J. N. Am. Benthol. Soc., 1993, 12(3):223-235

Transient storage in Appalachian and Cascade mountain streams as related to hydraulic characteristics

D. J. D'ANGELO[1,4], J. R. WEBSTER[2], S. V. GREGORY[1], AND J. L. MEYER[3]

[1] *Fisheries and Wildlife Department, Oregon State University, Corvallis, Oregon 97331 USA*
[2] *Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24060 USA*
[3] *Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA*

Abstract. Hydraulic characteristics were measured in artificial streams and in 1st- to 5th-order streams in the Appalachian and Cascade mountains. Appalachian Mountain stream sites at Coweeta Hydrologic Laboratory, North Carolina, were on six 1st-order streams and a 1st- through 4th-order gradient of Ball Creek-Coweeta Creek. Cascade Mountain sites were located on constrained and unconstrained reaches of Lookout Creek, a 5th-order stream in H. J. Andrews Experimental Forest, Oregon. At each site, a tracer solution (chloride or rhodamine WT) was released for 30–180 min and then discontinued. At the downstream end of the release site, the resulting rise and fall of the tracer concentration was measured. These data, along with upstream concentration and measured widths and depths, were used in a computer model to estimate several hydraulic parameters including transient storage and lateral inflow. Estimated transient storage zone size (A_s) ranged from near zero in artificial streams to 2.0 m^2 in 5th-order streams. A_s was largest relative to surface cross-sectional area (A) at 1st-order sites where it averaged 1.2 × A, compared with 0.6 × A and 0.1 × A in unconstrained and constrained 5th-order sites, respectively. Where measured, lateral discharge inputs per metre of stream length ranged from 1.9% of instream discharge in 1st-order streams to 0.05% of instream discharge at 5th-order sites. Our results show that surface water exchange with storage zones is rapid and extensive in steep headwater streams and less extensive but still significant at 3rd- through 5th-order sites. An understanding of relationships between stream morphology, storage zone size, and extent of interactions between surface and subsurface waters will assist comparisons of solute dynamics in physically diverse streams.

Key words: solutes, transient storage, transport model, retention, discharge, geomorphology.

Solute dynamics often play a critical role in streams because many solutes (e.g., phosphorus and nitrogen) are present in short supply and thereby regulate primary and secondary productivity (Stream Solute Workshop 1990). Additionally, linkages between terrestrial and aquatic ecosystems and between upstream and downstream reaches of streams strongly influence solute concentrations (Meyer et al. 1988). Evaluation of solute transport characteristics in physically complex, small mountain streams has typically been attempted with short-term tracer and nutrient releases (Stream Solute Workshop 1990). These studies (e.g., Elwood et al. 1981, Newbold et al. 1981, Elwood et al. 1983, Mulholland et al. 1985, Triska et al. 1989, Mulholland et al. 1990, Munn and Meyer 1990, D'Angelo and Webster 1991, D'Angelo et al. 1991, Hart et al. 1992) primarily focused on discovering processes that influence transport and transformation of biologically reactive solutes, and were limited by an inability to separate and quantify physical and biological determinants of solute transport.

Recent applications of transport equations (Fischer et al. 1979, Bencala and Walters 1983, Hart et al. 1990) to solute transport in streams allow us to explain transport dynamics quantitatively in terms of relationships between physical characteristics (e.g., geomorphology, flow and substrate) and hydraulic variables (e.g., dispersion, transient storage, transient storage exchange rate, and lateral inflow). A combination of tracer studies and solute transport simulations provides a means to quantitatively separate physical and biological controls, smooth out small scale variability, and compare studies done at different scales (Stream Solute Workshop 1990).

We suggest that dispersion, transient storage (pockets of slow water movement), transient

[4] Present address: Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

storage exchange rate, and lateral inflows are important hydraulic variables that reflect stream physical characteristics and determine both nonreactive and reactive solute dynamics. Dispersion and the exchange rate between the main channel and transient storage zones should respond to properties such as discharge, velocity, and channel cross sectional area, which correlate with stream order. Transient storage zone size should be influenced most by the presence or absence of instream complexity (e.g., leaves, wood, boulders). Inflow of water from lateral and sub-surface areas is expected to be a function of stream geomorphology (i.e., constrained versus unconstrained reach types), substrate and streambank porosity, total sub-surface water volume and flow, and height of the water table.

Our objective was to use short-term tracer-release studies coupled with a solute-transport computer model to quantify these hydraulic variables. We focused on how small scale physical obstructions (e.g., presence or absence of leaves) in artificial streams, stream order and discharge in 1st- through 4th-order natural streams, and geomorphic complexity in 5th-order streams affect the following hydraulic variables: dispersion, transient storage zone cross-sectional area, transient storage exchange coefficient, and lateral inflow. These hydraulic parameters should both reflect longitudinal changes in physical characteristics and assist in identifying those changes that are most important in determining solute transport dynamics.

Methods

Field sites

Solute releases were conducted in outdoor artificial streams, with and without leaves, and at sites on 1st- through 5th-order natural streams at low and high flows (Table 1). Outdoor artificial streams at Coweeta Hydrologic Laboratory, Macon County, North Carolina, were constructed of 15-m lengths of 20-cm wide plastic drain pipe and had a slope of 2%. The bottoms of the streams were layered with fine gravel to a depth of about 2 cm. Initial releases were conducted in the streams containing only gravel. Additional releases were conducted after loose dogwood or oak leaves (300 g AFDM/m^2) were evenly distributed throughout the streams (D'Angelo et al. 1991). Water depth ranged from 0.5 cm along stream edges to 3 cm at mid-channel.

Natural streams were studied at Coweeta Hydrologic Laboratory and at H. J. Andrews Experimental Forest, Lane County, Oregon. Streams studied at Coweeta are 1st-order streams with flows of 0.5–5.0 L/s that drain mixed-hardwood ($n = 3$) or white pine (*Pinus strobus*) forests ($n = 3$) that are 35–40 yr old (D'Angelo and Webster 1991). Additional Coweeta sites ($n = 5$) were located on a 1st- through 4th-order gradient of Ball Creek to Coweeta Creek. Discharges along this gradient ranged from 7 to 276 L/s when sampled.

Stream reaches studied at H. J. Andrews Experimental Forest are in Lookout Creek, a 5th-order stream with flows of 283–2830 L/s, which drains Douglas fir (*Pseudotsuga menziesii*) forests that are 50–350 yr old. Stream reaches studied were classed as either constrained ($n = 5$) or unconstrained ($n = 2$). Constrained reaches of Lookout Creek had ratios of valley floor width to active channel width of 1.3–2.8, while unconstrained reaches had ratios >6.0 (Lamberti et al. 1989).

Tracer dynamics

Slightly different methods were used in the four studies (artificial streams, 1st-order pine-hardwood comparison, 1st- through 4th-order gradient, and constrained vs. unconstrained reaches of Lookout Creek); but in general a solution containing chloride (as NaCl) or rhodamine WT (Lookout Creek) was released into each stream for a period sufficient to allow concentrations to reach a plateau. Time to plateau ranged from 10 to 180 min depending on size of stream and length of reach. Solutions added raised stream chloride from 1 mg/L to 3 mg/L and rhodamine WT from 0 μg/L to 10 μg/L.

Water samples were taken at the downstream end of the reach at set intervals. When concentrations reached a plateau, samples were also taken at several sites along the reach. Solute input was then discontinued and samples were taken at the downstream site until concentrations returned to near background levels. Cl was analyzed with a Technicon Autoanalyzer-II system using standard methods (APHA 1985). In the 1st- through 4th-order gradient study in Ball Creek-Coweeta Creek, we measured Cl concentrations in the field with an ion specific elec-

TABLE 1. Solute release site information.

Site	n	Location	Release date	Reach lengths (m)
Artificial streams				
Without leaves	6	Coweeta	19 November 1988	15
Dogwood, summer		3	19 November, 29 June 1989	15
Dogwood, winter		3	19 November, 18 December 1988	15
Oak, summer	3	3	29 June 1989	15
Oak, winter	3	3	18 December 1988	15
1st-order sites				
Pine, summer	3	Coweeta	19 September 1989	20, 20, 20
Pine, winter	3	Coweeta	19 December 1988	20, 20, 20
Hardwood, summer	3	Coweeta	19 September 1989	20, 20, 20
Hardwood, winter	3	Coweeta	19 December 1988	15, 20, 20
Gradient sites				
1st order, summer	1	Coweeta	30 July 1991	93
2nd order, summer	2	Coweeta	29 July, 20 August 1991	105, 105
3rd order, summer	1	Coweeta	30 July 1991	100
4th order, summer	1	Coweeta	19 August 1991	100
5th-order sites				
Unconstrained, summer	2	Andrews	26 August 1987	530
			1 September 1987	381
Unconstrained, winter	2	Andrews	2 March 1987	530
			4 March 1987	381
Constrained, summer	5	Andrews	20 August 1987	567
			5 August 1987	532
			27 August 1987	385
			2 September 1987	335
			31 August 1987	447

trode (Orion model #290A). In Lookout Creek, rhodamine WT was measured in the field with a Turner Designs fluorometer.

For 1st-order Coweeta streams and 5th-order H. J. Andrews stream reaches, discharge (Q) was calculated from weir stage-discharge relationships. For Ball Creek-Coweeta Creek 2nd- through 4th-order sites, discharge was calculated from chloride dilution by assuming no lateral inputs over the reach. Channel cross-sectional area (A, m^2) was calculated from mean depth and wetted channel width. This parameter was used in the model to calculate velocity as Q/A.

Model development

The model presented here is a modification of a one-dimensional advection-dispersion model (e.g., Thomann and Mueller 1987). We used the central difference scheme to formulate the finite difference equations and the Crank-Nicolson implicit method for numerical solutions of equations. The basic model includes advection and dispersion:

$$\frac{\partial c}{\partial t} = -u\frac{\partial c}{\partial x} + D\frac{\partial^2 c}{\partial x^2} \qquad (1)$$

where c is solute concentration in surface waters (mg/L), t is time, x is distance (m), u is velocity (m/s), and D is a dispersion coefficient (m^2/s). This equation is valid when discharge (Q, m^3/s) and stream cross-sectional area (A, m^2) are constant. The first term in the equation represents downstream transport (i.e., advection; Fig. 1A). The second term represents longitudinal dispersion, which determines scattering of the solute upstream and downstream and

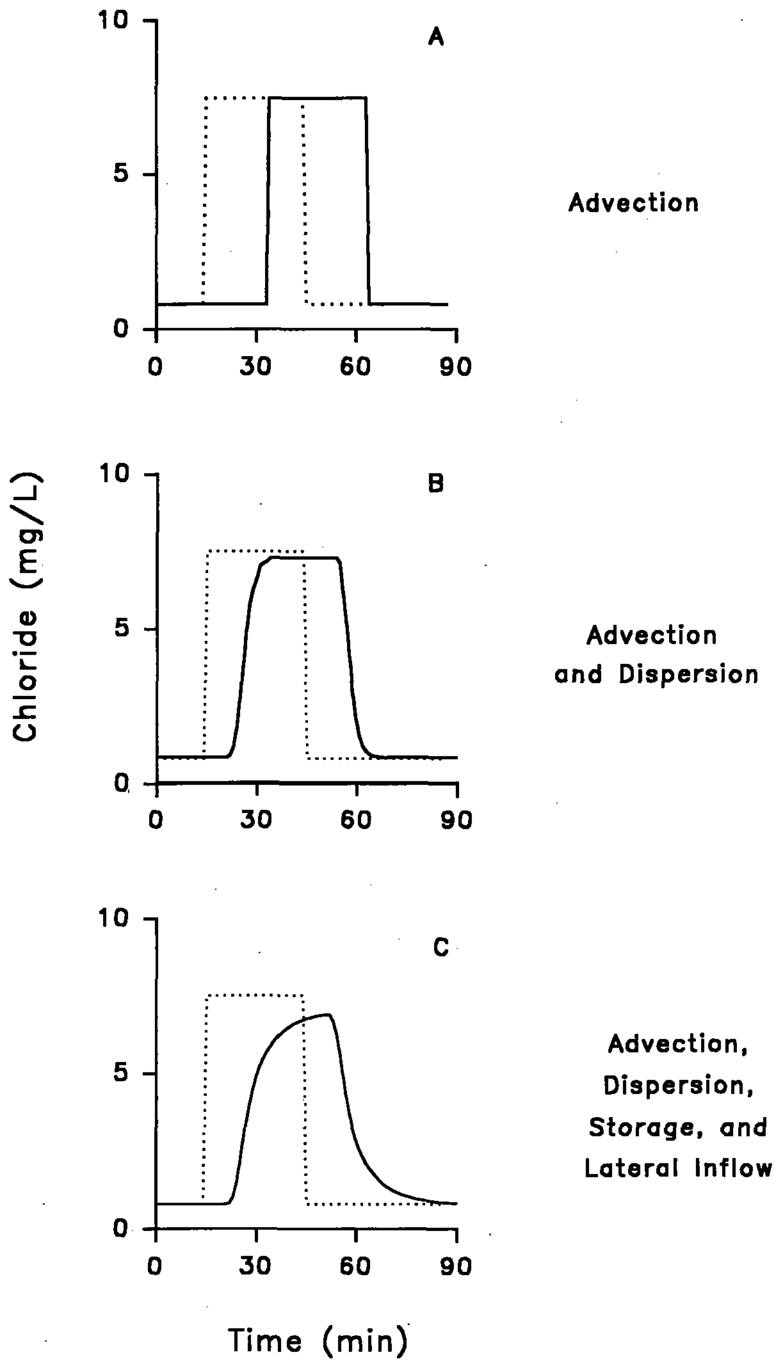

FIG. 1. Theoretical representation of a chloride curve from an upstream site, and model simulation of a downstream site depicting the shape of the solute curve with advection only (A), advection and dispersion (B), and advection, dispersion, transient storage and lateral inflow (C). Dotted lines represent the upstream curve (at the top of the release site) and solid lines represent the downstream curve (at the bottom of the release site).

results in spreading (in time) of the pulse of solute passing a downstream point (Fig. 1B).

The one-dimensional transport model can be expanded by including transient storage and lateral inputs as a pseudo two-dimensional mechanism (i.e., a kinetic submodel with no longitudinal velocity). Bencala (1983) illustrated that storage zones (e.g., behind rocks or in the sediments) can be essential for proper modeling of the descending limb of the solute-time curve:

$$\frac{\partial c}{\partial t} = \left(-\frac{Q}{A}\right)\frac{\partial c}{\partial x} + \frac{1}{A}\frac{\partial}{\partial x}\left[AD\frac{\partial c}{\partial x}\right] + \frac{Q_L}{A}(c_L - c) + \alpha(c_s - c) \quad (2)$$

where c_s is the solute concentration (mg/L) in transient storage zones, c_L is the solute concentration in lateral inflow (mg/L), Q_L is the lateral volumetric inflow rate ($m^3\ s^{-1}\ m^{-1}$), and α (1/s) is a coefficient of exchange with the storage zone area. Equation 3 models the change in solute concentration and must be solved simultaneously with equation 2:

$$\frac{dc_s}{dt} = \alpha\frac{A_s}{A}(c_s - c) \quad (3)$$

where A_s is the cross-sectional area of the storage zone (m^2). The transient storage component simulates removal of mass during the rising portion of the curve, temporary storage in transient storage zones, and release back into the stream after the main pulse has passed. This temporary storage and release produces a tail at the end of the solute pulse as typically observed in field data (Bencala and Walters 1983; Fig. 1C).

The transient storage model is based upon the following assumptions: 1) there is no downstream flow in the storage zone; 2) there is uniform and instantaneous distribution of solute within the storage zone; and 3) exchange between zones is a function of concentration and an exchange coefficient (Bencala and Walters 1983). Storage zones with little downstream flow can be found behind boulders, along stream edges, and in the hyporheic zone of streams. The criteria of uniform, instantaneous distribution of solutes along a concentration gradient between surface and subsurface waters is less likely to be met. However, Bencala and Walters (1983) argue that because solute mass is re-

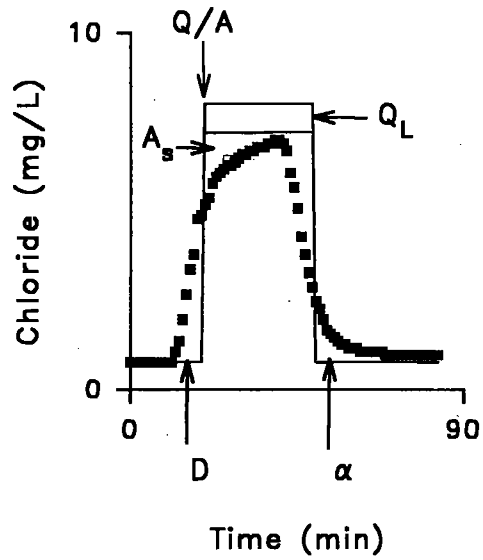

FIG. 2. Example chloride curve produced from samples collected at a downstream site. The height, width, and arrival time of the square wave are determined by the concentration and duration of the solute release, and velocity of the water. Additional parameters smooth the square wave into a curve. Parameters are positioned according to the region of the curve they most strongly influence. Q = discharge, A = stream cross-sectional area, Q/A = velocity, Q_L = lateral inflow, D = dispersion, A_s = transient storage zone cross-sectional area, and α = transient storage coefficient.

moved and temporarily stored in slow water zones during the rising phase of the pulse, and later returned to main channel flow, a mechanism exists in streams that presents itself as transient storage and can be simulated using these equations.

Field data were evaluated with the computer model by subjective curve fitting. Figure 2 is a depiction of theoretical data collected at a site downstream from the solute release and illustrates how parameters were used to fit different portions of the curve. Velocity (calculated from measured variables Q/A) and duration of the solute release were used to produce a square wave depicting when the solute pulse reached and passed the downstream station. Velocity was adjusted to center the square pulse over the data curve. Lateral inflow (Q_L) dilutes the solute pulse to achieve the peak downstream concentration. Dispersion (D) was then set to produce a leading edge of the curve that matched the

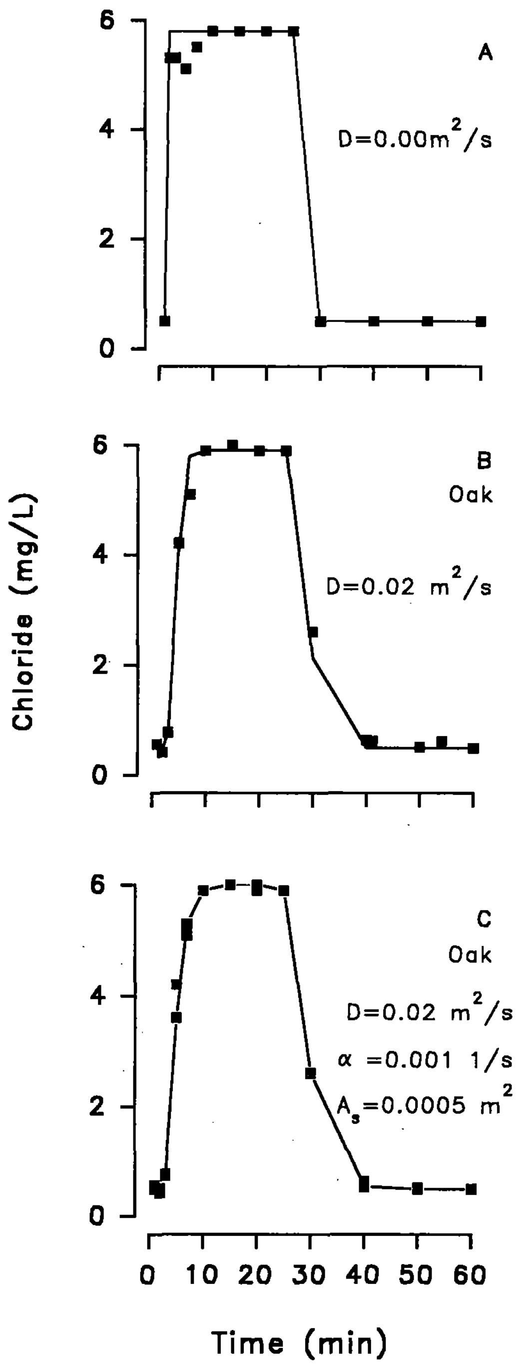

FIG. 3. A.—Model simulation (line) without transient storage compared with chloride data (squares) for an artificial stream in November 1987 when no leaves were in the streams. B.—Model fit when leaves had been in the streams for about four months (March 1988). C.—Model fit to the same data as B with transient storage included. Symbols as in Figure 2.

data. Finally, subsurface area (A_s) and the transient storage exchange coefficient (α) were adjusted to fit the left shoulder of the curve and the descending limb, respectively.

Results

Dispersion was estimated for all streams studied. Before leaves were added, dispersion in the artificial streams was negligible. The slight rounding of the left shoulder of the data curve suggests a very small amount of dispersion or transient storage (Fig. 3A). Leaves were added to the streams in November, and by March dispersion increased to 0.01–0.02 m^2/s (Fig. 3B). Dispersion in the artificial streams never exceeded 0.05 m^2/s (Table 2). For the natural streams, dispersion was lowest at 1st-order sites and generally increased with stream order (Table 2). Dispersion increased from an average of 0.04 in the 1st-order streams ($n = 5$) to 0.25 in 2nd-order sites ($n = 2$), dropped to 0.05 at the 3rd-order site ($n = 1$), and then increased to 0.2 at the 4th-order site ($n = 1$) and 2.2 in the 5th-order reaches ($n = 9$). Dispersion in the natural streams was positively correlated with discharge ($r = 0.92$, $p = 0.0002$; Fig. 4A) and more weakly correlated with velocity ($r = 0.51$, $p = 0.03$; Fig. 4B). The 3rd-order site, in a relatively straight section of stream, does not follow the expected pattern relating dispersion to discharge and velocity.

Transient storage zone size (A_s, m^2) and the exchange rate (α, 1/s) between A_s and A were negligible in the artificial streams. Adding a transient storage component to the artificial stream simulations improved model fit to only one data point (Fig. 3C). It did noticeably improve the fit in natural streams. Figure 5 shows example data sets and computer simulations for 2nd-order and 5th-order stream sites, respectively. Figures 5A and 5C show model fit to data without inclusion of transient storage zones. Model fit was improved when transient storage zones were included (Figs. 5B, D).

Transient storage zone size ranged from 0.02 m^2 at a 1st-order stream site to 2.0 m^2 at a 5th-order unconstrained site (Table 2). Transient storage zone area as a proportion of stream cross-sectional area (A_s/A) was highest in 1st-order streams (mean = 1.2; SE = 0.41) and least in 5th-order constrained reaches (mean = 0.1; SE = 0.21). In unconstrained 5th-order reaches, however, A_s/A (mean = 0.58; SE = 0.05) was higher than all except 1st-order sites. Along the gradient of 1st-order through 4th-order sites on Ball Creek, the 1st-order site had the highest A_s/A (1.3). A_s/A in 2nd-, 3rd-, and 4th-order sites was 0.35, 0.16, and 0.30, respectively. Note that the 3rd-order site has a lower ratio than the 2nd- or 4th-order sites due to a smaller transient storage zone (A_s) rather than a larger A. Overall, A_s/A was negatively correlated with discharge, with highest A_s/A at very low-discharge 1st-order sites, but the relationship was non-linear (Fig. 6A). A_s/A decreased more smoothly in relation to increasing velocity ($r = -0.55$, $p < 0.03$) (Fig. 6B).

The solute exchange rate (α) differed greatly between 1st- through 4th-order sites and 5th-order sites. Therefore, we evaluated these site groups separately and in combination. Exchange rate and discharge were negatively correlated when all sites were combined ($r = -0.42$, $p < 0.05$), but showed no correlation when 1st- through 4th-order sites were evaluated separately ($r = 0.59$, $p = 0.21$) from 5th-order sites ($r = 0.39$, $p = 0.37$) (Fig. 7A). There was no correlation overall between the exchange rate and velocity ($r = -0.045$, $p = 0.8$), but they were positively correlated when 1st- through 4th-order sites were grouped and evaluated separately ($r = 0.82$, $p < 0.04$) from 5th-order sites ($r = 0.58$, $p < 0.08$) (Fig. 7B).

Lateral inflows ($m^3\ s^{-1}\ m^{-1}$) were calculated for 1st-order Coweeta streams and H. J. Andrews 5th-order sites (Table 2) and were positively correlated with discharge ($r = 0.62$, $p < 0.07$; Fig. 8A). The percentage increase in stream flow per unit length (Q_L/Q) was higher in 1st-order streams (mean = 1.7%/m, SE = 1.9) than in 5th-order reaches (mean = 0.005%/m, SE = 0.044; Fig. 8B).

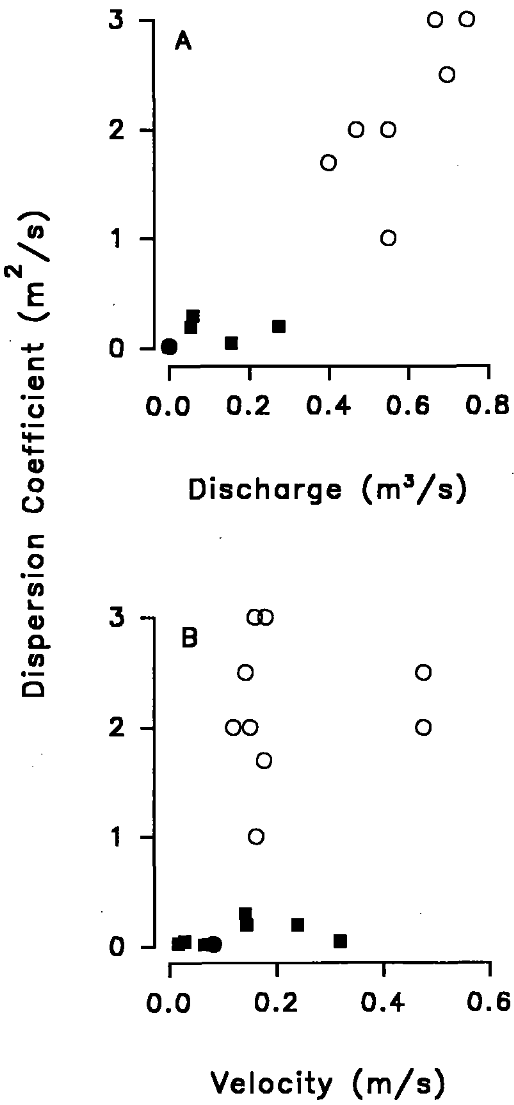

FIG. 4. A.—Correlation between dispersion and discharge for 1st- through 4th-order stream sites (filled squares) and 5th-order stream sites (open circles) ($r = 0.92$, $p < 0.0002$, $n = 12$). B.—Correlation between dispersion and velocity for 1st- through 4th-order stream sites (filled squares) and 5th-order stream sites (open circles) ($r = 0.51$, $p < 0.03$, $n = 17$).

Discussion

Results from this study demonstrate that quantified model parameters (D, A_s, and α) reflect differences in stream characteristics such as presence of obstructions (i.e., leaves), stream size (i.e., order), flow, and morphology (i.e., constrained vs. unconstrained), and are useful descriptors for comparisons of diverse and physically complex streams. In our study, dispersion was largely a function of discharge, while transient storage and exchange appeared to be most pronounced in headwater reaches where instream channel complexity (i.e., boulders, leaf packs, and woody debris) is most prevalent. The degree of exchange between the main channel and storage zones was strongly affected by discharge and stream morphology, especially at 5th-order sites where the presence or ab-

TABLE 2. Measured parameters (u, Q, A) and model parameters (D, A_s, α, Q_L) for solute releases. u = velocity, Q = discharge, A = stream cross sectional area, D = dispersion, A_s = transient storage zone cross sectional area, α = transient storage exchange coefficient, and Q_L = lateral inflow. * represents missing data.

Site	u (m/s)	Q (m^3/s)	A (m^2)	D (m^2/s)	A_s (m^2)	α (1/s)	Q_L ($m^3\ s^{-1}\ m^{-1}$)
Artificial streams							
Dogwood, summer	0.064	0.00024	0.0037	0.05	*	*	0.000000
Dogwood, winter	0.064	0.00024	0.0037	0.05	*	*	0.000000
Oak, summer	0.067	0.00025	0.0037	0.03	*	*	0.000000
Oak, winter	0.061	0.00025	0.0037	0.02	0.0005	0.001	0.000000
1st-order sites							
Pine, summer	0.064	0.002	0.025	0.02	0.025	0.0013	0.000046
Pine, winter	0.028	0.001	*	0.05	0.020	0.0008	0.000013
Hardwood, summer	0.081	0.002	0.022	0.02	0.040	0.0010	0.000000
Hardwood, winter	0.016	0.001	*	0.03	0.020	0.0005	0.000019
Gradient sites							
1st order, summer	0.027	0.007	0.103	0.10	0.400	0.0000	*
2nd order, summer	0.140	0.060	0.383	0.30	0.120	0.0009	*
2nd order, summer	0.143	0.055	0.383	0.20	0.160	0.0012	*
3rd order, summer	0.318	0.156	0.572	0.05	0.080	0.0020	*
4th order, summer	0.238	0.276	1.446	0.20	0.350	0.0015	*
5th-order sites							
Unconstrained							
Reach 4, summer	0.162	0.550	3.400	1.00	2.000	0.00007	0.000680
Reach 4, winter	0.476	0.600	*	2.00	0.500	0.00050	0.000000
Reach 7, summer	0.179	0.750	4.200	3.00	2.000	0.00008	0.000680
Reach 7, winter	0.476	2.000	*	2.50	1.000	0.00001	0.000000
Constrained							
Reach 1, summer	0.159	0.670	4.200	3.00	0.500	0.00005	0.000890
Reach 2, summer	0.142	0.700	5.680	2.50	0.200	0.00007	0.000018
Reach 3, summer	0.119	0.470	3.600	2.00	0.100	0.00005	0.000120
Reach 5, summer	0.176	0.400	2.270	1.70	0.400	0.00007	0.000320
Reach 6, summer	0.150	0.550	3.800	2.00	*	0.00006	0.000540

sence of large floodplain areas can strongly influence flow patterns. The influence of discharge and morphology emphasize the need to evaluate solute dynamics both annually and longitudinally when comparing catchments, rather than taking a "snap-shot" approach.

Dispersion as used in our study is not identical to classical dispersion defined as turbulent or eddy diffusion because this model incorporates transient storage as an additional mechanism to account for longitudinal spreading. However, classical dispersion and dispersion with transient storage both describe spreading at the leading edge of the curve and reflect the portion of water that arrives downstream faster than the main solute pulse. Up to some threshold, higher discharges in conjunction with instream obstructions may diversify flow paths, thereby increasing dispersion. Our finding that dispersion is strongly related to discharge is in line with the findings of Bencala and Walters (1983) who found strong relationships between dispersion, transient storage, and friction. Fischer et al. (1979) successfully estimated classical dispersion from stream velocity, depth, width, and shear velocity.

Perhaps of greater relevance to accessibility of nutrients for aquatic organisms are interactions between stream cross-sectional area (A, m^2), transient storage zone size (A_s, m^2), and transient storage exchange rate (α, 1/s). A_s/A provides a measure of storage area cross section relative to stream cross-sectional area. In 1st-order streams, debris dams, boulders, and back-

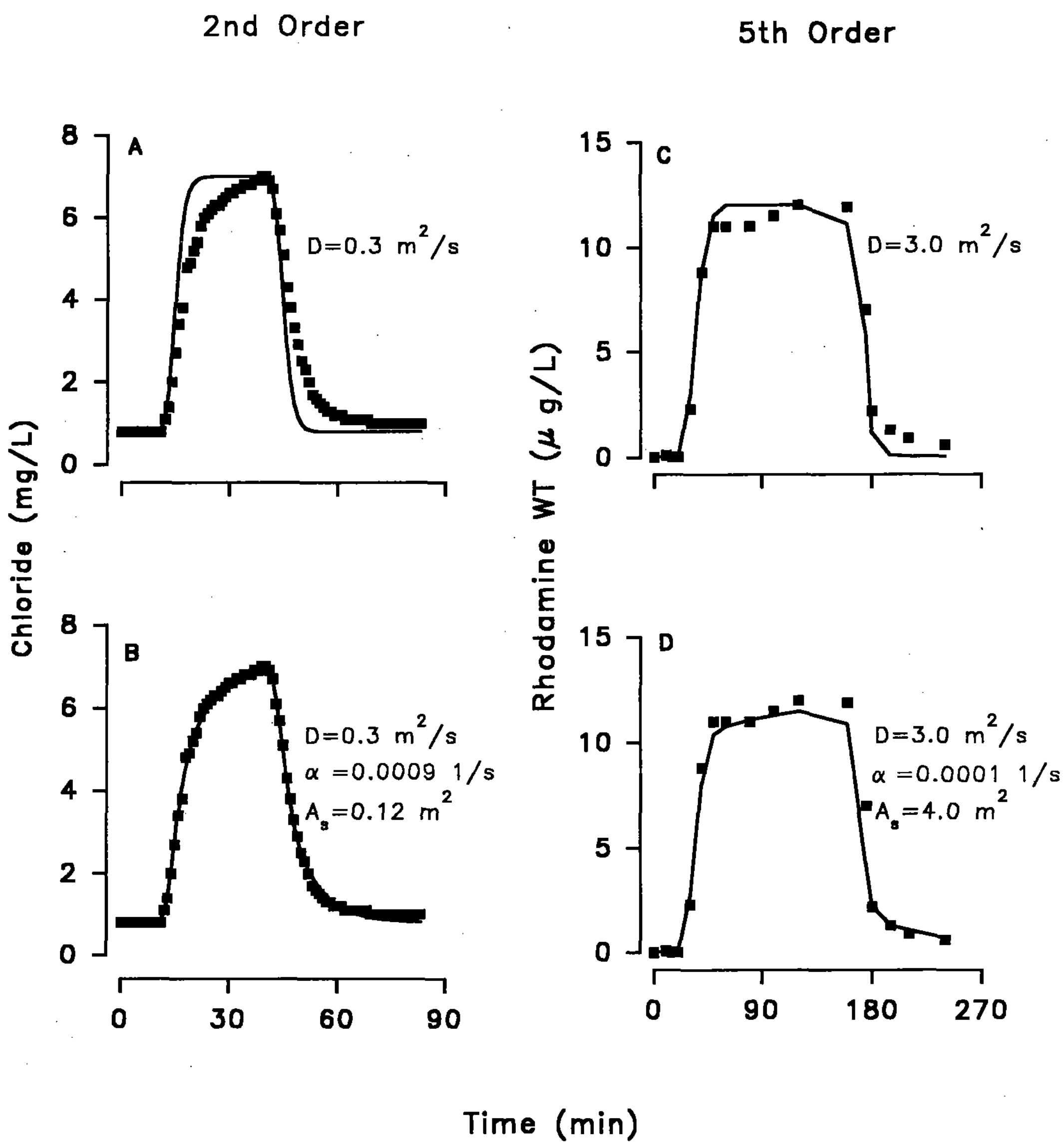

FIG. 5. A.—Model simulation (line) without transient storage compared with chloride data (squares) for a 2nd-order site on Ball Creek at the Coweeta Hydrologic Laboratory, July 1991. B.—Model fit to the data in (A) when transient storage is included. C.—Model simulation without transient storage compared with rhodamine WT data for a 5th-order stream at the H. J. Andrews Forest, September 1987. D.—Model fit to the data in (C) when transient storage is included. Symbols as in Figure 2.

water zones as well as a large and porous hyporheic zone produced relatively large amounts of transient storage (i.e., A_s/A was greatest in the 1st-order streams examined). A large A_s/A reflects a high potential for temporary storage of materials during downstream transport, resulting in a longer residence time for solutes and providing a hydrologic contribution to total stream retention. Of additional importance is that these regions of reduced water velocity may be biological "hot-spots": locations where longer residence times allow reactive solutes greater contact with sediments and time for physical, biological, and chemical interactions (Jackman et al. 1984, Cerling et al. 1990, Castro and Hornberger 1991). Facilitation of biotic and

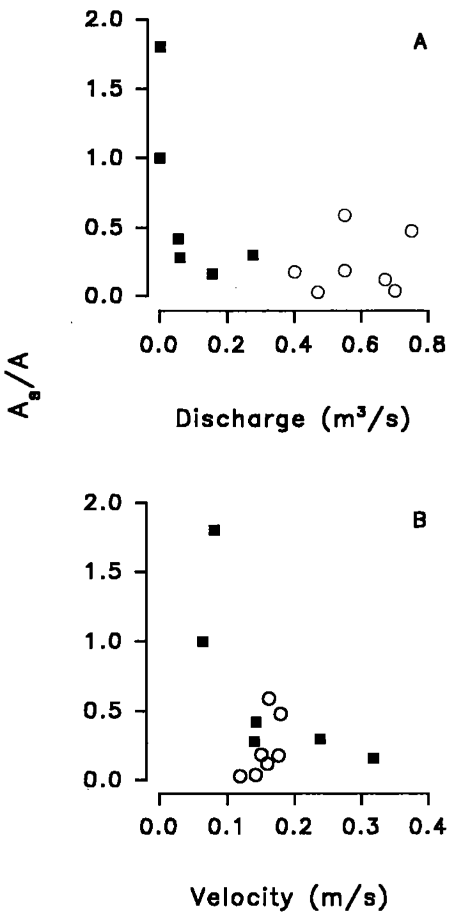

FIG. 6. A.—Relationship between A_s/A and discharge ($r = -0.82$, $p < 0.0005$, $n = 13$). B.—Relationship between A_s/A and velocity ($r = -0.55$, $p < 0.035$, $n = 15$) for 1st- through 4th-order sites (filled squares) and 5th-order sites (open circles).

abiotic interactions by longer residence time means that small increases in transient storage may translate into large impacts on overall retention of reactive solutes.

In our study, the ratio of transient storage to stream cross-sectional area (A_s/A) decreased downstream, concurrent with increases in velocity and discharge. We suggest two possible explanations for this pattern. First, decreases in in-stream channel complexity (e.g., substrate size and composition, amount of boulders and woody debris) between the headwaters and downstream reaches may result in a decrease in A_s/A by eliminating transient storage zones that would have formed behind these obstructions. Second, transient storage zones may be incorporated into the main current under higher flow conditions, while functioning more independently at low flows. We did not have sufficient data to examine a single site over a range of flow conditions or to evaluate storage zone response to flow. Comparisons of transient stor-

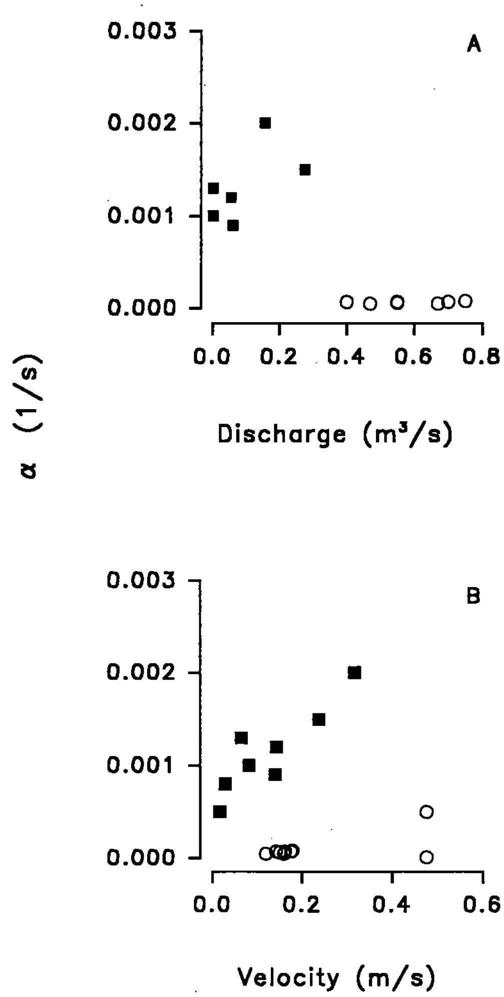

FIG. 7. A.—Correlation between exchange coefficient (α) and discharge for all 1st- through 5th-order sites. Overall r was -0.42 ($p < 0.05$, $n = 13$). Alpha and Q were not correlated for 1st- through 4th-order Coweeta sites (filled squares) or 5th-order H. J. Andrews sites (open circles) when evaluated separately. B.—Correlation between the exchange coefficient (α) and velocity was not significant for 1st- through 5th-order sites overall, or for 5th-order sites (open circles) evaluated separately. The correlation was significant ($r = 0.82$, $p < 0.04$, $n = 8$) for 1st- through 4th-order Coweeta sites (filled squares).

age zone size during storms and over an annual hydrologic regime will provide useful information on availability of flow refugia for biota, storage areas for nutrients limiting to periphyton, and degree of hyporheic and surface water interaction.

In contrast to A_s/A, the rate of exchange (α, 1/s) between the main surface water and the storage zone increased as discharge and velocity increased within a given range of stream orders (1st- through 4th-order, 5th-order groups). A positive relationship between flow and exchange may be a result of increased availability of solute per unit time and flushing of exchange sites at higher flows, as has been observed in algal kinetics studies (Whitford and Schumacher 1964, McIntire 1966).

Lateral inflows occur as subsurface water moves into the main channel. Quantification of lateral inflow, combined with dispersion and transient storage parameters, provides insight into the degree to which the stream may function multidimensionally (longitudinally, laterally, vertically, and temporally, sensu Ward and Stanford 1989). Lateral inflow as a percentage of total discharge per metre (Q_L/Q) was greater (1.9%/m) at 1st-order sites than at 5th-order sites (0.05%/m) (Fig. 8B). Therefore, even though lateral inflow (Q_L) was greatest in large streams (Fig. 8A), it may well be more important in small streams, especially during low flows when lateral inflow may provide temperature refugia and nutrient sources (H. Li, Oregon State University, personal communication). During winter months, Q_L was 0.0 at the 5th-order sites (n = 2). Extremely low to non-existent lateral inflows during winter releases may indicate a decoupling of main channel waters from lateral regions or a reversal of flow patterns, with main channel water entering lateral regions. Lateral inflow into the channel is estimated from dilution of the solute pulse, but this technique cannot identify when there is flow from the main channel to lateral areas.

Comparisons of parameters for 5th-order sites in the Cascade Mountains (H. J. Andrews Forest) did not follow expected downstream patterns obtained from 1st- through 4th-order sites in the Appalachians (Coweeta) for all variables. For example, velocities at the 5th-order sites were similar to those of 1st- through 4th-order sites, whereas discharge was double and dispersion was an order of magnitude greater at

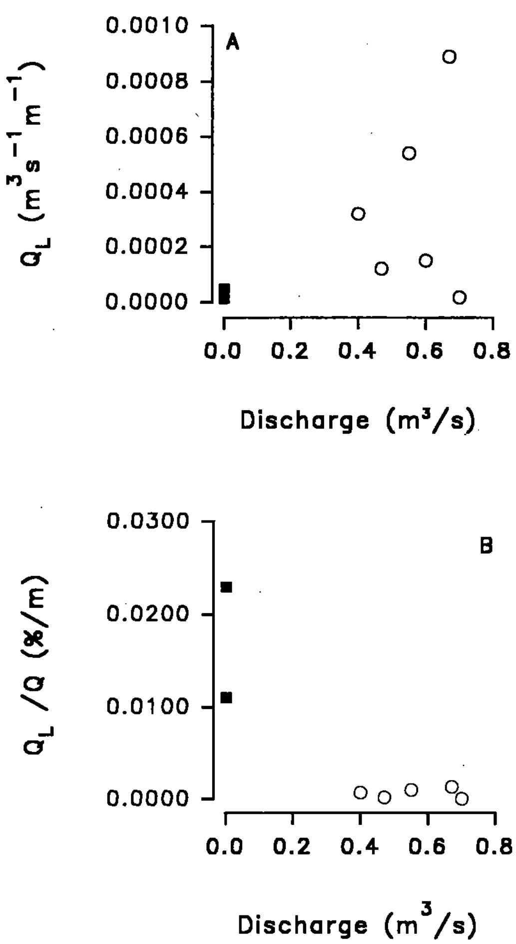

FIG. 8. A.—Relationship between Q_L and discharge for 1st-order Coweeta sites (filled squares) and 5th-order H. J. Andrews sites (open circles). B.—Relationship between Q_L/Q and discharge (symbols as in A).

5th-order sites than at the 4th-order sites. A_s/A followed the expected downstream decline, but α, rather than increasing, was sometimes more than an order of magnitude lower than the Coweeta sites (Figs. 7A, B). The apparent discontinuity of downstream trends from Coweeta sites and 5th-order H. J. Andrews Forest sites could be a result of geomorphic differences between the two stream systems (e.g., constrainment, geology, gradient) or could reflect a hydraulic transition zone, where decreases in slope and/or changes in channel dimensions (e.g., wetted perimeter and depth) reduce the exchange rate.

Comparisons of constrained and unconstrained 5th-order stream reaches revealed little difference between most parameters. In marked contrast are values for A_s and A_s/A, which were considerably higher in the unconstrained reaches and more closely approximated values for headwater streams. The prevalence of transient storage zones in unconstrained reaches supports predictions that these sections of stream may contain important refuge sites (i.e., slow water areas where organisms may avoid harsher conditions of main flow paths) required for organisms to survive spates or other disturbances (Sedell et al. 1990).

Our evaluation of conservative solute dynamics in artificial streams and streams from the Appalachian and Cascade mountains revealed patterns and some interesting discontinuities. Artificial streams had the lowest values for dispersion, storage, and exchange parameters because of their simple instream complexity consisting of gravel, leaves, and lack of a hyporheic zone. In natural streams, most parameters (u, Q, Q_L, D, A, A_s, and α) increased in magnitude from 1st-order through 4th-order. This increase continued through 5th-order streams for all parameters except α, which exhibited an order of magnitude discontinuity between 4th- and 5th-order sites (notably from different locations, Appalachian and Cascade mountains). In contrast, lateral inflow and subsurface area were greatest in 1st-order streams when examined relative to stream discharge (i.e., Q_L/Q) and cross-sectional area (i.e., A_s/A).

We suggest that parameters obtained from conservative solute releases provide information about stream hydraulics and reveal trends that are essential for comparison of solute dynamics in streams of different sizes, from different biomes, without requiring impractical microscale physical measurements. In this study, our evaluation revealed: 1) greater transient storage zone size, exchange rate, and lateral inflows in the headwater streams on a per metre basis; 2) a greater total lateral inflow (Q_L) at downstream sites; and 3) that 5th-order unconstrained stream reaches have storage parameters that more closely resemble upstream sites than 5th-order constrained sites. Studies of this type, which relate stream hydraulics to transport processes, and future studies relating catchment land use to hydraulics and transport will allow us to effectively link catchment and nutrient dynamics with stream hydrology and nutrient processes. An understanding of this linkage is critical if we are to evaluate the impacts of changes in stream, riparian, and catchment management practices on transport and transformation of solutes in physically diverse systems.

Acknowledgements

We would like to thank all those at the Coweeta Hydrologic Laboratory who provided assistance, especially Jim Deal and Kitty Reynolds. Dan Gallagher (Civil Engineering Department, Virginia Polytechnic Institute and State University) and John Mussen provided assistance with preliminary model equations. Gary Lamberti, Linda Ashkenas, and Randy Wildman conducted nutrient releases at the H. J. Andrews site. We would also like to thank Ken Bencala, United States Geological Survey, for his advice concerning model equations, and Fred Benfield, John Hutchens, and Jennifer Tank for critiques of the manuscript. This research was supported by a National Science Foundation doctoral dissertation grant (to DJD), and by NSF grants BSR 9011661 and BSR 9011663.

Literature Cited

APHA. 1985. Standard methods for the examination of water and wastewater. 16th edition. A. E. Greenberg, R. R. Trussell, and L. S. Clesceri (editors). American Public Health Association. Washington, D.C.

BENCALA, K. E. 1983. Simulation of solute transport in a mountain pool-and-riffle stream with a kinetic mass transfer model for sorption. Water Resources Research 19:732–738.

BENCALA, K. E., AND R. A. WALTERS. 1983. Simulation of solute transport in a mountain pool-and-riffle stream: a transient storage model. Water Resources Research 19:718–724.

CASTRO, N. M., AND G. M. HORNBERGER. 1991. Surface-subsurface water interactions in an alluviated mountain stream channel. Water Resources Research 27:1613–1621.

CERLING, T. E., S. J. MORRISON, R. W. SOBOCINSKI, AND I. L. LARSEN. 1990. Sediment-water interaction in a small stream: adsorption of ^{137}Cs by bed load sediment. Water Resources Research 26:1165–1176.

D'ANGELO, D. J., AND J. R. WEBSTER. 1991. Phosphorus retention in streams draining pine and hardwood catchments in the southern Appalachian Mountains. Freshwater Biology 26:335–345.

D'ANGELO, D. J., J. R. WEBSTER, AND E. F. BENFIELD. 1991. Mechanisms of stream phosphorus retention: an experimental study. Journal of the North American Benthological Society 10:225–237.

ELWOOD, J. W., J. D. NEWBOLD, R. V. O'NEILL, R. W. STARK, AND P. T. SINGLEY. 1981. The role of microbes associated with organic and inorganic substrates in phosphorus spiralling in a woodland stream. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 21:850–856.

ELWOOD, J. W., J. D. NEWBOLD, R. V. O'NEILL, AND W. VAN WINKLE. 1983. Resource spiralling: an operational paradigm for analyzing lotic ecosystems. Pages 3–37 *in* T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

FISCHER, H. B., E. J. LIST, R. C. Y. KOH, J. IMBERGER, AND N. H. BROOKS. 1979. Mixing in inland and coastal waters. Academic Press, New York.

HART, B. T., P. FREEMAN, I. D. MCKELVIE, S. PEARSE, AND D. G. ROSS. 1990. Phosphorus spiralling in Myrtle Creek, Victoria, Australia. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 24:2065–2070.

HART, B. T., P. FREEMAN, AND I. D. MCKELVIE. 1992. Whole-stream phosphorus release studies: variation in uptake length with initial phosphorus concentration. Hydrobiologia 235/236:573–584.

JACKMAN, A. P., R. A. WALTERS, AND V. C. KENNEDY. 1984. Transport and concentration controls for chloride, strontium, potassium and lead in Uvas Creek, a small cobble-bed stream in Santa Clara County, California, U.S.A. 2. Mathematical modeling. Journal of Hydrology 75:117–141.

LAMBERTI, G. A., S. V. GREGORY, L. R. ASHKENAS, R. C. WILDMAN, AND A. D. STEINMAN. 1989. Influence of channel geomorphology on retention of dissolved and particulate matter in a Cascade Mountain stream. Proceedings of the California Riparian Systems Conference. USDA Forest Service General Technical Report PSW-110.

MEYER, J. L., W. H. MCDOWELL, T. L. BOTT, J. W. ELWOOD, C. ISHIZAKI, J. M. MELACK, B. L. PECKARSKY, B. J. PETERSON, AND P. A. RUBLEE. 1988. Elemental dynamics in streams. Journal of the North American Benthological Society 7:410–432.

MCINTIRE, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiologia 27:559–570.

MULHOLLAND, P. J., J. D. NEWBOLD, J. W. ELWOOD, L. A. FERREN, AND J. R. WEBSTER. 1985. Phosphorus spiralling in a woodland stream: seasonal variations. Ecology 66:1012–1023.

MULHOLLAND, P. J., A. D. STEINMAN, AND J. W. ELWOOD. 1990. Measurement of phosphorus uptake lengths in streams: comparison of radiotracer and stable PO_4 releases. Canadian Journal of Fisheries and Aquatic Sciences 47:2351–2357.

MUNN, N. L., AND J. L. MEYER. 1990. Habitat-specific solute retention in two small streams: an intersite comparison. Ecology 71:2069–2082.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VAN WINKLE. 1981. Measuring nutrient spiralling in streams. Canadian Journal of Fisheries and Aquatic Sciences 38:860–863.

SEDELL, J. R., G. H. REEVES, F. R. HAUER, J. A. STANFORD, AND C. P. HAWKINS. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711–724.

STREAM SOLUTE WORKSHOP. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. Journal of the North American Benthological Society 9:95–119.

THOMANN, R. V., AND J. A. MUELLER. 1987. Principles of water quality modeling and control. Harper and Row Publishers, New York.

TRISKA, F. J., V. C. KENNEDY, R. J. AVANZINO, G. W. ZELLWEGER, AND K. E. BENCALA. 1989. Retention and transport of nutrients in a third-order stream: channel processes. Ecology 70:1877–1892.

WARD, J. V., AND J. A. STANFORD. 1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology. Pages 56–64 *in* D. P. Dodge (editor). Proceedings of the international large river symposium. Canadian Special Publication on Fisheries and Aquatic Sciences 106.

WHITFORD, L. A., AND G. J. SCHUMACHER. 1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. Ecology 45:168–170.

Received: 23 July 1992
Accepted: 20 April 1993