

RESEARCH ARTICLE

Macrophyte-driven transient storage and phosphorus uptake in a western Wisconsin stream

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Abstract

Investigations of phosphorus cycling and transport in streams lend insight into potential mechanisms of nutrient sequestration and can help mitigate human impacts. In this study, we examined the relationship between transient storage and phosphorus uptake in a cold-water stream in western Wisconsin. Hydrological characteristics, nutrient spiralling metrics, macrophyte biomass, and geomorphological properties were quantified in 7 reaches of Spring Coulee Creek using injections of a conservative tracer alone or with added PO_4^{3-} . Fraction of median travel time due to transient storage (F_{med}^{200}) was correlated with macrophyte biomass ($r = .794$, $p = .033$), and PO_4^{3-} uptake velocity was correlated with F_{med}^{200} ($r = .756$, $p = .049$). Stepwise linear regression was used to build models for transient storage and uptake velocity. Macrophyte biomass, stream bed slope, and riffle to pool ratio accounted for 99.6% of the variation in transient storage ($p < .001$). Transient storage, canopy cover, and slope accounted for 98.0% of the variation in uptake velocity ($p = .002$). This study shows that transient storage, primarily resulting from macrophyte beds, can be a significant factor regulating phosphorus uptake in stream ecosystems.

KEYWORDS

aquatic vegetation, macrophytes, nutrient transport, phosphorus uptake, stream ecosystems, tracer studies, transient storage

1 | INTRODUCTION

Excess nutrients from human activities often have an adverse effect on water quality (Allan, 2004). In landscapes dominated by agriculture, the pollutants of concern are often nutrients (e.g., nitrogen and phosphorus) originating from practices that include the use of inorganic fertilizer and manure (Carpenter et al., 1998). Excess amounts of these nutrients generated from raising crops and livestock make their way into the waterways and can cause disruptions in water quality that affect resident aquatic organisms and terrestrial species that use the impacted resource. Lakes, reservoirs, large rivers, and marine ecosystems suffer detrimental effects from harmful algal blooms and hypoxia (Dybas, 2005; Rabalais, Turner, & Wiseman, 2002). These effects intensify as anthropogenic nutrient inputs to the environment continue to increase because of human population growth and land use development. Small streams account for the greatest proportion of the drainage network, and the natural processes within these low-order streams have the potential to reduce loading of nutrients into downstream water bodies. Headwater streams can recycle nutrients, trap sediment and pollutants, and provide the resource base,

which maintains biological diversity downstream (Meyer et al., 2003). It is important to study and understand stream nutrient dynamics because of the continued influence humans have on nutrients in the environment.

Both biogeochemical and geomorphic variables influence nutrient dynamics in a stream. The latter have an indirect effect on uptake by controlling residence time, the amount of time water and solute are exposed to biochemically reactive substrates (Valett, Morrice, Dahm, & Campana, 1996). Increased exposure to these reactive substrates can facilitate biotic and abiotic uptake. Furthermore, geomorphic characteristics such as gradient, sinuosity, and cross-sectional area affect hydrological transport processes and ultimately dictate the size of the transient storage zone (anywhere water is temporarily retained, e.g., surface pools, macrophyte beds, and the hyporheic zone). Although it is intuitive that transient storage would be an important driver of nutrient uptake, a review of the nutrient spiralling literature has concluded that the relationship between transient storage and nutrient uptake remains unclear (Ensign & Doyle, 2006). Some studies have found no significant relationship between storage and uptake (Martí, Grimm, & Fisher, 1997; Webster et al., 2003), whereas

some assert the importance of surface sediments (over hyporheic storage) to nutrient retention (Butturini & Sabater, 1999; Hart, Freeman, & McKelvie, 1992). In contrast to these findings, other studies conclude hyporheic transient storage is important to nutrient uptake. For example, transient storage was responsible for about 43% of phosphorus retention in Hugh White Creek (Mulholland, Marzolf, Webster, Hart, & Hendricks, 1997) and for similar amounts of nitrate retention in another North Carolina stream (Thomas, Valett, Webster, & Mulholland, 2003). Furthermore, others have found that manipulating natural and artificial structures alter surface (in-channel) transient storage and subsequently influence nutrient uptake (Ensign & Doyle, 2005).

One reason for the inconsistency in the literature is that generic measures of transient storage do not distinguish between surface and hyporheic storage zones. These zones have very different implications for nutrient uptake at different times or in different locations (Hall, Bernhardt, & Likens, 2002; Thomas et al., 2003). For example, in some streams, benthic uptake predominates during peak autotrophic growth, whereas low benthic biomass conditions can shift uptake into the hyporheic zone (Orr, Clark, Wilcock, Finlay, & Doyle, 2009). However, in streams where the hyporheic zone is negligible relative to surface storage, surface storage will be more important (Jin & Ward, 2005; Stoffleth, Shields, & Fox, 2008), regardless of seasonal biomass conditions or channel flow obstructions. Ultimately, some studies found that the hyporheic zone has the larger potential for nutrient processing (Triska, Kennedy, Avanzino, Zellweger, & Bencala, 1989), whereas others emphasize the importance of surface storage for nutrient uptake (Ensign & Doyle, 2005). Because distinguishing between these two types of storage can be difficult, particularly when considering dynamic spatial and temporal scales, it is helpful if researchers attempt to identify the key features that contribute to storage. Information regarding these geomorphological and biogeochemical features, along with the non-specific measure of transient storage, can aid in understanding stream nutrient dynamics.

One transient storage feature that can play a key role in stream nutrient dynamics is macrophyte beds. They have a large indirect influence on nutrient dynamics by altering stream flow and sedimentation processes. Studies have found that dense macrophyte beds decrease near-bed water velocity and significantly increase residence time and the trapping of particulate sediment and organic matter (Sand-Jensen, 1998; Schulz, Kozerski, Pluntke, & Rinke, 2003; Gurnell, van Oosterhout, de Vlieger, & Goodson, 2006; Nepf, Ghisalberti, White, & Murphy, 2007), both of which can contribute to phosphorus retention in streams. Macrophytes also directly alter water chemistry and nutrient dynamics via photosynthesis and nutrients uptake through their roots (from sediment) and shoots (from water column). Furthermore, macrophytes provide surfaces for the establishment of epiphytic biofilms, which can be very efficient at removing nutrients from the water column (Hein, Pedersen, & Sand-Jensen, 1995; Levi et al., 2015; Pelton, Levine, & Braner, 1998). However, despite the numerous research efforts towards quantifying stream hydrology responses to macrophytes or nutrient uptake and retention associated with macrophytes, few studies specifically focus on the interactive effects of the contribution of macrophytes to whole-stream transient storage and subsequent effects on nutrient uptake.

The dynamic relationships between biogeochemical and geomorphic and other stream characteristics are complex, and determining their collective role in nutrient dynamics is challenging. Research in this field has often used whole-stream injections of conservative and reactive tracers and applied the theoretical constructs of nutrient spiralling (Ensign & Doyle, 2006; Newbold, Elwood, O'Neill, & Van Winkle, 1981; Runkel, 2007; Sheibley, Duff, & Tesoriero, 2014). Many studies that target these relationships are often conducted using interstream assessments examining a single reach from each study stream. The attraction of this approach is the assumption that the results would be more generally applicable to all streams; however, the results using this design can be confounded by variations in other important stream characteristics, for example, stream water chemistry, geology, stream biota, and land use. Another less used approach is to employ a longitudinal, intrastream assessment where the study can target a smaller set of independent variables without the need to account for high variation in the non-target stream characteristics. By avoiding the analytical noise of confounding characteristics, the method can provide a more robust assessment of certain target variables.

Much of the previous nutrient spiralling work in streams has focused on nitrogen (Mulholland et al., 2008; Peterson et al., 2001), partly because nitrogen spiralling can be readily studied using stable isotope additions. However, studies of phosphorus dynamics are particularly important because phosphorus is the nutrient often linked to eutrophication of freshwater systems (Schindler et al., 2008; Schindler, Carpenter, Chapra, Hecky, & Orihel, 2016). Knowledge regarding whole-stream phosphorus uptake in the unique geological region of western Wisconsin is lacking, but previous research in our study stream shows that phosphorus is limiting periphyton growth (Mooney, Strauss, & Haro, 2014), which allows us to quantify phosphorus uptake via nutrient addition experiments. The objectives of this study were (a) to quantify transient storage and phosphorus uptake in Spring Coulee Creek and (b) to identify the variables that have the greatest influence on transient storage and phosphorus uptake. It was hypothesized that transient storage and phosphorus uptake would be positively correlated in Spring Coulee Creek and the primary factor promoting both storage and uptake would be macrophyte biomass.

2 | METHODS

2.1 | Study area

Spring Coulee Creek is a first- to fourth-order cold-water stream located in south-western Wisconsin (43.712°N, -90.990°W). The Spring Coulee Creek watershed (~32 km²) drains predominantly Type B (82.9%) moderate infiltration hydrological soils (Gridded Soil Survey Geographic (gSSURGO), 2016), and land cover within the watershed is 42.8% deciduous forest, 33.8% cultivated crops, and 15.5% pasture (Homer et al., 2015). The stream is located in the U.S. Environmental Protection Agency Driftless Area Ecoregion (Ecoregion 52), which was bypassed by the last continental glaciation, resulting in a landscape dominated by karst topography with rolling hills, sinkholes, caves, and cold-water streams. Land use in the Driftless Area is largely agricultural (Juckem, Hunt, Anderson, & Robertson, 2008). About 60%

of the land is classified as cultivated or pasture. Driftless Area streams tend to exhibit relatively high nitrogen and low phosphorus concentrations, with summer median total dissolved N and P concentrations of 2.9 mg N/L and 15 μg P/L, respectively (Olmanson, 2014).

Seven reaches of Spring Coulee Creek were selected for investigation, herein referred to as SC-1 through SC-7 (Figure 1 and Table 1). All study reaches were third- or fourth-order segments, and criteria for reach selection were based on ~15-min travel time of a conservative pulse (slug) tracer to peak downstream concentration, no significant tributary inflow, accessibility, variable macrophyte abundance, and an acceptable mixing reach at the upstream point. Reach lengths,

measured with a field tape, ranged from 215 to about 315 m. Data were collected in August 2015, during stable baseflow conditions. Despite stable flow, larger discharges in SC-5, SC-6, and SC-7 were the result of a significant tributary entering the stream below SC-4. Stream substrate consisted of a sandy bed with overlying cobbles in areas with increased slope. During data collection, ambient PO_4^- concentrations ranged from 17 to 30 $\mu\text{g}/\text{L}$, pH 8.3–8.5, and conductivity 480–490 $\mu\text{S}/\text{cm}$, and temperature was generally between 16 and 18 °C. The motivation for this intrastream approach was an attempt to isolate grain size, canopy, sinuosity, and especially macrophyte abundance as the primary drivers of any patterns observed. A similar

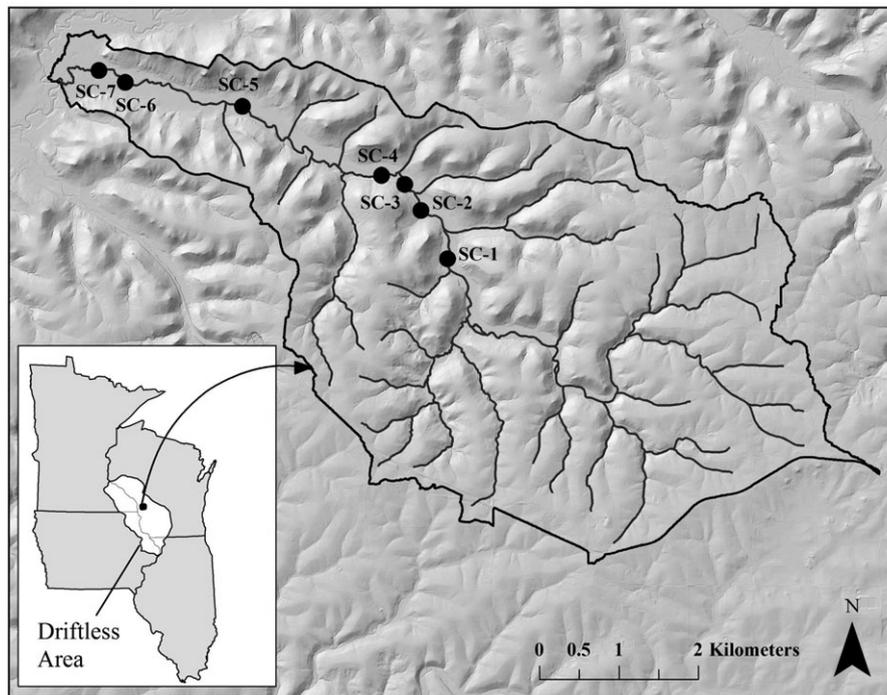


FIGURE 1 Location of study reaches (SC-1 to SC-7) within the Spring Coulee Creek watershed. General flow direction was southeast to northwest

TABLE 1 Channel geometry, geomorphic characteristics, and vegetation abundance of seven study reaches in Spring Coulee Creek

	SC-1	SC-2	SC-3	SC-4	SC-5	SC-6	SC-7
Baseflow discharge (L/s)	131	131	130	134	231	225	231
Length (m)	215	298	262	280	276	300	316
Width (m) ^a	4.77 ± 1.45	4.45 ± 1.48	4.18 ± 1.69	4.08 ± 1.00	4.52 ± 2.17	3.95 ± 0.84	3.91 ± 1.37
Depth (m) ^a	0.21 ± 0.07	0.24 ± 0.07	0.39 ± 0.13	0.28 ± 0.10	0.50 ± 0.33	0.41 ± 0.12	0.40 ± 0.17
Velocity (m/s) ^a	0.34 ± 0.13	0.34 ± 0.12	0.29 ± 0.15	0.43 ± 0.21	0.41 ± 0.28	0.39 ± 0.16	0.44 ± 0.28
Riffle:Pool	0.67	0.33	0.00	0.33	0.40	0.00	0.40
D ₅₀ (mm) ^b	53	51	33	53	34	9	8
Bed slope (%)	0.91	0.75	0.53	1.03	0.80	0.25	0.46
Sinuosity	1.08	1.16	1.22	1.22	1.22	2.19	1.28
Canopy (%) ^a	63 ± 24	14 ± 18	40 ± 36	62 ± 36	3 ± 6	39 ± 29	13 ± 20
M _c (%) ^{a,c}	26 ± 38	50 ± 44	42 ± 40	26 ± 41	36 ± 42	37 ± 42	25 ± 28
M _b (g/m ²) ^{a,d}	62 ± 103	93 ± 91	126 ± 183	123 ± 244	147 ± 239	45 ± 59	37 ± 41

^aMean and standard deviation reported from 11 transects.

^bMedian grain size.

^cMacrophyte cover.

^dMacrophyte biomass.

study across multiple streams would potentially have increased “noise” from variable hydrology, species, temperatures, and water chemistry. We do not know of another study that has used multiple-reach, single-stream approach to examine the connection between macrophyte-driven transient storage and nutrient uptake.

2.2 | Physical measurements

Each reach was divided into 11 equidistant transects where measurements of wetted width (w), thalweg depth (d), and thalweg velocity (v) were taken immediately following the series of releases. An OTT MF Pro velocity metre was used to measure velocity at 0.6 depth and determine discharge (Q) via the velocity–area method using at least 10 points measured. Froude number (Fr , Equation 1) was calculated to categorize habitat type at each transect.

$$Fr = \frac{v}{\sqrt{g \times d}} \quad (1)$$

where g is the gravitational acceleration constant (9.81 m/s^2), d is the thalweg depth (m), and v is the thalweg velocity at 0.60 depth (m/s). Froude numbers were used to classify each transect as a pool, riffle, or run (Jowett, 1993).

Macrophyte cover (M_c) and macrophyte biomass (M_b) were estimated using a grid technique modified from Bowden, Glime, and Riis (2006). A randomly placed quadrat at each of the 11 transects was used to estimate per cent M_c . Additionally, the macrophytes within each quadrat were harvested to determine macrophyte biomass (M_b) in the lab via ash-free dry mass. Canopy cover was measured using a convex Model A spherical densiometer during September 2015, before leaf fall. Measurements were taken facing four directions (90° intervals from one another) from the centre of the channel at each transect. To determine reach median grain size, D_{50} , grain size distributions were constructed from Wolman pebble count data that were collected along the entire reach. Reach length was determined manually using a field tape, whereas elevation change and valley length were determined from point measurements taken at the upstream and downstream end of each reach with a Trimble GEOXH 6000 GPS with centimetre accuracy following differential correction. From these measurements, bed slope (change in elevation \div channel length) and sinuosity (channel length \div valley length) were calculated.

2.3 | Tracer releases

A series of tracer releases were conducted in August 2015, during baseflow and peak biomass conditions. In each reach, a pulse (slug) release was conducted to measure phosphorus uptake, and a sustained injection release was done to quantify transient storage and other hydrological parameters. With the exception of SC-6, where 5 days separate the two releases, both releases were completed in either 1 day or in two consecutive days. In order to ensure adequate solute mixing, an area of turbulence was selected for at the upstream end, and an approximate 15-min travel time was targeted in each reach.

Rhodamine WT dye (RWT) was used as the conservative tracer during the pulse and injection releases. We acknowledge that RWT dye can be affected by sorption processes, so it should not be used

as a conservative tracer to investigate long flow paths or the hyporheic zone (Runkel, 2015). We warranted its use as a conservative tracer in this study on the basis of limited hyporheic transient storage in Spring Coulee Creek. Further justification was based on high (97–100%) mass recovery of RWT during slug releases, low organic matter in study stream, short-reach lengths (215 to 370 m), and short-duration injections (<1.5 hr). Target concentrations of RWT were 30 ppb. These concentrations were easily observed in the study reach and rapidly diluted to non-detectable levels downstream.

Pulse additions of RWT plus PO_4^{3-} to the surface water were used to determine dissolved phosphorus uptake. Target concentrations of PO_4^{3-} were $200 \mu\text{g P/L}$ above background. Slugs containing known amounts of phosphorus and RWT and were added at the upstream end of the stream reaches. Over the course of the pulse period, downstream concentrations of RWT were measured with a Hydrolab DS5 multi-parameter probe equipped with a Turner Designs® Rhodamine WT sensor. The probe was calibrated daily, and temperature corrections were applied to the RWT data (Wilson, Cobb, & Kilpatrick, 1986). Additionally, samples for phosphorus analysis were collected in 20-ml scintillation vials at the downstream end approximately every 60 s, beginning 10 min before the pulse arrived, and continuing until RWT concentrations returned to ambient levels. Samples were taken less frequently if change in dye concentration between time points was small. Samples were acidified ($\text{pH} < 4$) and kept refrigerated until dissolved phosphorus concentrations were measured on a Lachat QuikChem 8500 Series 2 Flow Injection Analysis System (QuikChem® Method 10-115-01-1-A). On average, 54 phosphorus samples were used to estimate phosphorus uptake in each reach.

Sustained injections of RWT were accomplished with a battery-powered FMI Lab Pump (Model QB) and voltage regulator to ensure constant injection rate. Pump rates during each release were between 55 and 95 ml/min. Injections persisted until a plateau was achieved at the downstream end (about 1 hr), and the pump was turned off. Concentrations of RWT were monitored throughout the injection period and until background levels returned.

2.4 | Uptake calculations

The nutrient spiralling approach (Webster, 1975) uses interrelated metrics to describe uptake dynamics in streams. Uptake length (S_w), the average distance a nutrient atom travelled in dissolved inorganic form before it is removed from solution, is a function of biotic demand and hydrology (Newbold et al., 1981). To standardize S_w by taking into account velocity and depth, it is converted to a mass transfer coefficient (Stream Solute Workshop, 1990) referred to as the uptake velocity, v_f (Peterson et al., 2001; Valett, Crenshaw, & Wagner, 2002). This value describes how quickly a solute in transport will become taken up and immobilized and is good for comparing uptake in reaches of differing sizes. These uptake metrics were calculated from the pulse releases using a mass balance approach (Tank, Rosi-Marshall, Baker, & Hall, 2008). Simply put, this method compares the recovery of both the conservative and non-conservative tracers over the duration of the pulse period to determine uptake. We compared the total mass recovery PO_4^{3-} to RWT at the downstream station (P:RWT_{ds}) to the mass ratio of the injectate (P:RWT_{inj}) and

assumed any mass reduction of phosphorus relative to RWT was the result of uptake. Uptake length (S_w) was a function of this difference and reach length (L ; Equation 2).

$$S_w = \frac{-1(L)}{\ln(\text{P:RWT}_{\text{ds}}) - \ln(\text{P:RWT}_{\text{inj}})}. \quad (2)$$

To calculate v_f , in order to compare channels of different sizes, discharge (Q) was divided by the product of channel width (W) and S_w (Covino, McGlynn, & McNamara, 2010; Stream Solute Workshop, 1990; Equation 3).

$$v_f = \frac{Q}{S_w W}. \quad (3)$$

Studies agree that this approach to calculating uptake is generally suitable and provides practical values (Powers, Stanley, & Lottig, 2009; Trentman et al., 2015).

2.5 | Storage calculations

We used the field data from the sustained injections in conjunction with one-dimensional transport with inflow and storage (OTIS and OTIS-P) models to characterize the channel and determine hydrological parameters of each reach (Runkel, 1998). This model uses the advection–dispersion equation (Equations 4 and 5), to determine hydrological channel characteristics including channel cross-sectional area (A), transient storage cross-sectional area (A_s), dispersion (D), and storage exchange rate (α).

$$\frac{\partial C}{\partial t} = -\frac{Q}{A} \frac{\partial C}{\partial x} + \frac{1}{A} \frac{\partial}{\partial x} \left(AD \frac{\partial C}{\partial x} \right) + \frac{q_{LIN}}{A} (C_L - C) + \alpha (C_s - C), \quad (4)$$

$$\frac{dC_s}{dt} = \alpha \frac{A}{A_s} (C - C_s), \quad (5)$$

where A is the main channel cross-sectional area, A_s the storage zone cross-sectional area, C the main channel solute concentration, C_L the lateral inflow solute concentration, C_s the storage zone solute concentration, D the dispersion coefficient, Q the volumetric flow rate, q_{LIN} the lateral inflow rate, t the time, x the distance, and α the storage zone exchange coefficient.

Lateral inflow rate (q_{LIN}) was set to 0 because baseflow in Spring Coulee Creek was stable, and change in discharge within each reach was negligible ($<\pm 2\%$). Preliminary values for A , A_s , D , and α were obtained by fitting the advection–dispersion equation to the data using a visualization tool in Mathematica™. The parameter estimates were then optimized with non-linear regression using OTIS-P computer software (Runkel, 1998). The ratio of A_s/A is the size of the transient storage zone relative to the size of the channel, but the term does not consider the interaction between flow velocity and the exchange rate (i.e., how much water is actually entering the storage zone). Thus, we also calculated a more robust metric of transient storage, F_{med}^{200} (Equation 6), the fraction of median travel time spent in storage if the reach were 200 m (Runkel, 2002).

$$F_{\text{med}}^{200} = \left(1 - e^{-200 \frac{\alpha}{(Q/A)}} \right) \frac{A_s}{(A + A_s)}. \quad (6)$$

Damkohler (Dal) values were calculated to evaluate if the length (L) of the experimental reach allowed for reasonable parameter estimates to be obtained (Wagner & Harvey, 1997; Equation 7).

$$Dal = \frac{L\alpha \left(\frac{A + A_s}{A_s} \right)}{Q/A}. \quad (7)$$

Parameter estimates are the most reliable when Dal is on the order of 1.0. Calculated Dal values that are much less than 1 indicate there was not enough interaction between the tracer and the storage zone to obtain reasonable parameter estimates. This could occur when stream velocity is very high, timescales of exchange are too long, and/or the reach length is too short. In contrast, calculated Dal values much greater than 1 indicate that too much (or even all) of the tracer was able to interact with the storage zone during the release (i.e., solute exchange with the storage zone was fast relative to water velocity). In addition to using Dal to evaluate parameter reliability, OTIS-P also provides the parameter estimate uncertainty (standard deviation and the ratio of the estimate to the standard deviation of the estimate).

2.6 | Statistics

A Pearson correlation matrix was constructed using the following variables: F_{med}^{200} , v_f , M_c , M_b , log of sinuosity, canopy, D_{50} , slope, and riffle:pool. This allowed for selection of variables for model building. Log transformations were applied to variables to satisfy the regression assumption of linearity. Stepwise linear regression was used for model building to predict storage (F_{med}^{200}) and uptake (v_f). Models were checked to ensure that added variables increased the adjusted R^2 and decreased Akaike information criterion. Statistical analyses were performed using SPSS (version 24) and RStudio (version 0.99.902).

3 | RESULTS

There were two overarching patterns in channel characteristics within the study reaches. One pattern was the longitudinal variation in channel geomorphology due to increased channel size and discharge. Discharge was greater downstream, and in general, downstream reaches had narrower widths, greater depths and velocities, less canopy cover, finer substrates, more gradual slopes, and were more sinuous (Table 1). Despite this overall trend, features of SC-4 were very similar to SC-1. Both reaches had steep slopes ($>0.90\%$), large median grain sizes (53 mm), and high canopy cover (60–65%). This is likely because SC-4 was confined by a bluff wall on one side of the channel and by a bed embankment protecting an agricultural field on the other. The meander-preventing obstacles resulted in channel incision and caused SC-4 to bear resemblance to SC-1. As a consequence of this “geomorphological reset,” channel characteristics from SC-1 to SC-3 are comparable to the changes observed from SC-4 to SC-7. Regardless of location along the longitudinal profile, reaches with greater slopes had greater canopy cover, median grain sizes, riffle:pool, and were less sinuous. Macrophyte cover and biomass followed less identifiable patterns.

Macrophyte cover was greatest in SC-2 (50%) and lowest (~25%) in SC-1 and SC-7. Macrophyte biomass was greatest in the mid-reaches (SC-3, SC-4, and SC-5) where it ranged from 123 to 147 g/m² and lowest in SC-7 and SC-8 (45 and 37 g/m², respectively). Aquatic vegetation consisted primarily of *Elodea*, but *Potamogeton* and *Ranunculus* were also present.

Hydrological parameter estimates obtained from OTIS-P were considered reliable (Table 2). Evidence of this included *Dal* on the order of one (2.5–7.7; Wagner & Harvey, 1997) and high ratios, which indicated that the uncertainties of estimates were small compared to the estimates themselves (Wagner & Gorelick, 1986). Mean size of the storage zone relative to size of the channel (A_s/A) was 0.15 ± 0.07 . One reach, SC-5, stood out with the greatest values for A , A_s , and A_s/A (1.54, 0.39, and 0.25, respectively). These high values are attributed to two very long (>30 m), wide (>5 m), and densely vegetated pools observed in the reach. The OTIS-P model used to obtain parameter estimates provided good fits with the data (e.g., Figure 2a–c), and all seven plots of predicted (modelled) versus observed (field data) RWT values had $R^2 > .99$.

The median travel time spent in storage if the reach were 200 m (F_{med}^{200}) was calculated from the OTIS-P parameter estimates and ranged from 1.01 to 6.16%. This storage metric was positively correlated with both macrophyte biomass (M_b ; $r = .794$, $p = .033$; Figure 3) and with uptake velocity (v_f ; $r = .756$, $p = .049$; Figure 4a). However, M_b and v_f were not correlated ($r = .606$, $p = .149$; Figure 4b). Uptake velocities, calculated from breakthrough curves of RWT and PO_4^{3-} (e.g., Figure 2d–f), averaged 2.33 ± 1.46 mm/min in Spring Coulee Creek.

The strongest predictors of F_{med}^{200} were M_b , slope, and riffle:pool ($p < .001$, adjusted $R^2 > .99$; Table 3). The strongest predictors of v_f were F_{med}^{200} , canopy, and slope ($p = .002$, adjusted $R^2 = .98$). Observed versus predicted plots for each of these models show a close fit to a 1:1 line (Figure 5).

4 | DISCUSSION

Understanding the dynamics of phosphorus retention and cycling in streams is important to the development of effective methods aimed at water quality improvement. By learning which variables are key players in phosphorus removal from streams, we can focus restoration efforts around them. Because of the potential to facilitate phosphorus uptake, we were interested in which factors affected transient storage. Our results supported the hypothesis that macrophyte biomass was positively correlated with transient storage. Of all the variables tested, M_b was the most important variable affecting transient storage; it accounted for 63% of the variation in F_{med}^{200} . An additional 34% of the variation in the model was explained by slope, which was negatively correlated with transient storage. Greater slopes increase advective velocity, which would decrease residence time of water and solutes. Stofleth et al. (2008) also demonstrated the inverse relationship between velocity and F_{med}^{200} in sand-bed streams. The third predictor variable, riffle:pool, was positively correlated with storage. The inclusion of riffle:pool in the model only explained an additional 2.5% of the variation in F_{med}^{200} . This storage was likely caused by eddies in the shallow riffles.

Because M_b accounted for most of the variation in F_{med}^{200} in the final predictive model, the primary mechanism of transient storage in Spring Coulee Creek was surface storage presumably caused by macrophyte beds. Others have likewise concluded that sand-bed streams have very little hyporheic storage (Harvey & Wagner, 2000; Jin & Ward, 2005; Stelzer, Strauss, & Coulibaly, 2017; Stofleth et al., 2008). Values of A_s/A in Spring Coulee Creek (0.15 ± 0.07) were similar to what Powers et al. (2009) found in other Wisconsin streams and were within range of the mean for sand-bed streams (0.36 ± 0.22 , as reviewed by Stofleth et al., 2008). We observed low F_{med}^{200} values (1.01 to 6.16%), compared to Jin and Ward's (2005) observation in

TABLE 2 Final advection–dispersion model parameters from seven study reaches in Spring Coulee Creek

Reach	Parameter estimates					
	Ratio ^a (95% CI)					
	A (m ²) ^b	A_s (m ²) ^c	D (m ² /s) ^d	α (/s) ^e	A_s/A	Dal
SC-1	1.00 426 (1.00–1.01)	0.07 34 (0.07–0.08)	0.50 59 (0.48–0.51)	1.04×10^{-4} 13 (8.87×10^{-5} – 1.20×10^{-4})	0.07	2.5
SC-2	0.63 76 (0.62–0.65)	0.08 9 (0.06–0.09)	0.83 13 (0.70–0.95)	3.02×10^{-4} 4 (1.69×10^{-4} – 4.34×10^{-4})	0.12	4.6
SC-3	0.80 241 (0.79–0.80)	0.19 60 (0.18–0.19)	0.78 33 (0.73–0.82)	2.94×10^{-4} 24 (2.70×10^{-4} – 3.19×10^{-4})	0.23	2.5
SC-4	0.71 129 (0.70–0.72)	0.10 19 (0.09–0.11)	0.83 17 (0.74–0.93)	2.40×10^{-4} 8 (1.83×10^{-4} – 2.98×10^{-4})	0.14	2.8
SC-5	1.54 110 (1.51–1.56)	0.39 31 (0.36–0.41)	0.87 19 (0.78–0.96)	2.74×10^{-4} 12 (2.29×10^{-4} – 3.19×10^{-4})	0.25	2.5
SC-6	0.89 100 (0.87–0.91)	0.09 10 (0.07–0.11)	0.65 13 (0.55–0.75)	4.82×10^{-4} 5 (3.04×10^{-4} – 6.60×10^{-4})	0.10	7.7
SC-7	0.97 193 (0.96–0.98)	0.09 21 (0.08–0.10)	0.73 24 (0.67–0.79)	2.69×10^{-4} 8 (2.05×10^{-4} – 3.33×10^{-4})	0.09	4.2

^aRatio = parameter estimate \div standard deviation.

^bMain channel cross-sectional area.

^cStorage zone cross-sectional area.

^dDispersion coefficient.

^eStorage zone exchange coefficient.

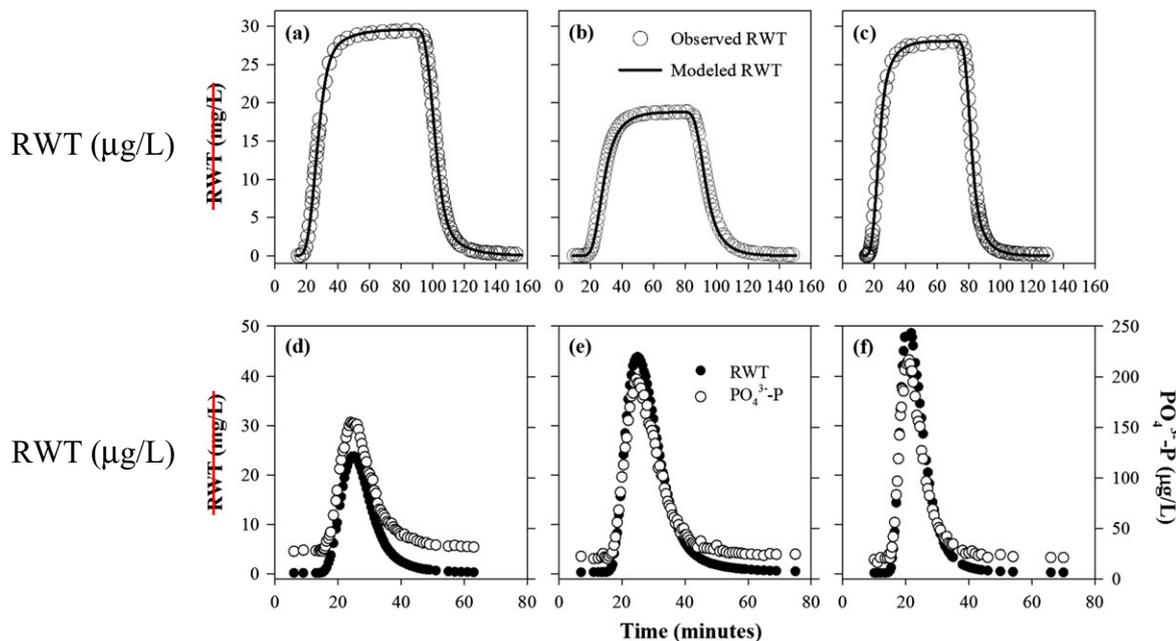


FIGURE 2 Representative breakthrough curves from (a–c) sustained and (d–f) instantaneous tracer releases performed in (a and d) SC-1, (b and e) SC-2, and (c and f) SC-7. RWT = rhodamine WT dye

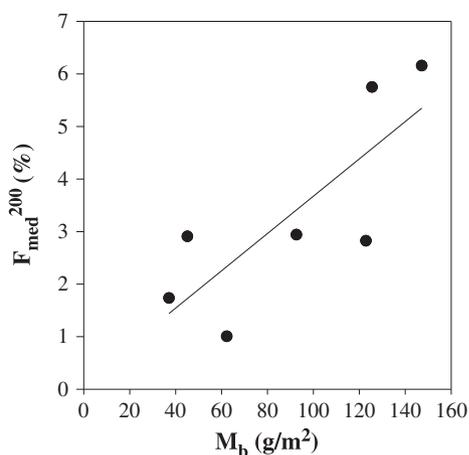


FIGURE 3 F_{med}^{200} as a function of M_b for seven reaches of Spring Coulee Creek ($r = .794, p = .033$)

their sand-bed stream (9.5 to 34.5%). Interestingly, values of F_{med}^{200} in Spring Coulee Creek were more akin to what is found in bedrock streams, like Walker Branch, and Tennessee (Hendricks, 1999; Mulholland et al., 1997)—indicating that permeability was low even for a sand-bed stream. This, in addition to high mass recoveries of RWT during the short-term pulse releases, further indicates that the effect of the hyporheic zone was negligible. In fact, the domination of surface storage in Spring Coulee Creek was likely key to the positive correlation between transient storage and phosphorus uptake velocity. This would be consistent with the findings of others who have shown the greater influence of surface storage (over hyporheic storage) on uptake (Ensign & Doyle, 2005; Gücker & Boëchat, 2004; O'Connor, Hondzo, & Harvey, 2010).

We were able to measure phosphorus uptake using the nutrient addition method because phosphorous was the limiting nutrient in our study stream. Phosphorus uptake metrics in Spring Coulee Creek were

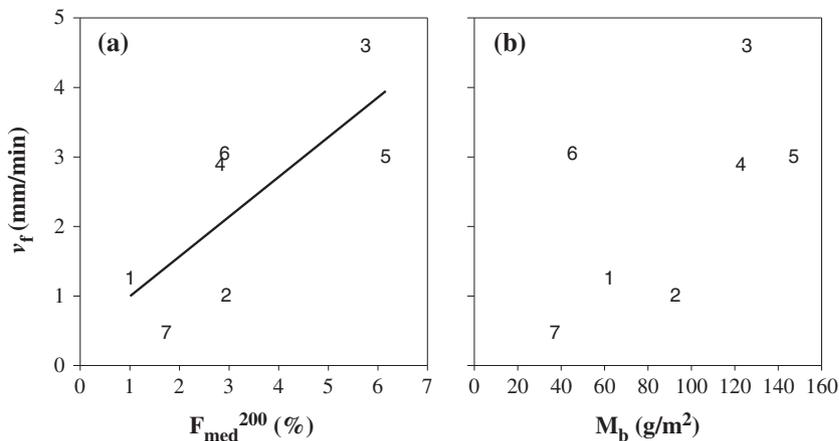


FIGURE 4 v_f as a function of F_{med}^{200} (a, $r = .756, p = .049$) and M_b (b, $r = .606, p = .149$). Numbers correspond to reach name

TABLE 3 Regression models predicting F_{med}^{200} and v_f in Spring Coulee Creek

Dependent variable	Predictor variables in model	Model	Model p value	R^2	Adjusted R^2	AIC
F_{med}^{200}	M_b^*	$F_{\text{med}}^{200} = 0.036 (M_b) + 0.121$.033	.631	.557	27.03
	M_b^{***}	$F_{\text{med}}^{200} = 0.052 (M_b) - 487.50 (\text{slope}) + 1.924$	<.001	.973	.960	10.57
	Slope**					
	M_b^{***} Slope*** Riffle:Pool**	$F_{\text{med}}^{200} = 0.061 (M_b) - 705.10 (\text{slope}) + 2.493 (\text{riffle:pool}) + 1.850$	<.001	.998	.996	-5.59
v_f	F_{med}^{200*}	$v_f = 0.572 (F_{\text{med}}^{200}) + 0.425$.049	.571	.486	24.18
	F_{med}^{200**}	$v_f = 0.770 (F_{\text{med}}^{200}) + 0.039 (\text{canopy}) - 1.533$.008	.911	.867	15.15
	Canopy*					
	F_{med}^{200***}	$v_f = 0.786 (F_{\text{med}}^{200}) + 0.045 (\text{canopy}) - 158.90 (\text{slope}) - 0.732$.002	.990	.980	1.90
	Canopy** Slope*					

Note. AIC = Akaike information criterion.

*** $p < .0001$.

** $p < .001$.

* $p < .01$.

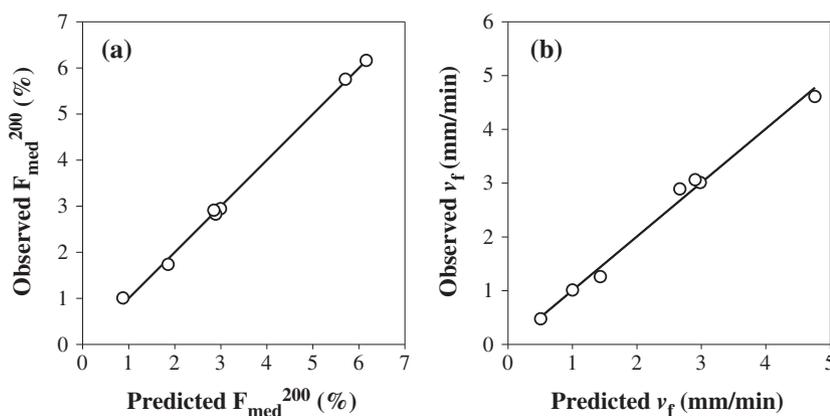


FIGURE 5 Predicted and observed F_{med}^{200} (a, $y = 0.999x + 0.002$, $R^2 = .998$) and v_f (b, $y = 1.001x + 0.005$, $R^2 = .990$)

similar to those observed in other streams (Niyogi, Simon, & Townsend, 2004; Powers et al., 2009; Valett et al., 2002). It is well known that uptake can be affected by ambient nutrient concentrations and/or added nutrients (Earl, Valett, & Webster, 2006; Mulholland et al., 2008; Reddy, Kadlec, Flaig, & Gale, 1999). However, we were unable to detect a relationship between uptake and ambient PO_4^{3-} or peak PO_4^{3-} concentration above ambient. Even if our PO_4^{3-} addition altered the measured phosphorus uptake kinetics, we would assume that all reaches were affected similarly because similar PO_4^{3-} levels were administered to each reach. Therefore, we should still be able to assess how relative rates of phosphorus uptake varied with transient storage, macrophyte biomass, and other physical characteristics of the stream.

Although our hypothesis that transient storage is the main driver of phosphorus uptake was supported, other variables also helped explain variation in v_f . The addition of canopy to the model for v_f explained about 34% more of the variation. Another 8% was accounted for by slope. These additional variables demonstrate that the channel structures and materials that develop storage zones, as well as environmental factors, can be significant influences on nutrient uptake (Argerich, Martí, Sabater, Haggerty, & Ribot, 2011; Drummond, Bernal, Schiller, & Martí, 2016). Canopy and slope can affect a wide array of features including light availability, substrate size, flow velocity, temperature, and organic material inputs, which in turn can have an effect on phosphorus uptake. Perhaps these factors altered algal biomass, or the nutrient composition of algal biofilms, both of which

have been correlated with phosphorus uptake velocity (McMillan, Tuttle, Jennings, & Gardner, 2014; Newcomer Johnson, Kaushal, Mayer, Smith, & Svirichi, 2016; Niyogi et al., 2004; Price & Carrick, 2014).

In Spring Coulee Creek, the main driver of uptake velocity was transient storage, and the main driver of transient storage was M_b . Despite the capability of macrophyte stems and leaves to take up large quantities of SRP from the water column following periods of availability (Baldy et al., 2015), there was no correlation between M_b and v_f . The lack of significant relationship between these variables could be a result of (a) differing timescales with which storage and uptake were measured and (b) ambiguity of the metric M_b . With regard to the first artefact, transient storage in each reach was determined using a 1- to 1.5-hr-long injection, whereas uptake was measured with a pulse release. On the basis of these timescales, it is reasonable to assume that some of the storage quantified by the sustained release had little to no effect on phosphorus uptake measured by the pulse release. In addition, we know that longer releases increase the measure of A_s . An unpublished study in SC-2 demonstrated that a longer injection period (6 vs. 1 hr) increased A_s/A by 16.7% (0.12 to 0.14) and decreased α by 25.5% (3.02×10^{-4} to 2.25×10^{-4}). The longer release resulted in a greater measure of A_s because RWT had the opportunity to travel deeper into macrophyte beds where it could not during the shorter release. Because our storage model indicates M_b as the primary driver of storage, we assume that our sustained

releases captured deeper storage within dense macrophyte beds. During our pulse releases, phosphorus had the opportunity to only enter storage on the periphery of the macrophyte beds; thus, deeper storage likely was not important for explaining our rates of phosphorus uptake. Instead, most of the uptake that was measured occurred in storage zones where the exchange rate was high, for example, the peripheral region of the macrophyte beds. Therefore, because storage was quantified on a longer timescale than uptake, we may not be able to observe a link between M_b and v_f .

Another reason why we observed no relationship between M_b and v_f might be because the metric, M_b , was ambiguous on several levels. Because canopy (e.g., light availability) was a driver of v_f , it is possible that metabolic activity of macrophytes or epiphytes could have affected uptake; however, our macrophyte metric does not account for metabolic activity in Spring Coulee Creek. Furthermore, there are a variety of factors, including plant shape and density, that can affect the movement of water in and around macrophyte beds (Luhar, Rominger, & Nepf, 2008; Nepf et al., 2007). The two-dimensional metric, M_b , provided no insight into these characteristics that would have affected v_f . Sand-Jensen (1998) demonstrated that flow velocity within dense macrophyte beds can be highly variable and even non-existent. Thus, dense beds can provide long-term storage, have very small exchange rates, and are not as important for uptake. However, two vegetated areas with similar biomass or cover can have differing effects on water residence time and flow dynamics depending on their continuity across a channel (Cotton, Wharton, Bass, Heppell, & Wotton, 2006). Residence time and potential for uptake would decrease if flow paths through or around a macrophyte bed were present. Conversely, a contiguous macrophyte bed would increase residence time and potential for uptake by slowing the velocity of the active channel. In addition to density, macrophyte shape is important as well. On a small scale, Levi et al. (2015) showed that macrophyte species with a higher perimeter-to-area ratio of their leaves had greater rates of ammonium uptake. On a larger scale, shape of a macrophyte bed dictates the amount of contact individual plants have with phosphorus in the water column. Although effects of macrophyte beds on stream hydrology and nutrient dynamics are complex and often difficult to understand (Clarke, 2002; Luhar et al., 2008; Nepf et al., 2007), additional information such as metabolic activity, macrophyte density within beds, density of stems, and frontal area per unit volume of beds would likely result in better understanding of the relationship between macrophytes and phosphorus uptake velocity.

5 | CONCLUSIONS

In Spring Coulee Creek, M_b , slope, and riffle:pool accounted for 99.6% of the variation in F_{med}^{200} , whereas F_{med}^{200} , canopy, and slope accounted for 98.0% of the variation in v_f . Our results indicate the importance of macrophyte-driven transient storage to phosphorus uptake. We can expect features of macrophyte beds, which create greater opportunity for phosphorus to interact with reactive substrates, would promote uptake. These characteristics include increased surface area and higher exchange rates between storage zones and the main channel. Although storage created by macrophytes was important for

phosphorus retention in Spring Coulee Creek, we cannot draw conclusions regarding relative importance of individual components within the macrophyte-driven storage. For example, we do not know the phosphorus uptake efficiency of the macrophytes themselves, their epiphytic biofilms, or the sediment within beds. These results call for further investigation into the effects of macrophyte beds on phosphorus uptake in this stream and for better metrics to describe aquatic vegetation in future studies.

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