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GLOBAL CHANGE AND RIVER ECOSYSTEMS

# Periphyton biomass and ecological stoichiometry in streams within an urban to rural land-use gradient

**Patrick J. O'Brien · John D. Wehr**

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**Abstract** This study examined the effects land use on biomass and ecological stoichiometry of periphyton in 36 streams in southeastern New York State (USA). We quantified in-stream and land-use variables along a N–S land-use gradient at varying distances from New York City (NYC). Streams draining different landscapes had fundamentally different physical, chemical, and biological properties. Human population density significantly decreased ($r = -0.739$; $P < 0.00001$), while % agricultural land significantly increased ($r = 0.347$; $P = 0.0379$) with northing. Turbidity, temperature, conductivity, and dissolved Mg, Ca, SRP, pH, DOC, and Si significantly increased in more urban locations, but $NO_3^-$ and $NH_4^+$ did vary not significantly along the gradient. Periphyton biomass (as AFDM and Chl-*a*) in rural streams averaged one-third to one-fifth that measured in urban locations. Periphyton biomass in urban streams averaged $18.8 \pm 6.0$ g/m$^2$ AFDM and $75.6 \pm 28.5$ mg/m$^2$ Chl-*a*. Urban Chl-*a* levels ranging between 100 and 200 mg/m$^2$, are comparable to quantities measured in polluted agricultural streams in other regions, but in our study area was not correlated with % agricultural land. Periphyton nutrient content also varied widely; algal C varied >20-fold (0.06–1.7 μmol/mm$^2$) while N and P content varied >6-fold among sites. Algal C, N, and P correlated negatively with distance from NYC, suggesting that periphyton in urban streams may provide greater nutrition for benthic consumers. C:N ratios averaged 7.6 among streams, with 91% very close to 7.5, a value suggested as the optimum for algal growth. In contrast, periphyton C:P ratios ranged from 122 to >700 (mean = 248, twice Redfield). Algal-P concentrations were significantly greater in urban streams, but data suggest algal growth was P-limited in most streams regardless of degree of urbanization. GIS models indicate that land-use effects did not easily fit into strict categories, but varied continuously from rural to urban conditions. We propose that the gradient approach is the most effective method to characterize the influence of land use and urbanization on periphyton and stream function.

**Keywords** Benthic algae · Periphyton · Rivers · Land use · Ecological stoichiometry · Urban–rural gradient · Nutrients · New York

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P. J. O'Brien · J. D. Wehr (✉)
Louis Calder Center—Biological Station and Department of Biological Sciences, Fordham University, Armonk, NY 10504, USA
e-mail: wehr@fordham.edu

## Introduction

The array of ecological variables that drive or limit algal production in streams, such as nutrient supply, light availability, physical disturbance, and grazing, have been studied extensively, both through correlative and experimental approaches (Bothwell, 1988; Chessman et al., 1992; Stevenson et al., 1996; Wehr & Sheath, 2003). The ongoing challenge in studying these systems lies in the inherent complexity of stream habitats and their communities, but also in understanding the multiple scales of factors that regulate algal production and composition (Biggs, 1995; Snyder et al., 2002). Interest in algal production has increased in light of recent studies (e.g., Finlay et al., 2002; Torres-Ruiz et al., 2007) that have demonstrated a greater importance for autochthonous matter in lotic food webs than was suggested in earlier models (e.g., Vannote et al., 1980). These studies indicate that benthic algae consist of higher quality organic matter than that terrestrial matter, which is essential for consumers in stream food webs.

The factors that affect the quantity and quality of this production are of importance to stream ecosystem theory. Biggs (1996) proposed a two-tiered conceptual model to characterize the multiple factors that regulate benthic algal production and structure in streams. Proximate variables directly regulate biomass accrual and loss, and include physical and chemical factors, water quality (dissolved nutrients) temperature, optics (light availability, turbidity), and hydrography. The main factors predicted to lead more directly to biomass accrual are nutrients and light availability, while the main factors leading to loss of production are disturbance, especially floods and droughts. Larger-scale environmental or landscape features, ultimate variables, include climate, topography, land use, geology, and human impacts. The connection between the effects of proximate and ultimate variables as they affect stream periphyton has not received extensive study. However, Snyder et al. (2002) demonstrated that periphyton biomass and diatom community structure in broad (>5th order) streams in Idaho (USA) were most affected by N and P supply, and that these were in turn affected by location, presumably reflecting land-use differences. Blinn & Bailey (2001) demonstrated that diatom community structure was strongly correlated with land-use practices, especially irrigation practices and dryland farming, in streams in Victoria, Australia. Carr et al. (2005) tested the ability to use land-use variables to replace local water quality variables in predictive models of periphyton chlorophyll-*a*, using a 21-year database of rivers in Alberta, Canada. Land use, especially human population density, explained roughly 25–28% of the variability in periphyton Chl-*a*, but the best models included both land use and local nutrient data. They suggested that within ecoregions, land use can be a good surrogate for nutrient data in predicting lotic periphyton Chl-*a* concentration.

Stream periphyton assemblages also vary in their nutritional quality. There is evidence suggesting that the importance of periphyton in stream food webs may be more a function of quality than quantity (Cross et al., 2003). Laboratory data suggest that the optimal stoichiometry of C:N:P content in freshwater periphyton should be around 119:17:1 to avoid nutrient limitation of growth (Hillebrand & Sommer, 1999), a ratio very close to that suggested for oceanic plankton: 106:16:1 (Redfield, 1958). However, unlike plankton in comparatively stable open oceans, autotrophs in more variable and spatially structured systems, like streams, show marked deviations from this C:N:P ratio (Wetzel, 2001; Hillebrand et al., 2004). Both the biomass produced and concentrations of essential nutrients contained in algal assemblages subsequently affect consumer growth rates (Frost & Elser, 2002; Stelzer & Lamberti, 2002), as well as nutrient cycling properties within the ecosystem (Dodds et al., 2004). A better understanding of the influence of different land-use conditions on periphyton stoichiometry in stream ecosystems is needed.

Urbanization exerts profound effects on the landscape and associated aquatic systems, such as redirection of rainfall by impervious surfaces (Hirsch et al., 1990), increased surface runoff (McMahon & Cuffney, 2000), increased sediment load, and decreases in sediment particle size (Paul & Meyer, 2001). Temperature changes have been attributed to removal of riparian vegetation, decreased recharge of groundwater, and the urban "heat-island" effect (Pluhowski, 1970; Pickett et al., 2001). Oxygen demand, conductivity, turbidity, and dissolved metals also tend to increase with urbanization (Paul & Meyer, 2001). Inputs of sewage, wastewater, and fertilizers, which typify many urban streams, result in greater dissolved N and P concentrations (Meybeck, 1998; Winter & Duthie, 2000). Elevated levels of base cations (Ca, Mg, Na, and K) may also cause an increase in specific conductance (Paul & Meyer, 2001).

These physical and chemical changes can have important effects on stream periphyton. Walker &

Pan (2006) demonstrated that diatom species composition in streams in the Portland region (Oregon, USA) significantly correlated with differences in water chemistry and land use along an urban–rural gradient. Periphyton chlorophyll-*a* accrual rates in one urban stream in Catalonia, Spain did not differ significantly among experimental nutrient (N, P) treatments, apparently due to shaded, canopy conditions (Schiller et al., 2007). Interestingly, substrata in the urban site also experienced accumulations of fine organic matter (detritus) on their surfaces, which was suggested to have inhibited periphyton growth. However, $NH_4^+$ treatments did result in significantly reduced $NO_3^-$ uptake rates in this stream. Periphyton growth in one urban stream near College Station, Texas was strongly affected by the high frequency of floods, but still reached 30 times the designated nuisance level (>100 mg Chl-*a*/m$^2$), and was composed of edible, early-stage algal species rather than late-stage, and less edible taxa (Murdock et al., 2004). How such changes may be mirrored by periphyton nutrient stoichiometry remains to be seen.

Here, we examine a suite of land-use factors that may influence the biomass and ecological stoichiometry of stream periphyton. We aim to link in-stream or proximate (e.g., temperature and nutrients) and ultimate (e.g., land use) variables to understand the key factors affecting streams along a land-use gradient at varying distances from a large urban center, NYC. We predict that (1) there will be significant changes in physical and water chemistry (proximate) variables in concert with identifiable land-use (ultimate) variables, and that (2) periphyton biomass and nutrient stoichiometry will be significantly affected by physical and chemical changes in these streams. Our goal is to identify which variables show greatest sensitivity to land-use changes and which may be most important to stream periphyton. We also aim to identify if periphyton nutrient stoichiometry data may be used to assess nutrient limitation among different land-use conditions.

## Materials and methods

### Design and site selection

The study area is a 6,000 km$^2$ region in southeastern New York State east of the Hudson River and north from Yonkers to Troy NY. Land use ranges from dense urban districts in the south to sparsely populated rural areas. Rural regions are mosaics of forested (mixed hardwood) and light- to moderate-intensity agriculture. Following a pilot study of 20 streams, a power analysis determined that a sample size of at least 32 streams was required to detect local and landscape effects. We identified 70 streams as potential sites which met the following criteria: (1) first to third order; (2) stream width $\geq$3 m; (3) cobble-boulder substratum with at least three riffles; (4) current velocity in riffles $\geq$25 cm/s; (5) streambed neither completely shaded nor fully open to sunlight. From this set, a stratified-random method (stratified by watershed) was used to select 36 streams of sample in 2001. All streams were sampled within a 6-week period during average summer base flow (no major rainfall events). These criteria ensured that streams had predominantly rocky substrata and differed mainly by land use along a gradient from urban to rural conditions (verified using GIS, below).

### Field sampling

Most field methods follow Stevenson & Bahls (1999). Geographic locations were determined using a Garmin 12-XL GPS unit. Stream width was measured with a measuring tape and depth with a meter stick. Current velocity was measured with a General Oceanics 2030 current meter from five riffles in the center of each reach. Water temperature and conductivity were measured with a YSI 30 S/C/T meter and canopy cover was measured with a Forest Model-C spherical densiometer. For periphyton samples, five rocks between 10 and 35 cm diameter were arbitrarily chosen from separate riffles, placed in 4 l plastic bags and stored on ice. Unfiltered water was collected for pH (25 ml polypropylene bottles) and turbidity (20 ml borosilicate vials) measurements and stored on ice. Two water chemistry samples were syringe-filtered in situ (Nalgene nylon membrane 0.2 µm poresize) and preserved by acidification (U. S. Environmental Protection Agency, 1987) to pH <2.0 with HCl (for dissolved organic carbon, DOC) or $H_2SO_4$ (for $NO_3^-$, $NH_4^+$, soluble-reactive-P [SRP], Si [as $SiO_3$]) and refrigerated (4°C) until analysis.

## Periphyton processing and analyses

Periphyton was scraped from rocks with razor blades and brushes to a final volume of 250–500 ml; processing was completed within 1 day of collection. Periphyton suspensions were homogenized and mixed using a small hand blender, and divided into aliquots for (1) dry mass (DM) and ash-free dry mass (AFDM), (2) Chlorophyll-*a* (Chl-*a*), (3) C and N analyses, (4) P analysis, and (5) taxonomic identification (preserved with Lugol's iodine). DM and AFDM were determined after filtration onto pre-ashed and pre-weighed (to 0.0001 g) 47 mm glass fiber filters (Whatman GF/F), dried ($\geq$18 h) at 80°C, weighed (=DM), then ashed at 450°C for 2–3 h and re-weighed (AFDM) to the nearest 0.0001 g (AFDM = difference between DM and mass of ash after combustion; American Public Health Association, 1985). Pheophytin-corrected Chl-*a* was measured after extraction with 90% buffered acetone and absorbances measured at 750, 665, and 664 nm (Lorenzen, 1967). The Autotrophic Index (AI) of each periphyton assemblage was calculated as the ratio of AFDM/Chl-*a*, after Biggs & Close (1989). This method classifies samples with ratios <200 ("low") to consist mainly of autotrophic algae, while "moderate" ratios (200–400) are regarded to be a mixture of autotrophic and heterotrophic periphyton, and values >400 to be dominated by heterotrophic organisms and/or detritus. In our study, we use this index to estimate algal versus non-algal periphyton in streams draining different landscapes. Periphyton C and N concentrations were measured from homogenized periphyton dried at 80°C in 9 × 10 mm tin cups and measured using a Perkin Elmer 2400 Series II CHNS/O analyzer. Periphyton-P was measured after digestion following Solórzano & Sharp (1980) and the digest analyzed as reactive-P as described below. After all scrapings were completed, rocks were measured for determination of surface area (SA), based on linear dimensions and formulas for appropriate geometric shapes. We defined "colonizable area" as the upper 50% of each rock area as all were embedded in streambed at time of collection.

## Water chemistry

Streamwater pH was measured with an Orion Model 720 pH Meter and turbidity with a Turner TD-40 nephelometer; both were analyzed in the lab immediately after returning from the field (<6 h). DOC was measured using a Shimadzu TOC-5050A TOC analyzer (American Public Health Association, 1985). Dissolved ammonium ($NH_4^+$–N) concentrations were measured as using the phenol–hypochlorite method (American Public Health Association, 1985; Bran+Luebbe Analyzing Technologies, 1986b); nitrite (measured as $NO_2^-$–N) using the sulfanilamide-NNED (American Public Health Association, 1985; Bran+Luebbe Analyzing Technologies, 1987a); nitrate ($NO_3^-$–N) by reduction to nitrite using a Cd–Cu column and analyzed as nitrite; reactive silica using the molybdate–ascorbate method (American Public Health Association, 1985; Bran+Luebbe Analyzing Technologies, 1987b); and soluble-reactive phosphate (SRP) using the antimony–ascorbate–molybdate method (American Public Health Association, 1985; Bran+Luebbe Analyzing Technologies, 1986a). Total dissolved phosphorus (TDP) was predigested using acid persulfate (Eisenreich et al., 1975) and analyzed as SRP. Nutrients were measured using a Bran & Luebbe TRAACS 800 autoanalyzer. Dissolved Ca and Mg were measured using a Perkin-Elmer 1100B atomic absorption spectrophotometer (American Public Health Association, 1985).

## Data variables

Nutrient stoichiometry of periphyton assemblages was calculated on a molar basis from nutrient content data and used as a broad measure of nutrient limitation (Redfield, 1958; Hillebrand & Sommer, 1999). The proximate stream variables stream width, maximum depth, current velocity, turbidity, temperature, and percent canopy cover were defined as physical properties. Conductivity, pH, DOC, $NH_4^+$, $NO_3^-$, Si, SRP, TDP, Ca, and Mg were defined as (proximate) water chemistry variables. The following were defined as periphyton variables (on DM and SA basis): % organic matter, AFDM, Chl-*a*, C, N, P, and C:N, C:P, and N:P ratios. Landscape-level variables were land use, bedrock geology, and population density. Data were obtained from the New York State GIS Clearinghouse and analyzed using Arc Info. Population density data (persons per square km) were derived from a layer of the U.S. Department of Commerce, Bureau of the Census 1990 coverage. Land use data were derived from a layer of the U.S. Geological Survey (USGS) 1990 1:250,000 Scale

Land use and Land Cover for New York, Hartford and Albany Quadrangles. Data were presented in the Anderson level 2 classification system (general land use and subdivisions), but for the purpose of this stream study only the level 1 classification was used, as suggested by Wang & Yin (1997). Bedrock geology data were derived from a layer of the New York Geologic Survey 1999 Bedrock Geology Lower Hudson and Hudson Mohawk coverages. Additional hydrography and boundary coverages for Westchester, Putnam, Dutchess, Columbia, and Rennssalaer counties were obtained from the U.S. Department of Commerce, Bureau of the Census 1998 TIGER Files.

### Data analysis

Analyses addressed correlations between northing (distance from NYC) and physical properties, water chemistry and periphyton variables, to establish if distance from a large urban area had a general influence on these variables. Multiple stepwise linear regression was used to determine which variables most affected periphyton biomass and nutrient content ($\alpha \leq 0.05$ for inclusion, $\alpha \geq 0.10$ for exclusion into the model). Multicollinearity was assessed by comparing individual $t$-values and $r^2$ with overall $r^2$ and $P$ values in each model (Graham, 2003); no issues were detected. Predictor (independent) variables included physical (temperature, canopy cover, turbidity, depth, width, and current velocity), and water chemistry (DOC, $NO_3^-$–N, $NH_4^+$–N, SRP, TDP, Ca, and Mg) variables. GIS analysis, correlation, and ANOVA were used to determine the effect of land use and urbanization on stream and periphyton variables. Data from physical, water chemistry, and periphyton variables for each stream were entered into an Arc Info data table, visualized as points by using location data, northing and easting, and then combined with population density, land use and geology coverages. For GIS, a 150-m buffer zone (radius) was created around each sample point in Arc Info (Tufford et al., 1998). Arc Info output files for population density, land use, and geology attributes were generated for the buffer zones of each stream. The weighted mean population density, bedrock geological data, and percent land use categories were determined for each 150-m buffer zone. Correlations were used to determine links between population density and the physical, water chemistry, and periphyton variables. ANOVA followed by Tukey post-hoc HSD tests were used to determine the effects of land use (Sokal & Rohlf, 1995). Each stream-reach site was classified into a predominant land-use category, determined by the landscape that occupied the largest percentage within each buffer zone (typically >60% of total area). Statistical analyses were performed using Systat 10.0 with $\alpha \leq 0.05$ set for a type I error. All quantitative data were tested for normality; non-normal data were transformed using standard transformation methods (Sokal & Rohlf, 1995). Most physical, chemical, and periphyton variables required $\log_{10}$ transformation with the exception of Si (square root transformation) and DOC and pH (normal). Of the landscape variables, population density was $\log_{10}$ transformed.

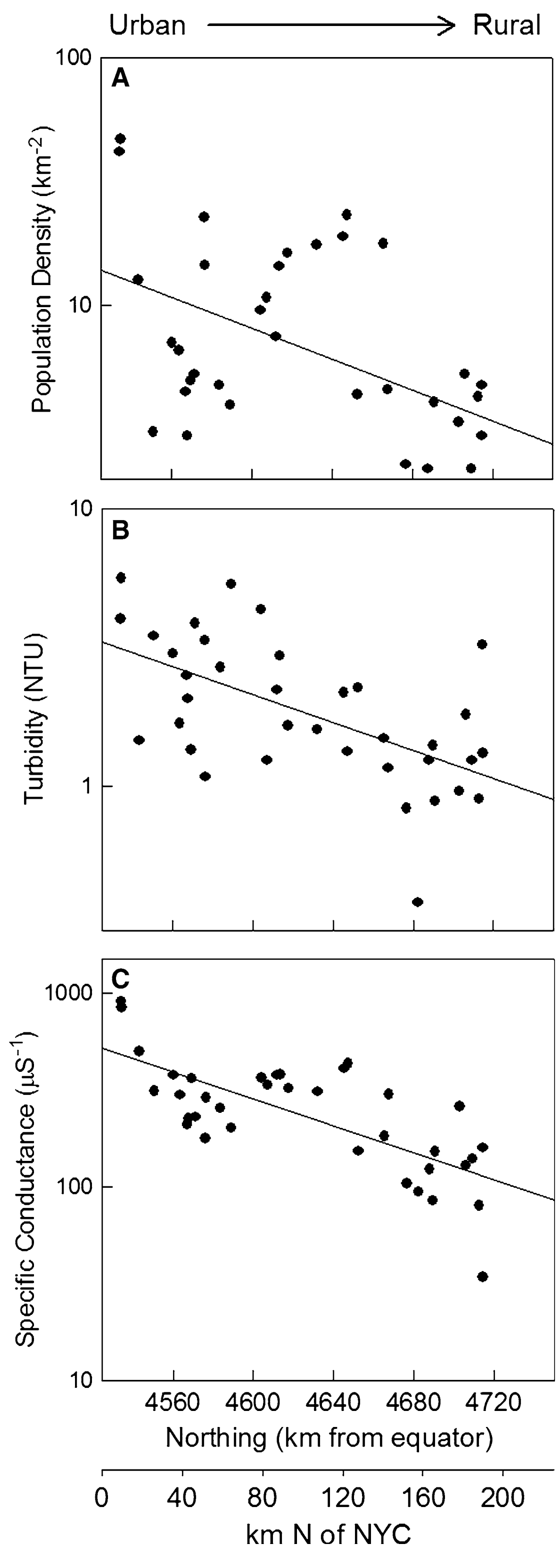
## Results

### Landscape patterns

Streams situated in urban landscapes were concentrated in the southern portion of the study area. Percent urban area (as determined by GIS) within respective 150-m buffer zones (radii) at each site, ranged from <0.01 to 100%, as did percent agriculture and forest area. These landscape variables were compared with geographic distance from NYC (northing). Human population density significantly decreased ($r = -0.739$; $P < 0.00001$; Fig. 1A), while % agricultural land use significantly increased ($r = 0.347$; $P = 0.0379$) with northing (Table 1). Percent urban and % forested land showed similar trends but were NS ($P > 0.10$; Table 1). Therefore, northing (distance from NYC) was used as a proxy variable to further test the effects of urbanization.

Among physical variables, stream water turbidity and temperature significantly decreased with northing (i.e., greater values in urban streams; Table 1; Fig. 1B). Turbidity ranged from 0.83 to 5.63 NTU, while summer temperatures ranged from 8.5 to 25.9°C. Percent canopy cover, stream depth, stream width, and current velocity were not significantly correlated with northing. Most of the water chemistry variables were negatively correlated with northing (i.e., greater in urban streams), including conductivity (Fig. 1C) and dissolved Mg, Ca, SRP, pH, DOC, and

**Fig. 1** Plots of the significant correlations between geographic distance from NYC (northing) and key land use (**A** human population density; $r = -0.739$, $P < 0.001$), physical (**B** stream turbidity; $r = -0.587$, $P < 0.001$), and water chemistry (**C** conductivity; $r = -0.722$, $P < 0.001$) variables measured at each of 36 stream sites along a putative urban to rural land-use gradient (see Table 1 for complete statistics)




Si, but were non-significant for dissolved $NO_3^-$ and $NH_4^+$. Water chemistry variables that differed most among streams were pH (6.1–8.9), Mg (0.6–22 mg/l), conductivity (34–908 µS/cm), and SRP (6.4–66 µg P/l). Each of these was significantly greater in urban streams.

Periphyton biomass and stoichiometry

Periphyton biomass, measured as Chl-*a* (per unit area), varied by two orders of magnitude among the 36 streams and by approximately one order when measured as AFDM (Table 2). Similarly, carbon content of algal periphyton ranged nearly 30-fold, from 0.06 to 1.7 µmol/mm$^2$ (unit area basis), but only about 6.6-fold on a DM basis (14.2–93.6 µmol/mg). Periphyton AFDM and Chl-*a* concentrations were very highly correlated ($r = 0.8625$; $P < 0.00001$), and the AI of these measures varied strongly among streams (mean 425 ± 44 [SE]), with 58% of the streams (21 of 36) with low (<200) or moderate (200–400) ratios.

Periphyton C, N, and P content also varied among streams (Table 2) and created a range of periphyton C:N ratios from 4.4 to 12.5 (mean = 7.6 ± 1.5; Redfield = 6.6) and C:P ratios from 122 to 706 (mean = 248 ± 109; Redfield = 106). The periphyton C:N ratios in 29 of 36 streams were greater than the Redfield ratio of 6.6, and all C:P ratios were greater than the predicted ratio of 106. The average C:N:P ratio of 191C:24N:1P was more C-rich than the idealized Redfield ratio of 106:16:1.

Periphyton biomass and nutrient content correlated either positively or negatively with northing (Table 3). Periphyton biomass, measured as AFDM ($r = -0.485, P = 0.003$; Fig. 2A) was significantly greater in streams at the urban end of the gradient (=negative correlation with northing), although Chl-*a* concentration per SA, while showing a similar trend, was non-significant. Correlations between calculated AI and

**Table 1** Correlations between northing (distance from NYC) and land-use properties, physical variables, and water chemistry from 36 streams from an urban–rural land-use gradient north of New York City ($r$, correlation coefficient; values with $P \leq 0.05$ are printed in bold)

| Northing versus | $r$ | $P$ |
|---|---|---|
| Land use | | |
| % Agricultural land | **+0.347** | **0.0379** |
| % Forested land | −0.245 | 0.1497 |
| % Urban land | −0.128 | 0.4564 |
| Population density | **−0.739** | **<0.0001** |
| Physical variables | | |
| Canopy cover | −0.179 | 0.2972 |
| Current velocity | −0.035 | 0.8397 |
| Depth | −0.114 | 0.5067 |
| Temperature | **−0.555** | **0.0004** |
| Turbidity | **−0.587** | **0.0002** |
| Width | −0.096 | 0.5792 |
| Water chemistry | | |
| Ca | **−0.575** | **0.0002** |
| Conductivity | **−0.722** | **<0.0001** |
| DOC | **−0.418** | **0.0111** |
| Mg | **−0.653** | **0.0002** |
| $NH_4^+$ | +0.171 | 0.3195 |
| $NO_3^-$ | −0.183 | 0.2843 |
| pH | **−0.525** | **0.0010** |
| Si | **−0.341** | **0.0416** |
| SRP | **−0.558** | **0.0004** |
| TDP | −0.217 | 0.2038 |

Negative correlations indicate greater values in urban streams

land-use measures were weak or inconsistent (correlations with northing, human population density, and % urban land NS; $P > 0.250$), but AI did correlate positively with % forested land ($r = 0.537$; $P = 0.0007$).

Periphyton in urban streams had significantly greater C, N, and P content (=negative correlation with northing; Fig. 2B; Table 3). Periphyton also had greater algal C:N in urban streams (negative correlation with northing) and lower N:P ratios (positive correlation with northing; Fig. 2C). Further, periphyton N:P ratios in a majority of streams were greater than Redfield predictions, although those in urban locations were closer to the predicted value of 16. The trend for periphyton C:P was positive with northing (relatively greater P in urban streams), but the trend was non-significant ($r = 0.277$; $P = 0.1068$).

Influence of in-stream variables on periphyton biomass and nutrient stoichiometry

Multiple linear regression (MLR) models were next used to identify the most important proximate predictors (local physical and water chemistry variables) of variation in periphyton biomass and nutrient content among the study streams (Table 4). Variation in AFDM ($r^2 = 0.646$) and Chl-$a$ ($r^2 = 0.561$) per unit area were more effectively predicted than was percent organic matter ($r^2 = 0.119$) for these streams. Collectively, the models suggest that benthic algal biomass was negatively influenced by percent canopy cover, stream depth, and in one measure (% organic matter), turbidity. These variables were all significantly greater in urban streams (decreased with northing). None of the major nutrients associated with urbanization (SRP, TDP, $NH_4^+$, $NO_3^-$) were included in any of the models, despite several positive bivariate correlations (e.g., SRP versus AFDM; $r = +0.366$, $P = 0.0304$; $NO_3^-$ vs. Chl-$a$; $r = +0.434$, $P = 0.0092$).

The influence of proximate, in-stream variables on periphyton nutrient content and stoichiometry were also examined using MLR (Table 5). Nutrient content was also best predicted by aqueous cation (Mg or Ca) concentration and canopy cover. However, stoichiometric ratios, particularly those with phosphorus, were predicted to be a function of aqueous P (as TDP).

Influence of land-use variables

Differences in human population density and landscape type were clearly identified within the study area (Table 1). From this, seven of nine major land use classes were identified from the NY State GIS database: urban, agricultural, rangeland, forested, water (lakes, ponds, and streams), wetlands, and barren land (non-vegetated but not impervious surfaces). Of these, only urban, agricultural and forested land occurred in large enough frequencies for analysis. Their potential influence on periphyton was first examined using correlations between landscape variables (three land-use types and human population density) and the biomass and nutrient stoichiometry of stream periphyton (Table 6). Biomass (as AFDM) was positively correlated with increasing population density (Fig. 3A), with percent of urban land, based on GIS estimates (Fig. 3B), and negatively with

**Table 2** Summary data for biomass, nutrient content, and stoichiometry of algal periphyton sampled from 36 streams from an urban to rural land-use gradient north of New York City (SD, standard deviation; AFDM, ash-free dry mass; DM, dry mass; SA, surface area; atomic stoichiometric ratios calculated from nutrient per unit area)

| | Min | Max | Mean | SD |
|---|---|---|---|---|
| Biomass | | | | |
| AFDM (g/m$^2$) | 1.6 | 47.0 | 9.8 | 10.4 |
| Chl-*a*/DM (μg/g DM) | 2.0 | 63.4 | 16.8 | 16.6 |
| Chl-*a*/SA (mg/m$^2$) | 1.7 | 226.4 | 37.5 | 49.9 |
| Ratio Chl-*a*/AFDM (%) | 0.2 | 6.3 | 1.7 | 1.7 |
| % Organic matter | 23.2 | 60.0 | 41.5 | 4.7 |
| Nutrient content | | | | |
| C/DM (μmol/mg) | 14.2 | 93.60 | 38.1 | 24.1 |
| C/SA (μmol/mm$^2$) | 0.06 | 1.70 | 0.39 | 0.41 |
| N/DM (μmol/mg) | 0.008 | 0.209 | 0.050 | 0.047 |
| N/SA (μmol/mm$^2$) | 1.8 | 12.2 | 0.05 | 0.05 |
| P/DM (μmol/mg) | 0.0016 | 0.0138 | 0.0020 | 0.0030 |
| P/SA (μmol/mm$^2$) | 0.0170 | 0.1360 | 0.0777 | 0.0274 |
| Nutrient stoichiometry | | | | |
| C:N | 4.4 | 12.5 | 7.6 | 1.5 |
| C:P | 122 | 706 | 248 | 109 |
| N:P | 14.3 | 93.8 | 33.7 | 15.6 |

**Table 3** Correlations between northing (distance from NYC) and biomass, nutrient content and stoichiometry of algal periphyton sampled from 36 streams from an urban–rural land-use gradient north of New York City (see Table 2 for abbreviations, values with $P \leq 0.05$ are printed in bold)

| Northing versus | *r* | *P* |
|---|---|---|
| Biomass | | |
| AFDM | **−0.485** | **0.0031** |
| Chl-*a*/DM | 0.023 | 0.8976 |
| Chl-*a*/SA | −0.301 | 0.0792 |
| Ratio Chl-*a*/AFDM (%) | −0.272 | 0.1080 |
| % Organic matter | 0.254 | 0.1408 |
| Nutrient content | | |
| Algal C/DM | −0.223 | 0.1982 |
| Algal C/SA | **−0.459** | **0.0056** |
| Algal N/DM | −0.141 | 0.4197 |
| Algal N/SA | **−0.425** | **0.0110** |
| Algal P/DM | −0.088 | 0.6171 |
| Algal P/SA | **−0.501** | **0.0022** |
| Nutrient stoichiometry | | |
| C:N / SA | **−0.334** | **0.0500** |
| C:P / SA | 0.277 | 0.1068 |
| N:P / SA | **0.402** | **0.0167** |

Negative correlations indicate greater values in urban streams

greater forest land cover (Fig. 3C). Biomass measured as Chl-*a* concentration correlated negatively with % forested land (Table 6). Periphyton C, N, and P concentrations each correlated positively with human population density (Fig. 4) and with % urban land cover (Table 6). Despite a wide range of % agricultural land across the streams-sites (from 0 to 100%; mean: 44.4 ± 43.5%), periphyton biomass was unrelated to this land-use attribute (Table 6). Periphyton N:P ratio correlated negatively with human population density, but none of the stoichiometric ratios correlated with any of the three main land-use categories.

The influence of land-use type on periphyton biomass and nutrient stoichiometry was contrasted among the three major GIS-based land-use categories, designated as either forested, agriculture or urban, based on the greatest land-use percentage within a 150-m radius at each geographic location. Not all periphyton variables exhibited clear patterns, but algal biomass (as Chl-*a*) was significantly different among the three land-use areas, with greatest amounts measured in urban streams (Table 7; Fig. 5). Similarly, periphyton in urban streams also had significantly greater C and N content. In each of

**Table 4** Multiple linear regression analysis identifying stream-variable (proximate) predictors of benthic algal biomass, measured as ash-free dry mass (AFDM), Chl-*a* per unit dry mass (Chl-*a*/DM), Chl-*a* per unit surface area (Chl-*a*/SA), and percent organic matter

| | Slope ± SE | *t*-Score | *P* |
|---|---|---|---|
| AFDM | | | |
| Mg | 0.697 ± 0.100 | 6.968 | <0.00001 |
| Percent canopy cover | −0.006 ± 0.002 | −2.729 | 0.01024 |
| Depth | −0.001 ± 0.004 | −2.488 | 0.01826 |
| ANOVA: $P < 0.00001$ | | Adjusted $r^2 = 0.646$ | |
| Chl-*a*/DM | | | |
| DOC | −0.029 ± 0.016 | −1.841 | 0.07521 |
| pH | 0.143 ± 0.042 | 3.390 | 0.00192 |
| Percent canopy cover | −0.003 ± 0.001 | −2.221 | 0.03376 |
| Depth | −0.007 ± 0.002 | −2.746 | 0.00994 |
| ANOVA: $P = 0.00003$ | | Adjusted $r^2 = 0.497$ | |
| Chl-*a*/SA | | | |
| pH | 0.592 ± 0.116 | 5.122 | <0.00001 |
| Percent canopy cover | −0.009 ± 0.003 | −2.968 | 0.00564 |
| Depth | −0.020 ± 0.006 | −3.280 | 0.00251 |
| ANOVA: $P < 0.00001$ | | Adjusted $r^2 = 0.561$ | |
| % Organic matter | | | |
| Turbidity | −11.341 ± 4.739 | −2.393 | 0.02236 |
| ANOVA: $P = 0.02236$ | | Adjusted $r^2 = 0.119$ | |

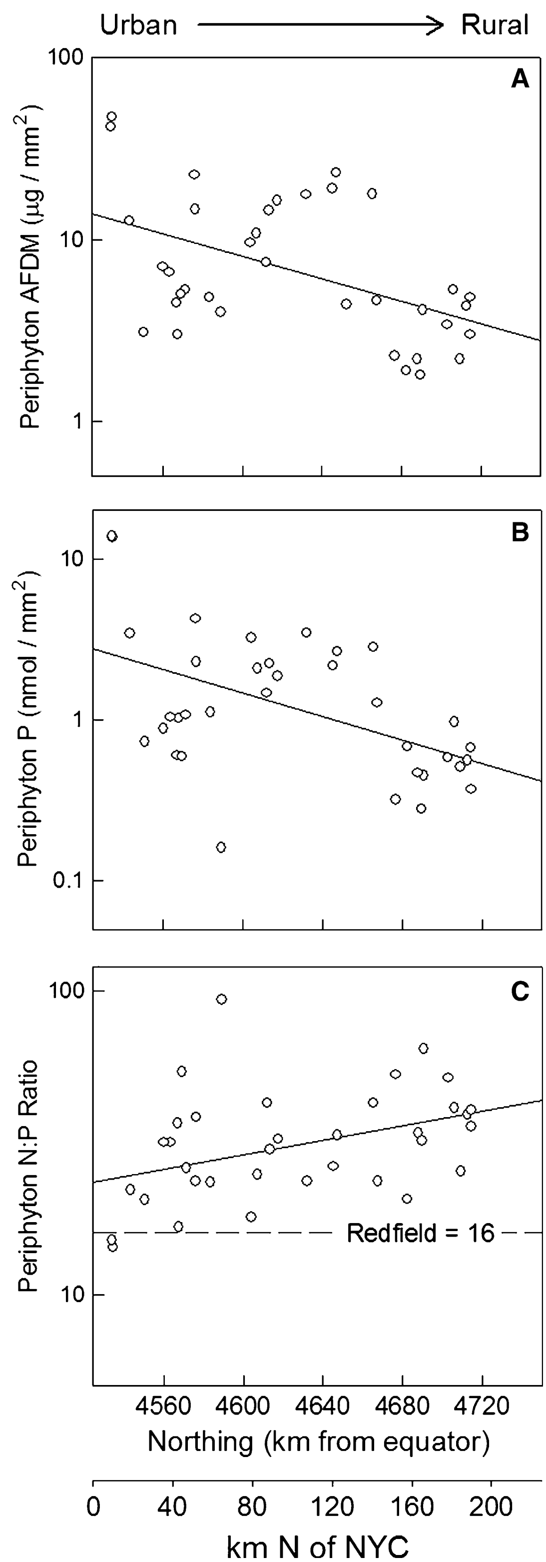
Independent variables were physical and water chemistry variables measured at each stream (independent variables listed in order of relative importance; $r^2$ = coefficient of determination for complete model)

**Table 5** Multiple linear regression analysis identifying stream-variable (proximate) predictors of periphyton nutrient content and stoichiometric ratios (per unit SA)

| | Slope ± SE | *t*-Score | *P* |
|---|---|---|---|
| C/SA | | | |
| Mg | 0.665 ± 0.111 | 5.984 | <0.00001 |
| Percent canopy cover | −0.006 ± 0.002 | −2.677 | 0.01162 |
| ANOVA: $P < 0.00001$ | | Adjusted $r^2 = 0.571$ | |
| N/SA | | | |
| Ca | 0.830 ± 0.140 | 5.923 | <0.00001 |
| Percent canopy cover | −0.005 ± 0.002 | −2.423 | 0.02121 |
| ANOVA: $P < 0.00001$ | | Adjusted $r^2 = 0.562$ | |
| P/SA | | | |
| Ca | 1.138 ± 0.182 | 6.256 | <0.00001 |
| ANOVA: $P < 0.00001$ | | Adjusted $r^2 = 0.529$ | |
| C:N | | | |
| Mg | 4.431 ± 1.484 | 2.986 | 0.00539 |
| Conductivity | −4.408 ± 1.962 | −2.247 | 0.03169 |
| ANOVA: $P = 0.00587$ | | Adjusted $r^2 = 0.230$ | |
| C:P | | | |
| TDP | −0.258 ± 0.098 | −2.620 | 0.01334 |
| Si | −0.297 ± 0.095 | −3.130 | 0.00372 |
| ANOVA: $P = 0.00087$ | | Adjusted $r^2 = 0.316$ | |
| N:P | | | |
| TDP | −0.317 ± 0.098 | −3.238 | 0.00281 |
| Si | −0.348 ± 0.094 | −3.688 | 0.00083 |
| ANOVA: $P = 0.00008$ | | Adjusted $r^2 = 0.410$ | |

Independent variables were physical and water chemistry variables measured at each stream (independent variables listed in order of relative importance; $r^2$ = coefficient of determination for complete model)

**Fig. 2** Plots of the significant correlations between geographic distance from NYC (northing) and periphyton biomass (**A** ash-free dry mass per unit area; $r = -0.485$, $P = 0.003$), periphyton nutrient content (**B** phosphorus concentration per unit area; $r = -0.501$, $P = 0.002$), and periphyton stoichiometry (**C** N:P ratio; $r = 0.402$, $P = 0.17$) measured at each of 36 stream sites along a putative urban to rural land-use gradient (see Table 3 for complete statistics)




these comparisons, those streams draining rural forested land were classified with the least biomass and nutrient content. Although the nutrient stoichiometric ratios varied along the urban–rural gradient (based on northing; Table 3), no significant differences were revealed when compared by land-use categories (Table 7).

## Discussion

### Streams in contrasting landscapes

Our data demonstrate that streams draining different landscapes in southern New York State have correspondingly different physical, chemical, and biological properties. Watersheds along this urban–rural gradient differ little with regard to soil type, geology, or forest type, but exhibit profound ecological differences, making this region a useful setting in which to test human impacts (McDonnell et al., 1997). In our study, urban streams were more nutrient-rich, had higher pH, greater concentrations of dissolved cations, and greater conductivity. The range of conductivities and nutrient concentrations equal or exceed that observed along other urban–rural land-use gradients in the U.S. (Walker & Pan, 2006; Sprague et al., 2007; Ponader et al., 2008).

All of the significant trends in water chemistry along the urban–rural gradient increased from rural to urban areas (Table 1; Figs. 1, 3). The elevated SRP concentrations likely resulted from sewage inputs, as well as fewer wetlands and altered soils (Walsh et al., 2005). Sonoda & Yeakley (2007) demonstrated that soils adjacent to urban streams have lower capacities for retaining P than those in non-urban areas. We observed a highly significant correlation between SRP in stream water and distance from an urban center, as well significant trends for dissolved Mg, Ca, Si, DOC, and pH, but not dissolved $NH_4^+$ or $NO_3^-$ (Table 1). Our data partly support earlier contentions (Pluhowski, 1970; Pickett et al., 2001) that streams along an urbanization gradient are warmer (Table 1: $r = -0.555$ versus northing). However, when compared among specific GIS land-use categories, stream temperatures were not significantly different (forested: 18.7 ± 1.0°C versus urban: 18.8 ± 3.9°C). While evidence of a "heat-island" effect was not seen, our data do agree with prior studies showing many other physical and chemical effects of urbanization (Paul & Meyer, 2001; Strayer et al., 2003), effects that likely have important effects on stream periphyton.

## Periphyton biomass and land use

Periphyton biomass was significantly greater in streams draining urbanized landscapes and in locations with greater human population density. Periphyton in rural, forested streams averaged roughly one-third to one-fifth the amount in urban locations (Figs. 3, 5; Tables 3, 6). Average biomass in urban streams of 18.8 ± 6.0 g/m$^2$ AFDM and 75.6 ± 28.5 mg/m$^2$ Chl-*a*, and maximal Chl-*a* levels exceeding 100 mg/m$^2$, are comparable to quantities measured in agricultural streams elsewhere (Biggs & Close, 1989; Chételat et al., 1999; Godwin & Carrick, 2008) and in experimentally nutrient-enriched streams (e.g., Greenwood & Rosemond, 2005). However, variation in stream algal biomass in our study area was not correlated with % agricultural land, despite dominating the watersheds of 13 streams. Instead, biomass was most closely correlated with human population density and % urban land (Table 6). Landscapes classified as agricultural in

**Table 6** Correlations between landscape variables and periphyton biomass, nutrient content and stoichiometry (*r*, correlation coefficient, with probabilities; * $P \leq 0.05$, ** $P < 0.01$, values with $P \leq 0.05$ are printed in bold)

| | Population density *r* | Percent urban land *r* | Percent agricultural land *r* | Percent forested land *r* |
|---|---|---|---|---|
| Biomass | | | | |
| AFDM/SA | **0.429*** | **0.414*** | −0.091 | −0.256 |
| Chl-*a*/SA | **0.356*** | **0.362*** | 0.159 | **−0.465**** |
| % Organic matter | −0.185 | 0.132 | 0.093 | −0.205 |
| Nutrient content | | | | |
| Algal C/SA | **0.443**** | **0.401*** | −0.052 | −0.284 |
| Algal N/SA | **0.445**** | **0.404*** | 0.005 | **−0.344*** |
| Algal P/SA | **0.491**** | **0.389*** | −0.037 | −0.289 |
| Nutrient stoichiometry | | | | |
| C:N | 0.168 | 0.164 | −0.263 | 0.128 |
| C:P | −0.286 | −0.116 | −0.020 | 0.117 |
| N:P | **−0.338*** | −0.170 | 0.101 | 0.041 |

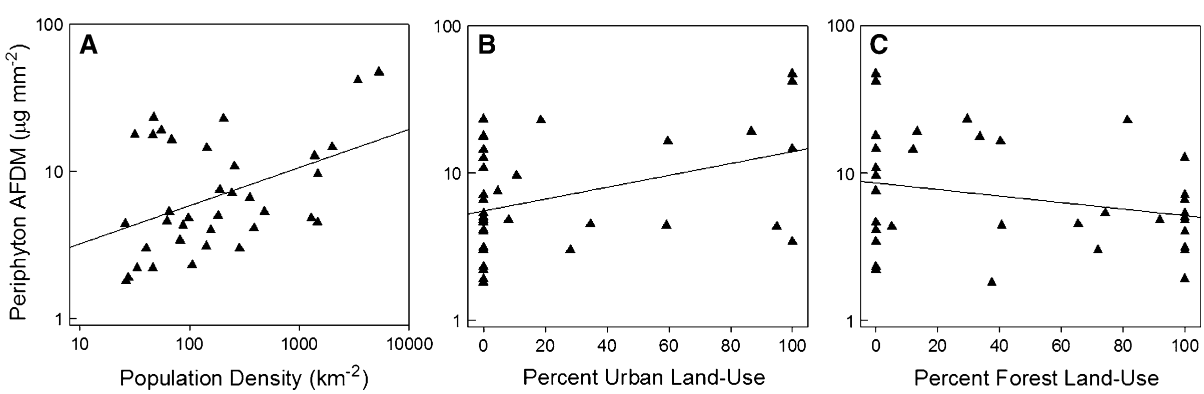



**Fig. 3** Relationships between periphyton biomass (ash-free dry mass per unit area) versus human population density, percent urban land use and percent forest land use across 36 stream sites along a putative urban to rural land-use gradient

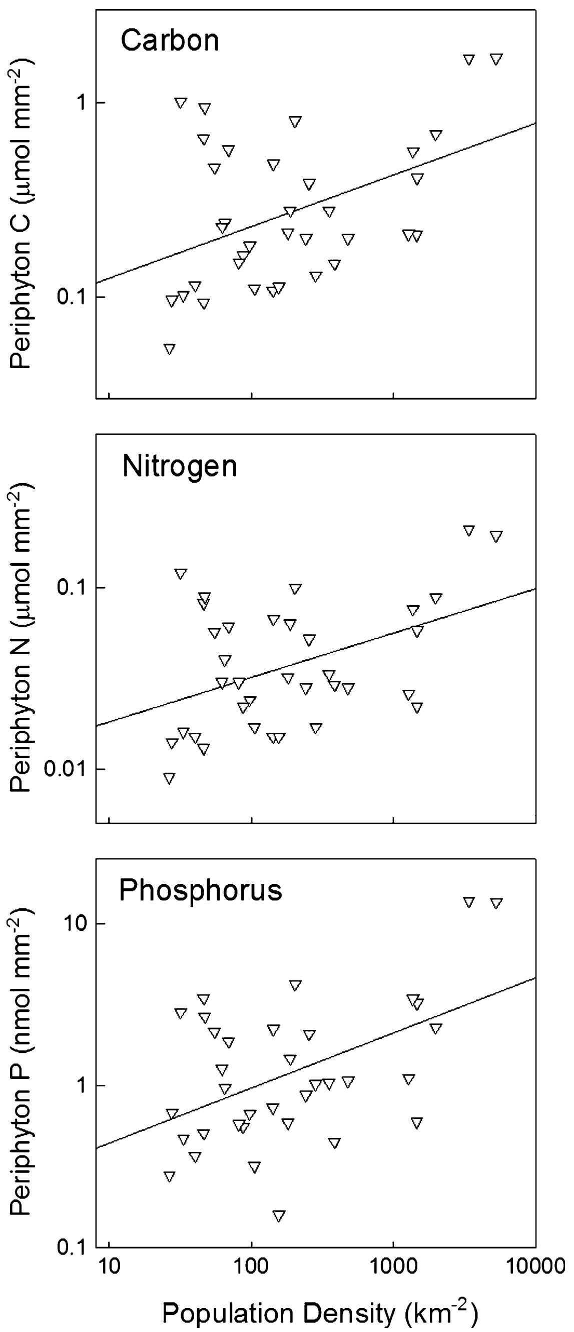



**Fig. 4** Relationships between algal carbon, nitrogen, and phosphorus (per unit area) versus human population density across 36 stream sites along a putative urban to rural land-use gradient

our study area had intermediate levels of periphyton biomass (mean AFDM: 9.1 ± 2.0 mg/m$^2$). Agricultural streams in other regions have much greater algal biomass (>20 g AFDM/m$^2$, 100–300 mg Chl-*a*/m$^2$; Biggs & Close, 1989). We attribute this difference to a lower intensity form of agriculture in our region, which is a mixture of grain crops and fallow fields.

Few studies have characterized periphyton biomass and stoichiometry in urban streams. However, a meta-analysis of data from more than 300 streams and rivers from the USGS National Stream Water-Quality Monitoring Network revealed significant positive correlations between benthic Chl-*a* and % urban land area (Dodds et al., 2002), which agrees with our data for the NYC urban–rural gradient. Murdock et al. (2004) reported that one urban stream in Texas accumulated periphyton biomass at very rapid rates, despite frequent floods that were capable of removing most of this production. Average total biomass in their system occasionally exceeded 500 mg Chl-*a*/m$^2$, which was five or more times the recognized nuisance level (Welch et al., 1988; Murdock et al., 2004). Just three streams in the present study (all urban) exceeded that criterion.

It has been suggested that algal biomass may exhibit inconsistent responses to increasing urbanization of streams (Walsh et al., 2005), but the present data and those cited earlier suggest that urban land use usually results in greater periphyton biomass. Some of this increased biomass may be facilitated by reduced canopy cover in the riparian zone, providing greater light for primary production (Table 4). Urban streams in our study area also had significantly greater dissolved SRP, Si, Ca, and Mg (negative correlations with northing; Table 1), suggesting that greater SRP supply may also have exerted a positive influence. Hill & Fanta (2008) have demonstrated that stream periphyton growth can be co-limited by P and irradiance, although experiments in other streams suggest that light may be a more important factor (Schiller et al., 2007). Canopy cover values estimated for our streams by spherical densitometer measurements indirectly measure light availability, but have the advantage of reflecting longer-term landscape properties of each site (e.g., Fitzpatrick et al., 1998; Pan et al., 1999).

One may also ask whether urban streams are more autotrophic, based on the presence of elevated periphyton biomass. In the present study, no direct measures of productivity were made. However, periphyton AFDM and Chl-*a* concentrations in our streams were

**Table 7** Results of analysis of variance comparing mean periphyton biomass and nutrient stoichiometry (per unit surface area) among three major land-use categories (Tukey HSD post-hoc analyses run following significant general ANOVAs; individual land use listed in order of their means; classes sharing underlines were judged not statistically different [$P > 0.05$])

| | *F* | *P* | Post hoc tests |
|---|---|---|---|
| Biomass | | | |
| AFDM/SA | 3.057 | 0.06053 | |
| Chl-*a*/SA | 5.615 | 0.00796 | Forest Agricultural Urban |
| % Organic matter | 1.613 | 0.21455 | |
| Nutrient content | | | |
| Algal C/SA | 3.484 | 0.04276 | Forest Agricultural Urban |
| Algal N/SA | 4.016 | 0.02780 | Forest Agricultural Urban |
| Algal P/SA | 2.874 | 0.07116 | |
| Nutrient stoichiometry | | | |
| C:N | 0.893 | 0.41928 | |
| C:P | 0.086 | 0.91784 | |
| N:P | 0.236 | 0.79117 | |

highly correlated ($r = 0.862$; $P < 0.00001$), suggesting that these streams have an algal-based metabolism. The geographic pattern of periphyton AFDM : Chl-*a* (AI), a relative measure (although approximate) of the degree of heterotrophy or autotrophy (Biggs & Close, 1989), was inconsistent among stream sites. The AI was significantly greater (=less autotrophic) in more rural streams in forested landscapes, but did not correlate with any measures of urbanization. However, the C:Chl-*a* ratio of epilithic periphyton among all of our streams averaged $\approx$200, which is broadly indicative of a relatively high algal content in the mixed periphyton, and is substantially less than a global average of 405 across many freshwater systems (Frost et al., 2005). Among our streams, this ratio was least (greater algal content) in urban streams (139 $\pm$ 25) and greatest in rural, forested streams (299 $\pm$ 42). It is possible that the degree of autotrophy may not be directly responsive to urbanization, but our AFDM, Chl-*a* and carbon data suggested that the majority of this carbon is algal based. For this reason, nutrient stoichiometry of stream periphyton may be important in studies of urban-to-rural gradients.

## Nutrient effects and algal stoichiometry

Nutrient content of periphyton varied widely among our study streams, with algal carbon ranging more than from 20-fold, from 0.06 to 1.7 μmol/mm$^2$, while N and P content each varied by more than 6-fold among streams (Table 2). Concentrations of all three elements correlated significantly along the land-use gradient (northing, distance from NYC, % urban land), with greater concentrations in urban streams (Tables 3, 6; Figs. 4, 5). This trend of greater N and P content suggests that algal matter in urban streams may provide greater nutrition for consumers, which require specific quantities of N and P for metabolism and growth. Mass gain in the larval caddisfly *Glossosoma nigrior* was positively correlated with greater periphyton N content on which they grazed (Hart, 1987). Similarly, growth of the stream-dwelling snail *Elimia flavescens* was significantly greater when provided with P-enriched periphyton (40% greater than controls), but only when food supply was low (Stelzer & Lamberti, 2002). The nutrient content of periphyton was also shown to affect the rates of excretion and retention of N and P by heptageniid mayfly larvae, although the animals retained or accumulated P in excess of immediate needs (Rothlisberger et al., 2008). A shift from nutrient-limited to nutrient-sufficient conditions in a stream, as occurs during urbanization, could alter interactions between grazers and algal food sources, and have important consequences for nutrient cycling.

Greater accumulation of P and N by periphyton in urban streams cannot be fully attributed to elevated aqueous sources of these nutrients, as dissolved $NH_4^+$ and $NO_3^-$ concentrations did not correlate with northing (Table 1) or appear in any of the multiple regression models for periphyton biomass (Tables 4, 5). The absence of aqueous nutrients in some of the regression models may be due to the fact that some of the carbon in periphyton was detrital rather than algal. However, we did observe significantly greater SRP concentrations in urban streams, which could have enhanced periphyton growth, as well as P and N content. An alternative explanation is that algal growth effectively diluted the detrital content (high C:P) of the periphyton, and thereby increased the net P concentration of the assemblage. Nonetheless, experiments using nutrient-diffusing substrata have shown directly that increased P can have a direct stimulating effect (Schiller et al., 2007). Such effects may also result when either N or P is limiting algal growth, and one nutrient is preferentially assimilated and stored (Liess & Hillebrand, 2006).

The C:N:P stoichiometry of periphyton from our study streams varied both above and below predicted Redfield ratios. However, C:N ratios averaged approximately 7.6 across our streams (Table 2), which is very similar to a median of 7.5 from a series of laboratory growth experiments with optimum growth rates (Hillebrand & Sommer, 1999). These authors also suggested that a range of C:N ratios between 5 and 10 are optimum for algal growth, while ratios >10 are indicative of N limitation. More than 91% of our measured periphyton C:N ratios (33 of 36) fell between 5 and 10, suggesting that most were within their "optimal" range. In contrast, periphyton C:P ratios in our streams were more variable, ranging from 122 to more than 700 (mean = 248; Table 2). While Redfield (1958) suggested an optimum or average value of around 106, Hillebrand & Sommer's (1999) results suggest that algal C:P ratios around 130 would achieve maximum growth rates. Only 5 of 36 streams had C:P ratios ≤130 (although all were >106), and were located within all three land-use types. By this evidence, it would appear that algal growth may have been P-limited in streams in all land-use types. In situ experiments indicate that P supply may often limit stream periphyton growth, although N + P or light + P co-limitation is more common, and such responses can be season-dependent (Bothwell, 1985; Francoeur et al., 1999; Francoeur, 2001; Hill & Fanta, 2008). However, other experiments have observed ≥90% maximal algal growth rates at SRP concentrations as low as 16 µg/l (Rier & Stevenson, 2006), a concentration that was exceeded in 44% (16 of 36) of our streams. While our data are suggestive of P limitation, they should be viewed with some caution, especially as periphyton assemblages likely have varying amounts of algal, bacterial, and detrital material.

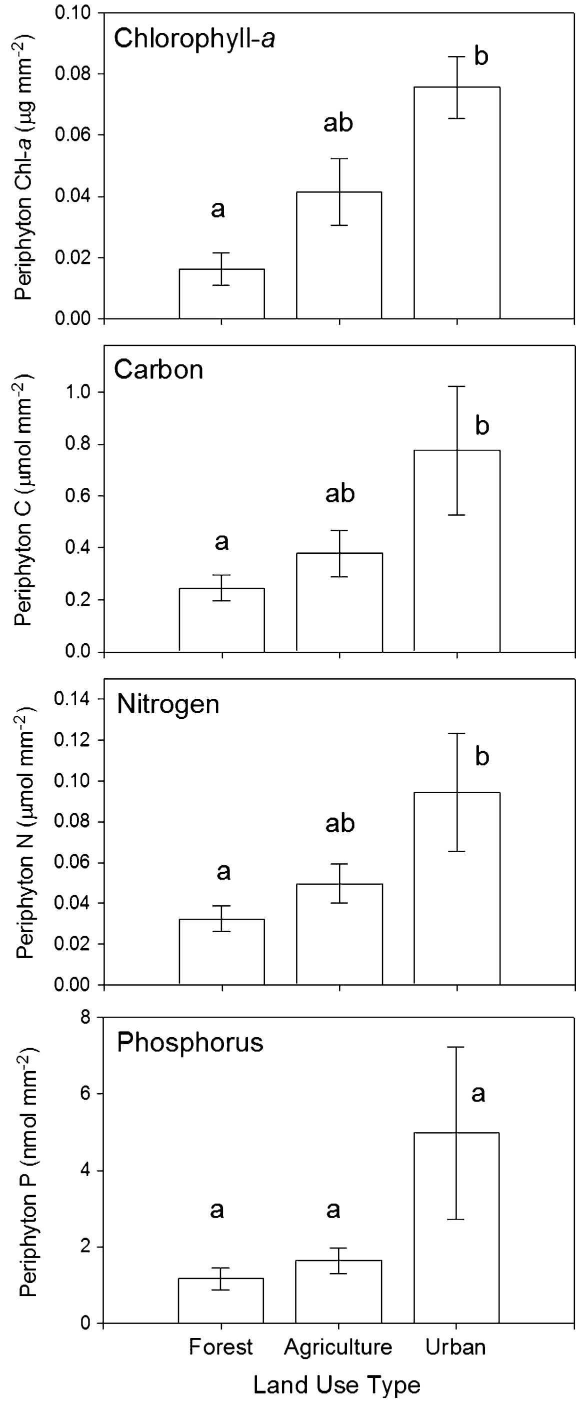



**Fig. 5** Mean periphyton biomass (µg chlorophyll-*a*/mm$^2$), and periphyton nutrient content (nmol or pmol C, N, P/mm$^2$) measured in streams located in one of three major land-use types (*bars* represent means ± 1 SE; $n_{forest} = 15$; $n_{agricultural} = 13$; $n_{urban} = 8$; *bars* sharing the *same letter* were judged not significantly different, based on Tukey's HSD test [$P > 0.05$])

Schiller et al. (2007) examined nutrient limitation and algal stoichiometry in three streams in NE Spain and observed that periphyton from a stream located in a forested site had greatest C:N ratios, with intermediate ratios at an urban site, and lowest ratios (greater relative N) in the agricultural stream. We observed a different pattern among our 36 streams in New York, with greatest periphyton C:N in urban streams (Tables 3, 6), as well as greater absolute concentrations of N and P (Fig. 5). However, the range of C:N ratios in stream periphyton was not broad, ranging only from 4.4 to 12.5, with most near Redfield predictions. These ratios were not significantly different among the three major land-use categories (Table 7). Perhaps unlike other parts of the world, urban streams in SE New York State received greater inputs of dissolved N and P than either rural forested or agricultural streams. This difference may be attributed to differences in the intensity of agriculture in southeastern New York state, but perhaps also from differences in perspective. Changes in the land use may not easily fit into strict categories, but more likely vary continuously from rural to urban conditions. As such we suggest that the gradient approach may reveal more about the influence of land use on stream function.

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