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The role of leaf litter macroinvertebrates in stream-floodplain dynamics

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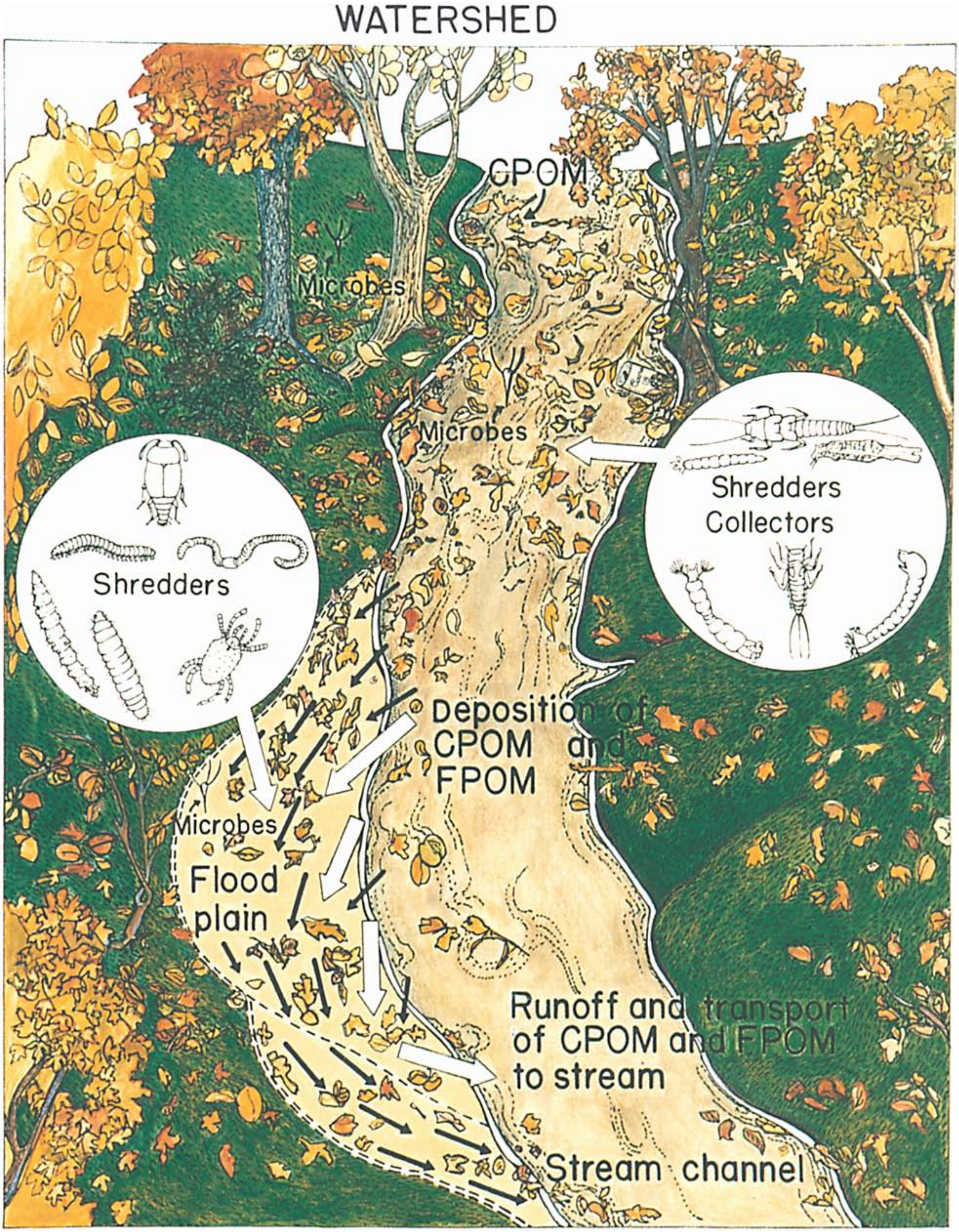
Abstract

The floodplain has been viewed as a transitional system or ecotone between aquatic and terrestrial habitats. This research has evaluated the role of floodplain macroinvertebrates in the degradation of leaf litter in a Michigan woodland floodplain, and examined the interrelationships among floodplain-stream macroinvertebrates, microbial colonization and selected environmental factors. Although taxonomically different decomposer groups operate in both systems, their functional roles as leaf litter detritivores are basically the same. Leaf litter processing rates were compared and contrasted between the stream and adjacent floodplain using leaf packs and litter bags, respectively. In the stream, the major time period for detritus processing by invertebrates is in the fall and winter, while in the floodplain it is during the spring. Therefore, the sequence of events involved in processing are similar, yet the timing and rate of these events are strikingly different. An understanding of the significant ecological processes linking the stream and floodplain as complementary systems is discussed within the context of watershed management.

Introduction

As early as 1887 Forbes, in his classic paper 'The Lake as a Microcosm', emphasized the importance of floodplains are breeding grounds and reservoirs of life. The critical importance of floodplains to the productivity of such large rivers as the Amazon and Congo is well known (Marlier, 1973; Welcomme, 1979; Junk, 1983; Lowe-McConnell, 1987). Within the past decade or so, the structure and function of stream ecosystems have emphasized the origins and fates of organic resources and inorganic nutrients in running waters, with the stream being viewed more as a parasite of the watershed than an isolated ecosystem by itself (Cummins, 1974, 1977, 1980; Hynes, 1975; Merritt *et al.*, 1984a). From this, the 'River Continuum Concept', has been developed as a holistic view of a river system describing the structure and function of lotic communities from headwaters to the mouth (Cummins, 1975; Vannote *et al.*, 1980; Minshall *et al.*, 1983). More recently, Ward (1989a) has conceptualized the dynamic and hierarchical nature of lotic ecosystems as a four-dimensional framework, whereby the lateral dimension includes interactions between the stream channel and riparian-floodplain systems. Gregory *et al.* (1991) also have proposed a conceptual model of riparian zones that emphasizes linkages between terrestrial and aquatic ecosystems and incorporates temporal and spatial patterns of hydrologic and geomorphic processes.


WATERSHED
CPOM
Microbes
Microbes
Shredders
Collectors
Shredders
Deposition of
CPOM and
FPOM
Microbes
Flood
plain
Runoff and transport
of CPOM and FPOM
to stream
Stream channel

Floodplains and riparian zones may be defined in various ways. To the geomorphologist, the floodplain is an area of a river valley covered with material deposited by floods (Leopold *et al.*, 1964); to the hydrologist, it is the area inundated by flood events in excess of the stream channel's capacity (Maddock, 1976); to the ecologist, it is a transitional system, or ecotone between aquatic and terrestrial habitats (Junk, 1983; Risser, 1990), that includes sharp gradients of both environmental factors and ecological processes (Gregory *et al.*, 1991). To planners and lawyers, it is an area defined by statute (Cooke & Doornkamp, 1974); and to developers it is often the ideal location to build a house.

In the context of our work, the floodplain is an environment subjected to erosional and depositional forces in equilibrium (Cummins, 1972; Merritt & Lawson, 1979) (Fig. 1). It is a depositional region where organic debris resulting from litter fall and lateral movement accumulates and is temporarily stored. It is also an area of high channel complexity and low velocity during storm events and high water periods where suspended detrital material is deposited. During flooding, it functions as an erosional region in that organic material deposited on the floodplain is washed and transported into the stream. Floods serve as a resetting mechanism for streams and rivers in that they scour attached algal communities and redistribute inorganic sediments and particulate detritus (cf. Cummins, 1977), creating new sites for macroinvertebrate colonization and renewing food resources.

Studies have shown that litter production and diversity in riverine floodplain forests (undergoing annual flooding) often exceeds corresponding values of forested wetlands (not undergoing annual flooding) and non-wetland habitats (Bell *et al.*, 1978; Brinson *et al.*, 1980, 1981; Gomez & Day, 1982; Shure & Gottschalk, 1985; Ward, 1989b). This suggests that the floodplain may serve as a temporary 'storage' and preprocessing area for detritus such as leaf litter prior to its entry into the stream. In addition to leaf litter, wood debris from floodplains provides a major habitat for stream organisms and serves as an important component of forested watersheds (Anderson & Sedell, 1979; Triska & Cromack, 1980). Thus, events in the riparian ecosystem largely determine the quantity, quality, and availability of allochthonous organic material received by streams (Hynes, 1975; Sedell *et al.*, 1978). The ecological processes occurring in the floodplain of a watershed provide insight into the important linkages between terrestrial and aquatic environments (Pinay *et al.*, 1990). Our research has evaluated the role of floodplain macroinvertebrates in the degradation of leaf litter and examined the interrelationships between floodplain-stream macroinvertebrates and selected abiotic and biotic factors.

Description of study site

Our study of stream-floodplain interactions was mainly conducted in the Augusta Creek watershed in southwestern Michigan, consisting of a third-order brownwater trout stream (*ca.* 10 m width, 0.7 m depth) and associated floodplain. The Augusta Creek floodplain is heavily forested, with the major species being black ash (*Fraxinus nigra* Marsh), basswood (*Tilia americana* L.), dogwood (*Cornus* spp.), and black cherry (*Prunus serotina* Ehrh.). The dominant lowland herbaceous vegetation consists of Jewel-weed (*Impatiens capensis* Meerb.), wood nettle (*Laporta canadensis* (L.)), running strawberry (*Euonymus obovata* Nutt), *Iris* sp. and violet (*Viola* sp.) (Merritt & Lawson, 1979). The floodplain is divided into three areas based on vegetation, elevation and soil parameter gradients (Fig. 2). The point bar is the area adjacent to the stream and most

Fig. 1. A conceptual model of the watershed ecosystem showing the ecological processes and interactions occurring between a stream and its floodplain. (CPOM-coarse particulate organic matter; FPOM-fine particulate organic matter). Black arrows indicate deposition of CPOM and FPOM onto floodplain from stream. White arrows indicate movement of CPOM and FPOM from floodplain to stream.

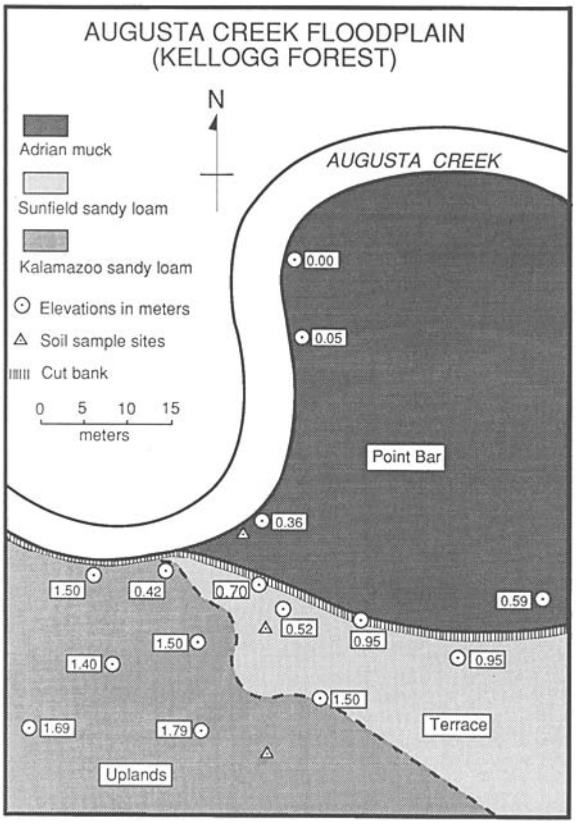


Fig. 2. Soils and elevational map of Augusta Creek (Kellogg Forest) floodplain.

frequently inundated during flooding. This area consists of poorly drained organic deposits and has the highest soil moisture and organic content of the three areas. The terrace and uplands sites consist of well-drained sandy loam soils with lower soil organic and moisture content. The bankfull flood recurrence interval for Augusta Creek is 1.75 years.

Methods of studying stream-floodplain processes

Leaf litter processing in running waters has been extensively studied with leaf packs of different species (Petersen & Cummins, 1974; Webster & Benfield, 1986; Stout, 1989). Processing was measured by a leaf pack bioassay technique described by Cummins (1977) and Merritt *et al.* (1979).

The litter bag method (Crossley & Hoglund, 1962) was used to examine the association of organisms and related processes that occur in the floodplain and upland areas of the watershed. Leaves collected at the time of abscission were air-dried for approximately one week, weighed into four to eight gram aggregations, soaked in non-chlorinated water until softened and then placed in 10 × 10 cm nylon mesh bags and sealed. Three mesh sizes were chosen to separate components of leaf litter degradation in a Michigan woodland floodplain: (1) 50 μm – to exclude all soil invertebrates and allow only leaching and microbial decomposition; (2) 500 μm to admit microinvertebrates (mites, Collembola and enchytraeids) and exclude most macroinvertebrates; and (3) 8000 μm – to admit all soil fauna (microinvertebrates and macroinvertebrates, including earthworms and Mollusca).

Since estimates of sample decay rates in confined litter bags have been substantially lower than those observed with individually tethered non-confined leaves (Witkamp & Olson, 1963), both techniques were used to estimate upper and lower limit rates of litter degradation. Litter bags and tethered leaves were buried in the fall between the litter and humus layers and secured by long nails or spikes.

In the floodplain, a subsample of litter bags was collected immediately after being placed in the field to assess weight loss due to leaching, or breakage due to handling during litter bag preparation. Bags were evaluated monthly during fall and winter and twice a month during spring and summer. The rate of leaf material loss was expressed as the percentage remaining after a given time period (Merritt *et al.*, 1979).

The role of specific floodplain macroinvertebrates in leaf litter processing was examined through the use of feeding chambers which enclose leaf litter and shredders (Knollenberg *et al.*, 1985). An experimental floodplain plot of homogenous soil composition and vegetation was chosen. In each of six rows, six holes were dug (27 cm apart, 18 cm deep) in a plot and the excavated soil was handsorted to remove large debris and steam heated to eliminate soil fauna. Perforated plastic feeding chambers (22 cm high × 20 cm diam), each lined with 50 μm aperature nylon mesh were filled to within 4 cm of the top with prepared soil. Each chamber was sealed with a tightly fitting 1 mm aperture nylon mesh top. The inner mesh prevented soil microfauna from entering the chamber while the top prevented the intrusion of the macrofauna from above.

Eight individuals of a representative floodplain macroinvertebrate, *Lumbricus terrestris* L., were placed in each chamber and then replaced in the holes dug in the study plot. Chambers without earthworms were placed within the plot to serve as controls. After 48 h of acclimation, a pre-weighed leaf pack was added to each chamber with earthworms and to each control chamber. The density of macroinvertebrates added to each chamber was based on natural field estimates for an equivalent volume of soil.

Chambers with earthworms and leaf controls were sampled weekly and every two weeks, respectively. Leaf and leaf fragments were washed, air-dried and weighed, and the portion of leaves not retrieved macroscopically was assumed to be consumed by earthworms. This took into account the correction factor for leaf control losses due to handling and microbial degradation (Knollenberg *et al.*, 1985).

A square box-type sampler (144 cm^2) modified from Healey & Russell-Smith (1970) was used to sample leaf litter macroinvertebrate abundance and diversity. Box samples containing litter and humus were returned to the laboratory and floodplain macroinvertebrates were extracted using a modified Ladell apparatus (Lawson & Merritt, 1979).

Results and discussion

Stream-Floodplain fauna

The major groups of invertebrates which specialize in the consumption of coarse particulate organic matter (CPOM) in Augusta Creek are shown in Table 1 and Fig. 1. They include a wide range of taxa, but mainly consist of amphipods, pteronarcid stoneflies, craneflies (*Tipula*) and limnephilid case-bearing caddisflies. The role of these litter-feeding animals in stream ecosystems has been shown to be of considerable significance, accounting for at least 20% of the degradation of CPOM, such as leaf litter, to fine particulate organic matter (FPOM), animal biomass, and CO_2 (Petersen & Cummins, 1974; Webster & Benfield, 1986). The FPOM generated by shredders makes up a significant component of the food resource base for stream collectors (Short & Maslin, 1977; Wallace & Merritt, 1980). These include blackflies (Simuliidae), some mayflies (Leptophlebiidae), and midges (Chironomidae).

Results of early faunal studies (Bornebusch, 1930; Eaton & Chandler, 1942; Crisp & Lloyd, 1954; and others) showed that the fauna of forest soils is comprised of communities that are closely associated with, and characteristic of, a particular type of soil, vegetation, and physical landscape. For example, the fauna of deciduous forests (oak and beech) with a mull humus formation (e.g. similar to our study site), are characterized by the numerical abundance of earthworms (50–80%), with the dominant arthropods being Diplopoda, Isopoda and Coleoptera. In spruce mull, however, the earthworms are less prominent and arthropods such as Acari, Diplopoda, larvae of Diptera and Coleoptera are dominant. In deciduous forests with a mor humus formation, earthworms also are fewer in number and the dominant arthropods are Diptera and Coleoptera larvae, Diplopoda, Collembola, and Acari. Intermediate stages between these contrasted types of arthropod communities can be found in a floodplain depending on local conditions of soil, vegetation and climate, and the extent of flooding (cf, Uetz *et al.*, 1979). In turn, the relative composition and abundance of riparian plant communities are major determinants of stream litter processing rates and consumer community structure (Cummins, 1974).

Six major groups of macroinvertebrates were found to be associated with leaf litter in the Augusta Creek floodplain, comprising 35 families, 40 genera and 55 species (Merritt & Lawson, 1979, 1981) (Fig. 1, Table 1). Although the Coleoptera

Table 1. Major macroinvertebrate groups associated with leaf litter processing in a Michigan woodland watershed (Augusta Creek).

Watershed habitat	Major macroinvertebrate groups	Comments
Stream	Amphipoda (mainly *Gammarus*); Insecta-Plecoptera (mainly Pteronarcidae, some Nemouridae and Capniidae); Ephemeroptera (some Leptophlebiidae); Trichoptera (Limnephilidae, Phryganeidae, Lepidostomatidae); Diptera (Tipulidae, some Chironomidae)*	Groups listed are primarily large particle feeders and totally aquatic as immatures. Amphipods, tipulids and chironomids have terrestrial analogues.
Floodplain	Oligochaeta (Enchytraeidae, Lumbricidae); Gastropoda (Pulmonata); Diplopoda (mainly Julidae); Isopoda (*Trachelipus* sp.); Diptera (mainly Tipulidae, Sciaridae and Chironomidae); Coleoptera (mainly predators)	Consists of both semi-aquatic and terrestrial groups. Many floodplain species have the physiological and morphological adaptations to survive in moist habitats subject to annual inundations. Higher diversity and abundance of specific groups, especially Diptera.
Uplands	Similar faunal representation as floodplain but species composition changes	Consists mainly of terrestrial species not capable of surviving periods of inundation and areas of high soil moisture. Lower abundance of some groups, particularly Diptera, Enchytraeidae and Gastropoda, and greater abundance of some Coleoptera.

* Taken from Petersen & Cummins (1974) and Merritt & Cummins (1984) who have worked on leaf litter processing in the stream of the Augusta Creek Watershed.

(beetles) were well represented, most species sampled were predators and therefore their indirect role in litter degradation was difficult to assess. The Tipulidae (craneflies) were represented by 24 species belonging to 15 genera. The habitat distribution for the majority of these species was linked to high soil moisture and organic content, thus greater densities (number m^{-2}) were recorded from the point bar than the uplands (Merritt & Lawson, 1981). This was generally true for the Gastropoda (9 species), enchytraeid worms and non-tipulid Diptera (16 families), which decreased in abundance on a elevational gradient running from the stream bank to the upland. Many representatives of these groups have the physiological and morphological adaptations to survive in moist habitats subject to annual inundations (Crisp & Lloyd, 1954; Kuhnelt, 1976). In other floodplain fauna (e.g. Diplopoda, Isopoda and *Lumbricus* spp.) the relationship between increased soil moisture and animal abundance was not as clear.

Seasonally, there was a bimodal distribution of floodplain macroinvertebrates in this Michigan watershed, with lows during the winter when the soil was both cold (often frozen) and saturated, and in summer when high evapotranspiration reduced soil and litter moisture to an annual minimum (Merritt & Lawson, 1979). The downward vertical migration by soil animals to escape cold surface temperatures during winter and desiccation in the summer has been documented (Wallwork, 1976), and probably explains the summer and winter lows in our study. Although snow covered the ground during most of the winter, earthworm activity was observed in the humus layer at temperatures as low as 2 °C (Knollenberg *et al.*, 1985).

Marked increases in Michigan floodplain macroinvertebrates occurred in spring and again in the fall (Merritt & Lawson, 1979). The annual spring peak coincided with warming soil temperatures which increased soil invertebrate activity, while the abundance in early fall coincided with an increase in precipitation and the fact that many soil animals begin to inhabit leaf litter and soil for winter hibernation.

The effects of flooding on the leaf litter fauna depend to a large extent on the wettability of their surface and their physiological adaptations to survive periods of inundation (Gifford, 1968; Wallwork, 1976). Earthworms, in regions where regular flooding occurs, are not harmed by water alone and remain there for extended periods. On the other hand, strictly terrestrial earthworms and enchytraeids are severely damaged by water; they swell up and die at varying rates depending on temperatures (Kuhnelt, 1976). Floodplain gastropods may escape flooding by finding elevated substrates to climb upon, while some craneflies exit their soil burrows in order to colonize moss and leaves (Freeman, 1967; Frey & Edgar, 1977). Irmler (1981) described three types of survival strategies for animals inhabiting Amazonian floodplain forests: (1) high reproductive rates and short development times; (2) life cycle adaptations to the seasonal rhythm of floods (e.g. diapause or change in habitat); and (3) an amphibious life pattern. All of these strategies could apply to temperate organisms which face seasonal floods.

Leaf litter processing in the floodplain

Our study showed that autumn leaves (*F. nigra*) placed within fine mesh bags (50 μm) in the point bar of a Michigan woodland floodplain had the slowest breakdown rates. Those leaves placed in coarse mesh bags (8000 μm), which admitted all soil fauna, had the fastest breakdown rates. Differences between breakdown rates in fine and medium bags (which admitted microarthropods) were not significant, suggesting that the role of microarthropods (e.g. Acari, Collembola) in leaf litter breakdown was not as significant in our floodplain as reported elsewhere (Madhe, 1969; Harding & Stuttard, 1974; Wharton, 1978).

The significant differences we found in leaf litter breakdown rates between coarse mesh bags or tethered leaves *vs.* fine and medium mesh bags reflected the importance of soil macroinvertebrates on floodplain litter breakdown. Previous *in situ* experiments demonstrated that, over a 4-week period in the spring, earthworms alone could consume leaves equivalent in amount to ca 95% of the total annual leaf fall (Knollenberg *et al.*, 1985). Other major groups involved in floodplain litter degradation were Diptera larvae (mainly tipulids), enchytraeids, millipedes, gastropods and isopods (Merritt & Lawson, 1979). Similar leaf litter breakdown studies in deciduous forests containing a 'mull' type soil have shown the greater importance of the macrofauna than microfauna in fragmenting and processing litter (Bocock & Gilbert, 1957, van der Drift, 1963; Edwards, 1974).

Litter processing in the point bar was significantly faster than that of the upland. Differences could be attributed to several factors, including a greater litter faunal diversity and abundance, higher soil moisture and differences in other edaphic conditions (Merritt & Lawson, 1979). Litter processing in the terrace (transition zone) fell between those values in the point bar and uplands. In the point bar only petioles and larger leaf veins remained after eight months, while in the terrace and uplands there was progressively more whole leaf material remaining.

Animal-microbial and environmental factors affecting stream-floodplain litter processing

Leaf litter degradation in stream and floodplain communities is influenced by a variety of abiotic and biotic factors. Abiotic factors can act to physically fragment leaf litter by, for example, the action of wind or by freezing-thawing or wet-dry cycles in terrestrial habitats. Of greater significance is the resident power of water flow in streams which provides the energy to abrade or fragment leaf litter as it travels down the channel. However, abiotic factors such as leaf chemical composition, temperature and moisture appear to be the most significant variables influencing leaf litter degradation and decomposition (see review by Brinson *et al.*, 1981 for freshwater wetlands). These factors alter the rate of microbial colonization and conditioning of leaf litter, which for many invertebrates appears to be necessary to promote significant feeding activity. Studies have demonstrated a preference of certain invertebrates for leaf species which are maximally colonized by microorganisms (Cummins & Klug, 1979). The conditioning process involves the leaching of soluble organics followed by colonization with microorganisms, mainly fungi, and bacteria (Suberkropp *et al.*, 1975; Kuhnelt, 1976). This process physically softens and chemically modifies the leaf, which can then be consumed and more efficiently assimilated than newly fallen leaves (Kaushik & Hynes, 1971; Bärlocher & Kendrick, 1981).

Deciduous leaves vary considerably in chemical composition which influences the rate at which microorganisms are able to colonize and condition them (Petersen & Cummins, 1974; Stout, 1989). For example, oak leaves decay very slowly and persist well beyond leaves of other species such as maple or ash under similar environmental conditions. This is primarily due to the thickness of the cuticle and to inhibitory substances (e.g. lignin, tannins) within the leaf, and to low leaf nitrogen content which retards microbial colonization. While a species of leaf imposes an ultimate biotic control on the maximal rate of leaf decomposition, abiotic environmental factors such as moisture and temperature modify the timing of leaf litter decomposition by controlling the pace of biological activity. Life in floodplain soils is more variable, with daily and seasonal temperature extremes being greater than in the stream environment. While there is no lack of moisture in stream habitats, terrestrial communities subject to variations in soil moisture can seriously impact soil microbial colonization, macroinvertebrate activity and seasonal cycles. Therefore, abiotic factors may act singly or in combination to influence the rates of microbial colonization and in turn the feeding activities of macroinvertebrates. As a result, biological processes in streams that are measured in days often may take weeks in terrestrial sites.

To demonstrate how environmental factors influence the degradation process, we introduced leaf litter to the floodplain that had undergone two levels of conditioning (Merritt *et al.*, 1984b). The first series of leaves was placed in the floodplain in mid-November, coincident with natural litter fall, and conditioned on the floodplain for 17 weeks. A second series of leaves was placed in the stream in mid-February and conditioned for a 5-week period. After this preconditioning period, the stream-conditioned leaves were removed from the water in late March and placed in the floodplain adjacent to the floodplain-conditioned leaves. Both sets of leaves were monitored for weight loss over time. Results showed that stream-conditioned leaves were processed rapidly in early spring while floodplain-conditioned leaves remained virtually untouched. The latter required an additional 30 days of conditioning before significant processing by the macroinvertebrate community occurred. Once this level of conditioning was achieved, the leaves were processed at approximately the same rate as stream-conditioned leaves.

Previously, it had been thought that low soil temperatures in late winter to early spring physically limited the activity of the macroinvertebrate community in the processing of leaf litter in floodplain habitats. However, from the above results it appears that if the soil fauna is provided with suitably conditioned leaf litter, the animals will process litter even at low soil temperatures. What appears to most limit faunal activity is the rate at which leaf litter is conditioned by the microbial community. It is likely that microbial conditioning occurred more rapidly in the stream habitat due to optimal moisture and uniform stream temperatures. Streams are known to maintain a highly adapted microbial community specialized to function at low winter temperatures (Suberkropp & Klug, 1976).

In contrast, floodplain conditioning is generally slowed due to the varying soil moisture and temperature, and the less cold-adapted rot fungi, which provide less optimal conditions for microbial colonization and growth.

Stream-floodplain litter processing: a contrast

Patterns of leaf litter processing and the annual dynamics of the associated fauna in Augusta Creek and its associated floodplain are shown in

Fig. 3. The major time period for detritus processing by stream invertebrates is in the fall and winter (Petersen & Cummins, 1974; Cummins *et al.*, 1989). The bimodal peaks shown in leaf pack animal densities represent the presence of different invertebrate functional groups (Merritt & Cummins, 1984) (Fig. 3A). Leaf packs in the fall are colonized by large particle detritivores (i.e. shredders) while in the winter, packs are mainly colonized by fine particle feeders (i.e. collectors) that feed on the surface of leaf material or aid in fragmentation. As shown, before animals readily feed on stream litter, leaves must go through a period in which much of the soluble organic material is lost to leaching, followed by a period of microbial colonization. A fast leaf (i.e. based on the percent dry weight loss; Petersen & Cummins (1974)) entering the stream in October would not be found in a recognizable form or in a leaf pack after April (Cummins *et al.*, 1989) (Fig. 5A).

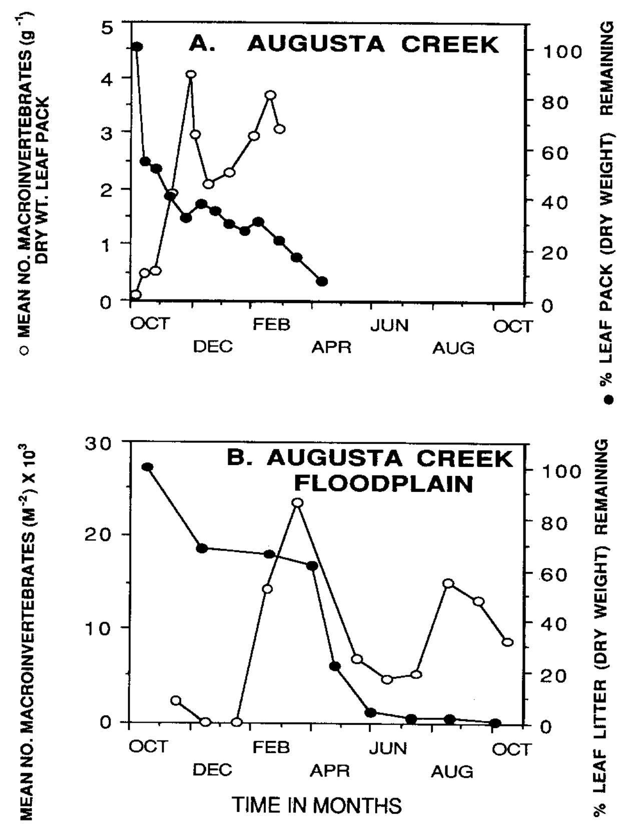


Fig. 3. A comparison of leaf litter (*F. nigra*) processing and seasonal changes in litter macroinvertebrate densities between the Augusta Creek floodplain and stream. Leaf pack and litter bag weight losses reported as percent remaining. Stream data taken from Petersen and Cummins (1974) and Cummins (unpubl. data).

In contrast, the major time period for litter processing in the floodplain was in the spring. During this time temperature was increasing, the greatest abundance of major floodplain macroinvertebrates occurred, and leaf litter had been sufficiently colonized by the microbial community (Fig. 3B). After March, there was a significant decline in the percent leaf litter weight remaining in coarse mesh bags and by July confined litter in the point bar was nearly gone. We assumed that the fall abundance of many floodplain invertebrates was due to increased invertebrate activity in response to climatic factors, such as increased soil moisture. However, it was not clear what the macroinvertebrate food resource was during late summer and early fall when there was little litter remaining on the floodplain to degrade, and freshly fallen litter had not yet been conditioned. We observed floodplain macroinvertebrates feeding on the abundant decaying lowland shrub and herbaceous summer ground vegetation, in addition to any decomposed organic matter that still remained from the previous spring.

Our studies have shown that the overall ecological processes occurring in the floodplain are similar to those occurring in the stream (Fig. 4). Although taxonomically different decomposer groups operate in the two systems (Fig. 1, Table 1), their functional roles are basically the same. The sequence of events involved in processing are similar, yet the timing and rate of these events are strikingly different. Spring flooding may serve as a mechanism to transport relatively high quality organic material (i.e. either conditioned CPOM or recently generated FPOM) into the stream when the energy reserves from the stream-processed litter of autumn are significantly diminished. This may be analogous to some marine environments where much of the macrophytic material enters the detrital pool of coastal systems in autumn, and differential rates of decompositon and related availability to macroconsumers mitigate this pulse of food and assure a

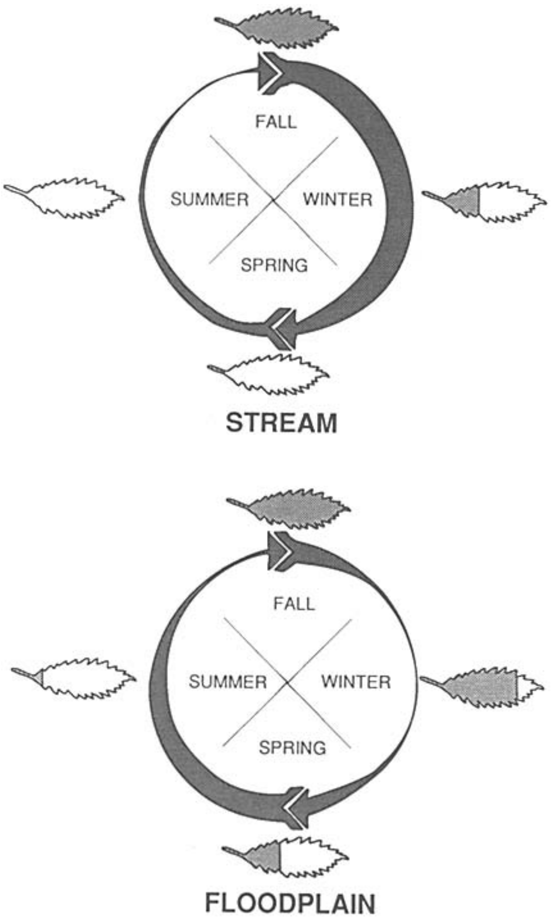


Fig. 4. A diagrammatic representation contrasting major time periods and rates of leaf litter processing in a stream and floodplain. Width of arrows depict maximal periods of litter processing, while leaf shading approximates the residual percent of leaf material left in the environment over time.

continual nutrient source to the benthos (Tenore 1977). Livingston *et al.* (1974) also have shown that annual pulses of organic and inorganic particulates from the watershed were the most important controller of secondary production of a Florida estuary.

Over time, annual meterological and hydrological events (i.e. rainfall, flooding) serve to transport particulate organic matter into the stream from the floodplain and/or onto the floodplain from the stream. Both systems are continually interacting, often making it difficult to determine in which system there is a net gain over annual or longer cycles (cf. Brinson *et al.*, 1981). Overall, this integral stream-floodplain system functions as a retentive mechanism, delaying the eventual downstream export of organic matter. For example, in an alluvial wetland system in North Carolina only 37% of the annual allochthonous input was lost as downstream transport with the remainder either oxidized (56.5%) or stored (6.5%) (Mulholland, 1981), demonstrating the interactive nature of undisturbed stream-floodplain habitats and their potential to efficiently utilize organic matter inputs (cf. Pinay *et al.*, 1990).

Junk *et al.* (1989) have viewed the life histories of major animal groups in a large river-floodplain as being analogous to a highway network with vehicles travelling in opposite directions. An observer may first surmise that resources for these vehicles are derived from the main highway; however, a closer look would reveal that these four-wheeled creatures, corresponding to the fish, need to leave highways periodically for sustenance, along with their apparently symbiotic occupants. The main stream channel therefore is used principally as a route for gaining access to adult feeding areas, nurseries, spawning grounds or as a refuge during low water periods or during the winter. This analogy can also be applied to some semi-aquatic floodplain invertebrates that have evolved adaptations to survive the 'ATTZ' or 'aquatic/terrestrial transition zone' of Junk *et al.* (1989). Likewise, Ward (1989b) has made the comparison of 'nutrient spiralling' of lotic systems (Webster, 1975; Newbold *et al.*, 1981) to riverine wetlands, where nutrients are temporarily stored in reservoirs (floodplains) lateral to the river channel. The mean spiralling length is decreased by increased path length and residence time on the floodplain, thereby increasing total system efficiency and lending stability to the stream-floodplain complex.

Relevence to watershed management

In the past, efforts to increase our energy outputs have received more attention than efforts to measure the damaging effects of society on our water resources. As a consequence, little research has been conducted on the effects of watershed modifications (e.g. dams, reservoirs, stream channelization, logging) on the dynamics of floodplains or other wetlands, or on the important linkages that exist between terrestrial and aquatic ecosystems (cf. Hasler, 1975; Swanson *et al.*, 1982; Amoros *et al.*, 1987; Ward & Stanford 1989). Increased importance is now being placed on the ecology and management of aquatic-terrestrial ecotones (Naiman & Décamps, 1990), as a result of the increased use and run-off of agricultural fertilizers and pesticides and alterations of the riparian zone. Floodplains are continually chosen as sites for construction of houses or industries in spite of flooding and river instability. A major axiom that must be recognized by those competing with the riverine environment is that flooding is a natural process rather than a natural hazard and that, if we are to maintain the integrity of the watershed ecosystem, we must consider the stream and floodplain as complementary systems. A better understanding of the significant ecological processes linking these two systems will enable biologists to influence proper water management decisions and more adequately predict the effects of proposed perturbations on these fragile environments.

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