

RESEARCH ARTICLE

Nutrient uptake in a simplified stream channel: Experimental manipulation of hydraulic residence time and transient storage

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Abstract

Stream restoration efforts have aimed at increasing hydraulic residence time (HRT) and transient storage (TS) to enhance nutrient uptake, but there have been few controlled studies quantifying HRT and TS influences on nutrient uptake dynamics. We assessed the effects of HRT and TS on ammonium (NH_4^+) and phosphate (PO_4^{3-}) uptake through controlled experiments in an artificial channel draining a pristine tropical stream. We experimentally dammed the channel with artificial weirs, to progressively increase HRT, and performed NH_4^+ and PO_4^{3-} additions to estimate uptake each time a weir was added. We also ran consecutive additions of NH_4^+ and PO_4^{3-} with no weirs, to evaluate short-term changes in uptake metrics. Also, NH_4^+ was injected alone to assess potential nitrification. We observed that NH_4^+ and PO_4^{3-} uptake rates were much greater in the very first addition, probably due to luxury uptake. The weirs increased mean HRT (from 8.5 to 12 min) and depth (from 6.5 to 8.9 cm) and decreased mean water velocity ($0.40\text{--}0.28\text{ m s}^{-1}$). Surprisingly, damming decreased the relative size of transient storage zone (storage zone area/channel area, A_s/A from 0.72 to 0.55), indicating that greater depth increased A , but not A_s . Greater HRT increased uptake rates and velocities of both nutrients ($p < 0.05$). The NH_4^+ conversion to NO_3^- was estimated at 18% of NH_4^+ consumption, indicating that joint additions to measure NH_4^+ and NO_3^- uptake would not be feasible in this system. Our results suggest that increases in HRT can lead to a greater short-term retention of nutrients, with implications for stream management and restoration initiatives.

KEYWORDS

ammonium, nitrification, nutrient assimilation, phosphate, tropical water bodies

1 | INTRODUCTION

Anthropogenic impacts from land use conversion, water pollution, hydraulic alteration, and geomorphologic simplification degrade freshwaters and decrease ecosystem services (Dodds, Perkin, & Gerken, 2013). Streams are not just drainpipes: They process and retain materials that enter them (e.g., Mulholland et al., 2008). Thus, humans have exploited the capacity of streams and rivers to reduce the concentrations of contaminants for many decades. For example, Streeter and

Phelps (1925) proposed an equation to predict longitudinal dissolved oxygen patterns in a stream/river reach in response to organic matter inputs, an approach that continues to this day (e.g., Fan, Ko, & Wang, 2009; Gotovtsev, 2010).

Ecosystem integrity and trophic state also link to nitrogen (N) and phosphorus (P; e.g., Dodds & Smith, 2016) through abiotic and biotic processes. In streams and rivers, these both nutrients can be removed from the water column through sedimentation (Bouwman et al., 2013; Gabriele, Welti, & Hein, 2013), adsorption to organic and inorganic

particles (Peterson et al., 2001), complexation (Reddy, Kadlec, Flaig, & Gale, 1999), and other chemical reactions in both aerobic and anaerobic conditions (González-Sanchis, Comín, Murillo, & García-Navarro, 2010; Small et al., 2016). N and P can also be stored in organic matter through biotic uptake by bacteria or algae (Mulholland et al., 2008; Tromboni, Dodds, Neres-Lima, Zandonà, & Moulton, 2017). Permanent removal of N through denitrification (releasing N_2 to atmosphere) is an important pathway accounting for 20–35% decrease in organic N concentrations in tropical streams (Potter, McDowell, Merriam, Peterson, & Thomas, 2010).

Nutrient uptake rates are influenced by characteristics of the water bodies such as transient storage and hydraulic residence time (HRT; Baker, Bledsoe, & Price, 2012), periphyton biomass (Mulholland, Steinman, Marzolf, Hart, & DeAngelis, 1994), and natural/anthropogenic disturbance (e.g., Bernhardt, Likens, Buso, & Driscoll, 2003; Diemer, McDowell, Wymore, & Prokushkin, 2015). Elevated background nutrient concentrations and chlorophyll standing stocks can increase nutrient uptake (Bernot, Tank, Royer, & David, 2006; Niyogi, Simon, & Townsend, 2004). In tropical areas of developing countries, where population growth is significant (Grimm et al., 2008) and N and P inputs are usually large, significantly less information is available on stream uptake and retention of these nutrients (e.g., Figueroa-Nieves, McDowell, Potter, & Martínez, 2016; Gücker & Boëchat, 2004; Tromboni et al., 2017). Urbanization can also decrease streams' nutrient retention capacity and efficiency as compared with more pristine ecosystems by altering hydrologic characteristics (Batchelor & Gu, 2014; Grimm et al., 2005).

As the transient storage zone increases in size, the probability of interaction between nutrients and organisms or abiotic materials increases (Argerich, Martí, Sabater, Haggerty, & Ribot, 2011). Stream restoration techniques use in-stream structures to increase the cross-sectional area of the water bodies and transient storage zones (Rana, Scott, & Hester, 2017), with different restoration typologies associated with positive, neutral, or negative effects on N and P removal (see Johnson, Kaushal, Mayer, Smith, & Sivirichi, 2016, for a comprehensive review). Controlled experiments on how these hydraulic changes influence short-term nutrient dynamics are lacking.

Methods developed in streams to measure whole-system nutrient uptake (Stream Solute Workshop, 1990) allowed inference about nutrient dynamics in natural ecosystems, incorporating benthic, hyporheic, and water column compartments. The dependence of nutrient uptake rates on concentrations allows characterization of dynamics of uptake (Dodds et al., 2002; Payn, Webster, Mulholland, Valett, & Dodds, 2005). The tracer additions for spiralling curve characterization (TASCC) method (Covino, McGlynn, & McNamara, 2010) was subsequently developed to characterize uptake kinetics using single pulses of nutrients in streams. The metrics derived by TASCC include dynamic uptake (stream's response to the range of concentrations from a nutrient addition), and this allows extrapolation to estimate gross uptake rate at ambient nutrient concentrations where net uptake is zero (Dodds, 1993). In addition, the use of TASCC could reveal times of hysteresis by quantifying differences in the rising and falling limbs of breakthrough curve (BTC; nutrient concentration curve created by pulse addition), which could potentially be attributed to transient storage.

There have been few controlled studies to understand how in-stream uptake is influenced by water residence time and transient storage in an experimental setting. We aimed at assessing how ammonium (NH_4^+) and phosphate (PO_4^{3-}) uptake in a tropical stream channel was influenced by manipulations in HRT and transient storage caused by artificial weirs. Also, we assessed the degree to which the dissimilatory nitrification process might influence estimates of NH_4^+ uptake, and the possibility of simultaneously measuring NH_4^+ and nitrate (NO_3^-) uptake. We considered a reach where a natural stream had been channelized into a concrete channel with a rectangular cross sectional area. We used artificial damming of such simplified channel to test the hypothesis that increased HRT leads to greater nutrient uptake. Thus, we used a system where transient storage would be dominated by slow-moving portions of the stream and the associated biofilms on the sides and bottom of the stream channel, which is also known to be involved in transient storage (Mulholland et al., 1994).

2 | METHODS

We studied a channelized reach of the Espirado Stream located in São Carlos municipality, São Paulo State, Southeast Brazil (21°58' 59.15"S, 47°52'24.74"W), with a length and width of 200 and 0.45 m, respectively. The concrete channel was built as part of a water supply system. The stream is located in a relatively well protected watershed with secondary vegetation representative of the Cerrado biome and has low turbidity and nutrient concentrations in the water, as it flows from a preserved Cerrado watershed through a dense riparian forest (Dodds, Tromboni, Saltarelli, & Cunha, 2017). However, the stream canopy is removed in the area with the channel and substantial biofilm (periphyton), and plants/macrophytes such as *Callicostella* sp. and *Eleocharis* sp. develop on the bottom and sides of the concrete channel. This experimental set-up (Figure 1) was ideal for testing the influence of HRT and transient storage on uptake, because the stream could be dammed to increase depth and slower water zones, without increasing average width, and there was a minimal hyporheic zone associated with unconsolidated substrata on the sides and bottoms of the channel.

We assessed uptake of NH_4^+ and PO_4^{3-} using Cl^- as conservative tracer and the TASCC method (Covino et al., 2010) for modelling nutrient uptake. Such modelling approach allowed us to quantify ambient-spiralling parameters and nutrient uptake kinetics. For each experiment, we dissolved 112.6-g Cl^- as NaCl, 10.9-g PO_4^{3-} as K_2HPO_4 , and 8.7-g NH_4^+ as NH_4Cl in approximately 10 L of stream water. We then introduced the solution into the stream at the head of the experimental reach consistently over 1 min (we used a timed pulse to allow modelling of transient storage; see below). The mass of conservative tracer added increased in-stream conductivity to measurable levels, whereas the mass of added nutrient was intended to raise in-stream concentrations to approximately two to three times above background (Covino et al., 2010). Electric conductivity (EC) was measured at 10-s intervals over the experiment with a multiparameter probe (Model HI 9829, HANNA Instruments, Woonsocket, RI, USA). We collected samples at the downstream end of reach over the full BTC, with sampling frequency ranging from 15 s to 1 min as

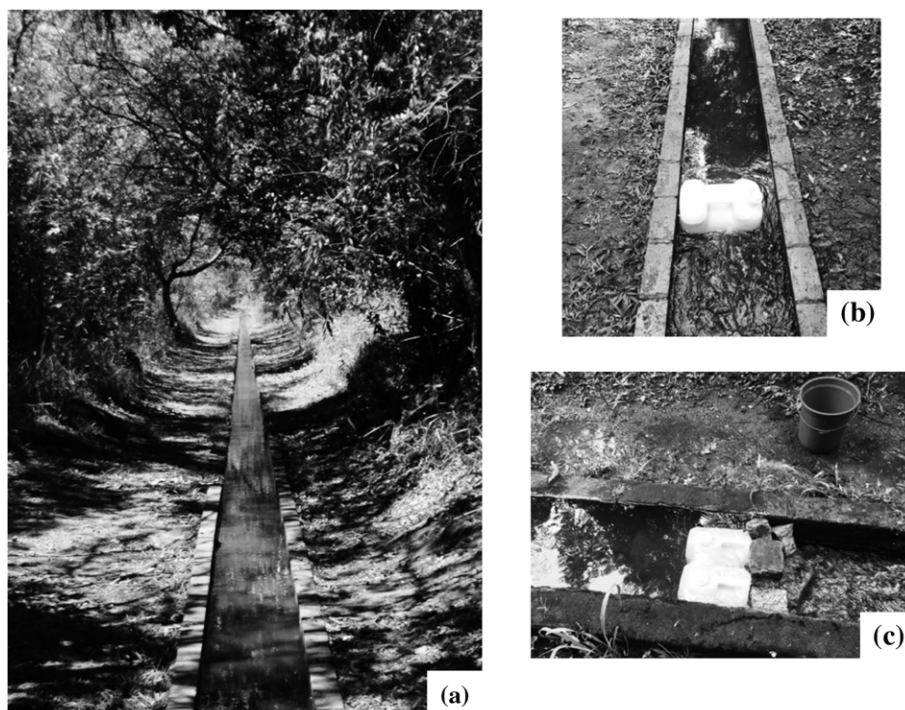


FIGURE 1 Experimental set-up for experimental manipulation of hydraulic residence time and transient storage: channelized reach of the Espriado Stream (a) and details of the plastic/rock weirs installed in the channel (b and c)

function of the rate of change of EC. We collected three blank samples to determine nutrient background concentrations immediately before each addition. Water samples were filtered immediately upon collection, transported to the laboratory in a cooler, and within 6 hr frozen at -18°C until analysis. All water samples were analysed within two weeks from collection. All nutrient concentrations were determined via colorimetry using a Hach DR 4000V spectrophotometer (Hach Environmental, Loveland, CO, USA). The method used for NH_4^+ was based on Solorzano (1969), modified for a 7-ml sample volume, and the ones used for PO_4^{3-} and NO_3^- followed APHA (2012).

We ran three sets of experiments in 2017 (Table 1) and estimated the following uptake metrics for each case (sensu Covino et al., 2010): $S_{w,amb}$ (ambient uptake length), $V_{f,amb}$ (ambient uptake velocity), and U_{amb} (areal ambient uptake). First, we added NH_4^+ and PO_4^{3-} together to assess if uptake metrics for these nutrients varied in the very short

term, following three sequential nutrient additions (Experiments 1–3). Second, we added artificial damming to the channel and assessed how uptake of NH_4^+ and PO_4^{3-} responded to the increase in HRT produced by damming (Experiments 4a–4f). We progressively added plastic/rock weirs (Figure 1) to increase mean HRT in the channel (minimum of 8.5 min to maximum of 12.0 min, Table 1). For these latter experiments, we modelled the change in the size of the transient storage using the concentration data from the conservative NaCl releases and a one-dimensional transient storage modelling approach with OTIS-P (Runkel, 1998). OTIS-P is a mathematical simulation model used to characterize the transport of solutes in streams and rivers based on a mass balance equation for transport that includes advection, dispersion, and transient storage. This application typically involves a trial-and-error approach wherein parameter estimates are adjusted to obtain an acceptable match between simulated and

TABLE 1 Characteristics of the nutrient addition experiments developed at the Espriado Stream Channel (total reach length: 200 m), including date, nutrient species added, the presence/absence of artificial weirs, and aim of each experiment

Experiment	Added nutrients	Artificial weirs	Aim	Date
1	NH_4^+ and PO_4^{3-}	No	Compare how uptake metrics change following three sequential additions	June 2017
2	NH_4^+ and PO_4^{3-}	No		
3	NH_4^+ and PO_4^{3-}	No		
4a	NH_4^+ and PO_4^{3-}	No	Investigate how uptake metrics change following sequential additions with manipulation of the hydraulic residence time in the channel by artificial damming	March 2017
4b	NH_4^+ and PO_4^{3-}	Yes (at 60, 120, and 180 m)		
4c	NH_4^+ and PO_4^{3-}	Yes (at 60, 90, 120, 150, and 180 m)		
4d	NH_4^+ and PO_4^{3-}	Yes (at 30, 45, 60, 90, 120, 150, and 180 m)		
4e	NH_4^+ and PO_4^{3-}	Yes (at 30, 45, 60, 75, 90, 105, 120, 150, 165, and 180 m)		
4f	NH_4^+ and PO_4^{3-}	No	Assess potential nitrification	July 2017
5	Only NH_4^+	No		

Note. Mean hydraulic residence time for Experiments 1, 2, 3, 4a, 4f, and 5: 8.5 min; for Experiment 4b: 9.3 min; for Experiment 4c: 10.3 min; for Experiment 4d: 11.3; for Experiment 4e: 12.0 min.

observed tracer concentrations. The hydraulic parameters we estimated with OTIS-P from the NaCl releases were the dispersion coefficient, channel cross-sectional area of the main channel (A), and transient storage cross-sectional area (A_s).

Previous additions with NO_3^- , PO_4^{3-} , and NH_4^+ together (unpublished data) in the same channel showed NO_3^- recovery above 100%, suggesting the occurrence of NO_3^- production. Thus, we also performed one pulse of NH_4^+ alone to estimate NO_3^- production and potential nitrification rates (Experiment 5). We measured the change in NO_3^- concentration during the NH_4^+ pulse addition for approximately 45 min after EC returned to background conditions. We integrated the area under the resulting NO_3^- BTC to calculate the mass of NO_3^- created via nitrification. The percentage transformation of NH_4^+ to NO_3^- attributable to nitrification was calculated by quantifying the new mass of NO_3^- formed after NH_4^+ addition compared with the total NH_4^+ uptake (estimated by integrating the NO_3^- and NH_4^+ break through curves).

3 | RESULTS

The three sequential additions of NH_4^+ and PO_4^{3-} showed a tendency of having much greater uptake rates in the first addition relative to subsequent additions (Table 2), all with no dams (refer to Table 1). Ambient uptake velocities, for example, were higher in Experiment 1 (20.1 mm min^{-1} for NH_4^+ and 6.5 mm min^{-1} for PO_4^{3-}), with lower and more stable values across Experiments 2 and 3 (9.0–10.6 mm min^{-1} for NH_4^+ and 5.3–5.6 mm min^{-1} for PO_4^{3-}). Uptake rates were higher (274.0 and 60.8 $\mu\text{g m}^{-2} \text{min}^{-1}$ for NH_4^+ and PO_4^{3-}) and uptake lengths were shorter (89 and 274 m for NH_4^+ and PO_4^{3-}) in the very first experiment. NH_4^+ and PO_4^{3-} background concentrations remained relatively similar across Experiments 1, 2, and 3, from 12.1 to 15.2 $\mu\text{g L}^{-1}$ and 9.3–9.7 $\mu\text{g L}^{-1}$, respectively, suggesting a luxury uptake in the first release.

Both NH_4^+ and PO_4^{3-} uptake metrics were significantly influenced by the increase in mean HRT with damming (Figures 2 and 3, all shown regressions significant at $p < 0.05$). The results from the very first experiment in this case (Experiment 4a, Table 1) are not shown because the uptake metrics from the first experiments were assumed

TABLE 2 Uptake metrics for ammonium (NH_4^+) and phosphate (PO_4^{3-}), including uptake length ($S_{w,amb}$), uptake velocity ($V_{f,amb}$), and uptake rate (U_{amb}), as well as background nutrient concentrations ($[C]_{amb}$) for the Espriado Stream Channel

Nutrient	Uptake metric	Experiment 1	Experiment 2	Experiment 3
NH_4^+	$S_{w,amb}$ (m)	89	201	166
	$V_{f,amb}$ (mm min^{-1})	20.1	9.0	10.6
	U_{amb} ($\mu\text{g m}^{-2} \text{min}^{-1}$)	274.0	136.7	128.7
	$[C]_{amb}$ ($\mu\text{g L}^{-1}$)	13.7	15.2	12.1
PO_4^{3-}	$S_{w,amb}$ (m)	274	325	336
	$V_{f,amb}$ (mm min^{-1})	6.5	5.6	5.3
	U_{amb} ($\mu\text{g m}^{-2} \text{min}^{-1}$)	60.8	53.6	49.0
	$[C]_{amb}$ ($\mu\text{g L}^{-1}$)	9.3	9.7	9.3

Note. The results are shown for three sequential nutrient additions (Experiments 1, 2, and 3; see Table 1)

as luxury uptake, whereas results from the subsequent experiments represent the uptake capacity once luxury capacity was fulfilled.

Artificial damming with weirs caused consecutive increments in HRT, leading to increases of 0% (no weirs), 9%, 21%, 32%, and 41% increases in water residence time (Table 1, Figures 2 and 3). Artificial damming also caused changes in the BTC for conductivity across Experiments 4b–4f (see Supporting Information). Mean water velocity decreased with damming (from 0.40 m s^{-1} with no weirs to 0.28 m s^{-1} with maximum number of weirs), and mean stream depth increased (from 6.5 to 8.9 cm; Table 3). For NH_4^+ and PO_4^{3-} , $S_{w,amb}$ decreased, $V_{f,amb}$ increased, and U_{amb} increased progressively with the increase in HRT. Comparing uptake during undammed experiments (no weirs) to uptake under a 41% increased HRT, $S_{w,amb}$ decreased about 28% (for NH_4^+ , Figure 2a) and 45% (for PO_4^{3-} , Figure 3a). The obstructions in the channel also led to greater uptake velocities for both dissolved

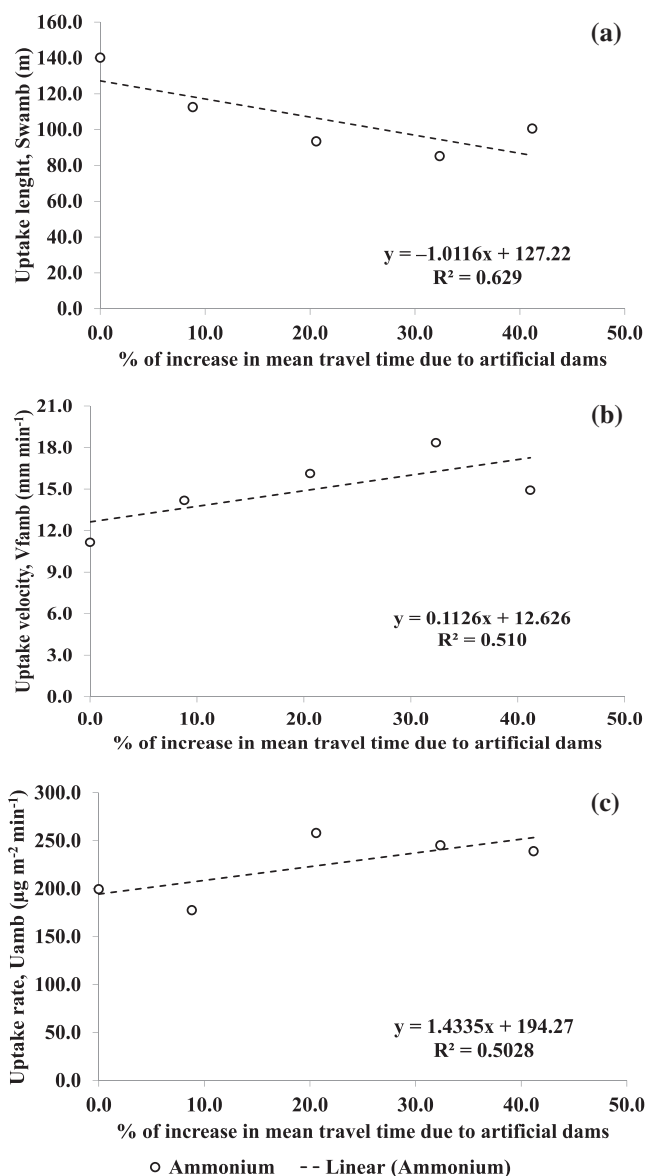


FIGURE 2 Ambient metrics for ammonium uptake in the Espriado Stream Channel as a function of percentage of increase in mean travel time (Experiments 4b to 4f; see Table 1): uptake length (a), uptake velocity (b), and uptake rate (c). All shown regressions are significant at $p < 0.05$

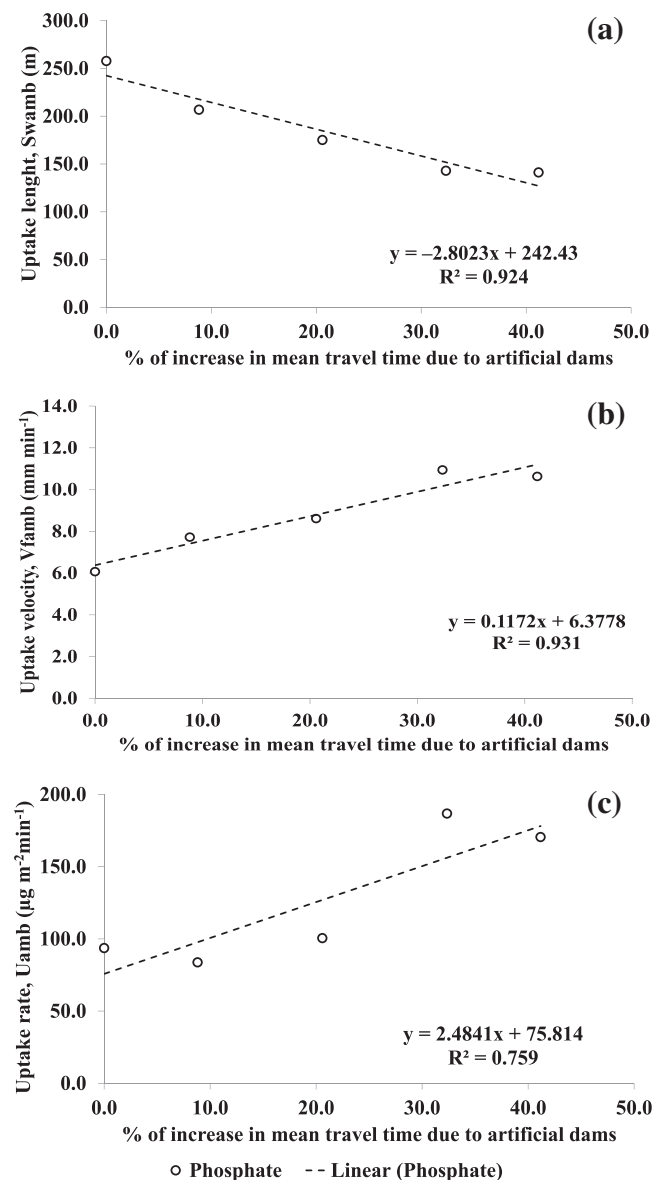


FIGURE 3 Ambient metrics for phosphate uptake in the Espirado Stream Channel as a function of percentage of increase in mean travel time (Experiments 4b to 4f; see Table 1): uptake length (a), uptake velocity (b), and uptake rate (c). All shown regressions are significant at $p < 0.05$

nutrients ($V_{f,amb}$ increased up to 63% for NH_4^+ and 79% for PO_4^{3-} , respectively, Figures 2b and 3b). This effect was also observed in the uptake rates (Figures 2c and 3c, Equations (1) and (2)).

$$U_{amb}(\text{NH}_4^+) = 1.4335TT + 194.27, \quad (1)$$

$$U_{amb}(\text{PO}_4^{3-}) = 2.4841TT + 75.814, \quad (2)$$

where $U_{amb}(\text{NH}_4^+)$ is the ambient uptake rate for ammonium ($\mu\text{g N m}^{-2} \text{min}^{-1}$), $U_{amb}(\text{PO}_4^{3-})$ is the ambient uptake rate for phosphate ($\mu\text{g P m}^{-2} \text{min}^{-1}$), and TT is the percentage of increase in mean HRT due to the addition of artificial weirs.

The relative size of the transient storage zone decreased as more weirs were added based on the ratios of cross sectional storage zone area to cross sectional area of the main channel (A_s/A). This was due to

TABLE 3 Ambient uptake lengths ($S_{w,amb}$, m) for ammonium (NH_4^+) and phosphate (PO_4^{3-}) for the Espirado Stream Channel

Nutrient	Experiment	$S_{w,amb}$ (m)		Water velocity (m s^{-1})	Mean depth (cm)	A_s/A
		rising limb	falling limb			
NH_4^+	4b	185	124	0.37	7.1	0.64
	4c	41	105	0.34	7.5	0.61
	4d	99	75	0.31	8.5	0.56
	4e	112	152	0.28	8.9	0.55
	4f (no weirs)	171	172	0.40	6.5	0.72
PO_4^{3-}	4b	517	219	0.37	7.1	0.64
	4c	763	178	0.34	7.5	0.61
	4d	261	71	0.31	8.5	0.56
	4e	565	158	0.28	8.9	0.55
	4f (no weirs)	604	206	0.40	6.5	0.72

Note. The results are shown for the experiments with weirs (Experiments 4b–4f; see Table 1) separating the rising and falling limbs. For each experiment, mean water velocity, mean depth, and the ratios of cross-sectional storage zone area to cross sectional area of the main channel (A_s/A) are also shown.

the increase in water depth created by the damming but not in the transient storage zone cross-sectional area. Thus, increases in depth by damming did not create dead spots that were modelled as subsurface zones. A_s/A for the experiment with no weirs (4f, see Table 1) was estimated as 0.72 and decreased to 0.64 (4b), 0.61 (4c), 0.56 (4d), and 0.55 (4e; Table 3).

For NH_4^+ and PO_4^{3-} , we observed clear hysteresis in all experiments with no dams (1, 2, 3, and 4f; see Supporting Information for detailed plots total dynamic concentrations against dynamic uptake lengths for each experiment). Differences in rising and falling limbs of total dynamic concentrations plotted against dynamic uptake lengths across experiments were observed for NH_4^+ and especially for PO_4^{3-} . In PO_4^{3-} plots, $S_{w,amb}$ in the rising limbs were greater than in the falling limbs for all experiments. The $S_{w,amb}$ reduction in falling limbs was 57%, 76%, 73%, 72%, and 65% for experiments 4b, 4c, 4d, 4e, and 4f, respectively (Table 3), suggesting higher retention with greater HRT. NH_4^+ plots showed the same general pattern ($S_{w,amb}$ usually greater in rising than in falling limbs). As more and more artificial weirs were added (Experiments 4b → 4c → 4d → 4e), the difference observed between the rising and falling limbs dynamics of the nutrient additions gradually diminished, indicating that the decrease in A_s/A probably led to a reduction of the hysteresis effect.

From the pulse of NH_4^+ alone (Experiment 5 from Table 1), 0.35 g of NO_3^- was produced through nitrification. Thus, approximately 18% of the added NH_4^+ was nitrified immediately. The uptake rate of NH_4^+ in this experiment was $26.1 \mu\text{g m}^{-2} \text{min}^{-1}$, and modelled nitrification rate was $4.7 \mu\text{g m}^{-2} \text{min}^{-1}$.

4 | DISCUSSION

Luxury uptake apparently can have a substantial effect on nutrient uptake parameters. This has long been known for lake phytoplankton for phosphorus assimilation to polyphosphate (Dodds & Whiles, 2010) but has not been as well established for NH_4^+ uptake in both lakes and streams to our knowledge. We also know of no whole-stream measurements that have directly measured the amount of luxury uptake

with a nutrient pulse. We observed different uptake metrics for the very first nutrient addition in the set of three sequential experiments (Table 2). S_{w-amb} was shorter, whereas U_{amb} and V_{f-amb} were significantly greater in the first addition for both NH_4^+ and PO_4^{3-} . The second and third additions showed similar values for both NH_4^+ and PO_4^{3-} uptake metrics, suggesting a decrease in nutrient assimilation in the stream following the first experiment. However, for NH_4^+ , the result could be due to saturation of the dissimilatory process of nitrification as well; our observed rates were substantial. Although we recognize that nitrification is a dissimilatory process, we refer to uptake and nitrification simply as uptake in this discussion unless otherwise noted.

Appling and Heffernan (2014) observed that organisms could adjust to nutrient limitation using elevated nutrient uptake and storage during periods of abundance (in this case, a short-term addition) in terrestrial and aquatic ecosystems. Periphyton was present in streambeds of our study site. Such biological community can play a major role in regulating P concentrations of the water column assimilating both organic and inorganic forms of P (Reddy et al., 1999). The luxury uptake capacity can be relevant for undisturbed streams, because nutrient concentration in these systems is generally low; therefore, the nutrient limitation is greater than in impacted sites. Background NH_4^+ and PO_4^{3-} in Experiments 1–3 varied between 12.1–15.2 $\mu\text{g L}^{-1}$ and 9.3–9.7 $\mu\text{g L}^{-1}$ (Table 2), respectively, which are low concentrations typical in the range described for reference tropical stream sites (e.g., see Cunha, Dodds, & Calijuri, 2011, and Fonseca, Mendonça-Galvão, Padovesi-Fonseca, Abreu, & Fernandes, 2014).

According to the results of the one-dimensional transient storage modelling (OTIS), the relative size of the transient storage area (A_s/A) decreased, as a result of an increase in water depth in the channel across the experiments with weirs and consequential increase in the cross-sectional area (A). The measured cross-sectional area of the storage zone (A_s) did not vary in the experiments with the weirs. We were expecting an opposite trend, with transient storage increasing as we dammed more and more the channel. However, this concrete channel did not have a hyporheic component of the transient storage zone, so likely modelled transient storage was associated with the biofilms attached to the bottom of the channel. Thus, as we increased depth, cross-sectional area increased, but the areas of slower water velocity apparently did not contribute to the area of the transient storage zone and the effect of damming was on depth and water velocity (Table 3) rather than width or interaction with hyporheic zone.

For the experiments with weirs, we noted hysteresis in both NH_4^+ and PO_4^{3-} additions and differences in uptake metrics for the rising and falling limbs, as noted by other researchers (Gibson, Reilly, Conine, & Lipshutz, 2015; Thomas, Valett, Webster, & Mulholland, 2003; Trentman et al., 2015). We interpret these patterns to be representative of uptake in different stream compartments. The first edge of the pulse initially had more contact with the main channel, whereas the trailing edge had more time to interact with transient storage zones and reactive substrates (Day & Hall, 2017; Thomas et al., 2003). Consistent with this interpretation, uptake length in the rising limb was generally longer than uptake length in the falling limb (e.g., for PO_4^{3-} , maximum uptake lengths in the rising and falling limbs were

763 and 219 m, respectively, Table 3). However, for the ambient uptake metrics (Figures 2 and 3) calculation, we used the entire BTC (both falling and rising limbs) as a representation of average stream conditions, although others (e.g., Day & Hall, 2017) have used only the falling limb of the curve.

We observed more hysteresis in the PO_4^{3-} than in NH_4^+ additions. The PO_4^{3-} hysteresis could be function of HRT and substrate physicochemical and biological characteristics (Reddy et al., 1999). This hysteresis effect could be due to PO_4^{3-} adsorption to the solid phase and is generally observed in substrata having active reaction surfaces (Small et al., 2016). We observed that the hysteresis effect tended to decrease as we added more weirs, depth increased, and the water column had less interaction with the channel margins.

Longer water residence times and more solute interaction with reactive areas should increase uptake (Ensign & Doyle, 2005; Johnson et al., 2016; Roberts, Mulholland, & Houser, 2007). We interpreted the positive effect on nutrient uptake derived from the weirs as a direct consequence of mean depth increase, leading to greater contact between solute and channel borders with a strong reactive stream compartment (Day & Hall, 2017). This interpretation follows the difference observed between rising (lower uptake) and falling limbs (greater uptake) as the falling limb has longer HRT and more interaction with reactive zones. The relationships between transient storage zones and stream nutrient uptake and retention have received much attention in recent years, with still controversial results of the net effects of transient storage zone increase on nutrient retention (e.g., see Mulholland & Deangelis, 2000, and O'Connor, Hondzo, & Harvey, 2010, for positive effects; Martí, Grimm, & Fisher, 1997; Niyogi et al., 2004, and Hall, Bernhardt, & Likens, 2008, for either weak or no effects). Such relationships can also vary depending on the nutrient form considered (e.g., Sheibley Duff, & Tesoriero, 2014, reporting different effects on NO_3^- , NH_4^+ , and PO_4^{3-}).

In-stream structures such as artificial weirs and log jams have been used for enhancing solute retention in the context of stream restoration. Rana et al. (2017) studied the effects of such structures on transient storage in a small forested stream and concluded that adding weirs increased both cross-sectional area of the stream and size of transient storage zone but decreased exchange with the transient storage. The authors highlighted that the net effect of the weirs on water quality improvement (e.g., solute retention) is complicated and depends case to case on the relative importance of reactions in weir backwater and hydrostatically driven hyporheic exchange versus hydrodynamically driven exchange.

In general, our results suggest that the changes in channel complexity (in our case, increases in the HRT and in mean depth by the weirs) can lead to a greater capacity of a stream to remove or transform nutrients through biological or physical processes. Our regression equations with HRT influencing uptake metrics (Figures 2 and 3) can be used to predict nutrient acquisition in the study channel as a function of HRT and highlight water velocity controls on uptake. Our results are consistent with findings from other studies in temperate streams. In general, N uptake rates were greater in streams having debris dams in comparison with other stream habitats as bedrock outcrops, gravel beds, or cobble-riffles (Munn & Meyer, 1990). PO_4^{3-} and NH_4^+ uptake rates decreased in a reference stream in

TABLE 4 Comparison of ammonium (NH_4^+) and phosphate (PO_4^{3-}) uptake metrics obtained in the Espraido Stream Channel through different sets of experiments and other studies worldwide. Ambient uptake length ($S_{w,amb}$), uptake velocity (V_f), and uptake rate (U_{amb}), as well as background nutrient concentrations ($[C]_{amb}$), are shown for each case when available

Nutrient	Uptake metric	Day and Hall (2017)	Ensign and Doyle (2005)	Johnson et al. (2016)	Our study	
		Colorado streams (US) ^a	First order streams compilation ^a	Reference streams compilation ^b	Espraiado Stream Channel—experiments with no dams (1, 2, 3, and 4f) Range (median)	Espraiado Stream Channel—experiments with dams (4b, 4c, 4d, and 4e) Range (median)
NH_4^+	$S_{w,amb}$ (m)	850–1,900	23–275	210.5	82–200 (153)	85–113 (97)
	V_f (mm min^{-1})	1.6–3.0	2.5–17.0	0.4	9.0–21.6 (10.9)	14.2–18.3 (15.5)
	U_{amb} ($\mu\text{g m}^{-2} \text{min}^{-1}$)	0.6–6.2	5.3–52.6	96	128.7–295.1 (168.0)	177.5–258.0 (242.1)
	$[C]_{amb}$ ($\mu\text{g L}^{-1}$)	0.6–3.5	—	—	12.1–17.9 (14.4)	12.5–16.0 (14.7)
PO_4^{3-}	$S_{w,amb}$ (m)	—	24–161	413	258–336 (299)	141–207 (159)
	V_f (mm min^{-1})	—	1.5–6.6	4.9	5.3–6.5 (5.8)	7.7–10.9 (9.6)
	U_{amb} ($\mu\text{g m}^{-2} \text{min}^{-1}$)	—	3.4–15.7	—	49.0–93.6 (57.2)	83.7–186.7 (135.4)
	$[C]_{amb}$ ($\mu\text{g L}^{-1}$)	—	—	—	9.3–15.4 (9.5)	10.8–17.1 (13.9)

^aRanges (min–max).

^bMedian.

response to litter exclusion (Webster et al., 2000) and wood and coarse wood debris (CWD) removal (Ensign & Doyle, 2005). PO_4^{3-} uptake rates were strongly correlated with CWD abundance and water residence time in mountain streams (Valett, Crenshaw, Wagner, & Oct, 2002). CWD addition had positive short-term effect on hydrodynamics complexity (water velocity decreased and transient storage zone area increased) and on nutrient uptake (NH_4^+ uptake rates increased; Roberts et al., 2007). In these studies, the authors highlighted the effect of CWD on hydrodynamics (increasing in HRT) and on aquatic metabolism (stimulation of heterotroph activity by introducing organic matter, as well as periphyton growth). As our weirs were made of plastic and previously dry rocks, and the period of the experiments was short, we considered that the weir effect was only on hydrodynamics, not on biofilm development.

Our data suggest that caution should be taken not to measure NH_4^+ to NO_3^- uptake simultaneously in single pulses but that pulse injections of NH_4^+ can be used to estimate whole-channel nitrification rates if those rates are high. In the studied stream channel, we estimated an 18% conversion percentage from NH_4^+ to NO_3^- . NH_4^+ uptake in forested streams is largely due to biotic process (Mulholland & Deangelis, 2000) and can be used for either assimilation or nitrification. At high levels of experimental NH_4^+ elevation, NH_4^+ uptake may be a result of abiotic sorption to the sediments (Triska, Packman, Duff, & Avanzino, 1994). Nitrification in other streams can vary from less than 1% (e.g., Ribot et al., 2013, in temperate streams from Barcelona, Spain) to 60% of NH_4^+ removal (e.g., Merriam et al., 2002, in a tropical rainforest stream in Puerto Rico). In eight streams across North America, 20% to 30% of NH_4^+ removal was due to nitrification, and 70% to 80% due to uptake on the streambed (Peterson et al., 2001). Thus, the 18% of nitrification in our study is similar to nitrification estimates for other aquatic systems, although tropical streams seem to be more effective on NH_4^+ removal, as observed by Merriam et al. (2002) and Koenig, Song, Wollheim, Rüegg, and Mcdowell (2017). In our study reach, the relatively high NO_3^- background concentration (approximately $300 \mu\text{g L}^{-1}$) can thus be a result of the nitrification process and loading from the broader watershed. In addition, the dissolved oxygen concentrations in the studied stream (usually between 5.5 and

7.5 mg L^{-1} , Saltarelli et al., 2018) probably favoured the nitrification process. Ribot et al. (2013) found that nitrification in a high-N stream (mean ambient $\text{NO}_3^- + \text{NH}_4^+$ concentration of approximately $800 \mu\text{g L}^{-1}$) was lower (0.2%) than in a low-N stream (mean ambient $\text{NO}_3^- + \text{NH}_4^+$ concentration of approximately $200 \mu\text{g L}^{-1}$; 0.2–7.6%). The authors highlighted that microbial assemblage composition and hydraulic exchange can be influential in regulation of stream nitrification.

Our study stream generally showed high retention in comparison with other studies especially for NH_4^+ (Table 4). Ambient uptake rates for NH_4^+ in our study reached a maximum of approximately 295 versus $96 \mu\text{g m}^{-2} \text{min}^{-1}$ as the greatest reported value for the other studies. Our NH_4^+ uptake rates are higher than those reported by Tromboni et al. (2017) for pristine Atlantic Rainforest streams. Some studies have highlighted the significant retention capacity of tropical streams. Gucker and Boëchat (2004) observed NH_4^+ uptake rates of up to $1,000 \mu\text{g m}^{-2} \text{min}^{-1}$ in Brazilian pristine streams from Cerrado and highlighted that channel morphology controlled transient storage and NH_4^+ retention in those tropical ecosystems. Merriam et al. (2002) observed elevated P retention ($V_{f,amb}$ of 87 mm min^{-1}) in streams located in Puerto Rico and attributed those results to the adsorption mechanism. Only a few researchers have explored nutrient uptake dynamics in tropical systems, and more data are necessary to understand how our results relate to the more abundant results from temperate streams.

5 | CONCLUSIONS

The controlled experimental set-up in a channelized reach of the pristine Espraido Stream was ideal for testing the effects of HRT and transient storage on NH_4^+ and PO_4^{3-} uptake. The studied channel was experimentally dammed to increase mean depth and HRT without an associated increase in width (as it is a rectangular channel). Our experiments showed that luxury uptake could be an important response to short-term pulses of nutrients, especially in undisturbed aquatic systems (for example, NH_4^+ uptake velocity was approximately two times higher in the very first addition). This highlights that

the biological communities in this tropical channel rapidly adapted to a new condition of nutrient availability. The significant differences in metrics for the sequential nutrient additions thus suggest that nutrient enrichments should be used with caution and luxury uptake should be considered accordingly.

Our experiments also showed that HRT can have strong and immediate influences on nutrient uptake parameters (a modest increase in water residence time—up to ~40%—had a measureable effect on both NH_4^+ and PO_4^{3-} acquisition). Maybe with a marginal effect as compared with the HRT issue, damming provided by the artificial weirs in the experiments also caused mean depth increase and presumably more significant contact between solutes and channel borders, a reactive stream compartment due to the presence of periphyton and aquatic plants. Also, the hysteresis effect derived from transient storage was more pronounced for PO_4^{3-} than NH_4^+ , probably due to different biotic and abiotic processes related to uptake of each nutrient form.

Our results demonstrated short-term variability of NH_4^+ and PO_4^{3-} uptake metrics in this tropical channel within sequential nutrient additions. This indicates that the temporal resolution of monitoring campaigns for assessing nutrient uptake might be adapted to capture quick temporal shifts in nutrient uptake. Channelized streams are common in anthropogenically dominated systems, and anthropogenic simplification of stream channels is widespread (Wohl & Beckman, 2014). Although these channels retain some nutrient retention ability, those with greater hydraulic residence will have more. Also, our study indicates that the net effects of restoration techniques using structures to increase in-stream HRT will probably vary case to case, depending on factors such as hyporheic exchange, hydrodynamics, and shifts in the A_s/A ratio. Overall, despite the low complexity and high homogeneity of the studied channel, we reported here high uptake rates and velocities in comparison with high-latitude water bodies, highlighting the need for more specific stream nutrient uptake estimations in tropical regions. Artificially increased HRT can directly enhance nutrient uptake and retention in tropical streams.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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