# Geomorphic Influences on Large Wood Dam Loadings, Particulate Organic Matter and Dissolved Organic Carbon in an Old-Growth Northern Hardwood Watershed

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## ABSTRACT

We quantified large wood loadings and seasonal concentrations of particulate organic matter (POM) and dissolved organic carbon (DOC) in three different geomorphic zones (each with unique hydrogeomorphic characteristics) of a pristine, old-growth northern hardwood watershed. The highest large wood dam loadings were in the high-gradient, bedrock controlled geomorphic type characterized by a cascading and step pool stream channel (19 dams $km^{-1}$), while the lowest loadings were in the low-gradient, bedrock controlled geomorphic type (5 dams $km^{-1}$). POM and DOC concentrations varied seasonally and were generally significantly correlated with discharge before and following leaf-off (mid to late September). The highest concentrations of POM were in the wetland dominated, low-gradient, bedrock controlled geomorphic type (3.74 mg $L^{-1}$), while the highest DOC concentrations were in the high gradient, bedrock controlled geomorphic type following leaf-off (14.55 mg $L^{-1}$). Our results suggest that organic matter dynamics vary both spatially and temporally in a watershed in response to changes in hydrogeomorphic conditions, and the processing of different types of organic matter may be intimately linked, resulting in the significant differences in how organic matter is processed and utilized in stream ecosystems flowing through forested watersheds.

## INTRODUCTION

In eastern North America, allochthonous inputs of organic matter are the primary energy resource for small streams in forested watersheds (Fisher and Likens 1973, Cummins 1974, Cummins et al. 1983). Once in the stream, much of this material (including trees, branches, twigs, leaves, and seston) is broken down by physical and biological processes into successively smaller forms of particulate organic matter (POM) and dissolved organic matter (DOM) that is transported downstream (Vannote et al. 1980). The retention of these various forms of organic matter is essential for a properly functioning stream ecosystem, as both POM and DOM serve as sources of energy and substrates for both stream microbes and macroinvertebrates, the foundation of the aquatic food web in heterotrophic systems (Cummins and Klug 1979, Bilby 1981, Lamberti and Berg 1995, Wallace et al. 1997).

The flux, retention, and processing of different forms of organic matter in streams are influenced by physical characteristics of the stream and its valley (Bilby and Likens 1980, Speaker et al. 1984, McDowell and Likens 1988, Palik et al. 1998). Differences in



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stream channel and valley morphology (e.g., discharge, channel width, stream gradient, stream substrate) influence the retention efficiency of stream ecosystems. For example, large wood and smaller forms of POM typically are retained in narrow or constrained stream channels, even at normal flow, especially if the channel is steep and the substrate is bedrock or rock plate (e.g., Trotter 1990, Nakamura and Swanson 1994, Rot et al. 2000). Conversely, entrenched channels may limit large wood dam formation because wood may not easily fall into deep, narrow channels, and flooding in entrenched channels usually creates sufficient water power to turn and transport logs, as well as POM (Downs and Simon 2001).

One result of the large wood and POM retained in streams is longer residence times for water, solutes, and suspended forms of organic matter that will either decompose, be consumed, or be dislodged and transported downstream (Speaker et al. 1984, Wallace et al. 1995). There are only limited examples of research that examine how watershed variation in channel and valley form effected the retention, accumulation, and processing of different types of organic matter (e.g., Bilby and Likens 1980, Naiman 1980, Bilby 1981). Lack of such an approach has limited our conceptual understanding of how changes in hydrogeomorphic conditions may affect the processing of organic mater and the possible seasonal linkages among different forms of organic matter and their relationship with hydrogeomorphic features of the watershed.

We examined patterns of large wood accumulation and seasonal patterns of POM concentrations and dissolved organic carbon (DOC) concentrations in stream reaches characterized by different hydrogeomorphic conditions. We worked in an old-growth northern hardwood-hemlock forest watershed of Upper Michigan which, unlike many watersheds in the eastern United States, has never been harvested and no large wood has been removed from the stream system. Specifically, we addressed the following questions. (1) How variable are large wood loadings among different hydrogeomorphic conditions in the watershed? (2) How do concentrations of POM vary both spatially and temporally in response to changes in hydrogeomorphic conditions? (3) How do concentrations of DOC, a major component of DOM, vary both spatially and temporally in response to changes in hydrogeomorphic conditions?

## MATERIALS AND METHODS

*Site Description*

We conducted our study in the Little Carp River watershed, a 42.2 km$^2$ northern hardwood-hemlock forest located in the Porcupine Mountains Wilderness State Park along the south shore of Lake Superior in Michigan's western Upper Peninsula (Fig. 1; 46°45'N, 89°47'W). The forests of the Little Carp River watershed have never been logged and are best characterized as uneven-aged (Lorimer and Frelich 1984, Frelich and Lorimer 1991). The climate is characterized by moderate precipitation (91 cm yr$^{-1}$), cold winters (January mean -7°C), and mild summers (July mean 19°C). The growing season typically lasts 100-140 days, with leaf-off occurring in mid to late September (McNab and Avers 1994). Over two-thirds of the precipitation usually occurs as snow from November to April, and the peak discharges along the Little Carp River and its tributaries usually occur following snowmelt in the spring. Average annual spring flooding following snowmelt often results in flood elevations 1-2 m above the bankfull channel.

The Little Carp River watershed consists of three different geomorphic sub-basins, each with characteristic hydrogeomorphic conditions that are largely dictated by geology, and stream channel and valley morphology. These include: (1) low gradient, poorly entrenched stream channel in an unconstrained bedrock-controlled valley in the upper portions of the watershed; (2) high gradient, moderately entrenched stream channel in a constrained bedrock-controlled valley in the middle of the watershed; and, (3) high gradient, deeply entrenched stream channel in a deeply incised clay lake plain valley in the lower portions of the watershed. The stream characteristics of each geomorphic zone are summarized in Table 1. Gravel and small cobbles compose the stream substrate of the low gradient geomorphic zone, and the stream morphology is best described as pool-riffle (Montgomery and Buffington 1993). Extensive alluvial wetlands (~18% of the watershed area) are located in the upper watershed along the low gradient channel of the Little Carp River. Conversely, boulders and cobbles interspersed with large, exposed slabs of bedrock characterize the streambed of the high gradient geomorphic zones of the Little Carp River. Stream morphology in these areas consists of either a step-pool or cascade, with pools, riffles and waterfalls (Montgomery and Buffington 1993).

The structure and composition of the riparian forests in each of the sub-basins reflect differences in stream valley geomorphology and its subsequent influence on fluvial disturbances. While the intensity of floodwaters in the low gradient, unconstrained bedrock-controlled zone is not as great as in the other two zones, the lateral extent of the floodwaters is far-reaching, often resulting in flooded or saturated soil conditions and a floodplain plant community dominated by tag alder (*Alnus incana* L.) and a mixture of grasses and sedges that can extend up to 100 m from the bankfull channel. In both of the high gradient geomorphic zones, floodplain development is minimal as the stream channel is often constrained by bedrock, resulting in floodplain plant communities dominated by herbaceous plants. However, the higher terraces and valley walls in both of these geomorphic zones are dominated by eastern hemlock (*Tsuga canadensis* L.) and northern hardwoods such as sugar maple (*Acer saccharum* Marsh.) and American basswood (*Tilia americana* L.).

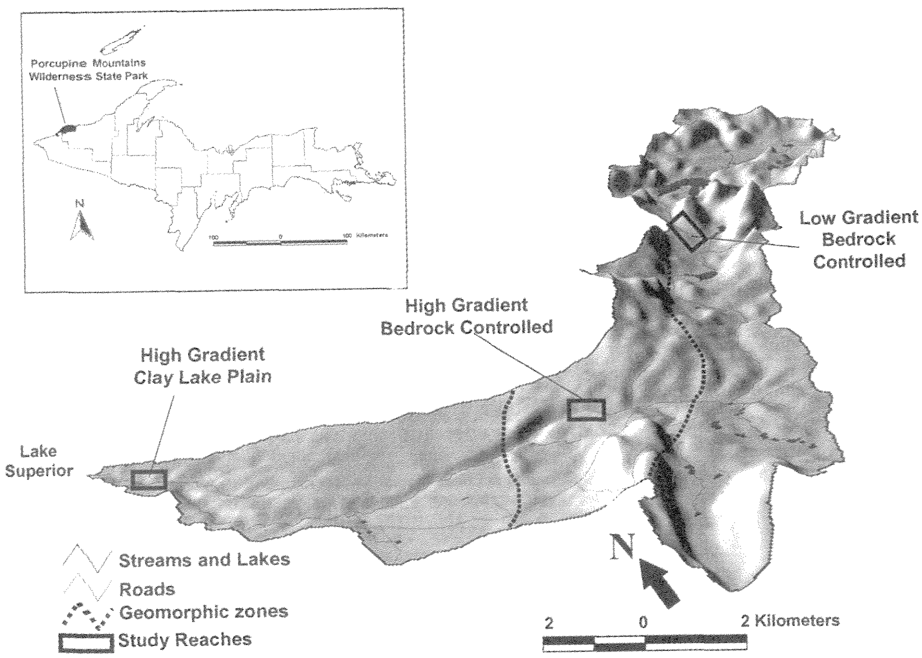


Figure 1. Geomorphic zones of the Little Carp River watershed, an old-growth northern hardwood dominated watershed of Michigan's Upper Peninsula.

Table 1. Stream channel and valley characteristics by geomorphic zone of the Little Carp River, Upper Michigan.

| Variable | Geomorphic zone: Low-gradient bedrock controlled | High-gradient bedrock controlled | High-gradient clay lake plain |
|---|---|---|---|
| Rosgen stream channel type[a] | C | B | F |
| Channel entrenchment | poorly | moderately | deeply |
| Channel slope (%) | 1.8 | 4.3 | 1.7 |
| Bankfull height (m)[b] | 0.5 | 0.6 | 0.6 |
| Bankfull width (m)[b] | 5.8 | 11.3 | 18.3 |
| Bankfull discharge (cms)[b] | 4.7 | 9.4 | 9.7 |
| Valley floor width (m)[b] | 148.0 | 122.0 | 223.0 |
| Valley constraint (%)[c] | 3.9 | 9.2 | 8.2 |

[a]Rosgen stream channel types – see text for explanation.
[b]Measurements taken at downstream boundary of each study reach from 1999-2001.
[c]Valley constraint = (bankfull width/valley floor width)*100

*Field Methods*

In the summer of 1999, we used a Trimble global positioning system to geo-reference the location of individual large wood dams along the 25 km length of the Little Carp River from Mirror Lake to Lake Superior (Fig. 1). Large wood dams were defined as accumulations of at least two stems with a mid-diameter > 10.0 cm that spanned at least 75% of bankfull channel (Bilby and Likens 1980, Hedman et al. 1996). Once geo-referenced, large wood summary statistics for each km of stream length located within each geomorphic zone were determined using ArcView® software (ESRI 1999).

Each month from June to December of 1999, we collected triplicate 1-L water samples from the approximate middle of the water column and downstream end of the study reach in each geomorphic zone to determine POM. Stream water samples were not collected over the winter or during peak snowmelt in the spring (January-May) as the research sites were inaccessible. We estimated discharge ($m^3$ $sec^{-1}$) using standard techniques (Gore 1996) at a single study reach characteristic of each geomorphic zone. Water samples were transported to the laboratory and frozen until processed. Prior to processing, samples were thawed and kept refrigerated at 4°C, and POM was determined as described in Wallace and Grubaugh (1996). POM was expressed as milligrams ash-free dry-weight per liter (mg AFDW $L^{-1}$).

Each month from June to December 1999, we also collected ten water samples from the approximate middle of the water column distributed evenly across each study reach to estimate DOC. Stream samples were transported to laboratory where they were acidified to a pH of ~ 2.0 with 2N HCl, and filtered through 0.45 $\mu$m filter. DOC was determined using a Shimadzu TOC-5000A total organic carbon analyzer.

*Data analyses*

Analysis of variance (PROC ANOVA) using SAS software (SAS 2001) was conducted to examine differences in large wood loadings, POM concentrations, and DOC concentrations among geomorphic zones. Where differences were significant, a

Bonferroni multiple-comparison was used to determine levels of significance between means. Specifically, we hypothesized that (1) the high gradient, bedrock controlled reach had higher large wood dam loadings, and subsequently higher concentrations of POM and DOC, than the high gradient, clay lake plain reach; and, (2) the high gradient, bedrock controlled reach had higher large wood dam loadings, and subsequently higher concentrations of POM and DOC, than the low gradient, bedrock controlled reach. Furthermore, to examine seasonal relationships between POM and DOC concentrations and discharge in each geomorphic zone, we calculated Pearson correlation coefficients (PROC CORR) using SAS software for (1) the entire sampling period (June to December), (2) prior to leaf-off (June to September), and (3) following leaf-off (mid September to December).

## RESULTS

The density of large wood dams varied considerably among the three geomorphic zones (Fig. 2). Average density of large wood loadings was significantly higher in the high gradient, bedrock controlled zone than the high-gradient clay lake plain and low gradient, bedrock controlled geomorphic zone ($P < 0.001$; Fig. 2). Although not examined directly, the spatial distribution of large wood dam loadings in each geomorphic zone was highly variable, with the majority of large wood dams located in broader portions or unconstrained segments of stream reaches compared to the narrower or constrained stream segments.

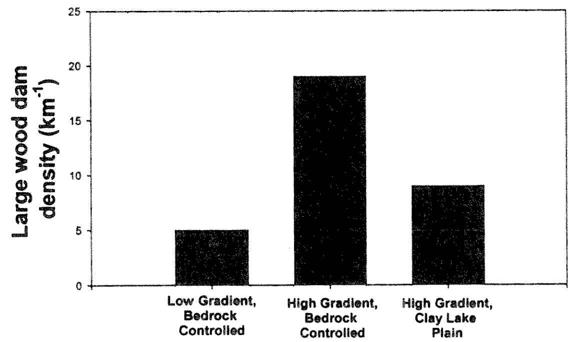


Figure 2. Density of large wood dams by geomorphic zone of the Little Carp River, Upper Michigan.

Average stream water concentrations of POM from June to December varied minimally among the three geomorphic zones (*F-statistic* = 0.15; $P = 0.85$; Table 2). Average concentrations of POM were 1.28 mg $L^{-1}$ in the clay lake plain geomorphic zone, 1.32 mg $L^{-1}$ in the low gradient, bedrock controlled geomorphic zone, and 1.45 mg $L^{-1}$ in the high gradient, bedrock controlled geomorphic zone. There also appeared to be several seasonal trends in POM concentrations (Fig. 3). Prior to leaf-off (June to mid-September) POM concentrations were significantly positively correlated with discharge in all three zones (Table 3). Concentrations of POM were negatively correlated with discharge in both of the high gradient reaches following leaf-off. In contrast, average POM concentrations in the low gradient, bedrock controlled reach increased nearly three-fold with increasing discharge, ranging from 1.25 mg $L^{-1}$ in late October to 3.74 mg $L^{-1}$ in late November (Fig. 3).

Average stream water concentrations of DOC from June to December were significantly higher in the wetland-dominated low gradient bedrock controlled

Table 2. Average (± 1 standard error) streamwater concentration (mg $L^{-1}$) of particulate organic matter (POM) and dissolved organic carbon (DOC) from June to December 1999 for study reaches by geomorphic zone of the Little Carp River, Upper Michigan. Values in a row followed by the same letter are not significantly different at $P < 0.05$.

| | Geomorphic Zone | | |
|---|---|---|---|
| Variable | Low gradient bedrock controlled | High gradient bedrock controlled | High gradient clay lake plain |
| Particulate organic matter (POM) | 1.32 (0.28)*a* | 1.45 (0.23)*a* | 1.28 (0.16)*a* |
| Dissolved organic carbon (DOC) | 6.82 (0.29 )*a* | 6.33 (0.54 )*ab* | 5.12 (0.43 )*b* |

geomorphic type than the clay lake plain geomorphic type (*F-statistic* 4.07; $P = 0.0186$; Table 2). However, no significant differences were observed between the wetland-dominated low gradient and high gradient bedrock controlled geomorphic types, or between the high gradient bedrock controlled and clay lake plain geomorphic types ($P < 0.05$).

Seasonal differences were evident in streamwater DOC concentrations among the three different geomorphic types (Fig. 4). In all three geomorphic zones, DOC concentrations were significantly correlated with discharge prior to leaf-off (Table 3). DOC concentrations also significantly increased with increased discharge during the last three sample periods following leaf-off (September 29 to November 29) in the high gradient, bedrock controlled geomorphic type, but not the low gradient, bedrock controlled or and high gradient clay lake plain geomorphic types (Table 3). The highest concentrations of DOC were observed in the high gradient, bedrock controlled geomorphic type, increasing from approximately 3 mg $L^{-1}$ to over 14 mg $L^{-1}$ following leaf-off (after the September 29 sample period). Similar results, although not as strong, were observed in the high gradient, clay lake plain geomorphic type (Fig. 4).

## DISCUSSION

Overall, large wood loadings were similar to other second-growth and old-growth forested watersheds in eastern North America (e.g., Bilby and Likens 1980, Hedman et al. 1996), and the concentrations of POM and DOC were well within the reported range of other streams across eastern North America (e.g., Naiman 1980, Mulholand and Kuenzler 1979, Bilby 1981, McDowell and Likens 1988, Webster et al. 1990). Yet within the watershed there were distinct differences in large wood loadings and differences in seasonal patterns of POM and DOC concentrations among the three different geomorphic zones. Thus, these results support the concept that channel and valley form are important factors controlling the retention and processing of organic matter in stream ecosystems (Naiman 1980, Hutchens and Wallace 2002).

Loadings of large wood dams in the Little Carp River varied considerably among geomorphic zones. In the low-gradient upper portion of the watershed, northern hardwood species and/or tag alder-grass-sedge communities dominate the streamside forests, limiting the input of wood into the stream ecosystem and resulting in fewer dams. Conversely, the continuous forest cover, steep adjacent slopes, higher stream gradient and streambed structures such as large boulders result in greater large wood recruitment and retention in the high gradient geomorphic zones. The decrease in large wood loading in the high gradient clay lake plain geomorphic zone, relative to the bedrock controlled high gradient zone, is most likely related to stream size, as large wood loadings typically decrease with an increase in stream size (Bilby and Likens 1980, Bilby and Ward 1989).

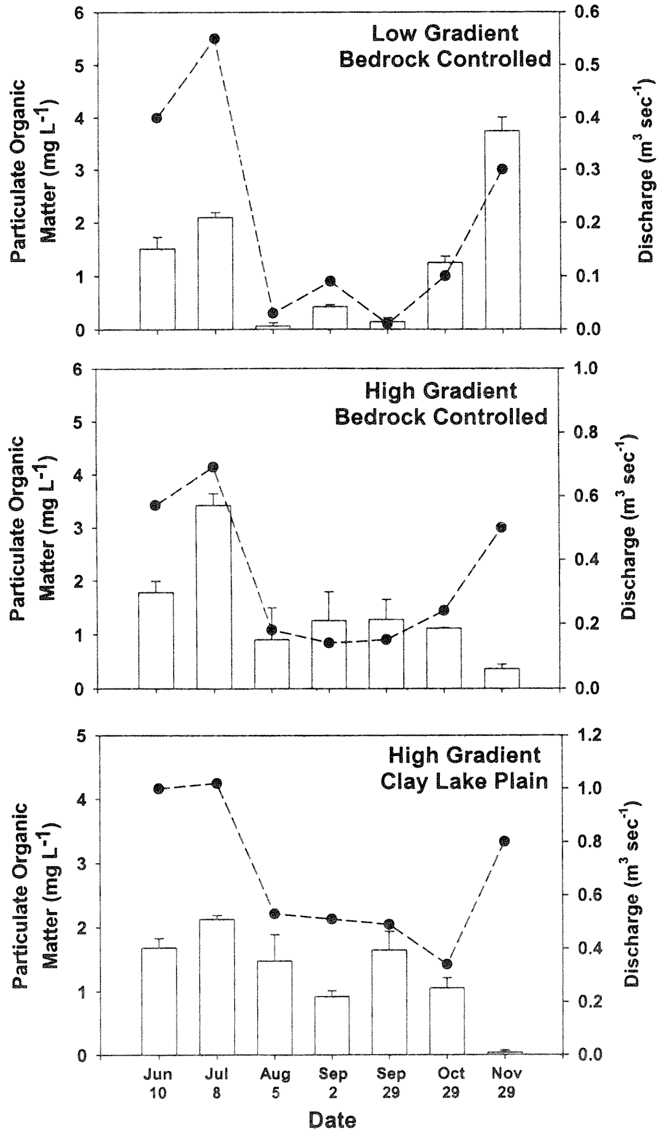


Figure 3. Mean concentration of streamwater POM (mg $L^{-1}$) and discharge ($m^3$ $sec^{-1}$) from June to December 1999 in the three geomorphic types examined in the Little Carp River watershed, Upper Michigan.

Although our results are based on observations over a single season, hydrogeomorphic conditions in the watershed also appear to affect seasonal in-stream POM concentrations. The increase in POM in the low gradient zone following leaf-off may be related to the large presence of alluvial wetlands and organic soils in this geomorphic zone (almost all of the wetland area in the Little Carp River watershed is located in the headwaters). As discharge increases in the fall, the amount of water flowing through these often saturated organic soils also increases, possibly providing a constant source of particulate forms of organic matter to the stream as the channel sides erode. Similar patterns in low-gradient streams with comparable streamside vegetation and streambed substrate have been observed in boreal watersheds (Naiman 1980).

A different mechanism may be operating in both high gradient geomorphic zones, where POM concentrations decreased following leaf-off. The nature of water movement in these high gradient cascading or step-pool reaches tends to be more turbulent that the low-gradient, pool-riffle reach type characteristic of the low-gradient geomorphic type, effectively transporting downstream all but the larger particles of organic matter such as leaves and twigs that tend to accumulate behind the large wood dams (Bilby and Likens 1980, Bisson and Montgomery 1996). Our results tend to support this pattern, as POM concentrations were negatively correlated with discharge following leaf-off.

One consequence of the large quantities of coarse POM trapped by the high loadings of large wood dams in the high gradient bedrock-controlled reaches is a seasonal increase in DOC, most likely originating from the leachate of trapped leaves (Bilby and Likens 1980). We observed such a trend, as DOC concentrations following leaf-off in the high-gradient bedrock controlled geomorphic type increased by 400%, while concentrations in the high gradient, clay lake plain geomorphic type increased more gradually in response to a variety of factors, including dilution and fewer large wood dams to trap leaves and other coarse POM. DOC concentrations following leaf-off in the wetland dominated low-gradient geomorphic zone were more variable, first increasing and then decreasing significantly with higher discharge, as the increased streamflow dilutes DOC concentrations.

The relationships we documented among large wood, POM, and DOC suggest that in the high gradient, bedrock controlled reaches large wood dams may help sustain the productivity of the stream ecosystem over the winter months. Large wood dams in

Table 3. Relationship between POM and DOC concentrations and discharge for study reaches by geomorphic zone of the Little Carp River, Upper Michigan.

| | Entire season | | Before leaf-off[a] | | Following leaf-off[b] | |
|---|---|---|---|---|---|---|
| Geomorphic zone | POM | DOC | POM | DOC | POM | DOC |
| Low gradient bedrock controlled | 0.664** | 0.010 | 0.977** | 0.817** | 0.987** | 0.090 |
| High gradient bedrock controlled | 0.517* | 0.278 | 0.742** | 0.917** | -0.779** | 0.694** |
| High gradient clay lake plain | 0.252 | 0.281 | 0.674* | 0.842** | -0.710** | 0.206 |

[a]Before leaf-off includes sample periods from June 10 to September 2, 1999.
[b]Following leaf-off includes sample periods from September 29 to November 29, 1999.
* $P < 0.01$; ** $P < 0.001$.

low-order streams are known to be major retention sites for coarser forms of POM. They also have correspondingly high densities of shredding macroinvertebrates and are net export sites of smaller particles of organic matter (Smock et al. 1989). Initially following leaf-off, most DOC originating from trapped leaves is of high quality and easily degradable (Hutchens and Wallace 2002). However, as concentrations of higher quality leaf leachate decreases, POM concentrations should increase as the leaves trapped by large wood are processed by shredding macroinvertebrates. Thus, in high gradient systems where annual POM concentrations are typically low because of the high streamflows, large wood dams may buffer the stream ecosystem by providing a source of POM during winter periods of lower streamflow that helps sustain the productivity of the stream ecosystem over the dormant season and into the next growing season. However, more research on winter POM concentrations and stream invertebrate communities is needed to test this hypothesis.

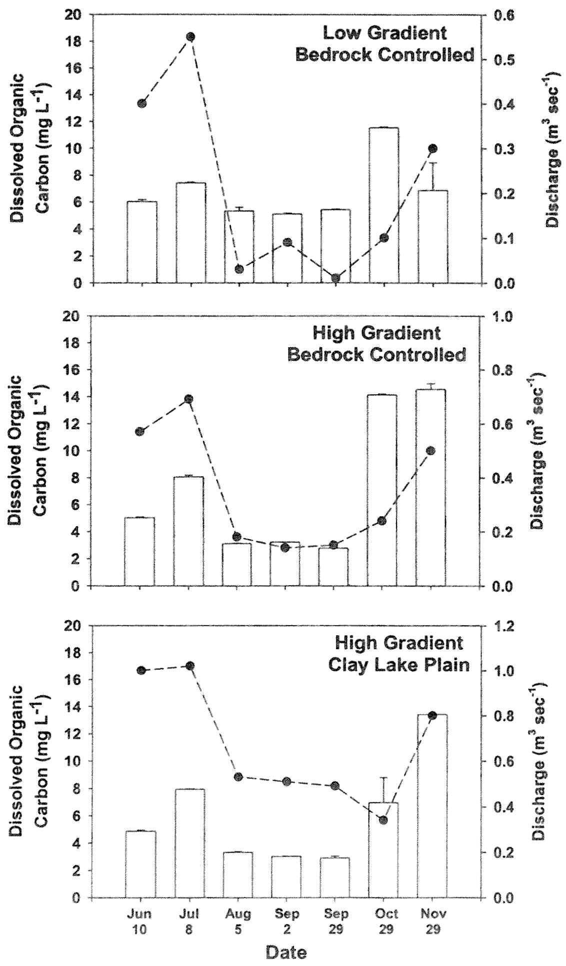


Figure 4. Mean concentration of streamwater DOC (mg $L^{-1}$) and discharge ($m^3$ $sec^{-1}$) from June to December 1999 in the three geomorphic types examined in the Little Carp River watershed, Upper Michigan. Averages are based on 10 samples per sample period.

Our results suggest that the hydrogeomorphic conditions of the watershed should be considered when designing stream ecosystem restoration programs that incorporate the addition of large wood. The accumulation and retention of large wood is highly variable among geomorphic conditions, suggesting that restoration of wood into streams should be equally variable. Engineered log additions that are installed improperly, in the wrong location, at the wrong density, have the potential to actually degrade the system by altering physical habitat but also by altering related storage and processing of POM and DOC. Although more research is needed to better understand how engineered logjams function ecologically in terms of organic matter retention and processing, the results of our research provide a baseline of reference conditions that can be used to help assess the proper functioning condition of streams in similar types of watersheds in the northern Lake States.

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## LITERATURE CITED

Bilby, R.E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate organic matter from a forested watershed. Ecology 62:1234-1243.

Bilby, R.E. and G.E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61:1107-1113.

Bilby, R.E. and J.W. Ward. 1989. Changes in characteristics and function of woody debris with size of streams in western Washington. Transactions of the American Fisheries Society 118:368-378.

Bisson, P.A. and D.R. Montgomery. 1996. Valley segments, stream reaches, and channel units. Pp. 23-52, in Methods in Stream Ecology. (F.R. Hauer and G.A. Lamberti, eds.). Academic Press, San Diego, CA.

Cummins, K.W. 1974. Structure and function of stream ecosystems. BioScience 24:631-641.

Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147-172.

Cummins, K.W., J.R. Sedell, F.J. Swanson, G.W. Minshall, S.G. Fisher, C.E. Cushing, R.C. Peterson, and R.L. Vannote. 1983. Organic matter budgets for stream ecosystems: Problems in their evaluation. Pp. 299-353, in Stream Ecology: Application and Testing of General Ecological Theory. (J.R. Barnes and G.W. Minshall, eds.). Plenum, New York.

Downs, P.W. and A. Simon. 2001. Fluvial geomorphological analysis of the recruitment of large woody debris in the Yalobusha River network, Central Mississippi, USA. Geomorphology 37:65-91.

ESRI. 1999. ArcView GIS 3.2. Environmental Systems Research Institute, Inc. Redmond, WA.

Frelich, L.E. and C.G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forest of the upper Great Lakes region. Ecological Monographs 61:145-164.

Fisher, S.G. and G.E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421-439.

Gore, J.A. 1996. Discharge measurements and streamflow analysis. Pp. 53-75, in Methods in Stream Ecology (F.R. Hauer and G.A. Lamberti, eds.). Academic Press, San Diego, CA.

Hedman, C.W., D.H. Van Lear, and W.T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research 26:1218-1227.

Huthcens, J.J. and J.B. Wallace. 2002. Ecosystem linkages between Southern Appalachian headwater streams and their banks: leaf litter breakdown and invertebrate assemblages. Ecosystems 5:80-91

Lamberti, G.A. and Berg, M.A. 1995. Invertebrates and other benthic features as indicators of environmental change in Juday Creek, Indiana. Natural Areas Journal 15:249-258.

Lorimer, C.G. and L.E. Frelich. 1984. A simulation of equilibrium diameter distributions of sugar maple (*Acer saccharum*). Bulletin of the Torrey Botanical Club 111:193-199.

McDowell, W.H. and G.E. Likens. 1988. Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook valley. Ecological Monographs 58:177-195.

McNab, W.H. and P.E. Avers (compilers). 1994. Ecological Subregions of the United States. USDA Forest Service Technical Report WO-WSA-5, Washington D.C.

Montgomery, D.R. and J.M. Buffington. 1993. Channel processes, classification, and responses. Pp. 13-42, in River ecology and management: lessons from the Pacific Coastal Ecoregion. (R.J. Naiman and R.E. Bilby, eds.). Springer-Verlag, New York.

Mulholland, P.J. and E.J. Kuenzler. 1979. Organic carbon export form wetland and forested wetland areas. Limnology and Oceanography 24:960-966.

Nakamura, F. and F.J. Swanson. 1994. Distribution of coarse woody debris in a mountain stream, western Cascade Range, Oregon. Canadian Journal of Forest Research 24:2395-2403.

Naiman. 1980. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Canadian Journal of Fisheries and Aquatic Sciences 39:1699-1718.

Palik, B.J., S.W. Golladay, B.W. Taylor, and P.C. Goebel. 1998. Riparian geomorphology and coarse woody debris recruitment in a Coastal Plain stream. Écoscience 5:551-560.

Rot, B.W., R.J. Naiman, and R.E. Bilby. 2000. Stream channel configuration, landform, and riparian forest structure in the Cascade Mountains, Washington. Canadian Journal of Fisheries and Aquatic Sciences 57:699-707.

SAS. 2001. The SAS System for Windows. Version 8.02. SAS Institute, Cary NC.

Speaker, R.W., K. Moore, and S.V. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verhandulungen der internationalen Vereinigung für Theoretische und Angewandte Limnologie 221:835-1841.

Smock, L.A., G.M. Metzler, and C. Gladden. 1989. The role of organic debris dams in the structuring and functioning of low-gradient headwater streams. Ecology 70:764-755.

Trotter, E.H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. Journal of the North American Benthological Society 9:41-156.

Wallace, J.B. and J.W. Grubaugh. 1996. Transport and storage of FPOM. Pp. 191-215, in Methods in Stream Ecology. (F.R. Hauer and G.A. Lamberti, eds.). Academic Press, San Diego, CA.

Wallace, J.B., J.R. Webster, and J. L. Meyer. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 52:2120-2137.

Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.
Webster, J.R., S.W. Golladay, E.F. Benfield, D.J. D'Angelo, and G.T. Peters. 1990. Effects of forest disturbance on particulate organic matter budgets of small streams. Journal of the North American Benthological Society 9:120-140.
Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.



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