater decreases in leaf-litter standing stock were observed in the stream (−609.83 g/m²) than in the swamp (−493.69 g/m²) between December 2007 and August 2008. By August, only 30% of the initial leaf-litter standing stock present in December 2007 remained in the dry stream channel, compared to 54% remaining in the swamp. Wood standing stocks (<5 cm diameter) did not change significantly over time in the swamp or stream.

Fungal biomass and temperature effects on litter-associated microbial respiration

Fungal standing crop (mg/m²) was higher in the swamp than in the stream (Fig. 4A) because of higher standing stocks of litter in the swamp and slightly higher fungal biomass/g leaf tissue in bald cypress litter (Fig. 4B). Bald
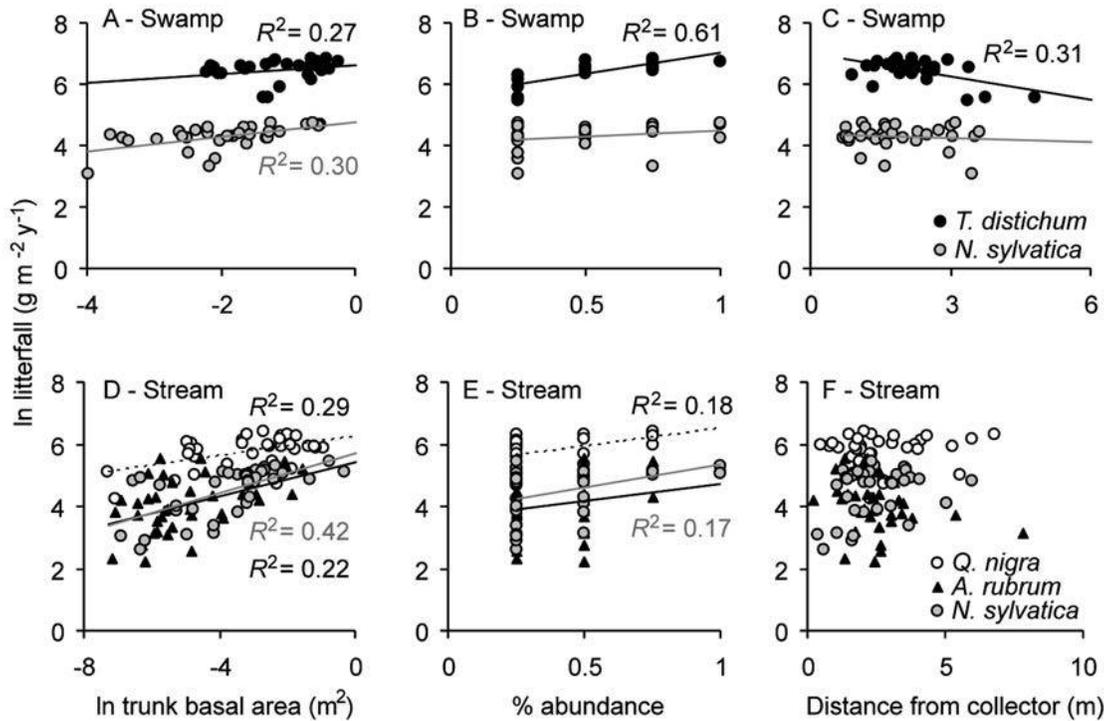
Figure 2. Litter production per tree species (*Taxodium distichum*, *Nyssa sylvatica*, *Quercus nigra*, and *Acer rubrum*) plotted against trunk basal area (A, D), % abundance (B, E), and distance from the litterfall collector (C, F) at the swamp (A, B, C) and stream (D, E, F) sites. Note *x*-axis scales.
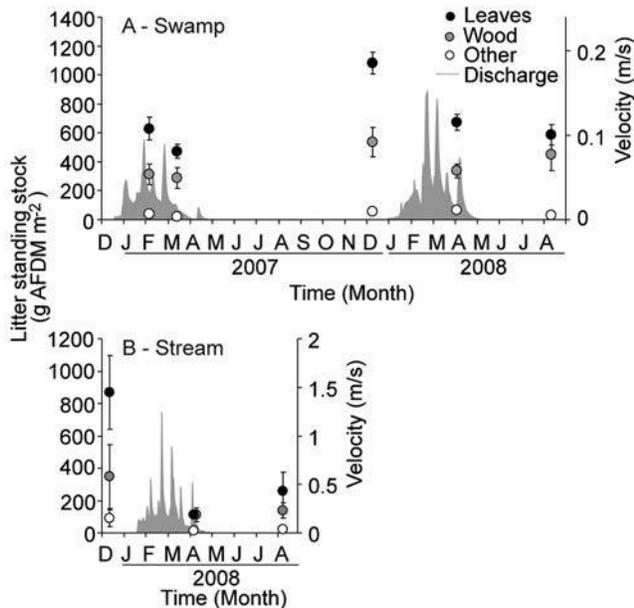

Figure 3. Mean (±1 SE) litter standing stock and water velocity over time in 2007 and 2008 at the swamp (A) and the stream (B) sites. Note axis scales in A and B and that some points overlap in B.

cypress supported significantly higher fungal biomass than did swamp tupelo litter in mid-February and late March 2007, but not in April 2008 (species × time, $F_{2,74}$ = 7.40, $p < 0.01$). Fungal biomass in bald cypress litter decreased significantly between mid-February and late March 2007 (Tukey's test, $p < 0.05$), but stayed relatively constant over time in swamp tupelo litter. O_2 uptake/g of leaf litter did not differ between the 2 tree species across sampling dates, and the relationship between fungal biomass and O_2 uptake was not significant.

In the stream, fungal biomass ($F_{3,31}$ = 27.89, $p < 0.0001$) and leaf-litter O_2 uptake differed among litter species ($F_{3,14}$ = 4.11, $p < 0.05$; Fig. 4C), with lowest levels of both measured in *Pinus* sp. litter (Tukey's test, all $p < 0.001$). Fungal biomass concentrations in red maple litter were significantly higher than those in water oak and *Pinus* sp. litter (Tukey's test, all $p < 0.01$), but not significantly different from swamp tupelo. Leaf-litter O_2 uptake was significantly correlated with the amount of fungal biomass present ($t_{1,15}$ = 3.26, $p < 0.01$, r^2_{adj} = 0.45; Fig. 4C).

Respiration at broader spatial scales

In the stream, shallow water depths prevented direct measurement of SOD for most of the flow period during 2007 and 2008, and as a result, concurrent measurements of SOD and leaf-litter respiration rates were not possible.
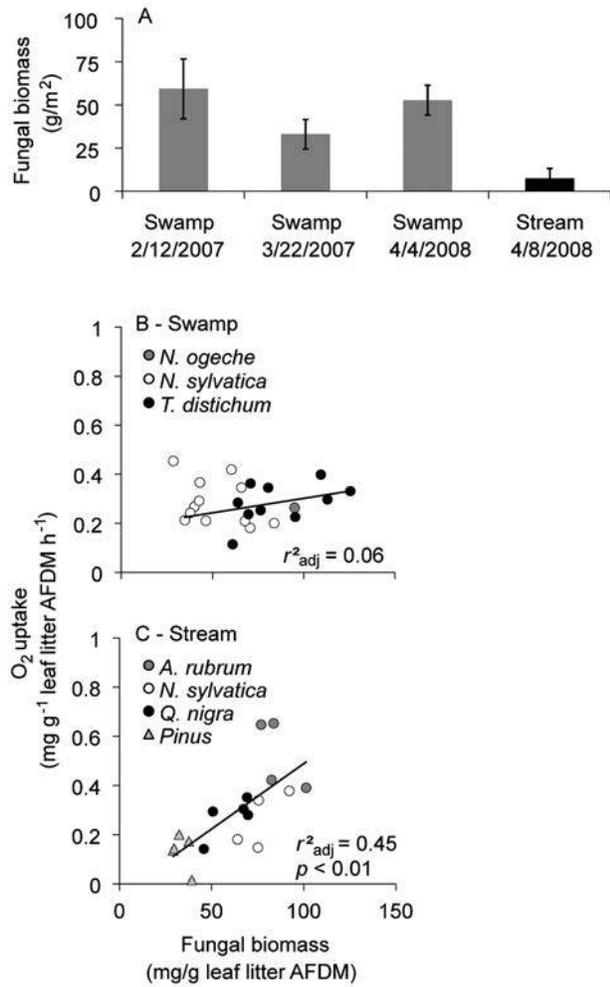
Figure 4. A.—Mean (±1 SE) fungal biomass g/m^2 of swamp and stream basin (A), and temperature-corrected (15°C) dissolved O$_2$ uptake per leaf-litter species (*Nyssa ogeche, Nyssa sylvatica, Taxodium distichum, Acer rubrum, Quercus nigra,* and *Pinus* spp.) vs fungal biomass in the swamp (B) and stream (C). AFDM = ash-free dry mass.

ER was measured only briefly in the stream during February 2007 because of time limitations and a lack of sonde availability, but direct comparisons between SOD and ER could be made at that time. Temperature-corrected ER in the stream (3.93 g O$_2$ m^{-2} d^{-1}) was roughly ½ (56%) that in the swamp (7.06 g O$_2$ m^{-2} d^{-1}) at that time ($F_{1,5}$ = 269.22, $p < 0.0001$; Fig. 5A, B), and did not differ significantly from SOD in the stream (3.33 g O$_2$ m^{-2} d^{-1}). Areal respiration rates from decaying leaf litter averaged 0.76 ± 0.30 g O$_2$ m^{-2} d^{-1} in April 2008 (range: 0.01–2.30 depending on the amount of litter present). These values were significantly lower than temperature-corrected SOD measurements during February 2007 ($F_{1,13}$ = 7.46, $p < 0.02$; Fig. 5B), which were 3.33 ± 1.05 g O$_2$ m^{-2} d^{-1} (range: 0.81–7.65).

In the swamp, temperature-corrected ER decreased from February to March within years ($F_{2,22}$ = 5.28, $p < 0.05$), but

increased among successive years ($F_{2,22}$ = 13.27, $p < 0.001$; Fig. 5A). Anoxia during nighttime hours prevented estimation of ER during early April, but ER could be compared directly to leaf respiration and SOD in February and March 2006–2007. SOD was the most variable of the 3 types of respiration measured in the swamp, where some measurements exceeded ER. In March 2006, SOD was significantly lower than ER ($F_{1,4}$ = 12.65, $p < 0.05$; Fig. 5A), but in March 2007, SOD and ER did not differ. In the swamp, temperature-corrected leaf-litter standing stock respiration rates did not change significantly over time, averaging 4.37 ± 0.55, 4.98 ± 0.51, and 4.16 ± 0.34 g O$_2$ m^{-2} d^{-1} in February and March 2007, and April 2008, respectively (Fig. 5A). It was significantly lower than ER in February 2007 ($F_{1,8}$ = 14.41, $p < 0.01$; Fig. 5A), but not (89% of ER) in March 2007. Across all dates, mean temperature-corrected leaf respiration (4.47 ± 0.97 g O$_2$ m^{-2} d^{-1}) accounted for 68% of mean total SOD (6.56 ± 1.55 g O$_2$ m^{-2} d^{-1}) and did not differ significantly among dates. However, SOD estimates ranged from 1.92 to 13.24 g O$_2$ m^{-2} d^{-1}, whereas leaf-litter respiration and ER estimates ranged from 2.48 to 6.74 and from 3.33 to 8.28 g O$_2$ m^{-2} d^{-1}, respectively.

DISCUSSION

Among the numerous forms of decomposing organic matter present (e.g., woody debris, fine particles, DOC, buried organic matter), microbial activity associated with surface leaf-litter breakdown is the dominant contributor to ER in the Little River. Our results suggest that forest composition may influence O$_2$ demand via the quality and quantity of litter produced. Different tree species: 1) produced different amounts of leaf litter/individual tree, which affected the amount of organic C entering the system (Fig. 2A–F), and 2) produced litter that harbored higher or lower amounts fungal biomass, thereby increasing or decreasing O$_2$ uptake rate/g leaf litter (Fig. 4B). For example, bald cypress produced the most litter/m^2 of the swamp, partially because of its dominance (basal area × density; Table 2), but also because it produced more litter per individual relative to the other tree species in the swamp (Table 3, Fig. 2A–C).
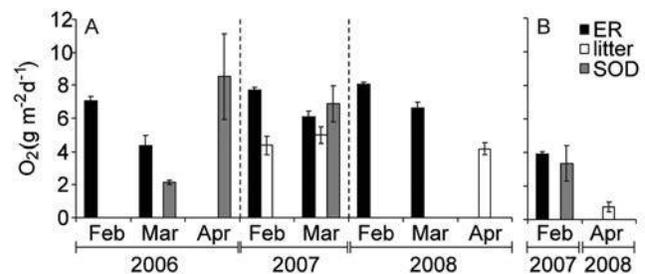

Figure 5. Mean (±1 SE) temperature-corrected (15°C) ecosystem respiration (ER), composite leaf-litter microbial respiration (litter), and sediment O$_2$ demand (SOD) at the swamp (A) and the stream (B) sites.

Despite faster litter breakdown rates, the swamp retained a higher percentage of litter inputs than the stream, possibly because of much lower water velocity and reduced export of particulate organic matter. Surface litter respiration accounted for 57 to 89% of ER in the swamp and did not differ significantly from bulk measurements of SOD. ER in forested streams and rivers is strongly influenced by the amount of organic C entering the system and the rate at which it is consumed or exported (Bernot et al. 2010), and therefore riverine swamps, such as the one studied here, may be exceptionally large sinks for dissolved O_2 in blackwater river networks.

Litter quality is often an area of focus when the effects of forest composition on aquatic ecosystem function are examined, but differences in the amount of litter produced per tree species are considered less frequently. Our results suggest that litter quantity is a species trait that deserves more attention, and that tree species may differentially affect O_2 demand via both quality and quantity of litter produced. For example, in the stream, water oak (*Quercus nigra*) litter supported significantly lower fungal biomass and microbial O_2 uptake rates/g litter than red maple (*Acer rubrum*) litter (Fig. 4C), but produced significantly more litter/individual than red maple or swamp tupelo (*N. sylvatica*) (Table 3, Fig. 2D–F). Oaks (*Quercus* spp.) generally produce litter of lower quality than red maple and support lower microbial biomass/g (Maharning and Bärlocher 1996, Mehring and Maret 2011), but their species-specific contributions to some ecosystem functions may be as large as those of trees that produce labile litter if they add a disproportionately large amount of organic C to the system, as our results suggest. Microbial O_2 uptake rates/g leaf litter did not differ significantly among tree species in the swamp, nor were they highly correlated with fungal biomass (Fig. 4B). However, *T. distichum* produced more litter/m^2 than other tree species in the swamp site because of its dominance (basal area × density; Table 2) and produced significantly more litter/individual than *N. sylvatica* (Table 3, Fig. 2A–C), possibly because conditions at the site favored growth and production by bald cypress: intermittent drying and flooding rather than permanent flooding (Megonigal et al. 1997), moderately elevated nutrient levels (Brown 1981), and low redox potential that favored elevated concentrations of metals more toxic to other tree species (McLeod and Ciravolo 2003). Their profuse production of pollen (male) cones also was a factor in the large quantity of litter inputs from *T. distichum* because those structures constituted ~13% of the total amount of leaf and pollen-cone litter entering the system. Litterfall within the Little River swamp site (917 g m^{-2} y^{-1}) was higher than average compared to other cypress-dominated swamps (693 g m^{-2} y^{-1}) and was within the upper ⅓ of previously reported values (79–1426 g m^{-2} y^{-1}) (Middleton and McKee 2004).

The Little River site, at lat 31.5°N, is not far from the latitude (31.9°N) where Middleton and McKee (2004) suggested that environmental conditions would allow for maximum litter production by *T. distichum.*

Riverine swamps may act as important O_2 sinks in blackwater river networks in part because slower water velocities enhance retention of organic matter. Decreases in litter standing stock throughout the wet season were greater in the stream than in the swamp. However, litter breakdown rates, measured concurrently at both sites, were significantly slower in the stream (Mehring 2012). Therefore, the stream appears to be less retentive than the swamp, possibly because of substantially faster water velocities in the stream. Maximum water velocity in the stream (1.23 m/s) was 8.2× higher than maximum water velocity in the swamp (0.15 m/s), suggesting lower potential for downstream transport of particulate organic matter in the swamp.

Given the high O_2 demand in the system, it is not surprising that hypoxic events are common from early April until the end of the flow season in the Little River. The wide, shallow channel morphology in the swamp allows uniformly high density of trees and large inputs of organic matter across the site (Table 2) and contributes to enhanced contact between water and O_2-consuming microbes in benthic organic matter. The frequency of large instream swamps throughout Georgia's coastal plain could help to explain differences in relative retentiveness and accumulation of particulate organic matter and resulting differences in O_2 demand among river reaches. Todd et al. (2010) estimated that 89% of all stream length within the LREW is found in smaller headwater streams (1st–3rd order) and 11% in >4th-order reaches. However, they found that swamps similar to the one in our study accounted for 52% of all floodplain areas in the LREW. These types of habitats may be relatively common throughout Georgia's coastal plain.

Agreement is generally good among the 4 methods used to measure O_2 demand in the swamp. Cathey (2005) estimated that an SOD calibration value of 6.00 g O_2 m^{-2} d^{-1} was required to validate a DO-prediction model (DoSag) in the Little River. This value is identical to the average uncorrected (for temperature) value of ER estimated in our study (6.00 ± 0.20 g O_2 m^{-2} d^{-1}), slightly lower than the average uncorrected SOD value of 6.37 ± 0.93 g O_2 m^{-2} d^{-1} measured previously in the swamp by Todd et al. (2009), and slightly higher than the average uncorrected value of leaf-litter standing stock respiration (5.69 ± 0.46 g O_2 m^{-2} d^{-1}) measured in our study. The mean ER reported for the swamp in our study falls in the middle of annual average ER rates reported for other southeastern blackwater rivers, which range from 3.01 g O_2 m^{-2} d^{-1} (Fuss and Smock 1996) to 9.44 g O_2 m^{-2} d^{-1} (Colangelo 2007). Therefore, although ER values in the

swamp were significantly higher than in an upstream reach of the Little River, they do not represent extremes for the region.

The similarity of average values measured by multiple methods suggests that hypoxia in the swamp is driven primarily by benthic O_2 demand that originates primarily from microbial decomposers inhabiting surface leaf litter. However, although areal leaf-litter respiration, which changed little throughout the wet season, accounted for 89% of ER in March 2007, it accounted for only 57% in February (Fig. 5A). FPOM or dissolved organic matter (DOM) both contribute to ER, but concurrent measurements of DOM-associated respiration rates in the swamp averaged only 4% of leaf-litter-associated O_2 demand on an areal (m^{-2}) basis (Mehring et al. 2013). Therefore, DOM respiration cannot fully explain the discrepancy between different estimates of O_2 demand. FPOM, which was not quantified in our study but is abundant in blackwater rivers (Jones 1997), probably makes an additional contribution to ER in the Little River. In February, lower temperatures (<10°C) and higher water-column DO concentrations (~5 mg/L) could have allowed greater oxygenation of subsurface sediments than in March. If that were the case, a greater proportion of total benthic O_2 demand and ER may have been generated by buried particulate organic matter at that time. This also may be the case in the stream, where water-column O_2 concentrations are higher (Fig. 1), sediments are coarser (Cathey 2005), and buried organic matter is present in high concentrations (Todd et al. 2010), potentially allowing more O_2 to enter subsurface sediments to be consumed by buried rather than surface organic matter.

Many of the blackwater rivers once cited for violation of Georgia's dissolved O_2 standards have been delisted. Surface litter decomposition is a substantial source of O_2 demand, and may explain a large proportion of the observed seasonal hypoxia in the Little River, but it is a driver that is vulnerable to anthropogenic disturbance. ER also is influenced by nutrient availability (Bernot et al. 2010), so nutrient loading could increase the frequency or duration of hypoxia in blackwater river systems that are already highly heterotrophic. In the Little River, nutrient concentrations are fairly low (Table 1). For all nutrient variables other than TKN, the average and maximum concentrations during the study period fell below nutrient standards proposed for the Southeastern Plains, the region that includes Georgia's coastal plain (Gruau et al. 2004). Feyereisen et al. (2008) calculated that loads of NO_3^-, NH_4^+, and TKN were 0.84, 0.32, and 5.58 kg ha^{-1} y^{-1}, respectively, in the swamp, and 0.70, 0.32, and 7.90 kg ha^{-1} y^{-1} in the stream. These values are considerably lower than values encountered in other agricultural watersheds (Feyereisen et al. 2008).

In other systems, nutrient additions significantly increased leaf-litter-associated microbial biomass and respiration (Gulis and Suberkropp 2003, Mallin et al. 2004, Suberkropp et al. 2010). If excess nutrient loading were to occur in the Little River or in other blackwater rivers, it could enhance microbial O_2 demand and lead to lower DO concentrations earlier in the wet season. In addition, agricultural water withdrawals, which have been increasing throughout the region (Lowrance et al. 2007), could lead to reduced river discharge and velocity, thereby increasing particulate organic matter retention and leading to enhanced hypoxia. Although regulatory opinions may have changed to view these systems as naturally low in O_2, a more thorough understanding of landuse impacts and variability of O_2 demand among river reaches will help to inform management strategies, and careful monitoring of water quality in coastal plain blackwater systems is still critical to their protection.

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