J. N. Am. Benthol. Soc., 2006, 25(4):998–1017

Uptake of nutrients and organic C in streams in New York City drinking-water-supply watersheds

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Abstract. Uptake of nutrients and organic C was measured once annually between 2000 and 2002 in each of 10 streams within the water-supply source areas for New York City. Nutrients (PO_4^{3-} and NH_4^+) and organic C (glucose and arabinose) were injected into the streams for 1 to 2 h, and uptake lengths were estimated from the longitudinal declines in downstream concentration relative to that of a conservative tracer. Uptake lengths increased with stream size and were converted to uptake velocities, V_f, to remove scaling effects. V_f s of PO_4^{3-} and NH_4^+ varied inversely with the ambient concentration of total dissolved P (TDP) and total dissolved N (TDN), respectively, and were described by a model based on Michaelis–Menten kinetics. However, V_fs of glucose and arabinose were unrelated to the concentrations of any solute. V_fs of PO_4^{3-}, NH_4^+, arabinose, and (with less certainty) glucose varied positively with measures of ecosystem metabolism (24-h community respiration and gross primary productivity). Uptake flux (U) of NH_4^+ also varied positively with ecosystem metabolism, but Us of PO_4^{3-}, glucose, and arabinose did not. The V_fs of PO_4^{3-} and NH_4^+ were positively related to invertebrate species richness and % forest cover, and negatively related to molecular tracer concentrations (polyaromatic hydrocarbons and fecal steroids [PO_4^{3-}-V_f], fragrance materials [NH_4^+-V_f]) and population density. Spiraling, as a measure of ecosystem function, was sensitive to human impacts, most clearly through responses to nutrient loadings, but very probably through responses to other impacts as well.

Key words: nutrient spiraling, uptake length, land cover, human impact.

The rates at which nutrients are used and cycled by ecosystem processes may be of practical interest both because nutrient cycling can be considered an ecosystem service (Palmer et al. 2004)—a process that directly or indirectly supplies human needs such as food production or water purification—and because such rates may provide a sensitive measure of human impact on an ecosystem, relative to what its condition or function would be in the absence of human activity (Odum 1985). In streams and rivers, nutrients move downstream as they cycle, and the combined processes are termed *spiraling* (Webster and Patten 1979). A nutrient atom moves some distance downstream as it undergoes various transformations that usually involve a transfer from a dissolved available form in the water column to the streambed and completion of the cycle by returning to the water column. The average or expected distance an atom moves is termed the spiraling length (Newbold et al. 1981). Early considerations of the spiraling concept (Wallace et al. 1977, Webster and Patten 1979, Newbold et al. 1982) suggested that evolutionary adaptations of stream-dwelling organisms can be expected to retain nutrients in place and cycle the nutrient supply efficiently, so that an intact or undisturbed stream ecosystem should cycle nutrients over relatively short distances or spiraling lengths. It follows that disturbance or stress should produce longer spiraling lengths and, thus, that

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spiraling length might prove a sensitive indicator of human impact on ecosystem function.

Human inputs or alterations to streams might increase spiraling length in several ways. First, a direct toxic depression of metabolic activity could reduce nutrient use, allowing nutrients to be transported farther downstream before uptake or transformation. Second, an alteration of ecosystem structure (e.g., the loss or substitution of species or functional groups) might reduce the efficiency of nutrient processing or retention. Third, pollution to streams and rivers in the form of surplus nutrients might saturate the uptake capacity, again allowing nutrients to travel farther between cycles. Last, physical alteration, such as the removal of streambed heterogeneity, might interfere with the ability of the stream to retain nutrients. Of course, other disturbances can be envisioned that could shorten spiraling length. Removal of forest canopy, for example, might be expected to increase primary production and attendant nutrient uptake, or an impoundment might slow downstream transport, thereby allowing shorter spirals.

Tests of the responses of spiraling to disturbance have been accomplished through field measurements of nutrient uptake length. Uptake length is the portion of the spiraling length involving transfer from a dissolved available form in the water column to a sequestered form on the streambed and is the parameter of choice because its measurement is straightforward and because uptake length makes up the major portion of the total spiraling length (Newbold et al. 1982). Disturbances reported to increase uptake length include logging (Butturini and Sabater 1998) and urbanization (Grimm et al. 2005, Meyer et al. 2005). PO_4^{3-} uptake lengths were longer in second-growth forests compared to old-growth forests, a phenomenon attributed to the greater storage of fine-grained sediments in streams within the latter (Valett et al. 2002). Opening the forest canopy also increased NH_4^+ uptake length because stream channels flowing through meadows were narrower than channels in woodlands, thereby reducing habitat per unit length (Sweeney et al. 2004).

These studies tend to support the underlying hypothesis that disturbance increases spiraling length, but they cannot yet be regarded as conclusive. Moreover, many questions remain regarding the specific mechanisms by which disturbance may affect spiraling. Our study reports the uptake lengths of NH_4^+, PO_4^{3-}, glucose, and arabinose measured in streams that were identified as key freshwater sources to the New York City (NYC) drinking-water supply. PO_4^{3-} and NH_4^+ represent easily assimilable forms of P and N, both of which potentially limit algal and microbial processes in streams and downstream reservoirs. Glucose and arabinose represent 2 monomeric carbohydrates that differ in bioavailability (Kaplan and Newbold 2003) and, thus, partially represent the range of bioavailability characteristic of natural dissolved organic C (Frazier et al. 2005). Carbohydrates were used in addition to the nutrients N and P because of their potential to reflect impacts on heterotrophic metabolism. NO_3^- uptake length was not measured, primarily because of logistical constraints. Uptake lengths of NO_3^- are typically several times longer (i.e., uptake rates several times smaller) than those of NH_4^+ (Webster et al. 2003, Hall and Tank 2003), particularly where ambient NO_3^- concentrations are elevated (Davis and Minshall 1999, Hall and Tank 2003). Thus, long reach lengths would have been necessary and, in many cases, the feasible length was constrained by tributary junctions and reservoirs. In addition, simultaneous addition of NO_3^- and NH_4^+ can confound estimates of NO_3^- uptake (Bernhardt et al. 2002).

The streams monitored in our study reflected a range of sizes, ambient solute concentrations, and watershed land uses/covers (hereafter land use) and were the subject of a comprehensive analysis of water quality, biological condition, and ecosystem function (a large-scale enhanced water-quality monitoring project [the Project], Blaine et al. 2006). Thus, they provided the opportunity for a relatively robust test of the hypothesis that human impacts increase spiraling length and for an examination of the proximate factors governing spiraling length.

Methods

Study sites

Ten study sites were established along streams flowing into NYC drinking-water reservoirs (integrative sites in figs 1 and 2 in Arscott et al. 2006). Six of these streams were located in the Catskill and Delaware watersheds west of Hudson River (WOH) and 4 were located in the Croton/Kensico watersheds east of Hudson River (EOH). Low population density, high forest cover, and agriculture characterized the WOH region, whereas the EOH region was more influenced by urban and suburban development (Arscott et al. 2006). Watershed areas of the WOH sites ranged from 100 to 272 km^2, whereas those EOH were considerably smaller (35–46 km^2). The stream reaches used in our study also were used for concurrent measurements of stream ecosystem metabolism (Bott et al. 2006).

Stream solute additions

Solute uptake length (S_w) for NH_4^+, PO_4^{3-}, glucose, and arabinose were measured once annually in the 10 streams for 3 y (2000–2002). Solute additions were made under baseflow conditions between June and October using the Stream Solute Workshop (1990) approach. Each addition involved simultaneous injections of a conservative tracer (sodium bromide), PO_4^{3-}, NH_4^+, glucose, and arabinose for 75 to 155 min at rates designed to achieve concentration elevations in the stream of 30 μg/L PO_4^{3-}-P, 30 μg/L NH_4^+-N, 14 μg/L glucose-C, and 12 μg/L arabinose-C. One day before additions, time-of-travel was estimated with rhodamine WT and channel width and depth were measured at 20 transects throughout the reach. The time-of-travel and depth measurements were used to finalize the reach length (300-5400 m) chosen to achieve an expected uptake of 35 to 70% of each added solute.

Immediately before solute addition, water samples for ambient concentrations were taken at each of 5 downstream sampling stations. Five subsequent water samples were taken from each station within the period of plateau concentration, or in the period of maximal concentrations, for assay of NH_4^+, soluble reactive P (SRP), glucose, and arabinose, in addition to the conservative tracer. Supplementary samples for total dissolved P (TDP), total dissolved N (TDN), and NO_3^-, in addition to NH_4^+ and SRP, were taken from just upstream of the injection site before and after the injection, and at the lowermost station before, during, and after each addition. Samples for N and P assays were field-filtered (0.45-μm Whatman® cellulose nitrate membrane) and frozen within 24 h of collection for analysis within 60 d. Samples for glucose and arabinose assays were sterile-filtered (0.2-μm HT Tuffryn Acrodisc®) and frozen within 24 h for analysis within 2 mo.

S_w for a given solute was estimated from the concentration elevations, $\Delta C(x,t) = C(x,t) - C(x,t_0)$, where $C(x,t)$ and $C(x,t_0)$ are the concentrations of the solute measured at a distance x (m) downstream of the injection point at time t after the beginning of the injection, and time t_0 (immediately before the injection), respectively. The ratio, r_c, is the concentration elevation relative to that of Br^- (the conservative tracer), $r_c = \Delta C/\Delta[Br^-]$, and was calculated to adjust for longitudinal dilution and dispersion. The longitudinal loss rate, k_l, of the solute was estimated by nonlinear regression from the relationship $r_c(x) = r_0 \exp(-k_l x)$, where r_0 is the concentration ratio elevation at $x = 0$. S_w for the respective solute was calculated as $S_w = 1/k_l$ (Newbold et al. 1981).

S_w is strongly scale dependent (Butturini and Sabater 1998), i.e., for a given nutrient concentration and uptake flux (U) of nutrient from the water column to the streambed, S_w varies in proportion to the product of the water depth, d, and water velocity, v_w (Stream Solute Workshop 1990). Therefore, S_w was converted to a mass-transfer coefficient, or uptake velocity (V_f), calculated as $V_f = k_l v_w d = v_w d/S_w$ to facilitate comparisons of spiraling among streams of varying size. The scaling factor, $v_w d$, is equivalent to the specific discharge (i.e., stream flow [Q] divided by stream width [w]), because $Q = v_w w d$.

Conservative tracer (Br^-) data were analyzed with a 1-dimensional advection–dispersion model that includes a transient storage component (OTIS-P; Runkel et al. 1998) to describe stream flow characteristics, including: Q, cross-sectional area ([A], from which $v_w = Q/A$, and $d = A/w$), cross-sectional transient storage area (A_s), longitudinal dispersion coefficient, and transient storage exchange coefficient (α). Transient storage represents short-term detention of the stream water in lateral zones, such as backwaters or eddies, or within the sediments where the downstream velocity is negligible (Bencala and Walters 1983). In our study, the size of the transient storage zone is reported as the ratio A_s/A, and the rate of transfer into the transient storage zone is reported as a hydraulic exchange velocity ($v_{hyd} = \alpha d$) for dimensional consistency with V_f.

Our study was not designed to assess nitrification of the added NH_4^+, but an approximate mass-transfer coefficient was calculated for nitrification using the supplementary samples for NO_3^- taken before and during the injections. Our approach was that of Mulholland et al. (2000), simplified by assuming that re-uptake of nitrification-produced NO_3^- within our relatively short reaches was negligible. The estimation required quantification of increases in NO_3^--N that were within the range of 0 to 30 μg/L above ambient concentration (because we added ~30 μg/L as NH_4^+-N). This quantification proved feasible only in streams where ambient NO_3^--N was ≤175 μg/L; at higher concentrations, our estimates were highly variable and often negative.

The results from 2 of 30 additions (i.e., site 40 in 2000, and site 5 in 2002) were not used in the analysis because they were affected by unusually high concentrations of suspended solids associated with minor flow fluctuations. In addition, the S_w for NH_4^+ at site 30 in 2000 could not be calculated because the variance in the sampled NH_4^+ concentrations was excessive.

Analytical methods

The carbohydrates, glucose and arabinose, were analyzed by high performance liquid chromatography (HPLC) with pulsed amperometric detection (Dionex 500) (Cheng and Kaplan 2001). Br^- was analyzed by ion chromatography with conductivity detection (Dionex

500). SRP was determined by the ascorbic acid method (EPA method 365.1; see USEPA 1983 for all methods). TDP was determined as SRP after ammonium persulfate digestion (EPA method 365.1). NH_4^+ was determined by the phenate procedure (EPA method 350.1), and NO_3^- (including NO_2^-) by Cd reduction (EPA method 353.2). Total dissolved N (TDN) was determined as the sum of NO_3^--N plus soluble Kjeldahl N (SKN, semiautomated phenate block digestion [modified from EPA methods 351.2 and 350.1]).

Covariates

Data from other components of the Project were used in the analyses of spiraling patterns. Site characterizations, including land use and population density, were generated by Arscott et al. (2006). Ambient dissolved organic C (DOC) and biodegradeable DOC (BDOC) were sampled annually from each of the reaches (Kaplan et al. 2006), but on different dates from the solute additions. Bott et al. (2006) measured ecosystem metabolism, as daily community respiration (CR_{24}), daily gross primary production (GPP), water temperature, and light (photosynthetically active radiation [PAR]) over 3-d periods that included the solute additions. Bott et al. (2006) also determined benthic stocks of chlorophyll *a* and periphyton-associated organic matter (BOM). Macroinvertebrate sampling was conducted in the spring of each year (Kratzer et al. 2006). Two variables derived from the macroinvertebrate data—the Hilsenhoff Biotic Index (HBI; Hilsenhoff 1988) and species richness/100 individuals—were used in our analyses. Concentrations of molecular tracers were sampled during baseflow in the summer of each year (Aufdenkampe et al. 2006), but not concurrently with the additions. Relationships were analyzed between V_f s and 5 groups of tracers: 1) total polyaromatic hydrocarbons (PAH), 2) toxic PAHs [the sum of benzo(b)fluoranthene, chrysene, benzo(a)pyrene, benzo(b)fluoranthene, and benzo(k)fluoranthene], 3) caffeine, 4) fragrance materials (the sum of tonalide and galaxolide, both used in perfumes and soaps), and 5) fecal steroids (the sum of 7 steroid compounds). Molecular tracer concentrations were log-transformed before calculation of 3-y means from each site. See appendix 2 in Blaine et al. (2006) for a comprehensive list of variable names and abbreviations.

Analysis of uptake kinetics

V_fs were compared among streams using a kinetic model based on the Michaelis–Menten equation, which describes enzyme kinetics, but has been used to describe the rate of nutrient uptake by natural streambed communities (e.g., McIntire and Colby 1978, Mulholland et al. 2002, Payn et al. 2005):

$$U = U_{max}C/(K_s + C) \qquad [1]$$

in which U represents the uptake flux of a nutrient or organic solute (mass per unit streambed area per unit time), U_{max} is the maximum uptake flux that would occur under high (saturating) water-column nutrient concentration (C) and K_s is the half-saturation concentration, i.e., the concentration at which $U = U_{max}/2$. The V_f reported here is related to the flux by $V_f = U/C$ (Stream Solute Workshop 1990) which, substituting for U in equation 1, yields:

$$V_f = U_{max}/(K_s + C) \qquad [2]$$

In equation 2, V_f reaches a maximum as C approaches 0; hence, $V_{fmax} = U_{max}/K_s$ and equation 2 becomes:

$$V_f = V_{fmax}K_s/(K_s + C) \qquad [3]$$

which we will refer to as the concentration-specific Michaelis–Menten curve.

V_{fmax} and K_s were estimated by nonlinear least squares (Proc NLIN, version 9.1, SAS Institute, Cary, North Carolina) using equation 3, the measured values for V_f and the ambient (pre-addition) concentrations (C) of the corresponding solute. Equation 3 was used rather than the more-familiar equation 1 because U, the dependent variable in equation 1, is the product of V_f and C, making it dependent on the independent variable, C. Equation 3 was fitted using not only SRP and NH_4^+ (the added nutrients), but also TDP and TDN, to represent C. Our rationale for using TDP and TDN was that the availability of alternative forms of either P or N might influence the demand for the added form.

Hypotheses and statistical analysis

Our primary hypothesis was that human impacts increase spiraling length or, equivalently (because streams of different sizes were compared), that human impacts decrease nutrient V_f. Possible mechanisms through which the effect of human impacts might have occurred were considered as secondary hypotheses. The relative influences considered were: 1) a saturating effect of human-induced nutrient enrichment, which would decrease V_f, 2) a stimulatory effect of nutrient enrichment, which would increase V_f, and 3) other unspecified impacts, such as the presence of toxins that would decrease V_f. Correlation coefficients and standardized regression coefficients in the framework of a path analysis were used to test these hypotheses (Fig. 1) (Wright 1934).

The 27 or 28 measurements from the individual

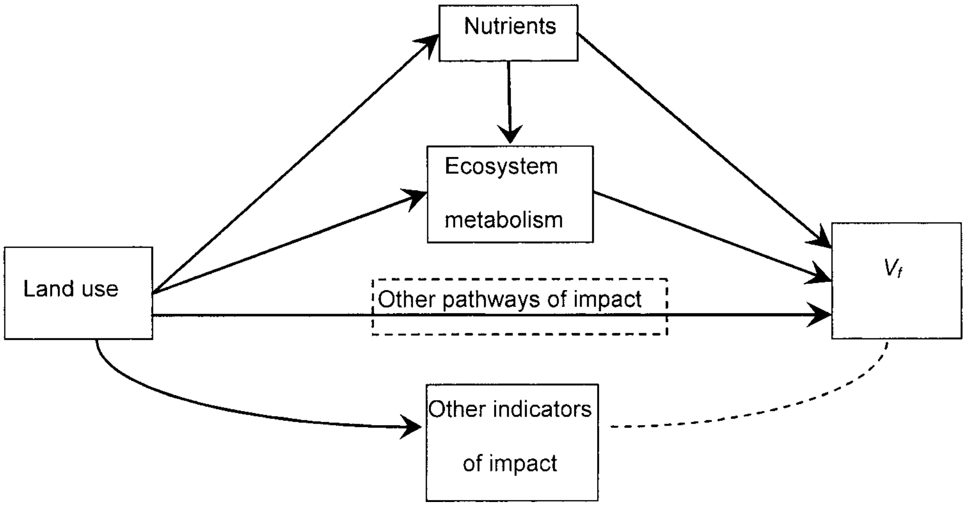

FIG. 1. Hypothesized links between human activity (land use) and nutrient uptake in the framework of a path analysis. $V_f =$ uptake velocity.

solute additions were used for the regressions and many of the correlations. We were cognizant that the multiple (usually 3) observations from each site cannot be regarded as truly independent samples. However, substantial within-site interannual variability in ambient concentrations, stream flow, and ecosystem metabolism introduced some degree of independence between the measures and, more important, should contribute explanatory power to the analysis. Because the lack of independence could produce spurious results, correlations also were computed using the values for each variable averaged across the 3 y at each site ($n = 10$). Results of the latter correlations are noted when they contradicted a major result obtained from the correlation of individual ($n = 27$ or 28) values. In cases of disagreement between the individual and 3-y-mean correlations, analysis of covariance (ANCOVA), with site as a main effect, was used to identify possible within-site (year-to-year) relationships that might have been masked by the 3-y averaging. For correlations and regressions involving variables that were not measured concurrently with the solute additions (invertebrates, molecular tracers, and land cover), only the 3-y means ($n = 10$) were used.

Results

Physical and chemical characteristics of streams

The experiments were conducted under baseflow conditions at stream flows ranging from 0.03 to 5.91 m^3/s, with correspondingly wide ranges in velocity, width, and depth (Appendix 1). A_s/A ranged from 0.04 to 0.65, and v_{hyd} ranged from undetectable to 0.057 mm/s. Ambient solute concentrations and conductivity are given in Appendix 2. SRP, TDP, TDN, NO_3^-, and conductivity were correlated ($r > 0.37$, $p < 0.05$, $n = 28$). NH_4^+ and arabinose were not correlated with any other chemical variables ($r < 0.36$, $p > 0.05$), and glucose was correlated only with conductivity ($r = 0.57$, $p < 0.01$). Despite covariation among nutrients, molar N:P ratios (based on TDN and TDP) varied by more than a factor of 10 (27–324, median = 76).

In addition, there were correlations of physical characteristics with chemical properties that were related to a regional interaction between watershed size and stream chemistry, but have bearing on subsequent data interpretation. TDN, TDP, and conductivity were negatively correlated with velocity, depth, and width ($r = -0.38$ to -0.74, $p < 0.05$), reflecting a general pattern of higher nutrient and major ion concentrations in EOH streams (where sites occupied smaller watersheds) than in WOH streams (Dow et al. 2006). TDN and conductivity (but not TDP) were positively correlated with A_s/A ($r = 0.44$ and 0.47, respectively, $p < 0.05$) which, in turn, was negatively correlated with velocity and depth ($r = -0.44$, $p = 0.02$ for both).

S_w and scaling with stream size

As expected from scaling considerations, S_w for all solutes varied with specific discharge (i.e., the scaling factor, $v_w d$; Fig. 2A–D) and converting S_w to V_f removed most of the influence of scale (Fig. 2E–H, Table 1). Of the 4 solutes, only NH_4^+-V_f was correlated with $v_w d$ (Fig. 2F, Table 1). This correlation may have represented stimulation of nutrient uptake by current velocity (Whitford and Schumacher 1961, Borchardt et al. 1994, Larned et al. 2004), but it appears at least as likely that it was an artifact of the higher TDN in the

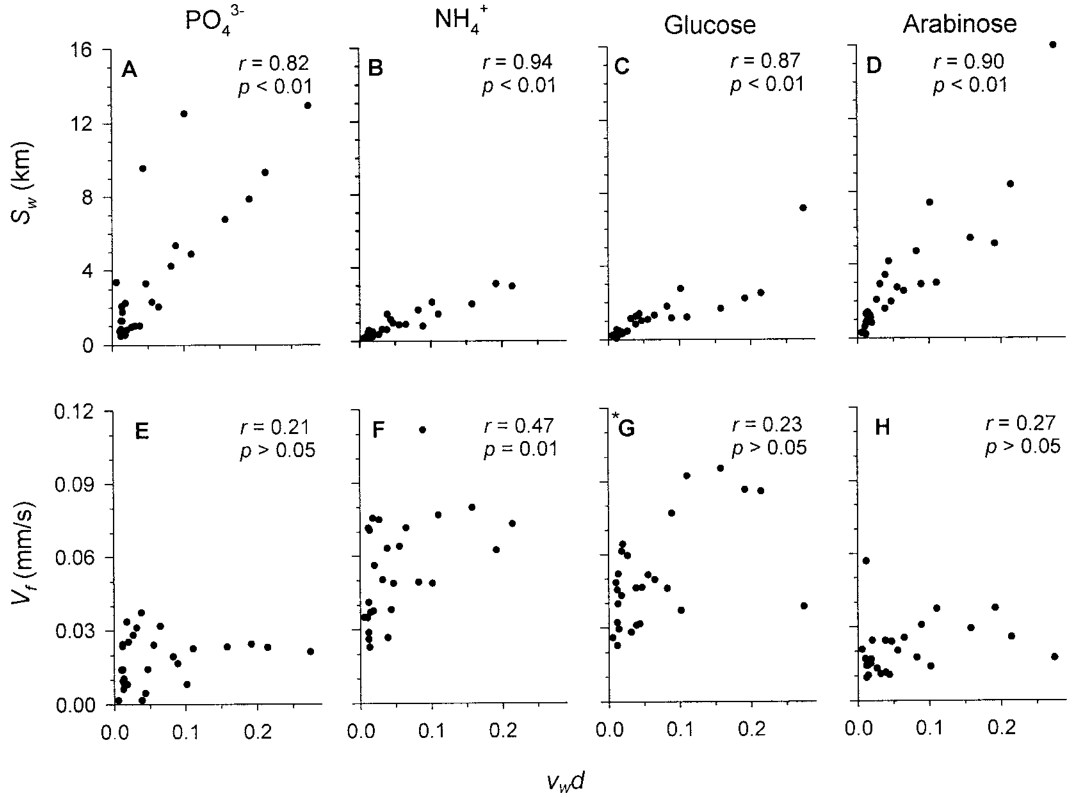

FIG. 2. Relationships between nutrient uptake lengths (S_w: A–D) and uptake velocities (V_f: E–H) and stream size, expressed as the product of velocity and depth ($v_w d$). The asterisk in panel G indicates a value (0.18 mm/s, 0.012 m^2/s) beyond the range of the vertical axis.

more-populated EOH sites where the study watersheds were smaller. V_fs were not related to v_{hyd}, A_s/A, PAR, or water temperature, except that NH_4^+-V_f was negatively correlated with A_s/A, and PO_4^{3-}-V_f was positively correlated with PAR.

V_f and ambient solute concentration

PO_4^{3-}-V_f varied inversely with ambient nutrient concentrations in a manner consistent with Michaelis–Menten kinetics. The nonlinear regression of the concentration specific Michaelis–Menten curve (eq. 3) using SRP as the concentration (C) explained 62% of the variance in V_f, as compared to ~40% (r^2) explained by correlation (Table 1). However, because TDP was more strongly correlated than SRP with PO_4^{3-}-V_f, equation 3 was fitted to the V_f again, using TDP in place of SRP. This regression explained 66% of the variance ($p < 0.01$), as compared to ~48% by correlation, and yielded parameter estimates of $V_{fmax} = 0.032 \pm 0.008$ mm/s and $K_s = 12 \pm 4$ µg/L (Fig. 3A).

NH_4^+-V_f was not correlated with the ambient NH_4^+ concentration, but it was negatively correlated with NO_3^- and TDN (Table 1). Ambient NH_4^+-N typically accounted for only 1 to 10% of the TDN and was only weakly correlated with TDN ($r = 0.32$, $p = 0.09$). Therefore, TDN, rather than NH_4^+, was used as the concentration (C) in equation 3 to fit the Michaelis–Menten curve. The nonlinear regression (Fig. 3B) explained 36% of the variance ($p < 0.01$), a result that was marginally better than simple correlation (r^2 = ~35%; Table 1). The nonlinear regression yielded parameter estimates of $V_{fmax} = 0.076 \pm 0.027$ mm/s and $K_s = 1020 \pm 450$ µg/L.

V_fs of arabinose and glucose were not correlated with concentrations of any solutes, including ambient concentrations of arabinose, glucose, DOC, and BDOC (Table 1). In contrast, both PO_4^{3-}-V_f and NH_4^+-V_f were negatively correlated with DOC, as was PO_4^{3-}-V_f with BDOC. However, DOC was strongly correlated with both TDP ($r = 0.81$, $p < 0.01$) and TDN ($r = 0.73$, $p < 0.01$), and BDOC was weakly correlated with TDP ($r = 0.37$, $p = 0.06$), so these associations probably reflect the influences of TDP and TDN, respectively.

Comparisons among V_fs

Similarities and differences among the V_fs of the various solutes are potentially useful in interpreting human impacts. V_fs of PO_4^{3-} and NH_4^+ were

Table 1. Pearson correlation coefficients between nutrient uptake velocities (V_f) and measured variables at 10 sites in the New York City drinking-water-supply watersheds (see appendix 2 in Blaine et al. 2006 for a comprehensive list of all variables). $v_w d$ = specific discharge, A_s/A = transient storage ratio, v_{hyd} = hydraulic exchange velocity, PAR = photosynthetically active radiation, SRP = soluble reactive P, TDP = total dissolved P, TDN = total dissolved N, DOC = dissolved organic C, BDOC = biodegradable DOC, CR_{24} = 24-h community respiration, GPP = gross primary production, BOM = periphyton-associated organic matter, HBI = Hilsenhoff Biotic Index, PAH = polyaromatic hydrocarbon. $n = 27$ or 28, except for variables designated 3-y mean for which $n = 10$ (see text for details). Bold font indicates $p < 0.05$.

	V_f			
	PO_4^{3-}	NH_4^+	Glucose	Arabinose
Stream flow	0.21	**0.46**	0.19	0.25
Water depth	0.28	**0.49**	0.12	0.20
Water velocity	0.23	**0.48**	0.28	0.32
$v_w d$	0.21	**0.47**	0.23	0.28
Stream width	**0.50**	0.35	–0.06	–0.04
v_{hyd}	0.10	0.17	0.07	0.12
A_s/A	–0.26	**–0.42**	–0.22	–0.28
log(PAR)	**0.45**	0.34	0.01	0.12
Stream water temperature	0.20	–0.16	–0.13	–0.13
SRP	**–0.64**	**–0.60**	–0.34	–0.27
TDP	**–0.70**	**–0.60**	–0.27	–0.19
NH_4^+	**–0.52**	–0.24	–0.27	–0.29
NO_3^-	**–0.57**	**–0.53**	–0.33	–0.25
TDN	**–0.64**	**–0.59**	–0.26	–0.21
Glucose	–0.30	–0.17	–0.01	–0.06
Arabinose	0.01	0.00	–0.13	–0.07
3-y mean DOC	**–0.74**	**–0.75**	–0.04	–0.11
3-y mean BDOC	**–0.69**	–0.53	–0.23	–0.33
CR_{24}	**0.47**	**0.47**	**0.51**	**0.61**
GPP	**0.52**	**0.45**	**0.40**	**0.48**
Chlorophyll *a* per unit streambed area	–0.28	–0.17	–0.03	–0.01
BOM	**–0.42**	**–0.41**	–0.35	**–0.45**
3-y mean HBI	–0.56	**–0.77**	–0.39	–0.41
3-y mean benthic macroinvertebrate species richness/100 individuals	**0.66**	**0.67**	0.15	0.14
3-y mean log(total PAHs)	**–0.70**	–0.36	–0.05	–0.14
3-y mean log(toxic PAHs)	**–0.82**	–0.43	0.04	–0.04
3-y mean log(caffeine)	–0.38	–0.38	–0.02	–0.08
3-y mean log(fragrance materials)	–0.58	**–0.71**	–0.48	–0.44
3-y mean log(fecal steroids)	**–0.82**	–0.57	–0.30	–0.37
Watershed-scale arcsin(% forest cover)[a]	**0.89**	**0.82**	0.16	0.22
Watershed-scale population density	**–0.67**	**–0.74**	–0.03	–0.05
Watershed-scale arcsin(% agricultural land use)[b]	**–0.65**	–0.42	–0.34	–0.41

[a] = sum of % coniferous + % deciduous + % mixed forest

[b] = sum of all agricultural land uses in table 2 of Dow et al. (2006)

correlated (Fig. 4A) reflecting, at least in part, a strong correlation between TDP and TDN ($r = 0.83$, $p < 0.01$). V_fs of glucose and arabinose, which were not clearly influenced by nutrient concentrations, were strongly correlated with each other (Fig. 4B) and less strongly correlated with NH_4^+-V_f (r = 0.57, 0.56, respectively, $p < 0.01$). Neither carbohydrate V_f was correlated with PO_4^{3-}-V_f ($r \leq 0.30$, $p > 0.05$).

NH_4^+-V_f averaged ~2.8× higher than PO_4^{3-}-V_f and exceeded the respective PO_4^{3-}-V_f in each of the individual measurements (Table 2). The mean glucose-V_f was the same as the mean NH_4^+-V_f, whereas the mean arabinose-V_f was nearly the same as of the mean PO_4^{3-}-V_f.

The residuals (i.e., the difference between observed and predicted values) from equation 3, as fitted using TDP and TDN for PO_4^{3-}-V_f and NH_4^+-V_f, respectively, were examined to investigate the possibility that high concentrations of one nutrient had a stimulating effect on the uptake of another. Neither set of residuals were correlated with any of the measured nutrient forms ($|r| < 0.3$, $p > 0.1$).

Nitrification

Among the 12 injections for which nitrification could be estimated (those with ambient NO_3-N $\leq$ 175 μg/L), nitrification-V_f (that part of the total NH_4^+ uptake that

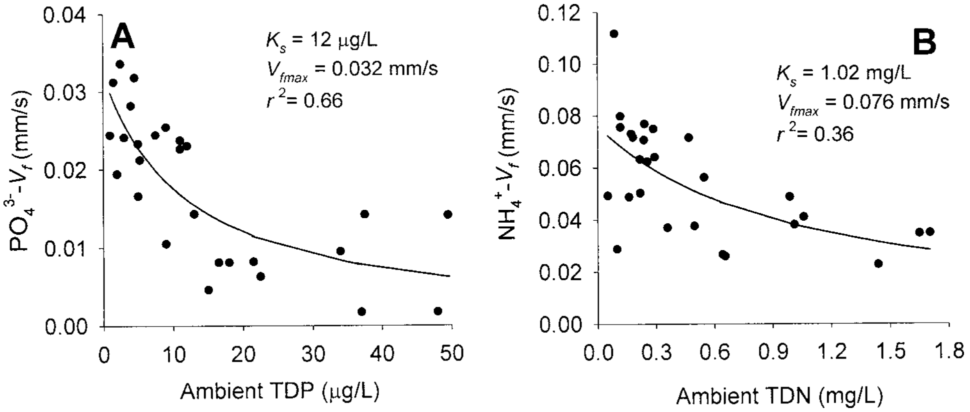

FIG. 3. PO_4^{3-}-uptake velocity (V_f) as a function of ambient total dissolved P (TDP: A) and NH_4^+-V_f as a function of ambient total dissolved N (TDN: B) concentration. The solid line represents the estimated concentration-specific Michaelis–Menten curve (eq. 3). K_s = half-saturation constant, V_{fmax} = maximum uptake velocity.

was nitrified rather than assimilated) ranged from 0 to 0.025 mm/s with a mean of 0.008 mm/s. Nitrification-V_f varied between 0 and 32% of NH_4^+-V_f with a mean of 11%. This proportion was correlated with ambient NO_3^- concentration ($r = 0.91$, $p < 0.01$). Nitrification-V_f also was correlated with ambient NO_3^-concentration ($r = 0.86$, $p < 0.01$).

Ecosystem metabolism, benthic chlorophyll, and BOM

Among the individual observations ($n = 26$–27), V_fs for all 4 solutes were correlated with CR_{24} and GPP (Table 1, Fig. 5A–D, E–H, respectively), both of which were measured concurrently with the solute additions (Bott et al. 2006). However, among the 3-y means of V_f values and metabolism measurements, only the correlations of NH_4^+-V_f with CR_{24} ($r = 0.78$, $p < 0.01$, $n = 10$) and GPP ($r = 0.85$, $p < 0.01$) and of arabinose-V_f with CR_{24} ($r = 0.67$, $p = 0.03$) were significant. ANCOVA, with V_f as the dependent variable, site as a main effect, and CR_{24} as a continuous covariate, was used to investigate whether year-to-year within-site variations might have contributed to the correlations among the individual observations. The year-to-year within-site variations in CR_{24} explained 24% ($p = 0.04$) of the residual variance (i.e., the variance unexplained by site effect) in PO_4^{3-}-V_f. Also, year-to-year within-site variations in GPP explained 29% of the residual variance in PO_4^{3-}-V_f ($p = 0.02$). These results point to an influence of ecosystem metabolism on PO_4^{3-}-V_f that may have been obscured in the correlations of the 3-y-mean data. CR_{24} explained 25% ($p = 0.04$) of the residual variance in arabinose-V_f, again providing evidence for an influence of metabolism. However, year-to-year within-site variations in CR_{24} and GPP did not influence NH_4^+-V_f or glucose-V_f, nor did year-to-year within-site variations in GPP influence arabinose-V_f.

None of the V_fs were correlated with benthic chlorophyll *a* (Table 1). Among the individual measurements, BOM was negatively correlated with the V_fs of NH_4^+, PO_4^{3-}, and arabinose. The negative

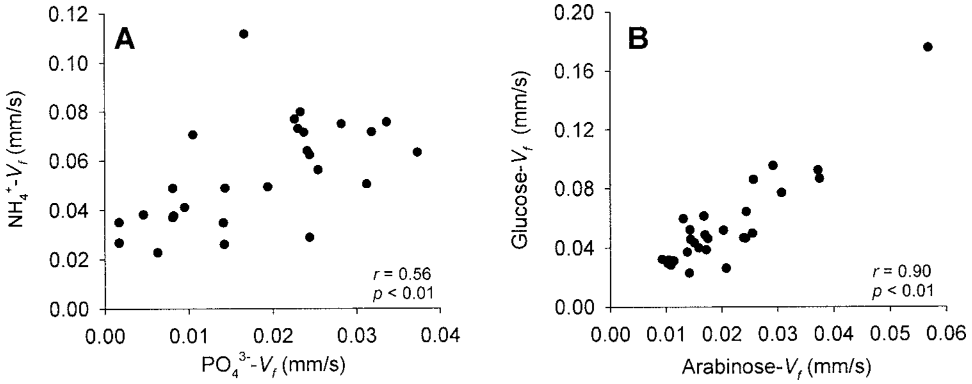

FIG. 4. Relationships between uptake velocities (V_f) of NH_4^+ and PO_4^{3-} (A) and of glucose and arabinose (B).

TABLE 2. Nutrient uptake velocities (V_f, mm/s) estimated from nutrient additions at 10 sites in New York City drinking-water-supply watersheds. * = V_f not significantly > 0 ($p > 0.05$), – = V_f not estimated.

Stream	Date	PO_4^{3-}	NH_4^+	Glucose	Arabinose
Bush Kill	13 July 2000	0.014	0.049	0.046	0.024
	27 June 2001	0.023	0.077	0.092	0.037
	19 June 2002	0.023	0.073	0.086	0.026
Cross	25 August 2000	0.025	0.056	0.064	0.024
	10 October 2001	0.010	0.071	0.052	0.014
	11 September 2002	0.008	0.037	0.030	0.010
Esopus	19 October 2000	0.017	0.112	0.077	0.031
	6 June 2001	0.024	0.062	0.087	0.038
	5 June 2002	0.023	0.080	0.095	0.029
Kisco	28 September 2000	0.002*	0.027	0.031	0.011
	17 October 2001	0.008	0.038	0.061	0.017
	9 October 2002	0.014	0.026	0.023	0.014
Main Branch Croton	24 October 2001	0.024	0.072	0.176	0.057
	28 August 2002	0.009	0.041	0.045	0.014
Muscoot	31 August 2000	0.014	0.035	0.049	0.017
	3 October 2001	0.006	0.023	0.040	0.016
	25 September 2002	0.002*	0.035	0.026	0.021
Neversink	12 October 2000	0.019	0.049	0.046	0.018
	15 August 2001	0.024	0.064	0.052	0.020
	7 August 2002	0.032	0.072	0.050	0.025
Rondout	20 July 2000	0.021	–	0.038	0.017
	29 August 2001	0.028	0.075	0.060	0.013
	25 July 2002	0.037	0.063	0.046	0.024
Schoharie	5 October 2000	0.031	0.050	0.028	0.011
	1 August 2001	0.034	0.076	0.043	0.015
	21 August 2002	0.024	0.029	0.032	0.009
West Branch Delaware	26 October 2000	0.008	0.049	0.037	0.014
	18 July 2001	0.005	0.038	0.032	0.011
Mean		**0.020**	**0.055**	**0.055**	**0.021**

correlation with BOM was opposite to the result expected from a nutrient demand exerted by heterotrophic microbes. However, these correlations were not significant ($p > 0.05$) when computed from the 3-y means, and ANCOVA yielded no significant year-to-year within-site effect of BOM on V_fs.

U

U expresses the transfer of nutrient to a unit area of streambed because mass per unit time is related to V_f by $U = V_f\ C$. No significant correlations were found among the *U*s of individual solutes ($|r| \leq 0.32$, $p \geq 0.12$, $n = 26–27$; e.g., Fig. 6A). NH_4^+-*U* was correlated with CR_{24} (Fig. 6B) and GPP ($r = 0.40$, $p = 0.045$, for both). These trends clearly reflect the correlation of NH_4^+-V_f with CR_{24} and GPP because NH_4^+ concentration was not correlated with either CR_{24} or GPP ($|r| \leq 0.06$, $p > 0.05$). No other *U*s were correlated with either measure of metabolism ($|r| < 0.014$, $p > 0.05$).

Benthic macroinvertebrates

The 3-y mean PO_4^{3-}-V_f was correlated with species richness (Fig. 7A), but was only marginally correlated with the HBI ($p = 0.09$, Table 1) reported in Kratzer et al. (2006). The 3-y mean NH_4^+-V_f was negatively correlated with the 3-y mean HBI (Table 1) and was positively correlated with the 3-y mean species richness (Fig. 7B). The HBI is an inverse index of water quality (Hilsenhoff 1988), so both results represent a positive association between NH_4^+-V_f and conditions favorable to the macroinvertebrate community. Benthic macroinvertebrates variables were not correlated with carbohydrate V_fs.

Molecular tracers

The 3-y mean PO_4^{3-}-V_f was negatively correlated with the 3-y mean concentrations of total PAHs, toxic PAHs (Fig. 7C), and fecal steroids, was marginally correlated with fragrance materials ($p = 0.08$; Table 1), but was not correlated with caffeine (Table 1). The 3-y mean NH_4^+-V_f was negatively correlated with fragrance materials (Fig. 7D), was marginally correlated with fecal steroids (Table 1, $p = 0.08$), but was not correlated with total PAHs, toxic PAHs, or caffeine (Table 1). No correlations were found between carbohydrate V_fs and molecular tracers.

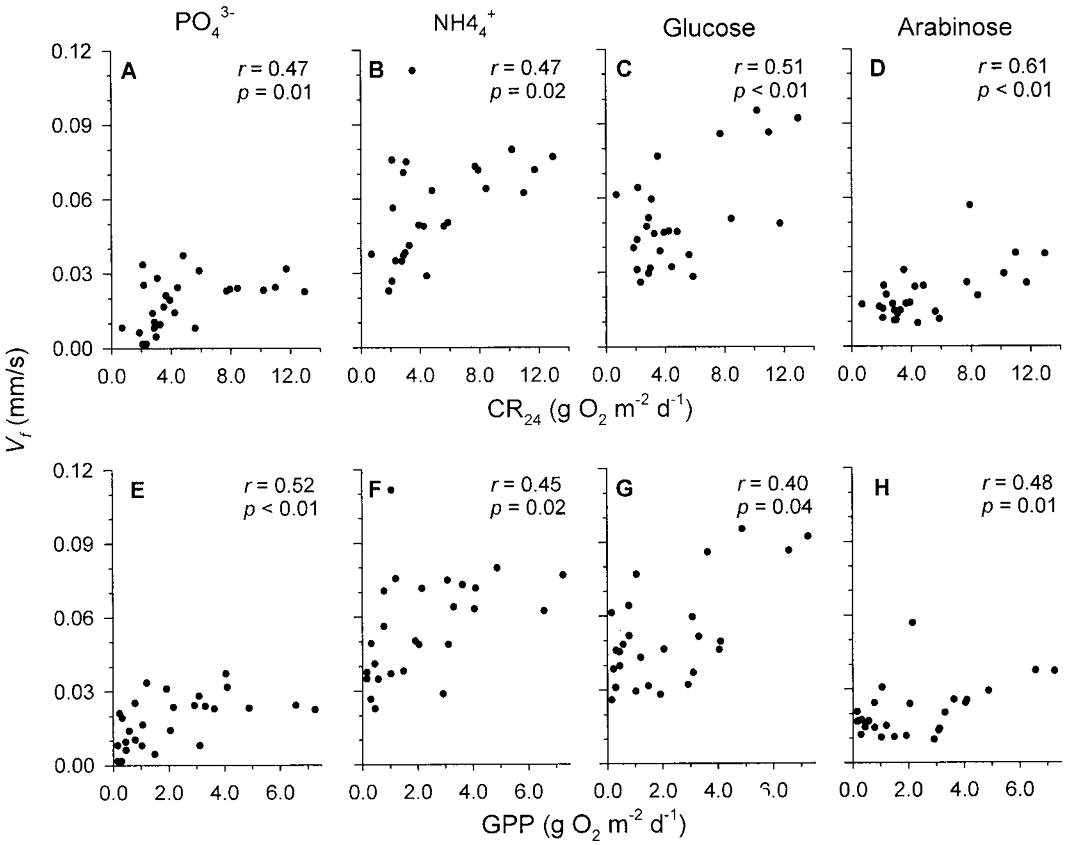

FIG. 5. Relationships between uptake velocities (V_f) of solutes and 24-h community respiration (CR_{24}: A–D) and gross primary production (GPP: E–H). Correlation coefficients were calculated from individual measurements at each site in each year ($n = 26–27$).

Land use

The 3-y mean PO_4^{3-}-V_f was positively correlated with % forest cover within the watershed (Fig. 8A), and negatively correlated with watershed population density (Fig. 8B) and % agricultural land use in the watershed (Table 1). The 3-y mean NH_4^+-V_f was positively correlated with % forest cover (Fig. 8C) and negatively correlated with population density (Fig. 8D), but not with % agricultural land use (Table 1). Neither of the carbohydrate V_fs were correlated with any descriptors of land use.

Spiraling and human impact

PO_4^{3-}-V_f path analysis.—Fig. 9A represents relationships among the measured variables in the form of a path analysis relating land use to PO_4^{3-}-V_f. To simplify the analysis, only one variable each was used among groups of variables representing land use (% forest cover), nutrients (TDP), and metabolism (CR_{24}). Despite the significance ($p < 0.05$) of the overall regression models and of the simple correlations represented in Fig. 9A, none of the individual path coefficients were significantly different from 0 ($p >$ 0.05). Thus, we interpret the path coefficients (standardized regression coefficients) only as estimates of the relative importance of the variables. Given this caveat, the analysis suggests that land use (as % forest cover) influenced P uptake through 3 main pathways. First, % forest cover negatively influenced TDP, which (through saturation mechanisms) varied inversely with PO_4^{3-}-V_f (path effect = the product of the path coefficients = 0.33). Second, % forest cover positively influenced CR_{24}, which varied positively with PO_4^{3-}-V_f (path effect = 0.11). Third, % forest cover positively and directly influenced PO_4^{3-}-V_f (path effect = 0.33). A 4th but minor pathway involved a slightly positive effect of TDP on CR_{24} (path effect = 0.05). The latter effect is consistent with a nutrient stimulation effect and was of the opposite sign of the negative correlation ($r = -0.38$, $p = 0.05$) between TDP and CR_{24}.

The preceding analysis suggests that nutrient saturation, while important, accounted for <½ of the overall influence of land use on nutrient uptake, i.e., that there were other mechanisms through which human activity impacted spiraling. To test for the influence of other mechanisms more directly, paths 2 and 3 were combined by eliminating CR_{24} from the

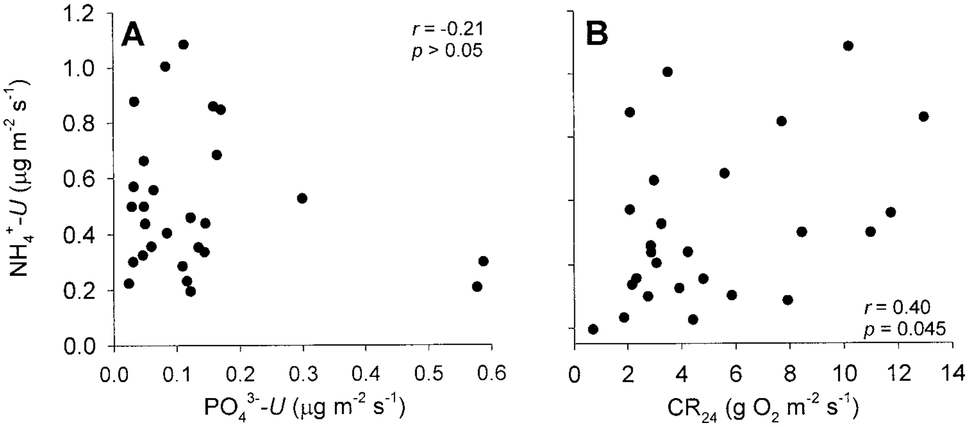

FIG. 6. Relationships between the uptake fluxes (*U*) of NH_4^+ and PO_4^{3-} (A), and between NH_4^+-*U* and 24-h community respiration (CR_{24}) (B).

analysis and regressing PO_4^{3-}-V_f on TDN and % forest cover. The resulting path coefficient for the direct effect of % forest cover on PO_4^{3-}-V_f, was 0.44 ($p = 0.055$).

Molecular tracers provided additional evidence that land use (human activity) affected PO_4^{3-}-V_f independently of the nutrient-saturation effect. Toxic PAHs were not significantly correlated with TDP ($r = 0.50$, $p = 0.14$, $n = 10$), despite strong inverse correlations with both % forest cover and PO_4^{3-}-V_f (Fig. 9A). Thus, multiple regression of PO_4^{3-}-V_f on TDP and toxic PAHs (using 3-y mean data) yielded significant ($p < 0.01$) standardized regression coefficients for both TDP (–0.56) and toxic PAHs (–0.54). This result does not imply that toxic PAHs necessarily affected PO_4^{3-}-V_f, but it does imply that either toxic PAHs or some covarying factor similarly reflective of human activity did affect nutrient uptake and that this effect was not confounded by nutrient enrichment. Invertebrate species richness also was strongly correlated with both % forest cover and PO_4^{3-}-V_f (Fig. 9A), supporting the overall hypothesis that spiraling reflects human impact. However, in contrast to the absence of a relationship between toxic PAHs and TDP, species richness covaried with TDP ($r = -0.29$, $p < 0.01$), so that species richness provided no additional evidence of an independent (non-nutrient-related) mechanism.

NH_4^+-V_f path analysis.—TDN (rather than TDP) was used to represent the primary nutrient in the path analysis for NH_4^+-V_f (Fig. 9B). As in the case of the PO_4^{3-} analysis, all of the regression models and all of the correlations represented in Fig. 9B were significant ($p < 0.05$), but none of path coefficients that were derived from multiple regression were significant ($p > 0.05$). Referring to the 3 pathways described for the PO_4^{3-} analysis, the path effect of % forest cover on NH_4^+-V_f via the TDN pathway was 0.22, the path effect of % forest cover on NH_4^+-V_f via the CR_{24} pathway was 0.12, and the direct path effect of % forest cover on NH_4^+-V_f was 0.33. Last, TDN had a slightly positive effect on CR_{24}, despite a negative simple correlation between these 2 variables. This analysis, like that of PO_4^{3-} uptake, pointed to a large role for mechanisms other than nutrient saturation. However, in contrast to the PO_4^{3-} analysis, multiple regression of TDN and % forest cover on NH_4^+-V_f failed to confirm a significant ($p = 0.12$) direct effect of % forest cover on NH_4^+-V_f. Fragrance materials provided confirmatory evidence for alternate pathways of influence analogous to that provided by toxic PAHs for PO_4^{3-}. That is, fragrance materials was strongly correlated with % forest cover and NH_4^+-V_f (Fig. 9B), but not with TDN ($r = 0.33$, $p = 0.35$), so that multiple regression of both TDN and fragrance materials on NH_4^+-V_f, yielded significant standardized regression coefficients (–0.54, –0.53, respectively, $p < 0.03$).

Discussion

Stream channel and flow characteristics

The scaling of S_w with stream size has been widely observed (Butturini and Sabater 1998, Peterson et al. 2001, Hall et al. 2002, but see Hall and Tank 2003 for an exception) and is expected if V_fs are relatively independent of stream-scaling influences (Wollheim et al. 2001). We saw no relationship between V_fs and either v_{hyd} or A_s of the streams except for a negative correlation of NH_4^+-V_f with A_s/A. A negative relationship, however, is inconsistent with any hypothesized role for transient storage in solute uptake, and we suspect it was an artifact of the regionally based covariation between TDN and A_s/A. Transient storage can influence solute uptake (Valett et al. 1996, Hall et al. 2002, Gücker and Boëchat 2004), particularly when the range of A_s/A is large, but several studies have

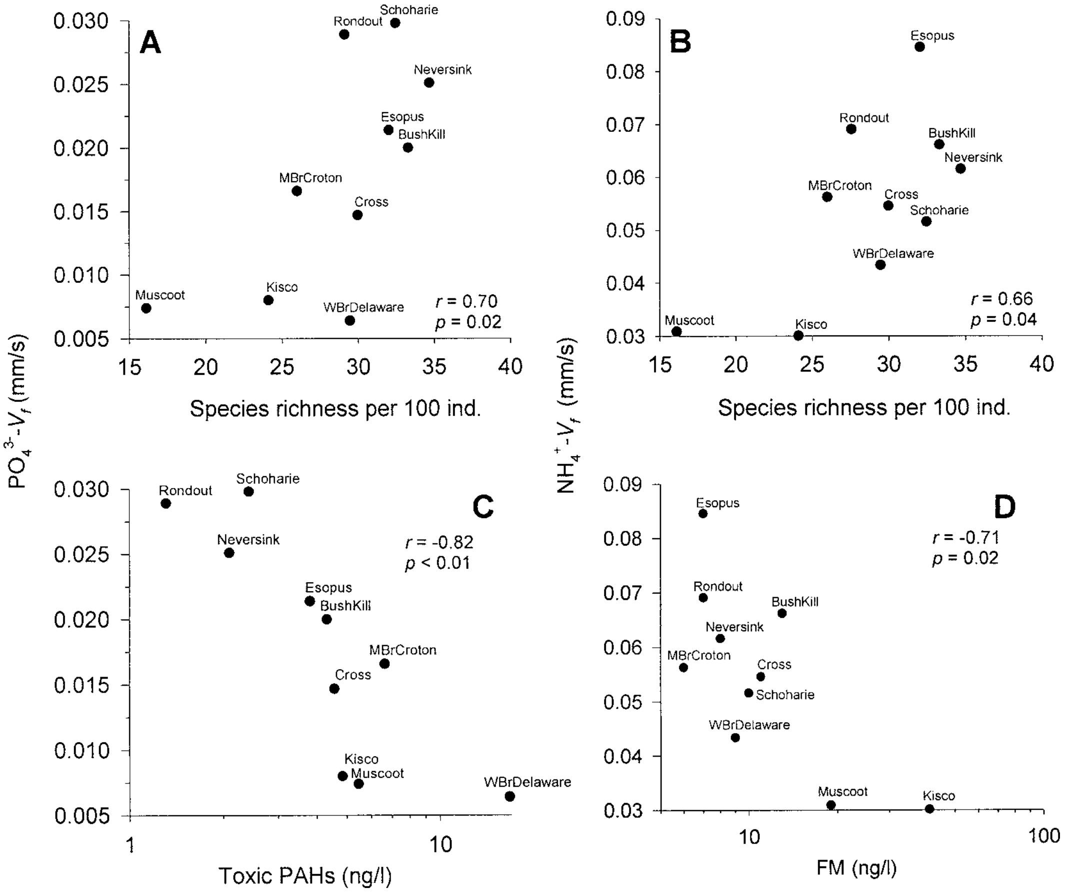

FIG. 7. Relationships between uptake velocities (V_f) of $PO_4^{3-}$and NH_4^+ and macroinvertebrate species richness/100 individuals (ind.) (A, B) and between PO_4^{3-}-V_f and concentrations of toxic polyaromatic hydrocarbons (PAHs) (C), and NH_4^+-V_f and concentrations of fragrance materials (FM: D). Points represent 3-y means. WBrDelaware = West Branch Delaware River, MBrCroton = Main Branch Croton River.

reported no statistical relationship between solute uptake and transient storage parameters (e.g., Webster et al. 2003, Niyogi et al. 2004, Meyer et al. 2005), or that additional factors produce a relationship opposite to that expected (Hall et al. 2002, Valett et al. 2002).

V_f and ambient solute concentration

Nutrient V_fs in streams respond to short-term variations in nutrient concentration in a manner consistent with the Michaelis–Menten model of saturation kinetics (Mullholland et al. 1990, 2002, Dodds et al. 2002a, Payn et al. 2005). The saturation concept also has been used to explain differences in V_f observed among streams of differing nutrient concentration (Davis and Minshall 1999, Niyogi et al. 2004), and several other interstream comparisons have observed inverse relationships between nutrient concentration and V_f (Webster et al. 2003, Dodds et al. 2002a, Bernhardt et al. 2002, Hall et al. 2002, Haggard et al. 2005).

The ability of the Michaelis–Menten model to explain significant variation in the V_fs of PO_4^{3-} and NH_4^+ among different streams has implications that are substantially different from application to a single stream. When the nutrient concentration is varied experimentally in a single stream, other factors that might govern nutrient demand, such as the biomass of nutrient-assimilating autotrophs and heterotrophs, light, temperature, and current, remain approximately constant. The response that is observed is clearly a response in the uptake kinetics. When different streams are compared, however, the uptake kinetics become only one of the many influences on nutrient demand. In the context of equation 3, these other influences would produce variability in V_{fmax} among streams, reducing the explanatory power of the model. Given these considerations, it is not surprising that equation 3 did not explain a higher proportion of the variance in V_f (66% for PO_4^{3-} and 36% for NH_4^+).

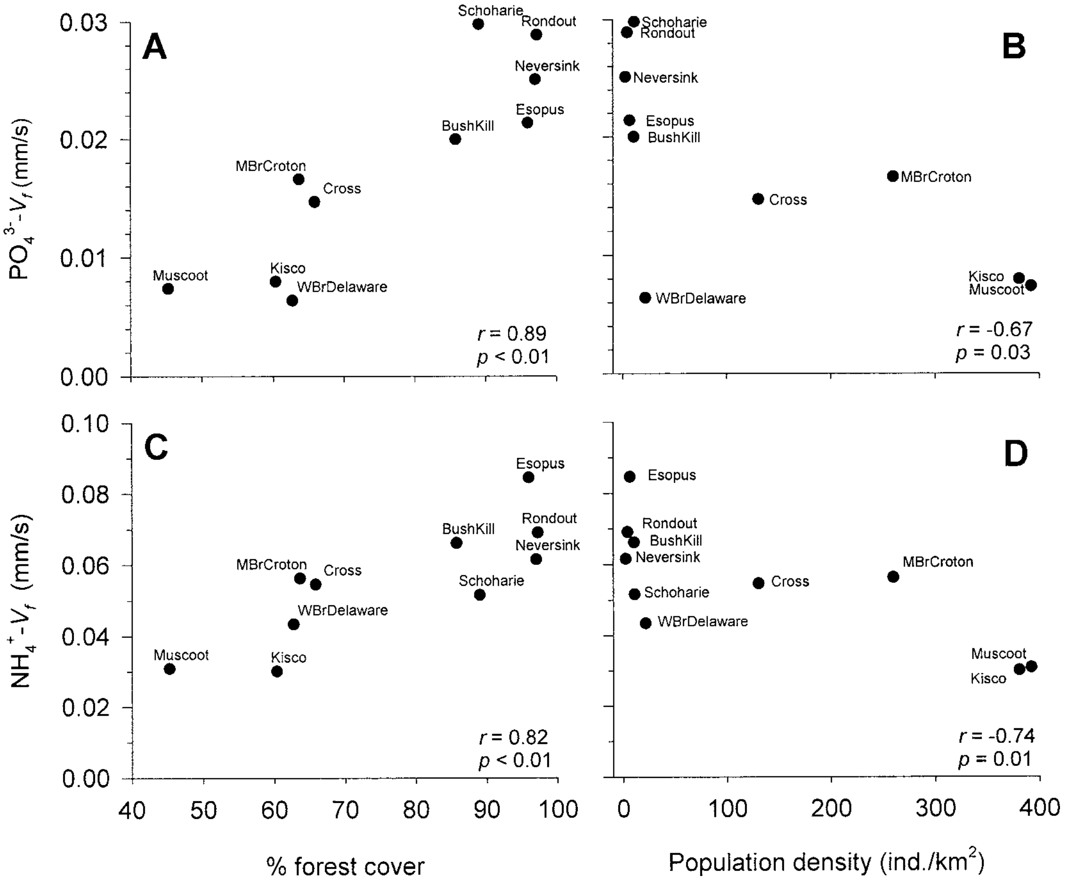

FIG. 8. Relationships between uptake velocities (V_f) of PO_4^{3-} and watershed-scale % forest cover (A) and population density (B), and NH_4^+-V_f and % forest cover (C) and population density (D). V_fs are 3-y means. % forest cover = sum of % coniferous + % deciduous + % mixed forest, ind. = individuals.

Rather, our results suggest that stream to stream variability in V_{fmax} is less than might be expected.

In fitting the concentration-specific Michaelis–Menten curve (eq. 3), we found that TDP explained more of the variance in PO_4^{3-}-V_f than did SRP, and that TDN explained more of the variance in NH_4^+-V_f than did NH_4^+ or dissolved inorganic N (DIN). These results suggest that various forms of the nutrients are used and that increases in one form reduce the demand for the other. In the case of NH_4^+ uptake we found, as well, that both NO_3^- and DIN explained more of the variance than NH_4^+. Bernhardt et al. (2002) similarly observed an inverse relationship between NO_3^- and NH_4^+-V_f among several streams in the Hubbard Brook Experimental Forest, New Hampshire. Thus, it appears that sufficiently high concentrations of NO_3^- can reduce the uptake of NH_4^+ even though both algae and heterotrophic microbes assimilate NH_4^+ preferentially to NO_3^- (Syrett 1962).

Our estimates of V_f for N and P were probably lower than the true V_f that would be measured at ambient concentrations using isotopic tracers (Mulholland et al. 1990, 2002). However, we believe that the utility of our results for comparisons among streams was not compromised because our nutrient additions were relatively low (~30 μg/L) and consistent among all injections. Limited data comparing ^{33}P additions to P enrichments suggest that our estimated V_fs may be 50 to 75% of the true V_f s (Mulholland et al. 1990). A more extensive paired comparison of ^{15}N-tracer with NH_4^+ enrichments in 10 streams suggests that the additions we used (30 μg/L) were likely to yield V_f estimates that were ~35% of their true value (Mulholland et al. 2002). Mulholland et al. (2002) reported a median NH_4^+-V_f, based on ^{15}N-tracer additions, of 0.20 mm/s for 9 sites where DIN concentrations were <62 μg/L. In our study, the median NH_4^+-V_f among 5 sites where DIN was <73 μg/L was 0.07 mm/s, which is 35% of the ^{15}N-based estimates of Mulholland et al. (2002) and consistent with their prediction.

Our estimated K_s values for P (12 μg/L for TDP, 8 μg/L for SRP) were higher than those reported by Bothwell (1985, 1988) (<1–4 μg/L) and very near those of Rosemond et al. (2002) (7–13 μg/L), but well below

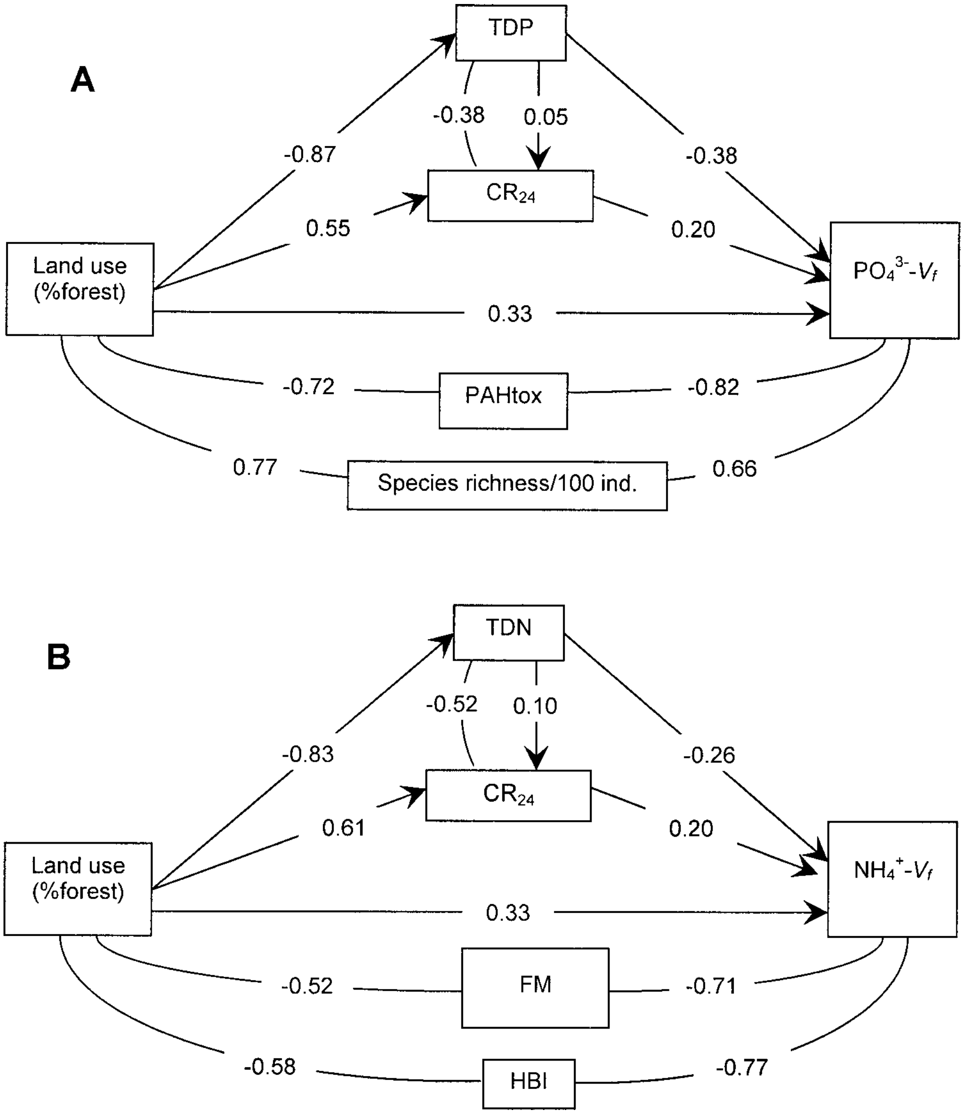

FIG. 9. Path analysis for effects of land use (represented as % forest cover [%forest]) on PO_4^{3-} uptake velocity (V_f: A) and on NH_4^+-V_f (B). The path coefficients (associated with solid arrows) represent standardized regression coefficients from the regression of a given (dependent) variable on all of the variables from which an arrow is drawn. Also shown are simple correlation coefficients represented by curves connecting the variables. For simple linear regressions of 24-h community respiration (CR_{24}) on % forest cover, and total dissolved P (TDP) or total dissolved N (TDN) on % forest cover, the path coefficient is the same as the correlation coefficient between the 2 variables. PAHtox = toxic polyaromatic hydrocarbons, FM = fecal materials, HBI = Hilsenhoff Biotic Index, ind. = individuals.

the concentrations (up to ~50 μg/L) sometimes observed to stimulate periphyton biomass accumulation in rivers (Borchardt 1996, Dodds et al. 2002b). Our estimates for K_s also were well below our additions of ~30 μg/L. The latter result implies that the short-term K_s governing uptake during our additions exceeded the long-term K_s to which the streams were equilibrated. This reasoning can be seen by tentatively assuming that equation 3 is equally applicable to both short-term and long-term kinetics. Representing the nutrient addition (ΔC) explicitly in equation 3 yields $V_f = V_{fmax}$ $K_s/(K_s + \Delta C + C)$ or V_{fmax} $K_s/(K_e + C)$, where $K_e = K_s + C$ (see Wright and Hobbie 1965). The assumption implies that we actually estimated K_e, rather than K_s, so that the true K_s (= K_e – ΔC) would be −18 μg/L, which is untenable. Because of longitudinal decreases from the target concentration, the typical effective concentration elevation (ΔC) was ~20 μg/L, but even using this corrected value still yields a negative (−8 μg/L) estimate for K_s. We infer that the short-term K_s (which we could not estimate because we added nutrients at only one concentration, cf. Payn et al.

2005), was much higher than the long-term equilibrated K_s, which we estimated from equation 3. The difference is expected theoretically as the result of variable cellular concentrations, or luxury consumption (Droop 1973) by streambed organisms. Rhee (1973) reported that the short-term K_s for PO_4^{3-} exceeded long-term K_s by a factor ~10, and Caperon and Meyer (1972) reported similar differentials for NH_4^+ and NO_3^- uptake.

Nitrification

Nitrification could be estimated only in streams with relatively low concentrations of ambient NO_3 ($\leq$175 µg/L) but, among these streams, nitrification accounted for an average of 11% of the NH_4^+ uptake, less than the mean of 56% measured in 19 mountain streams in New Hampshire (Bernhardt et al. 2002), and less than the mean of 26% estimated from ^{15}N-labeled NH_4^+ additions to 11 different streams from various biomes (Webster et al. 2003). However, nitrification was not detected during NH_4^+ additions to 11 mountain streams in Wyoming (Hall and Tank 2003), and the factors responsible for these differences remain unclear. The correlation between NO_3^- concentration and nitrification supports a similar finding of Bernhardt et al. (2002), who hypothesized that NO_3^- at high concentrations supplies much of the assimilatory demand for N, leaving more of the NH_4^+ available to nitrifying bacteria. Unfortunately, this relationship predicts that the highest nitrification rates in our study may have occurred in the high-NO_3^- streams where we could not estimate nitrification.

Spiraling and measures of ecosystem metabolism

The V_fs of all 4 solutes were positively related to ecosystem metabolism (CR_{24} and GPP), although a more conservative analysis left the relation between glucose-V_f and metabolism unconfirmed. Several other studies have found correlations between NH_4^+-V_f and either CR, GPP, or both (Hall and Tank 2003, Webster et al. 2003, Meyer et al. 2005). Our study appears to be the first that has observed a relationship between PO_4^{3-}-V_f and metabolism and between carbohydrate-V_f and metabolism. No influence of either benthic chlorophyll *a* or BOM on V_fs of any of the nutrients was observed, although these relationships have been reported in other studies (Mulholland et al. 1985, Niyogi et al. 2004, Meyer et al. 2005). The absence of these relationships in our study may be attributable to a relatively limited range of variation in these variables (Bott et al. 2006).

U can, in principle, be predicted from measures of stream metabolism under certain assumptions of stoichiometric coupling (Hall and Tank 2003, Webster et al. 2003). Therefore, we expected that CR_{24} and GPP would be more strongly correlated with *U* than with V_f. NH_4^+-*U* was correlated with both CR_{24} and GPP, but the correlations were weaker than the correlations of NH_4^+-V_f with CR_{24} and GPP. Moreover, no *U*s of other nutrients were correlated with either CR_{24} or GPP. For NH_4^+, the absence of a strong correlation probably reflected the variable and unknown contributions of NO_3^- and dissolved organic N (DON) to N uptake, and possibly reflected unmeasured nitrification in the high-NO_3^- streams. TDN (i.e., $NO_3^- + \text{DON} + NH_4^+$) was present in all of the streams at far higher concentrations than NH_4^+-N alone and, as implied by the influence of TDN on NH_4^+ uptake (Fig. 3B), dissolved N forms other than NH_4^+-N evidently accounted for much of the N assimilation. For P, the unmeasured contribution from dissolved organic P (DOP) may have been a factor. However, DOP averaged only 30% of TDP, and it seems unlikely that the influence of DOP could explain the lack of correlation. Rather, we suggest that variable stoichiometry, or luxury consumption, within the algal (Rhee 1973) and microbial (Senior and Dawes 1971, Makino et al. 2003) communities may have prevented a correlation. In our study, ambient TDP concentrations were negatively correlated with GPP (Bott et al. 2006) and CR_{24} ($p = 0.09$, TLB, unpublished data). If cellular C:P ratios varied inversely with P concentrations, they would have been lowest (and the ratio of P uptake to C metabolism would have been highest) at sites with the lowest metabolic rates. Thus, 2 opposing trends (1 in stoichiometry, the other in metabolism) may have balanced each other, leaving no net relationship between P concentration and *U*.

Spiraling and human impact

Our results generally support the hypothesis that spiraling, as measured by V_f, is a sensitive indicator of human disturbance. V_f s for both NH_4^+ and PO_4^{3-} were correlated with measures of human occupation of the landscape (% forest cover and population density), as well as with several measures of water quality that reflected human influences. These water-quality variables included nutrient concentrations, various molecular tracers, and macroinvertebrate-based indices of water quality. However, the carbohydrates, glucose and arabinose, showed little or no response to human impact despite their correlations with CR_{24}. Carbohydrates are consumed only by heterotrophs, whereas P and N are used by autotrophs as well as heterotrophs. Thus, it is tempting to suggest that autotrophs were preferentially impacted by human activities on the landscape. However, Bott et al. (2006) did not observe a greater sensitivity of GPP than CR_{24} to land use in these same streams. Another possibility is that human impacts affected the efficiency of (or otherwise altered) heterotrophic processes to reduce metabolism and nutrient consumption without affecting the demand for DOC from the water column.

The analysis of uptake kinetics, together with the path analyses, pointed to nutrient enrichment as a major causal link between human activity and spiraling. However, the path analysis supported other causal pathways as well. For example, community metabolism (in particular CR_{24}) had a positive influence on V_fs, but its inverse relation to human activity (e.g., % forest cover, see also Bott et al. 2006) was inconsistent with a nutrient-enrichment effect and evidently reflected other forms of human disturbance. We caution, however, that Bott et al. (2006) observed that human impacts on metabolism were potentially confounded by stream size and canopy cover. The associations with molecular tracers, particularly that of PO_4^{3-}-V_f with toxic PAHs, offer the possibility that nutrient uptake was affected by toxins. The concentrations of toxins observed in the Project (Aufdenkampe et al. 2006) were not clearly at levels that would impair ecosystem function, but they do demonstrate that the streams were receiving substances related to human activity. The streams with 2 of the 3 lowest V_fs (Kisco and Muscoot) have been reported by an independent study (Phillips et al. 2002, Phillips and Bode 2004) to receive several pesticides and herbicides, particularly during storm flows, at concentrations that may impair aquatic life. The stream with the lowest V_fs (West Branch Delaware) drains a watershed with larger % agricultural land use (= sum of all agricultural land uses in table 2 of Dow et al. 2006) than any other stream site in the Project, suggesting that pesticides and herbicides also were present in that stream. Thus, our study has shown that spiraling, as a measure of ecosystem function, was sensitive to human impacts and strongly suggests that this sensitivity included not only a response to nutrient loading, but to other impacts as well.

Acknowledgements

David Montgomery and David Arscott contributed significantly to field work, data management, and data analysis for this research. Chris Caine, Arlene Casas, Sarah Deonarine, and Nancy Parsons assisted with field work. Mike Gentile and Paul Kiry conducted the chemical analyses. This project was funded by a grant under the Safe Drinking Water Act from the New York State Department of Environmental Conservation and the US Environmental Protection Agency.

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Received: 17 February 2006
Accepted: 31 July 2006

APPENDIX 1. Channel and flow characteristics measured during nutrient injections at 10 sites in the New York City drinking-water-supply watersheds. See figs 1 and 2 in Arscott et al. 2006 for site locations. $A =$ cross sectional area of the stream, $A_s =$ cross-sectional transient storage area, $A_s/A =$ transient storage ratio, $v_{hyd} =$ hydraulic exchange velocity. Sites numbered ≤ 30 were west of Hudson River (WOH) and >30 were east of Hudson River (EOH).

Stream	Site	Year	Water velocity (m/s)	Stream flow (m^3/s)	Width (m)	Depth (m)	Longitudinal dispersion coefficient (m^2/s)	A_s/A	v_{hyd} (mm/s)
Bush Kill	11	2000	0.21	0.60	12.9	0.23	3.99	0.08	0.006
		2001	0.34	1.35	12.2	0.33	5.67	0.11	0.023
		2002	0.55	2.98	13.9	0.39	8.13	0.06	0.030
Cross	52	2000	0.12	0.16	8.0	0.17	0.56	0.08	0.009
		2001	0.07	0.07	5.0	0.19	0.21	0.24	0.057
		2002	0.09	0.08	5.5	0.16	0.36	0.18	0.030
Esopus	23	2000	0.33	1.70	19.1	0.27	6.06	0.04	0.007
		2001	0.56	4.37	22.8	0.34	2.57	0.12	0.099
		2002	0.53	3.16	20.0	0.30	8.71	0.04	0.010
Kisco	55	2000	0.17	0.39	10.1	0.23	1.28	0.13	0.009
		2001	0.11	0.17	9.4	0.17	0.83	0.19	0.021
		2002	0.07	0.10	8.3	0.18	0.41	0.15	0.014
Main Branch Croton		2001	0.09	0.09	7.8	0.13	0.50	0.14	0.010
		2002	0.11	0.09	7.3	0.11	0.52	0.08	0.005
Muscoot	46	2000	0.10	0.07	6.8	0.11	0.45	0.17	0.005
		2001	0.12	0.10	7.6	0.11	1.00	0.65	0.012
		2002	0.05	0.03	6.0	0.11	0.33	0.16	0.006
Neversink	29	2000	0.30	1.91	23.1	0.27	5.11	0.09	0.055
		2001	0.21	0.87	15.7	0.27	2.38	0.14	0.024
		2002	0.17	1.11	17.1	0.39	1.38	0.14	0.049
Rondout	30	2000	0.63	5.91	21.6	0.44	11.61	0.02	0.000
		2001	0.14	0.39	14.7	0.19	0.86	0.20	0.017
		2002	0.19	0.59	15.4	0.20	0.96	0.10	0.018
Schoharie	18	2000	0.16	0.77	24.3	0.20	2.42	0.17	0.012
		2001	0.10	0.43	23.7	0.18	0.55	0.25	0.029
		2002	0.08	0.23	19.4	0.15	0.57	0.21	0.017
West Branch Delaware	5	2000	0.29	2.21	21.7	0.35	1.24	0.20	0.053
		2001	0.18	0.87	19.8	0.24	1.03	0.21	0.031
Mean			**0.22**	**1.10**	**14.3**	**0.23**	**2.49**	**0.16**	**0.023**

APPENDIX 2. Ambient nutrient concentrations measured just prior to solute injections at 10 sites in the New York City drinking-water-supply watersheds. Dissolved organic C (DOC) and conductivity were measured at baseflow in the same season but on different dates from the additions (Kaplan et al. 2006). TDN = total dissolved N, SRP = soluble reactive P, TDP = total dissolved P, nd = no data. All ambient solute concentrations are in µg/L.

		Analytes								
Stream	Date	NH_4^+-N	NO_3-N	TDN	SRP	TDP	Glucose	Arabinose	DOC	Conductivity (µS/cm)
Bush Kill	13 July 2000	9	98	161	10	13	0.56	0.06	1360	69
	27 June 2001	11	156	242	7	11	0.71	0.05	1040	89
	19 June 2002	12	91	173	7	12	nd	nd	1500	71
Cross	25 August 2000	6	224	548	6	9	1.27	<0.02	2750	264
	10 October 2001	6	2	239	5	9	8.98	<0.02	3850	297
	11 September 2002	12	105	360	15	17	2.48	<0.02	3930	283
Esopus	19 October 2000	9	46	88	5	5	1.26	0.05	851	57
	6 June 2001	8	183	257	1	8	1	<0.02	752	71
	5 June 2002	14	92	117	5	5	1.34	<0.02	1040	60
Kisco	28 September 2000	21	348	643	19	37	1.01	0.02	4010	401
	17 October 2001	5	206	498	15	22	8.67	0.04	3000	465
	9 October 2002	8	367	657	41	38	10.32	0.04	2860	556
Main Branch Croton	24 October 2001	4	85	471	5	11	3.35	<0.02	3500	526
	28 August 2002	13	594	1060	32	34	1.12	<0.02	3990	511
Muscoot	31 August 2000	9	1220	1650	42	50	1.43	<0.02	6340	245
	3 October 2001	10	994	1440	18	23	2.29	<0.02	2920	634
	25 September 2002	10	1260	1710	36	48	3.13	<0.02	4200	444
Neversink	12 October 2000	7	36	53	2	2	0.97	<0.02	1470	26
	15 August 2001	8	191	294	2	3	0.39	<0.02	918	34
	7 August 2002	8	162	183	2	5	1.68	<0.02	1250	30
Rondout	20 July 2000	6	178	254	7	5	0.63	0.26	852	35
	29 August 2001	5	256	287	3	4	1.36	<0.02	827	42
	25 July 2002	6	186	218	4	nd	nd	nd	1030	38
Schoharie	5 October 2000	6	180	220	1	2	0.46	0.02	1510	67
	1 August 2001	12	62	118	1	3	1.31	<0.02	1540	108
	21 August 2002	8	22	99	1	1	<0.14	0.04	1580	107
West Branch Delaware	26 October 2000	14	866	988	20	18	0.67	0.07	2310	126
	18 July 2001	17	832	1010	11	15	0.89	<0.02	2160	174
Mean		**10**	**347**	**525**	**12**	**15**	**2.20**	**0.03**	**2281**	**205**