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Recovery of stream ecosystem metabolism from historical agriculture

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Abstract. Agriculture has influenced southern Appalachian streams for centuries, but recent socioeconomic trends in the region have led to extensive reforestation of agricultural land. Stream ecosystem metabolism might recover from agricultural influence as watersheds undergo reforestation, particularly when shade from terrestrial vegetation is restored. We determined historical (1950) and current (1993) forest cover in 2nd- and 3rd-order watersheds in 4 counties of the southern Appalachians using a geographic information system. Streams were placed into landuse categories based on % forested land cover in watersheds and riparian zones. Categories included forested (FOR; >98% forested) and 3 levels of agriculture (AG; ranging from 95% forest to <60% forest) with no change in % forest over the past 50 y, and 2 levels of recovery from agriculture (REC) indicated by reforestation after land abandonment. We selected 3 streams from each category and measured gross primary production (GPP) and 24-h respiration (R_{24}) using a 2-station diurnal O_2 change technique and gas releases to determine reaeration rates. We calculated net ecosystem production (NEP) and the ratio of GPP to R_{24} (P/R) to compare ecosystem energetics among landuse categories. We measured nutrient concentrations, photosynthetically active radiation (PAR), temperature (degree-days), suspended particle concentrations, and benthic algae (chlorophyll *a* and ash-free dry mass) to determine if these factors were affected by current or historical agriculture and were correlated with metabolism. Concentrations of inorganic nutrients, PAR, degree-days, suspended solids, and benthic algae were significantly higher in AG streams than in FOR streams. Nutrient and suspended solid concentrations also were higher in REC than in FOR streams, but PAR, degree-days, and benthic algae were similar in REC and FOR streams. GPP varied from <0.1 g O_2 m^{-2} d^{-1} in FOR streams to 1.0 g O_2 m^{-2} d^{-1} in AG streams. GPP was similar in REC and FOR streams, suggesting that shading caused by reforestation might reduce GPP to pre-agricultural levels. R_{24} was 4 to 20× greater than GPP in all stream types, resulting in highly negative NEP. NEP was less negative in AG streams than in FOR and REC streams. Negative NEP and P/R consistently <1 could have been caused by allochthonous organic matter from remnant forested land (up to 75% forested) in agricultural watersheds. GPP and P/R were strongly correlated with PAR, degree-days, and algal biomass, suggesting that reduced light limited primary production in the streams studied. R_{24} was positively correlated with nutrient concentrations. Shading caused by reforestation appears to be an important mechanism by which stream metabolism recovers from historical agriculture. Our results provide support for stream restoration efforts focused on developing and maintaining streamside forests.

Key words: primary production, respiration, light, nutrients, algae, agriculture, resilience, southern Appalachians.

Streams are intimately linked to their watersheds through fluxes of chemicals and water moderated by terrestrial vegetation (Hynes 1975). Light, nutrient, and organic matter supplies are strongly influenced by streamside vegetation (Sweeney 1993) and combine to influence instream organic matter processes. In particular, light and nutrients influence primary production, whereas nutrients and detritus input affect respiration. Metabolism in forested streams is generally heterotrophic (i.e., dominated by respiration with little primary production) because of shading and allochthonous inputs (Fisher and Likens 1973, Webster et al. 1995, Mulholland et al. 2001).

Humans have altered watersheds dramatically in forested biomes by removing terrestrial vegetation for agriculture and other land uses. Removal of vegetation has resulted in higher light inputs, increased temperatures, and reduced allochthonous C supply to stream ecosystems. In addition, agriculture often results in

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increased nutrient and sediment inputs to streams (Karr and Schlosser 1978, Lowrance et al. 1985, Waters 1995). The combination of higher light and nutrient availability may lead to high rates of primary production in agricultural streams and a subsequent shift in net metabolism to autotrophy (Brown and King 1987, Bunn et al. 1999, Young and Huryn 1999). In contrast, suspended sediment in agricultural streams may limit primary production by reducing the amount of light that reaches the stream bottom (Young and Huryn 1996) or by scouring algae from the surfaces of rocks (Horner et al. 1990). In addition, deposited sediment may provide inhospitable substrate for attached algae (Waters 1995) and reduce primary production in agricultural streams despite elevated light and nutrient availability.

Streams generally are regarded as resilient ecosystems (i.e., they recover quickly following disturbance; Webster and Patten 1979). However, after watershed-level disturbances such as logging or agriculture cease, recovery by terrestrial vegetation must precede recovery of stream conditions (Webster and Patten 1979, Gurtz et al. 1980, Valett et al. 2002). Changes in some stream attributes caused by watershed disturbance can be extremely long lasting and can persist after terrestrial areas revegetate. Streams in clear-cut logged watersheds show little recovery of water chemistry, wood input, and physical structure over decades, whereas other ecosystem properties (e.g., light inputs, quantity of allochthonous input) recover within a few years (Webster et al. 1992). Reforestation reestablishes shade and allochthonous inputs following logging (Webster et al. 1983). However, stream nutrients may remain elevated (Vitousek and Reiners 1975, Swank and Vose 1997), and the quality of allochthonous input is altered because of changes in tree species composition (Webster et al. 1983).

The influence of agriculture may last longer than the influence of logging because agricultural disturbance occurs over periods of decades or centuries rather than over the much shorter, discrete time frame of logging disturbance. Furthermore, reforestation of agricultural land is slow compared to postlogging reforestation because of the soil disturbance (e.g., compaction, erosion) caused by agriculture and because of limited recolonization by trees (Myster and Pickett 1994, Honnay et al. 1999). Thus, conversion of land from forest to agriculture acts as a press disturbance (sensu Bender et al. 1984) to streams that drain the disturbed watersheds. In comparison, logging can be thought of as a pulse disturbance (Bender et al. 1984), at least with respect to the forest. Old-field succession takes much longer than reforestation from logging (Foster 1992), so it is reasonable to predict that the influences of agriculture on streams will persist longer than the effects of clear-cut logging. The legacy of agriculture can affect biological community structure in streams (Harding et al. 1998) and might influence ecosystem metabolism as well.

In the southern Appalachians, large areas of historically agricultural land are undergoing reforestation as a result of socioeconomic changes in the region (Otto 1983, Clark 1984, Wear and Bolstad 1998). These changes provide an opportunity to study recovery of agricultural stream ecosystems during natural reforestation of their watersheds. We assessed effects of present and past agriculture on stream ecosystem metabolism using a comparative approach. Our objectives were to compare rates of gross primary production (GPP) and ecosystem respiration (R_{24}) among streams with different landuse patterns, determine how physical and chemical factors (e.g., nutrients, light, suspended sediment loads) are related to land use, and assess how these stream characteristics might influence metabolism. We addressed recovery from agriculture by comparing metabolism in streams with watersheds undergoing reforestation after historical agriculture with metabolism in streams in undisturbed forested watersheds and streams with watersheds currently being used for agriculture.

Methods

Study sites

The study streams (2nd and 3rd order) were in the Blue Ridge Physiographic Province in the southern Appalachian mountains of western North Carolina and southwestern Virginia, USA (Fig. 1). Headwater streams in the region are typically slightly acidic and have low conductivity reflecting granitic and micaceous parent lithology (Simmons and Heath 1979). Forests in the region are maturing 2nd-growth forests (logged ~75–100 y ago) and are dominated by oak (*Quercus* spp.), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*), with an understory of *Rhododendron*, mountain laurel (*Kalmia latifolia*), and dogwood (*Cornus florida*). Agricultural activity across the region is mainly cattle pasture with some row crops (primarily tobacco and corn), and fruit and vegetable farming appear to be increasing. Agriculture usually occurs in bottomland along streams, but many farmers have upland pastures. Riparian zones along agricultural streams often lack woody vegetation entirely or are vegetated with a narrow strip of trees, particularly black walnut (*Juglans nigra*), sycamore (*Platanus occidentalis*), black locust (*Robinia pseudoacacia*), red maple, and oak (Neatrour et al. 2004).

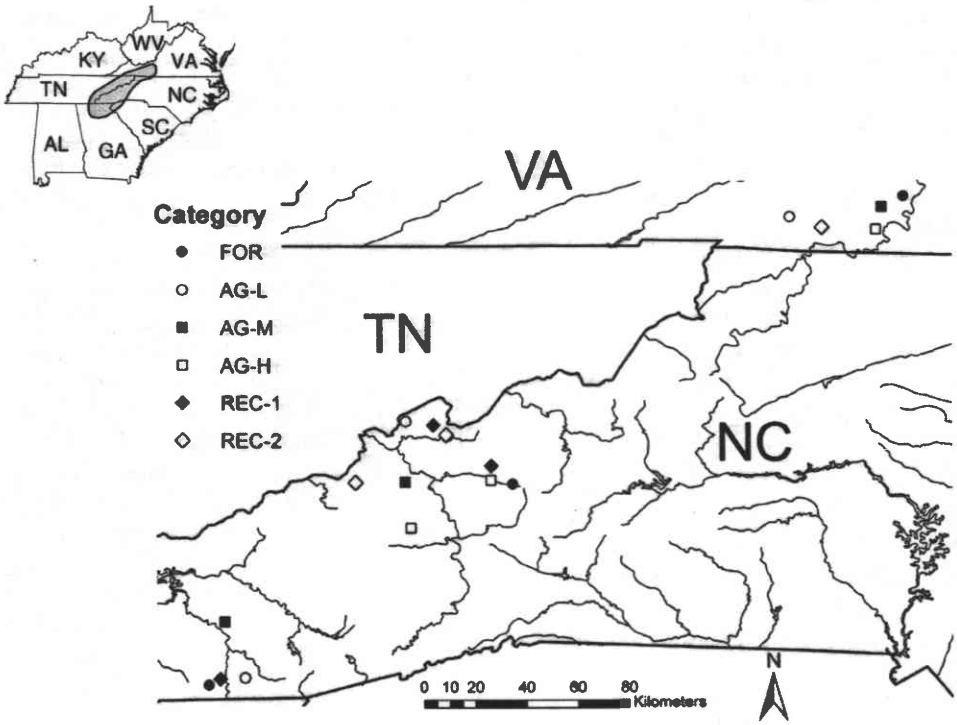

Fig. 1. Locations of study sites in the southern Appalachian region (gray area on inset). Sites are coded by landuse category. Landuse categories are defined in Table 1. AL = Alabama, GA = Georgia, KY = Kentucky, NC = North Carolina, SC = South Carolina, TN = Tennessee, VA = Virginia, WV = West Virginia.

Landuse categorization and stream selection

We used a chronosequence of landuse patterns to categorize streams based on present and past agricultural activity in their watersheds. The particular spatial distribution of land use in watersheds influences stream biota and ecosystem processes (e.g., Allan et al. 1997, Sponseller and Benfield 2001), making the appropriate scale for evaluating human effects on streams difficult to choose. Adding temporal variation can make these scalar influences on streams even more complicated. Therefore, we used a categorical approach to avoid these complications while still considering the history of human activity on the landscape. We prepared a database of past land use (% forest cover in 1950) and more recent land use (% forest cover in 1993) for watersheds in the southern Appalachians using a geographic information system (GIS). We obtained landuse data and watershed boundaries for 4 counties: Grayson County, Virginia, and Buncombe, Macon, and Madison Counties, North Carolina. We delineated watershed boundaries and 100-m-wide riparian corridors for streams (i.e., 50 m to each side of the stream) in each watershed for the entire stream length. We determined % forest cover for each watershed and associated riparian corridor by overlaying these spatial zones on a land-cover map from each year and quantifying % forest cover.

We selected watersheds with areas between 500 and 3000 ha and stream-outlet elevations between 600 and 1000 m above sea level (asl) to help standardize potentially confounding factors (i.e., stream size, slope, elevation). These restrictions reduced the number of possible watersheds to ~500. We grouped these 500 watersheds into 6 landuse categories based on historical and current amounts of forest in their watersheds. We chose 4 categories to represent a gradient of extant agriculture in watersheds with virtually no change in land use over time (forest watersheds: >98% forest [FOR]; agricultural watersheds: 90–95% forest [AG-L], 70–80% forest [AG-M], <60% forest [AG-H]) and 2 categories to represent different stages of watershed recovery from agriculture by reforestation (recovery watersheds: <60% forest in 1950 to >80% forest in 1993 [REC-1], <75% forest in 1950 to >90% forest in 1993 [REC-2]). REC-2 watersheds have shown the largest increase in forest cover over the past 50 y. REC-1 watersheds have undergone considerable reforestation (>20%) over the past 50 y, but they have less current forest cover than REC-2 watersheds, and, therefore, we

regarded them as being in an earlier stage of recovery than REC-2 watersheds. We used % forest cover in riparian corridors to verify category assignments, and streams with riparian-scale % forest cover that was dramatically different than watershed-scale % forest cover were not considered for our study. We selected study streams ($n = 3$ per category, 18 total) from the pool of candidate streams in each county by visually validating landuse category assignments and considering access to sampling locations, land-owner cooperation, and distribution across the region. After selecting the streams, we refined the landuse analysis to quantify % forest in 4 spatial zones (whole watershed, 100-m riparian corridor, and subcorridors: 100-m riparian corridors 2 and 1 km upstream) upstream of each study reach.

Physical and chemical measurements

We monitored physical and chemical characteristics of the study streams during baseflow conditions every 2 mo from November 2000 to August 2001. We estimated discharge from velocity measured with an electronic flow meter (Marsh–McBirney Flo-Mate; Marsh–McBirney, Frederick, Maryland) and cross-sectional area of the stream channel. We filtered triplicate 1-L water samples through precombusted and weighed glass-fiber filters (Gelman Type AE, 1-μm nominal pore size) for determination of suspended solids. We dried filters to constant mass, and weighed and combusted (550°C for 1 h) them to quantify organic (combustible) and inorganic (ash) suspended material. We collected 3 other water samples, filtered them in the field using presoaked membrane filters (Whatman nylon, 0.45-μm pore size), and froze them before analysis. We analyzed these samples for NO_3-N and soluble reactive P (SRP) using a Dionex DX500 Ion Chromatograph (Dionex Corporation, Sunnydale, California) and NH_4-N using the ortho-phthaldialdehyde fluorometric method (Holmes et al. 1999). We determined total dissolved inorganic N (DIN) as the sum of NO_3-N and NH_4-N. We measured specific conductance bimonthly using a field probe (YSI Model 30/50 conductivity meter; Yellow Spring Instruments, Yellow Springs, Ohio). We measured alkalinity once at the beginning of the study by acid titration (APHA 1998). We monitored temperature at 6-h intervals throughout the study using data loggers (HOBO Temp; Onset Corporation, Bourne, Massachusetts) to calculate cumulative degree days (>0°C).

Algae

We determined epilithic algal biomass on rocks collected in April, June, and August 2001. On each date, we placed 5 rocks from each stream in a cooler on ice for transport to the laboratory, where we scrubbed the upper surface of each rock with a wire brush in water to remove epilithon. We filtered scrubbed material onto precombusted and weighed glass-fiber filters (Gelman type A/E, 1-μm pore size) and cut each filter in half for separate analysis of photosynthetic pigments (chlorophyll *a*) and ash-free dry mass (AFDM). We measured chlorophyll *a* using a procedure similar to that outlined by Steinman and Lamberti (1996). We extracted chlorophyll *a* from each rock in 90% basic acetone for 20 h. After extraction, we measured absorbance at 750, 664, and 665 nm before and after acidification with 1N HCl on a Shimadzu UV-1601 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan). We determined epilithic organic standing stock by drying filters to constant mass, then combusting, rewetting, redrying to constant mass, and reweighing them to determine AFDM. We determined the area scrubbed on each rock by wrapping the upper surface of each rock in aluminum foil, weighing the foil, and using a mass–area conversion.

Metabolism

During summer 2001, we measured whole-stream metabolism once at each site using the open-system 2-station diurnal O_2 change method (Odum 1956, Marzolf et al. 1994). We recorded dissolved O_2 concentration and temperature at 5-min intervals over 24 h at 2 stations in each stream using Hydrolab sondes (Hydrolab Minisonde 4a; Hydrolab–Hach Company, Loveland, Colorado). We calibrated O_2 probes in water-saturated air at each site immediately before deployment. To correct for differences in calibration and probe drift, we placed probes together for 30 to 60 min at the beginning and end of each 24-h measurement period. Recording stations were 200 m apart in each stream. We secured sondes to the stream bottom in well-mixed stream segments with the probes pointing into the current at ~½ depth.

We estimated reaeration coefficients (K_2) using injections of volatile gas and conservative tracer at each site. We collected background water samples and made width and depth measurements at 50-m intervals along the 200-m study reach. We released volatile gas (sulfur hexafluoride [SF_6]) and conservative tracer (Cl^- or Br^-) at constant rates simultaneously into the stream ≥20 m upstream of the study reach to allow dispersion of solutes before sampling. We released SF_6 in deep runs through 3 bubbling air stones to maximize contact between gas and water, and we released Cl^- or Br^- using a fluid-metering pump (Fluid Metering, Incorporated, Syossett, New York) into a constrained riffle to

optimize mixing. We released gas and tracer for ≥3× the reach travel time (t) to reach steady-state (plateau) solute concentrations (Genereux and Hemond 1992, Marzolf et al. 1994). On the day before metabolism measurements were made, we determined t by releasing a slug of NaCl upstream of the study reach, recording conductivity as the slug passed upstream and downstream stations, and calculating the time for the slug to pass through the reach. We estimated water velocity through the reach by dividing reach distance by t (range: 20–50 min). We collected triplicate water samples every 50 m along the study reach after the stream reached plateau to determine concentrations of gas and tracer. We obtained gas samples by collecting 45 mL of stream water in a 60-mL syringe, adding 15 mL of atmospheric air (away from the sampling reach to avoid SF_6 contamination), and shaking for 10 min to equilibrate SF_6 in the headspace. We then injected the headspace into 15-mL evacuated, air-sealed glass vials. We quantified SF_6 with an SRI-8610 Gas Chromatograph (SRI Instruments, Torrance, California) equipped with an electron-capture detector. We filtered water samples for tracer analysis through Whatman nylon filters (0.45-μm pore size) and placed the samples on ice for transport to the laboratory where we measured Cl^- or Br^- using ion chromatography. We calculated K_2 for each stream using the method and equations of Wanninkhof et al. (1990) and Wanninkhof (1992). We converted K_2 values from ambient stream temperature to standard temperature (20°C) for comparison among sites (Elmore and West 1961).

We determined the change in dissolved O_2 (ΔDO) over each 200-m study reach by subtracting the O_2 concentration at the downstream site at time ($t_0 + t$) from the O_2 concentration at the upstream site at time t_0. We used O_2 saturation deficit and K_2 to correct ΔDO values for the flux of O_2 resulting from reaeration (Marzolf et al. 1994, Young and Huryn 1998). The saturation deficit was defined as the difference between measured O_2 values and equilibrium concentrations at ambient streamwater temperature and barometric pressure. We measured barometric pressure continuously using a Vaisala pressure transmitter equipped with a Campbell data logger (Campbell Scientific, Logan, Utah). We measured photosynthetically active radiation (PAR) continuously at the stream surface of each study site using a LI-COR quantum sensor (LI-COR Biosciences, Lincoln, Nebraska) and the Campbell data logger. We calculated discharge from velocity, width, and depth measurements at the upstream and downstream ends of the 200-m reaches. Discharge was nearly identical at upstream and downstream ends of each study reach, suggesting that the influence of groundwater and tributaries on ΔDO was negligible.

From the resulting reaeration-corrected ΔDO, we calculated GPP and R_{24} following Marzolf et al. (1994). We calculated GPP by integrating the reaeration-corrected ΔDO curve from dawn to dusk (times determined from PAR measurements). We calculated R_{24} by integrating the reaeration-corrected ΔDO from midnight to midnight using a linear change of ΔDO from dawn to dusk to estimate daytime R. We converted GPP and R_{24} to area estimates by dividing by mean depth along the reach. We used GPP and R_{24} to calculate net ecosystem production (NEP = GPP − R_{24}) and the ratio of GPP:R_{24} (P/R).

Statistical analysis

We used 1-way analysis of variance (ANOVA) to compare differences in metabolic variables among landuse categories with streams as replicates. Physical and chemical variables, chlorophyll *a*, and epilithic AFDM were compared using repeated-measures (RM) ANOVA with landuse categories as factors and streams as replicates. To explore factors controlling metabolism, we correlated metabolic parameters with physical and chemical variables, chlorophyll *a*, and epilithic AFDM using Pearson product-moment correlation. We tested all variables for normality prior to analysis and transformed them if necessary.

Results

Landuse patterns

In general, % forest cover was higher at broader spatial scales (watershed and riparian corridor) than at subcorridor scales within landuse categories (Table 1). In addition, % forest cover at all spatial scales was higher in 1993 than in 1950 in most landuse categories. However, reforestation was more extensive around streams in the REC landuse categories than in AG landuse categories. REC-1 and REC-2 watersheds had similar amounts of forest at the watershed scale, but streams in REC-2 watersheds had more extensively forested riparian corridors than did streams in REC-1 watersheds (Table 1). Watersheds in both categories had undergone extensive reforestation at all spatial scales, providing the potential for recovery of stream processes from historical agriculture. In AG watersheds, agriculture was found predominantly along the stream near sampling locations. However, some watersheds had extensive pasture in the uplands with more forested riparian zones.

Physicochemical variables

Stream elevation varied from 576 to 861 m asl and tended to be lower for AG than for FOR or REC

TABLE 1. Mean (±1 SE) historical and current % forest cover at different spatial scales (WS = whole watershed, RIP = 100-m-wide riparian corridor) and extents for 3 streams in each of 6 landuse categories: watersheds with >98% forest (FOR); watersheds with current agricultural land use (90–95% forest [AG-L], 70–80% forest [AG-M], <60% forest [AG-H]); and watersheds recovering from agriculture (<60% forest in 1950 to >80% forest in 1993 [REC-1], <75% forest in 1950 to >90% forest in 1993 [REC-2]). Percent forest cover of watersheds in FOR and AG categories has remained constant since 1950. Watersheds in REC categories are in different stages of reforestation; $n = 3$ streams in each landuse category.

Spatial scale	Year	FOR	AG-L	AG-M	AG-H	REC-1	REC-2
Watershed	1950	99.8 ± 0.2	87.8 ± 5.4	64.8 ± 9.8	58.1 ± 9.9	83.2 ± 5.3	73.2 ± 13.1
Watershed	1993	99.8 ± 0.1	94.6 ± 3.4	86.4 ± 3.9	81.1 ± 4.5	95.7 ± 0.9	93.7 ± 1.3
RIP, whole stream	1950	100.0 ± 0.0	87.4 ± 4.3	52.1 ± 9.1	34.2 ± 1.6	60.8 ± 11.0	69.6 ± 10.7
RIP, whole stream	1993	99.8 ± 0.2	97.1 ± 1.2	78.8 ± 5.1	63.1 ± 0.8	85.4 ± 4.3	93.2 ± 3.3
RIP, 2 km upstream	1950	100.0 ± 0.0	73.9 ± 6.3	19.6 ± 5.2	10.8 ± 10.4	41.8 ± 16.3	66.5 ± 9.2
RIP, 2 km upstream	1993	95.4 ± 3.7	87.5 ± 5.2	53.9 ± 3.2	27.4 ± 13.3	75.0 ± 6.6	90.1 ± 2.2
RIP, 1 km upstream	1950	100.0 ± 0.0	43.2 ± 12.2	18.7 ± 1.2	7.6 ± 6.1	29.5 ± 16.5	58.2 ± 10.5
RIP, 1 km upstream	1993	96.1 ± 2.1	68.9 ± 19.0	43.0 ± 6.2	17.6 ± 12.9	64.0 ± 6.1	83.6 ± 6.6

streams, but differences were not significant among streams in different landuse categories (Table 2). AG-M streams had the largest watershed areas, and REC-2 streams had the smallest watershed areas (ANOVA, $p < 0.001$); however, discharge at the time of sampling did not vary significantly among streams in different landuse categories. Specific conductance varied from 11.9 to 98.4 μS/cm among all streams and was highest in AG-L streams (ANOVA, $p = 0.011$). Alkalinity was slightly higher in AG-M, AG-H, and REC-1 than in streams in other landuse categories (ANOVA, $p = 0.031$), but mean values were generally low, ranging from 5.3 to 11.7 mg $CaCO_3$/L among streams in all landuse categories (Table 2).

Nutrient concentrations, PAR, and cumulative degree-days were strongly affected by agricultural land use. DIN was significantly higher in AG-H streams (582 μg/L) than in streams in other landuse categories and was lowest in AG-L and FOR streams (75 μg/L and 100 μg/L, respectively; Fig. 2A). DIN was significantly higher in REC streams than in AG-L and FOR streams. SRP was below or near the analytical detection limit in FOR and AG-L streams (mean < 5 μg/L, detection limit 4 μg/L; Fig. 2B). SRP concentration averaged 12 to 13 μg/L in REC streams and 8 to 9 μg/L in AG-M and AG-H streams, but this difference was not significant. PAR varied from a mean of 0.74 mol m^{-2} d^{-1} at FOR streams to 26.16 mol m^{-2} d^{-1} at AG-H streams (Fig. 2C). PAR was significantly higher at AG-M and AG-H streams than at streams in all other landuse categories, and PAR was higher at AG-L and REC-2 than at FOR streams. Cumulative degree-days were higher in AG-M and AG-H streams than in FOR, AG-L, and REC-2 streams (Fig. 2D).

The quantity and composition of suspended solids

TABLE 2. Mean (range) values for physical and chemical variables in 3 streams in 6 landuse categories. Discharge and conductivity were measured every 2 mo in each stream, and the values reported are means (range) for each stream. $K_{2(20°C)}$ = reaeration coefficient corrected to 20°C. See Table 1 for explanation of landuse categories; $n = 3$ streams in each landuse category.

	Landuse category					
Variable	FOR	AG-L	AG-M	AG-H	REC-1	REC-2
Elevation (m)	776 (693–832)	722 (588–861)	652 (576–762)	719 (671–762)	732 (646–838)	829 (766–861)
Watershed area (ha)	514 (241–922)	1231 (809-1539)	1815 (1551–2033)	1064 (925-1222)	731 (340–982)	333 (321–342)
Discharge (L/s)	73 (59–81)	90 (82–99)	66 (56–86)	70 (49–99)	62 (45–82)	59 (39–73)
Specific conductance (μS/cm)	20.8 (11.9–28.3)	75.0 (45.2–98.4)	31.5 (22.6–36.8)	43.0 (40.8–45.7)	50.0 (32.1–63.3)	65.2 (43.8–82.0)
Alkalinity (mg $CaCO_3$/L)	5.3 (4.9–6.1)	6.7 (4.8–8.3)	11.0 (9.2–12.5)	11.7 (8.4–15.9)	11.7 (8.7–16.2)	9.7 (9.1–10.3)
$K_{2(20°C)}$ (d^{-1})	113.5 (17.7–204.1)	48.2 (23.6–82.5)	46.9 (14.7–88.7)	29.5 (16.0–38.1)	69.8 (25.5–146.2)	86.9 (75.5–108.6)

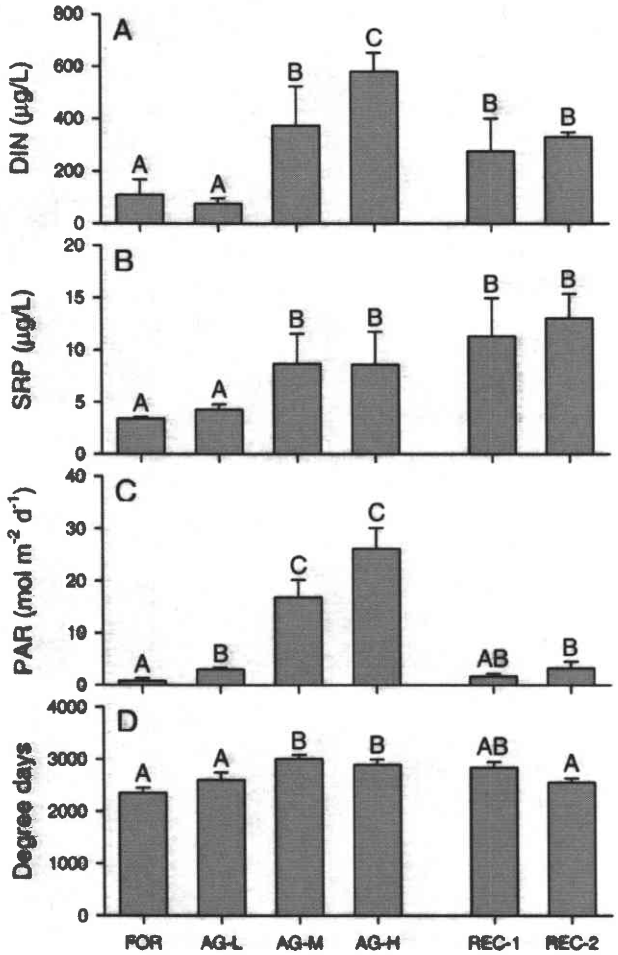

FIG. 2. Mean (+1 SE) dissolved inorganic N (DIN) (A) and soluble reactive P (SRP) (B) concentrations, photosynthetically active radiation (PAR) (C), and cumulative degree-days (days above 0°C from November 2000 to August 2001) (D) in streams in 6 landuse categories. Landuse categories are defined in Table 1. DIN and SRP values for each site were based on samples collected every 2 mo from November 2000 to August 2001. Bars with different letters are significantly different (Tukey's pairwise comparisons, $p < 0.05$); $n = 3$ streams in each landuse category.

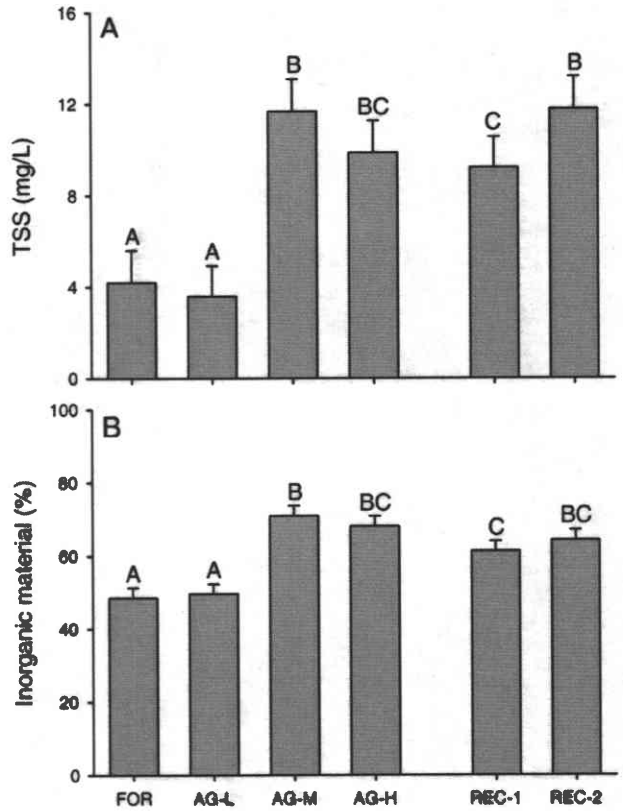

FIG. 3. Mean (+1 SE) total suspended solids (TSS) (A) and inorganic fraction of suspended material (B) in streams in each landuse category. Landuse categories are defined in Table 1. Bars with different letters are significantly different (Tukey's pairwise comparisons, $p < 0.05$); $n = 3$ streams in each landuse category.

differed among landuse categories. Total suspended solids (TSS) were lowest in FOR and AG-L streams and highest in AG-M and REC-2 streams (Fig. 3A). REC-1 and REC-2 streams had significantly higher TSS than FOR and AG-L streams. Approximately 50% of suspended material in FOR and AG-L streams and ~75% of suspended material in AG-M and AG-H streams was inorganic (Fig. 3B). Inorganic content of suspended material was higher in REC streams than in FOR and AG-L streams.

Algae and metabolism

$K_{2(20°C)}$ varied from 14.7 to 204.1 d^{-1} among all streams (Table 2). $K_{2(20°C)}$ was highest in FOR streams (113.5 d^{-1}), but values did not vary significantly among landuse categories because of high variability within landuse categories. In general, however, AG streams had lower $K_{2(20°C)}$ values than FOR or REC streams.

Chlorophyll *a* varied from ~2 mg/m^2 in REC-2, FOR, and AG-L sites in August to ~12 mg/m^2 in AG-H sites in June and REC-1 sites in April (Fig. 4A). Chlorophyll *a* values were highest in June in streams in all categories except REC-1. Across seasons, chlorophyll *a* was lower in REC-2 and FOR streams than in AG-H and REC-1 streams. Epilithic AFDM was generally highest in April and declined throughout the summer in streams in all landuse categories except AG-H (Fig. 4B). Epilithic AFDM was significantly higher in AG-H streams than in streams in any other

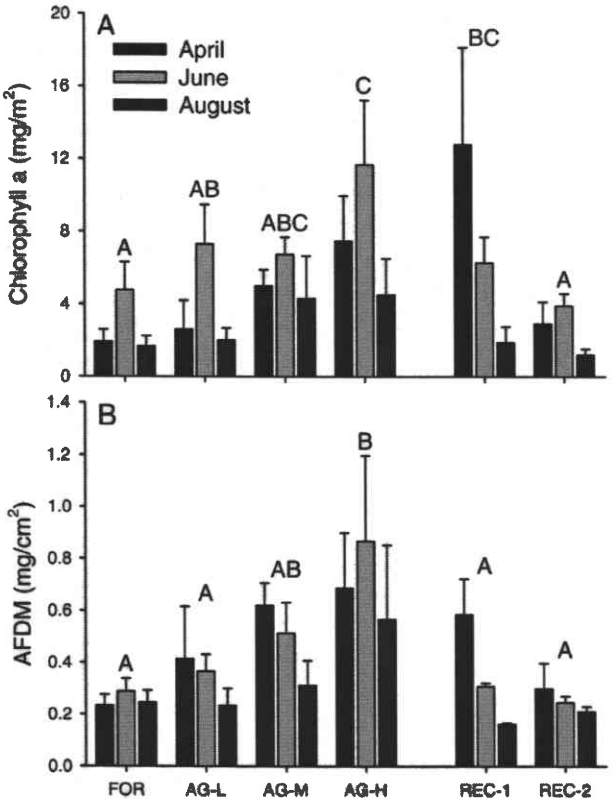

FIG. 4. Mean (+1 SE) chlorophyll *a* (A) and algal biomass (ash-free dry mass [AFDM]) (B) of epilithon on rocks collected from stream in each landuse category during 3 sampling periods. Landuse categories are defined in Table 1. Groups of bars with different letters are significantly different (Tukey's pairwise comparisons of values by landuse category, $p < 0.05$); $n = 3$ streams in each landuse category.

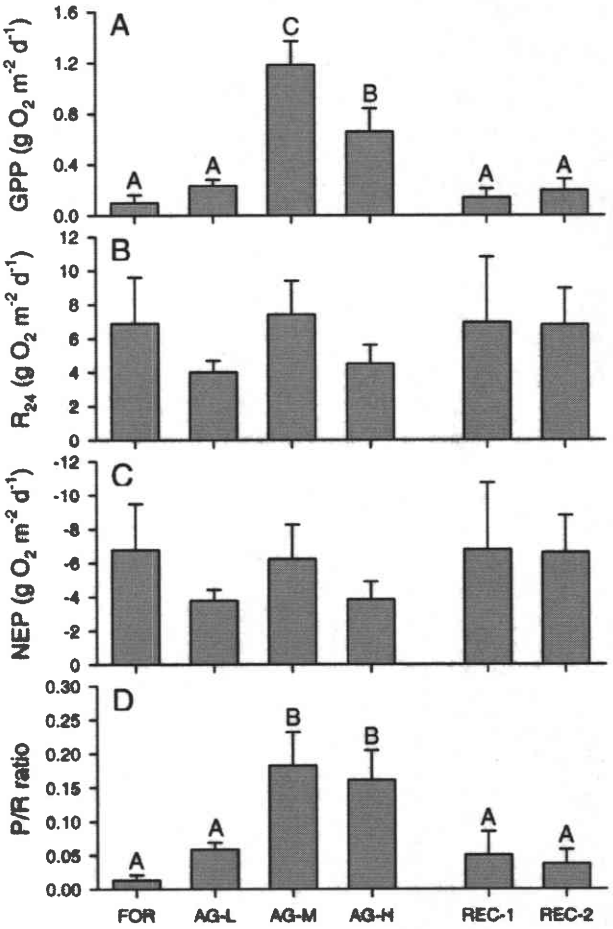

FIG. 5. Mean (+1 SE) daily rates of gross primary production (GPP) (A), ecosystem respiration (R_{24}) (B), net ecosystem production (NEP) (C), and photosynthesis/respiration (P/R) ratio (D) in streams in each landuse category. Landuse categories are defined in Table 1. Bars with different letters are significantly different (Tukey's pairwise comparisons, $p < 0.05$); $n = 3$ streams in each landuse category.

landuse category, but epilithic AFDM did not differ among streams in any other categories.

Metabolism varied greatly among streams within each landuse category. GPP was significantly higher in AG-M and AG-H streams (1.19 ± 0.19 and 0.66 ± 0.18 g O_2 m^{-2} d^{-1}, respectively) than in streams in all other categories, where rates varied from 0.10 to 0.23 g O_2 m^{-2} d^{-1} (Fig. 5A). GPP in REC-1 and REC-2 streams was similar to GPP in FOR and AG-L streams. R_{24} varied from ~4.0 to 7.5 g O_2 m^{-2} d^{-1}, was 4 to 40× greater than GPP, and did not differ significantly among streams in different landuse categories (Fig. 5B). High R_{24} relative to GPP resulted in negative NEP in all streams with NEP values similar to R_{24} values (Fig. 5C). Like R_{24}, NEP did not vary significantly among landuse categories. Mean P/R varied from 0.013 ± 0.008 in FOR streams to 0.183 ± 0.049 in AG-M streams and was significantly higher in AG-M and AG-H streams than in FOR, AG-L, and REC-2 streams (Fig. 5D).

Physical properties, water chemistry, and algal biomass (chlorophyll *a* and epilithic AFDM) were significantly correlated with metabolism (Table 3). DIN was positively correlated with GPP. SRP was positively correlated with R_{24} and negatively correlated with NEP. PAR and degree-days were both positively correlated with GPP and P/R. Like SRP, TSS was positively correlated with R_{24} but negatively correlated with NEP. Chlorophyll *a* and epilithic AFDM were positively correlated with GPP and P/R.

Table 3. Pearson product–moment correlation coefficients relating physical and chemical variables and algal biomass to metabolism variables. DIN = dissolved inorganic N, SRP = soluble reactive P, PAR = photosynthetically active radiation, TSS = total suspended solids, AFDM = ash-free dry mass, GPP = gross primary production, R_{24} = 24-h respiration, NEP = net ecosystem production, P/R = photosynthesis/respiration. Values in parentheses are p values for significant ($p < 0.05$) correlations ($n = 18$). NS = nonsignificant correlation.

	GPP	R_{24}	NEP	P/R
DIN	0.47 (0.048)	NS	NS	NS
SRP	NS	0.50 (0.034)	–0.52 (0.029)	NS
PAR	0.66 (0.003)	NS	NS	0.73 (0.001)
Degree-days	0.59 (0.009)	NS	NS	0.63 (0.005)
TSS	NS	0.57 (0.014)	–0.52 (0.027)	NS
Chlorophyll *a*	0.74 (0.001)	NS	NS	0.62 (0.007)
Epilithic AFDM	0.60 (0.008)	NS	NS	0.58 (0.012)

Discussion

Influence of agriculture on physical and chemical stream properties

Chemical and physical properties reflected the landuse gradient from forested to agricultural streams. PAR values from AG-H streams were similar to meadow stream reaches in Pennsylvania (Bott et al. 2006b), were as high as those recorded in prairie streams of Kansas (Mulholland et al. 2001), but were not quite as high as values reported for desert streams in Arizona (Mulholland et al. 2001). Thus, altering riparian vegetation through agriculture in a primarily forested region (the southern Appalachians) resulted in light conditions similar to those found in non-forested biomes in North America. PAR and degree-days were higher in AG streams than in FOR and REC streams and were similar between FOR and REC streams, suggesting that these variables recover in response to reforestation. However, several properties of REC streams were more similar to those of AG streams than of FOR streams, reflecting long-term effects of agriculture despite reforestation. DIN and SRP increased with increasing agriculture and were high in REC streams. Logging affects nutrients in a manner similar to agriculture in that nutrients may remain elevated for decades following postlogging reforestation (e.g., Swank and Vose 1997), but light and temperature return to prelogging conditions relatively rapidly (Marks and Bormann 1972, Vitousek and Reiners 1975, Webster et al. 1983).

Increased sediment load to receiving streams has been one of the most commonly reported influences of agricultural land use (Waters 1995). Young and Huryn (1996) showed that organic material in transport contributed to total reach respiration, whereas total suspended material reduced primary production by reducing light available to benthic algae. In our study, baseflow suspended particle concentrations were 3× higher in AG and REC streams than in FOR streams, and suspended material was composed of a higher fraction of inorganic sediment in AG and REC streams than in FOR streams. As a result, suspended inorganic sediment was ~4× higher in AG and REC than in FOR streams. Suspended organic particle concentrations were relatively similar among categories (<2× higher in AG than in FOR streams). Suspended material in AG streams was primarily inorganic; thus, one would expect suspended material in AG streams to reduce GPP but not to affect R_{24}.

Chlorophyll *a* was higher in AG than in FOR streams. We attribute this result to higher nutrient concentrations and PAR in AG than in FOR streams because grazer assemblages were similar in composition and density (McTammany 2004). High algal productivity in agricultural streams is associated with high light intensity and nutrient concentrations (Corkum 1996), and algal growth in the absence of light limitation has been strongly correlated with nutrient concentrations (Lohman et al. 1992, Mosisch et al. 2001). Chlorophyll *a* was ~3× higher in AG than in FOR streams in our study, but even the highest chlorophyll *a* values in our AG streams (~10 mg/m^2) were much lower than chlorophyll *a* values reported for some forested streams in the southern Appalachians (Walker Branch, Tennessee: 52–93 mg/m^2; White Oak Creek, Tennessee: 13–51 mg/m^2; Hill and Dimick 2002). Algal biomass was low in REC-1 streams relative to AG-H streams, a result that suggests that increased shading as a consequence of reforestation in REC watersheds may reduce PAR and algal growth. REC-1 streams exhibited the strongest seasonal trend in both chlorophyll *a* and AFDM. From April to August, algal biomass (chlorophyll *a* and AFDM) declined by ⅔ in REC-1 streams. This decrease corresponded to the transition from open winter canopies to closed summer canopies, and algal

biomass generally decreases over this period in forested streams (Hill et al. 2001).

If light limitation associated with canopy closure causes lower algal biomass in forested streams, then AG-M and AG-H streams should have had much higher algal biomass than FOR streams, particularly during summer. In general, AG streams did have higher algal biomass than FOR streams in each month, but differences were not greatest during summer months. Instead, the largest differences occurred during April. Thus, reductions in light following leaf emergence above forested streams may not limit algal growth relative to growth in agricultural streams. Other factors in AG streams may have been limiting algal growth and may have kept algal biomass low despite high light availability.

$K_{2(20°C)}$ values describe the propensity for gas exchange and reflect the physical interaction of flowing water with the stream channel (depth, velocity, slope, turbulence). $K_{2(20°C)}$ was positively correlated with site elevation and negatively correlated with watershed area and discharge. Small streams with high elevation and small watershed area tended to have steeper slopes, and these features probably contributed to higher $K_{2(20°C)}$ values. However, elevation, discharge, and $K_{2(20°C)}$ values did not differ among landuse categories. Metabolism estimates can be particularly sensitive to reaeration rates and the method used to determine reaeration (Wilcock 1982, McCutchan et al. 1998, Young and Huryn 1999). Making precise estimates of metabolism in streams with $K_{2(20°C)} > 100\ d^{-1}$ generally requires high R_{24} (McCutchan et al. 1998). $K_{2(20°C)}$ was $>100\ d^{-1}$ in only 4 streams, all from different landuse categories, suggesting that we can be relatively confident in our estimates of metabolism and in our comparisons among stream types.

Landuse effects on ecosystem metabolism

Reductions in % forest cover as a result of agriculture affected stream ecosystem metabolism by increasing GPP, but did not cause changes in R_{24}. GPP was nearly 0 in FOR streams and was highest in AG-M streams. AG-H streams had higher GPP than FOR streams but significantly lower GPP than AG-M streams. AG-H streams had the highest nutrient concentrations, PAR, and algal biomass, so we expected these streams to have the highest GPP. In fact, strong correlations between PAR, chlorophyll *a*, and GPP were evident among all study streams, but lower GPP in AG-H than in AG-M streams did not fit this trend. Young and Huryn (1999) suggested that canyon shading caused by channel incision in tussock grassland streams in New Zealand could reduce light and limit GPP. In addition, suspended particles reduce light reaching benthic algae in streams and may reduce GPP (Brown and King 1987, Wiley et al. 1990, Young and Huryn 1996). PAR and TSS data from our study do not support either of these possibilities as explanations for higher GPP in AG-M than in AG-H streams because PAR and TSS were similar in these 2 stream types. Intense agriculture may alter GPP by introducing toxic chemicals to streams and fine sediment to the stream bottom, changing particle size (Brown and King 1987). Many common herbicides are toxic to periphyton (Fairchild et al. 1998) and may reduce primary production in streams (Bott et al. 2006a), but their presence and effects on stream metabolism in our study are uncertain. Agriculture around our study sites was primarily pastures with limited row crops, so application of herbicides and pesticides was probably quite low in the watersheds. Increased sediment loads from agriculture were more likely to have affected stream metabolism in our study. Fine substrate generally supports lower algal standing crop (Dodds et al. 1996) and may scour larger particles when moved by storms, resulting in lower GPP in streams with shifting benthic substrate than in streams with stable substrates (Biggs et al. 1999). Inorganic sediment from watershed disturbances has been shown to negatively affect GPP during spring (when light is most abundant) in forested streams in Georgia (Houser et al. 2005). Higher GPP has also been associated with increased proportions of coarse substrates (cobble and boulder) in streams after accounting for the effect of PAR (Bott et al. 2006a). In our study, median particle size was lower and % fine sediment was higher in AG-H than AG-M streams (McTammany 2004), and this may have resulted in lower GPP in AG-H than AG-M streams despite higher PAR and nutrient concentrations. Moreover, comparisons of algal biomass among landuse categories were based on data from small cobbles, a substrate type that was less common in AG-H streams than in AG-M streams. This disparity may have influenced the outcome of scaling algal biomass to whole reaches to generate predictions for reach-scale GPP. Thus, sampling should include measurements of algae on different substrate types when making reach-scale estimates of GPP.

GPP in REC streams was similar to GPP in FOR and AG-L streams, probably because of light limitation from reforestation. GPP was strongly correlated with light availability (indicated by PAR and degree days) and was only weakly correlated with DIN in our study. Nutrient concentrations were higher in REC streams than in FOR streams, but canopy closure was

evident at all REC streams. Primary production in streams returns rapidly to normally low values in response to reforestation following clear-cutting despite persistent elevated nutrient concentrations (Webster et al. 1983). Furthermore, primary production decreases at the same time that nutrient concentrations increase during canopy closure from spring to summer in southern forested streams (Hill et al. 2001). Moreover, nutrients stimulate GPP in streams only in conditions where light is not limiting (Lowe et al. 1986, Hill et al. 1992). In a broad survey of streams, PAR explained 72% of the variation in GPP across North American stream ecosystems, whereas P concentration explained only an additional 18% (Mulholland et al. 2001). In our study, DIN was weakly correlated with GPP and including DIN did not improve regression models using PAR to predict GPP.

Unlike its influence on GPP, agriculture did not seem to affect R_{24} in our study. Some studies have suggested that respiration increases with agricultural activity in watersheds (King and Cummins 1989, Bunn et al. 1999). However, other studies have shown no increase or a decrease in respiration with agricultural activity (Young and Huryn 1999) and other watershed disturbances (Houser et al. 2005). Metabolism of forested southern Appalachian streams is dominated by respiration because light may limit primary production and allochthonous input is high (Webster et al. 1997), so high R_{24} may be the normal condition rather than a response to stress at the ecosystem level. In general, GPP appears to be more sensitive than R_{24} to differences in light regime (Mulholland et al. 2001), and removal of riparian vegetation appears to alter GPP more strongly than R_{24} (Bunn et al. 1999). R_{24} may not be affected by changing land use because loss of leaves is compensated by autotrophic respiration and respiration of autotrophic material. However, no mechanism exists to compensate for the changes in GPP caused by altering land use.

For all streams in our study, R_{24} was $\gg$GPP, resulting in negative NEP and P/R values $\ll$1.0. Agriculture did not appear to cause significant changes in NEP, most likely because R_{24} was 4 to 40× higher than GPP and dominated metabolism. Despite little change in NEP, streams with higher GPP had higher P/R values. At broader scales, stream P/R should reflect changing terrestrial–aquatic interactions. Vannote et al. (1980) predicted increases in P/R with distance downstream because increasingly open forest canopy in the downstream direction allows light to reach the stream and enhances GPP. However, Minshall et al. (1985) suggested that human activity in watersheds might cause higher P/R in lower-order streams than predicted by downstream distance or stream order. In our study, P/R was higher in small (2nd- and 3rd-order) AG streams than in small FOR or REC streams, supporting the assertion that land clearing alters typical longitudinal patterns of stream metabolism. However, the increase in P/R attributable to agriculture (i.e., from 0.01 in FOR streams to 0.22 in AG-M streams) in our study was not as dramatic as the increase observed in larger rivers (i.e., from 0.2 in 4th-order streams to 1.1 in 6th-order streams) in the southern Appalachians (McTammany et al. 2003). In addition, all P/R values were $\ll$1, indicating that even AG streams in our study were highly heterotrophic despite having open canopies. Several studies have found P/R ratios >1 in streams draining land used for various types of agriculture, including row crops (Midwestern USA; Wiley et al. 1990), pastures (New Zealand; Young and Huryn 1999), and arid-land cattle ranches (Australia; Bunn et al. 1999). GPP was 2 to 10× higher in these streams than in the streams in our study, but R_{24} was similar in all 4 studies (Wiley et al. 1990, Bunn et al. 1999, Young and Huryn 1999, our study). However, heterotrophic conditions may be more common among small streams in grasslands (Dodds et al. 1996) and meadows (Bott et al. 2006b) than previously thought.

What features might be limiting GPP in our AG streams relative to GPP in agricultural streams in other regions? The most agricultural watershed in our study was ~50% forested. In contrast, forest constituted only ~5% of the land cover in watersheds of streams draining tussock grassland and pasture in New Zealand (Young and Huryn 1999). Streams in Midwestern USA drained watersheds that were >90% row-crop agriculture (Wiley et al. 1990). Bunn et al. (1999) found higher P/R as canopy cover declined from agriculture and suggested a value of 73% canopy cover as the threshold for normal P/R in Australian streams. In addition, the mountainous terrain surrounding streams in the southern Appalachians may cause shorter photoperiods with subsequently lower GPP and P/R than in open canopy streams in areas with less topographic relief. Clearly, major differences in the baseline energetics of undisturbed streams across biomes affect interpretation of landuse effects on stream metabolism.

Metabolism was correlated with several factors that differed among AG categories. In most cases, those factors that were correlated with GPP and P/R were not correlated with R_{24} and NEP. Light availability seemed to be the main driver of GPP in most streams; however, other factors also may have been important. For example, AG-H streams had the highest PAR but did not have the highest GPP, possibly because of unstable substrate that was unsuitable for algae (Biggs

et al. 1999, Houser et al. 2005). Nutrient availability can limit GPP in streams receiving ample light (Lowe et al. 1986); SRP values were very low in all of our study streams. R_{24} was not correlated with PAR or temperature but was related to concentrations of nutrients and suspended particles. In summary, agriculture in the watersheds of southern Appalachian streams increases GPP and P/R, but leaves NEP dominated by R_{24}. Once agricultural land undergoes reforestation, stream metabolism returns to pre-agriculture levels. Active management of agricultural streams often entails restoring woody riparian vegetation. Our results suggest that such restoration could decrease GPP from the high levels characteristic of agricultural streams to levels seen in forested streams by limiting primary production and providing allochthonous detritus inputs.

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