

**ORGANIC MATTER DYNAMICS IN SMALL STREAMS
 OF THE PACIFIC NORTHWEST¹**

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ABSTRACT: Small streams in forested landscapes are tightly coupled to the vegetation of the surrounding forest, and one of the key drivers of the stream ecosystem is the nature of organic matter supplied to it. This paper is focussed on three questions related to organic matter dynamics in small, forested streams of the conifer dominated Pacific Northwest: (1) How do small streams differ from large streams? (2) How do small streams of the Pacific Northwest differ from those of other regions? and (3) How do forest practices alter organic matter dynamics of small streams in the Pacific Northwest? The organic matter dynamics of small streams in this region differ from temperate deciduous forests in the nature of the organic matter deposited (protective chemicals, hard epidermis, slower loss rates), the timing of inputs (distributed throughout the year), and the transport rates (smaller, hard needles are more easily transported). The large amount and persistence of wood in these streams provides an additional source of organic matter that can be consumed by particular species and contributes to biofilm and fine particulate organic matter (FPOM) production. Logging is commonly practiced in many forests of the region. This practice has been shown to alter the type, amount, and timing of organic matter delivery to small streams and reduce the amount and size of large wood. Changes in channel complexity and water temperature after logging also can contribute to reduced organic matter storage. Many of the processes controlling organic matter dynamics in small streams are well described in other regions. However, the climate, vegetation, and topography of the Pacific Northwest suggest that the rates and nature of some processes affecting stream organic matter may differ considerably from other regions. Further research on small streams of this area will be required to better understand these differences.

(**KEY TERMS:** aquatic ecology; detritus; food webs; headwaters; nutrients; particulate organic matter; rivers/streams.)

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INTRODUCTION

The importance of terrestrial organic matter in the food webs of streams, especially forested streams, has been appreciated since at least the early 1970s (Hynes, 1970; Cummins, 1974). Terrestrial ecosystems deliver many types of organic matter to streams including leaves, wood, dissolved organic compounds, and feces. In addition, dead animals from both the surrounding terrestrial system and in some cases from distant marine ecosystems may be deposited in streams. Organic matter delivered to streams from other systems is termed “allochthonous,” and organic matter generated within the stream is referred to as “autochthonous.” The influences of organic matter inputs on stream food webs and channel structure are well known (Hynes, 1970; Hassan *et al.*, 2005). The quantity and type of organic matter input to streams can control productivity of stream food webs, as demonstrated by experiments in adding or removing sources of leaf litter (Richardson, 1991; Wallace *et al.*, 1999; Johnson *et al.*, 2003).

Small streams in particular are heavily influenced by the strong coupling between the riparian forest and the channel, an observation dating back at least to Ross (1963). The heavy shading caused by closed canopy forests over small channels severely limits autotrophic production within the channel, and terrestrial organic matter often accounts for more than 90 percent of the total energy available to the food webs of these systems (Fisher and Likens, 1973). Small streams are frequently underappreciated

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(Meyer and Wallace, 2001) but export organic matter (in all its forms) and invertebrates to downstream reaches that often support fish (Wipfli and Gregovich, 2002). It is not clear if this energetic subsidy to downstream reaches is large relative to local input and production of organic matter, but there is evidence that it does make a substantial contribution in some systems (Wipfli and Gregovich, 2002).

A large proportion of the organic matter that provides energy from fixed carbon to food webs of small streams comes from leaf litter or ground water inputs of dissolved organic matter (DOM). This aspect of stream energetics has been well studied, particularly in temperate deciduous forests. A synthesis of the dynamics of organic matter inputs and processing in streams of the southeastern United States provides an excellent overview (Webster *et al.*, 1999).

In this paper the focus is on three questions related to organic matter dynamics in small forested streams of the conifer dominated Pacific coastal ecoregion: (1) How do small streams differ from large streams? (2) How do small streams of the Pacific Northwest differ from those of other regions? and (3) How do forest practices alter organic matter dynamics of small streams in the Pacific Northwest? For the purposes of this review, "small streams" are defined to include first-order and second-order channels (Strahler, 1957). Channels that fall into these orders in the Pacific Northwest include both ephemeral and permanently flowing streams. Generally, these systems are too small to support fishes, although a small proportion may seasonally provide spawning or rearing habitat for species of highly mobile fishes. Below is a brief review of organic matter dynamics before the primary questions of the paper are addressed.

GENERAL FEATURES OF ORGANIC MATTER DYNAMICS IN SMALL STREAMS

Terrestrial organic matter may enter a stream through several pathways and in various forms. Particulate organic matter (POM) is typically defined as organic matter larger than 0.63 μm (Webster and Benfield, 1986). Often POM is segregated into categories based on particle size, with FPOM from 0.63 μm to 1 mm and coarse particulate organic matter (CPOM) larger than 1 mm. Leaves and needles are often thought of as the primary form of POM input to streams, and many studies have examined the processing and transport of leaf litter in small streams (e.g., Webster and Benfield, 1986). However, wood forms the majority of POM contributed to streams in forested areas (Bisson and Bilby, 1998). In recent years the substantial contribution of terrestrial inver-

tebrates falling into streams as an energetic subsidy has come to be appreciated (Wipfli, 1997; Wipfli and Musselwhite, 2004). In some stream systems, carcasses of anadromous fishes may be an important source of POM (Gresh *et al.*, 2000; Chaloner *et al.*, 2004). Dissolved organic matter or dissolved organic carbon (DOC) is produced by the leaching of soluble organic compounds from CPOM (leaves, wood, fish carcasses, etc.) in the channel or delivered to the channel in ground water. These various forms of organic matter affect streams in different ways depending on their abundance in certain areas and the timing of inputs.

Particulate organic matter entering streams is colonized by fungi (CPOM, mostly by aquatic hyphomycetes) and bacteria, and this material is subsequently consumed by invertebrates (e.g., Hynes, 1970; Cummins, 1974). The microbial community on POM greatly enhances its nutritional value to consumers (Cummins, 1974). The consumption of POM by invertebrates produces smaller particles (FPOM) through fragmentation during feeding and production of feces (Heard and Richardson, 1995). These smaller particles are then recolonized by microbes and can be again ingested by invertebrate consumers.

The inputs of DOC from ground water and direct leaching provide a carbon source that contributes to the formation of biofilms (organic layers that encrust the stream substrate). These biofilm layers are biologically active, containing embedded algae, bacteria, and fungi and are an important food source for some stream invertebrates (McArthur and Richardson, 2002). DOC also provides a measure of protection for stream organisms from ultraviolet (UV) radiation. The UV radiation breaks DOC into smaller molecules, which diminishes the energy of the radiation (Kelly *et al.*, 2003).

Over the past two decades, the influence of hyporheic processes on organic matter dynamics of streams and rivers has become better appreciated (Edwards, 1998). The hyporheic zone is defined as the area below and adjacent to stream channels where surface and ground water mix. These areas can play an important role in governing the chemistry of surface waters and, as a result, influence nutrient availability (Triska *et al.*, 1989) and primary production (Edwards, 1998). The biofilm forming on hyporheic surfaces also can store or release large quantities of DOM (Pusch, 1996). Very extensive hyporheic systems develop along alluvial rivers. Small streams on the floodplains of such rivers also have large hyporheic systems. However, most headwater streams in the Pacific Northwest (PNW) are high gradient, and hyporheic systems are usually of limited extent. However, hyporheic zones do become established in the sediment deposits formed by large wood accumulations.

Wood contributes both dissolved and particulate organic matter to the stream as it degrades (Naiman and Sedell, 1979; Ward and Aumen, 1986). Leaching, the gradual dissolution of the wood by water, plays a minor role in wood decomposition due to its resistance to solution (Harmon *et al.*, 1986). Abrasion and fragmentation are the principal means of wood degradation in streams (Aumen, 1985). These degradation processes are accelerated by microbial decay that weakens the wood surface. Decay of wood in water is limited to a thin layer at the surface of the piece as high water content and low oxygen levels within the wood limit microbial penetration (Aumen, 1985). The surface layer of wood weakened by microbial action is subject to removal by abrasion or fragmentation during periods of elevated discharge (Bilby, 2003). Fragmentation is also enhanced by aquatic invertebrates specialized to burrow in or feed on wood (Anderson *et al.*, 1978). Both abrasion and fragmentation expose fresh wood surfaces for bacterial and fungal colonization and biofilm development.

Terrestrial invertebrates associated with riparian forest vegetation that fall into streams can form a large subsidy to stream food webs. Evidence from coastal forests in Alaska has demonstrated that these inputs can form up to half of the diet of some stream salmonids (Wipfli, 1997; Wipfli and Musselwhite, 2004). These inputs can be seasonally important and at times form the predominant prey source for stream fishes. These inputs of terrestrial invertebrates may even have indirect positive effects on other parts of the stream food web by diminishing the rates of fish predation on stream benthic invertebrates (Nakano *et al.*, 1999). The contribution in terms of nutrients and energy vary depending on forest age and type, with the greatest contributions typically associated with reaches supporting mostly alder trees or shrubs (Wipfli and Musselwhite, 2004).

Many species of fishes in the PNW, including some Pacific salmon (*Oncorhynchus* spp.) and the eulachon (*Thaleichthys pacificus*), die after spawning. As a result, they often deposit large quantities of organic matter in streams in the PNW. Most of this spawning occurs in moderate to large streams and rivers. However, several species of Pacific salmon can utilize streams of the size considered in this paper. In such streams the influence these fishes have on the organic matter and trophic dynamics can be substantial. The organic matter and nutrients that spawning salmon provide have been shown to affect stream productivity at multiple trophic levels (Bilby *et al.*, 1998; Zhang *et al.*, 2003; Chaloner *et al.*, 2004).

The materials transported to streams by spawning salmon are incorporated into the trophic system of streams both by direct consumption of carcass flesh and salmon eggs by fish and invertebrates and

biological or chemical uptake of dissolved materials released by fish metabolism and by carcass decomposition (Naiman *et al.*, 2002). Many of the stream invertebrates that consume POM also will consume dead fish carcasses (Minikawa *et al.*, 2002; Zhang *et al.*, 2003). This fish tissue is typically of a high quality and can support higher growth rates than leaf litter for some consumers (Minikawa *et al.*, 2002). Some stream fishes also consume salmon eggs and carcass tissue (Bilby *et al.*, 1998). Several studies have documented elevated primary production in response to nutrients released by decomposing carcasses (Richey *et al.*, 1975; Schuldt and Hershey, 1995). The presence of spawning salmon has been associated with increases in invertebrate production (Wipfli *et al.*, 1998; Minakawa *et al.*, 2002) and fish production (Bilby *et al.*, 1998).

As briefly mentioned above, the production of feces by stream dwelling animals is an important source of FPOM. The original food resources for these animals may be leaves, wood, fish carcasses, biofilm, algae, or other animals. The feces they produce are often of a characteristic size and shape depending upon species (Wotton *et al.*, 2003). Consumption of such particles by other organisms can render certain food sources available to consumers that may not have been able to process the original material (Wotton *et al.*, 2003). The nutritional quality of the feces is enhanced by microbes that colonize these particles following egestion (Cummins, 1974). The processing and repackaging of materials such that they augment another consumer's food resources (facilitation) is an example of a processing chain (Heard, 1994). In some cases, very fine organic matter particles (some small enough to be considered DOM) may be transformed into larger particles through production of feces. Some consumers, such as blackflies, strain very small particles from stream water, eat this material, and egest faecal particles much larger than the original material consumed (Wotton and Malmqvist, 2001). These FPOM particles can be subsequently eaten by other consumer species.

Organic matter input, export, and processing are greatly affected by disturbances, whether natural or anthropogenic. Disturbances affecting streams range in severity from relatively minor, predictable events, such as seasonal changes in flow, to less frequent, unpredictable, high-intensity events. Stream biota may be adapted to take advantage of predictable changes in organic matter input, such as seasonal input of leaf litter or deposition of salmon carcasses. However, severe disturbance events can fundamentally change the functional and structural properties of stream and riparian ecosystems and modify the amount, type, and/or timing of organic matter, wood, and nutrient delivery to small streams (Reeves, 1995).

Three types of catastrophic disturbance frequently affecting small streams in the PNW are flooding, fire, and debris torrents. Floods can impact stream organic matter dynamics by transporting stored particulate organic material downstream (Bilby and Bisson, 1992; Wallace *et al.*, 1995; Wipfli and Gregovich, 2002). Stored organic matter also might increase as a result of flooding, as large amounts of wood can be introduced into channels during storms, by both bank cutting and windthrow (Bisson *et al.*, 1987). Flooding in coastal areas and at lower latitudes in the PNW typically occurs during winter storms (Ziemer and Lisle, 1998). At higher elevations and latitudes and in noncoastal areas, high runoff typically occurs in spring and early summer, as much of the winter precipitation is stored as snow. Many rivers in the region are fed by glaciers, and these systems may experience high flows during warm summer weather. In non-glacial systems, high flows during late summer and autumn are very rare.

The frequency of occurrence of wildfires varies dramatically across the PNW. However, it is a major factor influencing small streams throughout the region. Fires recur at intervals of several centuries in the moist, coastal areas of the region, but fires may occur every few decades in the drier forests of the interior PNW (Agee, 1993). By altering the condition of the forests bordering small streams, fires affect input of terrestrial litter and large woody debris (Benda and Dunne, 1997). Loss of trees and other vegetation from along the stream reduces litter delivery and increases sunlight reaching the channel. Increased light can promote elevated primary production if nutrients are sufficient and effects from elevated UV radiation do not offset the benefit (Kelly *et al.*, 2003).

Storm events in the PNW often initiate landslides that generate debris torrents upon reaching steep stream channels. This process is more likely to impact small streams than larger ones due to the generally higher gradients of the smaller channels. Debris torrents remove much of the streambed substrate, organic matter, and riparian vegetation and may impact several kilometers of channel (Benda and Dunne, 1997). Large accumulations of wood and sediment form at the terminus of the torrent (Reeves *et al.*, 1995). Debris torrents often increase in frequency following fires as a result of the loss of soil cohesion as the roots of fire killed vegetation decompose (Benda and Dunne, 1997). As with fires, debris torrents alter organic matter dynamics and trophic structure in small streams. The simplification of the channel, removal of the source of terrestrial organic matter input, and exposure of the channel to sunlight cause autochthonous production of organic matter to dominate until the terrestrial vegetation growing along the

stream recovers to the point at which the channel is shaded (Lamberti *et al.*, 1991; Reeves *et al.*, 1995). The regrowing vegetation along debris torrented streams is typically deciduous, and this vegetation may persist for up to a century before being replaced by conifers.

HOW DO THESE PROCESSES DIFFER IN SMALL STREAMS VERSUS LARGE STREAMS?

Inputs and Retention

The relative importance of allochthonous and autochthonous organic matter sources generally changes with stream size (Vannote *et al.*, 1980). Small streams are often fully covered by a forest canopy. As a result, input of terrestrial litter and wood is similar to that received by the forest floor. In addition, the edge-to-area ratio is higher in the small streams; therefore, bankside inputs from litter being blown or washed into a small stream will be higher than in a larger channel. As stream size increases, the forest canopy does not cover the entire channel. As a result, terrestrial organic matter input decreases. These allometric relations indicate that small streams should have the highest organic matter inputs per unit area, relative to bigger streams in the same forest type and ecoregion.

In-channel production of organic matter typically varies inversely with terrestrial organic matter input. The shade provided by the covering forest canopy on small streams limits in-channel production of organic matter. The open canopy over larger channels enables more light to reach the stream, encouraging in-channel organic matter production. The systematic change in the predominant form of organic matter available to stream communities with changing stream size is one of the primary factors on which the river continuum concept (Vannote *et al.*, 1980) was based.

Standing stocks of organic matter in small streams of the PNW are estimated to be up to 25 kg dry weight per m² (Naiman and Sedell, 1979). A large percentage of this is of low nutritional quality, as most is wood, which has a high C:N ratio relative to smaller particles derived from leaves and feces (Naiman and Sedell, 1979).

Small streams tend to have a higher degree of roughness relative to their depth than larger streams (see Hassan *et al.*, 2005). The roughness is supplied both by inorganic substrate as well as large and small wood. Wood often makes up more than 90 percent of the organic matter stored in small streams (Naiman and Sedell, 1979; Bilby and Likens, 1980). In addition

to serving as a source of organic matter, wood influences the channel morphology through the formation of pools, depositional areas, and waterfalls (see Benda *et al.*, 2005). The effect of wood on channel structure influences the movement of organic particles through direct interception, creation of areas where organic material accumulates (Bilby and Ward, 1991; Webster *et al.*, 1999), and reduction of the transport efficiency of the channel through the formation of steps (Heede, 1979). The higher roughness and greater amounts of small and large wood per unit area in small streams, and especially streams bordered by forest, contribute to high rates of storage of particulate organic matter (Bilby and Bisson, 1998; Brookshire and Dwire, 2003). The storage occurs in pools, backwaters, debris jams, and traps under and behind cobbles and boulders. The significance of this process was illustrated in the McKenzie River watershed in Oregon, where CPOM storage in streams was directly related to the amount of wood in the channel and wood loading decreased with channel size (Naiman and Sedell, 1979). Similarly, Bilby and Ward (1989) reported that the amount of wood stored CPOM was about four times greater in channels less than 7 m wide than in channels more than 10 m wide for streams draining old-growth forests in western Washington.

Fine POM may constitute a large portion of the particulate organic matter pool in a small stream. This material can consist of fragments of leaves, feces of invertebrates (Wotton and Malmqvist, 2001), small wood fragments (Naiman, 1983), or flocs of DOM and very small particles (Petersen, 1986). There are large seasonal differences in the quality of these organic particles caused by the nature and timing of inputs of CPOM to small streams and increases in C:N of particles as organic matter is processed within a stream (Bonin *et al.*, 2000). For example, FPOM derived from wood typically has a high C:N and generally is a poor-quality food resource for consumers (Bilby, 2003), but FPOM derived from deciduous plant litter is of relatively high quality (Triska *et al.*, 1975). Forest age and type also may influence the quality of FPOM. The C:N of FPOM was found to be higher in old-growth forests in the PNW than in young forests (Bonin *et al.*, 2000).

Fine POM may be consumed by a large number of species and thus is an important resource in the food webs of streams. Naiman (1983) found that fine particles were generally of lower quality in terms of high C:N and of a larger size in smaller streams than larger channels. The diversity of particle types was found to increase downstream with increasing representation of algal cells in the FPOM.

Productivity of headwater streams is typically lower than that of larger channels for several reasons. These small channels are often heavily shaded by

overstory and understory vegetation, and the low light levels typically limit in-channel primary production (Fisher and Likens, 1973; Sedell *et al.*, 1975). The heavy shading coupled with the close association with ground water of many small streams produces lower water temperatures than in larger systems (Black, 2001). The low temperatures further limit productivity.

An additional factor influencing the productivity of small streams in the PNW is salmon. In recent years the contribution of marine derived nutrients and organic matter to streams along the northern Pacific coast of North America has received attention (Naiman *et al.*, 2002). In moderate sized streams supporting large spawning aggregations of Pacific salmon, the contribution can be enormous (Johnston *et al.*, 1997; Bilby *et al.*, 2003). However, by the definition of headwater streams used above, they provide limited spawning areas to Pacific salmon, and relatively few of these systems are likely to benefit from this upstream delivery process. However, in those small streams that do realize this subsidy, the impact on organic matter dynamics and productivity may be substantial (Naiman *et al.*, 2002). Streams that do not support salmon spawning may receive a small amount of marine derived nutrients carried upstream in the bodies of aquatic insects, bears, or other animals that consume carcasses (Cederholm *et al.*, 1989; Helfield and Naiman, 2001) or by insect eating birds (swallows, flycatchers) and bats. These animals distribute marine derived nutrients through the watershed by elimination of bodily waste. Although some of this material will ultimately make its way to headwater streams, the significance of this type of allochthonous organic matter to small streams is much less than it is for streams that support spawning fish. Studies by Chaloner *et al.* (2004) in Alaska have demonstrated that upstream reaches where Pacific salmon do not go have significantly lower productivity than downstream reaches where the salmon occur. Thus, most headwater streams may be more oligotrophic and less productive than downstream reaches where salmon carcasses can augment the availability of nutrients and organic matter.

Transport and Export

Most organic carbon is lost from small streams in the form of dissolved organic matter (actually colloidal in size), and up to 75 percent of export may be in this form (Benke *et al.*, 1988; Kiffney *et al.*, 2000). Fine POM makes up the next largest proportion, followed by CPOM. There also is variation in transport and storage of materials within the CPOM category. Estimates from small coastal streams in British

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Columbia suggest that 70 to 90 percent of leaf litter CPOM may be exported from streams during the year (Richardson, 1992b). However, only a very small proportion of the wood is typically exported (Bilby, 2003).

Transport efficiency of organic matter is influenced by discharge in small streams (Brookshire and Dwire, 2003). These streams transport relatively little FPOM or CPOM except at elevated flow (Bilby and Bisson, 1992; Wallace *et al.*, 1995; Wipfli and Gregovich, 2002). There are strong positive relations between rates of export of CPOM and instantaneous measures of discharge (Kiffney *et al.*, 2000). Lack of flow in ephemeral or intermittent channels essentially eliminates particulate organic matter transport at certain times of the year. Thus, there is the potential for large amounts of organic matter to be stored and transported only episodically. Even headwater channels that are usually perennially flowing may occasionally become intermittent during years of low precipitation, and this can result in increased storage that will be exported at a later time (e.g., Wallace *et al.*, 1995). Consumer organisms appear to be able to respond appropriately to changes in abundances of CPOM (Rowe and Richardson, 2001), suggesting that they have evolved a response to variation in the distribution and abundance of CPOM in small streams.

Despite the low transport capacity of headwater streams at low flow, in steep terrain periodically massive amounts of organic matter can be exported as a result of debris torrents (Keller and Swanson, 1979). Debris torrents are often triggered by a landslide that enters a small channel, propagating a wave of water, sediment, and organic matter that moves downstream until the channel gradient decreases. These events, although rare, can transport significant amounts of organic material, especially wood, to larger channels (May and Gresswell, 2003).

Transport in larger channels is also flow-related, but transport rates, especially of FPOM, are much higher and more constant than those in headwater channels at low and moderate flow levels. Export of fine particles from small catchments may be quite rapid, with export closely coupled to the timing of inputs and relatively low storage rates (Bonin *et al.*, 2003). Fine POM transport by small streams also has been shown to exhibit strong hysteresis, with concentrations at a given flow on the rising limb of a hydrograph being much higher than at the corresponding flow on the falling limb (Bilby and Likens, 1979; Wallace *et al.*, 1995). Thus, particulate organic matter transport tends to be more temporally variable in small streams than in larger reaches.

Coniferous trees predominate in forests of the PNW and in most other locations in western North America and the boreal region. Although deciduous trees are present, especially along larger stream channels, conifers generate most of the litter delivered to small streams in the region (Bilby and Bisson, 1992). Most research on organic matter dynamics has occurred in eastern North America and other regions where the predominant forest trees are deciduous (e.g., Webster *et al.*, 1999). These regional differences in vegetation may have a significant effect on organic matter dynamics in small streams, a pattern predicted by Ross (1963).

Leaves and Needles

The decomposition of conifer needles is generally slower than for most deciduous leaves (Webster and Benfield, 1986). The few studies of conifer needle breakdown have supported this view (Sedell *et al.*, 1975; Robinson *et al.*, 2000; Richardson *et al.*, 2004). There are several reasons that needles exhibit a lower rate of decomposition than leaves. Conifer needles typically possess a tough outer layer that retards microbial colonization. They also tend to have lower levels of nutritionally significant elements than deciduous litter. In addition, some needles contain protective chemical compounds that reduce the use of the tissue by fungi or bacteria (Quinn *et al.*, 2000). These factors affect the rate of development of microbial fauna on the needle, thereby decreasing the rate of degradation by decomposition.

Litterfall inputs to streams of the coniferous forests (Table 1) are somewhat less seasonal than those in deciduous forests. In the Hoh River Valley the highest input rates of senescent litterfall were during July to October (also see Table 1 in Edmonds and Murray, 2002). Litterfall from conifers can enter as green needles, although Edmonds and Murray (2002) report that only 3 percent of inputs were in that form. Inputs of litter from western red cedar during the autumn were about 65 percent of the total for that species based on three streams in British Columbia (two years of sampling), but the remaining 35 percent mostly entered during winter and spring (Figure 1). Hemlock and Douglas fir only dropped 19 percent of their annual inputs to streams during the autumn, with over 62 percent entering in spring and summer. Litter from deciduous trees in the PNW also may be less seasonal than in other regions. Red alder (*Alnus rubra*), a common deciduous tree in the PNW, drops green leaves throughout the growing season and can

TABLE 1. Input of Terrestrial Particulate Organic Matter and Instream Organic Matter Production in Streams of Varying Size (modified in part from Bilby, 1988).

Location	Order	Terrestrial Inputs (g/m ² /yr)	In-Stream Inputs (g/m ² /yr)	Percent Terrestrial of Total
WS 10, Andrews Forest, Oregon ¹	1st	477	5.3	98.9
Spring Creek, Mayfly Creek, and Blaney Creek, British Columbia ²	2nd	201-481	–	–
Bear Brook, New Hampshire ³	2nd	555	2.1	99.6
Fort River, Massachusetts ⁴	4th	384	609	38.6
Tributaries of the Hoh River, Washington ⁵	1st	359	–	–

¹Sedell *et al.*, 1975.

²Richardson, 1992b.

³Fisher and Likens, 1973.

⁴Fisher, 1977.

⁵Edmonds and Murray, 2002.

contribute a large proportion of its litter during summer periods, about 29 percent in the case of three small streams in British Columbia (Richardson, 1992b).

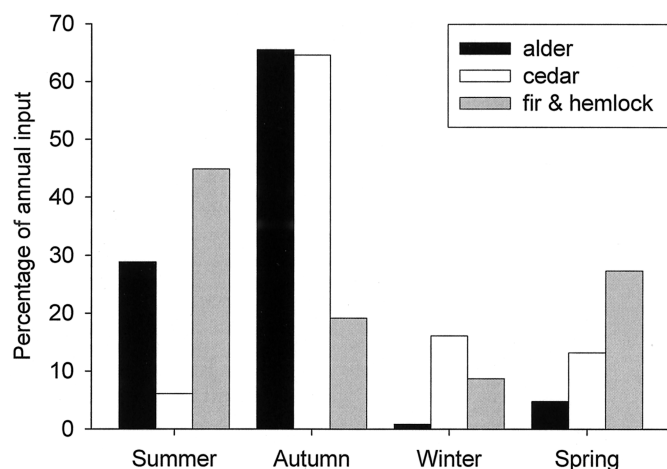


Figure 1. Average Seasonal Inputs of Leaf Litter as a Percentage of the Annual Total for Red Alder, Western Red Cedar, and Hemlock and Douglas-Fir (combined) Along Three Small Streams in Southwestern British Columbia. Data represent the averages for two years of litterfall data (methods in Richardson, 1992b). The amounts are based on litter dry mass.

The predominance of needles in the litter input to PNW streams also may influence CPOM transport rates. Conifer needles differ from deciduous leaves in how easily they are trapped along the stream channel. The large surface area and flexibility of deciduous leaves promotes capture on or around rocks, wood, or other channel roughness features, while small, stiff conifer needles “bounce” off most surfaces (Trent Hoover, University of British Columbia, January 2005, personal communication).

Despite the generally lower food value of needles, this material is utilized by stream biota (Richardson *et al.*, 2004). Needles are used by some stream invertebrates for nondietary purposes. Some larval caddisflies use needles in their case building. *Ecclisomyia conspersa* larvae always incorporate needles of species such as hemlock or Douglas fir into their cases, and early stages of *Dicosmoecus* spp. make their cases almost exclusively of conifer needles. Needles do provide an important food resource in streams as well. Although it takes longer for a microbial community to develop on needles than on deciduous litter, once a microbial community is established the nutritional value of needles to invertebrates increases substantially. Certain invertebrates may be able to consume needles even before they are fully conditioned by bacteria and fungi. Some chironomid larvae appear to burrow into needles consuming the tissue along the way. The fact that needles can make an important contribution to the structuring of aquatic communities of small streams was demonstrated by a study in the eastern United States where streams flowing through eastern hemlock stands in serious decline supported different aquatic communities than those streams in areas where hemlock was still predominant (Snyder *et al.*, 2002).

In addition to the relatively refractive nature of needles when compared with deciduous litter, organic matter decomposition rates in PNW streams also are depressed by low stream water nutrient concentrations and temperature. Nutrients from external sources supplement those contained by organic matter particles and accelerate microbial decay (Cowling and Merrill, 1966). Experimental additions of both N and P to stream water have accelerated the decomposition rate of organic matter (Mellilo *et al.*, 1983; Aumen, 1985). Nutrient levels in many PNW streams are low relative to other regions in North America

(McClain *et al.*, 1998). Water temperatures in this region also tend to be low relative to many other areas in North America (Beschta *et al.*, 1987), further slowing decay rate of organic matter in streams.

Wood

The coniferous trees that predominate in forests of the PNW tend to attain very large size. Coastal redwood, Douglas fir, Sitka spruce, western red cedar, and several other species common in the region can attain heights of over 150 m and diameters of more than 1 m. These large trees can deliver large pieces of wood to the streams that are stable (even at high flows) and often provide a foundation on which smaller pieces of wood can gather (Bisson *et al.*, 1987). As a result, wood has a more pervasive effect on stream ecosystem structure and function in this region than in most other forested areas of North America. For example, in New England streams wood is relatively rare in streams with channels wider than 6 m (Bilby, 1979), but wood is a major feature even in relatively large rivers in the PNW (Abbe and Montgomery, 2003; Meleason *et al.*, 2003). Although wood likely played a more prominent role in streams in eastern North America prior to the removal of the original forest, the fact that the trees in the PNW are capable of reaching much larger diameter and greater height suggests that even prior to human influence this regional difference existed.

The large size of the wood pieces delivered to streams in the PNW, coupled with the fact that many of the species common in the region are resistant to decay (Harmon *et al.*, 1986), enables wood to persist for a long time. The use of dendrochronological and ¹⁴C dating has demonstrated that pieces of wood often last more than a century, and pieces up to 1,400 years old have been identified (Hyatt and Naiman, 2001). In small streams, the lack of capacity for the channel to transport large wood further contributes to its longevity (Bilby and Bisson, 1998). Thus wood likely enjoys a longer "lifespan" in streams of the PNW than would be the case in many other forested regions of the world (Bilby, 2003).

Stream Roughness and Gradients

Streambeds on steeper terrain of the PNW typically consist of large rocks, which can contribute to the storage of organic matter beneath or behind them in streams. In a manipulation of boulder placements in a small stream, the addition of structural elements resulted in a large increase in the storage of organic

matter (Negishi and Richardson, 2003). Brookshire and Dwire (2003) demonstrated that wood in streams was a predominant feature in the retention of CPOM in headwater streams, and in meadow streams there was low retentiveness associated with lower wood amounts. These processes of organic matter retention are not unique to the PNW and have been shown in other regions. However, the size of the wood and the general large size of the streambed substrate in many PNW systems suggest that POM retention by these mechanisms may be particularly efficient in this region.

Water flowing across low lying, wet areas of the forest floor during storm events delivers organic matter to small streams from considerable distances from the stream edge. This may not be unique to streams of the PNW but perhaps only to areas with high rainfall intensities. The contributions of these very small, ephemeral channels to larger (more perennial) streams have not been quantified, but they appear to be capable of transporting CPOM to larger streams during storm events. It is unlikely that this is as important a process as may be experienced in other regions with soils having lower infiltration capacity and higher intensity rainfall events than in the PNW.

No processes of organic matter delivery, processing, or export are unique to the Northwest. Rather, the differences in organic matter dynamics between this region and other forested areas are primarily in rates and timing of these processes and the way the processes vary with position in the drainage network. Nevertheless, these differences do have implications for the timing, amounts, and quality of resources available to consumers. These regional variations in organic matter resource dynamics may generate different phenology and life history tactics and alter population dynamics and community composition (Richardson, 2001). These attributes of stream communities have not been compared between streams of the PNW and the temperate deciduous regions where most of the research has taken place.

Natural Disturbance Regimes

The types, intensity, and frequency of natural disturbances that influence streams in the PNW vary somewhat from disturbance regimes in other regions of North America. This region has a wide variation in hydrologic regimes (Ziemer and Lisle, 1998). Lower elevation and latitude systems are rain dominated, while those at higher latitudes and elevations and across much of the interior PNW are snowmelt dominated systems. Many high mountain small streams are fed primarily by glacial melt water. The seasonal

timing of high flows varies among these hydrologic regimes. Rain dominated systems are most likely to be impacted by flood flows during winter, snow melt systems during spring and early summer, and glacial systems during midsummer. Landslides and debris torrents are more common in the PNW than many other regions. Fires also are very common in some areas of the PNW (Agee, 1993) and have a much greater influence on small streams in the drier parts of this region than they do in watersheds in eastern North America. Organic matter input, transport, and processing may be altered for more than a century as a result of both fires and debris torrents (Reeves *et al.*, 1995; Benda and Dunne, 1997).

Anadromous Fishes

The great abundance (at least historically) of anadromous fishes in PNW watersheds distinguishes this region from most others in North America. Many of these fishes die after spawning, and the reproductive products and carcasses of spawners can contribute large amounts of organic matter and nutrients to streams (Naiman *et al.*, 2002). Some spawning by these fishes does occur in small streams, but most small streams have insufficient flow or inappropriate substrate to support spawning. However, carcasses can make a substantial contribution of organic matter and nutrients to the small streams that are utilized (Bilby *et al.*, 1998). This topic has been extensively studied over the past decade, but many questions regarding the impact of the organic matter subsidy provided by these fishes on small stream productivity remain to be investigated.

WHAT ARE THE EFFECTS OF FOREST MANAGEMENT AND HARVESTING ON ORGANIC MATTER DYNAMICS IN SMALL STREAMS OF THE PACIFIC NORTHWEST?

Removal of trees from along a stream during forest harvesting or land clearing prior to development alters the amount and type of terrestrial organic matter delivered to the channel. A study in western Washington demonstrated that litter delivery to a stream flowing through a logged area received about 20 percent of the litter delivered to a nearby stream flowing through an old-growth stand (Bilby and Bisson, 1992). The type of material delivered to these two streams also changed. In the old-growth system, the vast majority of terrestrial organic matter input to the channel was small pieces of wood and needles. In

contrast, about 90 percent of the material input to the stream in the logged area was leaves from deciduous trees, shrubs, and herbaceous vegetation. The alteration in the type of organic matter also altered the timing of input. Input at the old-growth site was relatively evenly distributed over the year, with needle input dominating during the summer and autumn and wood delivery dominating during the winter. The greatest amount of organic matter delivery to the stream in the logged area occurred from September through November, during leaf fall. The decrease in litter production at the logged site was partially offset by an increase in autotrophic production by algae in the stream (Table 2). However, total organic matter delivery to the old-growth site was still nearly double that at the logged location.

TABLE 2. Organic Matter Inputs to Two Stream Reaches in Western Washington, One Flowing Through a Logged Area the Other Through an Area With Old-Growth Forest.

	Organic Matter Input (g/m ² /yr)			
	Logged Site		Forested Site	
	1982-83	1983-84	1982-83	1983-84
Allochthonous Inputs	59	60	325	296
Autochthonous Inputs	185	167	111	109
Total	244	227	436	405

Notes: All trees along the stream channel were cut at the logged site. This study was conducted prior to the enactment of laws requiring the retention of standing trees along streams during logging (modified from Bilby and Bisson, 1992).

In the PNW the widespread conversion of the landscape to managed forest has led to an increase in the occurrence of deciduous forests along streams. Perhaps the most common tree species colonizing stream-side areas after logging in this region are red alder (*Alnus rubra*) or Sitka alder (*A. sinuata*). These species fix nitrogen, and the low C:N litter they produce tends to decay very rapidly. Headwater streams flowing through young stands of red alder have been shown to contain substantially more aquatic invertebrates than streams flowing through young conifer stands (Piccolo and Wipfli, 2002). The elevated invertebrate production in this study was attributed to the higher nutritional quality, and perhaps the higher surface area relative to mass, of the litter produced by the alder. Young, regenerating forests can also produce higher-quality fine particulates than old-growth forests, based on particles collected at the catchment outlet (Bonin *et al.*, 2003). Alder wood also breaks down more quickly than conifer wood (Bilby *et al.*, 1998) and contributes wood fragments and the biofilm

they support. The significance of these processes to overall stream productivity has yet to be adequately demonstrated. Alder also can add significant amounts of N to riparian forest soils, leading to elevated N concentration in stream water (Edmonds, 1980). Such increases in N can contribute to elevated autochthonous production (Stockner and Shortreed, 1978). The above changes in the quality of litter inputs after harvesting can result in the overall higher productivity noted in streams draining younger forests (Piccolo and Wipfli, 2002).

Larger peak flows may result from forest harvesting (see Moore and Wondzell, 2005), although this response is not unique to the PNW. If logging does occasionally increase peak flows, one might expect greater export rates of organic matter from headwater streams. These peak floods also tend to reduce channel complexity, reducing the storage capacity of a stream channel for organic matter. The evidence for a direct relation between forest harvest and peak flows is still uncertain, with the exception of evidence of large rain-on-snow peaks in areas with transient snow zones (Ziemer and Lisle, 1998; Moore and Wondzell, 2005).

Several other factors also could contribute to reduced organic matter storage in streams flowing through logged areas. The reduction in input rate is a major factor, and the alteration in the type of organic matter from relatively decay-resistant needles to leaves would lead to faster decomposition rates. Decay rate could be further accelerated by increased temperatures during the summer resulting from canopy removal (Anderson and Sedell, 1979; Short and Ward, 1980; Richardson, 1992a). Even a small increase in stream temperature could have large impacts on organic matter standing crops by changing the rates of breakdown (Karlsson *et al.*, 2005). Finally, a reduction in wood delivery to the channel after logging will diminish storage capacity for particulate organic matter. Bilby and Ward (1989) found that CPOM associated with wood decreased about tenfold following logging along small streams in western Washington. The combination of increased decay rate and accelerated transport could produce a substantial reduction in stored organic matter.

Logging, or any disturbance that removes the forest canopy, initiates a sequence of changes in the organic matter dynamics of headwater streams. The changes in these processes through time are driven by succession of the streamside forest and can persist for decades. In many areas of the PNW, red alder colonizes recently logged riparian areas. This species typically lives for 50 to 60 years and eventually is replaced by shade-tolerant conifers that establish under the alder canopy. The nature and amount of organic matter delivered to the stream as the riparian

stand conditions adjacent to the channel change through time will vary considerably, changing from leaves to needles and from small pieces of rapidly decaying wood to large, decay-resistant conifer wood. The changes in organic matter dynamics created by conversion of coniferous forests to alder dominated riparian areas after forest harvesting also influences the composition of the stream invertebrate community (Piccolo and Wipfli, 2002).

FUTURE DIRECTIONS FOR ORGANIC MATTER STUDIES IN THE PACIFIC NORTHWEST

It is noted above that wood not only contributes structurally to small streams but in itself is a source of organic matter. Anderson *et al.* (1978) demonstrated that a number of stream invertebrates consume wood. The nutritional value of wood is poor relative to most other types of organic matter (Bilby, 2003); however, wood contributes the largest proportion of the standing stock of organic matter in streams. The extent to which wood contributes to the total system energy flux that supports consumer growth is unknown. However, there are species of stream invertebrates that appear to be exclusively xylophagous (e.g., the beetle *Lara avara* and some tipulids) (Dudley and Anderson, 1982). Thus, wood (and its accompanying biofilm and microbial flora) can support invertebrate growth. As wood decomposes, it fragments into small pieces. Some of this material is stored in the stream, and some is transported as seston. The importance of this material to the microbial and macroconsumer production in streams is unknown but potentially large due to the vast amount of organic matter stored as wood in small streams (Bilby and Likens, 1980). A better understanding of the importance of wood in stream trophic dynamics is needed, including some understanding of the variation among tree species in the nutritional quality of wood.

Organic matter varies qualitatively among categories (wood, CPOM, FPOM, DOM) but also by species. Studies of consumer growth on different kinds of conditioned leaf litter have demonstrated large differences in growth rates (e.g., Sweeney and Vannote, 1986). However, there are few growth studies for any coniferous litter.

The PNW has large topographic relief and variation in local climate affecting forest composition and productivity. Bonin *et al.* (2000) found variation in the quality of FPOM related to elevation, forest age, and vegetation composition. These sources of variation are not well documented in general but may contribute to differences among streams in productivity

and community composition. These larger scale factors that drive patterns of forest composition, condition, and age should have effects on organic matter dynamics and stream biota. However, these linkages remain only poorly understood.

Leachates from different species of leaves differ considerably in composition and their support of bacterial production, with more than an order of magnitude difference in productivity, depending on litter source (McArthur and Richardson, 2002). Future studies should explore the variability of leachates from several species and how these differences affect instream productivity.

Much of the nutritional value of POM has been assumed to be provided by the biofilms and the fungi and bacteria they contain that encrust the particle. However, the extent to which organismal growth is actually supported by nutrition from the biofilm versus that derived from the particle substrate has never been thoroughly examined. Results of a recent study of the growth of crayfish displayed no difference in growth rate between specimens raised on leaf litter versus wood of red alder (Bondar and Richardson, unpublished manuscript), indicating that the sustenance achieved through these disparate sources may not differ substantially despite the difference in the nutrient content of the original source of the organic matter. This finding indicates that organisms are obtaining much of their nutrition and energy for growth through ingestion of the biofilms on the CPOM. Additional research on this question is required before the relative importance of the biofilm is understood.

CONCLUSIONS

The high relative inputs of organic matter and the high rates of storage in headwater streams support the conclusion that these channels are important sources of organic matter to downstream reaches (Wipfli and Gregovich, 2002). The retentiveness of these streams enables them to process organic matter on site, changing the form and nutritional characteristics of organic matter exported from these systems. While nearly all particulate organic matter delivered to headwater channels is delivered as CPOM, including wood, the greatest quantity of exported particulate organic matter is in the form of FPOM (Bilby and Likens, 1980). Thus, within these networks of headwater channels, organic matter is transformed into forms more readily used by much of the biota residing in larger stream channels.

The associations of stream communities with the vegetative composition of their watersheds, particularly of the riparian areas, were predicted by Ross (1963), Hynes (1975), and others. Aspects of organic matter physical attributes (size and toughness) and nutrient content can have profound influences on the types and productivity of organisms that inhabit a stream reach. For example, the storage of large quantities of organic matter in small streams promotes high productivity of many detritivores. Shredders, in particular, typically reach their highest productivity in small streams. There are very few studies that document changes in stream community characteristics as a result of alterations in the characteristics of the surrounding vegetation at a single site. However, there is increasing evidence that changes in vegetation do appear to be correlated with alterations in macroinvertebrate communities, such as those associated with conversion from conifer to alder dominated streambanks (Piccolo and Wipfli, 2002). This predicted relationship is likely to be broadly applicable to small streams everywhere, but in the remaining old-growth forests of the Pacific coastal ecoregion there is an opportunity to test this better than in many other parts of the world.

Small streams of the Pacific coastal ecoregion appear to differ in some key aspects from other small streams, but most of the differences are in rates of the main processes. Organic matter in all its forms is as important to small streams of the Pacific coastal ecoregion as other places where it has been considered. Key differences include the dominance of coniferous trees with needles of different physical and chemical properties from deciduous species, as well as a different phenology of leaf (needle) input that is not as strongly autumnal as for most deciduous species. The consequences of these differences are not all obvious, but some of the effects that can differ from small streams of other regions might be predictable.

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