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Controls on patterns of coarse organic particle retention in headwater streams

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Abstract. Organic matter retention is an integral ecosystem process affecting C and nutrient dynamics and biota in streams. Influences of discharge (Q), reach-scale channel form, and riparian vegetation on coarse particulate organic matter (CPOM) retention were analyzed in 2 headwater streams in northeastern Oregon. *Ginkgo biloba* leaves were released in coniferous forest reaches and downstream floodplain meadow reaches during spring high flow and summer baseflow. Transitional reaches were also analyzed during summer baseflow. Paper strips, simulating sedge blade retention, were released in meadow reaches during high flow. Mean transport distances (S_p) were calculated as the inverse of the longitudinal loss rate (k) of leaves in transport. The metrics S_p, width-specific discharge (Q_w = Q/stream width), and the mass transfer coefficient ($v_{dep} = Q_w/S_p$) were used to investigate retention. Values of S_p (0.9–97 m) were 2 to 11 times longer during high flow than baseflow. Mean S_p in forest reaches (29.3 m) was significantly shorter than in meadow reaches (68.9 m) during high flow but not during baseflow. Standardizing k for the scaling effects of Q by analyzing the relationship between Q_w and S_p, in which the slope equaled the inverse of mean v_{dep} of all *Ginkgo* releases, indicated times when v_{dep} was higher or lower than predicted by Q. Values of S_p were driven largely by Q, yet most experiments in which values of v_{dep} exceeded those predicted by Q_w occurred during high flow. Values of v_{dep} (0.3–32 mm/s) across experiments were generally inversely related to S_p but did not differ between forest and meadow reaches during high flow. Unlike meadow reaches, mean v_{dep} in forest reaches was higher during high flow (5.2 mm/s) than baseflow (1.1 mm/s). Values of v_{dep} were positively related to large wood volume and negatively related to the extent of floodplain inundation during high flow. Yet, in the meadow reach that had lower relative channel constraint, paper strips were transported farther onto the floodplain as Q rose, resulting in long-term (~1.5 mo) retention. Despite downstream increases in Q, there were no differences in mean baseflow S_p or v_{dep} among reaches in either stream, indicating some longitudinal compensation in retention. Alternating associations between retention metrics and structural elements of the stream channels between flow periods suggests dynamic reach-scale hydrologic-retention thresholds in response to changes in Q. Analysis of v_{dep} across experiments indicated that channel morphology, stream wood, and riparian vegetation are major controls on CPOM retention.

Key words: coarse particulate organic matter (CPOM), retention, stream ecology, seasonal flooding, spatial variability, meadows, forests.

Headwater streams in montane landscapes retain much of the detrital organic matter entering from adjacent riparian forests (Minshall et al. 1983, Speaker et al. 1984, Webster et al. 1994). Coarse particulate organic matter (CPOM: >1 mm) is often an important source of C and nutrients in small, forested streams (Cummins 1974, Hall et al. 2000) but efficient biological utilization largely depends on its deposition and storage in the channel (Lamberti and Gregory 1996). The fate of CPOM is ultimately controlled by 2 concurrent factors: breakdown and downstream transport (Webster et al. 1999). The ratio of retentive elements to stream discharge (Q) is generally high in small streams. These retentive elements include features of channel morphology (Speaker et al. 1984), wood accumulations (Bilby and Likens 1980), and riparian vegetation (Speaker et al. 1988). Efficient retention largely explains why CPOM is generally a small component of organic matter (OM) export from headwater catchments compared to fine particulate (FPOM) and dissolved OM forms (Bormann et al. 1969, Fisher and Likens 1973, Minshall et al. 1983, Wallace et al. 1995).

Retention can be quantified by releasing particles and expressing retention as % of particles in transport at a given distance downstream (Young et al. 1978, Speaker et al. 1984). The

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mean transport distance (S_p) of CPOM is analogous to the uptake length of a nutrient (Newbold et al. 1981). However, CPOM retention is largely physical, determined by the frequency and capture efficiency of retentive structures (Speaker et al. 1984, Webster et al. 1987), whereas nutrient retention in most streams has a strong biological influence (Newbold et al. 1982, Peterson et al. 2001). Studies of CPOM transport have focused on quantification of S_p (m), the longitudinal dimension of particle transport. Leaf-release experiments conducted globally in a wide variety of small forested streams found that S_ps of leaves are quite short, generally ranging from <10 to 200 m (Young et al. 1978, Speaker et al. 1984, Prochazka et al. 1991, Wallace et al. 1995, Ehrman and Lamberti 1992, Webster et al. 1994, Raikow et al. 1995). Releases of dowels to estimate small wood retention typically yield even shorter S_ps than leaves (Jones and Smock 1991, Webster et al. 1994, Wallace et al. 1995).

Most CPOM export in small streams occurs during periods of high Q (Fisher and Likens 1973, Webster et al. 1987, Wallace et al. 1995). Therefore, estimating transport dynamics during high flow can be critical to understanding long-term flux and retention of CPOM. Numerous studies have reported longer S_ps of CPOM during high flow (Speaker 1985, Webster et al. 1987, Jones and Smock 1991, Snaddon et al. 1992, Scarsbrook and Townsend 1994, Wallace et al. 1995), although some studies have also indicated increased retention by riparian vegetation (Speaker et al. 1988) and deposition on floodplains (Cuffney 1988, Jones and Smock 1991) during seasonal flooding. Clearly, the influence of channel morphology and vegetative structure (e.g., presence or absence of woody vegetation) on CPOM retention during high flows remains poorly understood.

Recent advances in the analysis of FPOM transport dynamics have highlighted the value of the transport parameter, deposition velocity (v_{dep}), in understanding POM retention in streams (Cushing et al. 1993, Minshall et al. 2000, Thomas et al. 2001). Deposition velocity (mm/s) is calculated by dividing the product of mean depth times velocity by S_p. Deposition velocity permits scale-independent investigation of retention by correcting for the increased probability of longer S_ps from increases in velocity and depth (Thomas et al. 2001). FPOM v_{dep} represents the vertical velocity at which a particle moves from the water column to the channel bottom. For CPOM, however, retention is primarily the probability of a particle being intercepted by objects (Speaker et al. 1984) and is not greatly influenced by sinking velocity over the range of velocities typically observed (Webster et al. 1999). Thus, for CPOM, v_{dep} more accurately represents the mass transfer coefficient, perpendicular to longitudinal flow, of particle collision and trapping by objects (e.g., wood and rocks).

Streams can be conceptualized as mosaics of different reach types and valley segments, with distinct fluvial and geomorphic processes and riparian vegetation (Pringle et al. 1988, Swanson et al. 1988, Gregory et al. 1991, Townsend 1996, Montgomery 1999). Most studies of CPOM retention have focused on the scale of channel units (e.g., riffles and pools) or retention structures (e.g., debris dams) rather than reach-scale longitudinal variation under varying flow conditions. For example, little is known about CPOM retention in streams with natural nonforested riparian zones such as meadows and grasslands or in streams draining mosaics of forest and grassland vegetation. Previous studies in grassland streams have suggested that dominant mechanisms of CPOM retention likely differ from forested streams because of differences in channel characteristics, flow dynamics, and a lack of large wood (Scarsbrook and Townsend 1994, Gurtz et al. 1988).

In our study, spatial and temporal patterns of CPOM retention were examined in 2 spring-snowmelt, headwater streams in northeastern Oregon. Large differences were previously found in these streams in CPOM inputs, transport, and storage between coniferous forest reaches and downstream floodplain meadows (Brookshire 2001). In our study, CPOM retention was quantified in forest, meadow, and transitional reaches of both streams, and differences in retention between high flow and baseflow were quantified using the metrics S_p, v_{dep}, and Q_w (Q/stream width). Controls on retention across reaches and under different flows were assessed by testing whether significant associations existed between S_p and v_{dep} and various channel characteristics of the streams. It was hypothesized that channel retention would be higher in forest than meadow reaches, and that the interaction among hydrology (Q, depth, ve-

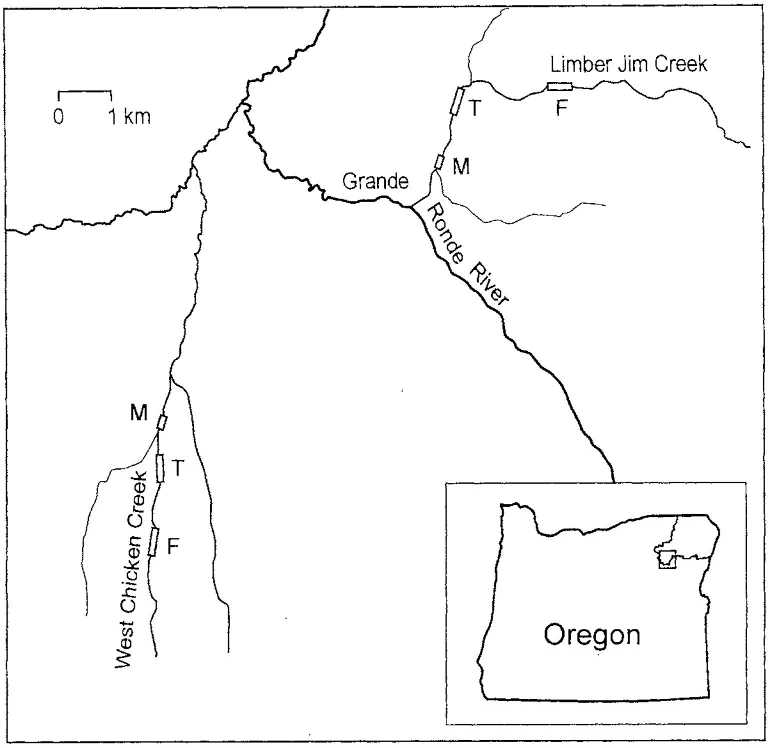

FIG. 1. Study area showing forest (F), transition (T), and meadow (M) study reaches of West Chicken Creek and Limber Jim Creek. Rectangles on each stream represent study reaches. The outlined area within the inset, extending from the focal study area (square), represents the Grande Ronde River Basin.

locity), channel form (width, relative channel constraint, channel structural elements), and reach-scale riparian characteristics (e.g., woody vegetation) would control retention rates among reaches.

Methods

Study sites

Experimental releases were conducted in 3 riparian reach types (forest, transition, and meadow) in West Chicken Creek (lat 45°3′17″N, long 118°24′11″W) and Limber Jim Creek (lat 45°06′15″N, long 118°19′41″W), both 2nd-order tributaries to the Upper Grande Ronde River in the Blue Mountains of northeastern Oregon (Fig. 1). Mean annual precipitation is 540 mm, which mostly occurs as snowfall from November to May (US Forest Service [USFS], PNW Research Station, La Grande, Oregon). Spring snowmelt characterizes the hydrographs with peak annual flow between April and June (USFS, La Grande). Limber Jim Creek has a larger drainage area, higher annual Q, and higher stream wood volumes than West Chicken Creek (Table 1).

Both streams flow through a geomorphically constrained section dominated by coniferous forest into an open, unconstrained meadow 1 to 3 km downstream. Three study reaches were selected along the longitudinal (forest-to-meadow) gradient in each stream: 1) a 500-m reach within the upstream forest; 2) a 500-m transition reach intermediate between forest and meadow; and 3) a 250-m reach in the downstream meadow section (Fig. 1). Meadow reaches were located within long-term livestock exclosures. In both streams, valley width increases and active channel:valley width ratio decreases downstream (Table 1). Stream channels are dominated by riffles (30–70%), but glides increase downstream. Pools account for 15 to 30% of channel area across all reaches. Dominant substrates are gravels and cobbles at all sites. In West Chicken Creek, a tributary entering downstream of the transition reach contributed ~30 to 40% of mainstem Q in the meadow reach

TABLE 1. Characteristics of the study reaches of West Chicken Creek and Limber Jim Creek.

	West Chicken Creek			Limber Jim Creek		
	Forest	Transition	Meadow	Forest	Transition	Meadow
Elevation (m)	1395	1361	1330	1396	1332	1311
Gradient (%)	3.2	3.0	1.8	3.8	2.0	1.8
Valley width (m)	49	55	97	36	56	77
Active channel width (m)	4.3	3.8	5.7	6.2	7.7	7.0
Baseflow stream width (m)	1.5	1.3	1.2	2.9	3.6	2.8
High-flow discharge (m^3/s)	0.32	0.32	0.42	1.45	1.98	1.98
Baseflow discharge (m^3/s)	0.007	0.007	0.010	0.06	0.10	0.10
Large wood ($m^3/100$ m)	2.9	3.8	0.9	12.1	6.2	5.7
Small wood ($m^3/100$ m)	0.1	0.04	0.01	0.06	0.03	0.02

throughout the year. Likewise, a tributary entering Limber Jim Creek upstream of the transition reach contributed ~5 to 36% of mainstem Q.

Overstory vegetation at the forest sites is dominated by several coniferous species, principally Engelmann spruce (*Picea engelmannii*). Mountain alder (*Alnus incana*) and currants (*Ribes* spp.) are common within the active channels of both streams and extend into the stream in many places (Case 1995). Large and small wood is abundant in the forested channels but decreases downstream (Table 1). Before our study, large wood had been placed within the channel of the meadow section of Limber Jim Creek by the USFS to improve fish habitat. Dominant vegetation in the meadow sites consists of graminoid plants (sedges [*Carex* spp.] and grasses), which often grow directly into the wetted channel. Canopy cover is low in the meadows with some scattered patches of conifers (primarily *Pinus contorta*). At Limber Jim Creek, alder and willow (*Salix* spp.) are also common. Riparian vegetation occurring in the transition reaches consists of a patchy conifer and alder overstory with an herbaceous, largely graminoid-dominated, understory. Although most work was concentrated in the forest and meadow reaches, transition reaches were used to evaluate patterns in baseflow retention along longitudinal gradients.

During high flow (May 1998), two 50-m (valley length) sites encompassing a wide range of channel features and variation in riparian vegetation were selected for experimental particle releases in each forest and meadow study reach. A total of 6 releases were conducted per stream (2 in each forest and 4 in each meadow). Stream lengths of high-flow sites ranged from 63 to 113 m depending on sinuosity. During summer baseflow (September 1998), three 50-m (stream length) sites were selected within each forest, transition, and meadow reach in each stream, for a total of 9 release sites per stream.

Leaf releases

Short-term CPOM retention was estimated by releasing batches of *Ginkgo biloba* leaves (n = 1000/release) into the study streams during spring high flow (rising limb of the hydrograph) and summer baseflow as a CPOM tracer in all study reaches. In the meadows, where most CPOM input consists of sedge leaf blades imported during spring high flow (Brookshire 2001), waterproof paper (Rite in the Rain®, J. L. Darling Corporation, Tacoma, Washington; Webster et al. 1994) cut into 1 × 28 cm strips (n = 770/release) was released during high flow. This material could be cut into the approximate shape of sedge blades, and the white color allowed easy detection within the channel.

Ginkgo leaves and paper strips were soaked in water for 12 h before release to impart neutral buoyancy (Speaker et al. 1984). During release, particles were distributed evenly across the width of the channel. Paper strips in the meadows were released shortly after *Ginkgo* leaves. Non-retained leaves were caught at the downstream end of the reach with a seine net staked to the channel bottom and stretched across the wetted width of the channel. During high flow, leaves were removed as necessary to avoid clogging. Nets were reinforced with fence posts pounded into the substrate. Leaves were collected and counted 2 to 3 h after release. Numbers of leaves were then visually estimated within 1-m increments downstream of the release point, noting the dominant retention feature for each leaf.

The meadow floodplains were searched for deposited strips in late June 1998, after high flow completely receded (42–45 d post-release). Lateral transport distance onto the floodplain was measured as the distance between the stream edge and the nearest edge of each deposited strip (perpendicular to flow). The spatial distribution of deposited strips was overlaid onto detailed maps of floodplain sections where most deposition occurred to illustrate patterns of floodplain retention.

Controls on retention

Large (>10 cm in diameter) and small (<10 cm) wood volumes were measured and numbers of debris dams were noted to quantify retention factors within reaches. Wood volumes occupying the active channel above or outside the baseflow wetted channel and within the wetted channel at baseflow were estimated (Lienkaemper and Swanson 1987). Accumulations of wood were considered debris dams if they spanned >½ the channel width. Approximately ½ of the debris dams in all reaches, including the wood installed by the USFS in Limber Jim Creek, spanned the entire channel width. Stream width, thalweg depth, and thalweg velocity were measured at regular intervals (1–3 m) in each site during high-flow and baseflow releases. Discharge was monitored at the downstream end of the meadow reach of both streams by the USFS during the study period with pressure transducers and stage–Q regressions. Velocity was measured in all reaches (Swoffer 2100 meter); Q in the forest reaches was calculated by multiplying velocity by cross-sectional area of flow. Width-specific discharge ($Q_w = m^2/s$) was calculated by dividing Q by mean stream width (Thomas et al. 2001). Relative channel constraint was defined hydrologically as the ratio of inundated floodplain width (high-flow width minus baseflow width) to total stream width during high flow. This value represents the proportion of high-flow stream width occurring outside the baseflow channel margins. Values were 0.66 and 0.41 in the forest reaches and 0.88 and 0.61 in the meadow reaches of West Chicken Creek and Limber Jim Creek, respectively.

Data analysis

The % of total released leaves caught in the net was fit to a negative exponential decay model (Young et al. 1978):

$$T_d = T_0 e^{-kd}$$

where T_d is the % of total released particles in transport at distance d (m) from the release point, T_0 is 100%, and k is the instantaneous retention rate. Turbidity during high flow greatly reduced our ability to positively identify leaves within the channel, so the calculation of slope (k) was based on 2 data points, T_0 and T_d (Lamberti and Gregory 1996). Variation in observed longitudinal leaf distribution explained by the model was then determined using linear regression, with modeled distribution as the explanatory variable. The mean transport distance (S_p) of particles is the inverse of the retention rate ($1/k$) (Young et al. 1978, Newbold et al. 1981). Deposition velocity (v_{dep}) was calculated by dividing Q by the product of mean stream width and S_p.

In 8 of 30 releases, all *Ginkgo* leaves were retained upstream of the net, so k was calculated by regressing the log-transformed % of leaves in transport (from visual surveys) against distance from the release site. Because visual inventories were less than the total number of leaves released, data were normalized to the % of leaves found (Speaker et al. 1984). Regressions for the 8 releases were significant (mean $r^2 = 0.76$, $p < 0.02$). To evaluate this 2nd approach, S_ps for the remaining 22 experiments were calculated using the regression technique and then compared with the results from the 2-point model using linear regression. This comparison indicated that the 2 methods produced very similar values of S_p (Observed S_p = 1.41 Model S_p − 5.23; $r^2 = 0.91$, $p < 0.0001$, $n = 22$). Values of S_p from the 2-point calculation were used for all analyses except the 8 releases for which the regression method was used because low detection rate of leaves during high flow (10–53%) resulted in potential bias in the estimation of their longitudinal distribution, and because we were more confident that we accounted for all leaves reaching the nets. Choice of method for calculating S_p did not affect the results of inferential analyses of spatial and seasonal retention patterns.

A 3-way analysis of variance (ANOVA) using stream, season (high flow versus baseflow), and

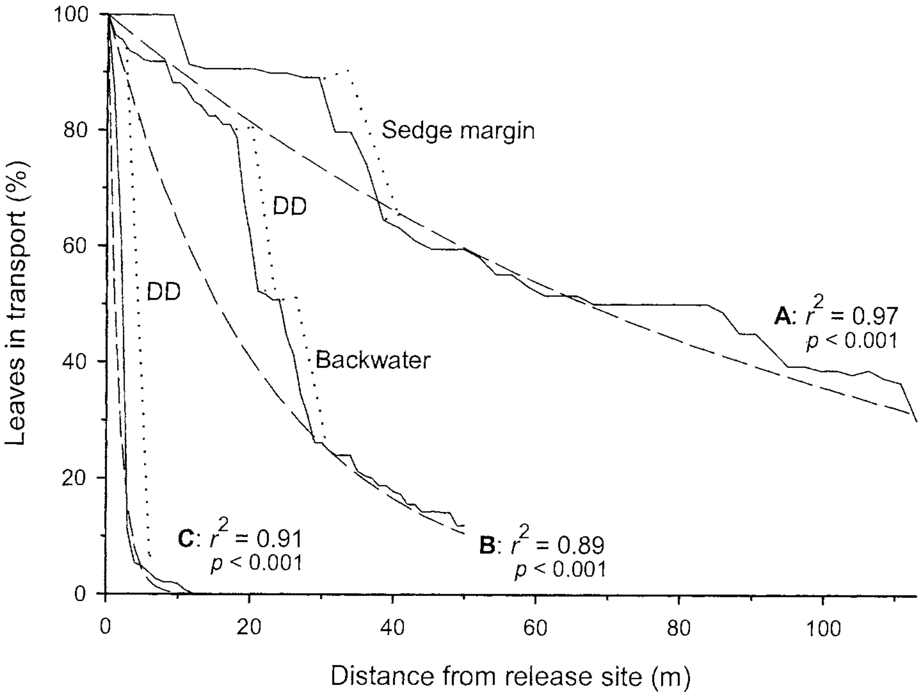

FIG. 2. Examples of model and regression (dashed lines) and observed (solid lines) retention curves for *Ginkgo* leaf releases conducted in the meadow reach of Limber Jim Creek during high flow (A), the forest reach of Limber Jim Creek during baseflow (B), and the transition reach of West Chicken Creek during baseflow (C). Included are the coefficients of determination for the associations between model and observed (A and B) and regression and observed (C) retention rates and major structural features (dotted lines) capturing most leaves in transport (DD = debris dams).

reach type (forest, transition, meadow) was used to test for differences ($p < 0.05$) in mean S_p and v_{dep} (i.e., the average S_p and v_{dep} of multiple releases) among releases (Ramsey and Schafer 1997). Post-hoc comparisons between reaches and seasons were conducted using Tukey's Honest Significant Difference (HSD) tests and t-tests. Transport distances and v_{dep} values were linearly regressed against hydrological and structural variables to assess reach-scale retention mechanisms.

Results

There was considerable variation in retention rates of *Ginkgo* leaves among releases and between streams: values of S_p ranged from 0.9 m to 97 m (k = 0.01–1.1) and values of v_{dep} ranged from 0.3 mm/s to 8.1 mm/s. Observed patterns of leaf retention (Fig. 2) conformed well to the negative exponential model with a mean r^2 (±1 SE) of 0.82 ± 0.03 across all regressions (n = 22). As observed previously (e.g., Speaker et al. 1984), intrareach variation was often substantial and largely related to the presence of retention structures (e.g., debris dams) and channel units that captured most leaves in transport (Fig. 2).

Reach-scale retention patterns

There were significant differences in mean S_p of *Ginkgo* leaves between streams, high flow and baseflow, and among reach types. There was also a significant interaction effect between reach and seasonal Q ($F_{8,17}$ = 12.72, $p < 0.0001$; Table 2). During high flow, mean S_p of *Ginkgo* leaves was >2 times longer (p = 0.019) in meadows (49–97 m; mean ± 1 SE = 68.9 ± 11.3 m) than in forests (21–38 m; 29.3 ± 4.5 m) of both streams (Table 3). Transport distances during high flow in forest reaches were significantly (p = 0.049) longer in Limber Jim Creek than in West Chicken Creek but did not differ (p = 0.204) between the 2 meadow reaches (Table 3).

TABLE 2. Results of 3-way ANOVA examining differences in transport distance (S_p) and deposition velocity (v_{dep}) of *Ginkgo* leaves between streams (West Chicken Creek and Limber Jim Creek), seasonal flow levels (spring high flow versus late-summer baseflow), and reach types (forest, transition, and meadow).

Variable	Source	df	F	p
S_p	Stream	1	15.09	0.0012
	Reach	2	13.17	0.0004
	Season	1	48.28	<0.0001
	Stream × Reach	2	0.01	0.9869
	Stream × Season	1	0.4	0.5368
	Reach × Season	1	11.6	0.0034
v_{dep}	Stream	1	0.02	0.895
	Reach	2	0.99	0.3919
	Season	1	8.4	0.01
	Stream × Reach	2	1.7	0.2132
	Stream × Season	1	12.95	0.0022
	Reach × Season	1	3.95	0.0754

The mean S_p of *Ginkgo* leaves in meadow reaches was >2 times longer ($p = 0.021$) than the mean S_p of paper strips (10–42 m; 33.2 ± 7.8 m; Table 3).

Mean S_ps of leaves were 2 to 11 times shorter during baseflow than high flow across all reaches (Table 3). There were no significant differences ($p > 0.18$, Tukey's HSD) in mean S_p among forest, transition, and meadow reaches in either stream. Mean whole-stream baseflow S_p (across all reaches, $n = 9$) was >4 times longer ($p = 0.002$) in Limber Jim Creek (21.8 ± 3.2 m) than in West Chicken Creek (4.9 ± 1.5 m).

Despite large differences in mean S_p of *Ginkgo* leaves among releases, mean v_{dep} did not differ significantly between streams or reaches (Tables 2, 3). During high flow, mean v_{dep} was higher in forest (5.2 ± 1.1 mm/s) than meadow reaches (2.7 ± 1.3 mm/s) but the difference was not significant ($p = 0.11$). However, a near-significant reach × season interaction (Table 2) was consistent with mean v_{dep} in the forests being >4 times higher ($p = 0.002$) during high flow than baseflow (1.1 ± 0.2 mm/s; Table 3). In contrast, in the meadow reaches, there was no difference ($p = 0.59$) in mean v_{dep} between high flow and baseflow (1.6 ± 0.3). Similar to mean S_p, there were no significant differences ($p > 0.2$) in mean v_{dep} among forest, transition, and meadow reaches in either stream at baseflow.

The significant stream × season interaction in mean v_{dep} (Table 2) indicated stream-scale differences between seasons: v_{dep} was >2 times higher in Limber Jim Creek during high flow ($p = 0.012$) but did not differ from West Chicken Creek during baseflow ($p = 0.39$; Table 3). Mean v_{dep} of paper strips (1–32 mm/s; 10.5 ± 7.3 mm/s) was ~4 times higher than *Ginkgo* leaves but this difference was not significant ($p = 0.41$). In addition, mean high-flow v_{dep} of *Ginkgo* leaves and paper strips combined was much higher in the meadow reach of Limber Jim Creek (12.4 ± 6.6 mm/s) than in the meadow reach of West Chicken Creek (0.9 ± 0.1 mm/s) but this difference was also not significant ($p = 0.18$).

Hydrologic controls on retention

Thalweg depth, thalweg velocity, and Q explained much of the variation in S_p of *Ginkgo* leaves across all releases (Fig. 3A–C). Thalweg depth explained 76% of the variation in *Ginkgo* S_p across all experiments ($p < 0.001$, $n = 26$) but the relationship was stronger for high flow than baseflow (Fig. 3A). Regressions between S_p and thalweg velocity ($r^2 = 0.54$) and Q ($r^2 = 0.51$) were also highly significant ($p < 0.001$) across experiments, but were only significant for base-

TABLE 3. Mean (±1 SE) transport distance (S_p) and deposition velocity (v_{dep}) of *Ginkgo* leaves and paper strips for forest (FR), transition (TR), and meadow (MR) reaches of West Chicken Creek (WC) and Limber Jim Creek (LJ). MR_S = paper strip releases in the meadow reaches.

		High flow			Baseflow		
		FR	MR	MR_S	FR	TR	MR
WC	S_p (m)	21.7 (1.0)	63.4 (14.1)	41.9 (0.4)	7.0 (4.0)	2.1 (0.6)	5.7 (2.2)
	v_{dep} (mm/s)	3.6 (0.4)	0.7 (0.1)	1.0 (0.1)	1.1 (0.4)	3.2 (1.2)	1.7 (0.6)
LJ	S_p (m)	36.9 (1.4)	74.6 (22.5)	24.6 (14.6)	19.8 (1.3)	18.3 (6.7)	27.6 (7.6)
	v_{dep} (mm/s)	6.9 (1.3)	4.7 (1.4)	20.1 (11.9)	1.0 (0.1)	1.9 (0.6)	1.5 (0.4)

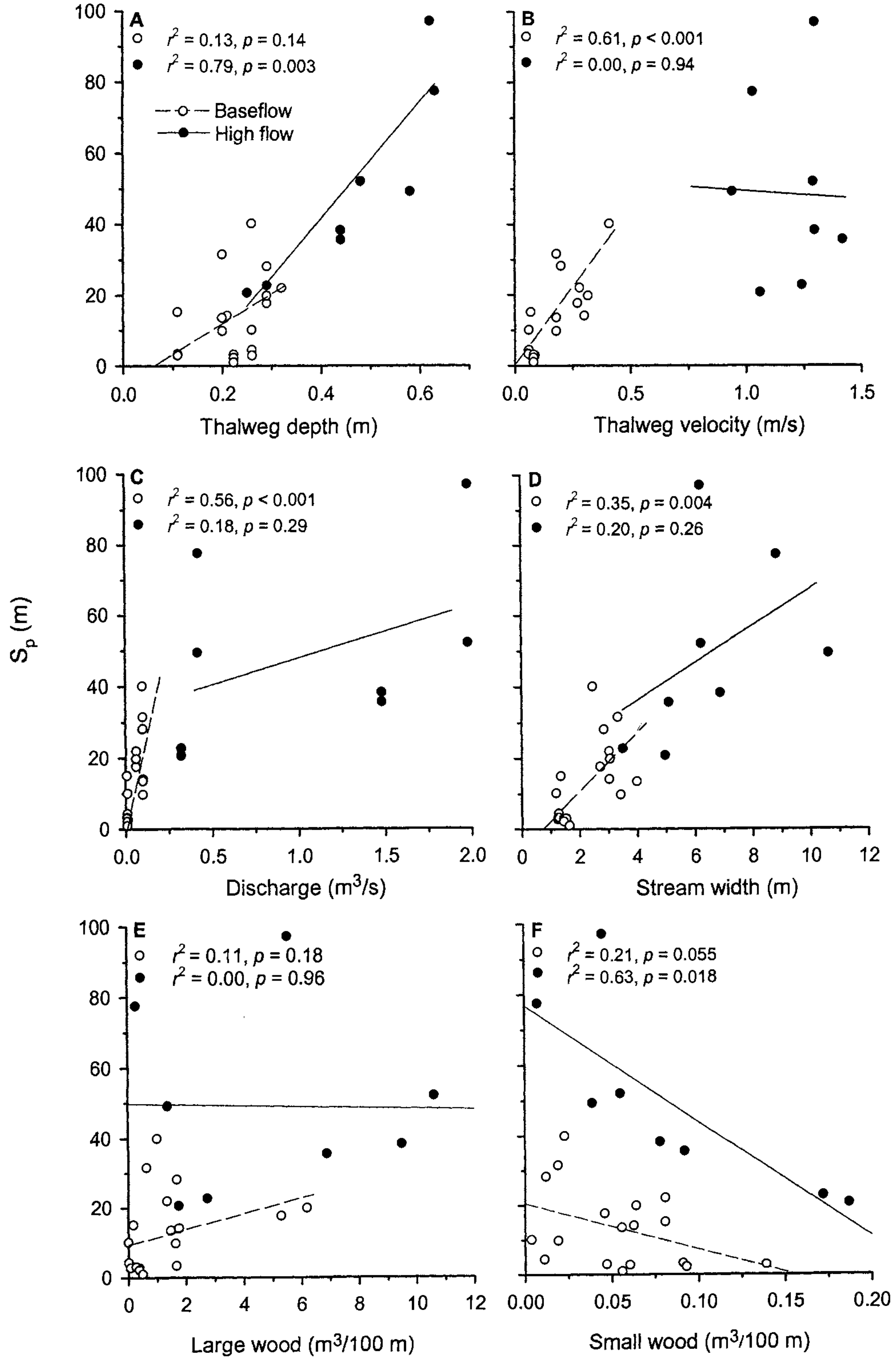

FIG. 3. Regressions of mean transport distances (S_p) of *Ginkgo* leaves against hydrological and structural variables for baseflow and high-flow experiments. A.—Thalweg depth. B.—Thalweg velocity. C.—Discharge. D.—Stream width. E.—Large wood. F.—Small wood.

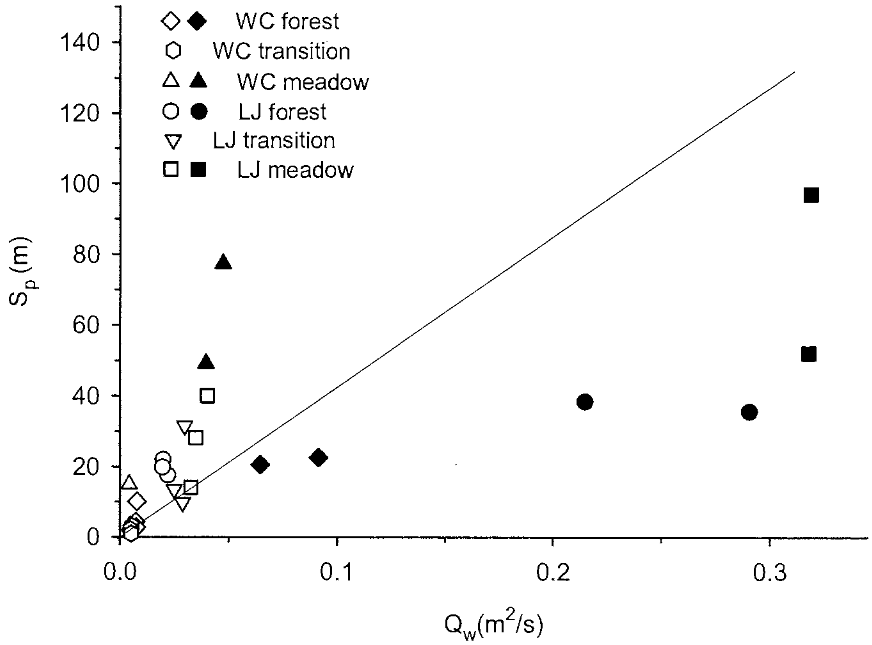

FIG. 4. Relationship between width-specific discharge ($Q_w = Q/W = m^2/s$, where Q = discharge and W = width) and mean transport distances (S_p) of *Ginkgo* leaves, illustrating variability in deposition velocity (v_{dep}). Solid symbols represent high flow and open symbols represent baseflow. WC = West Chicken Creek, LJ = Limber Jim Creek.

flow releases when separated by season (Fig. 3B, C).

Regressing S_p against Q_w improved the fit for baseflow releases ($r^2 = 0.68$, $p < 0.0001$) over that for Q. Q_w is directly related to v_{dep}, so deviation from the relationship between Q_w and S_p, in which the slope equals the inverse of mean v_{dep} for all *Ginkgo* releases (2.3 ± 0.4 mm/s), identified experiments in which S_p was either higher or lower than the mean predicted solely by Q_w over the range of conditions in all experiments (Fig. 4). Values above the line indicate experiments in which v_{dep} was driven primarily by hydrology, whereas values below the line indicate experiments in which v_{dep} was higher than expected if Q_w was the primary control of transport.

Channel form and riparian controls on retention

Deposition velocity was significantly associated with large wood volume during high flow but not baseflow (Fig. 5A), and was not associated with small wood during either period (Fig. 5B). Values of v_{dep} were also strongly associated with the floodplain inundation ratio of experimental reaches during high flow (Fig. 5C). In contrast, high-flow S_p was not associated with the floodplain inundation ratio ($r^2 = 0.019$, $p = 0.74$) but was associated with stream width across all *Ginkgo* releases ($r^2 = 0.62$, $p < 0.001$). However, this association was significant only for baseflow releases when separated by season (Fig. 3D). There was no relationship between large wood volume and S_p for high-flow or baseflow releases (Fig. 3E) but there were significant and near-significant associations between small wood volume and S_p for high-flow and baseflow releases, respectively (Fig. 3F).

There were distinct patterns among reaches in the % of leaf retention associated with various structures for the baseflow releases. Visual detection rates of leaves within the channel ranged from 14 to 79% (mean = 48.9 ± 4.2%). The % of leaves retained by streamside vegetation was significantly ($p < 0.05$) higher in transition and meadow reaches than in upstream forest reaches (Fig. 6A, B). Differences in riparian vegetation influenced retention through associated differences in wood abundance. Percent retention

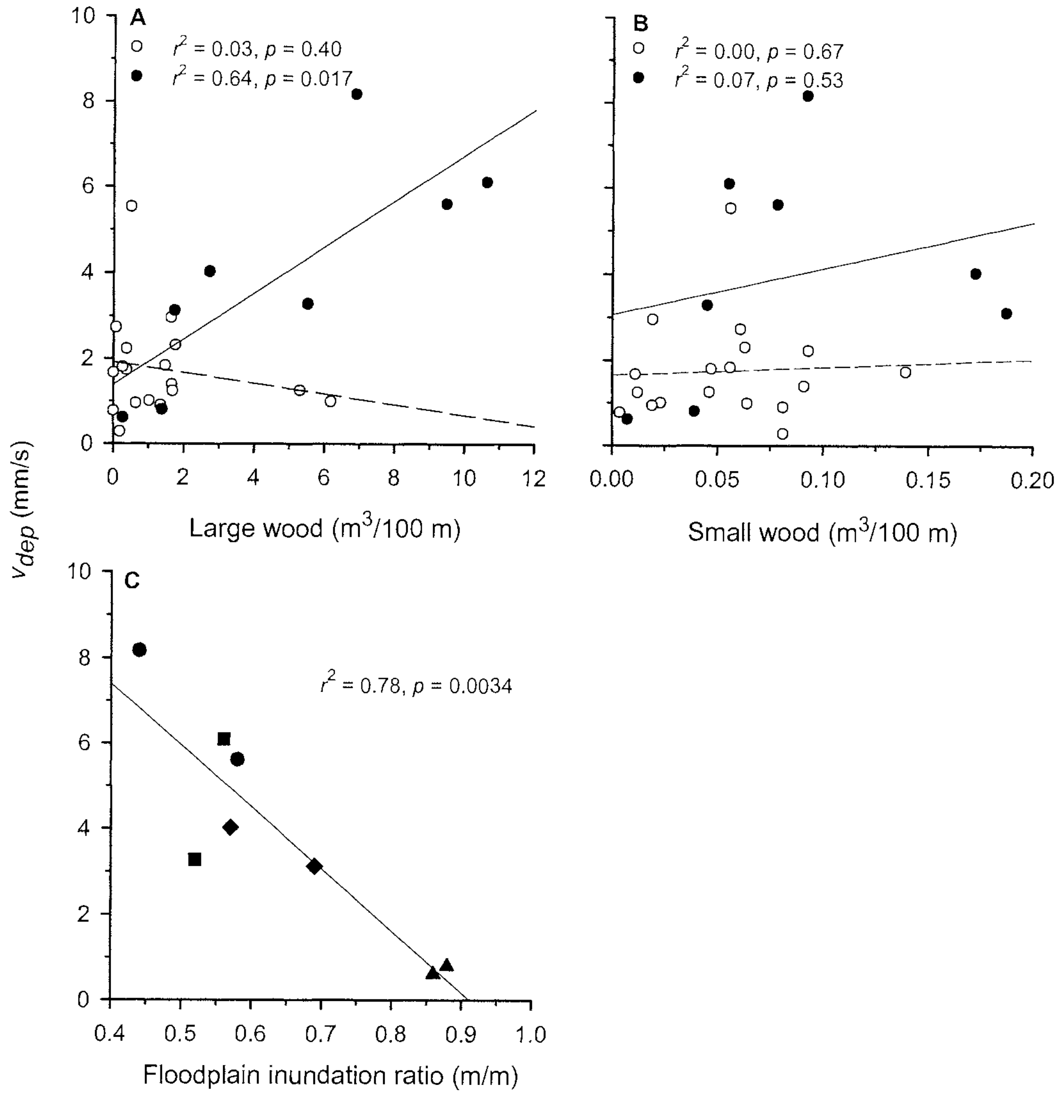

FIG. 5. Regressions of v_{dep} against wood volume and the floodplain inundation ratio. This ratio was calculated by dividing the difference between high-flow and baseflow stream width by high-flow stream width. Baseflow and high-flow symbols for panels A and B as in Fig. 3. Site symbols for panel C as in Fig. 4.

by small wood was significantly ($p < 0.05$) higher in forest reaches than in transition reaches. In West Chicken Creek, ~50% of retention in forest and transition reaches was associated with large and small wood. Wood, including debris dams, accounted for <10% of retention in the meadow reach of West Chicken Creek but ~55% of retention in the meadow reach of Limber Jim Creek where wood had been added. Retention by wood and rocks dominated in all reaches of Limber Jim Creek (Fig. 6B). Leaf retention within pools was minor at all sites.

Turbidity during high flow resulted in low detection of retained leaves (10–53%; mean = 27.8 ± 4.1). However, assuming that the relative proportions of effective retention sites remained constant regardless of detection ability, our results suggested that 33 to 54% of leaf retention in the forest reaches was associated with accumulations of wood and 30 to 62% was associ-

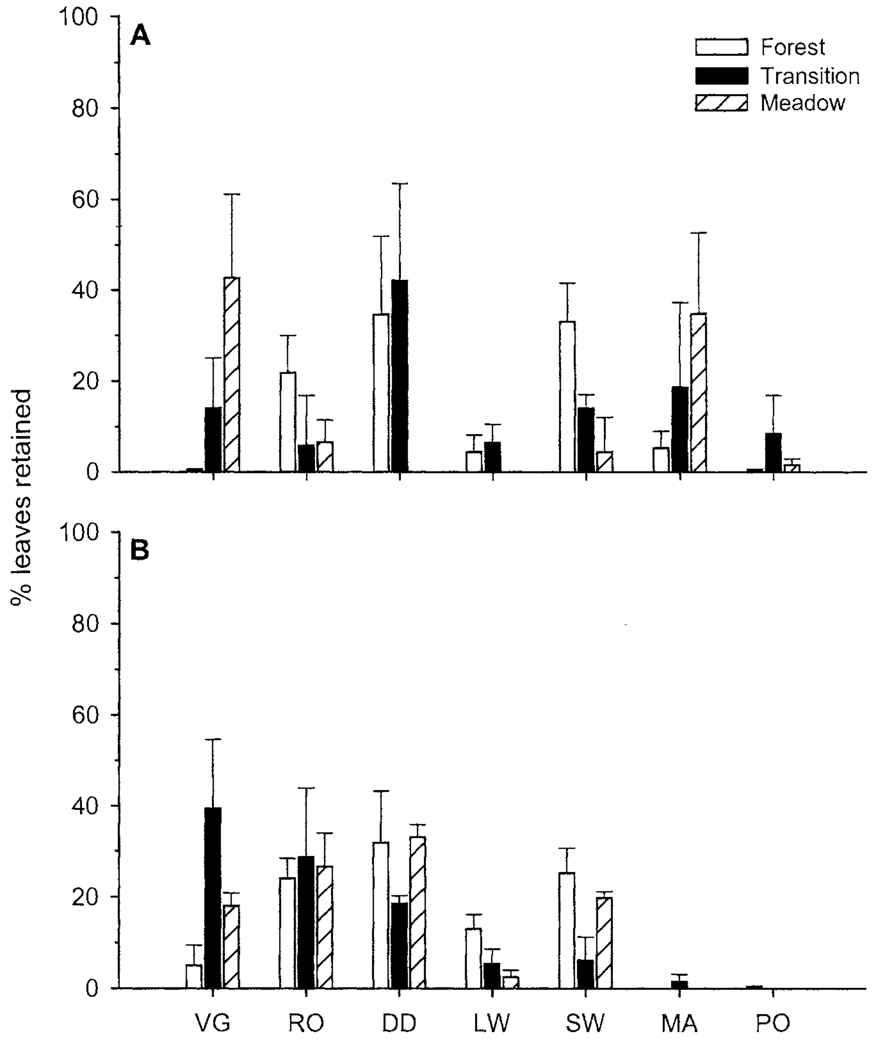

FIG. 6. Mean % (+1 SE) of *Ginkgo* leaves associated with various structures during baseflow in West Chicken Creek (A) and Limber Jim Creek (B). VG = streamside vegetation and associated slow water, RO = rocks, DD = debris dams, LW = large wood, SW = small wood, MA = macrophytes, and PO = pools.

ated with the stems of riparian shrubs (Fig. 7A, B). Mechanisms of retention were evenly divided among wood, shrub stems, and stream margins in the meadow reach of Limber Jim Creek (Fig. 7B), whereas streamside sedges accounted for most retention in the meadow reach of West Chicken Creek (Fig. 7A). Mechanisms of paper-strip retention in meadows were similar to *Ginkgo* leaves but appeared to be more associated with accumulations of wood (Fig. 7A, B).

Short-term retention of paper strips was high (84–99%) in both streams but many strips were subsequently transported farther downstream and onto the floodplains (Fig. 8) as Q rose (~0.42–1 m^3/s in West Chicken Creek and ~1.98–2.5 m^3/s in Limber Jim Creek). Twenty-seven percent (415/1540) of strips released into West Chicken Creek were deposited onto the floodplain within the study reach, particularly in areas of extensive over-bank flow, such as meander bends or high-flow side channels. In contrast, only 5% (76/1540) of released strips were deposited onto the meadow floodplain of Limber Jim Creek. The mean lateral transport distance of paper strips onto the floodplain was 1.5 ± 0.09 m (range = 0–9 m) at West Chicken

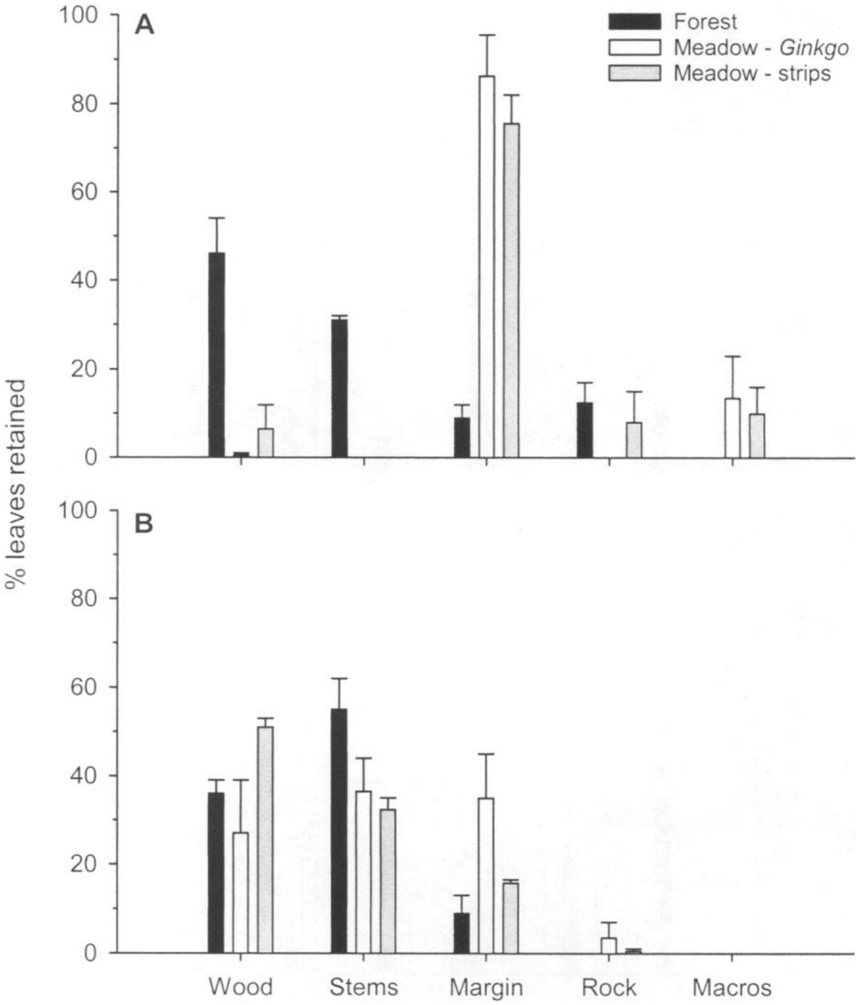

FIG. 7. Mean % (+1 SE) of *Ginkgo* leaves and paper strips associated with various structures during high flow in West Chicken Creek (A) and Limber Jim Creek (B). Wood = any large or small wood, Stems = stems of woody shrubs, Margin = rocky edges of the stream or streamside herbaceous vegetation, Rock = benthic rocks, and Macros = macrophytes.

Creek and 0.6 ± 0.08 m (0–4.2 m) at Limber Jim Creek.

Discussion

Spatial and temporal dynamics of retention

Transport distances of *Ginkgo* leaves increased predictably with Q, velocity, width, and depth in both streams (Fig. 3). These results are consistent with past studies reporting longer transport distances of CPOM (Speaker 1985, Webster et al. 1987, Jones and Smock 1991, Scarsbrook and Townsend 1994, Wallace et al. 1995), FPOM (Cushing et al. 1993, Minshall et al. 2000, Thomas et al. 2001), and N (Peterson et al. 2001, Wollheim et al. 2001) with increases in Q and stream size. In general, the probability that a particle will remain in transport increases with increasing stream size and velocity (Speaker et al. 1984, Webster et al. 1994). Although this relationship is important to understanding scaled patterns of material export, comparative analyses using S_p alone may be confounded by differences in stream size.

Quantifying longitudinal and seasonal vari-

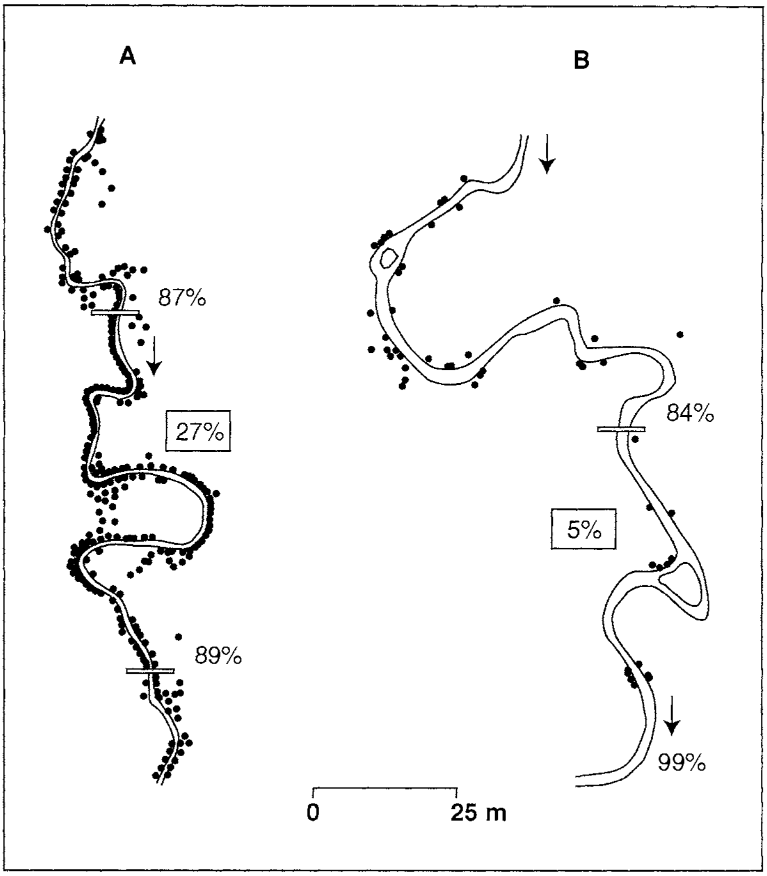

FIG. 8. Paper-strip distribution on the floodplains of the meadow study reaches of West Chicken Creek (A) and Limber Jim Creek (B) ~1.5 mo after short-term releases. Dots represent individual strips, arrows indicate leaf-release sites, and open horizontal bars represent the location of nets. Values in boxes represent the % of strips released that were retained on the floodplains and unboxed values are the % of strips retained during the short-term releases. The upstream release site in West Chicken Creek and the downstream net location in Limber Jim Creek are not shown.

ability in S_p and v_{dep} is critical to understanding controls on annual fluxes of CPOM in headwater catchments. Downstream increases in Q from tributaries resulted in much longer S_ps in the meadow reaches than in upstream forest reaches during high flow but not baseflow, suggesting that transport was longitudinally more conservative at lower flow because of some downstream compensation in particle trapping capacity, particularly by streamside vegetation (Fig. 6). Hydrological variables related to size and velocity explained most variability in S_p for baseflow experiments (Fig. 3), but because of the narrow range of S_p values within streams (Table 3), these relationships were driven primarily by large between-stream differences.

Scatter around the S_p and Q_w relationship reflected variability in v_{dep} and indicated the relative importance of transport controls other than hydrology (Fig. 4). For example, at high flow the meadow reach of Limber Jim Creek had >4 times higher Q than the meadow reach of West Chicken Creek, yet S_p was nearly equal, suggesting that the channel and riparian zone of Limber Jim Creek were proportionally more retentive than those of West Chicken Creek. Accordingly, v_{dep} of *Ginkgo* leaves was higher in Limber Jim Creek than in West Chicken Creek during high flow (Table 3). These observations highlight the utility of v_{dep} as a descriptor of particle retention and suggest that differences in riparian vegetation structure influenced rates of CPOM retention during spring floods.

Roughness coefficients for floodplain vegetation types are generally lowest for deeply inundated flexible graminoids and highest for dense shrubs (Arcement and Schneider 1987). Both forest reaches were characterized by an abundance of woody shrubs growing directly in the active channel (Case 1995) but only the meadow reach of Limber Jim Creek had abundant woody riparian vegetation; the meadow reach of West Chicken Creek consisted entirely of herbaceous, largely graminoid plants. The meadow reach of West Chicken Creek had the greatest proportional extent of floodplain inundation, yet particle releases here yielded the lowest v_{dep} values among all experiments (Fig. 5C).

Riparian vegetation strongly influenced retention via large wood. Wood presence and abundance was strongly related to intrareach patterns of particle retention (Fig. 2) and interreach variation in v_{dep} (Fig. 5A), and accounted for a high proportion of observed sites of leaf retention (Figs 6, 7). Although S_p was negatively associated with small wood volume (Fig. 3F), this pattern was no longer significant after converting to v_{dep} (Fig. 5B), suggesting the relationship with small wood was confounded by differences in hydrology. Large wood volume accounted for much of the variability in v_{dep} for high-flow experiments but had no influence on baseflow retention (Fig. 5A). Deviation from the expected S_p and Q_w relationship for the high-flow experiments matched the relationship between large wood and v_{dep} such that all points below the line in Fig. 4 corresponded to experiments for which v_{dep} was >3 mm/s and strongly influenced by large wood (Fig. 5A). The alternating pattern of wood being a significant predictor of v_{dep} during high flow but not during baseflow suggests a hydraulic threshold above which large wood effectively removed particles from transport and below which other factors (e.g., hydrology) predominated.

Our finding that wood was a key factor influencing v_{dep} of CPOM during high flow supports the importance of stream wood to the regulation of annual particulate losses (Bilby and Likens 1980, Wallace et al. 1995), given that most organic export in headwater streams occurs during periods of high flow (Fisher and Likens 1973, Webster et al. 1987). Associations between wood and retention were consistent with patterns of coarse benthic organic matter (CBOM) in the 2 streams. In autumn 1999, 69 to 94% of CBOM in the forest reaches was associated with debris dams, as was 87% of CBOM in the meadow reach of Limber Jim Creek, where wood had been added (Brookshire 2001).

Particle type affected retention patterns during high-flow releases in the meadow reaches. Mean S_p of paper strips was <½ the length of *Ginkgo* leaves (Table 3). Differences in mean v_{dep} between *Ginkgo* leaves and strips also suggested that strips were better retained. Strips wrapped around objects more than *Ginkgo* leaves, suggesting higher capture efficiency of graminoid-dominated riparian vegetation for sedge blades than for *Ginkgo* leaves. Scarsbrook and Townsend (1994) similarly found that S_ps of tussock grass leaves in a New Zealand grassland stream (1.9–6.4 m) were significantly shorter than elliptical tree leaves (5.5–14.7 m). The observation that the shape and size of particles affects transport behavior has important implications for our understanding of transport dynamics in streams with heterogeneous sources of organic matter (Thomas et al. 2001).

Our study found differential reach-scale responses in retentive capacity with stream flow. In the forest reaches, mean v_{dep} was significantly higher during high flow than baseflow, whereas mean v_{dep} in the meadow reaches did not change, suggesting a flood threshold response in mean v_{dep} in the forests, but flow-independent mean v_{dep} in the meadows. However, inferences from short-term releases should be limited to behavior observed at the Q and duration of the experiment because even slight flow increases can dislodge particles, increasing downstream transport (Young et al. 1978, Speaker et al. 1984). Increased Q can also move CPOM from stream channels to adjacent floodplains where it is retained (Jones and Smock 1991).

Patterns of long-term strip distribution on the floodplains were opposite those found for short-term releases (i.e., higher v_{dep} in Limber Jim Creek). In both streams, <1 to 16% of paper strips were exported downstream within 3 h of release; most were retained within 100 m of the release point. Yet, ~1.5 mo after peak flows (42–45 d after the releases), 5 to 30% of these retained paper strips occurred on the floodplains (Fig. 8). Thus, including the proportion of strips removed during the short-term releases, 39%

and 87% of strips were retained within the channels or exported downstream in West Chicken Creek and Limber Jim Creek, respectively. The exact sequence of capture and remobilization on the floodplains is unknown, but stream differences suggest that resuspension during the rising limb and deposition during the falling limb were tightly coupled at West Chicken Creek, whereas retention at Limber Jim Creek was dominated by resuspension and downstream transport. This result further suggests differential thresholds of retention in response to changing flow.

Very few strips were observed within the wetted channels and numerous strips were found >200 m downstream of the release sites. The relative proportions of strips retained within the channels and exported downstream were not determined, but low rates of *Ginkgo* leaf retention suggested that much naturally occurring CPOM is eventually exported downstream. This conclusion is consistent with relatively small standing crops of CBOM in the meadows.

Retention and flux of riparian detritus in headwater streams

In summary, we found that Q overwhelms the influence of channel form and structural features on S_p in these headwater streams, but that strong influences on retention of reach type, channel form, and structural features emerged when retention was analyzed in terms of v_{dep}. During high flow, large wood abundance, the degree of floodplain inundation, and riparian vegetation type were the major controls on CPOM retention. During baseflow, there were no differences in mean v_{dep} between streams or longitudinally within streams despite large differences in Q, suggesting that reach-scale differences in structural elements (e.g., wood versus streamside vegetation) compensated for the influence of Q.

A central tenet of stream ecosystem theory is that the headwater reaches of stream networks are highly retentive of organic C and nutrients (Vannote et al. 1980, Minshall et al. 1983). High physical retention is expected to contribute to energetic stability in aquatic ecosystems (Minshall et al. 1983, Elwood et al. 1983). Many studies have demonstrated high levels of organic retention in forested headwater streams but few have investigated retention within the context of longitudinal variability in physical structure (Lamberti et al. 1989, Webster et al. 1994). Our results demonstrate that processes and rates of detrital retention can be quite spatially variable because of reach-scale differences in channel and riparian structure, and temporally variable depending on how retention mechanisms function at different flow levels.

A comparison of Q_w, S_p, and v_{dep} from our study or calculated from published studies of CPOM retention in streams of similar size illustrates that S_p and v_{dep} are highly variable across CPOM types and a relatively narrow range of Q_w (Table 4). Mean S_p and v_{dep} for all experiments were 72 m and 5.5 mm/s, with both parameters having coefficients of variation >145%. The variation in S_p (0.9–97 m) and v_{dep} (0.3–32 mm/s) observed in our study spanned much of the range in these parameters over different biomes and stream types, although inclusion of data in Table 4 was limited by the availability of mean width, depth, velocity, and Q values needed to calculate v_{dep}. In addition, most of the entries, including ours, represent averages of multiple experiments. Unfortunately, no published study investigated associations between v_{dep} and various stream features to isolate retention mechanisms, apart from the influence of Q. Nevertheless, the range presented suggests that headwater streams vary greatly in their ability to retain CPOM, depending on hydrologic, channel, and riparian characteristics. The values of v_{dep} for CPOM are more variable and generally much higher than the range of v_{dep} values observed for FPOM across particle size classes and stream sizes (0.1–1.1 mm/s; Thomas et al. 2001). Such variability suggests that the idea of headwater streams being highly retentive for CPOM should be evaluated apart from the predictable Q_w and S_p relationship and viewed in context of the natural range of variability in spatial and hydrologic characteristics of headwater streams.

Assessment of spatial and temporal variability in physical retention is critical to the analysis of organic matter flow in headwater streams. Our results support the idea that longitudinal differences in channel and riparian structure are key elements affecting rates of organic matter flux and processing in headwater streams.

TABLE 4. Comparison of width-specific discharge (Q_w m^2/s), transport distance (S_p, m), and deposition velocity (v_{dep}, mm/s) for coarse particulate organic matter (CPOM) release experiments conducted in various headwater streams. All entries except for Young et al. (1978) represent averages of multiple releases. Values of v_{dep} were calculated from average Q_w and S_p for all entries except our study. Values of v_{dep} for our study represent averages of experimental releases. HF = high flow and LF = low flow.

Location	Site characteristics	Particle type	Q_w	S_p	v_{dep}	Reference
Pennsylvania	Deciduous forest	Leaves	0.038	192	0.2	Young et al. 1978
Virginia	Artificial stream	Leaves	0.005	13.9	0.4	Webster et al. 1987
Scania, Sweden	Deciduous forest, natural	Plastic strips	0.017	13	1.3	Petersen and Petersen 1991
	Agriculture, channelized	Plastic strips	0.051	87	0.6	
Virginia	Blackwater floodplain	Leaves	0.012	7.1	1.6	Jones and Smock 1991
		Dowels	0.008	7.7	1.0	
Indiana	Deciduous forest	Leaves	0.280	134	2.1	Ehrman and Lamberti 1992
Alaska	Glacial retreat floodplain	Leaves	0.179	407.6	0.4	Flory and Milner 1999
		Catkins	0.300	125	2.4	
North Carolina	Montane deciduous forest	Leaves	0.039	1.6	25.6	Webster et al. 1999
		Sticks	0.039	1.3	30.8	
Oregon	Montane coniferous forest, HF	Leaves	0.152	29.3	5.2	Our study
	Montane meadow, HF	Leaves	0.186	69.0	2.7	
	Montane meadow, HF	Paper strips	0.186	33.2	10.5	
	Montane coniferous forest, LF	Leaves	0.021	11.3	1.1	
	Montane meadow, LF	Leaves	0.033	16.3	1.6	

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