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Riparian–stream linkage paradigm

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Introduction

The study of streams has made great strides in the last four decades, emerging from its fish-centric and water quality foci up through the 1960s into analyses of community structure and ecosystem processes in the 1970s and 1980s and on to field and mesocosm experiments and assessment of ecological state ('health' or integrity) of the 1990s. Now the discipline of stream ecology, or lotic limnology, has a theoretical and applied base as rich as any field of ecology. In limnological and ecological publications and societies, the field has moved from invisibility to major coverage over this period. A significant component of this coming of age has been the recognition of the sentinel importance of land–water interactions in understanding running water ecosystems. This thesis was eloquently laid out early on by the father of modern stream ecology NOEL HYNES (1963, 1970) and the evolutionist with a love of caddisflies, HERB ROSS (1963). An extension of this paradigm is the Riparian Linkage or Litter Link Model (CUMMINS et al. 1989, GRUBBS & CUMMINS 1996), which couples characteristics of stream-side vegetation, i.e. the riparian zone, with highly predictable in-stream biology. The coupling of riparian plant litter with shredder invertebrates (detritivores specializing in coarse particulate organic matter for food) was an important feature of the River Continuum Concept (e.g. VANNOTE et al. 1980) and it represents a key component of overall riparian zone function (e.g. CUMMINS 1988, GREGORY et al. 1991). The nature and pervasiveness of this coupling has been explored on a world-wide basis (e.g. GRAÇA 1993; CUSHING et al. 1995).

The riparian linkage paradigm (litter link model)

The conceptual model of the riparian–stream linkage is now one of the most studied and best understood on the lotic horizon. The components of this model for forested watersheds can be summarized as follows:

1. A definable width of bank vegetation, the riparian zone, along both sides of the channel generates the majority of litter drop that reaches the stream, and measures of relative percentage cover for species in the riparian area accurately predict relative percentage accumulation of litter from these species in the stream channel.
2. Retention of riparian-derived litter in the channel is dependent on channel structure, such as the presence of large woody debris, and is followed by rapid leaching of dissolved organic matter (DOM) following normal abscission.
3. Stream temperature summation over the litter processing period and dissolved oxygen conditions in accumulations of the retained litter underlie the associated in-stream biological activity, because the key organisms are obligate aerobes with temperature-sensitive activity rates.
4. Conditioning of the leached litter is a process that depends on microbial colonization, especially by aquatic hyphomycete fungi, which results in increased quality of the litter as a food resource for shredders.
5. In-stream litter degradation rates, normalized for temperature, are predictable by species of riparian plant, allowing litter classification along a gradient from fast to slow.
6. Shredder CPOM (coarse particulate organic matter)-feeders, selectively utilize conditioned litter.
7. Resident gut microbial flora are involved in the production of compounds that are assimilable by host shredders.

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8. This co-evolved association between riparian litter and shredders can be found in forested streams worldwide.

Litter entrainment and leaching

Following abscission and the litter reaches the stream and is wetted, leaching can account for up to 30% dry mass loss in the first 48 h (Fig. 1; e.g. Petersen & Cummins 1974, Webster & Benfield 1986). This solution loss is relatively independent of temperature (Petersen & Cummins 1974) and leaves shed while still green can loose much less to solution (Gessner & Schwoerbel 1989). The dissolved organic matter (DOM) leachates readily complex with divalent cations, especially Ca^{2+}, to form flocs (Dahm 1981) and the biochemically mobile constituents are taken up directly by stream microbes. The flocs or foams are rare in low pH, soft-water streams and common in higher pH, hard-water streams when a plant litter source of DOM is present. A classic example can be found in Yellowstone National Park in the USA where the DOM-rich, cation-poor Gibbon River meets the Firehole River, with its high cation load, to form the Madison River. The massive flocs at the first bend in the Madison are legendary.

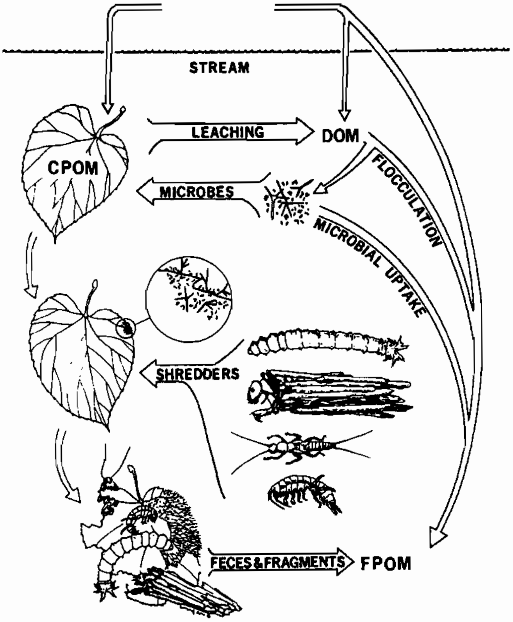

Fig. 1. The sequence of litter fall (represented by a leaf) into a stream through leaching of dissolved organic matter (DOM), microbial colonization (especially by aquatic hyphomycete fungi), and shredder feeding on the conditioned leaf litter. After Cummins & Klug (1979).

Entrainment of the litter is a critical feature of a given stream reach which allows shredders to use it as a food resource (e.g. Gregory et al. 1991, Haapala & Muotka 1998). This is particularly true in watersheds in which litter fall and annual high flows occur together as they do in the North American Pacific Northwest. Empirical methods have been developed to measure retentive capacity for litter and fine wood along a given stream reach (e.g. Speaker et al. 1984, 1988). Using autumn-shed leaves of the exotic Ginkgo tree, which are bright yellow and retain their color for months after introduction into stream water, Cummins et al. (1989) showed that none of the 5000 leaves introduced as a pulse into a second-order Appalachian stream were recovered further than 500 m downstream after 5 months of autumn–winter flows. Retention was provided by accumulations of large woody debris as well as geomorphic channel features. Hildrew et al. (1991) showed that retentive capacity of a stream reach for leaf litter was related to shredder abundance as well as the amount of litter retained.

Microbial colonization

Following entrainment and leaching, the next key step in the process is the colonization of the litter by aquatic hyphomycete fungi and bacteria (Fig. 1; e.g. Gessner & Chauvet 1994, 1997, Suberkropp 1998). Initial and subsequent colonization by hyphomycetes is rapid, by virtue of a simple life cycle in which spores settle out on litter and, if leaf surface conditions are suitable, hyphae grow from the spore tips into the leaf. When a growing hyphal tip repenetrates the leaf surface into the stream water, a new spore develops, breaks loose, and drifts to settle in a new location (e.g. Suberkropp & Klug 1974, 1980, Arsuffi & Suberkropp 1984, Barlöcher 1985, 1992, Baldy et al. 1995). Although bacteria are common on the surfaces of litter substrates in streams, their penetration into the inner matrix of leaves is slower, accomplished by following aquatic hyphomycete fungal hyphal tracks through the leaf cuticle or by entering at leaf stomates (SUBERKROPP & KLUG 1976). Hyphal development is maximal in the least lignified tissues (midrib and major veins) of a given leaf or those leaves with the thinnest cuticle and softest tissue (e.g. SUBERKROPP et al. 1983). In general, the hyphomycetes use the leaf substrate as a carbon source and take up nitrogen and phosphorus from the water column (SUBERKROPP et al. 1976). The hyphomycete fungi are rich in specific polyunsaturated fatty acids which have been shown to be attractants for detrital leaf-eating invertebrate shredders (HANSON et al. 1983, 1985, CARGILL et al. 1984, 1985). Also, hyphomycete species have been shown to differ in their attractiveness and palatability for shredders (BARLÖCHER & KENDRICK 1973, SUBERKROPP et al. 1983).

Litter processing

The term processing (degradation) is defined here as the total of all causes of leaf litter disappearance, not just decomposition (BOULTON & BOON 1991), once the terrestrially derived leaves, needles or other plant parts have been wetted and entrained in the channel. This includes leaching loss of DOM, microbial metabolism (i.e. conversion of litter to microbial biomass and CO_2), feeding by shredders (i.e. conversion of litter to invertebrate biomass), and mechanical breakage due to physical forces related to stream flow and sediment movement as well as inefficient feeding by shredders (CUMMINS 1974, CUMMINS et al. 1989). Because of differences in the quantities and qualities of leached biochemicals, microbial colonization, and the timing of shredder feeding, species of riparian plants differ in their instream processing times. If the processing times are normalized for temperature, which is expressed on a per degree day basis (HANSON et al. 1984), it is possible to classify riparian species as fast, medium, or slow (PETERSEN & CUMMINS 1974, WEBSTER & BENFIELD 1986, CUMMINS et al. 1989, GRUBBS & CUMMINS 1994b, 1996). Taking the 50% processed time when half the dry mass after 48 h leaching has been lost as a comparative point, and using North American species, fast litter, such as alder and basswood, would require approximately 300 degree days, medium litter, such as some maples and hickories, would require about 450 degree days, and slow litter, such as oaks, rhododendron, and most conifers, would require about 600 degree days (CUMMINS et al. 1989). Under fall–winter stream temperatures, averaging about 5 °C, 300 degree days would be accumulated in about 2 months. Studies involving exchanges of leaves between continents have shown that the processing categories – fast, medium and slow – remain largely predictable for the transplanted leaf types (e.g. CAMPBELL et al. 1991, GAZZERA et al. 1991, CAMPBELL 1994, PARKYN & WINTERBOURN 1997; Fig. 2). GRAÇA (1994) pointed to differences in processing rates of exotic leaves because of lack of adaptation of local shredders, but this can be interpreted only when a native and exotic leaf type in the same processing category are compared at a given site.

Methods for studying riparian leaf processing in woodland streams have been reviewed a number of times (e.g. PETERSEN & CUMMINS 1974, MERRITT et al. 1979, WEBSTER & BENFIELD 1986, BOULTON & BOON 1991) and all studies involve preparing artificially assembled leaf accumulations. The two main procedures entail either the use of mesh bag enclosures to hold pre-weighed amounts of leaves or tethering leaf accumulations, termed leaf packs (PETERSEN & CUMMINS 1974), to a stable object such as a common building brick (PETERSEN & CUMMINS 1974, MERRITT et al. 1979, CUMMINS et al. 1980). Both techniques allow for establishing initial conditions of leaf species, including initial mass, history (i.e. condition of the litter when selected for leaf pack construction, such as fresh or recently shed), whether preleached or not, and biochemical composition. Leaves in unconfined, free-moving conditions have also been studied using various techniques to establish processing times. Penetrometers have been used to measure leaf toughness,

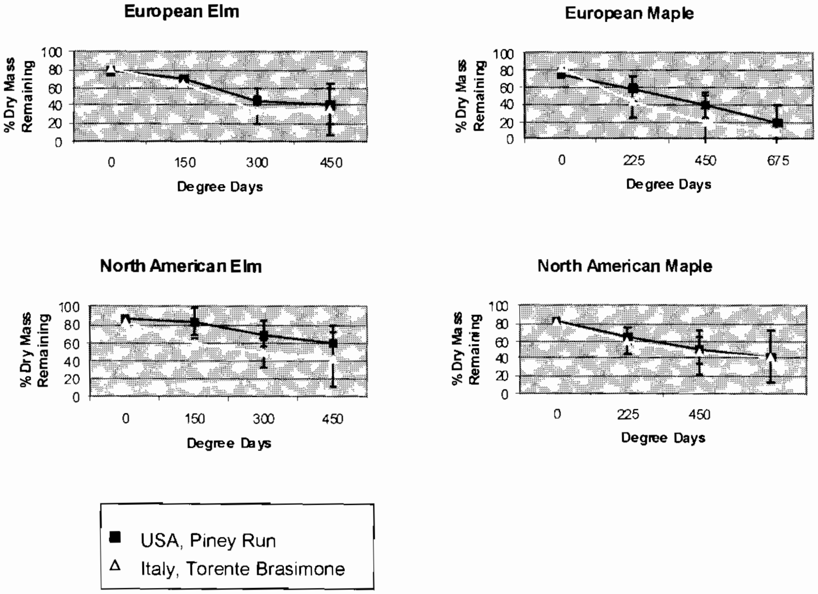

Fig. 2. Processing (percentage dry mass remaining vs. degree days) of elm (*Ulmus minor* and *U. americana*) and European and North American maple (*Acer pseudoplatanus* and *A. rubrum*) in an Appennine Italian stream (T. Brasimone) and an Appalachian North American stream (Piney Run). After GAZZERA et al. (1991).

which can be calibrated against processing time measured using leaf packs (e.g. GRUBBS & CUMMINS 1994a).

In 1977, in response to questions about methods of measuring the rates of riparian litter processing in woodland streams, an experiment was conducted to compare naturally entrained leaf litter with that confined in mesh bags (e.g. PARK 1974, DOBSON 1991) or tethered to bricks (CUMMINS 1974, PETERSEN & CUMMINS 1974, MERRITT et al. 1979). The experiment, conducted in the autumn in a first-order deciduous woodland stream in Michigan, involved the release of basswood leaves (*Tilia americana*) into a 58-m study section confined by mesh screens (CUMMINS et al. 1980). The only two basswood trees in the riparia (MAHAN 1980) were manually defoliated and the leaves introduced as a pulse into the study reach. Loss of mass of individual introduced leaves was estimated from regressions of dry mass on leaf length (n = 106). The free ranging leaves were collected and kept separate from two habitats: exposed (riffle or glide) or alcove (back waters, pools) locations. Leaves in leaf packs (PETERSEN & CUMMINS 1974) or 1-mm mesh, 18-cm^2 nytex™ bags (100 each) were placed along the thalweg of the channel at the same time as the basswood leaves were released at the upstream end of the 58-m study reach. Samples of free ranging leaves from both habitat types and packs and bags were collected at intervals during the experiment to compare processing rates. The results showed that processing of the leaf packs (tethered leaves) closely tracked free ranging leaves collected from exposed locations, showing that both mechanical and biological breakdown were similar. Processing of the leaves in mesh bags was significantly slower than pack and exposed free ranging leaves, and tracked the free ranging leaves collected from alcoves (Fig. 3). Qualitative examination showed that exposed free ranging and pack leaves had been colonized by hyphomycete fungi while alcove and bag leaves were poorly or not at all colonized by fungi. Thus, the normal processing rates of leaf litter by hyphomycete fungi and shredders were well simulated by leaf packs but not by leaf bags (Cummins et al. 1980).

Shredder feeding

Once the litter is appropriately conditioned, i.e. it has accumulated sufficient microbial biomass and become soft enough, shredders begin feeding on these substrates. Colonization of litter by shredders may precede feeding (Beiser et al. 1991) and green leaves may require no conditioning (Gessner & Schwoerbel 1989). In temperate North America, the shredder functional group is dominated by Plecoptera in the families Pteronaridae, Nemouridae, Capniidae, Leuctridae, and Taeniopterygidae; Trichoptera in the families Limnephilidae, Lepidostomatidae, and Calamoceratidae; Diptera in the family Tipulidae and in the subfamily Orthocladiinae of the Chironomidae; and Amphipoda, Isopoda, and Decapoda crustaceans. In semi-tropical South America, West Africa, and Australia, the shredder functional role of North American limnephilid caddisflies is played largely by the Leptoceridae.

An important feature of shredder feeding on riparian-derived plant litter is selectivity. The shredders select the most heavily microbially colonized leaf as well as the portion of the leaf that is most heavily colonized. The choice is keyed to the physical softness of leaf tissue, which is a result of conditioning, and the presence, at least in some cases, of certain polyunsaturated fatty acids (Cargill et al. 1985) traceable to the hyphomycete fungi present in the leaf tissue. Examples of these differences in leaf palatability can be readily seen when several different leaf types are incubated side by side in a stream over the same time period (Beiser et al. 1991).

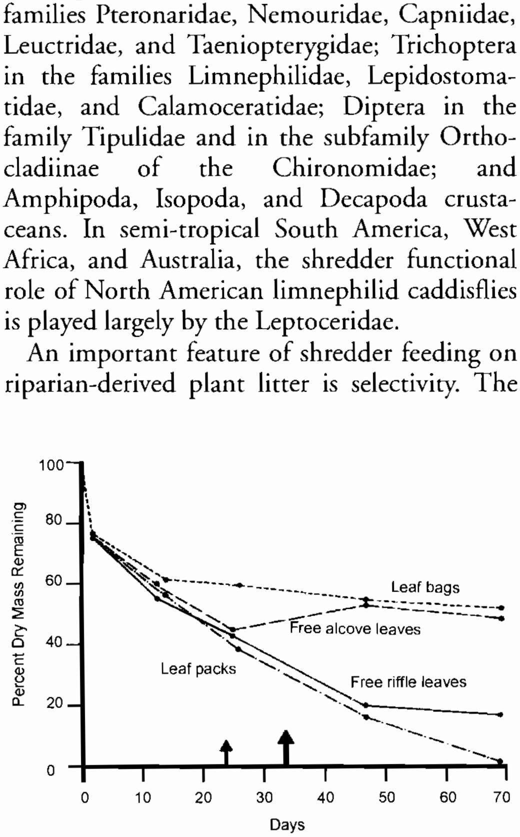

Fig. 3. Comparison of processing (percentage dry mass remaining vs. days in the stream) of basswood leaves in leaf packs (tethered on bricks), in mesh bags, and natural free ranging leaves collected from exposed (riffle) and depositional (alcoves) accumulations over 70 days. Totals of 10–44 leaf packs and bags and 22–186 natural leaves collected at each sampling; C. V. range for samples 20–50%. Arrows indicate spates. After Cummins et al. (1980).

The shredders, as a group, have been shown to house resident gut bacteria including filamentous spore-formers (Cummins & Klug 1979). Collectors, FPOM (fine particulate organic matter) feeders, have similar resident microbes, but scrapers (periphyton feeders) do not (Klug & Kotarski 1980). The resident flora is housed in the shredder hindgut. Microbial cellulase and other enzyme activity produces products, such as cellobiose, that can be further digested and/or assimilated by the host shredder once they are refluxed from the hindgut forward to the midgut. This presumed augmentation of nutrient assimilation could be critical for shredders that ingest such a high cellulose-content diet (Martin et al. 1981a,b, Walters & Smock 1991) (Fig. 4). Cummins & Wilzbach (1988) have proposed that some of the same microbes that aid in providing supporting nutrients to the host shredder may also be a significant source of mortality under appropriate conditions. This pathogenic mortality, termed inside-out control, likely occurs at molting when lesions develop at the junction of the foregut with the hind- and midgut. The lining of the former two is cast with the molt, whereas the midgut lining is not. A lesion would allow facultative anaerobic microbes access to the aerobic haemolymph and the resulting explosive population growth of the microbes would constitute the infection. This dual role of the resident microbes as both nutritional enhancers and pathogens is a key feature of shredders, making evolution of defenses against infection from the gut difficult.

It is possible to identify both obligate and fac-

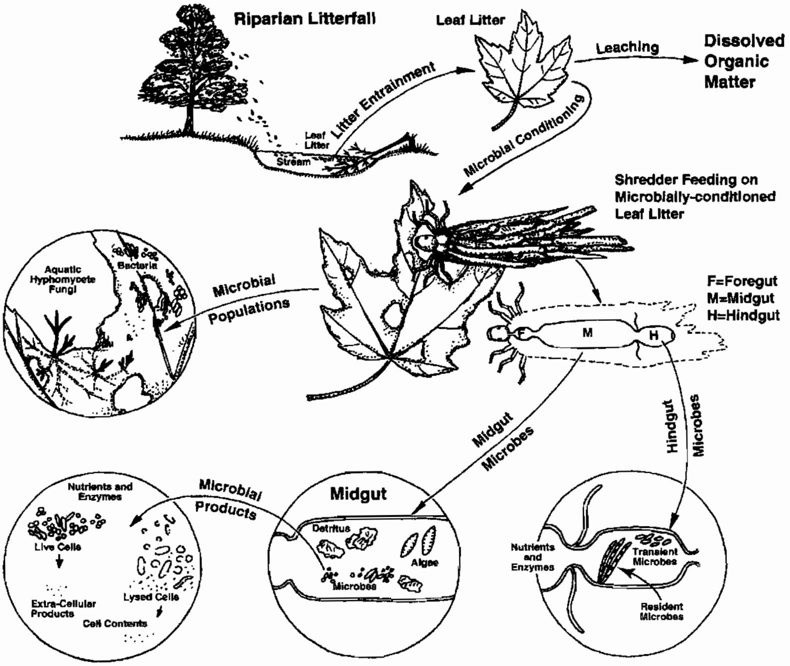

Fig. 4. Importance of stream microbes and resident gut flora to shredders in providing assimilable materials including those refluxed forward from the hindgut to the midgut. After Merritt & Cummins 1996.

ultative species of shredders with regard to their dependence on conditioned riparian litter as a food resource (e.g. Cummins et al. 1989, Merritt & Cummins 1996, Murphy & Giller 2000). A good example of a facultative shredder is the limnephilid caddisfly *Pycnopsyche lepida* of eastern North American woodland streams. *Pycnopsyche* feeds on conditioned litter into the terminal (fifth) larval instar, at which time it adds mineral grains to the leading edge of its case. Eventually the case is entirely mineral and, aided by the increased case weight, the larvae often feed as facultative scrapers, removing attached periphyton from cobbles and boulders in riffles, runs and glides (Cummins 1964). By contrast, species of two closely related limnephilid genera are representative of obligate forms in their terminal larval instars. *Dicosmoecus*, which builds its case of coarse sand grains, is an obligate scraper feeding on periphyton, and *Onocosmoecus,* which builds its case of leaf and bark material, is an obligate shredder, feeding primarily on litter from riparian deciduous hardwoods. In lab experiments, larvae of species from each genus showed normal growth and final pupal weights only when fed their obligate food resource (Cummins unpublished). As a general rule, most shredders appear to be obligate, or to feed preferentially on conditioned riparian litter (e.g. Merritt & Cummins 1996), and, therefore, this functional group is tightly coupled with the riparian vegetation setting of its parent stream (e.g. Grubbs & Cummins 1996). Both natural and anthropogenic alteration of the species composition or structural attributes of this riparian setting are likely to result in altered composition of the shredder assemblages, reduced shredder abundances, and lowered detrital processing rates (e.g. Cuffney & Wallace 1989).

Bird & Kaushik (1985) reported on collectors functioning as facultative shredders, but since FPOM was not directly offered, their relative growth efficiencies in functioning as shredders vs. collectors could not be evaluated. The presence of feeding shredders significantly enhances co-habiting collector growth (Short & Maslin 1977, Dieterich et al. 1997) and

Ward & Cummins (1979) demonstrated that the gathering collector midge *Paratendipes albimanus* grew better on FPOM produced by grinding conditioned leaf litter or on the feces of the cranefly shredder *Tipula abdominalis* than on natural FPOM from stream depositional areas. It seems clear that both obligate and facultative collectors would benefit from co-habitation with shredders in leaf litter.

Shredder life cycles and litter availability

An intriguing part of the shredder–riparian litter linkage is the timing of shredder life cycles that corresponds to both litter availability and conditioning time. In temperate regions where the litter drop from deciduous species of trees and shrubs occurs in the autumn, at the onset of the cold season, fall–winter shredder species (Cummins et al. 1989) emerge from pupae formed in late summer to early fall (August through October in North America). Adult oviposition and hatching of first instar larvae correspond, in general, with the onset of autumn inputs of deciduous litter (e.g. Grubbs & Cummins 1996). Thus, most shredder species having fall–winter generations grow during the coldest part of the year and spend the summer growing season in an inactive condition. For example, in North America, most full-grown fifth instar *Pycnopsyche* fasten their cases to a solid structure such as a large cobble, boulder or piece of wood and remain inactive until molting to pupae at the end of the summer. The digestive tract of the prepupal larvae atrophies but the legs remain functional, allowing the larvae to retain the ability to detach their case and move to a new location, if necessary, in response to falling water levels (Cummins 1964).

Spring–summer shredder species (Cummins et al. 1989) either have annual life cycles, with the growing period occurring in both cold and warm seasons but with most growth in summer, or they have a summer growing season that follows oviposition and hatching in the spring. The food resource for these spring–summer shredders is dominated by litter with slow processing rates, such as conifer needles, that requires a conditioning time of up to 8 months (Cummins et al. 1989; Fig. 5). The phenology of shredder species relative to litter inputs and their conditioning times was proposed by Cummins et al. (1989) and has been documented in a detailed study of a Pennsylvanian woodland stream (Grubbs & Cummins 1996) (Fig. 6). Of the 11 species of shredders identified in the study, the abundance and growth of nine fall–winter species and the two spring–summer species could be matched up with the litter inputs upon which they depended.

Field manipulation

Interest in the difference between shredder communities utilizing riparian litter in the fall–winter and those feeding on it in the spring–summer period led to an experiment in forested streams in the Oregon Cascade Mountains (Cummins & Gregory 2002, unpublished data). A pair of second order streams in the same watershed was selected to be similar in aspect, geology, geomorphology, hydrology, and chemistry. One stream flowed through a 15-year-old clear cut in which the riparian had come back in red alder (*Alnus rubra*), the other through a 400-year-old growth conifer stand

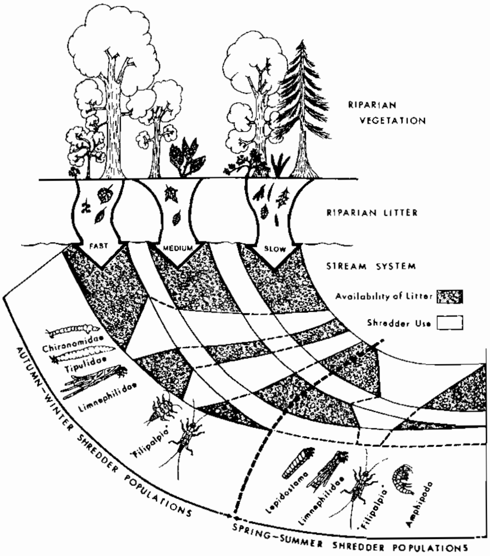

Fig. 5. Comparison of fall–winter shredders and spring–summer shredders and their feeding on fast, medium, and slow litter types. After Cummins et al. (1989).

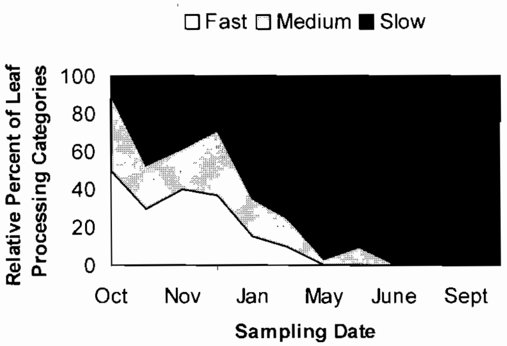

Fig. 6. Fast, medium, and slow leaf litter standing stock in Powder Mill Run, Pennsylvania, USA. After Grubbs & Cummins (1996).

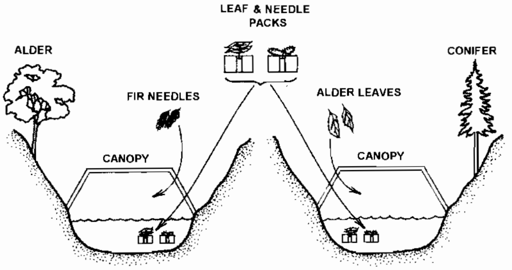

Fig. 7. Experimental design of litter drop exclusion experiment. Canopy cover of 100-m stream reaches of old growth conifer and second growth alder tiparian. Following channel cleaning of natural litter, inputs were reversed and leaf packs of both Douglas fir and alder were placed in each channel. After Cummins & Gregory (2001).

primarily of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). A 100-m study reach of each stream was covered with a flexible plastic sheeting canopy supported by wooden scaffolding (Fig. 7). Both upstream and downstream ends of the study reaches were blocked with 1-cm mesh hardware cloth to limit movement of litter or animals into or out of the canopied study reaches. The experiment was begun just prior to the major abscission of red alder leaves, and all leaf and needle litter was cleaned by hand from the canopied reaches of each channel. Amounts of litter were added to each canopied reach that approximated previously measured autumn litter standing crops. Douglas fir needles were introduced at the head of the canopied reach in the alder stand and red alder leaves at the head of the canopied reach in the old growth conifer stand. Shredders were abundant in the alder-bordered stream, especially the limnephilid caddisfly *Hydatophylax hesperus*, while no shredders, except the wood-eating riffle beetle *Lara avara*, were identified in the old growth conifer-bordered stream. Alder and Douglas fir leaf packs were also introduced into each channel and caged *Hydatophylax* containing either alder or needle litter were placed under the canopy in each reach.

Although caddisfly shredders used Douglas fir needles for case construction in the alder stream, no needle feeding was evident either in the channel or in the cages containing *Hydatophylax*. Within several weeks, all shredders in the alder stream, except those in alder leaf packs or cages with alder litter, appeared to have died. The alder leaves, either loose or in leaf packs, that were introduced into the canopy-covered old growth stream were not visibly processed during the experiment. *Hydatophylax* fed and grew normally in the cages containing alder leaves that were placed in the conifer stream. It seems clear that the alder stream was populated with fall–winter shredders whose presence was timed to the input of alder litter that would have normally occurred, whereas no such fall–winter shredder populations were in a position to utilize autumn litter inputs.

Conclusions

In this paper, an attempt has been made to establish the importance, predictability, and ubiquitous nature of the close linkage between litter derived from the riparian zone of forested streams and the invertebrate detritivores, termed shredders, that depend on the litter as a food resource. Despite the well-documented importance of the riparian zone in influencing the physical, chemical, and biological nature of the attendant stream, and the focus on the riparian zone as a major area of importance in the management of stream ecosystems, the litter–shredder linkage has yet to be employed in any standard assessment protocol for evaluating stream ecosystem ecological integrity, i.e. stream health. At the least, the seasonal pattern of taxa, numbers, and biomass of shredders per unit mass of entrained riparian litter could be used as an index of the degree to which the riparian–stream ecosystem coupling is intact.

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