7

Detrital Energy and the Decomposition of Organic Matter

The decomposition of organic carbon provides key energy inputs to most food webs, and this is especially true in fluvial ecosystems. These energy pathways are referred to as detrital or detritus-based, and the immediate consumers of this material are decomposers and detritivores. Detritus includes all forms of non-living, organic carbon including fallen leaves, the waste products and carcasses of animals, fragments of organic material of unknown origin, and organic compounds (Table 7.1). Some of this material originates within the stream (autochthonous), such as dying macrophytes, animal carcasses and feces, and extracellular release of dissolved compounds, and some is transported into the stream from outside the channel (allochthonous), such as leaf fall, soil particulates, and compounds dissolved in soil water. Carbon entering streams through detrital pathways can be stored, exported, or respired from a given reach. Estimates suggest that microbial decomposition of allochthonous detritus is responsible for a net efflux of more than 2 Pg C yr^{-1} globally from freshwater systems (Raymond et al. 2013; Battin et al. 2009). In many streams, energy derived from detrital resources can substantially exceed the energy fixed within streams by photosynthesis.

The division of non-living organic energy sources into size classes is widely employed in studying detrital dynamics in streams. The usual categories are coarse particulate organic matter (CPOM, > 1 mm), fine particulate organic matter (FPOM, < 1 mm and > 0.45 μm) and dissolved organic matter (DOM, < 0.45 μm). Each category can be divided further, but the dividing lines are arbitrary. Processes influencing the breakdown of forest leaves that enter steams, a dominant category of CPOM, have received extensive study and are comparatively well understood. FPOM can originate in a number of different ways but its origin and quality as a food resource can be difficult to establish. DOM, often referred to as dissolved organic carbon (DOC), likewise can be challenging to study; its entry into food webs is largely due to uptake by microbes in biofilms occurring on the stream bed and other surfaces, discussed in detail in Chap. 8. Regardless, it is clear that the dynamics of organic matter in streams are complex, microorganisms are critical mediators of organic matter processing, and climate conditions and the surrounding landscape significantly influence what takes place within the stream.

Detrital inputs moving across ecosystem boundaries from terrestrial, marine, and other freshwater habitats generate substantial sources of energy and nutrients in streams. Often referred to as "spatial subsidies" (Polis et al. 1997), the physical and chemical characteristics, quantity, timing, and duration of resources entering streams from other systems generate spatial and temporal variation in the availability of nutrients and energy, the distribution and abundance of aquatic organisms, and the rates of biogeochemical processes in rivers and streams (Marcarelli et al. 2011; Subalusky and Post 2019). Subalusky and Post (2019) developed an effective conceptual framework with which to examine interactions between spatial subsidies and the characteristics of donor and recipient systems that can be modified for our detrital discussion (Fig. 7.1). This figure highlights how the net impact of allochthonous subsidies on stream ecology is influenced by the size, species diversity, productivity, resource availability, and seasonality of both the donor and recipient systems, and the characteristics of the resources crossing ecosystem boundaries. Examining the large body of research about detrital resources through this conceptual lens is an effective way to begin to understand how the structural and functional integrity of streams depends on upstream, downstream, and lateral connectivity with other systems.

In this chapter we review the principal factors influencing the physical and chemical characteristics, quantity, timing, and duration of detrital inputs into streams, and the physical, chemical, and biological characteristics of streams that mediate the decomposition of organic matter (Fig. 7.2). Some of the concepts in this chapter are revisited or described in further detail in other sections of the book,

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Table 7.1 Sources of organic matter (OM) to fluvial ecosystems. Much OM originates outside the stream reach where it is measured. Some (sources marked with an asterisk) is produced by photosynthesis within the stream and subsequently enters the pools of dissolved or particulate OM

Sources of Input	Comments
Coarse particulate organic matter (CPOM)	
Leaves and needles	Major input in woodland streams, typically pulsed seasonally
Macrophytes during dieback*	Locally important
Woody debris	May be major biomass component, very slowly utilized
Other plant parts (flowers, fruit, pollen)	Relatively little information available
Other animal parts (feces and carcasses	Relatively little information available
Fine particulate organic matter (FPOM)	
Breakdown of CPOM	Major input where leaf fall or macrophytes provide CPOM
Feces of small consumers	Important transformation of CPOM
From DOM by microbial uptake	Organic microlayers on stones and other surfaces
From DOM by physical-chemical processes	Flocculation and adsorption, probably less important than microbial uptake route
Sloughing of algae*	Of local importance, may show temporal pulses
Sloughing of organic layers	Relatively little information available
Forest floor litter and soil	Influenced by storms causing increased channel width and inundation of floodplain, affected by overland versus sub-surface flow
Stream bank and channel	Little known, likely related to storms
Dissolved organic matter (DOM)	
Groundwater	Major input, relatively constant over time, often highly recalcitrant
Sub-surface or interflow	More important during storms
Surface flow	Possibly important during storms causing overland flow
Leachate from detritus of terrestrial origin	Major input, pulsed depending upon leaf fall
Throughfall	Smaller input, dependent on contact of precipitation and clouds with canopy
Extracellular release and leachate from algae*	Of local importance, may show seasonal and diel pulses
Extracellular release and leachate from macrophytes*	Of local importance, may show seasonal and diel pulses

especially the segments devoted to carbon dynamics, microbial ecology, and trophic interactions.

7.1 Inputs, Storage and Transport of CPOM

7.1.1 Sources of CPOM

Leaves and wood are the principal inputs of allochthonous CPOM to many streams, although other plant products, aquatic macrophytes, terrestrial invertebrates, and decomposing animal tissue also contribute to the total volume (Wenger et al. 2019; Webster et al. 1995; Wallace et al. 1995; Wipfli and Baxter 2010; Dalu et al. 2016). In some systems, macrophytes and algae from upstream may also represent important sources of energy and nutrients under certain conditions. The lability (referring to ease and speed of chemical transformation) and origin of particulate organic matter (POM), and the spatial and temporal distribution of particulate inputs, are highly variable among systems (Tank et al. 2010). Stream ecologists use the terms “standing stocks” or “standing crops” to describe the volume of POM in stream at a given time. The climate and land use history of a watershed strongly influence the lability, quantity, timing, and duration of allochthonous inputs entering a system (Thomas et al. 2016). Streams moving through forested landscapes in relatively undisturbed systems typically have greater inputs of POM (Golladay 1997; Webster et al. 1990). Heterotrophic microorganisms and other consumers utilize these carbon sources, and in some settings, allochthonous detritus is what fuels stream metabolism. Instream primary production

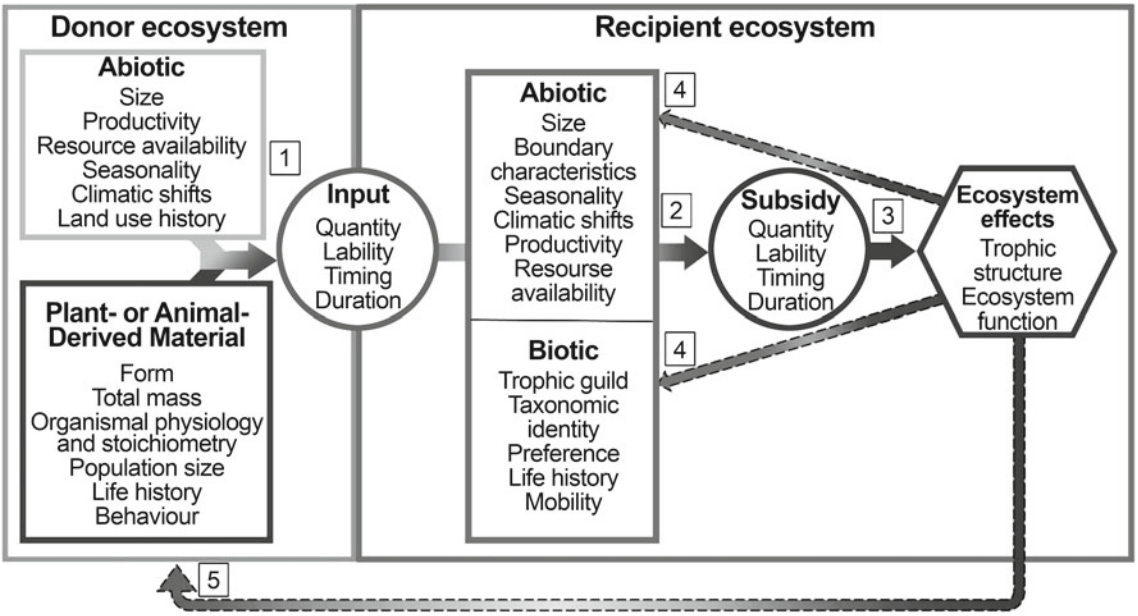


Fig. 7.1 Conceptual framework to consider the effects of detrital subsidies on ecosystem processes. (1) The abiotic features of the donor ecosystem will interact with characteristics of the plant- or animal-derived material and affect the quantity, lability, timing and duration (QLTD) of a given input to the system to the recipient ecosystem. (2) Resource inputs interact with the biotic and abiotic characteristics of the recipient systems to produce the QLTD of the resource subsidy. (3) The QLTD of the subsidy governs the ecosystem effects in the recipient ecosystem. (4) Changes in ecosystem processes in the recipient system alter the conditions that influence the QLTD of future subsidies, as there may be important feedbacks in certain abiotic and biotic conditions in the recipient system in response to the initial changes in ecosystem processes. (5) Changes to ecosystem processes in the recipient ecosystem may also generate feedback into the donor system that influence the QLTD of future inputs to the recipient system. (Modified from Subalusky and Post 2019)

may contribute to DOM pools by extracellular release after sloughing and dieback, and be incorporated into POM by microbial uptake, so the separation of allochthonous versus autochthonous sources can be imperfect.

Research examining CPOM dynamics has focused primarily on estimating changes in direct (vertical and upstream) inputs to stream surfaces. In contrast, much less work has been devoted to understanding within and among system variability in inputs from beyond the stream's banks (lateral); yet, in some systems they can represent a large proportion of the total. The timing, duration, and volume of lateral inputs depend on many factors including, but not limited to, wind patterns, precipitation regimes, bank slope, underlying geology, groundcover, litter accumulation, litter humidity, and the distance between the stream and the forest (Kochi et al. 2010; Tonin et al. 2017). Physical, chemical (e.g., leaching), and biological (e.g., microbial conditioning) processes in the terrestrial environment influence the characteristics of lateral inputs entering streams and may have subsequent impacts on ecosystem-level processes such as litter decomposition, ecosystem metabolism, and biomass production of higher trophic levels, termed secondary production (Tonin et al. 2017). In a study comparing leaf-litter decomposition rates between lateral and vertical inputs of leaf litter in third order stream in central Portugal, Abelho and Descals (2019) documented negative relationships between the length of litter exposure in terrestrial habitats and in-stream decomposition rates. Invertebrate colonization also tended to decline with increasing terrestrial exposure; however, the richness and biomass of invertebrates were more influenced by litter type than by whether litter originated from lateral or vertical inputs. These authors also measured the response of aquatic fungi, finding that the aquatic hyphomycete species richness of the community colonizing leaf litter and fungal sporulation rates were negatively related to the length of time spent by litter in the terrestrial environment.

In a review of litter inputs to streams of the eastern US by Webster et al. (2006), lateral inputs were estimated to contribute roughly one-fourth of the total CPOM. This is consistent with an estimate of about 30% of total inputs from lateral sources in a review of 18 streams from different biomes and continents by Benfield (1997). Lateral inputs can be especially dominant in some systems. For example, in the Ogeechee River, a blackwater river in the southeastern US, lateral inputs were fourfold greater than direct inputs, probably because the width of the river minimized direct litterfall, and floodplain inundation maximized inputs from

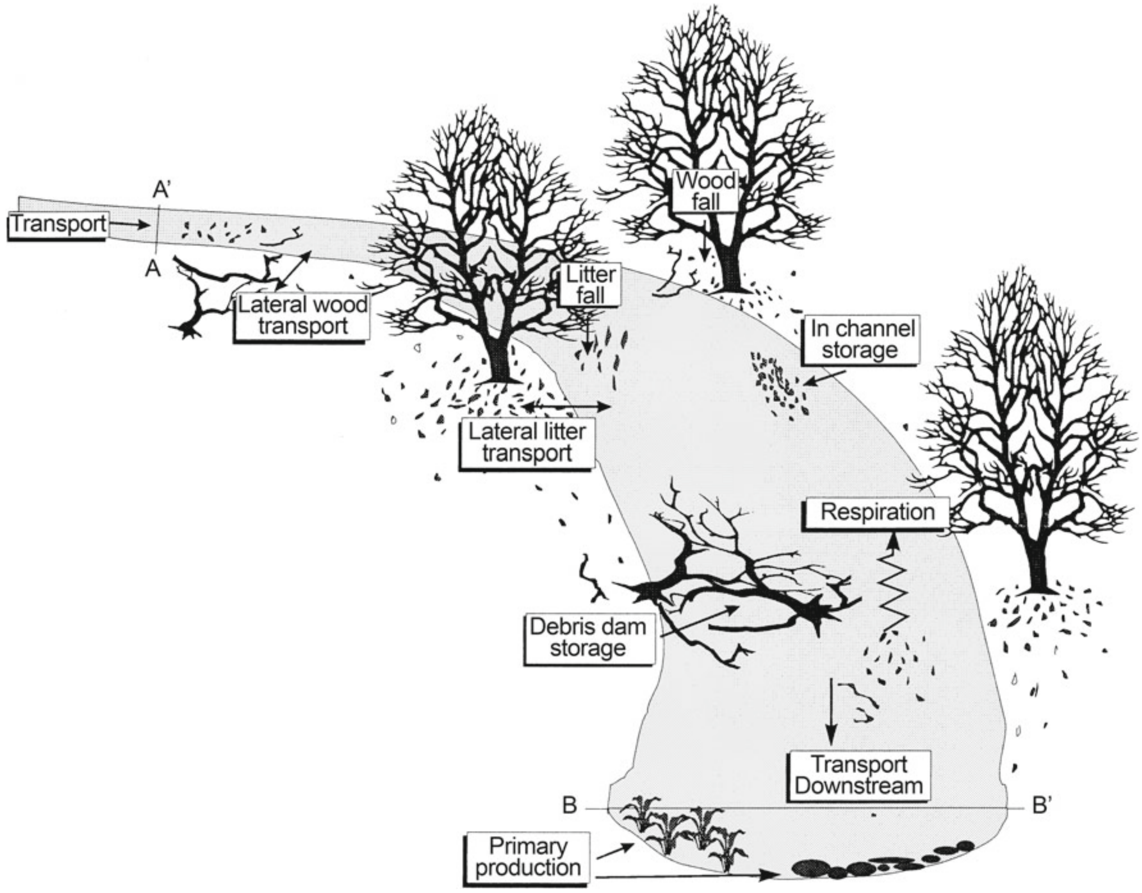


Fig. 7.2 Inputs, outputs and standing stocks of coarse particulates for a forest stream segment defined by the transects A–A' and B–B' (Reproduced from Minshall 1996)

outside of the channel. Lateral inputs, which were associated with increased precipitation and steep bank slopes, dominated CPOM inputs in a third-order stream on Santa Catarina Island in southern Brazil (Lisboa et al. 2015). The contribution of lateral inputs to CPOM can vary widely, even at smaller spatial scales. Work by Tonin et al. (2017) in streams from different tropical biomes emphasized the strong influence that local factors, including the density and diversity of riparian vegetation and site-specific topography, can have on the quantity, timing, and duration of lateral inputs.

The relative contribution of lateral and direct CPOM inputs often are temporally variable among systems. In temperate systems, seasonal variation in leaf inputs are common, with the greatest inputs occurring in the autumn, although lateral inputs of CPOM typically occur throughout the year. In an Austrian stream, direct CPOM inputs during the autumn contributed 61–65% of total inputs (Artmann et al. 2003). Similar results were obtained for a forest stream in Hokkaido, Japan, where leaf litter during October represented 58% of the annual inputs (Kochi et al. 2004). Additional seasonal variation in leaf fall can be attributed to diversity of terrestrial vegetation. In several small New Zealand streams, inputs of leaf litter peaked in the summer in streams running through native forest, but maxima were observed in autumn in pasture areas. In pine forests, litter inputs were lowest in the winter and peaked during the spring when large inputs of pollen heads were observed (Scarsbrook et al. 2001).

Litter inputs expressed per unit area of streambed are expected to decline as stream width increases, and be greater in warmer and wetter climates because of higher forest productivity. Inputs of CPOM are expected to decrease with increasing stream order owing to increasing stream width and lower retention. This is supported by data from first- through fourth-order streams throughout the US including Georgia-North Carolina (Wallace et al. 1982a), New Hampshire (Meyer and Likens 1979; Bilby and Likens 1980), and from sites in Michigan and Pennsylvania (Minshall et al. 1983). Litterfall inputs were less at fifth-order sites of a Pennsylvania stream compared with lower-order sites (Bott et al. 1985). However, the expected downstream decline in CPOM inputs has not been apparent in many comparisons, evidently because differences among sites in climate, floodplain connectivity, and anthropogenic influence exert a larger influence on CPOM dynamics. Blackwater streams of the southeastern US received very high litter inputs as a consequence of floodplain interactions. In contrast, litter inputs to desert and boreal streams can be relatively low.

Allochthonous sources of energy and nutrients are fundamental components of food webs and ecosystem processes in both temperate and tropical systems (Lamberti et al. 2017; Neres-Lima et al. 2017). In a comparison of litterfall estimates from 33 sites ranging from 78°S to 75°N and in six different biomes, Benfield (1997) concluded that litter inputs were primarily related to the presence of forested versus non–forested vegetation. However, litterfall was also positively related to annual precipitation and decreased with increasing latitude, reflecting the influence of climate on overall terrestrial productivity (Fig. 7.3). In a study of streams across three tropical biomes (Atlantic forest, Amazon, Cerrado) in Brazil, Tonin et al. (2017) found that larger litter inputs were associated with wetter climates among seasons, and litterfall in streams located in the two biomes with dry seasons (Amazon and Cerrado) was negatively related to increases in precipitation, indicating there was more litterfall in the dry season. Notably, this work highlighted the variability in the magnitude and timing of direct and lateral inputs of litter and the storage rates of OM among tropical biomes (Tonin et al. 2017).

Though dominant components, leaf litter and woody debris are not the only forms of OM inputs to rivers and streams. In some systems, macrophytes are important sources of OM in stream food webs. For example, OM surveys conducted seasonally in the Kowie River, a small temperate river, indicated that macrophytes significantly contributed to the pool of suspended particulates in the upper reaches of the stream (Fig. 7.4; Dalu et al. 2016). Animal movement may also introduce large pulses of OM into lotic systems from other habitats. A large body of work has examined the effects of marine- and lake-derived organic matter entering streams through the excretion, egestion, and the decomposition of gametes and carcasses of migrating fishes (e.g., Tiegs et al. 2011). Similarly, mass drownings of wildebeest (*Connochaetes taurinus*) commonly occur in the Mara River in Kenya during their annual migration, introducing more than 1,000 tons of biomass each year (Subalusky et al. 2017). In the same river system, hippos (*Hippopotamus amphibius*) contribute approximately 8,500 kg of terrestrially-derived OM to the river each day through their feces (Dutton et al. 2018). Though not as commonly studied, direct inputs of OM occur when animals in the riparian zone directly fall into streams, or via egestion when frass produced by insects in overhanging vegetation falls into the water below (Kochi et al. 2004). For instance, researchers have found significant changes in CPOM inputs and subsequent changes in nutrient dynamics and stream metabolism in response to periodic emergence of cicadas (Cicadidae: *Magicicada*) every 13–17 years (Menninger et al. 2008; Pray et al. 2009).

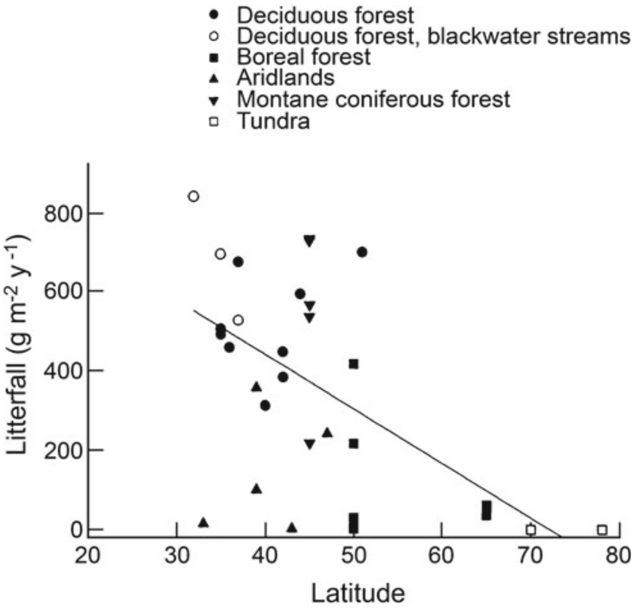


Fig. 7.3 A linear regression of litterfall versus latitude for 33 stream locations across six biomes (Reproduced from Benfield 1997)

7.1.2 Storage of CPOM

In relatively undisturbed systems, CPOM tends to be retained near the point of entry in the stream (Webster et al. 1994). This is particularly true in small streams (Golladay 1997). The retention of OM is affected by a number of stream features that vary with location and thus potentially determine the efficiency of a stream reach in processing inputs. Retention is likely to be greatest when current velocity is low, when boulders or other channel features create depositional locations and cause accumulation of organic material, when macrophyte beds reduce water velocity, and when floodplain connectivity allows flooding rivers to overflow their banks, slowing the passage of water and material downstream. By increasing the retentiveness of stream reaches, such features should increase the amount of organic matter respired by the consumer community and decrease the amount exported downstream. As retention varies among locations, seasons, or stream types, so should the relationship between processing and export.

The benthic storage of OM on or within the stream bed is influenced by the magnitude of terrestrial organic matter inputs and by the retention capacity of the river channel (Jones 1997). Wood generally comprises the largest proportion of stored OM (Pfeiffer and Wohl 2018), followed by

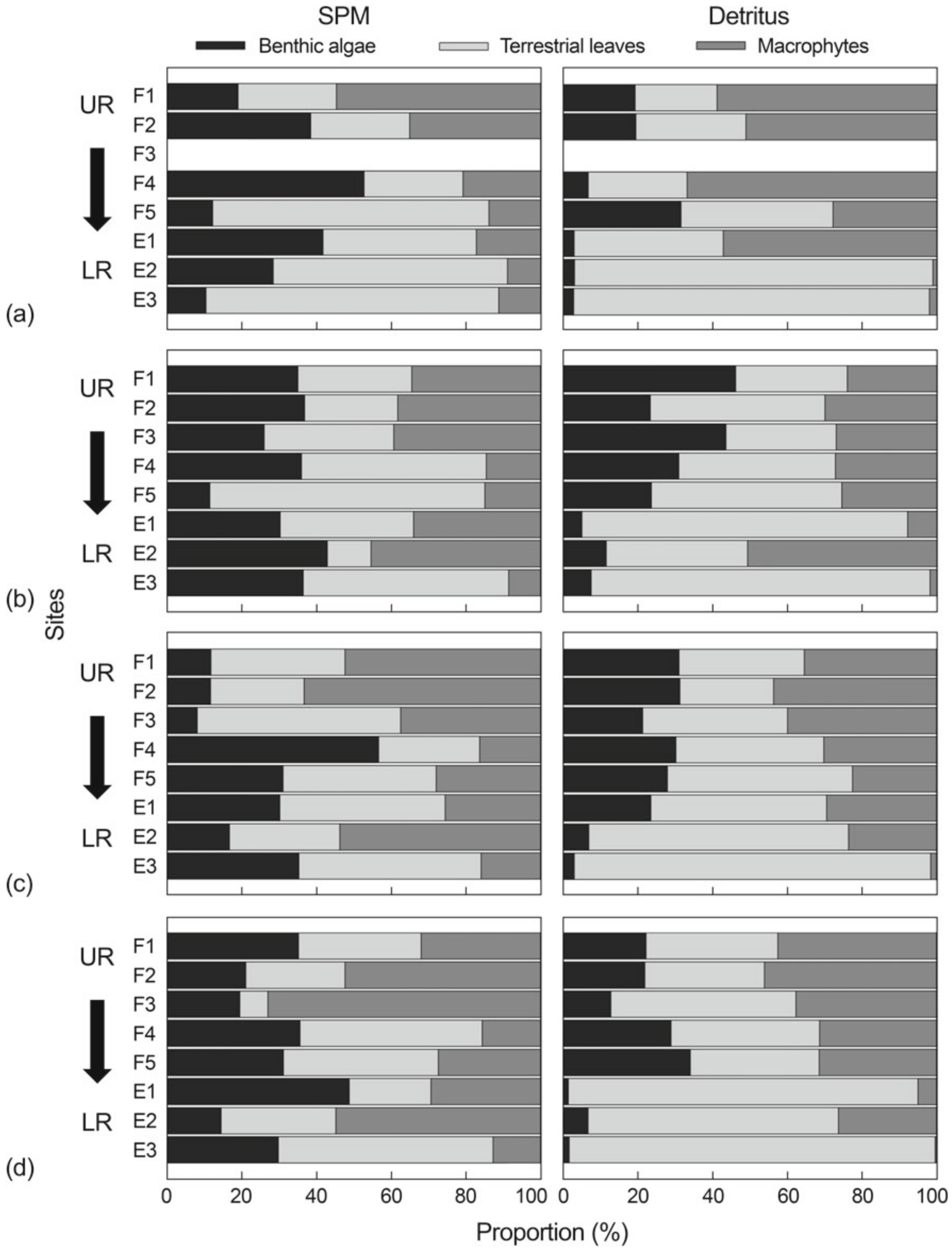


Fig. 7.4 Percentage contribution (relative mean) of benthic algae, macrophytes, and terrestrial plants to suspended particulate matter (SPM) and detritus in upper (UR) and lower reaches (LR) of the Kowie River, a small, temperate river in southern Africa in (**a**) early spring, (**b**) late spring, (**c**) summer, and (**d**) winter (Reproduced from Dalu et al. 2016)

coarse and fine materials; however, in some systems fines may be the largest component (Newbold et al. 1997; Martinez et al. 1998; Galas and Dumnicka 2003). In first- and second-order streams of the eastern US, FPOM can be more than 50% of the total amount of organic matter in the stream (Webster et al. 1995). Over 80% of stored OM was estimated to be buried in a Virginia coastal streams (Smock 1990), evidence of how challenging it is to make robust estimates of the standing stock of organic matter. High temporal variability was reported for the Njoro River in Kenya, where streambed OM accumulation ranged from approximately 93 to 6,700 g ash free dry weight m^{-2}, probably due to variability in litter inputs and discharge (Magana and Bretschko 2003).

Channel morphology can influence the retention of CPOM within a given reach. Retention rates of CPOM were higher in natural meandering sections than in straightened sections of a third-order stream in New Zealand (James and Henderson 2005). Similarly, Hoover et al. (2006) documented a number of effects of streambed geometry on leaf retention depending on flow and channel features. Protruding boulders were critical in retaining leaves in riffles, but not in pools, where leaves simply settled to the bottom. Leaf retention was greater in locations of greater depth and lower water velocity relative to reference streambed measurements across the river channel. The relative importance of pool versus riffle retention changed seasonally in the Njoro River, Kenya, where more CPOM was retained in pools than riffles during high flows (Magana and Bretschko 2003). Nakajima et al. (2006) also noted that CPOM accumulated in pools during periods of high flow, probably due to lower velocities near the streambed in pools.

7.1.3 Anthropogenic Activities and CPOM Inputs

Organic matter inputs are strongly influenced by anthropogenic activities. Logging and other activities that disrupt riparian vegetation can change the magnitude of leaf litter and wood inputs. Following logging in the catchment of a small forested stream in the southeastern US, leaf inputs fell to less than 2% of previous levels (Webster and Waide 1982). Allochthonous inputs recovered to near reference values after 5 to 10 years of regrowth and forest succession, but inputs were still detectably below reference levels after 20 years (Webster et al. 2006). Although litter inputs from early successional trees were less than observed prior to logging, these leaves were more rapidly broken down. Agricultural development disrupts links between aquatic and terrestrial environments by altering the timing and supply of terrestrial POM. Daily POM inputs and the standing stock of benthic OM were greater in reference headwater streams than agricultural streams in central Germany (Wild et al. 2019). Organic matter dynamics varied predictably with season in reference streams, but similar changes were more variable in agricultural systems (Fig. 7.5). Urbanization can also transform CPOM dynamics in many ways including, but not limited to, stream burial and channelization, changes in the abundance and diversity of riparian vegetation,

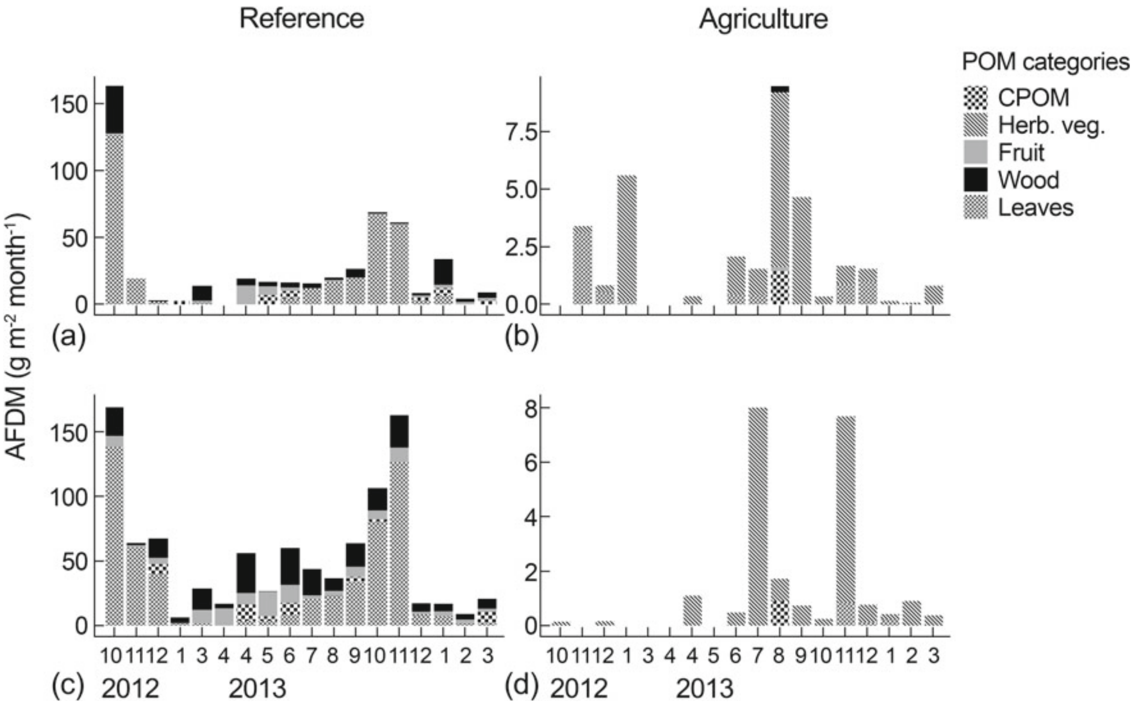


Fig. 7.5 Temporal variation in the inputs of particulate organic matter (POM) between October 2012 and March 2014 in reference (**a**, **c**) and agricultural (**b**, **d**) streams in north-central Germany (g AFDM m^{-2} d^{-1}). Values on the x-axes are months of the year beginning with October = 10. Please note that values on the y-axes are on different scales. Samples were taken twice in April (month 4) (Reproduced from Wild et al. 2019)

wastewater discharge, and the alteration of the volume, timing, and duration of surface runoff entering streams (Singer and Battin 2007; Kaushal et al. 2014; Smith and Kaushal 2015; Park et al. 2018).

Non-native riparian species can affect CPOM dynamics by altering the quantity and timing of leaf litter entering a stream reach. In Northern Spain, Pozo et al. (1997) noted that leaf litter input peaked during the summer in a stream dominated by non-native *Eucalyptus*, but similar OM peaks occurred during the autumn in a reference stream flowing through a native deciduous forest. Russian olive (*Elaeagnus angustifolia*) invasion has significantly changed the riparian habitats of many streams in the western US. Mineau et al. (2012) used a before-after-invasion comparison to document a ~25-fold increase in allochthonous inputs in sites where Russian olive was established. Introduced forest disease or parasites may also generate short- and long- term shifts in OM entering rivers and streams. Decades after chestnut blight (*Cryphonectria parasitica*) decimated the American chestnut populations from forests in the eastern US, dead chestnuts still contributed a large proportion of coarse woody debris in streams (Wallace et al. 2001). Similarly, eastern hemlock (*Tsuga canadensis*) populations have drastically declined in response to the invasion of the hemlock woolly adelgid (*Adelgis tsugae*), a parasitic insect, which was introduced from Japan to eastern North America in the 1950s. The adelgid has reduced populations of this once-dominant riparian evergreen tree and left large swaths of dead hemlocks in its wake, which are expected to influence the dynamics of wood entering streams. Riparian tree composition is expected to change after invasion, subsequently transforming CPOM dynamics (Pitt and Batzer 2015; Webster et al. 2012).

Climate change is expected to influence CPOM inputs through changes in temperature and precipitation, which are dominant controls on litterfall (Webster and Meyer 1997). In a nine-year study of a Mediterranean stream in the Montnegre-Corredor Natural Park in northeastern Spain, Sanpera-Calbet et al. (2016) demonstrated that changes in precipitation associated with the El Niño southern oscillation affected temporal dynamics in allochthonous inputs. Detrital inputs were influenced by the previous number of cumulative periods of no flow, as successive periods with no water flow progressively decreased the amount of riparian inputs entering streams. Instream flow events were also related to the timing of riparian inputs throughout the year. In years with permanent flow, streams were characterized by a single pulse of inputs in the autumn (~50% of total annual inputs) that was similar to values reported for streams in temperate climates. However, if a period of no flow occurred during the summer, the inputs were bimodal, occurring during the no flow event and in the autumn (Sanpera-Calbet et al. 2016).

Changes in the timing, duration, and intensity of forest fires and storms associated with climate change are also expected to have large impacts on allochthonous resources entering streams and rivers. Feedback between forest condition and fire management strategies and the severity, size, and configuration of forest fires is expected to alter allochthonous subsides through changes in riparian vegetation, hydrology, and post-fire debris flow (Bixby et al. 2015; Harris et al. 2015). Intense storms can also affect CPOM inputs to rivers and streams (Ramos Scharrón et al. 2012). Wohl and Ogden (2013) reported that bank erosion and landslides contributed to changes in wood export from the Upper Río Chagres watershed in central Panama after intense storms in 2010. They estimated that the carbon exported in wood during the storms (9.6–16 Mg C km^{-2}) was an order of magnitude larger than estimated background rates. Strikingly, their estimates were two orders of magnitude less than similar values of wood export from watersheds in Taiwan (Tsengwen Reservoir: 7800 ± 2200; Kaoping River: 4500–9200 Mg C km^{-2}) after Typhoon Morakot (West et al. 2011).

7.1.4 Transport of CPOM

Transport rates are expected to vary with particle size, flows, and the retentiveness of the stream channel. High discharges will entrain and transport even large particles, as can be seen from the export versus discharge relationship for a headwater stream in North Carolina (Fig. 7.6). Based on a small number of direct measurements, however, the distances traveled by CPOM are surprisingly short. Leaves typically are trapped by obstructions within a few meters of their point of entry to the channel (Webster et al. 1994) and often are broken down in place without further transport, although they can move tens of meters in storms. Using rectangles of waterproof paper, Webster et al. estimated an average distance of about 1.5 m from first entry to the stream, depending mainly on depth and likelihood of encountering an obstacle. Wallace et al. (1995) recorded movements of spray-painted red maple leaves and small pieces of colored plastic transparency sheets for up to four years. Although few natural leaves were recovered after about five months, no differences were observed between natural and artificial leaves, which, over the four-year study, moved on average 10–20 m yr^{-1}. The comparison of leaf breakdown to transport rates makes a strong case that, at least for the small streams where most research has been conducted, CPOM is

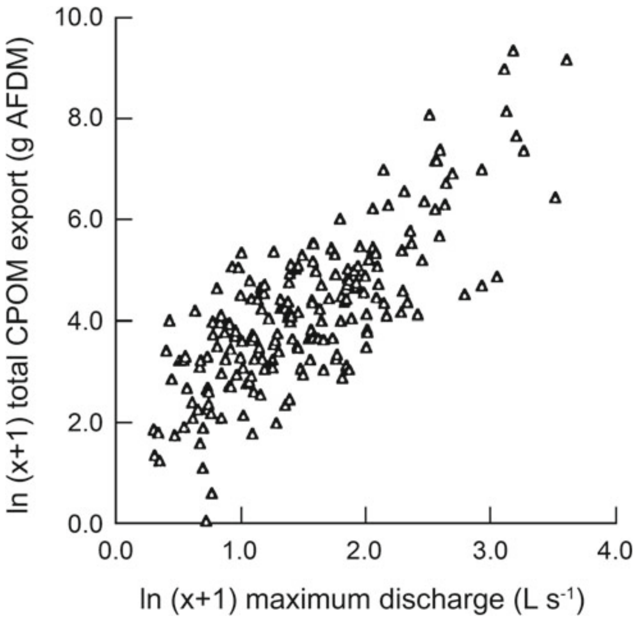


Fig. 7.6 CPOM export and maximum discharge in a headwater stream of the Coweeta Hydrologic Laboratory, North Carolina (Reproduced from Wallace et al. 1995)

transformed into other organic matter size classes or mineralized rather than exported.

7.2 The Decomposition of Organic Matter

Terrestrial leaf litter that enters streams from the surrounding landscape undergoes physical breakdown and decomposition, and in the process generates basal food resources for microbial and animal consumers. Leaf decomposition is a complex process that includes leaching of dissolved organic carbon (DOC) into the water column and leaf fragmentation into fine particulate organic matter (FPOM). Microbial colonization is rapid, and their secretion of extracellular enzymes transforms the organic matter into assimilable forms while their growth adds microbial biomass. Detritivorous animals of various feeding modes ingest both coarse and fine particles, obtaining nourishment from the leaf substrate and associated microbes. Organic inputs as leaf litter, often an abundant energy input to streams, are processed along multiple pathways (Marks 2019). Carbon compounds may be respired by microbes, ingested by detritivores, and transferred to higher trophic levels, or if especially recalcitrant, exported downstream. With the exception of OM buried in sediments or exported to the oceans, all constituent elements are mineralized and carbon is respired into CO_2.

It has long been recognized that leaf litter originating from a mixture of plant species includes material that undergoes rapid loss of mass, versus species that decompose much more slowly (Cummins et al. 1973; Kaushik and Hynes 1971). Typically quantified using an exponential decay coefficient obtained from measuring the loss of mass over time, and referred to as decomposition rate or breakdown rate (Benfield et al. 2017), species that decompose quickly are referred to as “labile”, and species that decompose more slowly are often labeled “refractory” or “recalcitrant”. The ease of measurement of leaf breakdown rate has resulted in a wealth of information on the differences among plant species and environmental conditions, and allowed global comparisons reviewed later in this chapter. Decomposition rates vary among plant species due to their structural and chemical traits. Leaves with higher concentrations of lignins and tannins and a tougher cuticle are more recalcitrant, and leaves with higher concentrations of sugars and nutrients are more labile (Gessner et al. 2010; Enríquez et al. 1993).

Rapidly decomposing leaves have traditionally been viewed as providing the greatest nutritional benefit to consumers, implying that a ranking of plant species by breakdown rate was equivalent to a ranking of food quality. Despite the appeal of such a convenient and easily obtained metric, Marks (2019) argues that equating breakdown rate with resource quality oversimplifies, and fails to distinguish the multiple pathways and fates of elements in leaf litter and their effects on organisms. A single measure of decomposition rate may fail to differentiate between resource availability to fungi versus to invertebrates, or recognize that different organisms may be limited by different elemental resources. During the early phases of decomposition, slowly decomposing litter retains most elements bound in more refractory litter, which subsequently becomes available to consumers (Fuller et al. 2015; Siders et al. 2018). By labeling trees with stable isotopes of carbon and nitrogen, and then incubating labeled leaves in a stream, Siders et al. (2018) showed that more carbon was assimilated by a shredding caddisfly from slowly decomposing oak litter than from rapidly decomposing cottonwood litter. However, carbon loss to leachate and to microbial biomass showed the opposite result, being higher from cottonwood leaf packs than from the oak litter.

In sum, the decomposition of detrital resources is a complex set of processes that support stream food webs and mediate biogeochemical cycling (Marks 2019). Elements bound in organic matter may cycle at different rates and elements limiting the growth and reproduction of organisms may shift with ontogeny or under different environmental conditions (Halvorson et al. 2018; Halvorson et al. 2015b). While rapidly decomposing leaves typically accrue microbial biomass more rapidly and are often preferred by macroinvertebrate consumers in feeding trials, equating leaf breakdown rate with food quality can mask the variety of the fates of the elements moving from detritus into stream food webs. Losses of the constituent elements of a leaf or other sources of OM follow multiple pathways and are influenced by structural and chemical characteristics of leaves that vary with tree species of origin and environmental conditions. Indeed, the presence of a mix of tree species with range of breakdown rates benefits consumers and the ecosystem, because it results in a more continuous resource supply for macroinvertebrates throughout their life cycles (Marks 2019). Though it does have its limitations, the relative ease and low cost of deploying leaf decomposition assays has allowed researchers to replicate experiments in streams and laboratories throughout the world. By employing loss of leaf mass as a proxy for OM decomposition, stream ecologists have made great advances in our understanding of the conditions governing the pathways and rates by which detrital resources are integrated into stream ecosystems.

7.2.1 Breakdown and Decomposition of Coarse Particulates

The rate of OM decomposition has been well studied because it can be measured easily and many of the physical, chemical, and biological factors that regulate decomposition can be detected within and among systems (Boyero et al. 2016; Tiegs et al. 2019). Decomposition is commonly estimated by measuring the change in mass of wood veneers or leaves or leaf discs (Benfield et al. 2017; Graça et al. 2005; Gregory et al. 2017). Briefly, the change in mass is calculated by drying and weighing OM, deploying the pre-weighed OM in streams or mesocosms for a known period of time, and again drying and re-weighing the OM to determine loss of mass. One can also measure changes in more homogenous organic substrates, such as strips of cotton, to reduce the influence of individual leaf and species-level trait diversity on decomposition rates (Tiegs et al. 2013; Tiegs et al. 2019). Once CPOM enters streams it undergoes a breakdown process or is exported (Webster et al. 1999). The sequence in the breakdown of CPOM, well documented for autumn-shed leaves in temperate streams (see reviews by Bärlocher 1985; Webster and Benfield 1986; Marks 2019), is illustrated in Fig. 7.7. Leaves fall directly or are windblown into streams, become wetted, and commence to leach soluble organic and inorganic constituents. Most of the leaching occurs within a few days and is followed by a period of microbial colonization and growth, causing numerous changes in leaf condition. The next stage, fragmentation by mechanical means and invertebrate activity, usually follows some period of softening of tissue by microbial enzymes, and is complete when no large particles remain. Although this model suggests sequential stages, leaf decomposition is a complex process and some of the events can occur simultaneously. For example, fragmentation can occur during microbial colonization and not just at the end of the process, and invertebrate colonization may begin shortly after leaves enter the stream (Gessner et al. 1999; Hieber and Gessner 2002). From a synthesis of many studies of 11 streams at the Coweeta Hydrologic Laboratory, the average leaf breakdown rate was found to be 0.0098/day, which implies the loss of 50% of initial mass after 71 days (Webster et al. 1999). Dissolved material and fine particulates can undergo further microbial degradation or be transported downstream.

The loss of leaf mass over time is approximately log-linear (Fig. 7.8), although some data have been interpreted as linear or as consisting of two or more distinct stages. Webster and Benfield (1986) argue that a simple exponential model provides a general description of the breakdown process

$$\mathrm{Wt} = \mathrm{Wie}^{-\mathrm{kt}} \tag{7.1}$$

where W_t = dry mass at time t, W_i = initial dry mass, and t is time, measured in days. The statistic k (in units days^{-1}), which is the slope of the plot of the natural logarithm of leaf mass versus time, provides a single measure of breakdown rate.

7.2.2 Physical and Chemical Conditions Influencing OM Decomposition

A number of physicochemical factors, including temperature, hydrology, and water chemistry, influence breakdown rates. Graca et al. (2015) outlined a useful framework to describe how physical, chemical, and biological factors interact across spatial scales in low-order streams (Fig. 7.9), and we discuss these themes below. The over-riding influence, however, is leaf type (Fig. 7.10), which results in a fast-to-slow continuum of leaf breakdown rates. Although leaf breakdown can occur at near-zero temperatures, breakdown rates generally are predicted to be faster at warmer temperatures (Follstad Shah et al. 2017). In an effort to estimate global patterns in OM processing, Tiegs et al. (2019) deployed cotton strips in streams and adjacent riparian areas at more than 1,000 sites throughout the globe, finding that the mean rate and variability of decomposition declined with latitude. Their findings suggested that lower temperatures may constrain rates of decomposition toward the poles, but that other factors, such as nutrient availability, may regulate rates of decomposition in tropical regions where warmer climates support greater rates microbial productivity.

Changing hydrology may also influence litter breakdown rates. Hydrologic fluctuations can cause abrasion and fragmentation, which may expose more surface area to microbial action (Benfield et al. 2001), and burial, which can reduce microbial activity by reducing the availability of oxygen

Fig. 7.7 Leaf litter bags deployed in a stream in the southeastern US. Each mesh bag contains the same quantity of previously dried and weighed leaves. Leaved are retrieved, dried, and re-weighed at subsequent time intervals to estimate the rate of leaf decomposition. Inset (**a**) shows bag dimensions. Photo by Carolyn Cummins

(Sponseller and Benfield 2001). Decomposition in the hyporheic zone can also be a substantial contributor to carbon dynamics in streams, and this may be especially true in intermittent systems. In streams in eastern Australia, Burrows et al. (2017) found that leaf litter processing rates were almost 50% greater and cotton strip processing rates were approximately 125% greater in the hyporheic zone when compared to surface environments under multiple saturation conditions. Furthermore, they documented similar rates of microbial respiration on substrates incubated in both habitats.

Ambient chemistry conditions can also influence breakdown rates. Using data from almost three decades of nutrient addition experiments in headwater streams in the southeastern US, Rosemond et al. (2015) found that that average residence time of terrestrial organic carbon declined by approximate 50% in streams subjected to added nutrients. They argued that nutrient pollution may alleviate nitrogen and phosphorus limitation of detrital food webs, and that increased carbon processing rates in polluted streams may negatively affect detrital food webs and alter rates of nutrient spiraling in streams. Variation in leaf breakdown rates along a stream in Costa Rica positively correlated with a natural gradient in phosphorus concentrations (Rosemond et al. 2002). Experimental addition of nitrogen and phosphorus to a stream in the southern Appalachians in the US enhanced the loss of wood mass and increased microbial respiration and fungal biomass (Gulis et al. 2004). However, nutrient additions to a stream in the Caribou National Forest in south-east Idaho in the western US did not affect leaf breakdown; the authors suggested this may have been because microorganisms were not nutrient limited due to relatively high ambient nutrient concentrations (Royer and Minshall 2001). Low pH and increased salinization have been shown to retard decomposition by inhibiting the activity of microorganisms and invertebrates (Dangles et al.

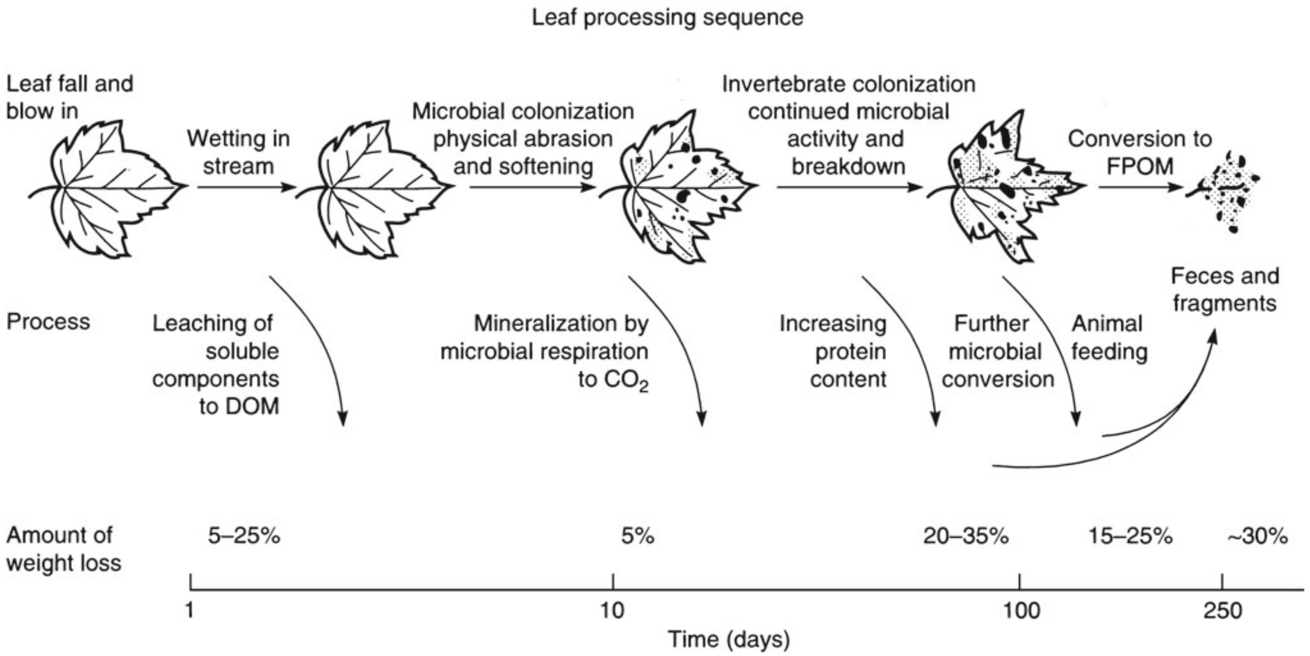


Fig. 7.8 The processing or "conditioning" sequence for a medium-fast deciduous tree leaf in a temperate stream. Leached DOM is thought to be rapidly transferred into biofilms by microbial uptake. Studies of organic matter breakdown start with the source material, often using leaves picked from riparian trees near the time of abscission, and follow its disappearance over time. The original leaf is transformed into several products including microbial and shredder biomass, FPOM, DOM, nutrients, and CO_2 (Gessner et al. 1999). Physical abrasion, softening of leaf tissue by wetting and the initial leaching of DOM, colonization by fungi and bacteria, and feeding by consumers all contribute to the conversion of CPOM into FPOM and DOM. Leaf breakdown can occur at very low temperatures, but rates typically increase with temperature, and are influenced by the presence of shredders, availability of nutrients, and whether leaves are buried or exposed

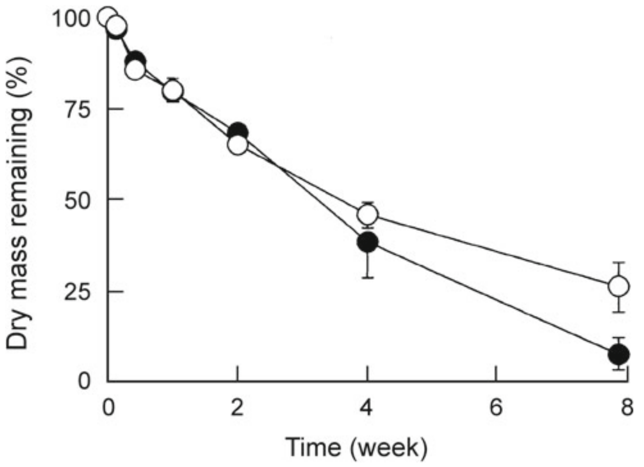


Fig. 7.9 Leaf dry mass remaining (as %) from alder (●) and willow (○) leaf packs in an experiment conducted in a Black Forest stream, Germany. Error bars represent 95% confidence intervals (Reproduced from Hieber and Gessner 2002)

2004; Canhoto et al. 2017). Metal pollution can decrease decomposition rates by negatively affecting shredders and microorganisms (Niyogi et al. 2001; Duarte et al. 2004; Carlisle and Clements 2005).

Addition of labile carbon, referred to as priming, may also influence decomposition rates of more recalcitrant organic matter. In streams, algae produce labile exudates, which may produce a priming response in OM decomposition by stimulating microbial activity. However, the relatively few results from experimental manipulations are equivocal (Bengtsson et al. 2018). Danger et al. (2013) suggested that the presence of diatoms had a positive priming effect on leaf decomposition rates in experimental microcosms. In contrast, Halvorson et al. (2019) tested algal-induced priming of decomposition of leaves from two species of trees, tulip poplar (*Liriodendron tulipifera*) and water oak (*Quercus nigra*), under light or dark conditions. Light enhanced algal biomass and production, thereby increasing bacterial abundance by 141%–733% and fungal production rates by 20%–157%. However, algal-stimulated fungal production rates were not related to long-term increases in litter decomposition rates, which were 164%–455% greater in the dark. Similar relationships were found with both leaf types, suggesting that the lability of leaves did not influence priming. Researchers suggested that algae may have supplied fungi with labile carbon and decoupled fungal activity from decomposition rates, and the fungi invested this carbon into growth and reproduction, instead of using the energy to

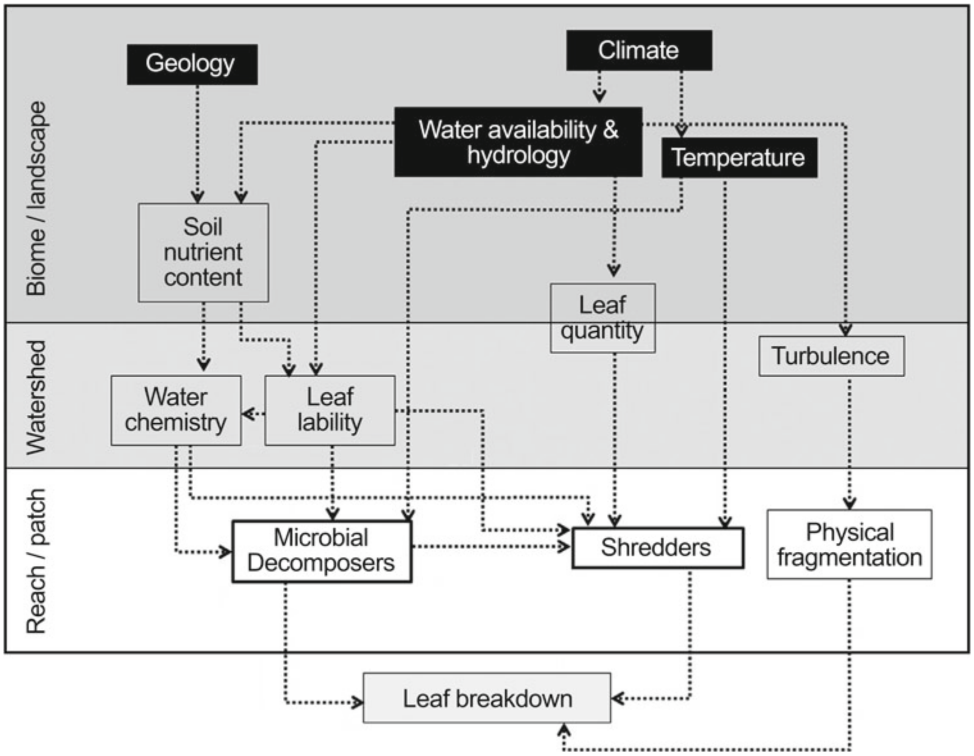


Fig. 7.10 Conceptual model of the drivers of litter breakdown. Arrows reflect the influence of one factor over the next one. The biological pathways are ultimately controlled by underlying geology and climate. (Modified from Graca et al. 2015)

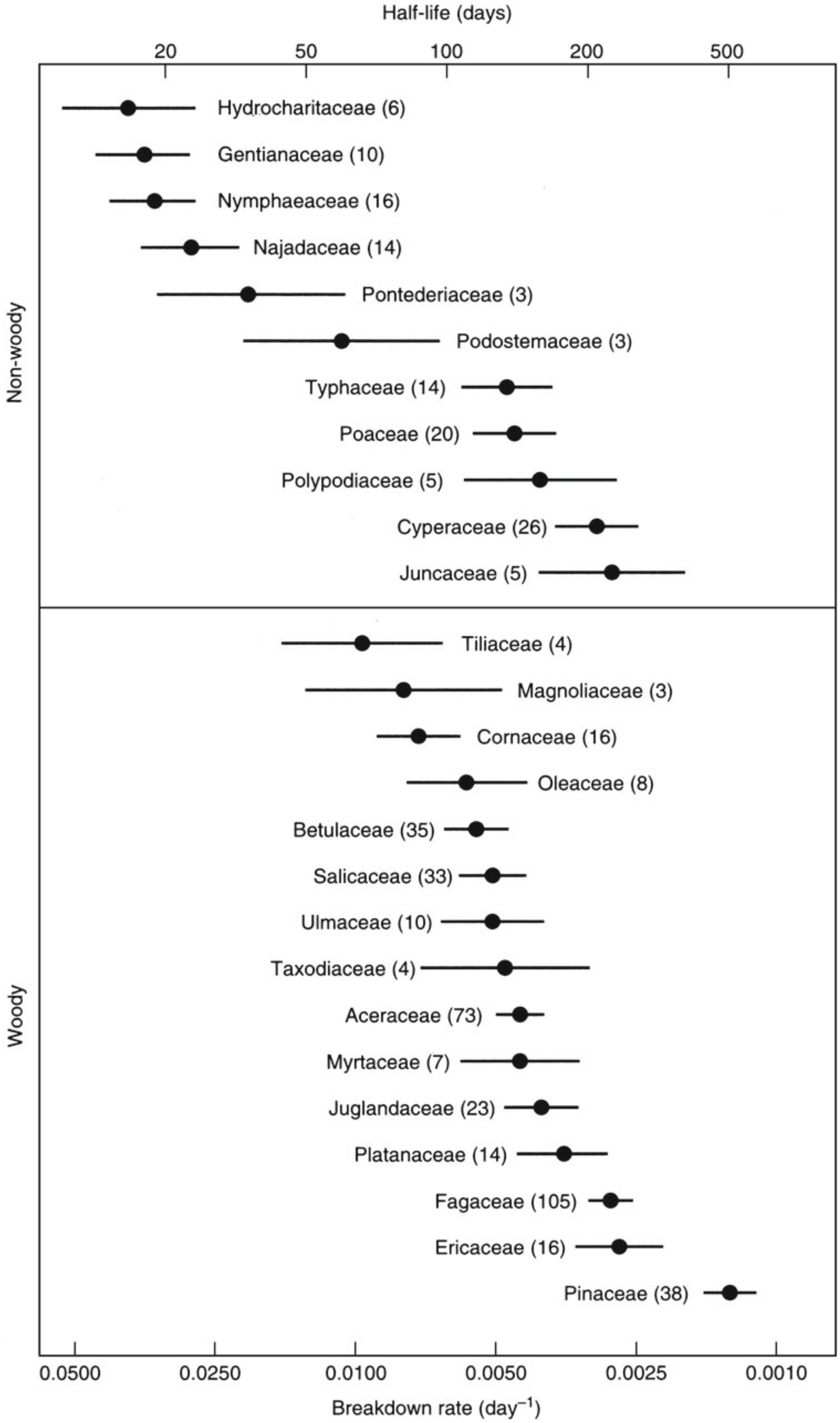
obtain nutrients and energy from leaves (Halvorson et al. 2019). Understanding functional feedback between autotrophic and heterotrophic communities is essential as human activities continue to modify the relative abundance of algal, fungal, and bacterial populations in streams.

7.2.3 The Lability of Organic Matter

Species-specific differences in physical, chemical, and ecological traits influence the initial lability of litter produced by plants, and affect the rate at which constituents are lost from the litter and move through aquatic food webs (Fig. 7.11; Irons et al. 1994; Boyero et al. 2017; Siders et al. 2018; Ferreira et al. 2016; Leroy and Marks 2006). Early research by Petersen and Cummins (1974) suggested a continuum of decomposition rates from slow to fast, based on the breakdown of leaves from six deciduous tree species in a small Michigan stream. They also recognized that this variation in leaf decomposition rates, which they termed a "processing continuum", had consequences for invertebrate consumers by extending the time interval over which microbially-colonized leaf litter was available. The wide variation in the breakdown rate of the leaves of different plant species has now been amply documented (Fig. 7.10). Non-woody plant leaves decompose much more quickly, on average, than do leaves of woody plants (mean half-lives in Fig. 7.10 are approximately 65 days and 100–150 days respectively). Submerged and floating macrophytes are among the fastest to decay, presumably because they contain the least amount of support tissue and often the greatest concentration of potentially limiting elements such as nitrogen and phosphorus.

The physical structure of leaf litter affects the rate at which elements are lost through leaching. As much as 25% of the initial dry mass of freshly-abscised leaves is lost due to leaching in the first 24 h. Constituents lost during leaching are primarily soluble carbohydrates and polyphenols (Suberkropp et al. 1976). Leaves of different plants show species-specific leaching rates: alder (*Alnus rugosa*) lost only about 4% of dry mass over several days whereas elm (*Ulnus americana*) lost 16% in an early study by Kaushik and Hynes (1971). Release of DOC by leaves of several plants in a stream in British Columbia, Canada, also revealed substantial differences in leaching rates (McArthur and Richardson 2002). During the first day, Western hemlock needles (*Tsuga heterophylla*) lost 14% of the total DOC released over a 7-day period, compared with 30% for western red cedar (*Thuja plicata*) and 74% for red alder (*Alnus rubra*). By the end of the experiment, hemlock and cedar had released 40% and 20% respectively of the DOC released by alder (Fig. 7.12). More recent work has also provided evidence that rapidly decomposing litter tends to lose more carbon and nitrogen through leaching relative to more recalcitrant species (Siders et al. 2018; Wymore et al. 2015).

Fig. 7.11 The breakdown rates for various woody and non-woody plants, based on 596 estimates compiled from field studies in all types of freshwater ecosystems. Means ±1 standard error are shown, and the variation is due to (at least) effects of site, technique, and numerous environmental variables. The number of individual rate estimates is shown in parentheses (Reproduced from Webster and Benfield 1986)



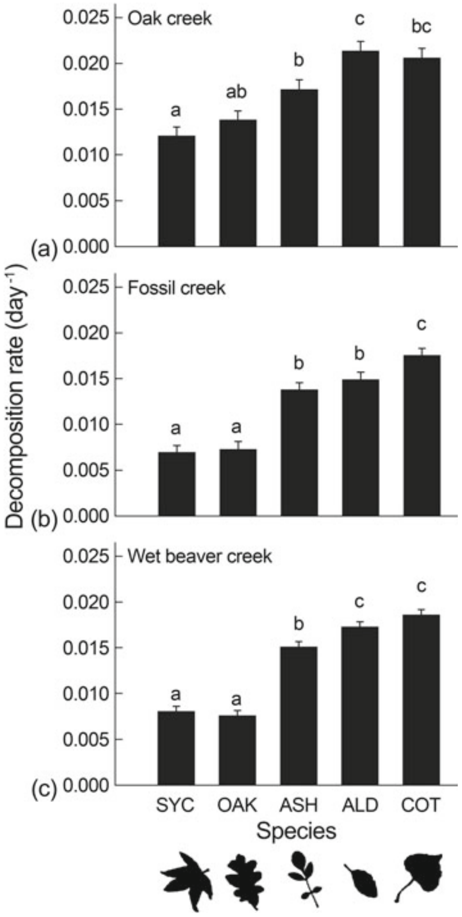


Fig. 7.12 Rates of leaf-litter decomposition for five species in three streams in the verde River catchment of Arizona, US (SYC *Platanus wrightii*, OAK *Quercus gambelii*, ASH *Fraxinus velutina*, ALD *Alnus oblongifolia*, COT *Populus fremontii*). Plotted values are the regression slopes ±1 SE for the ln-transformed regression model of the rate of decomposition. Significant differences among leaf types are represented by lower-case letters (Reproduced from Leroy and Marks 2006)

Differences in leaf chemistry and structure result in wide variation in decomposition rates (Webster and Benfield 1986; García-Palacios et al. 2016). Complex compounds including lignin, tannin, and phenols tend to reduce decomposition, whereas OM rich in labile carbohydrates, such as sugars, decompose more rapidly (Marks 2019). Similarly, leaves with higher initial nutrient concentrations tend to decompose more rapidly than leaves of lower nutrient content. Leaves that contain lower lignin and condensed tannin concentrations tend to be initially preferred by leaf-shredding invertebrates. However, as leaf conditioning proceeds in less labile, more slowly decomposing leaves, loss by leaching of some constituents that initially rendered the leaf less labile, as well as microbial growth, may reduce or even reverse initial palatability differences. Compson et al. (2018) demonstrated that, over time, a shredding caddisfly (*Hesperophylax magnus*, Limnephilidae) shifted its preference from a fast to a slow-decomposing leaf type, assimilating more carbon and nitrogen from the latter. Leaf chemistry also explained differences in decomposition of *Croton gossypifolius* (Euphorbiaceae) and a species of *Clidemia* (Melastomataceae) in an Andean stream (Mathuriau and Chauvet 2002). Higher decomposition rates in *Croton* than in *Clidemia* appeared to be related to lower tannin and higher N content in *Croton*, which resulted in earlier peaks in ergosterol (a compound found primarily in fungi), sporulation activity, and macroinvertebrate colonization.

Intraspecific variation in leaf structure and chemical composition may also affect patterns in decomposition. In a study of the decomposition of five genotypes of each of four different cottonwood cross types (*Populus* sp.) that were grown under common conditions, LeRoy et al. (2007) found that polymorphism markers in the genotype and differences in genetically-controlled chemical characteristics explained a large proportion of the variation in leaf-litter decomposition rates. Similarly, Compson et al. (2016) studied how plant genetics influenced the composition and timing of emerging insects using a subset of the same cross types. They found that litter from more closely related genotypes of *P. angustifolia* were more similar in decomposition rates, leaf thickness, and litter nitrogen concentrations. Additionally, they had more similar communities of emerging insects. Conversely, the researchers found only marginally significant differences in emerging insect composition between *P. fremontii* and *P. angustifolia*. They also documented reductions in the influence of genetic effects in mixed litter packs relative to leaves from single genotypes. Their results provide additional evidence that intraspecific variation in riparian forests can affect leaf decomposition rates, and suggest that the genetic structure of tree communities may influence characteristics of aquatic insect emergence.

Evolutionary relationships between tree species and detritivores may help explain patterns in decomposition, as detritivore communities may be adapted to break down litter with which they have co-evolved (Jackrel and Wootton 2014; Jackrel et al. 2016). Similar to cottonwood studies, Jackrel and Wootton (2014) documented significant intraspecific variation in decomposition rates for red alder (*Alnus rubra*) in reciprocal transplant experiments in two smaller and two medium-sized rivers in the western US. Detritivores processed local litter more rapidly that litter from other riparian habitats, suggesting that stream consumers are adapted to local intraspecific variation in litter. Studies in the same rivers suggested that intraspecific variation in leaf chemistry may drive local detritivore adaptation to food resources (Jackrel et al. 2016). Concentrations of plant defensive compound such as ellagitannins, and flavonoids influenced decomposition rates, a pattern that may have been driven by local adaptation of detritivores to local chemical conditions in leaf litter. Collectively, these results suggest that land cover change may influence the chemistry of OM entering streams, subsequently altering the rates at which OM is converted into animal tissue.

In a global survey of the physical and chemical characteristics of leaves and leaf litter decomposition, Boyero et al. (2017) found that mean annual temperature and temperature seasonality, and thus latitude, were related to the stoichiometry, or ratio, of nitrogen to phosphorus in litter. In warmer and less variable climates, litter typically had greater amounts of nitrogen relative to phosphorus. Nutrient concentrations of leaves are thought to be governed by soil nutrient concentrations, and tropical soils are thought to be depleted in phosphorus relative to their temperate counterparts because they are often older and have been subjected to more weathering and leaching (Reich and Oleksyn 2004; Chadwick et al. 1999). However, nitrogen content is thought to be relatively similar between temperate and tropical regions as it is regulated, in large part, by biological nitrogen fixation (Houlton et al. 2008; Vitousek et al. 2010). Notably, Boyero et al. (2017) found that tropical litter was not particularly nutrient poor, but their data suggested that relative to nitrogen, phosphorus was limiting in tropical litter, which may cause stoichiometric imbalances that influence the diversity and abundance of aquatic consumers (Boyero et al. 2017; Frost et al. 2006).

Plants invest in chemical inhibitors that may also impede leaf decay. Tough outer coatings such as the cuticle of conifer needles slow fungal invasion (Bärlocher and Oertli 1978), and complexing of protein to tannins is a principal cause of slow breakdown in many broad-leafed woody plants. Toxic chemical constituents also may influence breakdown rates (Webster and Benfield 1986), just as secondary plant compounds defend against terrestrial herbivores, although evidence is scant. Somewhat surprisingly, chemical measures of tannins (total phenolics and condensed tannins) of 48 deciduous trees were unrelated to published breakdown rates (Ostrofsky 1993). However, Canhoto et al. (2002) found that oils of *Eucalyptus globulus* inhibited the growth of hyphomycetes and the activity of their enzymes, which could explain the delayed decomposition of eucalyptus in rivers. In the aforementioned global survey, Boyero et al. (2017) found that investment in plant defenses typically declined with increasing latitude, and tougher and more chemically defended litter is generally found near the equator.

Microbial colonization plays a fundamental role in altering the palatability of leaves for detritivores (Arsuffi and Suberkropp 1985) and in the fragmentation of leaf material. This colonization is primarily by fungi and bacteria, although protists also can be substantial contributors to leaf fragmentation (Ribblett et al. 2005). Microbial activity also softens plant tissue, favoring the release of compounds that can be incorporated into microbial biomass (Gessner et al. 1999; Graca 2001). In general, nitrogen typically increases as a percent of remaining dry mass during leaf conditioning, and sometimes increases in absolute terms as well. Because protein complexed to lignin and cellulose is very resistant to breakdown, nitrogen compounds remain while other leaf constituents are lost, resulting in a relative increase of nitrogen.

Microbial immobilization of nutrients from external sources can also lead to increases in either relative or absolute quantities of nitrogen or phosphorus. When increases in total nitrogen are recorded, this immobilization of nitrogen usually is attributed to an increase in microbial biomass and incorporation of nitrogen from the surrounding water into new protein. In a headwater stream reach in Coweeta Hydrologic Laboratory, North Carolina, that received experimental additions of ammonium, nitrate, and phosphate, the nitrogen content of maple (*Acer rubrum*) and rhododendron (*Rhododendron maxima*) leaves increased significantly relative to a control (Fig. 7.13), suggesting higher microbial biomass under enrichment conditions (Gulis and Suberkropp 2003). The slower breakdown of rhododendron leaves compared to maple is attributable to their lower initial nitrogen content and lower surface area relative to leaf volume. In a study of oak and hickory leaves incubated in a Michigan stream over the winter (Suberkropp et al. 1976), cellulose and hemicellulose declined at about the same rate as total leaf mass, while lignin was processed more slowly and increased as a percentage of remaining weight. Lipids were lost more rapidly than total mass, and thus were a declining fraction of remaining dry mass of leaf material.

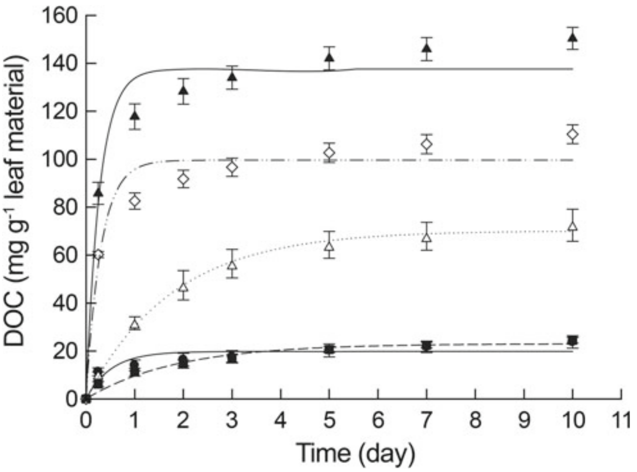


Fig. 7.13 Cumulative release of dissolved organic carbon (DOC) leachate over 10-day period for four tree species and grass cuttings (a common yard waste) in urban streams of southern Australia. Grass cuttings (●), English elm (*Ulmus procera*) (Δ), London plane (*Platanus acerifolia*) (■), river red gum (*Eucalyptus camaldulensis*) (◊) and white poplar (*Populus alba*) (▲) (Reproduced from Wallace et al. 2008)

Tracking the flow of energy and elements from individual riparian species into consumers may provide insights about links between biodiversity and ecosystem function in riparian and stream habitats. All elements stored in OM will eventually be mineralized and will cycle through various components of stream food webs. However, the rate at which elements cycle is governed by site-specific conditions, such as ambient nutrient concentrations, and the route by which elements move through organisms and abiotic pools. Transformations from one pool to another can occur rapidly—elements leached from leaf litter can be integrated into microbial biomass and respired within hours of entering a stream (Marks 2019).

Stable isotope labeling has generated a greater understanding about the rates and pathways of elements moving from CPOM into stream food webs (Cheever et al. 2013). Labeling allows scientists to quantitatively track carbon and nitrogen as they flow from leaf litter into microorganisms and macroinvertebrates. Unlike many commonly employed approaches, it can be used to compare the rates of elemental flux from the litter of different plant species and estimate the contribution of a given plant species to the productivity of higher trophic levels such as microbes and macroinvertebrates (Compson et al. 2015). Tracer studies have demonstrated that the carbon and nitrogen from slowly decomposing litter (frequently considered to be of lower quality) often supports biomass production in higher trophic levels comparable to faster decomposing species (Compson et al. 2015; Siders et al. 2018).

In more recalcitrant species, leaf chemistry influences assimilation rates of elements into higher-order consumers. Data from tracer experiments suggest that litter from rapidly decomposing species tends to support more microbial biomass and higher bacterial productivity, while resources from slowly decomposing litter tends to support the growth of fungi (Pastor et al. 2014; Wymore et al. 2013). Compson et al. (2018) found that lignin concentrations were positively correlated with nitrogen assimilation rates in macroinvertebrates, but that soluble condensed tannins were negatively correlated with tannin concentrations. They demonstrated that a 1% increase in lignin concentrations was expected to increase assimilation rates by 23% of its daily mean, and a similar increase in tannin concentrations was expected to reduce daily mean assimilation of nitrogen by 57% (Compson et al. 2018). Collectively, this body of work suggests that increased concentrations of plant structural compounds may initially impede nutrient cycling from litter, but the slower release rates of energy and nutrients from more recalcitrant species may increase the efficiency and longer-term transfer rates of elements to higher trophic levels (Marks 2019; Compson et al. 2018).

7.2.4 Microbial Succession and Decomposition Rates

Microbes typically have lower ratios of carbon to limiting nutrients when compared to the substrate they are colonizing, a pattern that supports the “peanut butter and cracker” analogy in which microbes function as the nutritious peanut butter covering a less nutritious cracker (Cummins 1974). However, this analogy fails to acknowledge some of the aforementioned interactions between microbes and macroconsumers that occur during leaf decomposition (Marks 2019). Though invertebrates often prefer to consume and grow faster when feeding on leaves that have been colonized by microbes, microbes are also consuming leaves and competing with macroinvertebrates for limiting resources. Microbes can produce chemical deterrents that retard macroinvertebrate consumption rates (Danger et al. 2016). Additionally, rapid microbial processing can enhance elemental loss from OM to the water column or atmosphere, preventing the resources from supporting productivity of higher trophic levels (Marks 2019).

Studies are in agreement that leaves submerged in a stream for some days to allow microbial colonization support higher invertebrate growth rates. Referred to as “conditioned leaves”, microorganisms, especially aquatic hyphomycetes, increase in mass over a period of days to weeks, contributing to leaf breakdown and influencing the palatability of leaves to shredders (Cummins and Klug 1979; Kaushik and Hynes 1971). Fungal mycelia are much more readily assimilated than leaf tissue, which explains why conditioned leaves invariably are preferred over unconditioned or sterile leaves. Colonization of aspen leaves by aquatic hyphomycetes resulted in weight loss, leaf tissue softening, and increases in the ATP (adenosine triphosphate, an indicator of microbial biomass) and nitrogen content of leaves (Arsuffi and Suberkropp 1984). However, the timing of these changes varied among species, as some initiated leaf degradation in 5–10 days, and other fungal species required as much as 20 days to reach comparable stages of degradation. Feeding preferences of larval caddisflies varied with fungal species composition and the duration of fungal colonization. For any given fungus-leaf combination, optimum palatability generally accords with the period of greatest microbial growth, as measured by nitrogen and ATP content and activity of degradative enzymes (Bärlocher 1985). The amphipod *Gammarus pseudolimnaeus* assimilated the mycelia of 10 fungal species with average efficiencies of 64%, compared with 11% average efficiency with unconditioned leaves of elm (*Ulmus americana*) and maple (*Acer saccharum*) (Barlocher and Kendrick 1974). Two crustacean shredders, *Gammarus pulex* and *Asellus aquaticus* preferentially fed on conditioned rather than on unconditioned elm leaves, and conditioned leaves were highly assimilated by both shredders (Graça et al. 1993). Fungal carbon accounted for 100% of the growth of third instar larvae of the limnephilid caddis *Pycnopsyche gentilis*, and 50% of the growth of fifth instar larvae, when fed a diet of tulip poplar (*Liriodendron tulipifera*) leaf discs colonized by a radiolabeled aquatic hyphomycete, *Anguillospora filiformis*. When fed a diet of sterile leaves, however, both instars lost weight (Chung and Suberkropp 2009).

Fungal colonization of leaves takes place primarily in the water, because freshly abscised leaves exhibit low fungal biomass (measured as ergosterol content) before entering the stream (Gessner and Chauvet 1997; Hieber and Gessner 2002). Rates of fungal growth and production on leaf litter peaks soon after submergence, and growth rates are typically greatest when fungal biomass is relatively low (Kuehn 2016). Fungi can degrade the polysaccharides present in the cell walls of the leaves by the production of extracellular enzymes (Jenkins and Suberkropp 1995), and their hyphae also penetrate leaf tissue, facilitating the softening process (Wright and Covich 2005b). Propagules of soil fungi, although commonly carried into the stream on shed leaves, appeared to contribute little to decomposition (Suberkropp and Klug 1976). Bärlocher (1982) reported that typically 4–8 species of aquatic fungi dominate throughout the decomposition of leaves, while a similar or larger number of rare species appear erratically. Apparently, no particular succession occurs on a single leaf, and whichever fungal species arrives first as a waterborne spore establishes numerical dominance. Hieber and Gessner (2002) identified 30 species of hyphomycetes on decomposing leaves of alder and willow, but two species, *Flagellospora curvula* and *Tetrachaetum elegans*, were dominant. Bacteria from biofilms growing on decomposing leaves in a stream in Ohio were mostly of one type known as *α-Proteobacteria,* although representatives of *β-Proteobacteria* were occasionally abundant (McNamara and Leff 2004).

The relative influence of fungi and bacteria upon the decomposition process likely varies with substrate, habitat, and time. Suberkropp and Klug (1976) followed in detail the succession of dominant microorganisms on oak and hickory in a Michigan stream from November until June. Fungi, primarily aquatic hyphomycetes, dominated during the first half (12–18 weeks) of the processing period. Bacteria, whose numbers gradually increased throughout, dominated the terminal processing stage and perhaps were benefited by fungal-induced changes in leaf surface area or by the release of labile compounds. Although fungal biomass was found to be several times greater than bacterial biomass on alder and willow leaves in a stream in Germany's Black Forest region (Fig. 7.14), the fungal contribution to leaf mass loss was only about twice that of bacteria, whose shorter turnover times partly compensated for their lower biomass (Hieber and Gessner 2002). Findlay et al. (2002) found that fungi dominated microbial biomass in large organic matter such as wood and leaves, whereas bacterial biomass was dominant in fine benthic organic matter (Fig. 7.15). Because fine benthic organic matter was more abundant than coarse detritus at the study sites, when bacterial biomass was weighted for the abundance of detritus in the reach, it was similar to or higher than that of fungi. In addition, bacterial biomass was less variable per unit of organic matter mass than fungal biomass, suggesting that bacteria could be a more reliable food resource than fungi. In a study of seasonal variation in fungal and bacterial colonization of leaf litter, Mora-Gómez et al. (2016) documented that the relative influence of microbes in decomposition shifted seasonally; fungi were more dominant decomposers in spring, but bacteria seemed to become more important in summer months.

Bacteria and fungi may interact synergistically and antagonistically during POM decomposition. In their study of decomposing leaf litter under low and high nutrient levels, Gulis and Suberkropp (2003) reported that microbial

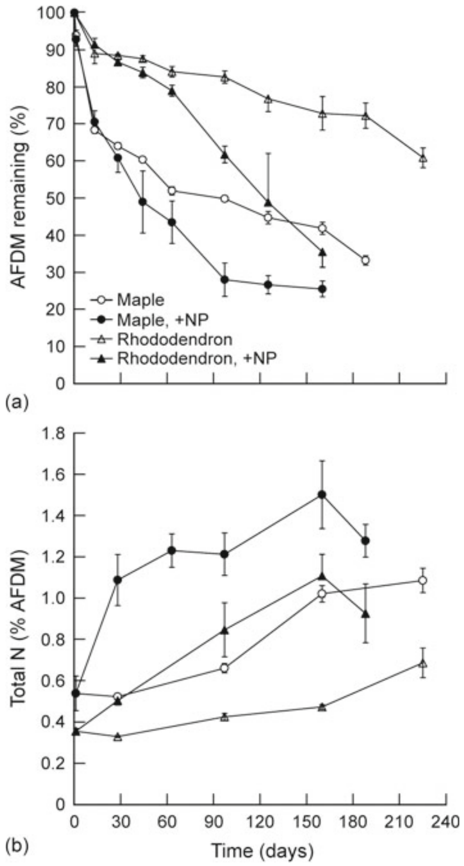


Fig. 7.14 (**a**) Ash free dry mass (AFDM) and (**b**) total nitrogen content in a decomposition experiment using maple and rhododendron leaves in control and nutrient-enriched reaches of a headwater stream at the Coweeta Hydrologic Laboratory, North Carolina, US (Reproduced from Gulis and Suberkropp 2003)

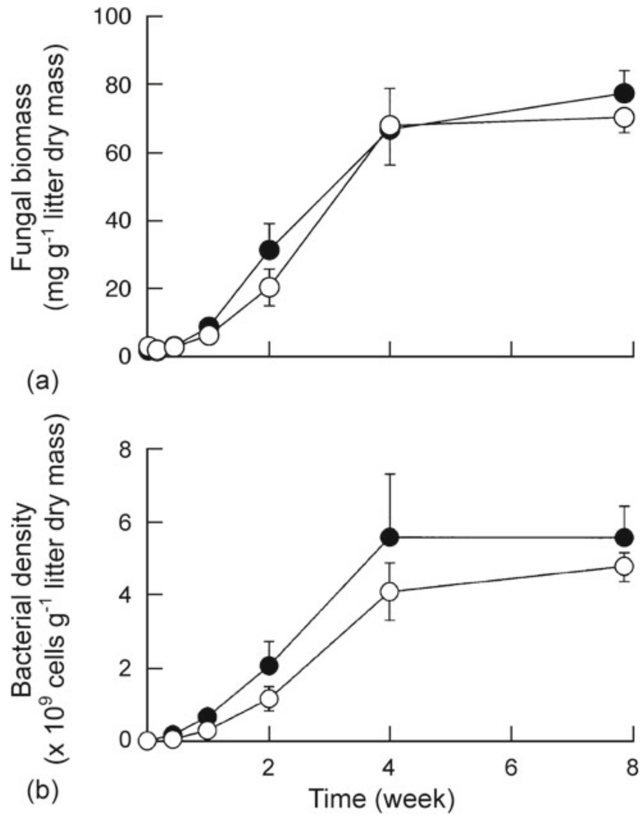


Fig. 7.15 (**a**) Fungal and (**b**) bacterial biomass in a leaf decomposition experiment conducted with alder (●) and willow (○) leaves in a Black Forest stream, Germany. Error bars represent 95% confidence intervals (Reproduced from Hieber and Gessner 2002)

biomass and production were always dominated by fungi. The bacterial contribution increased in treatments where fungi were excluded, suggesting competition between bacteria and fungi for resources. This interaction may be symbiotic as well, as researchers also found evidence that bacteria may benefit from fungal activity during leaf decay (Gulis and Suberkropp 2003). When leaf disks treated with antibacterial and antifungal solutions were incubated in two tropical streams in Venezuela, results indicated that fungi contributed more to total microbial biomass than did bacteria, while bacterial were responsible for a higher proportion of total microbial (Abelho et al. 2005). In a tropical headwater stream in Puerto Rico, leaf decomposition rates were faster when both bacteria and fungi were present, compared to treatments in which one was excluded. However, fungi reached higher biomass alone than in the presence of bacteria, suggesting an antagonistic effect (Wright and Covich 2005b). These results suggest that the interaction between bacteria and fungi can be synergistic in facilitating leaf decomposition but antagonistic in the mutual demand for a carbon source.

Even when encountered on a leaf, microbes may not be actively contributing to decomposition. New techniques are allowing stream ecologists to understand more about when microbes are actively dividing and consuming resources. For instance, quantitative isotope probing, a technique that measures the isotopic composition of specific nucleic acid sequences to differentiate between dormant and actively replicating cells, has begun to be used to study the bacterial and fungal contribution to leaf-litter decomposition in streams. In a pilot study, researchers found that of the 150 fungal species found on submersed leaves, only ~35% were actively dividing (Marks 2019).

7.2.5 Decomposition of Macrophytes, Wood, and Other Sources of CPOM

Thought not as well-studied as leaf-litter decomposition, the decomposition of macrophytes and wood also generates sources of carbon and nutrients for streams. Macrophytes can be key sources of detritus where they are abundant, typically in larger rivers and in floodplains. Polunin (1984) reviewed studies of the decomposition and fate of this material, which is similar to that of terrestrial leaves. Breakdown rates are relatively fast, although less so for emergent macrophytes that contain more support tissue. Bacteria appear to play a greater role in macrophyte decomposition than is true for leaves of terrestrial origin (Webster and Benfield 1986).

Wood ranging from small branches to large tree trunks is abundant in small to mid-sized streams flowing through forested landscapes (Pfeiffer and Wohl 2018; Sutfin et al. 2016). Wood influences channel structure and stream habitat in a number of ways, and also contributes to the nutrition of some consumers (Anderson and Sedell 1979). Not surprisingly, wood decays very slowly. The high lignin and cellulose content of wood fiber, combined with low concentrations of N and P, relatively small surface area, and low penetrability, results in very slow breakdown with microbial activity confined to surface layers. Even small wood chips (0.75–1.5 cm size range) placed in coarse mesh bags in Quebec streams showed very slow loss rates (Melillo et al. 1983). Alder chips (*Alnus rugosa*) had a half-life of about 7 months, while spruce (*Picea mariana*) chips would require roughly 17 years to achieve a 50% reduction in weight. Anderson et al. (1978) retrieved sticks (2.5 × 2.5 92 cm) of alder, hemlock (*Tsuga*) and Douglas fir (*Pseudotsuga*) after 15 months in an Oregon stream, with similar results. Webster et al. (1999) estimated breakdown rates for sticks of different diameter (<20 mm, 20–25, and >25 mm) of yellow poplar (*Liriodendron tulipifera*), white pine (*Pinus* *strobus*), and red oak (*Quercus rubra*) in a 5-year experiment conducted in streams at Coweeta Hydrologic Laboratory. Breakdown rates were more rapid for sticks of smaller diameter, and for poplar relative to the pine and oak. Breakdown rates for sticks were one to two orders of magnitude slower than those reported for leaves of woody plants. Logs (20–32 cm diameter) that were placed in this stream lost their bark after 4–5 years and showed some signs of surface decomposition after 8 years, but still no differences in density were detected. Natural wood pieces, such as branches and twigs, have slower decomposition rates than commercial wood substrates such as chips, sticks, cubes, and disks, probably because the latter have a higher surface to volume ratio and because leaching losses are higher from the processed surfaces of wood products (Spanhoff and Meyer 2004).

Nutrient availability may have some influence on wood decomposition in streams. Comparison of alder, pine, oak, and eucalyptus branches at three sites in the Agüera River, Spain, that differed in nutrient levels suggested phosphorus limitation of wood breakdown (Diez et al. 2002). An initial weight loss (5–9%) due to leaching occurred during the first few weeks, and phosphorus was rapidly lost during the first six weeks in all but eucalyptus. Breakdown rates were most rapid for alder, followed by oak and eucalyptus, and then pine, which also showed the lowest values of ergosterol. In two streams in Germany, the decomposition rate for black alder (*Alnus glutinosa*) was higher and the half-life shorter at a site with higher nitrate and phosphate levels (Spanhoff and Meyer 2004). Experimental addition of nutrients enhanced the decay of wood (oak veneers and natural maple sticks), more so for veneers than sticks (Gulis et al. 2004). The faster breakdown rate of the veneers was accompanied by higher nitrogen and ergosterol content and microbial respiration, which was thought to be primarily fungal (Fig. 7.16).

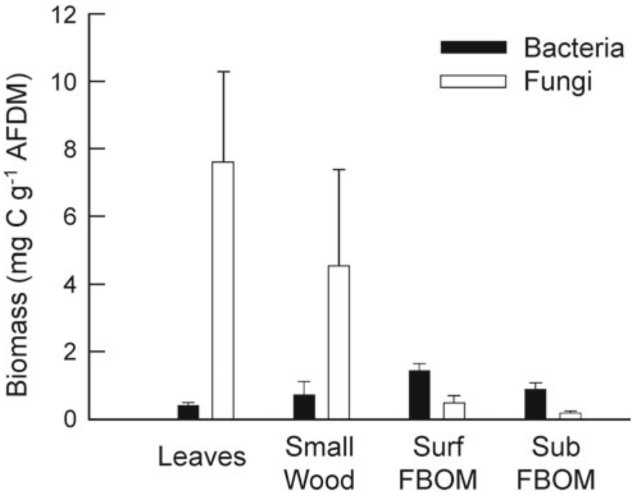


Fig. 7.16 Biomass of fungi and bacteria on leaves, wood, and surface and subsurface fine benthic organic matter (FBOM). Means and standard deviations of 7–9 streams are shown (Reproduced from Findlay et al. 2002)

When present, animal tissue can also represent substantial sources of organic matter in streams. For example, in a study comparing detrital inputs of cicadas to leaf litter from a dominant riparian tree species, researchers documented that cicada tissue had relatively lower carbon to nutrient ratios, released carbon and nutrients at a faster rate, and decomposed more quickly than leaf litter (Pray et al. 2009). The content and form of nutrients and carbon stored in animal tissue may vary among types of tissue and this may influence biogeochemical cycling. For example, Subalusky et al. (2018) found varied rates of decomposition associated with different animal tissues (e.g., hippo feces, wildebeest soft tissue and bone). Feces and soft tissue had relatively quick turnover times and rapid nutrient leaching, whereas bone decomposed at much slower rates.

7.2.6 Macroconsumers and Detritivory

The fragmentation of leaves by detritivores is an important process in leaf breakdown. Aquatic insects and crustaceans are the most common consumers of CPOM. During the decomposition of autumn-shed leaves in temperate woodland streams, microbial populations play a central role not only in decomposing the leaf substrate, but also in altering the chemical nature of the leaf material, rendering it more palatable and nutritious to consumers. In turn, the feeding activities of detritivores significantly accelerate the decomposition process. Their contribution to the fragmentation of coarse particles through feeding activities and production of feces significantly accelerates breakdown rates and influences subsequent biological processing of the original CPOM.

Several lines of evidence indicate that insects that shred larger pieces of leaves, or shredders, accelerate the breakdown of leaves in streams (Webster and Benfield 1986). The finding that leaf packs in mesh bags decomposed more slowly than those tethered to bricks with fishing line indicated that the former method underestimated breakdown rate, presumably because of the exclusion of detritivores. In addition, leaf breakdown was more rapid when bags with larger mesh size were used, presumably because invertebrate access was greater. Comparison of decay rates in experiments with and without insect detritivores provides further evidence that as much as half of leaf degradation can be attributed to the presence of animals in some systems. Processing rates in two experimental streams, one lacking invertebrates and another stocked with detritivores (*Tipula*, *Pycnopsyche*, and *Pteronarcys*) at densities believed to represent natural maxima, indicated that 21–24% of the loss of hickory leaves was due to the influence of detritivores (Petersen and Cummins 1974). The contribution of macroinvertebrates to the breakdown of *Phragmites*, a macrophyte, was comparable (Polunin 1982). In an Appalachian stream, exclusion of macroconsumers, primarily crayfish, using electric fences resulted in lower breakdown rates of rhododendron leaves (Schofield et al. 2001). When present, crayfish were responsible for 33% of leaf breakdown in summer and 54% in autumn. Sponseller and Benfield (2001) observed faster leaf breakdown with higher shredder density and biomass (Fig. 7.17). In addition to direct consumption, possible influences of detritivore feeding include release of nutrients and dissolved organic matter, comminution of litter, and modification of water circulation (Polunin 1984). The freshwater shrimp *Xiphocaris elongata*, a consumer of large leaves in tropical streams, increased the concentration of both total dissolved nitrogen and dissolved organic carbon, and also the concentration and transport of POM (Crowl et al. 2001).

The experimental removal of detritivorous insects from a small mountain stream in North Carolina provides a particularly convincing demonstration that animal consumers regulate rates of litter decomposition. Wallace et al. (1991, 1982b) added the insecticide methoxychlor to one small stream in February, with supplemental treatments in May, August, and November. Massive downstream drift of invertebrates occurred, and insect densities subsequently were reduced to less than 10% of numbers in an adjacent, untreated reference stream, while oligochaetes increased roughly threefold. Leaf breakdown rates were significantly slower in the treated stream, presumably due to the great reduction in insect density, and the magnitude of the effect was greatest for the most recalcitrant leaf species. Export of suspended fine particulates also was reduced in the treated stream, consistent with the finding of reduced leaf processing.

Studies conducted in Colombia, Costa Rica, Venezuela, Papua New Guinea, and Kenya found that insect shredders were scarce, despite the fact that densities of other invertebrates were similar to those reported in the temperate zone (Yule 1996; Dobson et al. 2002; Rincon et al. 2005; Wantzen and Wagner 2006). In these tropical locales, shredders represented less than 7% of total macroinvertebrate abundance, while in European rivers this value ranged from 10–43% (Dobson et al. 2002; Hieber and Gessner 2002). Nonetheless, leaf breakdown rates in streams in Costa

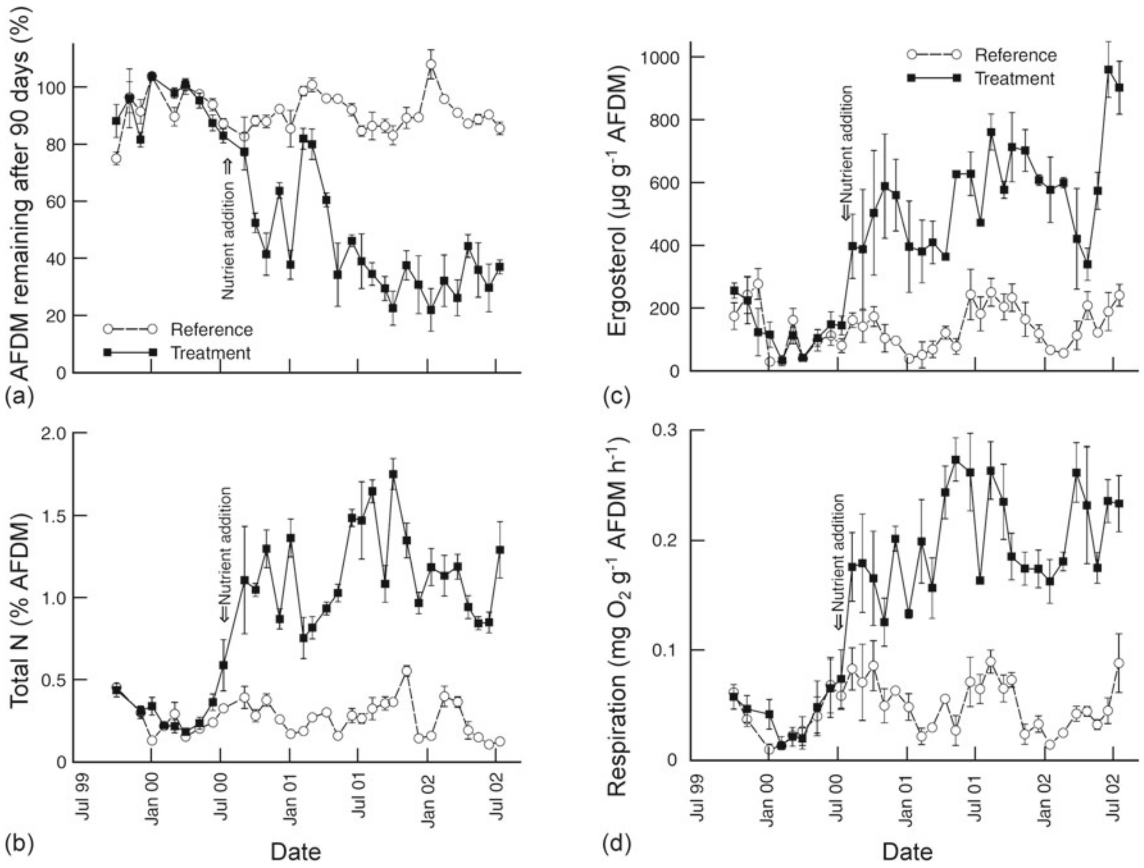


Fig. 7.17 Variation in (**a**) AFDM, (**b**) total N (as % of AFDM), (**c**) ergosterol and (**d**) respiration during a 90-day decomposition experiment using oak veneers incubated in a treatment stream (N and P additions) and a reference stream (no nutrient addition) (Reproduced from Gulis et al. 2004)

Rica (Rosemond et al. 1998) and in Colombia (Mathuriau and Chauvet 2002) were rapid, suggesting a greater role of microorganisms in tropical streams. Possible explanations for these findings include higher temperatures in the tropics, reduced lability of leaves due to the presence of defensive compounds, incorrect assignment of tropical invertebrates to trophic roles, or failure to detect the presence of large shredders (Irons et al. 1994; Schofield et al. 2001; Wantzen et al. 2002). In contrast to some reports of low shredder density in tropical streams, Cheshire et al. (2005) found that shredders represented 20% of total macroinvertebrate abundance in the Australian tropics, similar to values reported from the temperate zone. These authors suggested that shredder scarcity in tropical streams may reflect historical biogeography rather than a strict latitudinal effect, because in some temperate regions such as New Zealand, shredder insects also are scarce. Studies in streams in Colombia (Chará-Serna et al. 2012), Malaysia (Yule et al. 2009), and Panama (Camacho et al. 2009) also suggest that tropical shredders may be key in some locations, and that in tropical systems, site-specific shredder diversity may vary predictably with elevation, water temperature, and water chemistry.

Understanding how the lability, quantity, timing, and duration of allochthonous inputs to streams influence the structure aquatic food webs is a complex undertaking, but the importance of detrital resources in supporting stream food webs is well documented. Studies that have experimentally manipulated the quantity of subsidy inputs have enhanced our understanding of the importance of detritus in supporting ecosystem productivity (Venarsky et al. 2018). Drawing upon decades of observational and experimental data of research in forested, headwater streams in the southeastern US, Wallace et al. (2015) describe how the abundance and diversity of aquatic macroinvertebrates changes in response to whole-stream manipulations of benthic organic matter. Long-term data comparing reference streams to those subjected to whole-stream organic matter manipulations showed that in mixed substrate habitats, the amount of benthic OM was positively related to monthly invertebrate biomass and annual secondary production (Fig. 7.18), and this was especially pronounced in shredder populations. Their work emphasized that the organic matter remaining in the stream following litter exclusion and wood removal was more recalcitrant than that in the reference streams, whereas the litter inputs to reference streams was more labile and more easily incorporated into invertebrate biomass. Predator production was strongly correlated with total invertebrate production, providing evidence that terrestrially-derived resources are essential in supporting freshwater food web structure.

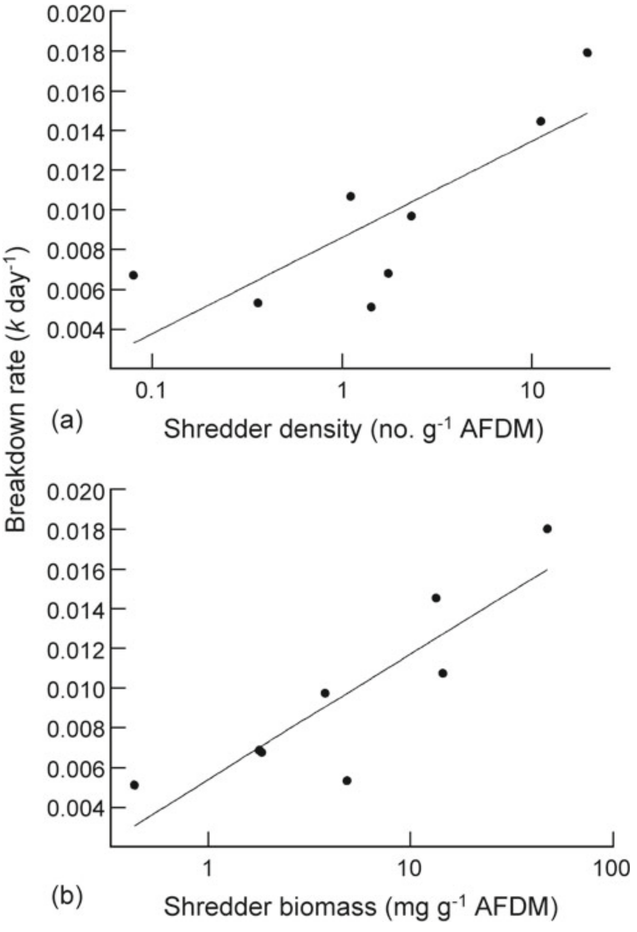


Fig. 7.18 Correlations between leaf breakdown rates and (**a**) density and (**b**) biomass of shredders expressed per g of leaf AFDM (Reproduced from Sponseller and Benfield 2001)

Investigations into CPOM dynamics have frequently been conducted in forested streams, where detrital inputs typically exceed consumer energy demands and where many populations of freshwater organisms have evolved to take advantage of specific temporal and spatial characteristics of subsidies. However, in streams with limited or no riparian vegetation, including cave, tundra, and desert systems, CPOM inputs may be reduced and seasonality not apparent (Tank et al. 2010). For instance, cave systems typically have relatively limited autochthonous production, and allochthonous inputs may be scarce as well; therefore, consumer demand for carbon is predicted to be high relative to carbon availability. Upon addition of maize to an experimental reach of the Bluff River Cave in the southeastern US, the abundance and biomass of organisms increased at all trophic levels, suggesting that carbon from the maize was rapidly assimilated by fungi and bacteria (Fig. 7.19), and that this energy was transferred to higher trophic levels (Venarsky et al. 2018). Intriguingly, only facultative cave taxa, which were also found in the connected surface streams, contributed to the community-level response and increased in abundance. In contrast, obligate cave species showed no

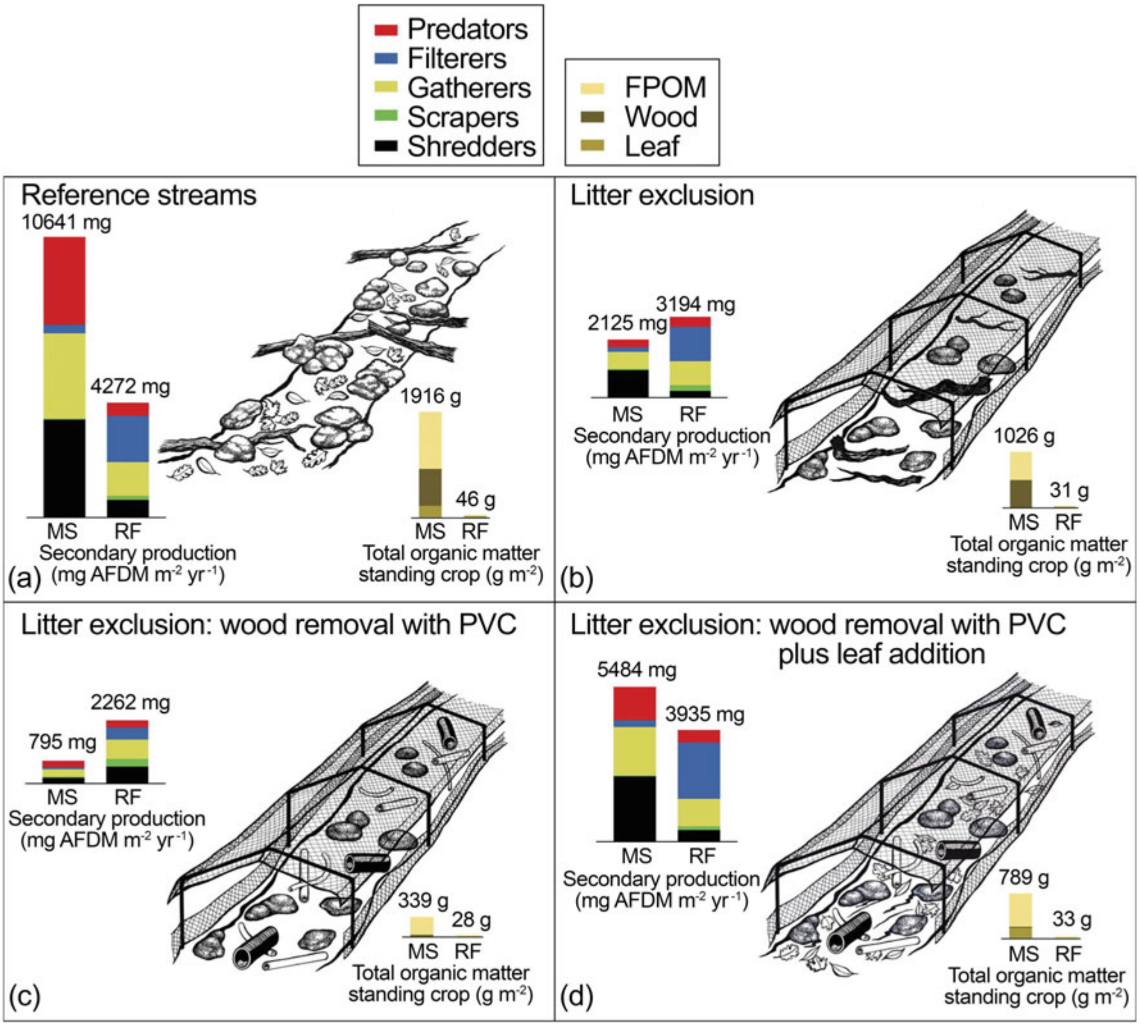


Fig. 7.19 Organic matter standing crops (g m^{-2}) and secondary production (mg AFDM m^{-2} yr^{-1}) in mixed substrate (MS) and rockface (RF) habitats, for (**a**) reference streams (n = 24 years); (**b**) end of third year of litter exclusion period; (**c**) end of small- and large-wood removal (n = 4 years) and the first year of PVC pipe addition period, and (**d**) end of fifth year of leaf addition. The litter exclusion canopy was maintained during the experimental period over the treatment stream. The values reflect total secondary production and organic matter standing crops for the reference streams, and the totals at the end of each experimental period for the litter exclusion stream. Rock face habitats characterized by low organic matter standing crops are drawn at a different scale from the mixed substrate organic matter standing crops. In contrast, secondary production values are drawn at the same scale for both habitats (Reproduced from Wallace et al. 2015)

response to the experimental treatment, indicating that evolutionary history may constrain the response of taxa to novel subsidies (Venarsky et al. 2018). In other words, this work suggests that species may have evolved under conditions of fluctuating nutrients and energy in order to be able to effectively respond to changes in resource availability.

Because of variation in the timing of leaf fall, species-specific rates of leaf conditioning by fungi, and the diversity of fungi present, leaves on the streambed are a mosaic of patches of microbial populations. The extent of this variation is shown by Bärlocher's (1983) study of a Swiss stream flowing through an alder-willow-maple forest. The standing crop of CPOM was maximal in October-November, and by April only veins and petioles remained for an 85% loss of leaf mass. Soluble protein also decreased after November, indicating that nutritional value declined from that time on. However, on any one date, the chemical characteristics of individual leaves were so variable that the amount of soluble protein in the richest 10% of leaves in mid-April exceeded the median value of leaves sampled in mid-November. Detritivores capable enough or fortunate enough in patch choice could enjoy food quality well above average.

Studies have found that shredders can discriminate among leaves colonized by different fungal species, showing preference for the fungi that induced the greatest growth. *Gammarus pseudolimnaeus* preferentially consumed leaf disks colonized by three of ten fungal species examined

(Bärlocher and Kendrick 1973). Similarly, limnephilid caddisflies showed a preference for aspen leaves colonized by fungal species linked to higher growth rates (Arsuffi and Suberkropp 1986). However, animals may not always effectively select higher quality food items. Growth of third and the fifth instars of *Pycnopsyche gentilis* larva fed with fungal-colonized leaves was always significantly greater than the growth of larvae fed with diets of un-colonized leaves; however, larvae did not show feeding preferences for leaves colonized with aquatic fungi (Chung and Suberkropp 2009). Final instars of the limnephilid caddisfly, *Clistoronia magnifica* require triglycerides for reproductive success, and preferentially consumed alder leaf-disks coated with lipids extracted from aquatic hyphomycetes, but third and fourth instars did not exhibit preference (Cargill et al. 1985a; Cargill et al. 1985b).

Where leaf shredding insects are rare or absent, other organisms may play a similar role in litter decomposition. Fish, shrimp, and crabs enhanced leaf breakdown in Costa Rican streams (Rosemond et al. 2002), as did shrimp and other macroinvertebrates in a stream in Puerto Rico (Wright and Covich 2005a). In New Zealand headwater streams, the crayfish *Paranephrops zealandicus* has a strong influence on the decomposition of leaf litter and the production of POM (Usio and Townsend 2001).

Though not as commonly studied, detritivores may also contribute to the processing of wood material via consumption (Benke and Wallace 2010; Eggert et al. 2007). Wood-eating organisms (xylophages), appear to be relatively rare, especially in the temperate zone. However, some caddisflies, beetles, and flies have been classified as obligate xylophages (Hoffmann and Hering 2000). In Neotropical rivers, several members of the suckermouth-armored catfishes (Loricariidae) feed on coarse woody debris. Interestingly, the ability to consume wood appears to have evolved multiple times, as species from two unrelated evolutionary lineages have evolved jaw morphologies that allow them to gouge and eat wood (Lujan et al. 2011).

7.2.7 Anthropogenic Change and Decomposition

Dominant land use may influence in-stream rates of decomposition, but findings are inconsistent among studies. Paul et al. (2006) found that leaves decomposed faster in agricultural (0.0465 day^{-1}) and urban (0.0474 day^{-1}) streams than in suburban (0.0173 day^{-1}) and forested (0.0100 day^{-1}) streams in the southeastern US. Faster breakdown in agricultural streams was attributed to enhanced biological activity supported by higher ambient nutrient concentrations, whereas increased rates of decomposition in urban settings likely were due to enhanced physical fragmentation resulting from higher storm runoff. In contrast, in Puerto Rican streams, Classen-Rodríguez et al. (2019) found that urbanization negatively affected decomposition rates relative to forested streams, possibly because of enhanced sedimentation and burial of leaf bags and fewer macroinvertebrate decomposers in urban streams. Organisms colonizing leaf packs in the urban system were limited to species tolerant of low-oxygen conditions.

Increasing carbon dioxide concentrations and subsequent increases in temperature associated with anthropogenically-driven climate change are also expected to influence OM decomposition in streams. Elevated temperature may increase decomposition rates by increasing metabolic rates of microbial and macroinvertebrate decomposers (Flury and Gessner 2011). Higher temperatures may also enhance leaching rates (Batista et al. 2012), which can result in fast litter decomposition by removing the recalcitrant compounds (Amani et al. 2019). As long as they do not exceed the upper limits of species tolerance, elevated temperatures may also increase the abundance, growth rates, and reproduction of microbes, subsequently enhancing decomposition rates (Moghadam and Zimmer 2016). In contrast, elevated carbon dioxide concentrations decrease litter decomposition rates by shifting the carbon to nutrient ratios of organic matter and reducing the lability of litter (Tuchman et al. 2003). Higher carbon dioxide concentrations, induce changes in plant physiology, increasing the production of carbon-based secondary and structural compounds (Stiling and Cornelissen 2007).

Climate change is predicted to increase average temperatures and the frequency of extreme weather events, and affect the composition of freshwater communities through changes in temperature and hydrology (Wenisch et al. 2017). Therefore, it is essential to understand how environmental variables influence the distribution and density of organisms through periods of climatic variability (Gutierrez-Fonseca et al. 2018). In a 15-yr study examining changes in stream macroinvertebrate communities in lowland Costa Rica, Gutierrez-Fonseca et al. (2018) demonstrated that macroinvertebrate richness and abundance declined with increasing discharge and were positively related to the number of days since the last high flow event. Their work suggests that macroinvertebrate community structure is ultimately the result of large-scale climatic phenomena, such as El Nino/Southern Oscillation (ENSO), and changes in hydrology associated with climate change have the potential to restructure the invertebrate community and alter their functional contribution to ecosystem-level processes (Gutierrez-Fonseca et al. 2018). In two streams in the Palatinate forest, south-western Germany, Wenisch et al. (2017) compared bulk leaf decomposition rate and the leaf processing efficiency of shredders in enclosures containing three shredder diversity treatments, where species loss was simulated based on their sensitivity to climate change. They found that litter decomposition rates were strongly affected by changes in the macroinvertebrate community, with a 33% increase and 41% decrease in decomposition following species loss at the first and second site, respectively. Researchers attributed the conflicting results to the traits of sensitive taxa. In the first site, the least sensitive taxa had more biomass that may have compensated for the loss of sensitive taxa. However, in the second site, species that were sensitive to shifts in climate played a larger role in decomposition that was not compensated for by the remaining species. Their findings highlight how local diversity in species trait composition may buffer the potential effects of climate change on ecosystem processes (Wenisch et al. 2017).

Temperature-mediated shifts in microbial respiration may enhance the flux of carbon dioxide from streams, reducing the capacity of streams to store carbon. Tropical watersheds emit large amounts of carbon dioxide to the atmosphere (Raymond et al. 2013); therefore, shifts from macroinvertebrate shredding to microbially-mediated decomposition has the potential to alter carbon dynamics at larger spatial scales (Boyero et al. 2012). The interactive effects of increasing temperature and carbon dioxide on decomposition in streams are still emerging. From a meta-analysis of data from about 40 field and laboratory studies conducted between 1993 and 2017, Amani et al. (2019) found that elevated temperature significantly increased litter decomposition rates, but elevated carbon dioxide concentrations did not.

Anthropogenically-derived changes in nutrient concentrations also may have large effects on OM decomposition rates (Rosemond et al. 2015). At lower concentrations, increasing nutrient levels can enhance the nutrient content of leaf litter and accelerate litter breakdown by microbes and macroinvertebrates (Demi et al. 2018; Cross et al. 2006). This can be especially pronounced in more recalcitrant species, and reduce species-specific differences in decomposition (Manning et al. 2015). Though carbon storage in systems might initially buffer subsequent changes to stream food webs, persistent increases in microbial respiration and carbon export could have significant impacts on the duration of litter resources in streams. This may negatively affect the quantity of carbon stored in litter and the carbon transferred to macroinvertebrates within a given reach (Rosemond et al. 2015; Wallace et al. 2015; Kominoski et al. 2018), suggesting that nutrient pollution may limit macroinvertebrate productivity as carbon resources become limited (Halvorson et al. 2017).

Introduced plant species can influence the relative lability of leaf litter entering streams. In an investigation comparing CPOM in streams dominated by native riparian vegetation, pasturelands, or introduced rhododendron (*Rhododendron ponticum*), Hladyz et al. (2011) reported that CPOM in rhododendron-dominated sites had much greater carbon to nutrient ratios, suggesting they were more recalcitrant. Introduced species may also affect interactions between detritivores and organic matter. Kiffer et al. (2018) compared the effect of leaves from native species and non-native *Eucalyptus globulus* on the feeding activity and performance of larvae of a common caddisfly shredder, *Triplectides gracils*, in an Atlantic Forest stream in Brazil. The larvae preferred to feed on softer leaves, regardless of the nutrient content and concentrations of secondary compounds. When softer, native species were not present, caddisfly larvae preferred the exotic species to tougher native species. However, larva that were fed the non-native species lost biomass through time, and larval survival was lower on *Eucalyptus* compared to four of the five native species. These data provide further evidence that species-specific traits of litter, such as leaf toughness, influence the behavior of detritivores, and highlight that changes in the composition of riparian vegetation may negatively impact the growth and survival of native taxa (Kiffer et al. 2018).

Native biodiversity loss is a threat to aquatic communities and ecosystems throughout the world, and may influence OM processing rates in rivers and streams. Though the effects of plant species richness on decomposition are variable among studies, litter mixing studies suggest the greater species richness of litter tends to accelerate decomposition rates (Handa et al. 2014) and the rate of FPOM production (López-Rojo et al. 2018). Within streams, the effects of increased macroinvertebrate diversity tend to be greater in enhancing rates of litter decomposition when litter packs are more diverse. As consumers specialize on different types and sizes of organic matter, increasing trophic diversity in streams tends to enhance the volume and rate of energy moving to higher trophic levels (Tonin et al. 2018). Hence, anthropogenically-induced changes in the spread of disease, land use, and climate are expected to alter detritivory in streams.

The decline of stream-breeding amphibians in response to the spread of Chytridiomycosis, a disease caused by infections of the *Batrachochytrium dendrobatidis* fungus, has ecosystem-level consequences. Experimental manipulations of *Smilisca*, a widespread and abundant genus of frog in Central American streams, demonstrated that tadpoles affect leaf decomposition by influencing microbial community dynamics through their excretion of nutrients and feeding activities (Rugenski et al. 2012). This research, and the collective body of work examining amphibian declines in streams, suggests that the loss of a suite of species may have widespread consequences on fundamental ecosystem processes, such as OM decomposition (Whiles et al. 2013; Colon-Gaud et al. 2010).

7.3 Sources and Processing of Fine Particulate Organic Matter

Fine particulate organic matter (FPOM) is found suspended in the water column as seston, and in the benthos of streams as fine benthic organic matter (FBOM). It includes all of the fine material, including algae, bacteria, detritus, and sediment, that ranges from 0.45 µm to 1 mm in size (Hutchens et al. 2017). The origin of FPOM in streams can vary widely, and it includes both allochthonous and autochthonous sources. Fine particulates arise from the physical breakdown of instream CPOM, microbial processing and animal waste, flocculation or complexation of dissolved substances, and runoff from the surrounding terrestrial environment.

7.3.1 Temporal and Spatial Variation in FPOM

Much less is known about the energy pathways involving FPOM than CPOM. One source of FPOM obviously is the breakdown of leaf litter (Fig. 7.7) as fragments from mechanical breakdown and shredder activity enter the water column. When one includes the production of feces and the eventual contribution of leached DOC to formation of fine particles, it is apparent that a large fraction of leaf litter eventually becomes fine particulate matter. In addition, microbial activity on the leaf can result in the release of leaf and bacterial cells and the hyphae and conidia of fungi (Gessner et al. 1999). Fine particulates are also transported into streams from the terrestrial landscape by wind and runoff, and can be formed from dissolved organic matter primarily by the incorporation of DOC into microbial biomass. These sources are difficult to trace and potentially of greater magnitude than FPOM derived from leaf fragmentation.

The amounts and characteristics of FPOM fluctuate along and within a river network, and they are linked to season, climate, dominant land use, and underlying geology. Particulate concentrations often show a positive relationship with regional precipitation, probably due to the influence of precipitation on terrestrial production and the subsequent effect on the supply of CPOM. Floodplains can be a large source of organic matter, and FPOM concentrations often increase in lowland rivers during inundation (Golladay 1997). Terrestrially-derived FPOM inputs are typically low during base flow and increase during storms and seasonal high flows as rising flows entrain particles from stream banks and side channels (Mulholland 1997a). A comparison of 31 streams and medium-sized rivers in North America, Europe, the Arctic, and Antarctica found FPOM to range between 0.14 and 15.30 mg L^{-1} (Golladay 1997). In streams and rivers of eastern US, POM estimates ranged between 0.5 and 52 mg L^{-1} (Webster et al. 1995); in undisturbed forested catchments, mean annual concentrations often are less than 2 mg L^{-1} (Fisher and Likens 1973; Naiman and Sedell 1979).

The concentration of FPOM is also affected by changes in particle availability. Controls of particle availability include terrestrial production, instream seasonal change in biological processing, and discharge, which varies both seasonally and unpredictably. In streams of the eastern United States during normal flows, FPOM concentrations are higher during spring and summer than during autumn and winter (Fig. 7.20), probably because lower biological activity during the colder months results in less instream particle generation (Webster et al. 2006). If the particle supply is relatively constant, then an increase in discharge will cause a dilution effect, even if the total amount of FPOM in transport is greater.

An increase in streamflow in response to a rainstorm results in a corresponding increase in particle concentrations as POM generated during low flows and stored in depositional areas is entrained by rising stream levels (Fisher and Likens 1973; Meyer and Likens 1979). This indicates that the major pool of particulate organic matter lies in areas already wet or adjacent to the stream's wetted perimeter, where FPOM accumulates during low flows. Inputs of POM from outside of the stream also are likely to be greatest during the rising limb of the hydrograph, due to the erosive effects of rainfall on soil and streambank litter and generation of flow in previously dry channels. During the descending limb, water enters the stream principally by subsurface flow, and carries little or no POM. Thus, concentrations are highest on the rising limb of the hydrograph (Fig. 7.21) and then decline due to exhaustion of the particle supply and dilution of the entrained material.

Because particulate concentrations usually are higher when discharge is greater, most FPOM is transported during episodic and seasonal floods, and thus flow conditions that occur during only a small fraction of the annual discharge cycle can account for a very large fraction of annual transport. Some 75–80% of POM transport in small streams in the southeastern US occurred during storms (Webster et al. 1990), demonstrating the importance of accurately sampling these episodic events. In fact, unless sampling is continuous or captures high flows very thoroughly, total transport may be seriously under-estimated.

In addition to weather and climate, other factors, including the composition of riparian vegetation, land use, and the presence of impoundments are expected to alter the quantity and timing of FPOM in streams. Forested streams frequently exhibit higher FPOM concentrations that non-forested streams, as was observed in a comparison of native forest to pasture sites in a New Zealand stream (Young and Huryn 1999), and in the aforementioned 31

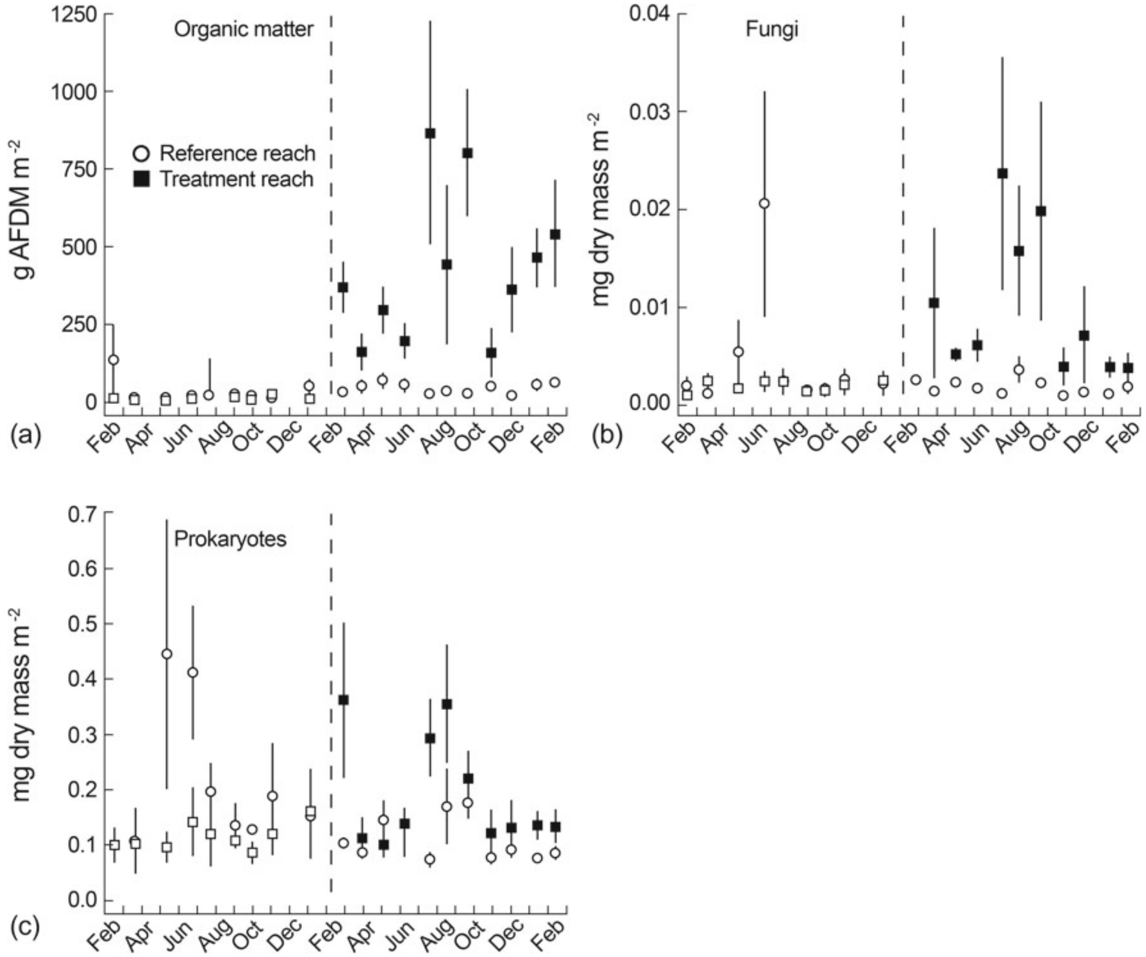


Fig. 7.20 Average values of (**a**) organic matter, (**b**) fungal biomass, and (**c**) prokaryotic biomass in the Bluff River Cave stream in Alabama in the southern US. Samples collected in the reference sites are represented with open circles and samples collected from the treatment reach are represented with open (pre-litter addition) and closed (post-litter addition) squares. The vertical, dashed line in each plot indicates when the litter addition began. Error bars are standard error (Reproduced from Venarsky et al. 2018)

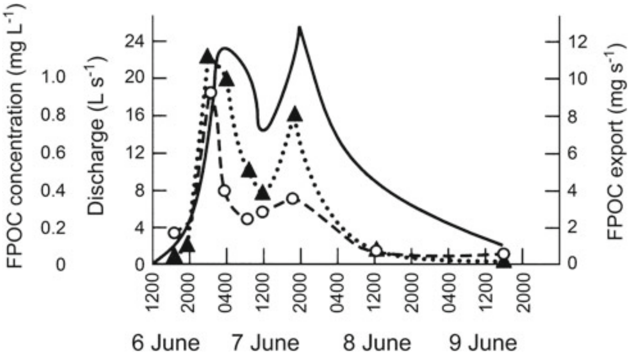


Fig. 7.21 Changes in discharge, FPOC concentrations, and FPOC transport during a summer storm in a small forested catchment in New Hampshire. Note that FPOC concentrations peak on the rising limb of the hydrograph, indicating rapid entrainment of small particulates. A second hydrograph peak resulted in a much smaller FPOC concentration peak, evidence that wash-out rapidly depletes the available FPOC supply. Solid line indicates discharge; O—O denotes FPOC concentration; and, ▲…▲ denotes FPOC export (Reproduced from Bilby and Likens 1979)

streams from different regions (Golladay 1997). However, high FPOM concentrations also are seen in low gradient streams flowing through agricultural or multiple-use catchments (Malmqvist et al. 1978), and especially in larger lowland rivers (e.g., Berrie 1972; Ward 1974).

Animals can also directly contribute to the FPOM pool through their feces (Wotton and Malmqvist 2001). Litter consumption rates and subsequent FPOM production can be influenced by the diversity of leaf litter (Fernandes et al. 2015), as macroinvertebrates that specialize in consuming leaf litter appear to be sensitive to changes in litter species and leaf conditioning by microbes (Santonja et al. 2018). Organisms specializing in FPOM consumption, such as black flies (Simuliidae, Diptera), can also contribute to the FPOM pool. Black fly larvae ingest FPOM and DOM and produce larger particulate material in the form of fecal pellets (Wotton et al. 1998). Hershey et al. (1996) observed a 28% increase in the mass of FPOM and an alteration of the particle size distribution downstream of a filtering black fly aggregation. Each larva can produce on average 575 pellets per day, and so in dense aggregations (~600,000 per m^{-2} within a 40 m reach of an Arctic tundra stream), the daily production of pellets was estimated at 1.3–9.2 × 10^9.

Because the production of FPOM is often dependent on in-stream consumer populations, changes in aquatic species composition may influence FPOM dynamics. For example, Greig and McIntosh (2006) demonstrated that an invasive trout in New Zealand streams reduced invertebrate density and, consequently, the rates of leaf decomposition and FPOM production. However, an introduced species may increase OM processing when the invader generates FPOM through feeding activities. Red-swamp crayfish *Procambarus clarkii* have introduced populations throughout the world. In a comparison of leaf consumption rates between the invasive crayfish and a native shredding caddisfly, researchers documented that decomposition rates and FPOM production were much greater in the presence of the invader (Carvalho et al. 2016).

Land use change also can influence FPOM inputs, as Epstein et al. (2016) showed from the carbon budget of the Jordan River, a regulated urban river that connects Utah Lake to the Great Salt Lake in the western US. Stable isotope analyses indicated that FPOM in the river was more isotopically similar to autochthonous source materials, including productive, eutrophic water released from Utah Lake and in-stream primary producers, than it was to terrestrially-derived CPOM. Temporal changes in FPOM concentration in the river reflected the flow release patterns from Utah Lake, indicating that eutrophication and water regulation associated with urban development can have strong effects on FPOM dynamics in streams.

7.3.2 Storage and Transport of FPOM

Depositional areas, especially pools and around wood accumulations, are key locations of FPOM retention in the benthos. Logs are a particularly effective retention device in low-order streams of forested catchments. Accumulations of organic matter formed when wood becomes lodged against obstructions trapping smaller material and leaves into a nearly watertight structure. Sediments and organic matter settle in the pools formed upstream of these dams, creating potential hotspots of detrital processing. Following experimental removal of all organic dams from a 175-m stretch of a small New Hampshire stream, organic matter export increased several-fold (Bilby 1981; Bilby and Likens 1980). When beaver *Castor canadensis* were unexploited they must have contributed greatly to organic matter storage over large areas of the north temperate zone. Where beaver occur at natural densities today, their activities influence 2–40% of the length of second- to fifth-order streams, and increase the retention time of carbon roughly six-fold (Naiman et al. 1986). In large rivers, the floodplain can be a primary site of POM deposition and storage and macrophyte beds are important retention features for POM (Wanner et al. 2002).

Fine particulate transport distance can be estimated by releasing a known quantity of particles into the stream and measuring water column concentrations at various distances downstream. The decline in particle concentration is fit to an exponential decay equation, and the inverse of the decay coefficient is a measure of average transport distance of a particle before being retained on the streambed. Using corn pollen as a surrogate for FPOM (it is similar in diameter but less dense), Miller and Georgian (1992) estimated mean transport distances of 100–200 m in a second-order stream in New York. Estimated transport distance for natural FPOM labeled with radiocarbon in the Salmon River headwaters of Idaho ranged from 150 to 800 m (Cushing et al. 1993; Newbold et al. 2005). Assuming that particle resuspension occurs every 1.5 to 3 h and an average transport distance per event of 500 m, Cushing et al. (1993) calculated an average downstream transport of 4 to 8 km day^{-1}. Much greater transport distances, between 3,000 and 10,660 m, were estimated for a sixth-order lowland river, using spores of *Lycopodium clavatum* with a fluorescent label, and distances were greater under faster currents (Wanner and Pusch 2001). Longer transport distances in larger rivers may reflect fewer opportunities for particle entrapment, whereas the extent of water exchange between surface flows and the hyporheic zone has been shown to correlate with transport distances in smaller streams (Minshall et al. 2000). Owing to the relative slow rate of utilization of FPOM estimated from respiration measurements and the combination of relatively long transport distances with frequent re-suspension, export rather than mineralization appears to be the dominant fate of FPOM from studies of smaller streams and rivers.

Effectively measuring the inputs and standing stocks of FPOM can be challenging, as they require estimates of concentrations in suspension and standing stocks on the stream bed (Hutchens et al. 2017). Instantaneous seston concentrations (mg L^{-1}) can be measured by filtering a known volume of stream water through a glass fiber filter that has been weighed and ashed to remove organics. The filters are dried, weighed, ashed, and re-weighed to calculate ash-free dry mass, an estimate of organic matter content. In larger systems, seston concentration estimates may need to be depth-integrated and velocity-weighted to account for differential settling rates and current velocities along the width and depth of the river. Newer methods to estimate FPOM concentrations integrate data collected with sensors or through remote sensing tools that assess turbidity or total suspended solids (measurements that include organic and inorganic constituents) with the aforementioned methods to account for the organic content of the suspended material. Sampling for benthic FPOM should account for the diversity and distribution of habitat types within a reach. Specifically, characteristics of the stream, including presence or absence of retention features (e.g., large wood, floodplains, dams), current velocity, and substrate particle size need to be taken into account when estimating the standing stock of fine particles in the benthos (Pfeiffer and Wohl 2018). In smaller systems, substrate cores can be filtered through sieves to estimate benthic FPOM. However, larger sites may require the use of SCUBA equipment or dredges and may require trained operators to safely support sample collection (Hutchens et al. 2017). Fluorescently labeled latex particles (Harvey et al. 2012) and titanium dioxide particles (Karwan and Saiers 2009) have been used to investigate deposition and entrainment of ultrafine particles (Hutchens et al. 2017). A review of FPOM sampling and processing methods and detailed protocols can be found in Hutchens et al. (2017).

7.3.3 Lability of FPOM

As discussed previously, the lability of organic matter is only approximated by some aggregate measure of the rate at which it is processed, as in reality, a number of different measures are informative. Lability of FPOM can be assessed by such characteristics as stoichiometry, enzymatic activity, respiration, and extractable amounts of nitrogen and phosphorus, among others. The physical and chemical aspects of fine particulates originating from terrestrial ecosystems are affected by the composition of the terrestrial vegetation, position along the river network, and temporal variation in discharge. Several characteristics of benthic FPOM differed among Oregon stream sites in old growth forest dominated by Douglas fir and western hemlock, and young growth stands of Douglas fir and herbaceous vegetation with abundant deciduous trees in the riparian zone (Bonin et al. 2003). The FPOM of streams flowing through young growth stands had lower carbon to nitrogen ratios and higher denitrification potential, as well as greater extractable ammonium, phosphatase activity, and respiration rates, suggesting greater lability and microbial activity compared with streams in older stands. The lability and amount of inputs of terrestrial POM likely are higher at young growth sites, and an observed increase in microbial activity following a storm is evidence of system response to a pulsed input. Benthic respiration and thus microbial activity have also been observed to increase as one proceeds downstream (Webster et al. 1999), which may be the result of changes in organic matter lability as well as higher temperatures, greater nutrient availability and increases in substrate lability related to higher algal POM inputs (Fig. 7.22).

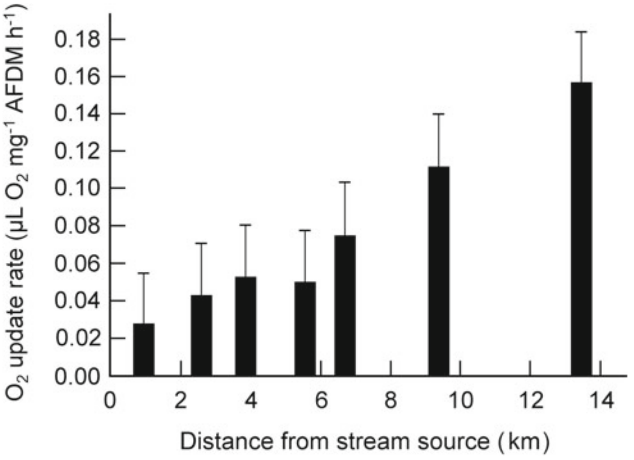


Fig. 7.22 Downstream variation in benthic FPOM respiration in Ball Creek-Coweeta Creek at the Coweeta Hydrologic Laboratory. Values shown are means and standard errors for all sampling dates for each site (Reproduced from Webster et al. 1999)

Even in headwater streams, FPOM originates from sources other than fragmentation of leaves, and this influences the palatability and physical and chemical recalcitrance of FPOM. Based on rough calculations of the magnitudes of inputs attributable to soil organic matter and the breakdown of wood, Ward and Aumen (1986) concluded that leaves and needles were minor sources of FPOM. Using flotation to separate organo-mineral particles from fragmented plant material collected from small forested streams in Oregon, Sollins et al. (1985) found that the majority of detrital carbon and nitrogen was present as organic material adsorbed on mineral surfaces, rather than as plant fragments. In an analysis of FPOM in the Amazon River, Hedges et al. (1986) compared the signatures of river particles to various potential organic sources, finding that the majority originated as soil humic material. At least for large rivers, this conclusion appears to be general (Bernardes et al. 2004; Onstad et al. 2000; Townsend-Small et al. 2005). Based on the ratio of carbon to nitrogen atoms in river seston world-wide, the majority of riverine FPOM most closely resembles soil organic matter. For instance, Spencer et al. (2016) demonstrated that organic particulates in the Congo River appeared to be sourced from soil-derived, mineral-associated organic matter. However, the relative proportion of fresh vascular plant material in the particulates increased with increasing discharge.

Lower C:N in FPOM relative to CPOM and DOM could be related to the presence of microbial biomass or clay minerals (Hedges et al. 1986; Devol and Hedges 2001). The ratio of C:N in particulates that have been measured in three of the world's largest rivers are similar (Congo River, 9.9–12.4 (Spencer et al. 2016); Amazon River, 6.8–13.2 (Hedges et al. 1986; Hedges et al. 1994); lower Mississippi River, 9.1–11.6 (Bianchi et al. 2007)). The values reported for FPOM are lower (i.e., more enriched in N) relative to the values reported for CPOM. Researchers have asserted that this enrichment may be due to nitrogen-enriched microbial biomass in soils and the preferential sorption of nitrogen-rich compounds to fine particulates (Spencer et al. 2016).

Evidence also suggests that the stoichiometry of FPOM is linked to climate and underlying geology. In a survey of the chemical characteristics of coarse and fine particulates from biomes of diverse climates (i.e., tropical montane forest, temperate deciduous forest, boreal forest, and tallgrass prairie), Farrell et al. (2018) documented greater average carbon and nitrogen concentrations and more variable carbon to nutrient ratios in CPOM that in FPOM. When compared to FPOM chemistry, phosphorus content was comparatively reduced and nitrogen to phosphorus ratios were greater in CPOM from tropical montane and temperate deciduous forests. However, CPOM was richer in phosphorus concentrations and had similar nitrogen to phosphorus ratios as observed for fine particulates in grassland and boreal systems (Fig. 7.23). The authors suggest that the microbial processing that transforms CPOM to FPOM results in more tightly constrained elemental composition, and subsequently less variability in the stoichiometry of FPOM. Stable isotope data collected in the same study suggested that fine particulates originated primarily from CPOM in tropical montane and temperate deciduous climates, but were derived from a mixture of detrital and non-detrital resources in the other biomes (Farrell et al. 2018). These observed patterns in CPOM and FPOM dynamics may influence trophic dynamics, as shredding invertebrates that depend on relatively carbon-rich and nutrient-poor food resources may more commonly experience nutrient limitation. In contrast, organisms feeding on FPOM may be more prone to carbon limitation, as their food sources are relatively nutrient rich.

The ingestion of particles by collector-gatherers and filter-feeders acts both as retention and utilization, as some fraction of the ingested material is digested and metabolized by the animal consumer. There does not appear to be any estimate of the potential magnitude of this effect owing to benthic collector-gatherers. However, filter-feeders typically consume only a small fraction of transported particles, less than 1% of annual transport in one estimate (Webster 1983). Thus microorganisms, mainly bacteria, appear to be responsible for most of the breakdown and re-mineralization of the organic carbon of FPOM that occurs within stream ecosystems. However, this interpretation may reflect inadequate study of benthic detritivores. Rosi-Marshall and Wallace (2002) estimated considerable ingestion of amorphous detritus by macroinvertebrates in a mid-order river in North Carolina, but the influence on system-level degradation of benthic FPOM is largely unknown.

While the quantity of FPOM consumed is poorly documented, it can be approximated by the measurement of respiration rates. Using laboratory measurements of benthic FPOM respiration, Webster et al. (1999) estimated breakdown rates 0.00104/day, for a half-life of about 1.8 years. Respiration rates are expected to decline over time as FPOM mass is lost, leaving more recalcitrant material behind, but

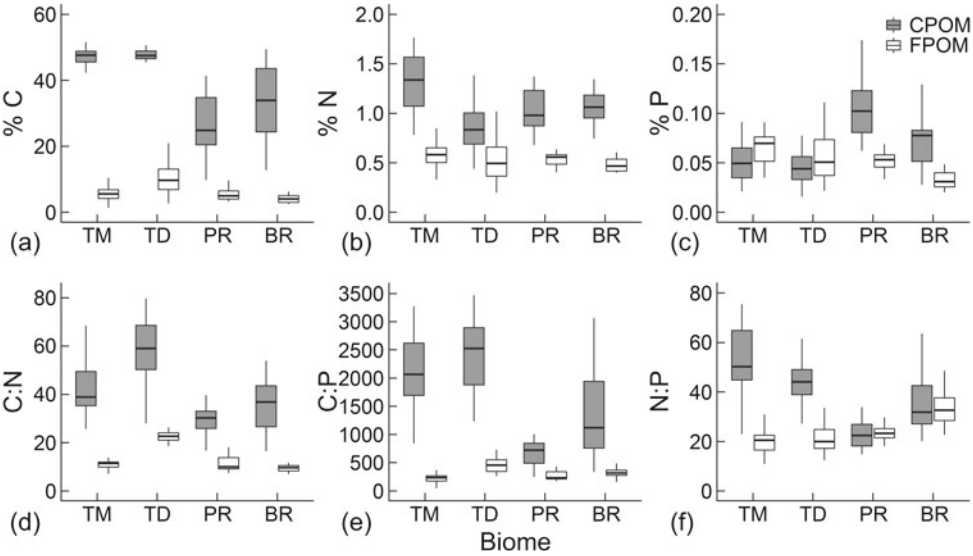


Fig. 7.23 Box and whisker plot of the elemental mass (%) of (**a**) carbon, (**b**) nitrogen, and (**c**) phosphorus, and the stoichiometric ratios (molar) for (**d**) carbon/nitrogen, (**e**) carbon/phosphorus, and (**f**) nitrogen/phosphorus. Coarse particulate matter (CPOM) is denoted by gray bars and fine particulate matter (FPOM) is denoted by white bars. All organic matter was collected from benthic habitats within stream networks in four biomes: Tropical Montane (TM), Temperate Deciduous (TD), Prairegrass (PR), Boreal Forest (BF). Boxes reflect the 25th and 75th percentiles and whiskers reflect the 10th and 90th percentiles. (Modified from data presented in Farrell et al. 2018)

supporting evidence is weak (Sinsabaugh et al. 1992). Seasonal and latitudinal variation in temperature has a strong influence on respiration rates and thus on the utilization of FPOM (Webster et al. 1999). Microbial decomposition of FPOM correlates with rates of the original CPOM, but FPOM decomposes more slowly (Marks 2019). This may be because macroinvertebrate processing removes nutrients and labile carbon from detritus, producing FPOM with higher carbon to nutrient ratios and greater lignin concentrations (Santonja et al. 2018; Yoshimura et al. 2008).

Though aquatic shredders produce large quantities of FPOM as fragments and egested material, the comparative significance of shredder FPOM as a pathway of nutrient transformation remains understudied. In an experiment conducted with three invertebrate shredders, *Pycnopsyche lepida, Lepidostoma* sp., and *Tipula abdominalis*, Halvorson et al. (2015a) fed organisms conditioned oak or maple litter of varying dietary carbon to nutrient ratios. FPOM production differed significantly among species. Additionally, insects fed high-nutrient diets produced FPOM with greater microbial decomposition rates, which varied with types of leaf litter. This work suggests that changes in litter type and ambient nutrient concentrations may modify production rates, elemental composition and stoichiometry, and decomposition rates of FPOM produced by detritivores that may vary among shredder species.

7.3.4 The Influence of Anthropogenic Activities on Fine Particulates

Human-mediated environmental pressures may alter the physical and chemical characteristics, quantity, timing, and duration of fine particulates entering the environment, potentially with profound effects on stream ecology. For example, changes in water chemistry may influence the lability and toxicity of FPOM. Nutrient enrichment resulted in greater increases in both fungal and bacterial biomass for CPOM than FPOM (Tant et al. 2013). The potential for FPOM to interact with chemical stressors in streams is also exceedingly high due to sorption and complexation processes (Bundschuh and McKie 2016). When coupled with intense rain events in the Amazon, deforestation and petroleum development have resulted in major changes in the timing, quantity, and composition of fine particulates entering the watershed. Increased sedimentation buried CPOM and negatively affected all macroinvertebrates, even the filter-feeding invertebrates that may have benefitted from increased organic particulates (Couceiro et al. 2011). In a study examining downstream changes of POC composition and biodegradability in a mixed land-use watershed in South Korea, Jung et al. (2015) documented significant differences in the concentrations of particulates within the watershed; particulates were greatest in the agricultural stream, but declined in downstream reaches.

The intensification of storms associated with anthropogenic climate change may also affect the lability, timing, and quantity of particulates entering streams. In a study of particulate exports in runoff from storm events in a small (~12 ha) watershed in Maryland in the eastern US, Dhillon and Inamdar (2013) documented that a single storm, Hurricane Irene, generated 56% of all of the organic particulates for 2011. This work suggests that the intensification of storm events may govern fine particulate dynamics in streams.

7.4 Sources and Processing of Dissolved Organic Matter

Dissolved organic matter (DOM) typically is the largest pool of organic carbon in running waters (Fisher and Likens 1973; Karlsson et al. 2005), and fluctuations in quantity and lability can strongly affect microbial metabolism and community structure (Bott et al. 1984; Judd et al. 2006). Dissolved organics comprise a variety of organic compounds that are potential carbon sources for microorganisms, and for this reason and because many studies now rely on automated carbon analysis by combustion of water samples, it often is reported as dissolved organic carbon (DOC). For all practical purposes these terms can be interconverted by assuming that DOM is 45–50% organic carbon by mass. Dissolved organics include labile organic compounds that are available to microorganisms for biological uptake as well as recalcitrant material that is less easily assimilated. Organic forms of nitrogen and phosphorous can be quantitatively significant fractions of DOM, and potentially are available for uptake by algae and heterotrophs. Groundwater, rainfall, throughfall, and leaching of leaves are primary sources of DOM in many systems, but this varies with climate, geology, and land use. Streams and rivers transport large quantities of DOM for great distances (Table 7.2), and some of the world's biggest rivers transport large amounts of DOC to the ocean. The 30 rivers with the greatest annual discharge export 90.2 Tg C year^{-1} as DOC, which represents 36% of global DOC flux by rivers to the ocean (250 Tg DOC-Cyear^{-1}). The Amazon River alone exports 11% of the total DOC flux to the oceans (Raymond and Spencer 2015).

The number of investigations focused on DOM in rivers has increased as new analytical approaches, continuous sensor technology, and advances in statistical analysis have allowed stream ecologist to address questions that were once untenable. This research has established that DOM is comprised of a mixture of compounds whose makeup significantly affects stream food webs, biogeochemical cycling, and the transport and uptake of contaminants (Creed et al. 2015). Methods used to evaluate changes in the lability, quantity, and composition

Table 7.2 Discharge, watershed area, and DOC fluxes and yields for the top 30 rivers ranked by discharge globally. (Reproduced from Raymond and Spencer 2015)

River Rank by Discharge	River Name	Discharge (km^3 yr^{-1})	Area (Mkm^2)	DOC Flux (Tg C yr^{-1})	Global DOC Flux (%)	DOC Yield (gC m^{-2} yr^{-1})
1	Amazon	6590	6.112	26.900	10.8	4.4
2	Congo	1325	3.698	12.400	5.0	3.4
3	Orinoco	1135	1.100	4.98	2.0	4.5
4	Changjiang (Yangtze)	928	1.808	1.58	0.6	0.9
5	Yenisey	673	2.540	4.65	1.9	1.8
6	Lena	588	2.460	5.68	2.3	2.3
7	Mississippi	580	2.980	2.10	0.8	0.7
8	Parana	568	2.783	5.92	2.4	2.1
9	Brahmaputra	510	0.580	1.90	0.8	3.3
10	Ganges	493	1.050	1.70	0.7	1.6
11	Irrawaddy (Ayeyarwady)	486	0.410	0.89	0.4	2.2
12	Mekong	467	0.795	1.11	0.4	1.4
13	Ob’	427	2.990	4.12	1.6	1.4
14	Tocantins	372	0.757	1.12	0.4	1.5
15	Amur	344	1.855	2.50	1.0	1.3
16	St. Lawrence	337	1.780	1.55	0.6	0.9
17	Mackenzie	316	1.780	1.38	0.6	0.8
18	Zhujiang (Pearl)	280	0.437	0.40	0.2	0.9
19	Magdalena	237	0.235	0.47	0.2	2.0
20	Columbia	236	0.669	0.40	0.2	0.6
21	Salween (Thanlwin)	211	0.325	0.23	0.1	0.7
22	Yukon	208	0.830	1.47	0.6	1.8
23	Danube	207	0.817	0.59	0.2	0.7
24	Essequibo	178	0.164	0.89	0.4	5.4
25	Niger	154	1.200	0.53	0.2	0.4
26	Ogooue	150	0.205	1.25	0.5	6.1
27	Uruguay	145	0.240	0.50	0.2	2.1
28	Fly	141	0.064	0.55	0.2	8.6
29	Lkolyma	136	0.650	0.82	0.3	1.3
30	Pechora	131	0.324	1.66	0.7	5.1
Total		**18,553**	**41.64**	**90.24**	**36.30**	**70.20**
Average		***618***	***1.39***	***3.01***	***1.21***	***2.34***

of DOM are varied, and are reviewed in Findlay and Parr (2017) and Ruhala and Zarnetske (2017). The installation of wells or lysimeters, the use of continuous sensors, and the collection of water samples are all methods used to measure DOM inputs to streams. Optical properties of DOM can be evaluated using fluorescence, which can be used to characterize the origin and lability of DOM. Advances in spectroscopic techniques, including absorbance and fluorescence, have also advanced our understanding of the role of DOM in supporting aquatic communities and ecosystems. Biochemical characteristics of DOM can be related to optical properties; hence, the characterization of DOM fluorescence can generate information about the source, redox state, and biological reactivity of DOM (Fellman et al. 2010).

7.4.1 Sources of DOM

Concentrations of DOM vary with terrestrial vegetation, soil flow pathways, and the presence of wetlands, and may be enriched by domestic sewage or agricultural runoff. Allochthonous DOM enters streams primarily through groundwater inputs at low flows, while more DOM enters via lateral flows during storms (Mulholland 1997b). Autochthonous sources of DOM are often seasonally dominant (Raymond and Spencer 2015) and are added to the organic pool via algae (Adams et al. 2018) and macrophytes (Kautza and Sullivan 2016). Wastewater treatment plants can also be a locally important source of DOC, where instream processing can generate abundant DOC from an allochthonous source, human waste (Yates et al. 2019). Much of the DOC exported from smaller systems, especially headwaters, is of terrestrial origin (Royer and David 2005), and this is especially true in forested regions of the temperate zone. In a review of rivers in the US, Spencer et al. (2012) suggest that the DOM in the great majority of rivers is predominantly from allochthonous sources. Exceptions to this pattern, the Colorado, Colombia, Rio Grande, and St. Lawrence, are highly modified with large impoundments that generate large inputs of DOM derived from photosynthetic plankton.

Dissolved organic matter concentrations ranged between 0.5 and 36.6 mg L^{-1} in a survey of 33 streams and rivers in the Caribbean, North America, Europe, and Antarctica (Mulholland 1997b). On a world-wide basis, DOC exceeds POC by approximately 2:1, but this depends on river type and discharge regime. Based on annual means, reported DOC:POC ratios for North American streams range from 0.09:1–70:1 (Moeller et al. 1979). The total export of organic matter from more than 80 Finnish catchments was dominated by DOC, which made up 94% of total organic carbon (Mattsson et al. 2005). In headwaters streams of British Columbia, DOM also represented a high percentage (84%) of the total organic matter export, and the remainder was mostly FPOM (Karlsson et al. 2005). In larger rivers, however, POC and DOC concentrations are similar, and at high discharge POC can exceed DOC (Thurman 2012).

The size division between FPOM and DOM is one of convenience, usually determined by what passes through a 0.45 μm filter. In reality, the dissolved fraction is likely to include some smaller bacteria, viruses, and some colloidal organic matter. Lock et al. (1977) used ultra-centrifugation to examine the colloidal fraction, which was defined by a sedimentation coefficient and estimated to correspond to a spherical diameter between 0.021 and 0.45 μm (perhaps 0.01- 0.5 μm should be considered the general size range for colloidal organic matter). In water from a variety of sources in Canada, the colloidal fraction constituted between 29 and 53% of total DOC.

Between 10–25% of DOM consists of identifiable molecules of known structure: carbohydrates and fatty, amino, and hydroxy acids. The remainder (50–75%, up to 90% in colored waters) can be placed in general categories such as humic and fulvic acids and hydrophilic acids. Humic acids separate from fulvic acids by precipitating at a $pH < 2$ while fulvic acids remain in solution. Fulvic acids also are smaller than humic acids, which often form colloidal aggregates of high molecular weight and may be associated with clays or oxides of iron and aluminum. Fulvic acids generally are the majority of humic substances (Thurman 2012). In the Amazon, for example, fulvic acids were approximately 50% and humic acids 10% of riverine DOC (Ertel et al. 1986).

Leachate from leaf litter and other POM is often a labile source of DOM. There are species-specific differences in DOC leached from leaves. As discussed previously, leaf leachate often is generated rapidly, incorporated into microbial biomass, and respired by microbes. Labile organic molecules are frequently lost from litter within the first few days after entering streams (Meyer et al. 1998). Typically, they are low molecular weight compounds that often account for a small proportion of pool of DOC but may play a disproportionally large role in supporting bacterial production in aquatic systems (Marks 2019). Some 42% of the autumnal DOC inputs to a small New England stream were attributed to this source (McDowell and Fisher 1976). Exclusion of leaf litter inputs to a stream at the Coweeta Hydrological Laboratory resulted in lower DOC concentrations than in a nearby, untreated reference stream (Meyer et al. 1998). Instream generation of DOC from leaf litter was estimated to contribute approximately 30% of daily DOC exports, and to be greatest in autumn and winter and during periods of increasing discharge rather than at baseflow. DOC concentrations were higher during the fall and early winter in a deciduous woodland stream in Tennessee (Mulholland 2003).

Inputs of DOC are also influenced by catchment characteristics such as geology, soils, and topography. The size of soil carbon pool is a strong predictor of stream DOC concentration (Aitkenhead et al. 1999). Water moving through shallow flowpaths has greater contact with the organic horizon of the soils, and so generally has higher DOC concentrations than are found in groundwater (Frost et al. 2006). Shallow flowpaths can be the result of steep slopes, shallow soils, and the presence of infiltration barriers or of saturated soils, such as wetlands and peatlands (Aitkenhead-Peterson et al. 2003). Deeper flowpaths increase the exposure of DOC to microbes and mineral soils, which can assimilate and adsorb DOC respectively. In the Amazon, differences in texture between oxisols and spodosols, the dominant soil types in clearwater and blackwater river catchments, result in different concentrations of DOC in groundwater and pronounced differences in DOC concentration and composition between these two types of rivers (McClain et al. 1997).

Soil organic matter originating in above-ground and below-ground terrestrial production is a quantitatively dominant source of DOC to fluvial ecosystems (Demars et al. 2018; Demars et al. 2019). Grasslands contain the highest soil organic matter, deserts the least, and forests are intermediate. The interstitial water of soils usually contains higher DOC concentrations due to solubilization of organic litter (Thurman 2012). Most soil DOC is produced in the organic horizon and from leaf litter and root exudate and decay. Enzymes released by soil microorganisms also contribute to the soil DOC pool (Aitkenhead-Peterson et al. 2003). Dissolved OM that reaches stream channels by surface and shallow sub-surface flowpaths is frequently more labile and in higher concentrations than DOM in groundwater, where low concentrations are a consequence of biological and chemical degradation of organic matter and physical adsorption. Mineral soils can also adsorb organic molecules, and an increase in the content of clay and aluminum and iron oxides is usually accompanied by higher adsorption of DOC (Aitkenhead-Peterson et al. 2003).

The contribution of groundwater to instream DOC concentrations is often underestimated (Webster and Meyer 1997; Tank et al. 2010). However, research has demonstrated that connections between groundwater supplies and streams can mediate patterns in stream carbon concentrations (Lupon et al. 2019; Dick et al. 2015). Median values for groundwater DOC are usually less than DOC in shallow soil water (Thurman 2012). In small streams in North Carolina, Meyer and Tate (1983) recorded DOC concentrations of 2–12 mg L^{-1} in soil water in contact with the active root zone, compared to 0.2–0.7 mg L^{-1} in subsurface seeps. Similarly, in the catchment of an Alberta stream, the median DOC concentration in soil interstitial waters was 7 (range 3–35) mg L^{-1}, whereas shallow groundwater in the saturated zone contained 3 mg L^{-1} DOC (Wallis et al. 1981). DOC of terrestrial origin is rich in aromatic components such as lignin and tannins because these compounds are abundant in terrestrial vegetation (Benner 2003), and as we shall see, these compounds are less accessible to microorganisms.

In catchments with a substantial area of wetlands, streams have elevated DOC concentrations due to the accumulation of organic acids that reduce pH, thus slowing bacterial decay (Thurman 2012; Lottig et al. 2013). The proportion of wetlands in their catchments explained up to 70% of the variation in DOC concentrations of Wisconsin rivers (Fig. 7.24), and was a better predictor than riparian wetland extent (Gergel et al. 1999). In catchments of the Adirondack Park of New York state, wetlands contribute 30% of DOC inputs but occupy just 12% of the surface area (Canham et al. 2004). Rivers draining permafrost catchments like the Kuparuk in Alaska also exhibit high DOC concentrations due to surface flowpaths through organic-rich soil layers (Mulholland 1997b). Based on radiocarbon analysis, DOC exported from wetlands in Ontario, Canada, DOC was of recent origin despite the fact that peat at a depth of 50 cm had an age between 1000 and 2000 years, suggesting that carbon was exported from wetlands primarily through shallow flowpaths (Schiff et al. 1998).

Precipitation is a highly variable source of DOC, influenced by contact with dust and pollen (Aitkenhead-Peterson et al. 2003), and by the intensity of a storm event (Chen et al. 2019; Wise et al. 2019). When rainwater is intercepted by leaves of the forest canopy, leaching removes significant amounts of organic matter. Fisher and Likens (1973) estimated an average value of 17.8 mg L^{-1} for canopy drip in a hardwood forest in New England. Precipitation indirectly affects riverine DOM through its influence over soil moisture and hydrologic flowpaths. Water that moves near the soil surface has greater contact with the organic horizon of soils, resulting in higher DOC concentrations (Mulholland 2003).

A large fraction of seasonal or annual DOC export can occur over short periods of time during high flows (Raymond and Spencer 2015; Yoon and Raymond 2012). In the Yukon River, Canada, DOC concentrations were highest in May and 50% of annual DOC transport took place during spring under high flow (Guéguen et al. 2006). High DOC concentrations were also observed at the beginning of the snowmelt season in a Colorado headwater stream (Hood et al. 2005). Even when DOC concentrations do not increase with discharge, the total annual transport is strongly influenced by hydrological regime because seasonal variation in discharge usually exceeds seasonal variation in DOC concentrations. In pristine boreal forest streams in Quebec,

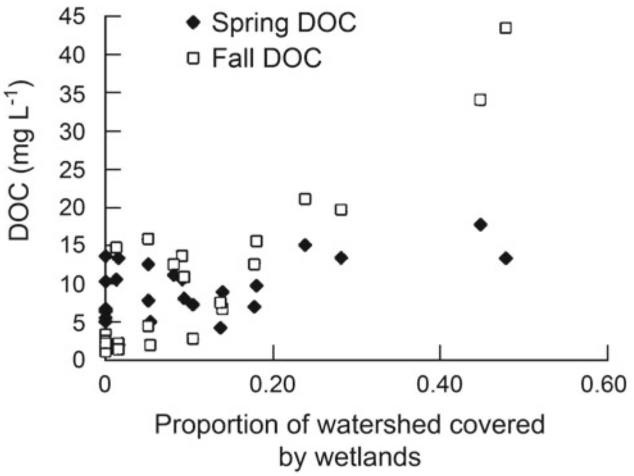


Fig. 7.24 The relationship between DOC concentrations and the proportion of wetlands in catchments for rivers in Wisconsin (Reproduced from Gergel et al. 1999)

Canada, DOC concentrations were relatively low and constant during the spring freshet, and higher during the productive summer and autumn (Naiman 1982). Nonetheless, the two-month stream freshet accounted for roughly half of annual discharge and 50% of DOC export.

Inputs of DOC increase during storms due to flushing of locations of DOC accumulation (particularly in organic-rich riparian zones and surface soils on hillslopes), canopy throughfall, and possibly due to leaching of newly entrained material (Meyer and Tate 1983; McDowell and Likens 1988). In well-drained soils, an increase in stream water DOC during a storm is expected due to shallow sub-surface flowpaths and flushing of soil DOC. In contrast, in streams draining wetlands, surface flow is dominant and increased rainfall may produce a decrease in DOC concentrations as a dilution effect (Mulholland 2003). In two small catchments in Ontario, Canada, DOC transport during storms represented 57–68% of the total during autumn and 29–40% of the total during spring (Hinton et al. 1997). During tropical storm Irene, a 500-year storm event in the northeastern US, Yoon and Raymond (2012) estimated that 40% of average annual DOC export occurred in the few days during and after the storm.

Primary producers can generate large amounts of DOM, releasing exudates from cell lysis that are typically of low molecular weight and labile (Bott et al. 1984; Bertilsson and Jones 2003). This organic carbon source may be most available during episodes of high primary production when exudates are produced, and within surface biofilms where exudates and products of cell lysis become concentrated. During springtime periphyton blooms, stream DOC concentrations have been noted to increase as much as 37% from a pre-dawn minimum to a late afternoon maximum, apparently due to extracellular release by algae (Kaplan and Bott 1989).

Animals also generate DOM in streams and rivers (Parr et al. 2019). A large body of work has examined the influence of animal consumers on the cycling of inorganic nitrogen and phosphorus in lotic systems (Atkinson et al. 2017; Vanni et al. 2017), but less is known about the influence of animals on DOM dynamics. Animal consumers may mediate the composition of dissolved organics directly via the excretion and egestion of more labile forms of organic matter, or indirectly by consuming photosynthetic organisms that produce labile exudates (Parr et al. 2020). In a headwater stream in the eastern US, Parr et al. (2019) demonstrated that the flux of DOM through animal communities via excretion can be substantial and that the energy derived from animal-mediated excretion may be important to microbial consumers, as it is more labile relative to other common sources of DOM in streams.

7.4.2 Spatial and Temporal Variability in DOM

The amount of DOM in river water varies on daily, seasonal, and yearly time scales; spatially, in accord with local geology, vegetation, rainfall and temperature; and with human activities in a watershed (Table 7.2). The river continuum concept (Vannote et al. 1980) assumed that DOM dynamics were in a steady state and functioned independently of time (Creed et al. 2015). However, subsequent research has demonstrated how the temporal dynamics of DOM are fundamental in supporting stream food webs and biogeochemical cycling (Raymond and Saiers 2010). Changes in flow affect DOM in distinct ways and at distinct time scales (hours to years) along a river continuum (Creed et al. 2015). Over longer time periods, DOM dynamics are affected by climatic cycles (e.g., El Nino–Southern Oscillation) and vary with long term changes in the physical and chemical environment (e.g., global warming, acid rain deposition). Over shorter times hydrological events, such as snowmelt and storms, influence the transport of DOM from terrestrial to aquatic environments.

Changes in DOM concentrations along the river continuum can be explained largely by changes in the nature of terrestrial-aquatic connectivity and the flow of terrestrially-derived DOM moving from smaller to larger systems. Lower-order systems are often characterized by high spatial and temporal variation in DOM concentrations. Site-specific variation can be explained by the diverse sources of DOM and their ability to respond rapidly to short-term events. For example, storm flows often shift flowpaths from deeper mineral soils to more shallow organic-rich soils, resulting in substantial variation in DOM between baseflow and stormflow events.

7.4.3 Lability and Uptake of DOM

The origin of DOM influences the chemical structure of the organic matter. In addition to influencing the concentration of DOM entering streams, factors including, but not limited to, weather and climate, land use, and changes in hydrology can alter the lability of DOM and cause its chemical characteristics to change seasonally The chemical composition of DOM derived from leachate varies among tree species. Additionally, microbial species can, in part, determine the chemical characteristics of DOC that is respired, integrated into higher trophic levels in stream food webs, or transported downstream (Wymore et al. 2018).

The composition of DOM governs the role of DOM in supporting biological communities and biogeochemical cycling (Raymond and Spencer 2015). The physical and chemical structure and volume of DOM influences the structure and function of the microbial community, with subsequent effects on upper trophic levels and ecosystem processes (Battin et al. 2016; Findlay 2010; Findlay and Parr 2017). Additionally, DOM composition can influence the formation of carcinogenic and mutagenic disinfection byproducts that threaten drinking water quality, and mediate the transport and reactivity of toxic substances, such as metals (Raymond and Spencer 2015).

Over the past few decades, researchers have employed many methods to characterize the composition of riverine DOM (Raymond and Spencer 2015). They include methods relying on carbon to nitrogen ratios, stable isotopes (e.g., $\delta^{13}C$, $\delta^{15}N$), and radiocarbon isotopes ($\Delta^{14}C$). Analytical techniques, such as advanced nuclear magnetic resonance spectroscopy and Fourier transform ion cyclotron mass spectrometry, are commonly employed to gain high-resolution data about the composition of DOM (Raymond and Spencer 2015). Optical properties of DOM, including florescence and UV absorbance at specific wavelengths, can help to distinguish specific natural and anthropogenic sources (Fellman et al. 2010). Using the US Geological Survey's Water Data for the Nation to analyze the composition of DOM in rivers in the US, Creed et al. (2015). observed a shift in UV absorbance suggesting that DOC rich in humic matter was characteristic of smaller rivers. However, there were exceptions to this pattern as humic-rich DOC also has been documented in larger black water rivers (Sun et al. 1997). Fluorescence components are typically classified as protein-like, humic-like, or fulvic-like (Fellman et al. 2010). Compounds including lignin, tannins, polyphenols, and melanins most likely generate most of the humic DOM fluorescence, which comprise a large portion of the fluorescence occurring in natural rivers. Research in aquatic systems has demonstrated that protein-like fluorescence can be correlated with bacterial production, bacterial respiration, and community respiration. Furthermore, protein-like fluorescence may also reflect DOM lability, as laboratory incubation experiments have documented relationships between biodegradable DOC and protein-like fluorescence (Fellman et al. 2010).

As previously mentioned, the contribution of aquatic animals to the pool of labile DOM pool via excretion and egestion may be functionally relevant in some systems. For instance, research in an Alaskan stream demonstrated that salmon-derived DOM was chemically distinct from the humic-rich, wetland-derived DOM that typically dominated the river, and was characterized by protein-like fluorescence (Fellman et al. 2010). In a forested, headwater stream in the US, Parr et al. (2019) found that the DOM excreted by stream invertebrates was two to five times more bioavailable to microbial heterotrophs than ambient stream water DOM, and could meet a significant proportion (40 ± 7%) of the microbial demand of labile carbon in the stream.

Dissolved organic matter is removed from stream water by both abiotic and biotic processes. Dahm (1981) estimated that adsoption onto clays and chemical complexing with oxides of aluminum and iron accounted for up to one-third of the initial removal of DOC from the water column. Over a period of several days, however, microbial uptake was responsible for the majority of DOC disappearance from the water column into the sediment layer. Photochemical degradation results in the transformation of DOC into other inorganic and organic compounds. Although it is not clear whether these organic products are more or less available to bacteria than the initial DOC, most studies conducted in freshwater systems using humic compounds or DOC from vascular plants have found that photochemical degradation enhances biological availability (Moran and Covert 2003). Increased biotic sorption and transformation into other compounds by photodegradation and relatively reduced concentrations of DOM tend to occur in watersheds dominated by soils that have high adsorption capacity (Tank et al. 2010).

The uptake of DOC by stream organisms is a key part of OM processing in streams, and it is a fundamental parameter to quantify in order to understand the contribution of rivers and streams to the global carbon budget (Mineau et al. 2016). Uptake of dissolved organic matter is primarily by microbes to sustain their respiration and growth (Bott et al. 1984), but research has suggested that some aquatic macroinvertebrates including black fly larvae and zebra mussels may also be able to directly utilize DOM (e.g., Ciborowski et al. 1997; Roditi et al. 2000). The bioavailability of ambient DOC varies among streams (Meyer 1994), flow conditions (Wilson et al. 2013), and seasons (Fellman et al. 2009). Hence, the parameters governing uptake are expected to vary accordingly (Mineau et al. 2016).

The incorporation of DOC into microbial biomass is of interest because of its potential as an energy input into stream food webs. It is a central tenet of this chapter that detrital energy pathways can be as or more important than primary production, and DOC can be a major carbon source for heterotrophic microorganisms. Bacteria likely play an even greater role in this regard than do fungi, but it also is apparent that different microorganisms are intimately intertwined with various OM sources, as well as with algae in complex energy-processing sites known as biofilms, the subject of Chap. 8. Experimental studies of the response of bacterial abundance and biomass to different carbon sources and nutrient levels are the basis for most current knowledge of DOC uptake by microbes. However, rapid advances in molecular microbial ecology including the ability to assay for key enzymes and to survey microorganisms for the functional genes that encode particular enzymes promise new insights into DOM dynamics.

Nutrients, temperature, oxygen, and many other environmental factors will influence the incorporation of these carbon sources into microbial biomass. High uptake rates for dissolved organic carbon are reported for labile molecules including leachate from leaves and highly productive algal mats, and the addition of nutrients often increases DOC uptake. However, because the majority of DOC enters streams from soil and groundwater and includes a heterogeneous mix of bioavailable, recalcitrant, and perhaps inhibitory compounds, total DOC is a poor predictor of microbial metabolism.

By measuring uptake coefficients of DOC using ^{13}C-labeled leaf leachate in mesocosms, Wiegner et al. (2006) estimated that the most readily assimilated DOC fraction would travel 175 m in White Clay Creek before being immobilized, and a second DOC pool they described as of intermediate lability would travel 3,692 m. These distances represented 7% and 150% of the third-order reach length, respectively, suggesting that readily available DOC was an energy input at the reach scale, whereas more recalcitrant material was exported and potentially served as a subsidy to downstream ecosystems. Because this experiment used fresh leachate rather than material aged by passage through the soil, uptake distances may be underestimated. Other studies have found that DOC in transport can support 11 to 55% of the benthic bacterial metabolism in streams and rivers (Bott et al. 1984; Findlay et al. 1993; Sobczak and Findlay 2002; Fischer et al. 2002). In the mesocosms studied by Wiegner et al. (2006), DOC met from one-third to one-half of the bacterial carbon demand, depending on the relative contribution of algal production.

Despite many measures of DOC concentrations and a reasonably good understanding of factors that influence spatial and temporal variation, neither input nor utilization rates are well quantified on an areal basis in streams. The cellular respiration resulting from the consumption of DOC contributes to the net flux of carbon dioxide from aquatic ecosystems to the atmosphere (Hotchkiss et al. 2015), and research suggests that a large proportion (27 to 45%) of DOC exported from terrestrial ecosystems to streams may be removed in watersheds before reaching coastal areas (Mineau et al. 2016). At least in small streams, downstream transport rather than utilization appears to be the fate of most DOC entering stream reaches.

7.4.4 Anthropogenic Influences on DOM

Anthropogenic activities may influence the lability, quantity, timing, and duration of DOM in streams and rivers. Increases in terrestrially-derived DOC concentrations have been measured in aquatic ecosystems over the last few decades (Marx et al. 2017). Anthropogenically-derived changes in precipitation, temperature, and land use have all been attributed to these changes.

Uptake rates of organic matter are expected to change with changing climate. By adding acetate, a labile form of DOC, to European streams from different ecoregions, Catalán et al. (2018). found that climate and the composition of DOC, rather than seasonal variation, had large effects on uptake. Specifically, mean annual precipitation explained half of the variability of acetate uptake velocity, a measurement that estimates demand for an element. Streams characterized by higher rates of precipitation, more recalcitrant DOM, and high respiration rates had the lowest uptake velocities. Semiarid streams that were characterized by more labile organic compounds and lower rates of respiration had higher uptake velocities, suggesting they were carbon limited. These findings emphasized the importance of interactions between climate and DOM composition in mediating DOC uptake in streams.

Changes in precipitation are linked to alterations in the chemical composition of DOC that reflect changes in the origin of the organic matter (Hood et al. 2006). In Mediterranean streams, drought can shift systems from lotic to lentic environments, fragmenting hydrologic connectivity and increasing autochthonous DOM relative to allochthonous DOM (Vazquez et al. 2011). Extreme flows associated with tropical storms and hurricanes are also expected to interact with land use to influence DOC dynamics. In the wake of hurricanes Harvey and Irma in 2017, high flows in streams in the southeastern US were linked to an increase in terrestrially-derived DOM relative to instream DOM. However, the total flux of more labile DOC was much higher at peak discharge, indicating materials transported by large storm flows could enhance microbial activity in streams. Watersheds with more urban development exported large loads of nutrients and labile DOC, and the watershed that had greatest percentage of wetland cover had a prolonged, but relatively subdued, export of DOC and nutrients (Chen et al. 2019).

Changes in temperature can alter the flow and lability of DOM entering lotic ecosystems, as temperature controls dissolution (Raymond and Spencer 2015). As temperatures warm in cooler climates, the retreat of glaciers may also influence DOM fluxes into riverine environments. Though relic glacial water has relatively low concentrations of DOM, the land that is exposed after glacier retreat exports much more DOM than previously ice-covered landscapes. Additionally, the DOM composition of glacier-derived water may be compositionally unique. Hence, glacier decline may affect the volume and lability of DOC entering certain aquatic environments.

Dominant land use often governs the source of DOM, with implications for the lability and processing rates of organic matter in streams (da Costa et al. 2017; Stanley et al. 2012).

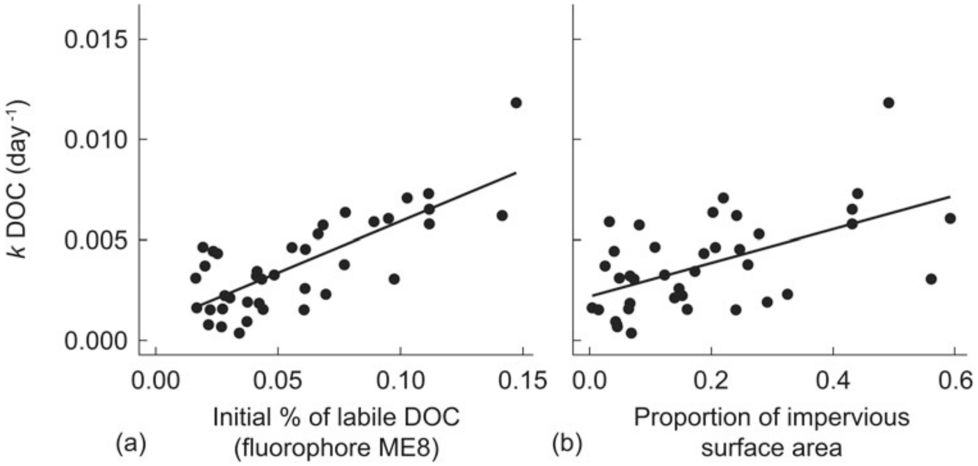


Fig. 7.25 (**a**) The relationship between the breakdown rates of dissolved organic carbon (*k* DOC) and the initial % dominance of a relatively labile form of DOC (fluorophore ME8), and (**b**) the relationship between the breakdown rate of DOC and impervious surface area (proportion ISA) in the study region (Reproduced from Parr et al. 2015)

Multiple studies have reported declines in the contribution of terrestrially-derived DOM relative to the contribution of DOM from autochthonous production and instream microbial sources in response to urban and agricultural development (Lu et al. 2014; Westerhoff and Anning 2000). As more land is converted to agricultural and urban landscapes, increases in the lability of DOM may fuel increases in microbial activity, subsequently altering rates of carbon cycling and the amount of carbon that is exported downstream (Williams et al. 2010; Parr et al. 2015). In headwater streams, urbanization did not have a strong effect on instream DOM concentrations, but did significantly increase the relative amount of bioavailable, hence labile, DOM derived from autochthonous microbial sources (Fig. 7.25). In a study examining the impacts of agricultural expansion in the Amazon on riverine carbon dynamics, Spencer et al. (2019) reported that agriculturally-impacted streams received lower total quantities of relatively labile DOC when compared to reference sites, resulting in lower instream DOC concentrations and greater rates of microbial degradation of DOM. Seasonal variation in the origin of DOM can also be affected by land use. In the Mara River in Kenya, Maese et al. (2017) reported that forest streams primarily transported DOM derived from terrestrial sources, whereas streams draining agricultural areas transported a mixture of DOM that was dominated by autochthonous sources during the dry season, but primarily DOM from terrestrial sources in the wet season (Masese et al. 2017). The increased soil erosion, organic matter oxidation rates, and relatively shallow soil-to-stream flow paths that often characterize agricultural landscapes can lead to higher DOC concentrations with large proportions of soil-derived, humic-like DOM, and greater DOC bioavailability (Shang et al. 2018).

Wastewater effluent can also introduce large volumes of chemically-distinct DOM (Singer and Battin 2007; Raymond and Spencer 2015). Yet, it is very challenging to estimate anthropogenic inputs of DOC from sewage because our knowledge of the state and structure of wastewater infrastructure is limited (WWP 2017; ASCE 2017, 2011). As Webster et al. (1995) emphasize, with over 24,000 sewage treatment plants in the eastern US, natural levels of DOC are typically unknown for larger rivers (>3rd order) in that region. Wastewater inputs to streams are commonplace and poorly quantified (Capps 2019); thus, the concern voiced by Webster et al. (1995) most likely applies to watersheds throughout the globe. Organic matter concentrations may also affect how chemical contaminants enter and subsequently influence aquatic ecosystems (Wohl 2015; Schmidt et al. 2012). Metals, such as zinc, copper, and mercury, bind to DOC and can enter aquatic food webs (Tomczyk et al. 2018a; Tomczyk et al. 2018b; Chaves-Ulloa et al. 2016).

7.5 Outgassing of Carbon from River Networks

The amount of CO_2 evasion currently estimated from inland waters and wetlands (2.9 Pg C yr$^{-1;}$ Sawakuchi et al. 2017) is the same order of magnitude as uptake of carbon by marine environments (2.4 ± 0.6 Pg C year^{-1}), uptake of carbon by terrestrial environments (2.7 ± 1.2 Pg C year^{-1}), deforestation and land use change (1.0 ± 0.7 Pg C year^{-1}), and anthropogenic CO_2 emissions from the burning of fossil fuels (7.9 ± 0.5 Pg C year^{-1}) (Ward et al. 2017). Because headwaters make up a large proportion of river networks (> 96% of the total number of streams globally), they potentially contribute large amounts of CO_2 to the atmosphere. Conservative estimates suggest 0.93 Pg C yr^{-1}, or 36% of all CO_2 outgassing from rivers and streams comes from headwater systems (Marx et al. 2017). Evasion estimates are poorly characterized for many of the world's rivers, and this is especially true for medium and large systems. However, existing estimates suggest that individual systems can emit large volumes of CO_2 into the atmosphere (Ward et al. 2017; Reiman and Xu 2019). For example, Sawakuchi et al. (2017) estimated that the Amazon River contributed 54% of global river and stream CO_2 outgassing. This is a remarkable estimation because the surface area of the Amazon only corresponds to 3% of the estimated surface area covered by all rivers globally.

In a study of the lower Mississippi River in the US, Reiman and Xu (2019) found that water in the river was constantly supersaturated with CO_2. In general, pCO_2 was much higher in the wet and the dry season and was positively associated with discharge and temperature (Fig. 7.26). Similar seasonal trends in pCO_2 have been documented in other rivers of the world, a pattern that could be explained by increasing heterotrophy associated with higher temperatures, or increased amounts of soil pore-water CO_2 entering the river due to increased mineralization and leaching of organic matter in the soil. This study documented an increase in riverine DOC concentrations (607 ± 158 µmol L^{-1}) from those that had been reported 5–15 years ago (296–489 µmol L^{-1}), reflective of the increase in air and water temperatures in the Mississippi River Basin. Coupled with greater discharge over the past few years, annual export of total dissolved carbon (16.2 Tg C) from the Mississippi River Basin to the Gulf of Mexico was higher than just seven years previously (15.5 Tg C). High partial pressures of CO_2 in the river water also resulted in a large quantity of carbon released into the atmosphere annually from the lower portion of the Mississippi. Both discharge and temperature have increased in the Mississippi River during the past few decades, and so both likely have contributed to changes in DOC levels. Specifically, discharge has increased more than 30% in the past 80 years and average annual air temperatur during the study were 0.2–0.4 °C warmer than their respective 5-year average ten years prior to the study, and 0.8–1.1 °C warmer than twenty years ago. Coupled with increasing DOC concentrations, the predicted changes in future temperature and discharge are expected to increase the rate of outgassing from the Mississippi (Reiman and Xu 2019).

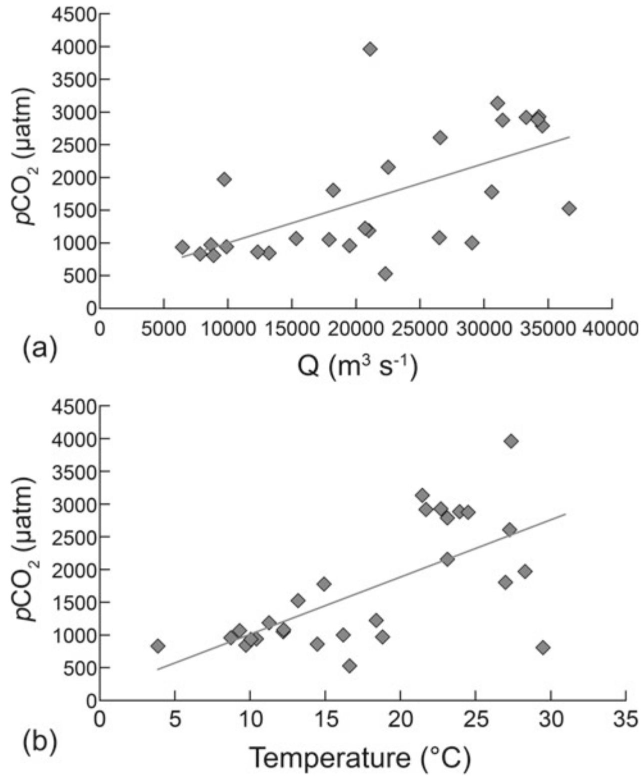


Fig. 7.26 Relationship between pCO_2 and (**a**) discharge (Q) and (**b**) water temperature in the Mississippi at Baton Rouge (Reproduced from Reiman and Xu 2019)

7.6 Summary

Particulate and dissolved organic matter originating both within the stream and in the surrounding landscape are substantial basal resources to fluvial food webs. Detritus-based energy pathways can be particularly important relative to pathways originating from living primary producers in small streams shaded by a terrestrial canopy and in large, turbid rivers with extensive floodplains. Coarse, fine, and dissolved organic matter originate from a myriad of sources. Leaves, fruits, and other plant products that fall or are transported by wind and gravity into the stream are major CPOM inputs, and the carcasses and feces of insects and larger animals also contribute to this pool. Most FPOM originates from the fragmentation of larger particles, particularly terrestrial vegetation, and is likewise transported into the channel or is produced by the breakdown of larger particles within the stream. Water that has been filtered through soil is usually the major source of DOM, which is a heterogeneous pool of molecules of widely varying bioavailability. The lability of non-living organic matter as a basal resource typically depends on the presence of bacteria or fungi whose degradative activity can alter palatability or accessibility of OM to consumers. Microorganisms are critical mediators of organic matter pathways, aiding in the processing of POM and uptake of DOM, and markedly increasing the energy available to consumers both small and large.

Autumn-shed leaves are a primary CPOM input to forested streams in temperate regions, and their decay serves as the primary model of CPOM processing. Leaves, which serve as the organic matter or carbon substrate, quickly release DOM when wetted, and soon are colonized by microorganisms and invertebrates, which enhance fragmentation and mineralization. The original leaf is transformed into several products including microbial and shredder biomass, FPOM, DOM, nutrients, and CO_2. Leaf breakdown rates vary considerably and, as a consequence, the supply of CPOM to the stream food web, although pulsed seasonally, is less so than would be the case if all leaves had similar breakdown rates. Temperature, oxygen availability, and nutrient supply are key environmental variables that influence the decomposition process. Colonization by microorganisms, particularly fungi, is critical to leaf decomposition as well as the leaf's nutritional value, although bacteria play a greater role as particle size diminishes, and the presence of leaf-shredding invertebrates also is functionally relevant. When detritivorous invertebrates are excluded, the breakdown process is significantly slowed.

Fine particulate matter is an amorphous collection of particles less than 1 mm, originating from instream CPOM breakdown, sloughed cells of algae, invertebrate fecal pellets, and fragments derived from the terrestrial environment. The uptake of DOM within biofilms provides another avenue for FPOM production. Black fly larvae, by consuming bacteria and very small FPOM and producing fecal pellets that are larger than some of the material that they ingest, illustrate yet another pathway for the generation of organic particles. The sources, processing, and eventual fate of FPOM is less well accounted for than is the case for CPOM. Although the breakdown of CPOM within the stream is the best-studied pathway, it seems likely that FPOM originates from many other sources. Because of the small size of FPOM, bacteria likely are more important than fungi in its microbial processing.

Dissolved organic matter typically is the largest pool of organic carbon in running waters and is incorporated into POM due primarily to uptake by microorganisms. Soil and groundwater are major pathways of DOM transport from terrestrial vegetation and wetlands into river water, whereas leaf leachate from leaves and from extracellular release by algae and higher plants can be temporally dominant instream sources. Because it comprises a heterogeneous mix of bioavailable, recalcitrant, and perhaps inhibitory compounds, total DOM is a poor predictor of microbial metabolism. DOM is removed from stream water by both abiotic and biotic processes.

Particulate and dissolved organic matter are key energy sources in almost all lotic ecosystems and frequently can be the dominant energy source. Detritus and the associated microbial biomass, along with algae and other primary producers, form the basal resources for the various trophic levels occupied by invertebrates, fishes and other consumers in stream food webs. We turn now to the diversity of consumers and the feeding adaptations that govern their effectiveness with the diverse producer and detrital resources described in this and the preceding chapter.

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