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Inter-annual, Annual, and Seasonal Variation of P and N Retention in a Perennial and an Intermittent Stream

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Abstract

Headwater streams represent the key sites of nutrient retention, but little is known about temporal variation in this important process. We used monthly measurements over 2 years to examine variation in retention of soluble reactive phosphorus (SRP) and ammonium (NH_4^+) in two Mediterranean headwater streams with contrasting hydrological regimes (that is, perennial versus intermittent). Differences in retention between streams were more evident for NH_4^+, likely due to strong differences in the potential for nitrogen limitation. In both streams, nutrient-retention efficiency was negatively influenced by abrupt discharge changes, whereas gradual seasonal changes in SRP demand were partially controlled by riparian vegetation dynamics through changes in organic matter and light availability. Nutrient concentrations were below saturation in the two streams; however, SRP demand increased relative to NH_4^+ demand in the intermittent stream as the potential for phosphorus limitation increased (that is, higher dissolved inorganic nitrogen:SRP ratio). Unexpectedly, variability in nutrient retention was not greater in the intermittent stream, suggesting high resilience of biological communities responsible for nutrient uptake. Within-stream variability of all retention metrics, however, increased with increasing time scale. A review of studies addressing temporal variation of nutrient retention at different time scales supports this finding, indicating increasing variability of nutrient retention with concomitant increases in the variability of environmental factors from the diurnal to the inter-annual scale. Overall, this study emphasizes the significance of local climate conditions in regulating nutrient retention and points to potential effects of changes in land use and climate regimes on the functioning of stream ecosystems.

Key words: nutrient retention; nutrient spiralling; uptake length; temporal variation; nitrogen; phosphorus; intermittent stream.

Introduction

Along the land-to-ocean aquatic continuum, headwater streams represent the key sites of nutrient storage, transformation, and removal (Alexander and others 2000; Peterson and others 2001), processes generally compiled under the term nutrient retention. Over the past three decades, the nutrient spiraling concept (Webster and Patten 1979; Newbold and others 1981; Stream Solute Workshop 1990), which combines the processes of

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nutrient uptake and transport, has provided an excellent framework to advance research on nutrient retention in streams. Numerous studies have used this concept to evaluate the variation of nutrient retention among different streams and to examine controlling factors (for a review see Ensign and Doyle 2006). Even though streams are highly dynamic ecosystems (Ward 1989; Palmer and Poff 1997), few studies have addressed the temporal variation of nutrient retention within streams.

Information on temporal variation in stream nutrient retention is important for several reasons. Firstly, it allows researchers to evaluate how many measurements of nutrient retention are needed to characterize adequately a stream. Secondly, it may help determine key factors driving nutrient-retention processes. Thirdly, it is critical for improving models of nutrient dynamics at larger spatial and temporal scales (Doyle 2005; Ensign and Doyle 2006; Wollheim and others 2006). Finally, it is needed to evaluate the utility of reference conditions as a managing tool (Nijboer and others 2004) and allows better predictions of how the ability of streams to retain nutrients will vary in response to changes in land use and climatic regimes.

Results from the few studies that have examined temporal variation of nutrient retention within streams indicate substantial variation at different time scales, from diurnal (for example, Martí and Sabater 1994; Mulholland and others 2006) to annual (for example, Simon and others 2005; Hoellein and others 2007). This finding is not surprising, considering that many of the environmental factors shown to influence nutrient retention, such as discharge (Wollheim and others 2001; Peterson and others 2001), temperature (Butturini and Sabater 1998; Simon and others 2005), and nutrient concentrations (Mulholland and others 2002; O'Brien and others 2007), may change dramatically over time. The temporal pattern of these environmental factors varies among streams, ultimately due to the influence of local catchment and climate conditions (Hynes 1975; Allan 1995). Thus, each stream is characterized by its own ''heartbeat'' of environmental factors, which results from a combination of factors following gradual seasonal patterns (for example, temperature), factors displaying an abrupt temporal regime (for example, discharge), and factors showing gradual seasonal patterns with abrupt changes associated with periods of flood or drought (for example, nutrient concentrations). The autotrophic (that is, algae, macrophytes, and bryophytes) and heterotrophic (that is, bacteria and fungi) compartments responsible for biotic nutrient uptake vary with time in response to changes in some of these factors (Minshall 1978; Bott and Kaplan 1985; Francoeour and others 1999). Nutrient retention is expected to follow these changes and, thus, to exhibit a characteristic temporal pattern within each stream.

Most studies on the temporal variation of stream nutrient retention have been constrained to time scales of 1 year or less (but see Martí and Sabater 1996). Nutrient retention is, however, expected to vary not only within and among seasons but also among years. This is of particular interest in Mediterranean streams, where a pronounced seasonality and high inter-annual variability are typical (Gasith and Resh 1999). Additionally, although studies of nutrient retention performed over 1 year have been used to draw conclusions about seasonality (for example, Mulholland and others 1985; Simon and others 2005; Hoellein and others 2007), the consistency of seasonal patterns can be verified only by examining its repeatability among years. Additionally, the variability of nutrient retention is expected to increase with the time scale covered by the study because of a higher probability of longer-term studies in capturing a greater variability in environmental factors.

Because processing rates in streams are strongly influenced by transport, the study of nutrient retention under variable flow conditions or hydrologic regimes can contribute to a better understanding of temporal variation in stream nutrient retention (Fisher and others 2004). Hydrological intermittency, which is also characteristic of Mediterranean and other arid and semi-arid streams, can exert a strong influence on nutrient dynamics (Dahm and others 2003; Bernal and others 2005; Lillebo and others 2007), including the effects of prior drought conditions on nutrient retention, which are largely unknown. Temporal variation in nutrient retention is, therefore, expected to be larger in intermittent than in perennial streams because of the additional effect of droughts on the biological communities responsible for nutrient uptake (Lake 2003).

Phosphorus (P) and nitrogen (N) are the nutrients that most commonly limit primary production in streams (Elwood and others 1981; Borchardt 1996). Thus, studies of nutrient retention have focused on one or both of these elements, normally using soluble reactive phosphorus (SRP) and ammonium (NH_4^+) because these are the P and N forms taken up preferentially by most organisms. Yet, simultaneous experiments with both nutrients can provide interesting information from a stoichiometric perspective because the retention of one nutrient is expected to be dependent on its relative availability with respect to other nutrients. Both SRP and NH_4^+ are subjected to abiotic and assimilatory biotic retention processes, but NH_4^+ can additionally undergo dissimilatory processes (for example, nitrification). Consequently, NH_4^+ retention is expected to be less influenced by changes in environmental variables and, therefore, to be less variable than SRP retention.

Our goal was to explore temporal variation in nutrient retention by addressing the three aspects of temporal extent, hydrologic regime, and nutrient stoichiometry. Thus, we analyzed temporal variation of both SRP and NH_4^+ retention in two Mediterranean streams with contrasting hydrological regimes: a perennial and an intermittent stream. The study was done over two complete hydrologic years to cover seasonal, annual, and inter-annual variation. To examine within-stream temporal variation, we considered the magnitude, temporal pattern, and range of retention metrics in relation to changes in associated environmental drivers (that is, discharge, temperature, and nutrient concentrations). Finally, we compiled published data on nutrient retention worldwide to explore further the relationship between variability of nutrient retention and environmental drivers over different time scales.

Methods

Study Sites

This study was conducted in La Tordera catchment (Catalonia, NE Spain). With an area of 868.5 km^2 dominated by siliceous geology, the catchment covers an altitudinal gradient of approximately 1,700 m in less than 30 km horizontal distance from the highest peaks (Montseny mountain range) to the river mouth at the Mediterranean Sea. The climate is Mediterranean, with warm, dry summers and mild, humid winters, but the pronounced altitudinal gradient results in a mosaic of microclimates with contrasting local temperature, precipitation, and evapotranspiration regimes. Within this catchment, we selected a perennial and an intermittent stream located at the extremes of the altitudinal gradient. The perennial stream (Santa Fe: 2° 27′ 40′E, 41° 46′ 34′N) is located in the Montseny Natural Protected Area. Monthly mean temperatures range from 3 in January to 20°C in August. Mean annual precipitation is approximately 900 mm, occurring mostly as rain in autumn and spring but with occasional snow in winter. At the study site (1,136 m asl), the stream drains a 2.6-km^2 granitic catchment forested primarily with silver fir (*Abies alba*) at higher elevations and beech (*Fagus sylvatica*) at lower elevations. Human use is mainly recreational, with some dispersed shepherding. Based on the influence of temperature, precipitation, and vegetation dynamics on stream hydrology, we divided each hydrologic year into two periods: (1) from December to April (the cool-wet and dormant period, or *wet period*), and (2) from May to November (the warm-dry and vegetative period, or *dry period*).

The intermittent stream (Fuirosos, 2° 34′ 55′E, 41° 42′ 12′N) is located in the Montnegre-Corredor Natural Protected Area. The climate is warmer and drier than at the perennial stream, with monthly mean temperatures ranging from 5 in January to 24°C in August. Annual precipitation varies greatly among years, with a mean of approximately 750 mm. At the study site (115 m asl), the stream drains a 14.4-km^2 granitic catchment covered mostly by perennial cork oak (*Quercus suber*) and Aleppo pine (*Pinus halepensis*) at the lower elevations and a deciduous forest of chestnut (*Castanea sativa*), hazel (*Corylus avellana*), and oak (*Quercus pubescens*) at the higher elevations. Human land use is restricted to the periodic harvesting of bark from cork trees and agricultural fields that occupy less than 2% of the catchment area. Stream discharge is intermittent in summer with no flow periods of variable duration among years. Only during the wettest years (annual precipitation >800 mm), does the stream not dry in summer. Due to the influence of drought, we divided each hydrologic year into three periods: (1) from December to mid-March (the cool-wet and dormant period, or *wet period*), (2) from mid-March to August (the warm-dry and vegetative period or *dry period*), and (3) from September to November (the transition from dry to wet conditions, or *transition period*).

We selected a representative reach of each stream for experiments. In the perennial stream, the reach was 140-m long and riffle-pool dominated with a slope of 0.094 m m^{-1}. The streambed was composed of cobbles (47%), boulders (25%), and pebbles (21%), with patches of gravel and sand. Riparian vegetation was well developed and dominated by beech, with some stems of common elder (*Sambucus nigra*) and poorly developed herbaceous understory. In the intermittent stream, the study reach was 80-m long and riffle-pool dominated with a slope of 0.074 m m^{-1}. Dominant substrate was finer than in the perennial stream and was composed of sand (56%) and boulders (30%), with patches of cobbles, pebbles, gravel, and bedrock. Riparian vegetation was dense, consisting mainly of alder (*Alnus glutinosa*) and sycamore (*Platanus hispanica*), with substantial herbaceous understory.

Field Sampling and Laboratory Analyses

This study covered two hydrologic years, from September 2004 through August 2006. During this period, the two streams were sampled approximately bi-weekly for water temperature, discharge, and concentrations of nitrate (NO_3^-) + nitrite (NO_2^-), ammonium (NH_4^+), and SRP. These data allowed a detailed characterization of the temporal variation of environmental variables known to affect nutrient retention. To examine temporal variation in nutrient retention, we conducted short-term, constant-rate additions of SRP (as $Na(H_2PO_4) \cdot 2H_2O$) and NH_4^+ (as NH_4Cl) into each stream once a month (coinciding with some of the regular sampling dates). Chloride (Cl^-, as NaCl) was added as a conservative tracer. A total of 25 additions in the perennial stream and 20 additions in the intermittent stream were completed. No flow or high-discharge conditions were avoided due to methodological constraints.

The methodology for nutrient additions followed Webster and Valett (2006). A Masterflex (Vernon Hills, Illinois, USA) L/S battery-powered peristaltic pump was used to deliver nutrient/tracer solution to the stream. Additions began at approximately 11 a.m. and lasted until conductivity reached a plateau at the bottom of the study reach (that is, 1–4 h, depending on stream discharge on each date). Conductivity was automatically recorded at the bottom of the reach every 5 s using a WTW (Weilheim, Germany) 340i portable conductivity meter connected to a Campbell Scientific (Logan, Utah, USA) data logger. We measured conductivity and collected water samples at eight stations along the reach prior to the addition to determine background concentrations (two to three replicates per station), and we collected samples at the same stations when conductivity reached a plateau (hereafter, ''plateau'' concentrations; five replicates per station). Water samples for nutrient chemistry were immediately filtered through Whatman (Kent, UK) GF/F glass–fiber filters (0.7 µm), stored on ice in the field, and refrigerated at 4°C or frozen in the laboratory until analysis.

On each addition date, stream discharge was estimated based on a mass-balance approach using the time-curve conductivity data recorded at the bottom of the reach (Gordon and others 2004). Discharge values from additions were compared with discharge measurements done at a single transect on the regular sampling dates, and the calculated correction factor was applied to the latter. Wetted width was determined on cross-sectional transects located at each sampling station along the reach. Water temperature was measured with the conductivity meter at each station during background and plateau samplings, and the values were averaged.

Concentrations of $NO_3^- + NO_2^-$ and SRP in stream water samples were analyzed in the laboratory using a Bran + Luebbe (Norderstedt, Germany) TRAACS 2000 Autoanalyzer II. NH_4^+ concentration was analyzed on a Skalar (Breda, The Netherlands) San$^+$ Autoanalyzer. All nutrient analyses were performed following standard colorimetric methods as described in APHA (1995). Analysis of the concentration of NO_2^- in more than 50% of the samples showed that it was negligible, accounting for less than 4% of dissolved inorganic nitrogen (DIN) in both study streams; thus, NO_3^- is used hereafter to refer to the concentration of $NO_3^- + NO_2^-$. DIN concentration was calculated as the sum of NO_3^- and NH_4^+ concentrations.

Calculation of Nutrient Retention Metrics

Using data from the nutrient additions, we calculated three metrics of retention for each nutrient (that is, NH_4^+ and SRP) and each addition date and stream: uptake length (S_w, m), uptake velocity (V_f, mm min^{-1}), and uptake rate (U, µg m^{-2} s^{-1}). S_w, the average distance traveled by a nutrient molecule before being removed from the water column (Newbold and others 1981), was calculated as the negative inverse of the longitudinal uptake rate (k_w, m^{-1}). This rate is the slope of the regression of the ln-transformed and background-corrected nutrient:conductivity ratio versus distance downstream from the addition point. S_w is an indicator of the nutrient-retention efficiency at the reach scale (Webster and Valett 2006). V_f, the velocity at which a nutrient is removed from the water column, was calculated as the stream-specific discharge (that is, discharge/width) divided by S_w. V_f is an indicator of nutrient demand relative to concentration in the water column (Hall and others 2002). U, the mass of a nutrient taken up from the water column per unit streambed area and time, was calculated as V_f multiplied by ambient nutrient concentration. U is used as an indicator of stream nutrient-retention capacity (Webster and Valett 2006). Finally, we calculated the nutrient-demand ratio (V_f-NH_4^+:V_f-SRP) by dividing the demand of NH_4^+ over that of SRP.

Nutrient concentrations in plateau samples are slightly enriched relative to background and, thus, may overestimate ambient S_w (Mulholland and others 2002). To minimize this effect, nutrient concentration of the added solution and pump flow rate was adjusted for each addition to reach a relatively low and similar nutrient-enrichment level among addition dates and streams. In the perennial stream, increases in nutrient concentration relative to background nutrient concentration at the top sampling station (mean ± SE) were 65 ± 8 µg P l^{-1} for SRP and 54 ± 9 µg N l^{-1} for NH_4^+. In the intermittent stream, these increases were 79 ± 16 µg P l^{-1} for SRP and 65 ± 14 µg N l^{-1} for NH_4^+. We found no relationship between the increase in enrichment concentration and S_w, except for NH_4^+ in the intermittent stream ($r^2 = 0.23$, $P = 0.032$, $n = 20$).

Data Analysis

All k_w used to estimate S_w values reported in this study are from statistically significant ($P < 0.05$) regressions of nutrient-addition data. Standard errors for each nutrient retention metric (that is, S_w, V_f, and U) were calculated based on error estimates for k_w. This error estimate is a practical approach to real measurement uncertainty associated with each nutrient addition (Hanafi and others 2007). We used Pearson's product-moment correlation to explore relationships between environmental parameters and nutrient-retention metrics. The independent t-test was used to compare environmental parameters and nutrient-retention metrics between streams, and the dependent t-test was used to compare retention metrics between nutrients in each stream. We applied linear regression analysis to examine relationships between environmental parameters and specific nutrient-retention metrics as follows. Firstly, the influence of discharge was explored using S_w. Secondly, the influence of water temperature was analyzed using V_f because this metric corrects S_w for discharge. Finally, we examined the influence of nutrient availability using either V_f or U. Additionally, potential U saturation was investigated with a Michaelis-Menten model (with Levenberg-Marquardt estimation algorithm and non-log-transformed data). To explore whether or not the influence of measured environmental drivers varied depending on time of year, regressions were also estimated separately with data for each hydrological period (as described in the ''Study site'' section). Variability of environmental parameters and retention metrics was compared within and among streams employing the range quotient, R_q (that is, maximum value/minimum value). Patterns of variability across time scales were further examined using linear regressions between R_q of nutrient-retention metrics and environmental parameters, based on data compiled from studies addressing temporal variation of stream nutrient retention at different time scales. In this analysis, we considered only studies for which data on retention metrics and environmental factors were available for three or more dates. Data were log-transformed as needed to meet assumptions of parametric statistics. Statistical analyses were done using Statistica 6.0 (Statsoft, Tulsa, Oklahoma, USA).

Results

Environmental Parameters

Water temperature and discharge followed seasonal patterns (Figure 1) and were negatively correlated in both the perennial ($r = -0.62$, $P < 0.001$, $n = 49$) and the intermittent stream ($r = -0.45$, $P = 0.004$, $n = 39$). Temperature was higher and spanned a broader range in the intermittent stream (Table 1). Conversely, discharge was relatively similar in both streams, but the range was larger in the intermittent stream (Table 1). Discharge was generally low from late-spring to early autumn (that is, dry period), and high, especially in the second study year, from late-autumn to early spring (that is, transition and wet periods) (Figure 1). The intermittent stream dried out in the summer, with a shorter no flow period in the first year (20 days) than in the second year (65 days).

Ambient concentrations of SRP and NO_3^- and their temporal patterns differed between streams. The concentration of SRP was higher, and that of NO_3^- was lower, in the perennial stream (Table 1). The concentration range of both nutrients was broader in the intermittent stream, especially for NO_3^- (Table 1). In the perennial stream, SRP and NO_3^- concentrations were positively correlated ($r = 0.55$, $P < 0.001$, $n = 49$) and followed a marked seasonal pattern that was consistent between years, with higher values during the warm, dry period than during the cold, wet period (Figure 1). Accordingly, both nutrients correlated positively with water temperature (SRP: $r = 0.72$, $P < 0.001$, $n = 49$; NO_3^-: $r = 0.73$, $P < 0.001$, $n = 49$) and negatively with discharge (SRP: $r = -0.71$, $P < 0.001$, $n = 49$; NO_3^-: $r = -0.27$, $P = 0.065$, $n = 49$). In contrast, SRP concentration showed a similar pattern as in the perennial stream in the intermittent stream, whereas NO_3^- concentration showed a nearly opposite pattern (Figure 1). The concentration of NO_3^- correlated negatively with water temperature ($r = -0.55$, $P < 0.001$, $n = 39$) and correlated positively with stream discharge ($r = 0.59$, $P < 0.001$, $n = 39$), whereas SRP concentration only correlated

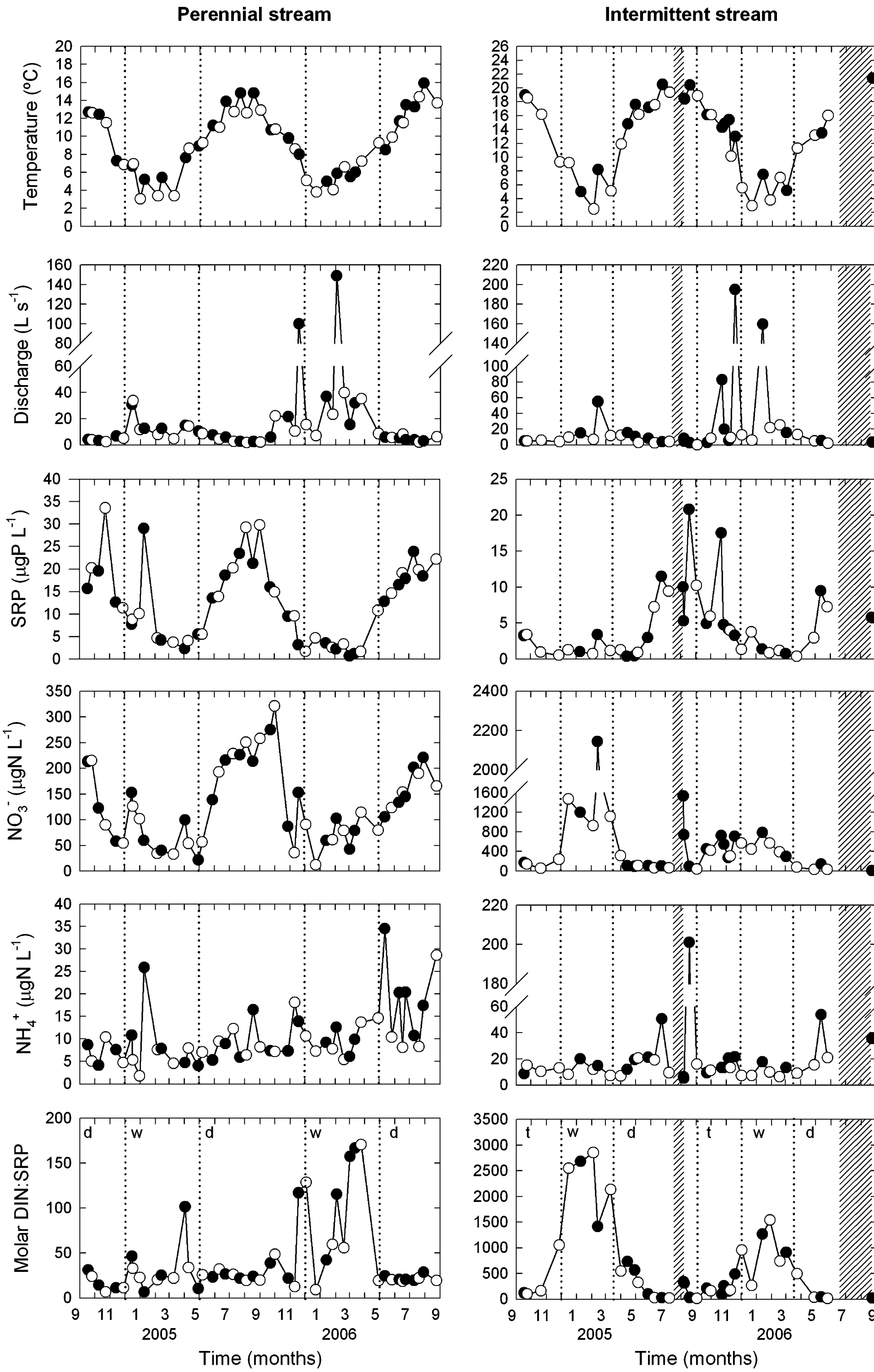


Figure 1. Temporal variation of stream water temperature, discharge, soluble reactive phosphorus (SRP), nitrate (NO_3^-), ammonium (NH_4^+), and molar DIN:SRP in the perennial stream ($n = 49$) and the intermittent stream ($n = 39$). Data are from regular samplings carried out during the 2-year study period. *Open symbols* denote days when nutrient additions were conducted. *Dotted lines* separate the hydrological periods, which are labeled with *small letters* in the lower panels (d, dry period; w, wet period; t, transition period). *Dashed bars* indicate the no flow periods in the intermittent stream. Notice different scales in *y*-axis for clarity of patterns.

positively with water temperature ($r = 0.50$, $P < 0.001$, $n = 39$). Concentrations of both nutrients increased dramatically after the first year's drought in the intermittent stream (Figure 1).

The concentration of NH_4^+ averaged less than 13% of DIN in both streams, but it was higher and showed a broader range in the intermittent stream (Table 1; Figure 1). The NH_4^+ concentration was positively related to water temperature ($r = 0.34$, $P = 0.035$, $n = 39$) and SRP ($r = 0.39$, $P = 0.015$, $n = 39$) and negatively related to NO_3^- concentration ($r = -0.42$, $P = 0.008$, $n = 39$) in this stream

Table 1. Mean, Standard Error (SE), Minimum (min), Maximum (max), and Range Quotient (R_q, max/min) of Physicochemical Parameters in the Perennial Stream (n = 49) and the Intermittent Stream (n = 39) over the 2-year Study Period

Parameter	Perennial stream				Intermittent stream				*P*
	Mean	SE	Min–Max	R_q	Mean	SE	Min–Max	R_q	
Temperature (°C)	9.3	0.5	3.1–15.9	5	13.1	0.9	2.5–21.4	9	**<0.001**
	(8.8)	*(0.5)*	*(3.1)–(14.4)*	*(5)*	*(11.5)*	*(0.9)*	*(2.5)–(19.4)*	*(8)*	*(0.054)*
Discharge (L s^{-1})	15.9	3.6	1.6–148.8	93	20.0	6.4	0.1–194.9	1,820	0.558
	(12.6)	*(1.6)*	*(4.5)–(52.0)*	*(12)*	*(9.0)*	*(1.0)*	*(0.7)–(24.9)*	*(36)*	*(0.107)*
SRP (μg P L^{-1})	13	1	1–34	49	5	1	0–21	56	**<0.001**
	(13)	*(1)*	*(2)–(34)*	*(20)*	*(3)*	*(1)*	*(0)–(10)*	*(26)*	***(<0.001)***
NO_3^- (μg N L^{-1})	129	11	12–321	26	452	78	14–2,143	156	**<0.001**
	(125)	*(12)*	*(12)–(321)*	*(26)*	*(369)*	*(64)*	*(35)–(1,468)*	*(42)*	***(0.019)***
NH_4^+ (μg N L^{-1})	10	1	2–35	20	20	5	5–201	39	**0.034**
	(10)	*(1)*	*(2)–(29)*	*(19)*	*(12)*	*(1)*	*(6)–(21)*	*(3)*	***(0.047)***
Molar DIN:SRP	40.8	6.0	6.5–170.7	26	614.1	125.6	11.5–2,853.1	247	**<0.001**
	(35.4)	*(5.3)*	*(6.6)–(170.7)*	*(26)*	*(695.9)*	*(127.4)*	*(11.5)–(2,550.4)*	*(222)*	***(<0.001)***

Data in italics within parenthesis represent values of parameters on nutrient addition dates (perennial stream, n = 25; intermittent stream, n = 20). SRP, soluble reactive phosphorus; NO_3^-, nitrate; NH_4^+, ammonium; DIN, dissolved inorganic nitrogen. The P values are the results of independent t-tests comparing physicochemical parameters between streams. Significant (P < 0.05) t-test results are highlighted in bold.

only. Pre- and post-drought increases of NH_4^+ were also observed in the intermittent stream (Figure 1).

The mean and range of the DIN:SRP molar ratio was larger in the intermittent stream (Table 1), although it showed a similar seasonal pattern in both streams, with its highest values during the wet period (Figure 1). Water temperature and DIN:SRP correlated negatively in both the perennial ($r = -0.34$, $P = 0.015$, $n = 49$) and the intermittent stream ($r = -0.74$, $P < 0.001$, $n = 49$), whereas discharge was positively related to DIN:SRP only in the perennial stream ($r = 0.54$, $P < 0.001$, $n = 49$). Dates when nutrient additions were performed captured a considerable part of the variation in environmental parameters observed in the richer data set from the regular bi-weekly samplings (Table 1).

Nutrient Retention

Nutrient-retention Efficiency. In the perennial stream, mean S_w-NH_4^+ was 4.2-fold shorter than mean S_w-SRP (Table 2), and S_w-NH_4^+ never exceeded S_w-SRP. S_w for the two nutrients was

Table 2. Mean, Standard Error (SE), Minimum (min), Maximum (max), and Range Quotient (R_q, max/min) of Retention Metrics for Both Added Nutrients on Nutrient Addition Dates in the Perennial Stream (n = 25) and the Intermittent Stream (n = 20) over the 2-year Study Period

Retention metric	Nutrient	Perennial stream				Intermittent stream				*P*
		Mean	SE	Min–Max	R_q	Mean	SE	Min–Max	R_q	
Uptake length, S_w (m)	SRP	406.4	81.3	97.3–1,556.8	16	384.6	86.0	66.1–919.2	14	0.800
	NH_4^+	96.4	19.3	18.6–618.4	33	223.4	50.0	23.8–568.1	24	**0.002**
P		**<0.001**				**0.012**				
Uptake velocity, V_f (mm min^{-1})	SRP	0.7	0.1	0.2–1.4	8	0.6	0.1	0.1–2.2	32	0.166
	NH_4^+	3.4	0.7	0.7–11.5	17	1.1	0.2	0.2–3.1	14	**<0.001**
P		**<0.001**				**0.012**				
Uptake rate, U (μg m^{-2} min^{-1})	SRP	8.5	1.7	0.3–33.2	112	1.5	0.3	0.1–5.9	77	**<0.001**
	NH_4^+	31.1	6.2	3.7–83.1	23	13.8	3.1	2.7–59.1	22	**0.001**
P		**<0.001**				**<0.001**				

NH_4^+, ammonium; SRP, soluble reactive phosphorus. The P values are the results of independent t-tests comparing retention metrics between streams and dependent t-tests comparing retention metrics between nutrients. Significant (P < 0.05) t-test results are highlighted in bold.

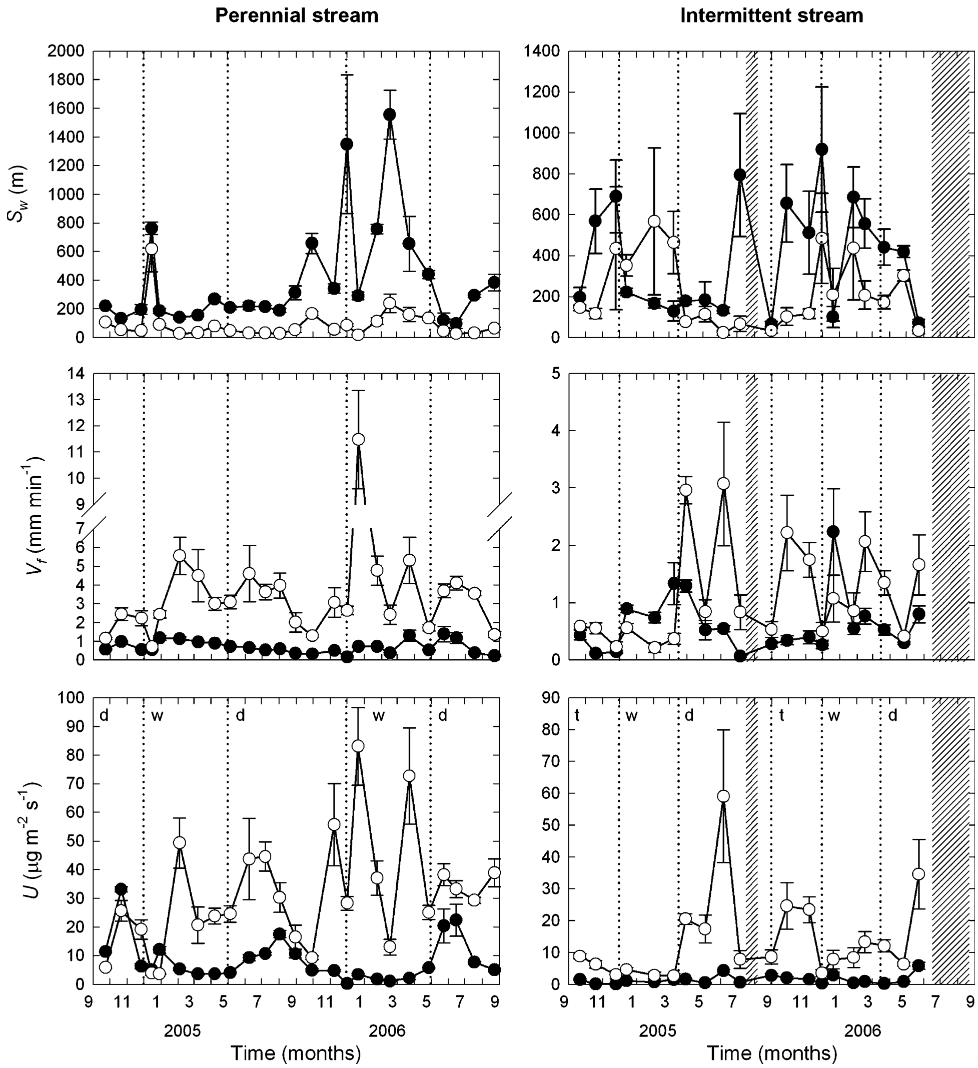


Figure 2. Temporal variation of the uptake length (S_w), uptake velocity (V_f), and uptake rate (U) of soluble reactive phosphorus (SRP) (*closed symbols*) and ammonium (NH_4^+; *open symbols*) in the perennial stream (n = 25) and the intermittent stream (n = 20). Data are from monthly nutrient additions done over the 2-year study period. Error bars are ±SE (see text for detailed explanation). *Dotted lines* separate the hydrological periods, which are labeled with *small letters* in the lower panels (d, dry period; w, wet period; t, transition period). *Dashed bars* indicate the no flow periods in the intermittent stream. Notice different scales in y-axis for clarity of patterns.

positively correlated (r = 0.72, P < 0.001, n = 25) and tended to be longest during the wet period, especially in the second study year (Figure 2). In the intermittent stream, mean S_w-NH_4^+ was 1.7-fold shorter than mean S_w-SRP (Table 2), but they were not correlated. S_w-NH_4^+ tended to be longest during the wet period when it exceeded S_w-SRP, but no clear seasonal pattern was observed for S_w-SRP (Figure 2). A comparison between streams showed that mean S_w-NH_4^+ was 2.3-fold shorter in the perennial than in the intermittent stream, whereas S_w-SRP was similar between streams (Table 2).

Nutrient Demand. In the perennial stream, V_f-NH_4^+ was positively correlated with V_f-SRP (r = 0.46, P = 0.022, n = 25), although it was consistently higher (4.9-fold, on average; Table 2) and reached maximum value during the wet period (Figure 2). In the intermittent stream, mean V_f-NH_4^+ was 1.8-fold higher but uncorrelated with mean V_f-SRP (Table 2). V_f-SRP was highest during the wet period when it exceeded V_f-NH_4^+, which showed no clear seasonal pattern (Figure 2). In this stream, V_f-SRP was higher than V_f-NH_4^+ only during the wet period, especially in the first study year (Figure 2). A comparison between streams showed that mean V_f-NH_4^+ was 3.1-fold higher in the perennial stream, whereas a similar mean V_f-SRP was found in both streams (Table 2).

Nutrient Uptake Capacity. In the perennial stream, mean U-NH_4^+ was 3.7 times higher than mean U-SRP (Table 2), and they were not correlated. Only U-SRP showed a clear seasonal pattern, with its highest values during the dry period (Figure 2). In the intermittent stream, mean U-NH_4^+ was 9.2 times higher than mean U-SRP (Table 2). U for both nutrients correlated positively (r = 0.53, P = 0.015, n = 20), showing its highest values during the dry period (Figure 2). An increase in U-NH_4^+ during the transition period was also apparent, especially in the second study year (Figure 2). A comparison between streams showed that mean U-SRP and U-NH_4^+ were 5.7 and 2.3-fold higher, respectively, in the perennial than in the intermittent stream (Table 2).

Variability of Nutrient-retention Metrics. Retention of both nutrients showed high variability in our study streams. Metrics spanned ranges of one ($R_q > 10$) or even two ($R_q > 100$) orders of magnitude, except for V_f-SRP in the perennial stream (Table 2). Furthermore, R_q increased as the time scale was expanded from seasonal to inter-annual for all three retention metrics and in both streams (Figure 3). R_q was lowest when computed per period (that is, seasonal scale) and highest when computed for the two study years (that is, inter-annual scale), with intermediate R_q at the annual scale (Figure 3). A comparison between streams showed that R_q was similar or higher in the perennial stream, except in the case of V_f-SRP (Table 2; Figure 3).

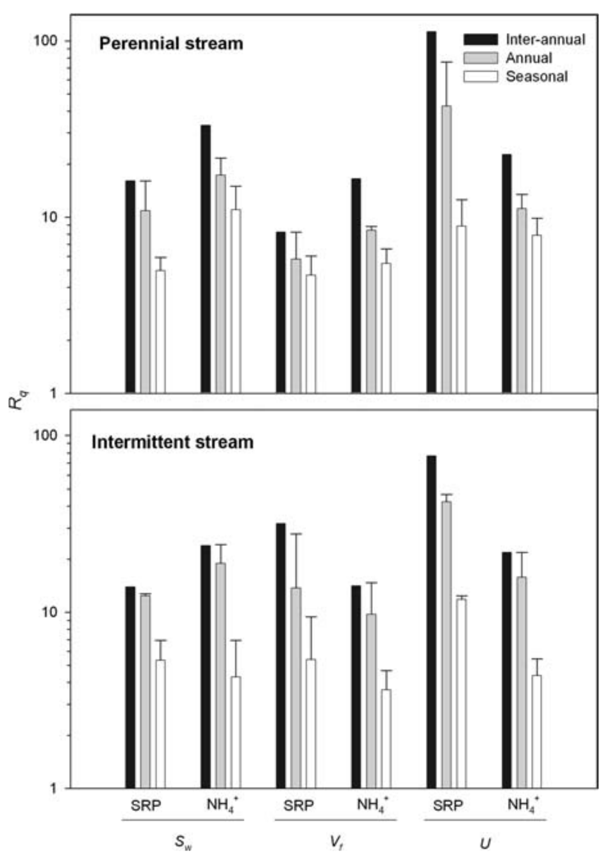


Figure 3. Average range quotient (R_q) of uptake length (S_w), uptake velocity (V_f), and uptake rate (U) of soluble reactive phosphorus (SRP) and ammonium (NH_4^+) in the perennial stream (*upper panel*) and the intermittent stream (*lower panel*) computed for the 2 years together (that is, inter-annual scale), each year separately (that is, annual scale; $n = 2$ for both streams), and each period of each year separately (that is, seasonal scale; $n = 4$ for the perennial stream, and $n = 6$ for the intermittent stream). Error bars are + SE.

Environmental Drivers of Nutrient Retention

Discharge. In the perennial stream, both S_w-SRP and S_w-NH_4^+ increased with discharge following power functions (Table 3). These relationships held for both nutrients when the analysis was restricted to the wet period (Table 3). When data from the dry period were analyzed, only S_w-NH_4^+ showed a significant relationship with discharge, and it was best fitted by a linear function (Table 3). In the intermittent stream, the relationships of discharge with both S_w-SRP and S_w-NH_4^+ also followed power functions, but these accounted for a lower proportion of the variation of S_w than in the perennial stream (Table 3). When each period was analyzed separately, only S_w-SRP showed a linear relationship with discharge during the wet period (Table 3).

Temperature. With data from all addition dates used together, V_f-SRP was not related to temperature in the perennial stream. When the extremely low V_f-SRP value measured in December 2005 (Figure 2) was excluded, however, a negative exponential relationship was found (Figure 4). Considering data from each period separately, we found only a negative exponential relationship of V_f-SRP with temperature during the dry period (Figure 4). In the intermittent stream, using data from all addition dates together, V_f-SRP showed a negative exponential relationship with temperature (Figure 4). This relationship lost its significance when data from each hydrological period were analyzed separately. No relationship between V_f-NH_4^+ and temperature was found in any of the streams, but the nutrient-demand ratio (that is, the ratio between V_f-NH_4^+ and V_f-SRP) exponentially increased with temperature in the intermittent stream (Figure 5).

Nutrient Availability. Considering data from all addition dates used together, neither V_f-SRP nor V_f-NH_4^+ was related to their respective nutrient concentrations (that is, SRP and NH_4^+) in any of the streams. When we analyzed each hydrological period separately, we found only a positive logarithmic relationship for V_f-SRP in the intermittent stream during the transition period (V_f-SRP $= 0.285 \cdot \log$ SRP $+ 0.202$, $r^2 = 0.76$, $P = 0.023$, $n = 6$). The nutrient-demand ratio did, however, decline exponentially with the DIN:SRP molar ratio in the intermittent stream with data from all addition dates

Table 3. Relationships of the Uptake Length, S_w (m) of Soluble Reactive Phosphorus (SRP) and Ammonium (NH_4^+) with Discharge, Q (L s^{-1}) in the Perennial and the Intermittent Stream using All Data Together (that is, ALL) or Separated into Periods (that is, Dry, Wet, Transition)

Nutrient	Period	Perennial stream	Intermittent stream
SRP	ALL	S_w-SRP = 49.73 · $Q^{0.79}$ r^2 = 0.49, p < 0.001	S_w-SRP = 122.01 · $Q^{0.45}$ r^2 = 0.20, p = 0.045
	Dry	n.s.	n.s.
	Wet	S_w-SRP = 37.13 · $Q^{0.89}$ r^2 = 0.54, P = 0.004	S_w-SRP = 30.44 · Q–130.50 r^2 = 0.82, P = 0.013
	Transition	–	n.s.
NH_4^+	ALL	S_w-NH_4^+ = 9.27 · $Q^{0.85}$ r^2 = 0.47, P < 0.001	S_w-NH_4^+ = 41.89 · $Q^{0.68}$ r^2 = 0.38, P = 0.004
	Dry	S_w-NH_4^+ = 12.25 · Q–24.87 r^2 = 0.47, P = 0.014	n.s.
	Wet	S_w-NH_4^+ = 6.45 · $Q^{0.96}$ r^2 = 0.46, P = 0.010	n.s.
	Transition	–	n.s.

n.s, not significant (P > 0.05).

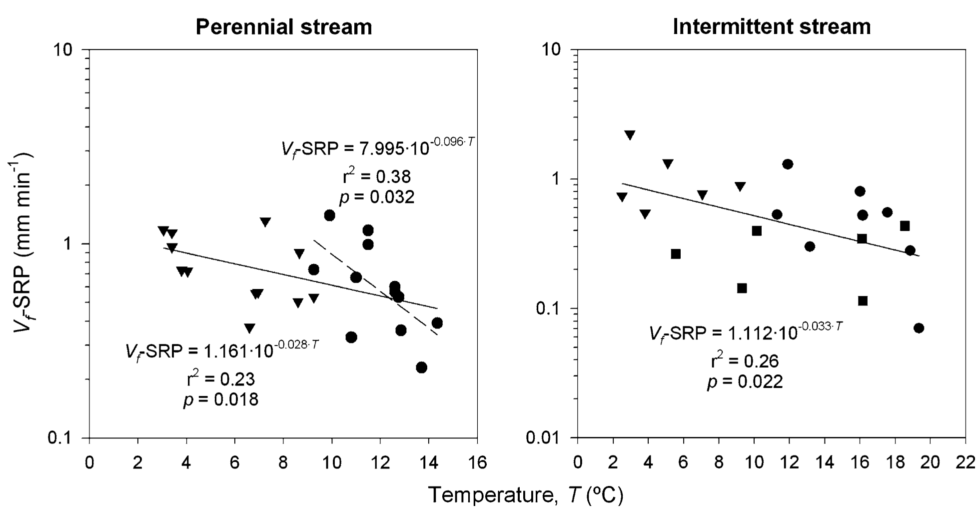


Figure 4. Relationships of the uptake velocity of soluble reactive phosphorus (V_f-SRP) with stream water temperature (T), in the perennial stream (n = 24, outlier from December 2005 excluded) and the intermittent stream (n = 20). *Symbols* indicate the different hydrological periods as follows: dry period (●), wet period (▼), and transition period (■). *Straight lines* represent significant (P < 0.05) linear regressions for data from all seasons in each stream. *Dashed line* represents a significant (P < 0.05) linear regression for the dry period in the perennial stream (n = 12).

(Figure 5). No relationship between the nutrient-demand ratio and DIN:SRP was found in the perennial stream or in any of the streams when data from each period were considered separately.

Michaelis-Menten models were poor predictors of nutrient uptake rates in both streams, regardless of whether data from all additions were used together or separated into hydrological periods. The model fits were not significant, or estimated half-saturation constants were outside the range of nutrient concentrations measured in this study when significant. The relationships between ambient nutrient concentrations and uptake rates were better explained by linear regression models.

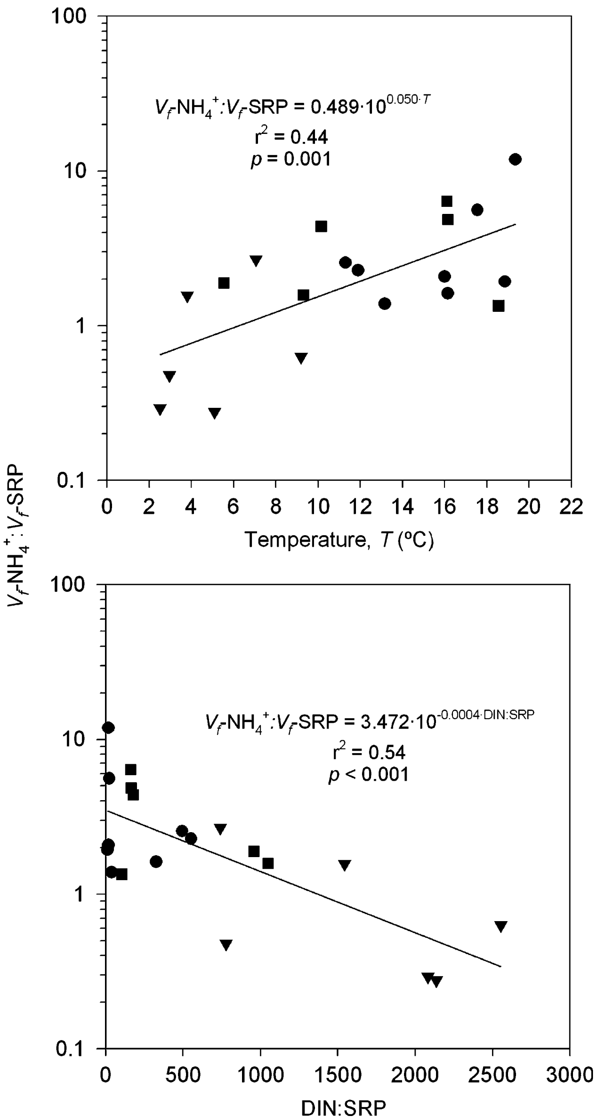


Figure 5. Relationships of the nutrient-demand ratio (V_f-NH_4^+:V_f-SRP) with stream water temperature (T) and the DIN to SRP molar ratio (DIN:SRP) in the intermittent stream (n = 20). *Symbols* indicate the different hydrological periods as follows: dry period (●), wet period (▼), and transition period (■). *Straight lines* represent significant ($P < 0.05$) linear regressions.

In the perennial stream, both U-SRP and U-NH_4^+ were positively related to their respective ambient nutrient concentrations following a power function (Table 4). This relationship held when each period was analyzed separately. In the intermittent stream, U-SRP was related to the ambient SRP concentration following a power function with both all data together or separated into periods (Table 4). Conversely, this relationship was linear in the case of U-NH_4^+, and no relationships were found when periods were analyzed separately.

Patterns of Variability Across Time Scales

The compilation of data from studies on the temporal variation of stream nutrient retention showed that R_q for all three retention metrics increased as the time scale considered was expanded from diurnal to inter-annual (Figure 6). Furthermore, variation in R_q of retention metrics among studies was related to the estimated R_q of specific environmental drivers. In particular, S_w-R_q was positively related to discharge-R_q, whereas V_f-R_q and U-R_q were positively related to concentration-R_q (Figure 6). No relationship between R_q of retention metrics and temperature-R_q was found.

Discussion

Comparison of the Magnitude of Nutrient Retention Between Streams and Nutrients

Nutrients in our study streams traveled, on average, only a few hundred meters before being removed from the water column, indicating high efficiency in nutrient retention, as has been observed in other headwater streams (see for a review Ensign and Doyle 2006). One major difference between the two streams was found for NH_4^+ retention, which, based upon all three retention metrics, was greater in the perennial than in the intermittent stream. This difference could be attributed to the relatively high DIN and low SRP availability in the intermittent stream, indicative of a lower potential for N limitation. Although the average retention efficiency (that is, uptake length) and demand (that is, uptake velocity) for SRP were similar between streams, the SRP uptake capacity (that is, uptake rate) was higher in the perennial stream due to its higher SRP availability because uptake capacity is a function of the ambient nutrient concentration (Webster and Valett 2006).

Both streams showed a higher ability to retain NH_4^+ than SRP. NH_4^+ is subject to a greater diversity of biotic assimilatory and dissimilatory retention processes than SRP, especially in reaches with fine substrata (Butturini and Sabater 1999). In addition, co-precipitation of SRP with calcium carbonate, which is an important abiotic removal process in calcareous streams, was probably negligible in our study streams due to the siliceous geology (Reddy and others 1999). In fact, Martí and Sabater (1996) reported similar findings in nearby catchments for a sand-cobble reach of the siliceous Riera Major, but higher SRP retention for a similar

Table 4. Relationships of the Uptake Rate, U (μg m^{-2} min^{-1}) of Soluble Reactive Phosphorus (SRP) and Ammonium (NH_4^+) with their Respective Nutrient Concentration in the Perennial and the Intermittent Stream using All Data Together (that is, ALL) or Separated into Periods (that is, Dry, Wet, Transition)

Nutrient	Period	Perennial stream	Intermittent stream
SRP	ALL	$U\text{-SRP} = 0.70 \cdot \text{SRP}^{0.95}$ $r^2 = 0.71$, $P < 0.001$	$U\text{-SRP} = 0.53 \cdot \text{SRP}^{0.81}$ $r^2 = 0.49$, $P = 0.001$
	Dry	$U\text{-SRP} = 1.04 \cdot \text{SRP}^{0.80}$ $r^2 = 0.34$, $P = 0.046$	$U\text{-SRP} = 0.59 \cdot \text{SRP}^{0.69}$ $r^2 = 0.54$, $P = 0.037$
	Wet	$U\text{-SRP} = 0.57 \cdot \text{SRP}^{1.09}$ $r^2 = 0.65$, $P = 0.001$	$U\text{-SRP} = 1.29 \cdot \text{SRP}^{3.12}$ $r^2 = 0.70$, $P = 0.037$
	Transition	–	$U\text{-SRP} = 0.18 \cdot \text{SRP}^{1.51}$ $r^2 = 0.81$, $P < 0.001$
NH_4^+	ALL	$U\text{-}NH_4^+ = 2.69 \cdot NH_4^{+1.03}$ $r^2 = 0.47$, $P < 0.001$	$U\text{-}NH_4^+ = 1.56 \cdot NH_4{-}4.95$ $r^2 = 0.28$, $P = 0.017$
	Dry	$U\text{-}NH_4^+ = 2.99 \cdot NH_4^{+0.94}$ $r^2 = 0.39$, $P = 0.031$	n.s.
	Wet	$U\text{-}NH_4^+ = 2.47 \cdot NH_4^{+1.12}$ $r^2 = 0.52$, $P = 0.005$	n.s.
	Transition	–	n.s.

n.s, not significant ($P > 0.05$).

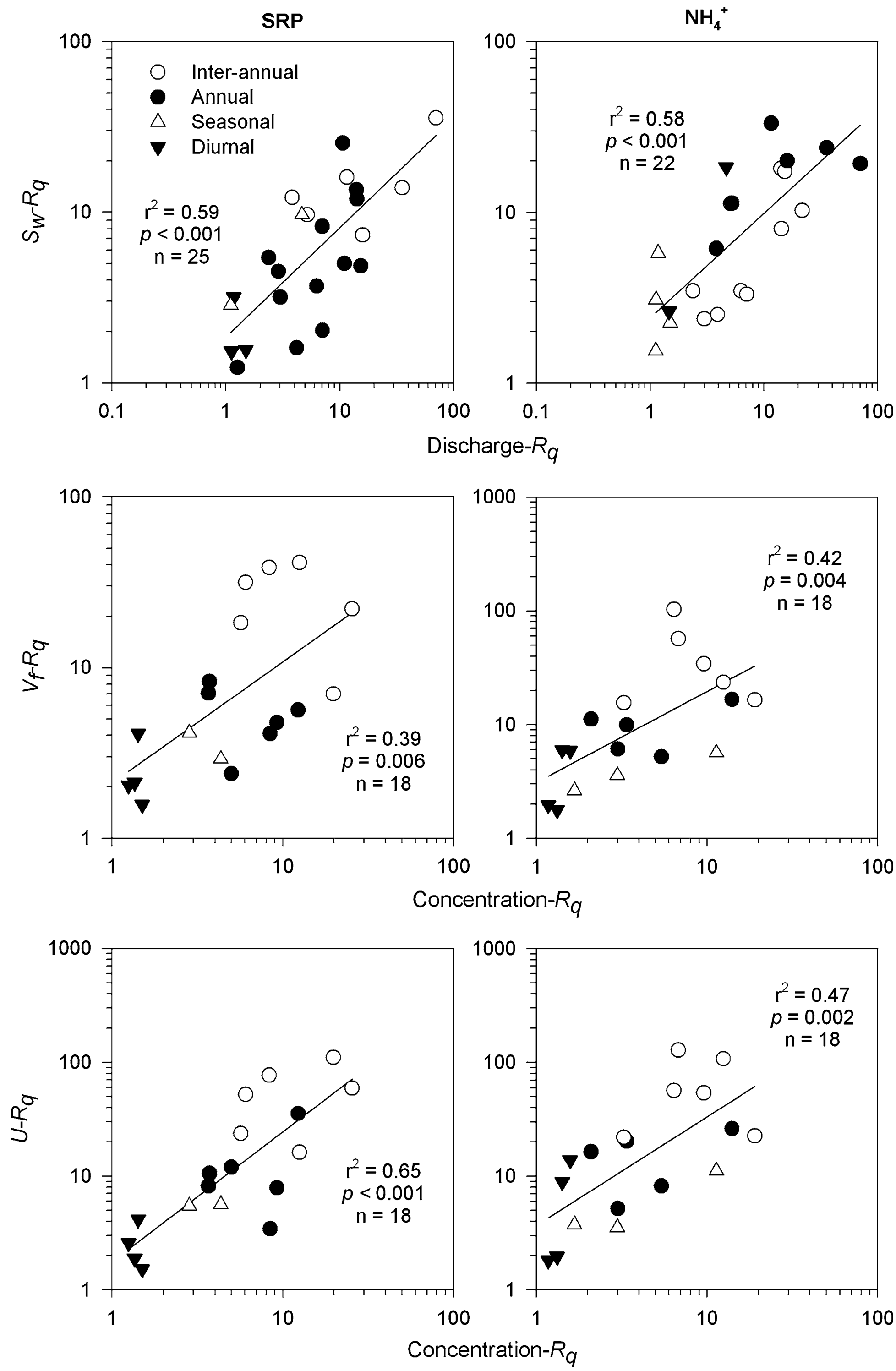
reach of the calcareous La Solana stream, a pattern that did not hold when bedrock-dominated reaches were included. Published studies conducted at an annual scale have found either higher retention of NH_4^+ (for example, Simon and others 2005), higher retention of SRP (for example, Hanafi and others 2006), or no differences between nutrients (for example, Hoellein and others 2007). These contrasting findings could be explained by differences in geology, substrate types, or nutrient limitation status among streams.

Drivers of the Temporal Patterns of Nutrient Retention in the Perennial and Intermittent Streams

The two study streams exhibited differences in the temporal patterns of nutrient retention. In the perennial stream, temporal variation in both NH_4^+ and SRP retention efficiency and demand were coupled, as shown in other studies (for example, Butturini and Sabater 1998; Martí and Sabater 1996; Simon and others 2005). In contrast, retention efficiency and demand for the two nutrients exhibited contrasting temporal patterns in the intermittent stream, as found in other studies (Sabater and others 2000; Simon and others 2005; Hanafi and others 2006). Coupled temporal variation of NH_4^+ and SRP retention suggests that the same factors or mechanisms influence retention of both nutrients in the perennial stream, whereas, in the intermittent stream, each of the nutrients may be subjected to different driving factors. Uptake rates of NH_4^+ and SRP, however, showed the opposite pattern: they were coupled in the intermittent stream but not in the perennial stream. This reflects the strong influence that temporal patterns of concentration exert on this metric, which were similar for the two nutrients in the intermittent stream and nearly opposite in the perennial stream.

Seasonal patterns observed for most environmental factors considered in this study, which were consistent between the 2 years, did not translate into equally clear patterns of variation in nutrient retention. The patterns of temporal variation of nutrient retention were instead a result of the combined influence of antecedent weather conditions and of different environmental drivers, as indicated by regression results. More importantly, as our regression analysis indicates, the influence of each factor differed between periods; therefore, no model of environmental controls on nutrient retention can be formulated for a full hydrologic year that does not fully take into account seasonal differences.

The use of three standard retention metrics allowed us to explore the relative importance of each environmental driver on the variation of nutrient-retention response over time. Nutrient-retention efficiency was negatively influenced by discharge in the two study streams. This is consistent with previous studies and has been attributed to a decrease in contact time between the water



column and the stream bottom in faster and deeper streams (Wollheim and others 2001; Peterson and others 2001). Our results also indicate that the effect of discharge was more relevant during the wet period in both streams, when base flow was higher as a result of lower evapotranspiration and frequent floods. The latter can additionally reduce nutrient retention by scouring benthic organic matter (Argerich and others 2008) and periphyton growing on substrates (Martí and others 1997), thus disturbing heterotrophic and autotrophic biological communities responsible for nutrient uptake. Previous studies in the intermittent stream suggest, however, that removal of benthic organic

◀**Figure 6.** Relationships between the range quotients (R_q) of: (*upper panels*) uptake length (S_w) and discharge, (*middle panels*) uptake velocity (V_f) and ambient nutrient concentration, and (*lower panels*) uptake rate (U) and ambient nutrient concentration, for soluble reactive phosphorus (SRP) (*left panel*) and ammonium (NH_4^+; *right panel*). We used data reported in the literature from stream reaches in which $n \geq 3$ additions were performed, and data for both retention metrics and environmental factors were available. Studies were grouped into four different time scales, indicated in the graphs with different symbols, based on the study period covered: (○) Inter-annual (two full years), including Martí and Sabater (1996) and this study; (●) Annual (at least three seasons of 1 year), including Mullholland and others (1985), Butturini and Sabater (1998), Hall and others (2002), Simon and others (2005), Hoellein and others (2007) (Δ) Seasonal (1–2 seasons of 1 year), including Sabater and others (2000), Haggard and Storm (2003), Hall and others (2003), Argerich and others (2008), and (▼) Diurnal (one full day), including Martí and Sabater (1994), Martí (1995). *Straight lines* represent significant ($P < 0.05$) linear regressions. The discrepancy in the number of points (n) among regressions is due to differences in the availability of data.

matter by floods reduces ecosystem respiration but enhances gross primary production by allowing light to reach primary producers until then covered by stored organic matter (Acuña and others 2004). Thus, floods may enhance the relative role of autotrophic over heterotrophic nutrient retention processes in these streams, but our data do not allow us to test this hypothesis. During the dry period, consistently low discharge became less important as a driver of the variation in nutrient retention, and other factors assumed a greater influence.

To examine the influence of these other factors, we focused on uptake velocity (that is, nutrient demand), a metric that corrects uptake length for the influence of stream size (that is, discharge) (Webster and Valett 2006). In contrast to discharge, which showed an episodic temporal regime, changes in water temperature were gradual and followed a consistent seasonal pattern. Thus, relationships with temperature would indicate seasonality. In this sense, we found no clear seasonal patterns in NH_4^+ demand in any of the two streams, likely due to the high complexity of mechanisms governing NH_4^+ dynamics in streams. In contrast, SRP demand was negatively related to water temperature in the two streams, suggesting similar mechanisms at work in the two streams. SRP demand was highest during the wet period and lowest during the dry and transition periods, in contrast to what would have been expected from a direct effect of temperature on the physiological activity of stream biofilms (DeNicola 1996). We should note, however, that, in these well-forested streams, the wet period includes ''hot moments'' of energy availability, which may favor nutrient demand by both heterotrophic and autotrophic organisms. In both study streams, leaf fall occurs mainly in autumn (that is, October to November), but, in the intermittent stream, leaf fall may extend from late summer to autumn (that is, August to November) during dry years, due to hydrologic stress (Acuña and others 2007). As a consequence, large inputs of organic matter accumulate on the streambed and may fuel heterotrophic activity during the transition and wet periods. Mulholland and others (1985) found that retention efficiency of SRP was highest in a perennial stream of a temperate region during the leaf-fall period. Although ecosystem respiration peaks are characteristic in the intermittent stream during autumn (Acuña and others 2004), neither our data nor other studies in Mediterranean catchments (Martí and Sabater 1996; Argerich and others 2008) showed evidence of a clear peak in nutrient demand associated with this period. Heterotrophic organisms may fulfill most of their nutrient needs through uptake of nutrients contained in the fresh organic matter during decomposition, thus showing low demand for nutrients in the water column. Additionally, the leaf-fall period coincides with high flood frequency in streams from the Mediterranean region (Gasith and Resh 1999), which may reduce the accumulation of large amounts of benthic organic matter (Acuña and others 2004; Argerich and others 2008). Inputs of leaves that accumulate in adjacent riparian soils during winter, when floods are less frequent than during fall, may further mask the relevance of a discrete period of organic matter inputs for heterotrophic organisms in these streams, compared to streams in temperate regions.

The wet period also is characterized by higher light availability than the dry period, especially before leaf out, due to the absence of riparian shading. Although forested headwater streams are typically heterotrophic (Battin and others 2008), increases in light availability can favor the development of photoautotrophic organisms, which are important players in nutrient retention. In fact, an increase in algal biomass with a concomitant shift from net heterotrophy to net autotrophy is characteristic in the intermittent stream during spring just before leaf out (Acuña and others 2004). In addition, light was shown to be an important limiting factor of periphyton growth in our perennial stream and other streams with well-developed riparian vegetation located in the same catchment during summer (von Schiller and others 2007). Although heterotrophic processes related to inputs of organic matter have been posited to control nutrient retention in forested streams (Webster and Meyer 1997), many other studies demonstrate that autotrophic processes can be important during periods of high light availability (for example, Mulholland and others 1992; Mulholland and others 2006; Hoellein and others 2007). Moreover, Sabater and others (2000) showed that removal of riparian vegetation-enhanced growth of photosynthetic organisms and increased SRP retention in a nearby stream. A stronger relationship of water temperature with SRP demand during the dry period, found only in the perennial stream, indirectly suggests a contrasting influence of riparian vegetation on SRP retention between the two streams through the regulation of the light regime. In fact, although riparian vegetation was well developed in the two streams, the structure and dynamics differed between the streams due to local climate conditions. In the perennial stream, riparian vegetation was very dense and dominated by a single-tree species, the phenology of which created two clearly contrasting seasons (that is, dormant and vegetative). In contrast, the riparian vegetation in the intermittent stream was sparser and dominated by a variety of species with differing phenologies and was also subject to hydrologic stress in the summer that caused leaf fall during this season and, thus, relatively higher light availability (Acuña and others 2007).

The lack of relationships between demand of SRP and NH_4^+ and their respective nutrient concentrations, as well as a better fit of uptake rates to linear rather than Michaelis-Menten models, suggests that nutrient concentrations were below saturation in the two study streams. These results support previous findings in headwater streams (for example, Simon and others 2005; Hanafi and others 2006; Hoellein and others 2007). Results from regressions between uptake rate and nutrient concentration done separately for each period, however, suggest saturation conditions for SRP in both streams during the dry period. The relationship between SRP uptake rate and concentration was best explained by a power function for each of the periods in the two streams, but exponents less than 1, which indicate potential saturation conditions (O'Brien 2007), were obtained only with data from the dry period in the two streams, coinciding with the highest SRP concentrations. Uptake of NH_4^+ did not show any signs of saturation, probably due to the relatively low concentrations and weak seasonal changes of NH_4^+ in both streams.

Although variation in nutrient demand was not influenced by nutrient availability, variation in the relative demand of the two nutrients (that is, V_f-NH_4^+: V_f-SRP ratio) in the intermittent stream responded to the relative availability of both N and P (that is, DIN:SRP ratio). Demand of SRP tended to increase relative to that of NH_4^+ as the potential for P limitation increased (that is, higher DIN:SRP ratios). In fact, the few dates when demand of SRP surpassed that of NH_4^+ coincided with times of extremely high DIN:SRP ratios. This pattern was driven by dramatic increases in NO_3^- concentration during the wet period, which may be attributed to a combination of a decline in NO_3^- uptake by terrestrial vegetation and soil microbial activity (Bernal and others 2005) and NO_3^- release in the stream edge zone due to the elevation of the groundwater table (Butturini and others 2003). This pattern did not hold in the perennial stream, likely due to the less clear seasonality and relatively low range of DIN:SRP ratios in this stream. Other studies have demonstrated temporal changes in the relative demand of N over P (Martí and others 1996; Simon and others 2005), which may be attributed to structural and functional adaptations of biofilm communities to the temporal variation of relative nutrient availability.

Variability of Nutrient Retention Between and Within Streams

Results from this study demonstrated differences not only in the magnitude and pattern of nutrient retention between the streams but also in the range of variation of this functional response. We expected larger variability in the intermittent stream in response to the higher variability observed in most measured environmental factors and to the anticipated negative effect of droughts on biological communities responsible for nutrient uptake (Lake 2003). Results were contrary to our expectations, however, with the perennial stream showing a similar or even broader range of variation in most retention metrics. This unexpected result suggests high resilience of biotic communities in the intermittent stream after disturbance (that is, drought), as supported by previous studies in the same stream (Acuña and others 2005, 2007). Our initial expectation held, however, when we analyzed the patterns of temporal variability measured across a variety of published studies. Our review analysis indicated that within-stream temporal variability in nutrient retention metrics tends to increase as the variability of specific environmental drivers becomes larger.

More evident patterns of variability emerged when we considered different time scales within each stream. We found an increasing range of variation of all retention metrics with increasing time scale in both streams, with the highest value at the inter-annual scale. This indicates that sampling any one period, or even a whole year, would not have been enough to capture the full range of nutrient retention observed over the two study years. In addition, we must take into account that we likely did not capture all the potential variability in nutrient retention of our study streams due to the constraints of the methodology employed (Webster and Valett 2006).

The high variability observed in our streams was comparable to that found by Martí and Sabater (1996) in two other Mediterranean streams located in nearby catchments. To the best of our knowledge, this is the only other existing study covering the variation of nutrient retention over a similarly extensive period. Our analysis of the variability across time scales with data from compiled studies further supports our findings. The variability of nutrient retention tended to increase as the time scale considered increased; it was lowest in studies at the diurnal scale, intermediate at the annual or seasonal scales, and highest in studies performed over an inter-annual scale. This interesting result may be explained by the higher probability of longer-term studies capturing greater variability in environmental drivers. Nevertheless, one unexplored subject of great interest is if the within-stream pattern across time scales observed for Mediterranean streams holds for streams found in other climate regimes.

Overall, results from this study emphasize the significance of local climate conditions in regulating the magnitude, temporal pattern, and variability of nutrient retention by dictating the disturbance regime and temporal windows of energy and resource availability in streams. As these factors may vary in response to changes in land use and climate regimes, our study contributes to a better understanding of the potential effect of these changes on stream ecosystem functioning and highlights the importance of long-term studies for the correct characterization of stream nutrient retention and its controlling factors. Models of nutrient dynamics at larger spatial and temporal scales that incorporate the temporal variation of stream nutrient retention would become valuable tools for the prediction and management of nutrient-related environmental problems in present and future scenarios.

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