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PRIMARY RESEARCH PAPER

Shifts in allochthonous input and autochthonous production in streams along an agricultural land-use gradient

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Abstract Relative contributions of allochthonous inputs and autochthonous production vary depending on terrestrial land use and biome. Terrestrially derived organic matter and in-stream primary production were measured in 12 headwater streams along an agricultural land-use gradient. Streams were examined to see how carbon (C) supply shifts from forested streams receiving primarily terrestrially derived C to agricultural streams, which may rely primarily on C derived from algal productivity. We measured allochthonous input, chlorophyll *a* concentration, and periphyton biomass in each stream, and whole-stream metabolism in six streams. Our results suggest a threshold between moderate- and heavy-agriculture land uses in which terrestrially derived C is replaced by in-stream algal productivity as the primary C source for aquatic consumers. A shift from allochthonous to autochthonous production was not evident in all heavy-agriculture streams, and only occurred in heavy-agriculture streams not impacted by livestock grazing. We then compared our findings to rates of allochthonous input and GPP in streams with minimal human influences in multiple biomes to assess how land-use practices influence C sources to stream ecosystems. The proportion of C derived from allochthonous versus autochthonous sources to heavy-agriculture streams was most similar to grassland and desert streams, while C sources to forested, light-, and moderate-agriculture streams were more similar to deciduous and montane coniferous forest streams. We show that C source to streams is dependent on land use, terrestrial biome, and degradation of in-stream conditions. Further, we suggest that within a biome there seems to be a compensation such that total C input is nearly equal whether it is from allochthonous or autochthonous sources.

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Introduction

Stream ecosystems receive energy from two sources: allochthonous inputs, which consist of terrestrially derived carbon (C) that is produced within the catchment and imported into the stream channel (e.g., Kaushik & Hynes, 1971), and autochthonous production, which includes C fixed within the stream channel by algae and macrophytes (e.g., Minshall, 1978). Ecologists have long recognized the importance of allochthonous C as the main energy source for forested stream communities (Fisher & Likens, 1973; Cummins, 1974; Vannote et al., 1980; Wallace et al., 1997b). Heavy shading by riparian vegetation often limits primary production in forested streams; consequently, forested stream food webs tend to be dependent on allochthonous material as an energy base (Webster & Meyer, 1997). Leaf litter generally makes up the largest component (69–80%) of allochthonous organic material entering deciduous forest streams (e.g., Wallace et al., 1995), and the majority of this input occurs during autumnal leaf fall (e.g., Benfield, 1997; Wallace et al., 1997a; Abelho & Graça, 1998).

Catchment land use can alter the overall quantity and relative importance of different sources of C to stream ecosystems (Quinn et al., 1997). For example, changes in catchment land use and riparian vegetation have been shown to influence allochthonous inputs (Benfield, 1997; Scarsbrook et al., 2001) and autochthonous production (Young & Huryn, 1999). Agricultural practices, in particular, are expected to significantly alter C sources to stream ecosystems. Removal of riparian trees not only reduces allochthonous inputs to streams (Delong & Brusven, 1994), but results in more light reaching the stream, potentially increasing primary production (Feminella et al., 1989). These changes to C supply along an agricultural gradient may be analogous to patterns observed along river continua in forested biomes (Minshall et al., 1983).

Streams draining agricultural areas often have higher nitrogen and phosphorus concentrations due to applications of fertilizer to agricultural fields (Cooper, 1993) and urine and manure from grazing livestock (Lemly, 1982; Shimura & Tabuchi, 1994; Quinn, 2000). Elevated nutrient concentrations have been associated with higher algal chlorophyll *a* concentrations (e.g., Delong & Brusven, 1992). On the other hand, Young and Huryn (1996) found that despite high nutrient loads, high sediment loads associated with agricultural land use decreased light availability at the streambed, potentially limiting algal growth. Unstable sediments, common in agricultural streams, may prevent algal establishment as well (Kjeldsen et al., 1996; Young & Huryn, 1996).

Conversion of forest to agriculture may also affect stream function, as higher nutrient loads, reduced shading, increased light input, and warmer temperatures may indirectly result in higher rates of primary productivity, mainly by algae (Young & Huryn, 1996; Bernot et al., 2006). Previous studies show that terrestrial biome (e.g., Mulholland et al., 2001) and land use (Young & Huryn, 1999) have strong effects on stream metabolism. For example, Houser et al. (2005) found a negative correlation between ecosystem respiration and upland soil and vegetation disturbance, but no relationship between gross primary production (GPP) and catchment disturbance. While several studies have compared metabolism along a grassland river continuum (e.g., Young & Huryn, 1996), variation in metabolism along an agricultural land-use gradient has received little attention (but see Fellows et al., 2006; McTammany et al., 2007; Young & Collier, 2009).

Here, we measured allochthonous input and periphyton (chlorophyll *a* and biomass) in 12 streams along an agricultural land-use gradient to examine how C sources to streams vary in response to varying levels of agriculture. Second, we compared annual allochthonous input to GPP in six of these streams to quantify if and where along an agricultural land-use gradient a shift in C sources occurs. Third, we compared our rates of allochthonous input and autochthonous production to reference (minimally influenced by humans) streams in a range of biomes.

Methods

Site description

This study was conducted in the southern Appalachian Mountains in Macon County, North Carolina,

and Rabun County, Georgia, USA. We selected 12 study streams that drain separate tributaries of the upper Little Tennessee River. This region is characterized by forest cover at high elevations and agriculture concentrated in river valleys (SAMAB, 1996). Agricultural land comprises approximately 10% of the upper Little Tennessee River watershed, but over 40% of the land within 30 m of the river channel (McTammany, unpublished data). Due to steep hill slopes and high soil erosion rates, the primary use of agricultural lands in the southern Appalachians is as pasture.

Our 12 study stream reaches ranged from 1st to 4th order and elevation ranged from 613 to 880 m. Study streams were placed into four land-use categories: forested, light agriculture, moderate agriculture, and heavy agriculture. The 12 sites (100-m length reaches) were assigned to land-use categories based on the influence of agriculture (0 = agriculture not present in catchment; 1 = active agriculture present in catchment, no livestock grazing adjacent to stream; 2 = active agriculture in catchment, livestock fenced from stream; 3 = active agriculture in catchment, livestock had historic access to stream; and 4 = active agriculture in catchment, livestock have current access to stream) and the extent of forested riparian zone along each study reach (Table 1). Extent of riparian forest along each stream reach was quantified as riparian tree density (number of trees ha^{-1} within 3 and 10 m of the stream), riparian tree basal area (m^2 ha^{-1} within 3 and 10 m of the stream), % riparian canopy cover, % stream canopy cover, and % grass ground cover (Table 1, methods described in Appendix in Electronic supplementary material).

Principal components analysis (PCA) was used to verify land-use categories using the variables in Table 1 (except for 10-m riparian tree basal area; Hagen et al., 2006). Variables were standardized (mean = 0, SD = 1) and transformed when necessary to meet the assumptions of PCA. Stream scores were plotted on the first two principal component axes, and the plot was examined for clusters of streams. Based on the results of PCA ordination, one stream was reclassified from light agriculture to moderate agriculture, and another was reclassified from moderate agriculture to heavy agriculture, resulting in an unbalanced design (three forested streams, two light-agriculture streams, three moderate-agriculture streams, and four heavy-agriculture streams).

Riparian vegetation along forested streams consisted of deciduous trees dominated by birches (*Betula* spp.), yellow-poplar (*Liriodendron tulipifera* L.), maples (*Acer rubrum* L. and *A. saccharum* Marsh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and a dense understory of rhododendron (*Rhododendron maximum* L.). Dominant riparian vegetation along light-agriculture streams consisted of yellow-poplar, yellow buckeye (*Aesculus octandra* Marsh.), and red maple trees. Riparian vegetation along moderate-agriculture streams was primarily red maple and alder (*Alnus serrulata* (Aiton) Willd.) trees. Riparian vegetation along heavy-agriculture streams was sparse and consisted of alder and sycamore (*Plantanus occidentalis* L.) trees.

Physicochemical variables

We measured stream water chemistry approximately monthly for 1 year (September 2002–September 2003) in each stream. Replicated (3X) water samples were analyzed for NO_3–N, NH_4–N, and soluble reactive P (SRP; methods described by Hagen et al., 2006). We measured dissolved O_2 (DO, mg l^{-1}) and specific conductance (μS cm^{-1}) in each stream using YSI DO and conductivity probes (Model 55 DO probe and Model 30 conductivity probe, Yellow Springs Instruments, Yellow Springs, OH). Stream temperatures were recorded every 4 h from September 2002 to September 2003 using temperature data loggers (HOBO, Pocasset, MA). Percentage silt and % silt plus sand were estimated once for each stream reach during the summer 2003 as described by Hagen et al. (2006). Photosynthetically active radiation (PAR) was measured continuously at four sites, one site in each land-use type, using a Li-COR sensor and Campbell data logger during metabolism measurements (July 2001). Individual PAR measurements were taken every 10 min and used to calculate average daily incident PAR (mol m^{-2} d^{-1}).

Allochthonous input

Allochthonous input to each study stream was measured September 2002 through September 2003 using litter traps consisting of plastic buckets (surface area = 0.066 m^2) anchored approximately 0.5 m above the stream to metal fence posts. Holes drilled into the bottom of the buckets allowed for water

Table 1 Characteristics of each stream site including riparian tree basal area (BA) and tree density (TD) within 3 and 10 m of each stream reach, stream canopy cover (SCC) along each 100-m stream reach, riparian canopy cover (RCC) within 10 m of each stream reach, grass groundcover (GGC) within 10 m of each stream reach, and agricultural influence

Land use	Stream	Stream code	3-m BA (m^2 ha^{-1})	10-m BA (m^2 ha^{-1})	3-m TD (no. trees ha^{-1})	10-m TD (no. trees ha^{-1})	SCC (%)	RCC (%)	GGC (%)	Agricultural influence
Forest	Ball Creek	BAL	47.2	34.8	1251.9	1178.7	39	83	0	0
	Hugh White Creek	HWC	31.8	39.2	1299.0	1620.2	33	86	0	0
	Jones Creek	JON	33.6	36.6	1161.1	1554.1	37	83	0	0
Light agriculture	North Prong Ellijay	ELL	21.6	35.5	586.5	568.4	30	84	6	1
	Tessentee Creek	TES	34.9	15.4	771.9	367.3	27	61	17	1
Moderate agriculture	Dryman Fork	DRY	32.1	1.9	459.7	70.4	25	61	42	2
	North Shope Fork	SHO	30.6	19.7	869.9	448.1	26	80	31	2
	Sutton Branch	SUT	10.7	6.1	692.6	77.2	32	37	29	2
Heavy agriculture	Caler Fork	CAL	4.6	0.3	31.8	62.5	8	13	67	3
	Hoglot Branch	HOG	0.0	0.0	0.0	0.0	1	0	95	4
	North Fork Skeenah Creek	SKE	0.6	0.3	92.1	49.4	7	1	70	2
	Payne Creek	PAY	0.8	0.4	13.7	6.8	2	6	90	4

See text for description of agricultural influence

drainage, and buckets were lined with aluminum screen with 2-mm openings. Ten litter traps were evenly dispersed along each 100-m stream reach. Litter was collected twice per month during heavy leaf fall (September through November) and monthly during the remainder of the study.

Litter was dried to a constant weight and sorted into the following categories: leaves, wood, fruit and flowering parts, and grasses. Samples were weighed, ground, ashed (550°C, 45 min), and reweighed to determine ash-free dry mass (AFDM) for each category. We then converted values for g AFDM to g C using a standard conversion of 1 g C = 2 g AFDM (e.g., Meyer & Edwards, 1990; McTammany et al., 2003).

Metabolism

Whole-stream metabolism was measured once during summer leaf out (July) in six of the study streams using the open-water two-station diel oxygen change technique (Odum, 1956; Marzolf et al., 1994; Bott, 2007) as described by McTammany et al. (2007). We measured dissolved oxygen (DO) concentrations and temperature in each site at upstream and downstream locations at 5-min intervals using calibrated submersible mini-sondes (Hydrolab Minisonde 4A, Hydrolab-Hach Company, Loveland, Colorado) for 48 h. Discharge did not change along the reaches during measurements, so we assumed negligible influence of inflowing water. Atmospheric gas exchange was estimated by sulfur hexafluoride (SF_6) injection. DO change (ΔDO) was then adjusted for flux of O_2 due to gas exchange using O_2 saturation deficit and the atmospheric exchange rate. We calculated GPP by integrating adjusted ΔDO from dawn to dusk and ecosystem respiration (R_E) by integrating corrected ΔDO over nighttime and daytime, assuming linear interpolation of R_E from dawn to dusk. We calculated a P/R ratio (GPP/R_E) to determine the relative importance of allochthonous versus autochthonous C to study streams. To compare the estimates of GPP to allochthonous inputs of C, we converted daily metabolism units (g O_2 l^{-1} d^{-1}) to g C m^{-2} y^{-1} as:

$$\mathrm{GPP}\,(\mathrm{g\ C\ m^{-2}\ y^{-1}}) = \left[\mathrm{GPP}\left(\mathrm{g\ O_2\ l^{-1}\ d^{-1}}\right)\right] \times \frac{(d)(0.375)(365)}{(1.2)} \quad (1)$$

where d is mean depth (m), 0.375 is the molar ratio of C to O_2, 1.2 is the photosynthetic quotient (Hill & Dimick, 2002), and 365 is the number of days in a year. Daily R_E rates were converted to g C m^{-2} y^{-1} as:

$$R_E\left(\text{g C m}^{-2}\ \text{y}^{-1}\right) = \left[R_E\left(\text{g O}_2\ \text{l}^{-1}\ \text{d}^{-1}\right)\right] \times (d)(0.375)(0.85)(365) \quad (2)$$

where 0.85 is the respiratory quotient (Wetzel, 1983). Metabolism measurements from four of the sites (Ball Creek, Tessentee Creek, North Shope Fork, and Caler Fork) were made as part of the Coweeta LTER Regionalization study (McTammany et al. 2007). Metabolism measurements in Hugh White Creek and Hoglot Branch were made by the same methods as part of the Lotic Inter-site Nitrogen eXperiment (LINX) II study (Mulholland et al., 2008; J. R. Webster, H. M. Valett, and B. R. Niederlehner, unpublished data) in the same study reaches where the allochthonous input measurements were made.

Chlorophyll *a* and periphyton biomass

Periphyton biomass and chlorophyll *a* were measured monthly, July through September 2003, in each stream using the AFDM method (Steinman & Lamberti, 2007) and hot ethanol extraction (Sartory & Grobbelaar, 1984), respectively. Three to five samples, consisting of three to five rocks each, were collected from each stream reach and were frozen until analysis. Periphyton was removed from the rock surface with a wire brush, subsampled, and a known volume was filtered onto two pre-ashed and weighed glass fiber filters (Whatman GF/F, 47 mm diameter). One filter was dried at 50°C, ashed (550°C, 45 min) to determine periphyton AFDM, and biomass was converted to g C. The second filter was frozen until chlorophyll *a* analysis could be completed. To express periphyton biomass and chlorophyll *a* measurements per unit area we estimated the surface area of each rock using the "aluminum foil method" (Steinman & Lamberti, 2007).

Inter-biome comparison

Webster and Meyer (1997) published a data set on organic matter budgets for 31 streams in a range of biomes. The majority of streams are from the United States; but the data set also included streams from Antarctica and Canada. We extracted data on terrestrial leaf litter input and GPP from 19 of those streams that were similar in size to the streams we studied. We used this data set to compare measured rates of allochthonous input and autochthonous production from our streams to C sources to streams with minimal human influence from different biomes worldwide.

Statistical analysis

Differences in riparian vegetation, mean annual water chemistry (NO_3–N, NH_4–N, SRP, DO, and specific conductance), mean annual stream temperature, total allochthonous input, and total leaf input were compared among streams in the four land-use categories using a one-way analysis of variance (ANOVA) followed by Tukey's post hoc multiple comparison tests. Kruskal–Wallis tests and Dunn's multiple comparison tests were used when data and data transformations did not satisfy the assumptions of ANOVA. Differences in chlorophyll *a* and periphyton biomass among land-use categories were analyzed using repeated measures (RM) ANOVA with land-use category as a fixed variable and time as repeated variable. We used Pearson product–moment correlation analysis to examine relationships between biological and physicochemical variables measured. To calculate correlations between litter input and physicochemical variables, we used annual means. When calculating relationships between metabolism and physiochemical variables, we used physiochemical values collected during the same month that metabolism values were measured.

Results

Physicochemical characteristics

Stream discharge measured during base flow conditions ranged from 21 to 760 l s^{-1}, with no pattern among land-use types. Mean monthly air temperature was 13.8°C and annual precipitation was 176 cm in 2002 (LTER, 2008). Nutrient concentrations generally increased along the gradient from forested to agricultural land use, but this difference was not significant (Table 2). Stream temperature, and sedimentation significantly increased along the land-use gradient from forest to agricultural streams (temperature: one-way ANOVA, $F_{2,7} = 46.1$, $P < 0.001$; % silt: one-way ANOVA, $F_{3,8} = 5.0$, $P = 0.03$; % silt

Table 2 Mean (±SE) chemical and physical characteristics of each stream site

Land use	Stream code	NO_3–N (μg l^{-1})	NH_4–N (μg l^{-1})	SRP (μg l^{-1})	DO (mg l^{-1})	Specific conductance (μS cm^{-1})	Temp. (°C)	Silt (%)	Silt plus sand (%)	PAR (mol m^{-2} d^{-1})
Forest	BAL	11.0 (1.8)	3.3 (0.9)	1.8 (0.7)	7.4 (0.7) AB	11.0 (0.3)	10.7 A	1 A	13 A	0.18
	HWC	10.9 (2.1)	3.1 (0.8)	1.6 (0.5)	7.4 (0.7) AB	11.2 (0.5)	11.2 A	2 A	13 A	
	JON	69.3 (6.2)	3.2 (0.7)	1.8 (0.6)	7.4 (0.7) AB	20.2 (1.9)	10.9 A	2 A	11 A	
Light agriculture	ELL	77.3 (4.1)	3.0 (1.6)	3.8 (1.0)	7.9 (0.7) A	30.7 (1.2)	–	0 A	12 AB	
	TES	53.0 (7.5)	2.8 (3.6)	3.8 (0.9)	7.6 (0.6) A	29.2 (2.2)	11.6 AB	8 A	23 AB	2.40
Moderate agriculture	DRY	25.5 (4.1)	2.5 (1.2)	2.2 (0.5)	7.3 (0.7) AB	28.8 (2.5)	11.7 B	13 AB	23 BC	
	SHO	24.7 (1.5)	5.0 (2.8)	2.6 (0.6)	7.0 (0.6) AB	40.4 (1.1)	12.3 B	18 AB	34 BC	2.72
	SUT	191.7 (55.2)	15.5 (0.6)	4.0 (1.4)	7.1 (0.6) AB	15.7 (0.4)	12.3 B	33 AB	45 BC	
Heavy agriculture	CAL	63.3 (5.0)	7.6 (0.7)	2.2 (0.6)	7.3 (0.7) B	32.8 (1.1)	13.5 C	14 B	34 C	10.20
	HOG	165.6 (26.9)	12.4 (0.6)	3.6 (0.8)	6.6 (0.6) B	18.3 (0.3)	13.6 C	31 B	44 C	
	SKE	98.5 (12.6)	7.2 (3.4)	5.3 (1.5)	6.9 (0.6) B	23.7 (0.8)	13.3 C	21 B	42 C	
	PAY	211.0 (19.8)	6.4 (1.8)	2.4 (0.7)	6.7 (0.7) B	26.3 (0.8)	14.4 C	46 B	48 C	

Land uses with the same letter for a particular variable do not have significantly different means for that variable ($P < 0.05$). Stream codes in Table 1

plus sand: one-way ANOVA, $F_{3,8} = 12.0$, $P = 0.002$; Table 2). Dissolved oxygen was significantly higher in light-agriculture streams than heavy-agriculture streams (one-way ANOVA, $F_{3,8} = 8.1$, $P < 0.01$; Table 2). PAR was lowest in forested streams, intermediate in light- and moderate-agriculture streams, and highest in heavy-agriculture streams (Table 2).

Riparian vegetation

Riparian tree basal area within 3 m of the stream (3-m basal area; one-way ANOVA, $F_{3,8} = 12.5$ $P = 0.002$), percentage stream canopy cover (one-way ANOVA, $F_{3,8} = 60.7$, $P < 0.001$), and percentage riparian canopy cover (Kruskal–Wallis one-way ANOVA on Ranks, $P = 0.03$) were significantly lower in heavy-agriculture streams compared to other land-use types (Fig. 1). Riparian tree basal area within 10 meters of the stream (10-m basal area; Kruskal–Wallis one-way ANOVA on Ranks, $P = 0.02$) and tree density within 3 m of the stream (3-m tree density; Kruskal–Wallis one-way ANOVA on Ranks, $P = 0.02$) were significantly higher along forested streams than heavy-agriculture streams; light- and moderate-agriculture streams had intermediate values. Tree density within 10 m of the stream (10-m tree density) was significantly higher along forested streams than other land-use types (1-way ANOVA, $F_{3,8} = 44.9$, $P < 0.001$). Percentage grass ground cover significantly increased along the gradient from 0% in forested to 85% heavy-agriculture land use (one-way ANOVA, $F_{3,8} = 46.1$, $P < 0.001$).

Allochthonous input

Annual allochthonous input ranged from 2.8 g C m^{-2} y^{-1} in Hoglot Branch (heavy agriculture) to 264.8 g C m^{-2} y^{-1} in Dryman Fork (moderate agriculture; Table 3). Annual allochthonous input was only significantly higher in moderate-agriculture streams than in heavy-agriculture streams (one-way ANOVA, $F_{3,8} = 12.1$, $P = 0.002$). Tree leaf input followed a similar pattern, ranging from 1.4 to 172.1 g C m^{-2} y^{-1} in Hoglot Branch and Dryman Fork, respectively. There was significantly lower annual leaf input to heavy-agriculture streams (Kruskal–Wallis one-way ANOVA on Ranks, $P = 0.03$; Table 3). Leaves comprised 51 to 87% of total allochthonous input with no pattern among land-use category.

Autochthonous production

GPP was lowest in forested streams (3.0 and 3.3 g C m^{-2} y^{-1} in Ball Creek and Hugh White Creek, respectively), which were characterized by heavy shading and low PAR (Tables 2, 3). GPP was higher

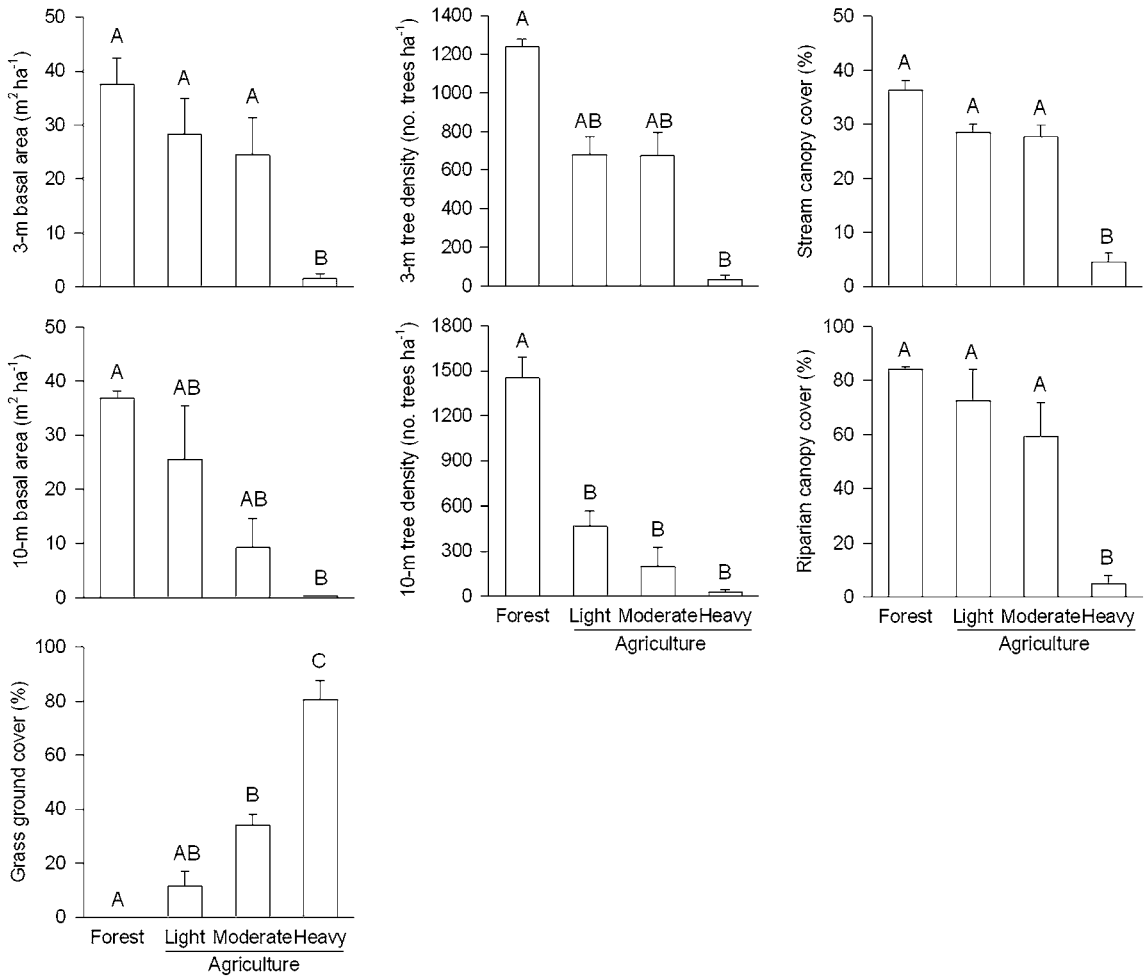

Fig. 1 Mean (±SE) riparian vegetation basal area and tree density within 3 and 10 m of each stream reach, stream canopy cover along each 100-m stream reach, riparian canopy cover within 10-m of each stream reach and grass groundcover within 10-m of each stream reach for each land-use category (forested $n = 3$, light agriculture $n = 2$ moderate agriculture $n = 3$, and heavy agriculture $n = 4$). Land uses with the same letter for a particular variable do not have significantly different means for that variable ($P < 0.05$)

in light- and moderate-agriculture streams (16.7 and 17.1 g C m^{-2} y^{-1} in Tessentee Creek and North Shope Fork, respectively), which had intermediate canopy cover and PAR. GPP was highly variable in heavy-agriculture streams (10.3 g C m^{-2} y^{-1} in Hoglot Branch and 103.8 g C m^{-2} y^{-1} in Caler Fork), which had little canopy cover (Fig. 1; Tables 1, 2, 3). R_E ranged from 89.6 g C m^{-2} y^{-1} in North Shope Fork (moderate agriculture) to 496.8 g C m^{-2} y^{-1} in Caler Fork (heavy agriculture; Table 3). Net ecosystem production (NEP) was quite variable across the agricultural land-use gradient ranging from −393.0 g C m^{-2} y^{-1} in Caler Fork (heavy agriculture) to −72.5 g C m^{-2} y^{-1} in North Shope Fork (moderate agriculture). NEP was negative and *P*/*R* ratios were <0.25 in all study streams (i.e., respiration exceeded photosynthesis, even in streams with the highest rates of GPP).

We found significant and positive relationships between both allochthonous input and leaf input, and dissolved oxygen, 3-m basal area, and 3-m tree density (Table 4). We found significant negative relationships between allochthonous input and leaf input, and NO_3–N, water temperature, % silt, % silt plus sand, and PAR (Table 4). In addition, leaf input was positively related to 10-m basal area (Table 4).

Table 3 Annual allochthonous input, leaf input, gross primary production, respiration, net ecosystem production, and primary production to respiration ratio at stream sites along an agricultural land-use gradient

Land use	Stream name	Allochthonous input (g C m^{-2} y^{-1})	Leaf input (g C m^{-2} y^{-1})	GPP (g C m^{-2} y^{-1})	R_E (g C m^{-2} y^{-1})	NEP (g C m^{-2} y^{-1})	*P/R*
Forested	BAL	206.3 AB	153.6 A	3.0	352.5	−349.6	0.01
	HWC	197.0 AB	149.8 A	3.3	241.0	−239.7	0.01
	JON	240.7 AB	143.3 A	–	–	–	–
Light agriculture	ELL	180.2 AB	155.1 A	–	–	–	–
	TES	185.7 AB	145.6 A	16.7	293.2	−276.5	0.06
Moderate agriculture	DRY	264.8 A	172.1 A	–	–	–	–
	SHO	184.4 A	152.1 A	17.1	89.6	−72.5	0.19
	SUT	201.6 A	158.2 A	–	–	–	–
Heavy agriculture	CAL	104.7 B	80.1 B	103.8	496.8	−393.0	0.21
	HOG	2.8 B	1.4 B	10.3	191.0	−184.2	0.04
	SKE	105.2 B	91.8 B	–	–	–	–
	PAY	22.8 B	17.1 B	–	–	–	–

Land uses with the same letter for a particular variable do not have significantly different means for that variable (one-way ANOVA, $P < 0.05$). Stream codes in Table 1

GPP gross primary production, R_E respiration, *NEP* net ecosystem production, *P/R* primary production to respiration ratio

–, No data

GPP was positively related to PAR, and *P/R* was positively related to specific conductance. Total C was negatively correlated with NO_3–N and NH_4–N and was positively related to DO (Table 4).

Mean chlorophyll *a* concentration ranged from 1.5 mg m^{-2} in forested streams in August to 6.7 mg m^{-2} in light-agriculture streams in September. Overall, chlorophyll *a* concentration was not significantly related to land-use category or sampling date (Fig. 2). Mean periphyton biomass ranged from 0.9 g C m^{-2} in forested streams in July to 3.5 g C m^{-2} in moderate-agriculture streams in September and was not related to land-use category or sampling date (Fig. 2).

Carbon source

Total C supply (annual allochthonous input and GPP, only given for the 6 streams in which both sources of C were measured) ranged from 13.1 g C m^{-2} y^{-1} in Hoglot Branch (heavy agriculture) to 209.3 g C m^{-2} y^{-1} in Ball Creek (forested; Table 5; Fig. 3a). Total C supply was consistently high in forested, light-, and moderate-agriculture streams (approximately 202 g C m^{-2} y^{-1}), while total C supply in heavy-agriculture streams was highly variable, ranging from 13.1 to 208.5 g C m^{-2} y^{-1} in Hoglot Branch and Caler Creek, respectively (Table 5; Fig. 3a). Forested streams received over 98% of their annual C supply from allochthonous sources and less than 2% from autochthonous production (Fig. 3b). Even light- and moderate-agriculture streams received 91.8 and 91.5% of their C supply from allochthonous sources, respectively (Fig. 3b). Carbon supply from allochthonous sources was substantially lower to heavy-agriculture streams (50.2% for Caler Fork and 21.2% for Hoglot Branch; Fig. 3b). Moreover, annual terrestrial input and GPP were high to Caler Fork (104.7 and 103.8 g C m^{-2} y^{-1}, respectively) but quite low to Hoglot Branch (2.8 and 10.3 g C m^{-2} y^{-1}, respectively; Table 3).

Inter-biome comparison

Total C supply in streams varies considerably across biomes ranging from 54 g C m^{-2} y^{-1} in tundra streams to 1771 g C m^{-2} y^{-1} in desert streams (Fig. 4a). Carbon sources to streams draining forested catchments, including deciduous forests, montane coniferous forests, and boreal coniferous forests,

Table 4 Pearson product-moment correlations between biological, physical, and chemical characteristics measured

Parameters	Allochthonous input (g C m^{-2} y^{-1})	Leaf input (g C m^{-2} y^{-1})	GPP (g C m^{-2} y^{-1})	R_E (g C m^{-2} y^{-1})	NEP (g C m^{-2} y^{-1})	*P*/*R*	Total C supply (g C m^{-2} y^{-1})
NO_3–N (μg l^{-1})	−0.65, 0.021	−0.66, 0.020	NS	NS	NS	NS	−0.92, 0.009
NH_4–N (μg l^{-1})	NS	NS	NS	NS	NS	NS	−0.87, 0.025
SRP (μg l^{-1})	NS	NS	NS	NS	NS	NS	NS
DO (mg l^{-1})	0.69, 0.013	0.74, 0.006	NS	NS	NS	NS	0.84, 0.036
Specific conductance (μS cm^{-1})	NS	NS	NS	NS	NS	0.89, 0.019	NS
Temperature (°C)	−0.88, 0.000	−0.84, 0.001	NS	NS	NS	NS	NS
Silt (%)	−0.63, 0.029	−0.64, 0.025	NS	NS	NS	NS	NS
Silt plus sand (%)	−0.69, 0.013	−0.65, 0.023	NS	NS	NS	NS	NS
PAR (mol m^{-2} d^{-1})	−1.0, 0.001	−0.98, 0.025	0.99, 0.007	NS	NS	NS	NS
3-m BA (m^2 ha^{-1})	0.81, 0.001	0.78, 0.003	NS	NS	NS	NS	NS
10-m BA (m^2 ha^{-1})	NS	0.58, 0.050	NS	NS	NS	NS	NS
3-m TD (no. trees ha^{-1})	0.76, 0.004	0.75, 0.005	NS	NS	NS	NS	NS
10-m TD (no. trees ha^{-1})	NS	NS	NS	NS	NS	NS	NS
SCC (%)	0.93, 0.000	0.94, 0.000	NS	NS	NS	NS	NS
RCC (%)	0.84, 0.001	0.85, 0.000	NS	NS	NS	NS	NS
GGC (%)	−0.81, 0.001	−0.81, 0.001	NS	NS	NS	NS	NS
Agricultural influence	−0.80, 0.002	−0.80, 0.002	NS	NS	NS	NS	NS

Pearson correlation coefficients and *P* values are shown for significant relationships

NS non-significant relationship

were dominated by allochthonous sources (Fig. 4b). Annual allochthonous inputs to these streams ranged from 31 to 368 g C m^{-2} y^{-1} in boreal coniferous forest and montane coniferous forest streams, respectively (Table 5). GPP in streams in forested biomes was also lower than any other biomes measured, ranging from 1.9 to 264.5 g C m^{-2} y^{-1} in deciduous forest streams (Table 5; Fig. 5b). GPP and litter inputs to August Creek, Michigan, and Walker Branch, Tennessee, were similar to light- and moderate-agriculture streams in the present study. GPP in the single grassland stream in the data set, Kings Creek, Kansas, was more than double litter inputs (Fig. 4b). Total C supply to the three desert streams was dominated by GPP (Fig. 4b), ranging from 944 to 2700 g C m^{-2} y^{-1}, while allochthonous inputs were quite low, ranging from 1 to 121 g C m^{-2} y^{-1} (Fig. 5a). C supply to the two tundra streams was also dominated by autochthonous production (Fig. 4b), but rates of GPP were considerably lower than desert streams (Fig. 5a).

Discussion

Relative contributions of allochthonous organic matter and autochthonous production shift along an agricultural land-use gradient; forested, light-, and moderate-agriculture streams were strongly heterotrophic with *P*/*R* ratios <0.2, and these streams received more than 90% of their C from terrestrial sources. Autochthonous C sources only made up a substantial portion (>50%) of total C supply in heavy-agriculture streams. Further, the proportion of autochthonous C to the four heavy-agriculture streams was highly variable, and anecdotal evidence from two of these streams suggests that autochthonous production dominates when livestock grazing

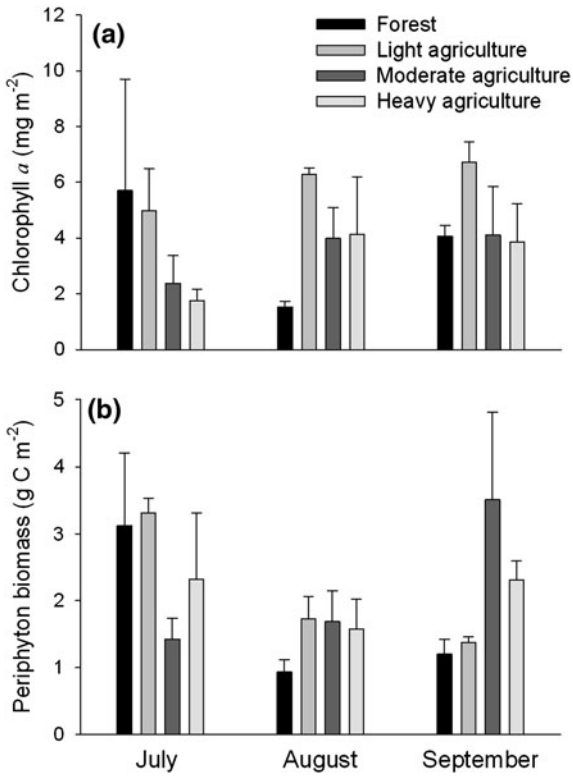

Fig. 2 Monthly mean (±SE) chlorophyll *a* (**a**) and periphyton biomass (**b**) from rocks collected from replicate streams in each land-use type during July, August, and September

was not present. Relative contribution of C supplied from allochthonous versus autochthonous sources varied across terrestrial biomes as well; C originating from allochthonous sources dominated energy budgets in deciduous forest and coniferous forest streams, while autochthonous production was much higher than allochthonous input to desert streams.

Effects of agricultural land use on C source to streams

We expected allochthonous input to decline linearly along the land-use gradient from forested to heavy-agriculture streams. Surprisingly, our results show similar annual allochthonous and leaf input to forested, light-, and moderate-agriculture streams. Allochthonous and leaf inputs were significantly related to both 3-m basal area and 3-m tree density, and only leaf input was significantly related to 10-m tree density (Table 4) suggesting that a narrow band of riparian vegetation is sufficient to provide shading and leaf inputs to stream systems. Most likely, light- and moderate-agriculture streams received allochthonous material equivalent to that of forested streams because individual trees along the agricultural streams contributed larger quantities of litter input than individual trees along the forested streams. Widely spaced trees tend to grow larger and produce more leaves due to lack of competition for resources (light, nutrients, and water) with surrounding trees (Pinkard & Neilsen, 2003). While individual trees along forested streams may contribute less to annual allochthonous input, the greater overall tree basal area and density in forested watersheds likely compensated for lower leaf inputs per individual tree. Annual contributions of terrestrial litter to forested, light-, and moderate-agriculture streams were similar to each other and to that measured in eastern deciduous forested streams (Webster et al., 1995; Wallace et al., 1999). Annual litter inputs to heavy-agriculture streams (2.8–105.2 g C m^{-2} y^{-1}) were within the ranges reported for streams in arid regions (8.3 g C m^{-2} y^{-1}; Schade & Fisher, 1997), high latitude streams (0 to 31 g C m^{-2} y^{-1}; Benfield, 1997), and New Zealand pasture streams (112 g dry mass m^{-2} y^{-1}; Scarsbrook et al., 2001).

We expected autotrophy to become an important energy pathway in agricultural streams (Wiley et al., 1990; Scarsbrook & Halliday, 1999), resulting in increased algal growth and higher rates of primary production due to warmer temperatures (Bott et al., 1985; Sinsabaugh, 1997) and increasing nutrient availability (Corkum, 1996). However, we did not see the sharp contrast we saw with allochthonous inputs. Chlorophyll *a* concentrations and periphyton biomass did not vary significantly along the agricultural land-use gradient and were similar to values typical of forested (Sponseller et al., 2001; Hill & Dimick, 2002), agricultural (McTammany et al., 2007). and reforested (McTammany et al., 2007) streams in the southern Appalachians. Low chlorophyll *a* concentration and periphyton biomass were likely due to heavy shading in forest, light-, and moderate-agriculture streams and the negative effects of sediment in heavy-agriculture streams.

GPP was low in forested, light-, and moderate-agriculture streams, and was similar to streams draining deciduous and coniferous forests worldwide (Lamberti & Steinman, 1997). Heavy shading by the forest canopy is the most reasonable explanation for low GPP. Several studies of streams draining small,

Table 5 Sites from Webster & Meyer (1997) and present study showing annual allochthonous input (without lateral inputs), gross primary production (GPP), and total C supply to streams

Stream	Location	Biome	Allochthonous input (g C m^{-2} y^{-1})	GPP (g C m^{-2} y^{-1})	Total C supply (g C m^{-2} y^{-1})	Reference
Augusta Creek	Michigan, USA	DF	224	32	256	Webster & Meyer (1997)
Hugh White Creek	North Carolina, USA	DF	253.15	2.9	256.1	Webster et al. (1997)
Satellite Branch	North Carolina, USA	DF	246	1.9	248	Wallace et al. (1997b)
Walker Branch	Tennessee, USA	DF	229.5	35.5	265	Mulholland (1997)
White Clay Creek	Pennsylvania, USA	DF	156.5	263.5	420	Newbold et al. (1997)
Creeping Swamp	North Carolina, USA	DFBW	348	28.2	376	Webster & Meyer (1997)
Devil's Club Creek	Oregon, USA	MCF	368	18.25	386	Webster & Meyer (1997)
Mack Creek	Oregon, USA	MCF	365	38.8	404	Webster & Meyer (1997)
WS 10, 1973	Oregon, USA	MCF	268.5	38.5	307	Webster & Meyer (1997)
WS 10, 1974	Oregon, USA	MCF	283.5	38.5	322	Webster & Meyer (1997)
Beaver Creek	Quebec, Canada	BCF	108.3	29.2	137.5	Naiman & Link (1997)
First Choice Creek	Quebec, Canada	BCF	208.8	17.4	226.2	Naiman & Link (1997)
Monument Creek	Alaska, USA	BCF	31	63.5	95	Irons & Oswood (1997)
Kings Creek, prairie site	Kansas, USA	GRAS	50	111.5	162	Gray (1997)
Deep Creek	Idaho, USA	DES	1.2	1770	1771	Webster & Meyer (1997)
Rattlesnake Springs	Washington, USA	DES	121	2700	2821	Cushing (1997)
Sycamore Creek	Arizona, USA	DES	8.25	944	952	Jones et al. (1997)
Canada Stream	South Victoria Land, Antarctica	TUND	0	53	53	McKnight & Tate (1997)
Kuparuk River	Alaska, USA	TUND	0	55	55	Harvey et al. (1997)
Ball Creek	North Carolina, USA	DF	206.3	3.0	209.3	Present study
Hugh White Creek	North Carolina, USA	DF	197.0	3.3	200.3	Present study
Tessentee Creek	North Carolina, USA	DF, light agriculture	185.7	16.7	202.4	Present study
North Shope Fork	North Carolina, USA	DF, moderate agriculture	184.4	17.1	201.5	Present study
Caler Fork	North Carolina, USA	DF, heavy agriculture	104.7	103.8	208.5	Present study
Hoglot Branch	North Carolina, USA	DF, heavy agriculture	2.8	10.3	13.1	Present study

Data are reproduced with permission from Webster and Meyer (1997)

TUND tundra, *DES* desert, *GRAS* grassland, *BCF* boreal coniferous forest, *MCF* montane coniferous forest, *DF* deciduous forest, *DFBW* deciduous forest, blackwater

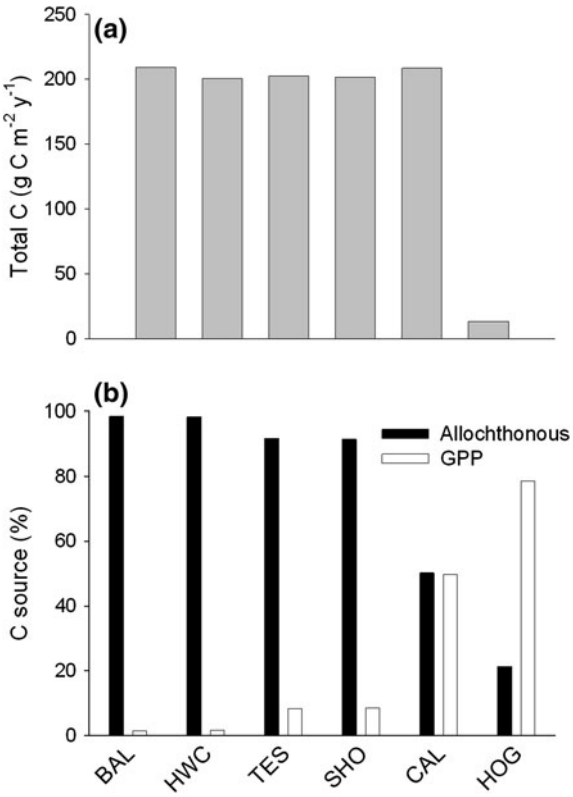

Fig. 3 Total carbon supply (**a**) and percentage carbon source (**b**) to study streams. Total carbon inputs is the sum of annual allochthonous input and GPP. In **b**, allochthonous origin consists of total annual litterfall (*filled bar*) and autochthonous origin includes in stream gross primary production (*unfilled bar*). BAL and HWC are forested streams, TES is a light-agriculture stream, SHO is a moderate-agriculture stream, and CAL and HOG are heavy-agriculture streams

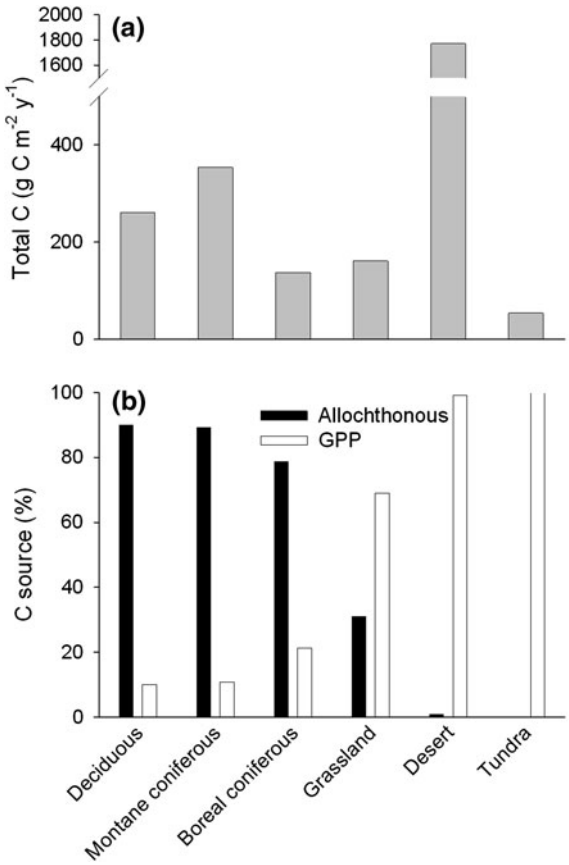

Fig. 4 Total carbon supply (**a**) and percentage carbon sources (**b**) to streams across multiple biomes. In **b**, allochthonous origin (*filled bar*) represents median total annual litterfall and GPP (*unfilled bar*) shows median GPP to streams in each biome. Data include 19 streams of similar size to our study streams (from Webster & Meyer 1997)

forested catchments show that heavy shading and low PAR contribute to low primary production (Vannote et al., 1980; Minshall et al., 1985; Webster & Meyer, 1997; Mulholland et al., 2001). Further, high R_E in these streams is likely in response to high allochthonous inputs and high retention of large wood (Hedman et al., 1996). GPP in heavy-agriculture streams was highly variable. GPP in Caler Fork was similar to streams in desert and grassland biomes, while GPP in Hoglot Branch was more characteristic of streams in deciduous forest biomes. Comparison of streams influenced by agricultural land use to reference streams in multiple biomes suggests that human alteration to terrestrial ecosystems can have significant effects on stream function. Here, we show that agricultural land-use practices can change stream metabolism to the point that they no longer function like other streams within the same biome.

We only measured metabolism along the agricultural land-use gradient during the summer leaf-out period. Extrapolation of single metabolism measurements to annual rates is a limitation of this data set; however, this allowed comparison of metabolism values from the current study with those collected by Webster & Meyer (1997). We argue that these data provide a baseline to compare metabolism both across an agricultural land-use gradient and to reference streams in multiple biomes. Further, metabolism data in the Webster & Meyer (1997) data set were collected using various methods and were not necessarily collected during an entire year. Rather, these data represent a best estimate of

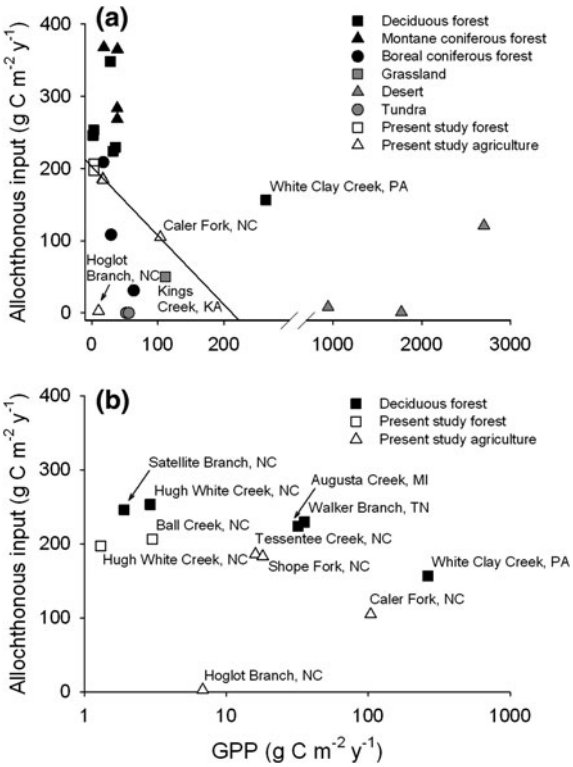

Fig. 5 Gross primary production and annual allochthonous input to streams with multiple biomes (**a**) and in deciduous forests (**b**). Data are reproduced with permission from Webster & Meyer (1997). The *line* in **a** is a linear regression extended to the axes for the streams in our study for which we have measurements of both allochthonous and autochthonous inputs with exception of Hoglot Branch ($R^2 = 0.99$)

metabolism values for streams in a variety of terrestrial biomes.

Previous studies have shown that GPP does not exhibit significant seasonal variation in southern Appalachian deciduous forest streams (Valett et al., 2008). GPP in 2 deciduous forested streams in the southern Appalachians was low and did not differ significantly throughout the year, while GPP in two New Mexico open canopy streams was higher in summer and autumn than winter (Valett et al., 2008). In studies that do show seasonal variation in GPP, variation is small relative to that across biomes (Roberts et al., 2007; Hoellein et al., 2009). Interestingly, the light- and moderate-agriculture sites in our study (Tessentee and Shope, respectively) were similar in leaf input and GPP to Walker Branch, Tennessee, a second-growth deciduous forest stream that demonstrates seasonal changes in metabolism (Roberts et al., 2007). Seasonal peaks in biomass of the green algae *Oedogonium* likely contributed to high spring GPP rates (Roberts et al., 2007) making Walker Branch behave similarly to agricultural streams.

Instead of following the expected pattern of lower allochthonous input and higher GPP as agricultural land use increases, autochthonous production was highly variable in heavy-agriculture streams. Caler Fork, which is characterized by little riparian shading, low allochthonous input, high nutrient concentrations, and warm stream temperatures (Table 1), had the highest GPP and seemed to follow the expected pattern of C source shifting. By contrast, GPP was substantially lower in Hoglot Branch than Caler Fork despite higher nutrient concentrations in Hoglot Branch. One factor that may have contributed to the difference between these two heavy-agriculture streams was the presence of heavy livestock grazing immediately along Hoglot Branch. Cattle trampling the banks and streambed likely contributed to higher sedimentation, less streambed heterogeneity, and less stable substrate in Hoglot Branch than in Caler Fork. The study reach of Hoglot Branch has a narrow, deep channel except for one cattle crossing area, and we often observed cattle walking in the stream. Lower GPP in response to trampling by livestock has been previously reported (Armour et al., 1991). The predominance of fine silty sediments in Hoglot Branch may have limited the establishment of algal communities and suppressed primary production, as constantly shifting sediment does not provide suitable habitat for attached algal growth (Waters, 1995). In a study of metabolism in 18 streams across an agricultural gradient (including the data from four of the streams in the current paper), McTammany et al. (2007) showed that heavily impacted streams had lower GPP than moderately impacted streams, despite higher nutrient concentrations, available light, and water temperatures. In their study, GPP rates among streams in the heavy-agriculture category were also highly variable, reflecting the influence of site-specific properties on stream ecosystem processes.

Overall, metabolism parameters were not related to physical and chemical characteristics. In fact, the significant relationship between GPP and PAR may have resulted from not having PAR data for Hoglot Branch. It is not surprising that R_E was not related to physical and chemical variables because R_E includes

both heterotrophic respiration (R_H) and autotrophic respiration (R_A) and variables that increase R_H tend to decrease R_A (e.g., shading). This is also true for NEP and P/R. For example, the relationship between P/R and specific conductance was significant because the two streams with high P/R and specific conductance (North Shope Fork and Caler Fork) had high P/R for different reasons. North Shope Fork had low R_E, mostly supported by R_H because GPP and therefore R_A was low, but Caler Fork had high R_E, mostly supported by R_A but offset by high GPP.

Carbon source shifting

Stream metabolism, which includes autotrophic primary production, R_A, and R_H, provides information on the relative sources of C to stream ecosystems. It has been suggested that total C input is approximately equal among streams across biome and land-use type (Dodds, 2006). This suggestion is partially supported by our data—for the six streams for which we have measurements of both allochthonous and autochthonous input, total C inputs are almost identical with the exception of streams with extreme disturbance (e.g., Hoglot Branch). Thus, within a biome there seems to be compensation between inputs such that total C input per unit area is nearly the same whether it is from allochthonous or autochthonous sources (Fig. 3, regression line in Fig. 5a). However, across biomes this does not appear to be the case—streams within a biome are dominated by either allochthonous or autochthonous C sources. There are only a few examples where both sources are intermediate: Caler Fork (heavy agriculture but no cattle access to the stream), Kings Creek (tall grass prairie; Gray, 1997), and White Clay Creek (majority of watershed was agriculture; Newbold et al., 1997). Conditions that appear to result in approximately equal allochthonous input and autochthonous production include highly productive terrestrial vegetation and good conditions for algal growth in streams (insolation of streambed, nutrient availability, stable substrate). In these streams, productive terrestrial vegetation will generate detritus to provide allochthonous input to streams, even if it is dead grass. However, shading by terrestrial vegetation did not limit primary production and algal growth. The other "reference" biomes have either low terrestrial production and low shading that favors high autochthonous production (tundra, desert) or high terrestrial production that limits algal growth by limiting light (deciduous and coniferous forest). Thus, total C supply to low order southern Appalachian streams is likely equivalent, regardless of extent of agricultural land use, aside from streams with extensive sedimentation. Total C supply, however, is not equivalent across biomes, suggesting that total C supply to streams is driven more by climatic factors that determine predominant plant communities associated with terrestrial biomes rather than localized land use.

A shift in C sources may have consequences to aquatic consumers, as terrestrially derived C is typically of lower quality than C originating within the stream itself (e.g., Elser et al., 2000; Cross et al., 2005). Thus, heavy-agriculture, grassland, and desert streams that exhibit higher rates of autochthonous production relative to allochthonous inputs have higher quality organic matter forming their trophic base. If total C input is similar among streams with variable contributions of allochthonous and autochthonous C input, net autotrophic streams may exhibit faster aquatic consumer growth rates, higher assimilation rates, different species composition, and higher secondary production than more heterotrophic systems. More research into supplies and uses of C from different sources could further our understanding of this potential carbon compensation.

Our findings contribute to previous studies that have measured whole-stream metabolism and deepen our understanding of the linkages between riparian vegetation and stream structure and function. We have documented a metabolic shift in stream ecosystems along an agricultural land-use gradient and suggest that this shift is influenced by factors associated with agricultural land use such as reductions in riparian vegetation and subsequent litterfall and streambed insolation. Access of livestock to the stream and resulting sedimentation due to trampling of the bank and stream bed further contribute to a metabolic shift. Furthermore, the shift from allochthonous to autochthonous production dominating C supply is not limited to streams draining agricultural catchments, as we have found evidence of C source shifting in other biomes, in particular, desert, tundra, and grassland streams. The next logical step is to examine how stream metabolic shifts and variable quality of allochthonous versus autochthonous C

sources influence stream community structure and function.

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