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Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance

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Abstract. Catchment characteristics determine the inputs of sediments and nutrients to streams. As a result, natural or anthropogenic disturbance of upland soil and vegetation can affect instream processes. The Fort Benning Military Installation (near Columbus, Georgia) exhibits a wide range of upland disturbance levels because of spatial variability in the intensity of military training. This gradient of disturbance was used to investigate the effect of upland soil and vegetation disturbance on rates of stream metabolism (ecosystem respiration rate [ER] and gross primary production rate [GPP]). Stream metabolism was measured using an open-system, single-station approach. All streams were net heterotrophic during all seasons. ER was highest in winter and spring and lowest in summer and autumn. ER was negatively correlated with catchment disturbance level in winter, spring, and summer, but not in autumn. ER was positively correlated with abundance of coarse woody debris, but not significantly related to % benthic organic matter. GPP was low in all streams and generally not significantly correlated with disturbance level. Our results suggest that the generally intact riparian zones of these streams were not sufficient to protect them from the effect of upland disturbance, and they emphasize the role of the entire catchment in determining stream structure and function.

Key words: ecosystem respiration, primary production, catchment disturbance, land use, seasonal patterns, military reservation.

Catchment land use affects sediment and nutrient inputs, physical habitat variables, and biological community composition in streams (Omernik 1976, Richards et al. 1996, Huryn et al. 2002, Strayer et al. 2003). Inputs of sediments and nutrients often increase with the proportion of urban or agricultural land use (Allan et al. 1997, Strayer et al. 2003). Land use also affects physical habitat variables such as abundance of coarse woody debris (Richards et al. 1996). The role of the riparian zone in mitigating some impacts of land use has been well studied (e.g., Lowrance et al. 1984, Gregory et al. 1991, Osborne and Kovacic 1993, Richards et al. 1996), but less is known about how localized, intense disturbance of upland areas affects streams.

Despite the growing number of studies of stream metabolism (e.g., Bott et al. 1985, Young and Huryn 1996, Uehlinger and Naegeli 1998, Mulholland et al. 2001, Acuña et al. 2004), rates of ecosystem processes (e.g., ecosystem respiration rate [ER] or gross primary production rate [GPP]) in streams have not been used frequently to quantify the effects of catchment disturbance. Efforts to quantify the effects of land use on the biology of stream ecosystems have emphasized community-scale metrics such as abundance or diversity of fish or macroinvertebrates (e.g., Steedman 1988, Richards and Host 1994). Changes in ecosystem processes are an integrated response to catchment disturbance, and have only recently been advocated as useful measures of stream health (Bunn et al. 1999, Young and Huryn 1999, Gessner and Chauvet 2002).

Military reservations present a unique oppor-

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TABLE 1. Selected physical and chemical characteritics of the study-stream reaches. Width, depth, discharge, and velocity values are means (SD) based on measurements made during quarterly NaCl/propane injections from summer 2001 through spring 2003 (n = 8 for width, depth, discharge, and velocity; n = 16 for nutrient measurements except for BC2, HB, and LPK where n = 15). Nutrient measurements were taken at the beginning and end of each measurement period. SRP = soluble reactive P, DIN = dissolved inorganic N. Stream abbreviations are as in Fig. 1.

Stream	Width (m)	Depth (m)	Discharge (L/s)	Velocity (m/s)	SRP (μg/L)	DIN (μg/L)	Catchment area (ha)	Disturbance intensity (% catchment)
KM2	1.6 (0.4)	0.15 (0.10)	16.6 (19.6)	0.04 (0.03)	6.2 (2.9)	14.2 (10.4)	231	1.8
BC2	1.0 (0.1)	0.10 (0.03)	4.6 (2.7)	0.04 (0.02)	5.1 (1.9)	31.3 (15.3)	74.9	3.2
LC	1.9 (0.2)	0.12 (0.03)	16.6 (14.4)	0.07 (0.04)	5.1 (2.3)	21.8 (18.3)	332	3.7
KM1	1.9 (0.2)	0.13 (0.04)	25.6 (13.7)	0.1 (0.02)	4.6 (2.4)	16.1 (4.9)	369	4.6
HB	1.7 (0.1)	0.10 (0.02)	14.2 (5.5)	0.08 (0.02)	4.0 (2.3)	68.3 (25.6)	215	6.6
SB2	1.5 (0.1)	0.06 (0.02)	13.5 (5.3)	0.14 (0.03)	2.5 (1.7)	47.9 (13.2)	123	8.1
BC1	1.3 (0.2)	0.14 (0.03)	8.3 (4.1)	0.04 (0.01)	4.3 (2.2)	11.0 (10.6)	210	10.5
SB3	1.0 (0.1)	0.05 (0.03)	5.5 (3.7)	0.11 (0.03)	1.9 (0.9)	23.6 (24.2)	71.7	10.5
LPK	0.8 (0.1)	0.04 (0.02)	3.1 (1.5)	0.10 (0.02)	3.2 (1.4)	67.8 (37.8)	33.1	11.3
SB4	1.3 (0.5)	0.04 (0.02)	6.1 (3.8)	0.12 (0.03)	2.6 (1.2)	50.3 (18.6)	100	13.7

tunity for examining ecological processes because land use within these reservations is often strikingly varied. Military reservations are often regional islands of biodiversity and have areas of high-quality habitat (Cohn 1996), yet local areas dedicated to training exercises often experience a high degree of soil and vegetation disturbance (e.g., Quist et al. 2003). As a result, these reservations contain a wide range of anthropogenic disturbance levels within a small region of relatively homogenous geography.

We selected a set of streams spanning a gradient of disturbance at the Fort Benning Military Installation (FBMI) to address 2 questions: 1) What are the effects of upland soil and vegetation disturbance on ER and GPP? 2) What is the magnitude and seasonal variation of ecosystem respiration and primary production in low-gradient headwater streams of the Southeastern Plains ecoregion?

Methods

Site description

Ten 2nd- to 3rd-order streams on the FBMI and within the Chattahoochee River catchment of west-central Georgia were selected for study (Table 1, Fig. 1). Until purchased by the US military in 1918 and 1941 to 1942, the land use was primarily row-crop agriculture and pasture. Subsequent to purchase, the forest has regrown and, within the undisturbed areas on the base, land cover consists primarily of oak-hickory-pine and southern mixed forest, with underlying sandy or sandy-clay-loam soils (Omernik 1987). Certain areas of the reservation are used for military training involving infantry and mechanized heavy equipment (e.g., tracked vehicles such as tanks). As a result, some catchments have localized areas with high soil and vegetation disturbance resulting in high rates of erosion. Other catchments have remained essentially undisturbed for the last 60 to 80 y.

The streams included in our study are typical low-gradient, sandy, Southeastern Plains streams (Felley 1992) with an intact riparian canopy and forested catchment. Leaf emergence usually occurs in late March or early April, and leaf abscission usually occurs in early November. Thus, from late spring through early autumn, the riparian trees provide a closed canopy, and the streams are generally evenly shaded. The riparian forest is almost entirely deciduous, resulting in little shading of the streams during winter and early spring. Precipitation (averaging ~1 m annually) is distributed evenly throughout the year, but stream discharge exhibits seasonal patterns. High rates of evapotranspiration in summer and early autumn result in lower stream discharge in summer and autumn relative to winter and spring. The study reaches (Fig. 1) were selected from within

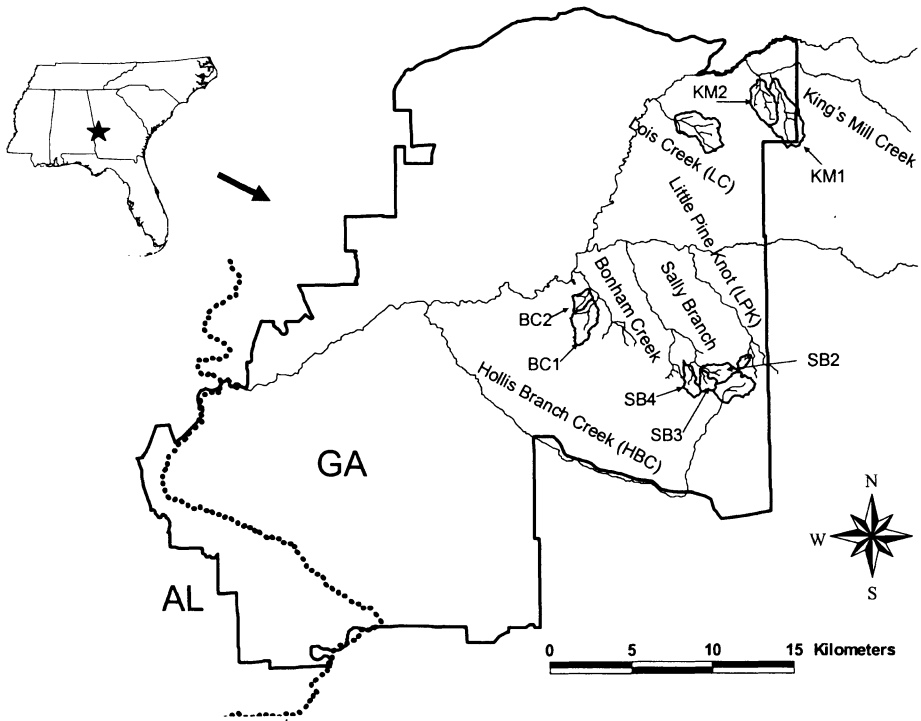

FIG. 1. Study catchments located on the Fort Benning Military Reservation near Columbus, Georgia. Study catchments included 2 tributaries of Bonham Creek (BC1, BC2), 3 tributaries of Sally Branch Creek (SB2, SB3, and SB4), 2 tributaries of Kings Mill Creek (KM1, KM2), 1 tributary of Little Pine Knot Creek (LPK), Hollis Branch Creek (HBC), and Lois Creek (LC).

stream reaches of relative homogeneity with respect to morphology, shading, and discharge. Study reaches had minimal lateral inflow, and increases in discharge from the upper to lower stations were <10%.

Disturbance

Disturbance intensity for each catchment was quantified by Maloney et al. (2005), and the methods are briefly reviewed here. Land use in the study catchments was quantified using geographic information system (GIS) data sets (streams: 1:24,000 [1993], soils: 1:20,000 [1998], and roads: 10 m [1995]), available digital orthophotography (1:5000 [July 1999]), digital elevation models (DEMs) (1:24,000, grid size = 10 m [1993]), and Landsat imagery (28.5 m [July and December 1999]) provided by Fort Benning personnel. Disturbance intensity was defined as the % of bare ground on slopes >5% in each catchment. Bare ground refers to areas with no vegetative cover and includes unpaved roads. Road cover was quantified by multiplying road length by average road width, estimated in the field, for each road class. The areas of soil and vegetation disturbance were in upland areas away from the perennial streams, but the upland areas were hydrologically connected to the perennial streams during storms via ephemeral drainages. Two-hundred forty-five of the 249 Fort Benning catchments have disturbance levels between 0 and 17%. The 10 catchments included in our study spanned much of this disturbance gradient, and disturbance intensities ranged from 1.8 to 13.7% (Table 1).

Field methods

Stream metabolism.—ER and GPP were determined using an open-system, single-station approach (Owens 1974, Bott 1996). Diel dissolved O_2 (DO) and temperature data were collected using YSI Model 6000 or 600 series sondes equipped with a YSI model 6562 DO probe. The sondes were calibrated in water-saturated air before deployment and immediately after retrieval. The calibration data were subsequently corrected for barometric pressure recorded during sonde calibration. Pre- and postdeployment calibrations were used to detect instrument drift. The sondes were deployed for 7 to 21 consecutive days each season (winter, spring, summer, and autumn) from summer 2001 through summer 2003 (data collection in Little Pine Knot Creek [LPK] began in winter 2002). DO concentrations were recorded at 15-min intervals (30-min intervals in summer 2001). Sondes were placed in a laterally constrained section of each stream to ensure that readings were taken from a representative, well-mixed area of the stream. Sondes were deployed in 5 streams at a time and moved to the other 5 streams immediately thereafter because of equipment limitations. The streams included in the 1st and 2nd sampling groups were varied to the extent possible within the constraints of military-base access restrictions. Winter deployments were during January and February; spring deployments were during March and April; summer deployments were during June, July, and August; and autumn deployments were during October and November. No usable metabolism data were available for some streams in summer 2001 (LPK and King Mills Creek [KM] 1), summer 2002 (Sally Branch Creek [SB] 2), summer 2003 (Lois Creek [LC] and SB4), autumn 2001 (LPK and LC), and winter 2003 (KM1) because of equipment malfunction during deployment.

Stream velocity, discharge, and gas exchange.—Reaeration coefficient, stream discharge, and stream velocity were determined using simultaneous, continuous injection of propane gas (volatile tracer) and a concentrated NaCl solution (conservative tracer) (Genereux and Hemond 1992). The injection sites were 15 to 20 m upstream of the study reaches, which ranged from 40 to 100 m long. The downstream station in each reach was ≤5 m from the site at which the DO sondes were deployed. Background conductivity (γ_b) was recorded at the upstream and downstream ends of the study reach before the injection. During the injection, a concentrated NaCl solution was delivered to the stream at a constant rate using an FMI model QBC pump (Fluid Metering, Syosset, New York), and propane gas was injected at a constant rate through a 30-cm × 6-cm aeration stone. Conductivity was recorded every 30 s at the upstream station and every 60 s at the downstream station. The difference in time between the occurrence of maximum rate of change in conductivity (maximum slope) at the upstream and downstream stations and the distance between the stations were used to calculate average water travel time and stream velocity.

Propane reaeration coefficients were determined from steady-state propane and NaCl concentrations at the upstream and downstream stations (Genereux and Hemond 1992). The O_2 reaeration coefficient, k_{O2} (/d), was calculated from $k_{propane}$ using the standard conversion $k_{O2} = k_{propane} \times 1.39$ provided by Rathbun et al. (1978). Propane samples were collected from the thalweg in a laterally constrained, well-mixed area of the stream reach. A 10-mL plastic syringe was rinsed once with stream water to remove air bubbles, and refilled with 6 mL of stream water. The sample was injected into a 7-mL pre-evacuated vacutainer. Six replicate samples were collected at each of the upstream and downstream sampling stations. Equilibrated headspace gas from each vacutainer was analyzed on a Hewlett Packard Model 5890 Series II gas chromatograph equipped with a 7.62 m Poropak Q column and a flame ionization detector.

Stream discharge (Q, L/s) was calculated as:

$$Q = (C_{NaCl} R_{inj})/(\gamma_{ss} - \gamma_b) \qquad [1]$$

where γ_b is the background conductivity (μS/cm), γ_{ss} is the steady-state injection conductivity (μS/cm), C_{NaCl} is the conductivity of the NaCl injection solution (μS/cm), and R_{inj} is the injection rate (L/s). Mean depth (z_{mean}, m) was calculated from stream width (W, m), Q, and velocity (U, m/s) using the equation $z_{mean} = Q/(1000[UW])$. Stream width was the average of wetted-width measurements taken every 5 m along the study reach.

Organic matter.—Percent benthic organic matter (%BOM) and coarse woody debris (CWD) data are from Maloney et al. (2005). Briefly, %BOM was determined from replicate sediment cores (1.6 cm wide × 10 cm long) taken at 3 thalweg sites in each stream 3 times/y from August 2001 to May 2003. Sediment cores were oven-dried at 80°C for 24 to 48 h, weighed, ashed in a muffle furnace at 550°C for 3 h, and reweighed. %BOM was calculated as the difference between dry and ashed masses divided by total dry mass. The relative abundance of CWD in each stream was quantified in April 2002 and

March 2003 using a modified transect method (Wallace and Benke 1984). Fifteen transects were set up in each stream and all submerged CWD >2.5 cm in diameter along each transect was quantified. Transects were perpendicular to the stream and spaced 5 m apart. CWD data were converted to planar area (m^2 of CWD/m^2 of stream bed) by multiplying CWD diameter by length and then dividing this value by the area sampled within each transect.

Metabolism calculations

ER and GPP were determined using a single-station, open-system method similar to the 2-station method of Marzolf et al. (1994). The rate of change in DO concentration was calculated as the difference between consecutive DO concentration readings instead of the difference between an upstream and downstream station as in the 2-station method. Ecosystem metabolism was determined from the change in DO over 15-min intervals (30-min intervals for summer 2001) based on the equation:

$$\Delta DO = P - R + k_{O_2}(D) \qquad [2]$$

where ΔDO is the change in DO concentration (g O_2/m^3), P is volumetric gross primary production (g O_2/m^3) and R is volumetric ecosystem respiration (g O_2/m^3) between consecutive DO measurements. The 3rd term in the equation represents the net exchange of O_2 with the atmosphere; k_{O2} is the O_2 reaeration coefficient, and D is the average DO deficit (g O_2/m^3) over the measurement interval. During the night, P = 0 and R was calculated from the ΔDO, k_{O2}, and D. During the day, R was determined by interpolating between R averaged over the last hour before dawn and the first hour after dusk. Total daily ER (g m^{-2} d^{-1}) was the sum of nighttime and daytime R over 24 h (from 2400 h to 2400 h). Total daily GPP (g m^{-2} d^{-1}) was the sum of the differences between the interpolated daytime R and the observed total metabolism. ER and GPP were both converted to areal units (g m^{-2} d^{-1}) by dividing the volumetric rates (g m^{-3} d^{-1}) by the mean depth of the stream reach.

Meteorological data

Meteorological data, including solar radiation and precipitation, from 3 meteorological stations at the FBMI were used in our study. Data from days with low solar irradiation or more than a trace of rainfall were omitted from analyses of disturbance impacts on stream metabolism to minimize the variability in stream metabolic rates caused by storms and variation in solar radiation among days. Low solar irradiation days were determined by calculating mean irradiance for every day in each month in which metabolism was measured. Any days with mean irradiance <70% of the maximum daily mean irradiance observed in that month were omitted from the analysis.

Data analysis

Seasonal mean ER and GPP (across all streams and years) were tested for significant differences using the Scheffé adjustment method for multiple comparisons. The effects of disturbance on GPP, ER, %BOM, and CWD were tested by regression analysis. Stream mean GPP and ER were regressed against catchment disturbance intensity to detect general trends across the disturbance gradient. Season-specific trends across the disturbance gradient were tested using the sampling episode mean (one sampling episode for each stream in each season of each year) GPP and ER for each stream in a stepwise regression analysis that included disturbance intensity, solar irradiance (GPP analysis), and temperature (ER analysis). Spearman correlation analysis was used to detect correlations between ER and %BOM or CWD. %BOM and CWD were not included in the stepwise regression analysis of ER and GPP because of their high covariance with disturbance intensity. All statistical analyses were conducted using SAS (version 8.0, SAS Institute, Cary, North Carolina).

Results

Physical and chemical characteristics varied moderately among our study streams (Table 1). Streams were generally 1 to 2 m wide with mean depths of 5 to 15 cm. Nutrient concentrations were low. Discharge rates were generally higher in winter and spring than in summer and autumn (Table 2). Rainfall was distributed approximately evenly among seasons, and the seasonal differences in stream discharge were primarily a result of seasonal differences in rates of evapotranspiration. Stream tempera-

TABLE 2. Mean discharge and temperature of the study-stream reaches for summer (2001–2003), autumn (2001–2002), winter (2001–2002), and spring (2002–2003). Means are based on quarterly NaCl tracer injections (n = 2 for all seasons except summer where n = 3). Stream abbreviations are as in Fig. 1.

	Discharge (L/s)				Temperature (°C)			
Stream	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
KM2	21.5	39.2	8.7	0.8	11.3	16.0	22.6	16.5
BC2	4.5	8.3	3.1	2.4	8.3	17.6	22.4	15.4
LC	17.2	34.8	11.5	5.7	9.4	16.4	23.7	21.2
KM1	28.6	44.9	17.1	16.2	9.6	15.9	22.7	17.4
HB	30.5	21.3	9.3	12.4	9.8	16.6	22.2	15.3
SB2	13.7	20.0	11.1	9.9	13.2	17.3	21.5	12.0
BC1	6.6	13.0	7.6	6.5	8.7	16.9	21.7	12.7
SB3	5.6	9.3	3.7	3.2	12.8	16.5	22.4	11.2
LPK	3.0	4.8	2.3	2.5	10.2	16.5	21.4	20.8
SB4	6.4	9.1	4.4	3.8	10.6	17.0	23.1	15.5

tures were lowest in winter, highest in summer, and intermediate in spring and autumn (Table 2).

The streams exhibited a broad range of reaeration coefficients, from 2 to 341/d; ~75% of the values were between 8 and 85/d. k_{O2} was negatively correlated with z_{mean} ($r = -0.71$, $p < 0.01$) and positively correlated with U ($r = 0.45$, $p < 0.01$).

Stream metabolism

A wide range of ER was observed, but GPP was generally quite low. ER was generally an order of magnitude higher than GPP, indicating that these streams were highly heterotrophic. Maximum ER and greatest variability in ER among streams occurred in winter and spring (Fig. 2A). ER was significantly higher in spring than in summer and autumn (Scheffé adjustment for multiple comparisons, $p < 0.05$); the difference between winter and autumn ER was marginally significant ($p = 0.08$); and no significant differences were found between summer and autumn or summer and winter (Fig. 2A). GPP was highly variable with a coefficient of variation usually >1 (Fig. 2B), and no significant differences were found among seasons. The low GPP and high variability among sites made seasonal patterns difficult to detect. ER and GPP were not correlated in winter, spring, or autumn, but were correlated in summer ($r = 0.6$, $p < 0.01$).

Effects of disturbance on stream metabolism

Increased disturbance negatively affected mean stream ER but did not have discernable effects on mean stream GPP (Fig. 3A, B). Mean ER declined from 5.7 ± 1.9 g O_2 m^{-2} d^{-1} (stream mean ±1 SE) at the least disturbed site to 2.4 ± 0.58 g O_2 m^{-2} d^{-1} at the most disturbed site (Fig. 3A). Mean GPP ranged from 0.04 ± 0.01 to 0.37 ± 0.22 g O_2 m^{-2} d^{-1} among streams and was not significantly related to disturbance level (Fig. 3B). One stream (Bonham Creek [BC] 1), which drained a catchment with anomalous morphometry, was omitted from all statistical analyses. This catchment had a notably broader, flatter floodplain than the rest of the study catchments, and this broad floodplain appeared to protect the stream from the effects of disturbance.

ER (means for each stream for each sampling episode) ranged from 1.3 to 16.3, 0.8 to 10.7, 0.2 to 5.2, and 0.1 to 3.3 g O_2 m^{-2} d^{-1} for winter, spring, summer, and autumn, respectively (Fig. 4A–D). The relationship between catchment disturbance and ER varied seasonally. ER decreased significantly with increasing disturbance in winter, spring, and summer, but not in autumn (Table 3, Fig. 4A–D). Streams in highly disturbed catchments had consistently low ER throughout the year. However, streams in catchments with low disturbance had a more pronounced seasonal cycle with lower ER in summer and autumn, and higher ER in winter and spring (Fig. 4A–D). Stream means from individ-

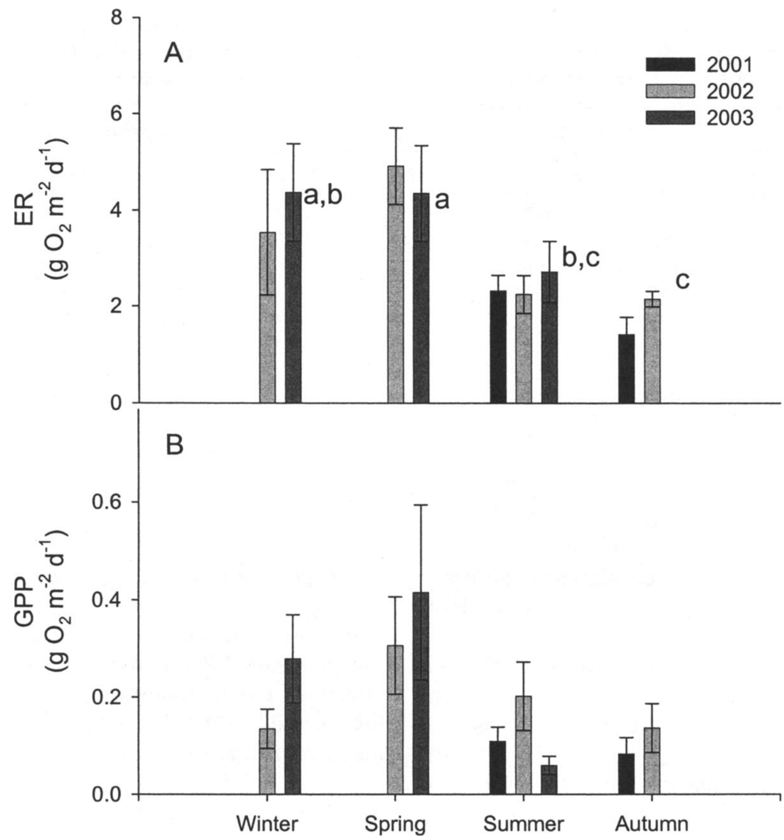

FIG. 2. Mean ($\pm$1 SE) seasonal ecosystem respiration rate (ER) (A) and gross primary production rate (GPP) (B). Separate bars are shown for each year. Groups of bars labeled with the same letters are not significantly different (Scheffé adjustment for multiple comparisons; $p < 0.10$). GPP did not differ among seasons. Years were pooled for the statistical analysis.

ual seasonal sampling episodes ranged from 0.23 to 5.3 g O_2 m^{-2} d^{-1} for streams in the 3 most disturbed catchments and from 0.5 to 16.3 g O_2 m^{-2} d^{-1} for streams in the 3 least disturbed catchments. Thus, disturbance level appeared to affect the magnitude of seasonal variation in ER.

GPP (means for each stream for each sampling episode) ranged from <0.01 to 0.92, <0.01 to 1.75, <0.01 to 0.29, and <0.01 to 0.44 g O_2 m^{-2} d^{-1} in winter, spring, summer, and autumn, respectively (Fig. 5A–D). When analyzed by season, no significant relationship was found between GPP and disturbance, except for spring 2002 (Table 3, Fig. 5A–D). Separate analysis of spring 2002 data indicated a significant negative relationship between disturbance and GPP. Stream means for individual seasonal sampling episodes ranged from <0.01 to 0.87 g O_2 m^{-2} d^{-1} in streams in the 3 most disturbed catchments and from <0.01 to 0.96 g O_2 m^{-2} d^{-1} for streams in the 3 least disturbed catchments.

Disturbance intensity, but not temperature, was a significant predictor of ER for winter, spring, and summer (Table 3). In contrast, stream temperature, but not disturbance intensity, was a significant predictor of ER in autumn (Table 3). Similar analyses of the relationships between seasonal mean GPP and 1) disturbance level and 2) solar irradiance showed that disturbance intensity was not a significant predictor of GPP at the seasonal scale, but was a significant predictor for GPP in spring 2002 when these data were analyzed separately. Solar irradiance was a significant predictor of GPP in summer and autumn (Table 3). The effect of solar irradiance probably would have been more pronounced had days with mean solar irradiance <70% of the monthly maximum daily

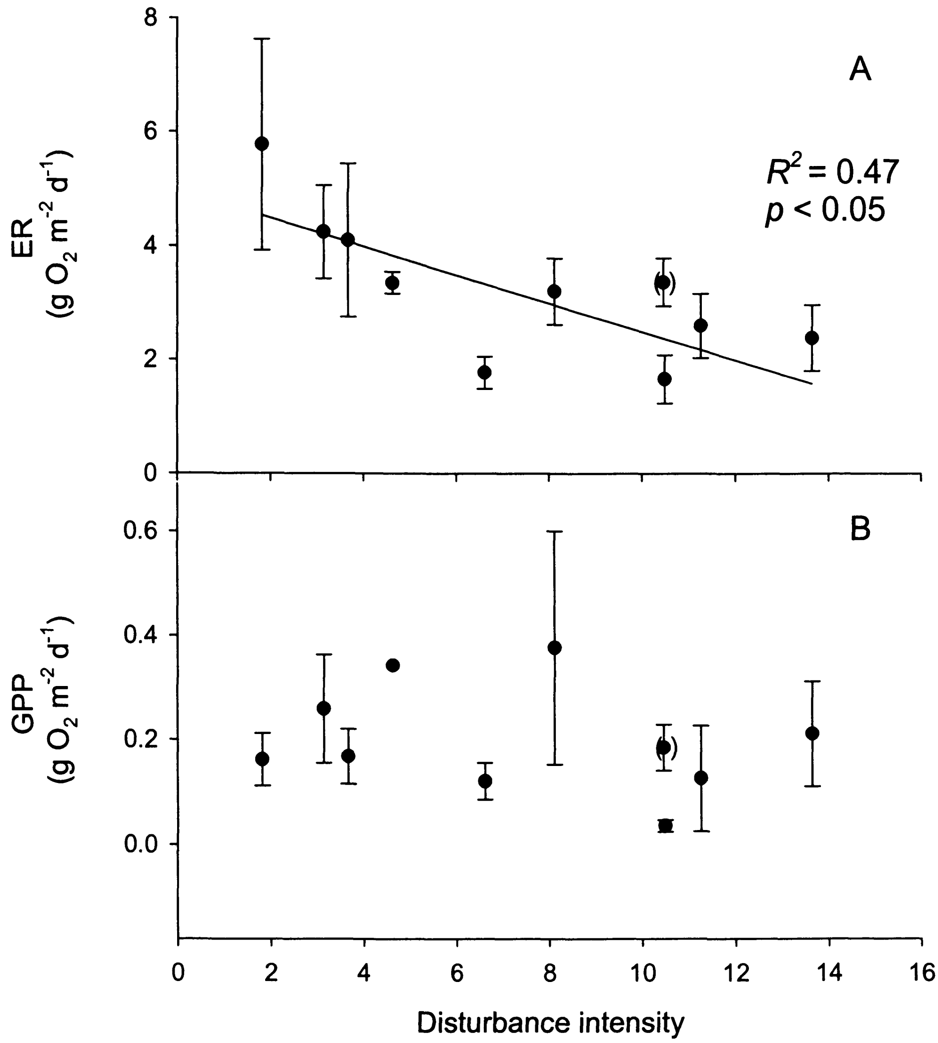

FIG. 3. Relationship between disturbance intensity and ecosystem respiration rate (ER) (A) and gross primary production rate (GPP) (B). Data are means (±1 SE) across all seasons and years. Parentheses indicate site BC1, which was excluded from the statistical analyses (see Results).

mean irradiance not been omitted from analysis.

Organic matter

Both %BOM (R^2 = 0.32, p = 0.06) and CWD (R^2 = 0.76, p = 0.001) abundance declined significantly as disturbance increased (Fig. 6A, B). %BOM, CWD, and disturbance covaried strongly, so inclusion of >1 of these predictors in the stepwise regression analysis (Table 3) would have been redundant. Mean stream ER was not correlated with mean stream %BOM (r = 0.48, p = 0.2; Fig. 7A), but was correlated with CWD abundance (r = 0.85, p < 0.01; Fig. 7B).

Discussion

Our results describe the pattern in stream metabolism observed across a range of disturbance levels in low-gradient, headwater streams in the Southeastern Plains region of the southeastern US. Open-system techniques for measuring stream metabolism are now used commonly (e.g., Odum 1956, Grimm and Fisher 1984, Edwards and Meyer 1987, Wiley et al.

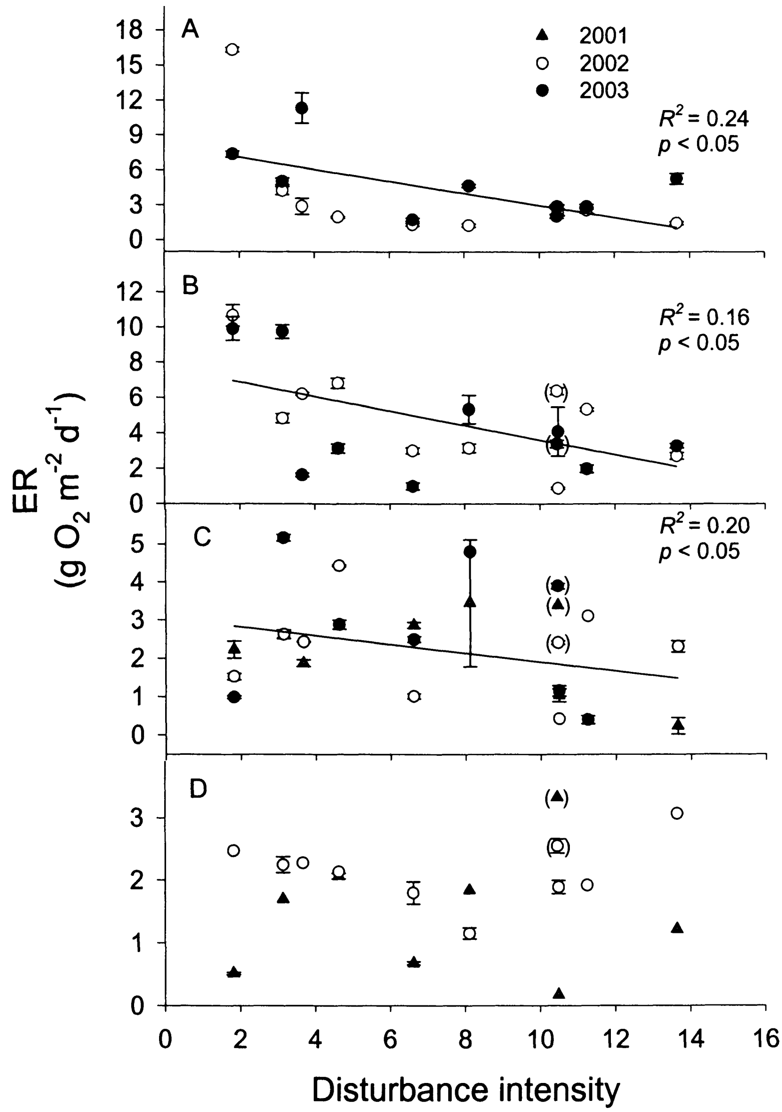

FIG. 4. Relationship between ecosystem respiration rate (ER) and disturbance intensity for winter (2001–2002) (A), spring (2002–2003) (B), summer (2001–2003) (C), and autumn (2001–2002) (D). Seasonal means for each year are shown as separate points. Regression lines are plotted for relationships that were significant. Parentheses are as in Fig. 3.

1990, Young and Huryn 1996, Uehlinger and Naegeli 1998, Mulholland et al. 2001, Hall and Tank 2003, McTammany et al. 2003, Acuña et al. 2004), but this approach has rarely been used to examine the effects of catchment land use or disturbance on stream ecosystems. Two years of quarterly data showed that ER in headwater streams decreased as the upland catchment disturbance increased, but that GPP generally was not affected by upland disturbance.

Disturbance and ER

Two possible mechanisms for the relationship between disturbance level and ER were examined in our study: %BOM and CWD abundance. Both CWD and %BOM were negatively correlated with disturbance level in our streams (Maloney et al. 2005; Fig. 6). High sediment inputs can bury CWD in highly disturbed streams, reducing the abundance of CWD in the stream

TABLE 3. Significant regression analyses for ecosystem respiration rate (ER) and gross primary production rate (GPP) by season. Unless otherwise indicated, seasonal sampling years are as in Table 2.

Season	Dependent variable	Independent variable	Slope ±1 SE	R^2	p
Winter	Log ER	Disturbance	−0.088 ± 0.041	0.24	<0.05
Spring		Disturbance	−0.087 ± 0.041	0.16	0.05
Summer		Disturbance	−0.11 ± 0.045	0.20	<0.05
Autumn		Temperature	0.10 ± 0.037	0.32	<0.05
Spring 2002	Log GPP	Disturbance	−0.37 ± 0.12	0.51	<0.05
Summer		Solar irradiance	0.025 ± 0.11	0.16	<0.05
Autumn		Solar irradiance	0.031 ± 0.15	0.18	0.05

channel. High input of inorganic sediments in highly disturbed catchments also may reduce %BOM by diluting or burying the organic material, reducing its availability for stream metabolism. Abundant CWD can increase the retention of organic material in streams (Bilby and Likens 1980), and we observed substantial accumulation of leaves and other organic matter in the debris dams formed by CWD in the low-disturbance streams. A significant relationship between %BOM and ER was not found, suggesting that %BOM was not an important mechanism underlying the relationship between ER and disturbance intensity. In contrast, ER and CWD were strongly positively correlated in these streams (Fig. 7B). The strong correlation between CWD and ER, but not %BOM and ER, supports the idea that CWD and the organic material it traps may be hot spots for ecosystem respiration in streams, as has been found in other studies (Hedin 1990, Fuss and Smock 1996).

Disturbance and GPP

GPP did not show significant trends across the disturbance gradient, except during spring 2002. GPP was generally low and temporal variation was high. The deciduous forest canopy is closed over these streams for much of the year (April–October), and the days are relatively short in the open-canopy season (except for late spring). Light availability often limits production in such streams (Hill et al. 1995). In addition, the unstable sandy bottoms of these streams are a poor substrate for benthic algae. The surficial geology in the area is prone to erosion and the climate is humid, so the substrate of these streams is particularly susceptible to resuspension and transport during storm events. Precipitation is frequent during most of the year, and even small amounts of precipitation could cause sufficient redistribution of stream sediments to partially bury sampling equipment, especially in the highly disturbed streams (JNH, personal observation). Such conditions restrict the development of stable primary producer communities. As a result, the observed GPP (and to a lesser extent ER) at any given time may have been affected by preceding storm frequency (Uehlinger and Naegeli 1998), making the influence of catchment disturbance difficult to discern.

Catchment disturbance was quantified using a simple metric with modest data requirements (% bare ground on slopes >5%), but additional factors that were not included may be important for understanding the effect of catchment disturbance on stream processes. Two such factors are the length and slope of potential flow paths between the disturbed area and the stream, and the type of soil and vegetation present in the catchment. More complex indices of disturbance would capture these additional catchment characteristics and might explain additional variation in stream metabolism.

Seasonal patterns

The observed seasonal patterns in metabolism did not covary with temperature, indicating that temperature was not the primary driver of seasonal patterns in these streams. However, ER was positively correlated with temperature in other studies (Bott et al. 1985, Fuss and Smock 1996, Uehlinger et al. 2000). In our study, higher ER occurred in winter and spring, and lower ER occurred in summer and autumn. This pattern

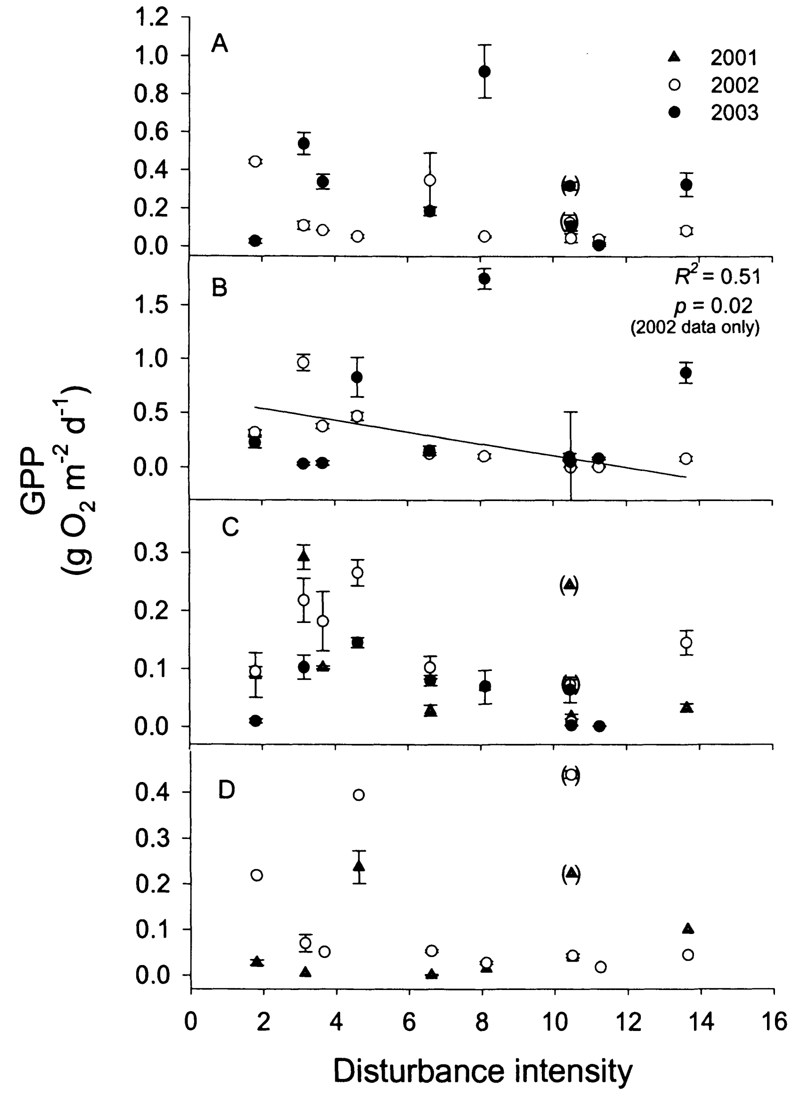

FIG. 5. Relationship between gross primary production rate (GPP) and disturbance intensity for winter (2001–2002) (A), spring (2002–2003) (B), summer (2001–2003) (C), and autumn (2001–2002) (D). Seasonal means for each year are shown as separate points. Regression line for spring data was based only on 2002 data (see Table 3). Parentheses are as in Fig. 3.

probably was driven by increased availability of labile organic matter in winter and spring. Deciduous riparian trees drop their leaves in late autumn, providing abundant labile organic matter through winter and spring. In addition, winter and spring are periods of high stream flow (because of low evapotranspiration rates), and higher flow may result in higher rates of labile organic matter input. Seasonal differences were less pronounced for GPP than ER (Figs 4, 5), and significant differences in mean values of GPP among seasons were not observed (Fig. 2). Maximum GPP occurred during spring, as has been observed in other studies (e.g., Acuña et al. 2004). This result was not surprising because spring conditions are particularly favorable for photosynthesis, i.e., light levels are relatively high because leafout has not yet occurred, temperatures are relatively warm, and day length is increasing.

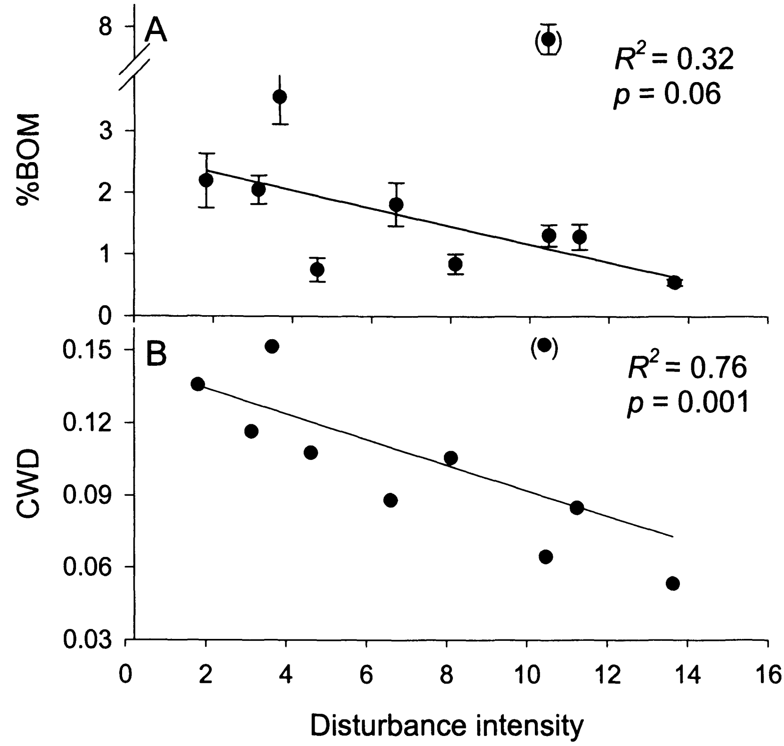

FIG. 6. Relationship between % benthic organic matter (%BOM) (A) and coarse woody debris (CWD) (B) and disturbance intensity. Parentheses are as in Fig. 3. Figure modified from Maloney et al. (2005).

Comparisons with other stream ecosystems

The range of ER observed in our study (0.3–16.3 g O_2 m^{-2} d^{-1}) spanned the range of rates observed in most other studies that used similar open-channel methods. Our range was slightly broader than the ranges observed by Mulholland et al. (2001) in a survey of stream metabolism across several biomes (2.4–11 g O_2 m^{-2} d^{-1}), and by Fellows et al. (2001) in headwater streams in northern New Mexico (2.3–14.7 g O_2 m^{-2} d^{-1}). It was ~2× the range (1.59–5.76 g O_2 m^{-2} d^{-1}) reported by Hall and Tank (2003) for streams in the Teton Mountain Range in Wyoming. Wiley et al. (1990) found respiration rates of 1st-order streams in a prairie river system in central Illinois (6.2–15.4 g O_2 m^{-2} d^{-1}, with one stream at 34 g O_2 m^{-2} d^{-1}) in the upper ½ of the rates in our study. A substantially broader range of ER (0.4–32 g O_2 m^{-2} d^{-1}) was observed in a Mediterranean stream (Acuña et al. 2004). The lowest ERs in our study were the lowest values observed in any of these studies.

GPP in our streams ranged from <0.01 to 1.75 g O_2 m^{-2} d^{-1}. Mulholland et al. (2001), Fellows et al. (2001), and Acuña et al. (2004) found similar ranges of GPP (0.1–1.8, 0.2–1.7, and 0.05–1.9 g O_2 m^{-2} d^{-1}, respectively). The range of GPP observed by Hall and Tank (2003) (0.13–0.6 g O_2 m^{-2} d^{-1}) was in the lower ½ of the range observed in our study. Much higher rates (generally >5.0 g O_2 m^{-2} d^{-1}) were observed by Wiley et al. (1990) in open-canopy prairie streams.

The occurrence and strength of the relationship between ER and GPP differs among stream systems. Some studies have found positive relationships (Wiley et al. 1990, Bunn et al. 1999), whereas others have found weak or nonexistent relationships (Mulholland et al. 2001). In our study, ER and GPP were not strongly correlated; the only significant correlation between them occurred during summer. ER was consistently much higher than GPP, indicating that these streams are strongly heterotrophic, as would be expected for headwater streams in forested catchments (Vannote et al. 1980).

In conclusion, our results add to the growing

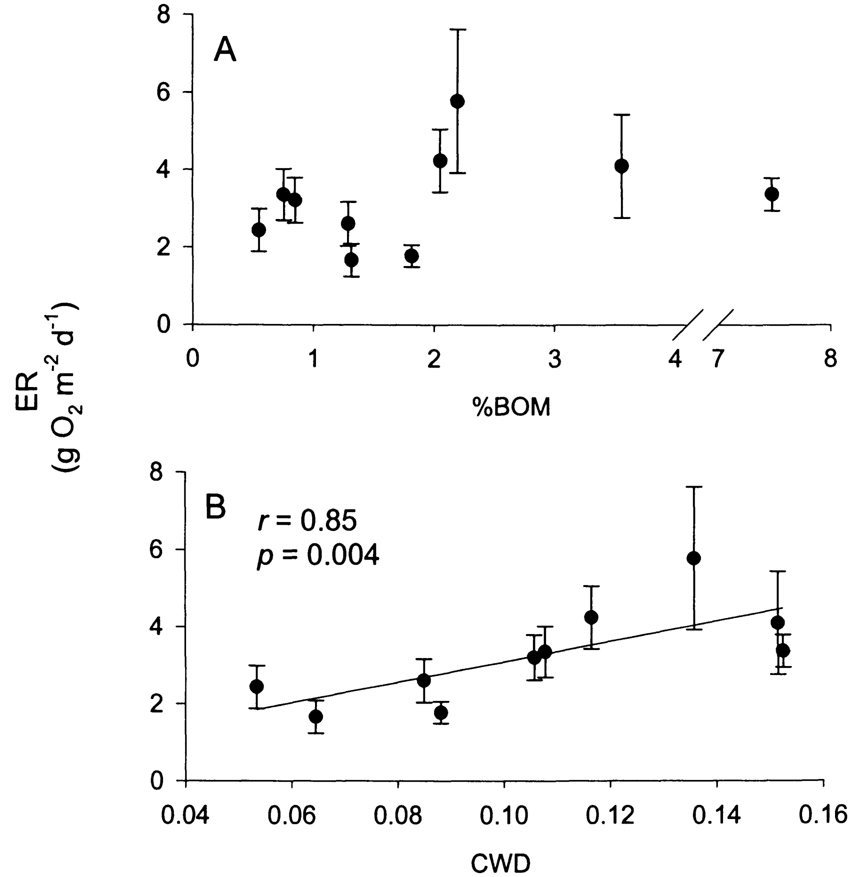

FIG. 7. Relationship between ecosystem respiration rate (ER) and % benthic organic matter (%BOM) (A) and coarse woody debris (CWD) (B).

body of work documenting the effects of catchment land use and disturbance on stream structure and function (e.g., Lowrance et al. 1984, Richards et al. 1996, Allan et al. 1997, Bunn et al. 1999, Huryn et al. 2002, Quist et al. 2003, Strayer et al. 2003). Much of this work has focused on measures of stream status such as nutrient concentrations, biotic communities (e.g., fish and macrophytes), and physical habitat variables (Richards et al. 1996, Huryn et al. 2002, Quist et al. 2003, Strayer et al. 2003). Few studies have focused on the effects of catchment land use and disturbance on biological processes such as ER and GPP (e.g., Bunn et al. 1999, our study), and rates of litter breakdown (Gessner and Chauvet 2002). We showed that disturbances to upland vegetation and soils, even when limited in its areal extent, can negatively affect the rate of biological processes in streams. The effect of upland disturbance on ER in these streams suggests that the generally intact riparian zones of these streams were not sufficient to protect them from the effects of upland disturbance. This result emphasizes the role of the entire catchment in affecting stream structure and function.

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