

PERSPECTIVES

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Controls on leaf processing in streams from spatial-scaling and hierarchical perspectives

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Abstract. The importance of leaf litter to streams is well known, as is the series of events involved in leaf decay (leaf processing). What is currently missing, however, is an understanding of how the numerous, interacting variables controlling leaf-processing rates in streams can be organized. We suggest that leaf processing is scale-dependent and that factors controlling processing rates will largely depend on the spatial scale of study. Such factors may interact across spatial scales, creating problems in extrapolating results beyond the scale at which the study was conducted. We present a hierarchical framework that relates constraints on leaf processing to specific spatial scales. This framework reveals a predictable structure regarding the factors controlling leaf processing, providing a means for explicit incorporation of spatial scale into studies of leaf processing. Our framework also allows for developing scale-specific predictions of how various environmental changes might affect rates of leaf processing in streams.

Key words: leaf litter, organic matter, stream decomposition, hierarchy, scale, conceptual models.

Leaf litter in forested streams is a major source of organic C, fueling much of the secondary production (e.g., Wallace et al. 1997, 1999). The physical breakdown of leaves and the conversion of leaf material into microbial and animal tissue (= leaf processing) have been investigated in streams for >30 y. This work has resulted in a general understanding of the functional role of leaf litter as it is converted into smaller particles, microbial biomass, and animal tissue (Cummins 1974, Petersen and Cummins 1974, but see Gessner et al. 1999). The sequence of events occurring during processing and the factors limiting rates of processing are well known (e.g., Webster and Benfield 1986). Still lacking, however, is a conceptual framework for

understanding the numerous, and often interacting, environmental variables affecting leaf processing in streams.

A hierarchical approach often is useful in yielding important insights for processes and systems that can be reduced to independent levels of organization (O'Neill et al. 1986). Hierarchy theory may be a profitable means of organizing and understanding ecosystems and ecological processes (Allen and Starr 1982, O'Neill et al. 1986, Allen and Hoekstra 1992). We believe a hierarchical approach is applicable to understanding leaf processing in streams. The goal of our paper is to examine leaf processing from a perspective of spatial scaling and hierarchy, and to present an organizational framework for the factors controlling leaf processing rates in streams. We do not attempt an extensive review

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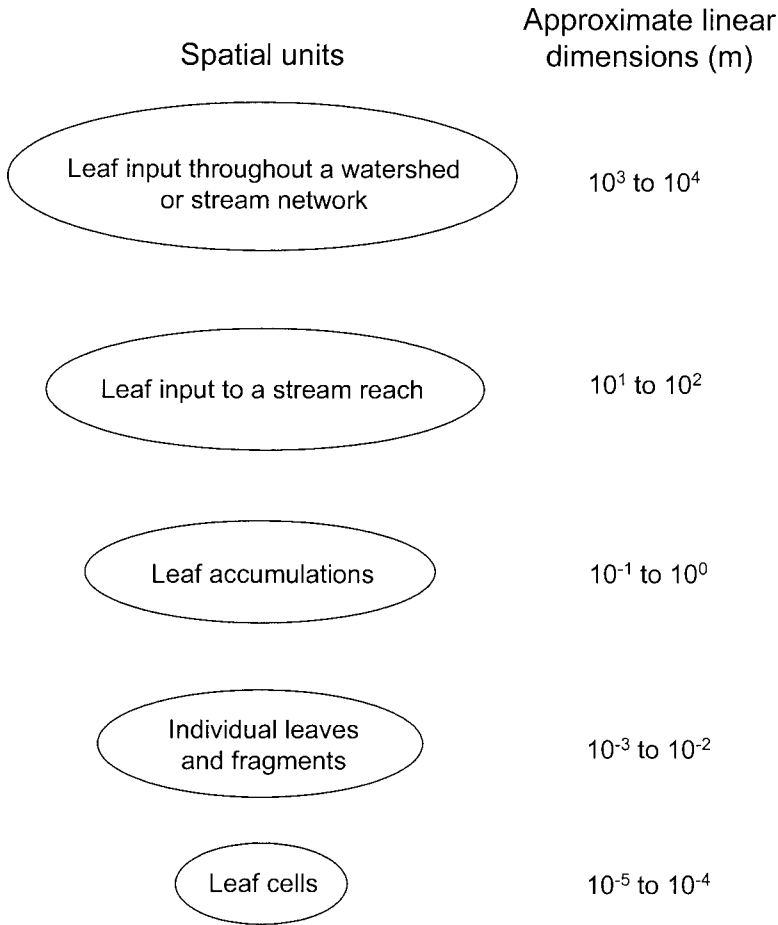


FIG. 1. Spatial units and their approximate linear dimensions relevant to leaf processing in streams. Leaf processing encompasses multiple spatial scales; studies can be conducted within or among various scales.

of the literature on leaf processing (see Webster and Benfield 1986, Boulton and Boon 1991), but rather we present selected examples of studies that illustrate the importance of spatial scaling and controls on leaf processing in streams.

Spatial Scales and Leaf Processing in Streams

Scale is one of the most pervasive and fundamental concepts in ecology because all observations and measurements are scale-dependent (Wiens 1989, Levin 1992). The processing of leaf litter in stream ecosystems occurs (and can be studied) across a range of spatial scales. For example, enzymes produced by aquatic fungi and bacteria act at the scale of molecules and leaf cells, whereas consumption by aquatic macro-invertebrates operates generally at the scale of

individual leaves or small accumulations of leaves. Factors such as water temperature, water chemistry, or riparian composition commonly act at scales of a stream reach or larger, although some factors (e.g., temperature and chemistry) can influence processing at several spatial scales. Together, these scales span 9 to 10 orders of magnitude in linear dimension (Fig. 1), approximately corresponding with the habitat scales presented by Frissell et al. (1986).

The traditional conceptual model of leaf processing in streams (Cummins 1974) was developed primarily from work conducted within individual riffles or short stream reaches (e.g., Kaushik and Hynes 1971, Petersen and Cummins 1974). Riffles and short reaches continue to be the most frequently studied spatial scales for leaf processing. Several factors are known to

cause variation in rates of processing within and among stream reaches, including pH, alkalinity, dissolved nutrients (Suberkropp and Chauvet 1995, Rowe et al. 1996, Rosemond et al. 2002), leaf quality (Gessner and Chauvet 1994, Royer and Minshall 2001), and the types and abundance of invertebrates (Oberndorfer et al. 1984, Robinson et al. 1998, Jonsson et al. 2001, March et al. 2001). Few studies have been conducted at spatial scales smaller than a riffle, but some studies have examined leaf processing at larger spatial scales, such as across biomes. For example, Minshall et al. (1983) compared processing rates among sites in Oregon, Idaho, Michigan, and Pennsylvania, all within temperate latitudes, and Irons et al. (1994) examined leaf decay at sites in Costa Rica, Michigan, and Alaska. Both studies concluded that interbiome differences in temperature altered the relative importance of microbial decomposers and macroinvertebrate shredders (Cummins 1974), thereby causing large geographic variation in litter-processing rates.

Can the environmental factors regulating leaf processing in streams interact or vary in relative importance across different spatial scales? Royer (1999) examined the processing of aspen (*Populus tremuloides* Michx.) and dogwood (*Cornus stolonifera* Michx.) leaves in 9 streams of southeast Idaho, and found that NO_3 concentration, temperature, and the abundance of shredders controlled rates of leaf processing. However, these factors were not equally important to dogwood and aspen leaves, nor were factors contributing to variation among the 9 streams equally important at smaller spatial scales (Royer 1999). Other recent studies have suggested that the importance of aquatic fungi to leaf processing varies among streams (Hieber and Gessner 2002) and that microbes and insects operate at different scales, depending on the availability of resources and local habitat conditions (Robinson and Gessner 2000). Given these examples, we believe there is strong evidence that factors controlling leaf processing can interact across spatial scales, thereby making scale an important factor in understanding differences in processing rates among studies and systems. It is, therefore, worthwhile to address the implications of scale-dependency for studies of leaf processing in streams.

The concepts of **grain** and **extent** place limits on our ability to extrapolate results across dif-

ferent scales (Wiens 1989). The size of the smallest sampling unit is considered the grain of a study, and patterns cannot be quantified at scales below the grain (Wiens 1989). Grain is a leaf pack for most leaf-processing studies; consequently, patterns and dynamics at a scale smaller than a leaf pack are undetectable. Unfortunately, this constraint prohibits addressing many interesting questions requiring a smaller grain size, such as: How tightly are nutrients cycled within leaf packs? Does the interior of a leaf pack become hypoxic or anoxic and in turn support anaerobic processes? What is the nature of the interactions between various consumers within the 3-dimensional space of a leaf pack? Each of these questions requires observations conducted at a spatial scale that largely has been overlooked (but see Cummins et al. 1980, Graça 1993, Gessner et al. 1999). The extent of a study is the overall spatial dimension across which measurements are made (Wiens 1989). In this context, results should not be extrapolated beyond the extent of the study unless the process under investigation is scale-independent or appropriate scaling relationships have been established; unfortunately, these conditions usually are not met in ecological research (Wiens 1989). For leaf-processing studies, the extent commonly has been a single stream reach or, less commonly, multiple reaches in >1 stream.

If a particular factor is found to control leaf processing in a stream reach, is it then appropriate to *scale-up* and conclude that the factor also controls leaf processing in other streams or stream reaches? To do so requires extrapolation beyond the extent of the study and, thus, accepting the assumption that the process is independent of scale. Alternatively, if we do not extrapolate to other systems we face the situation where each result is considered a special case, making it difficult to draw general conclusions (Wiens 1989, Hoekstra et al. 1991). We believe a hierarchical approach can incorporate the scale-dependent nature of leaf processing in streams and also reveal broad patterns among the factors controlling rates of leaf processing. Below is a conceptual, hierarchical framework for leaf processing in streams, which we suggest is applicable across all relevant spatial scales.

Hierarchical Organization of Constraints and Spatial Scales

Figure 2 depicts a hierarchy of environmental factors known to influence leaf processing in

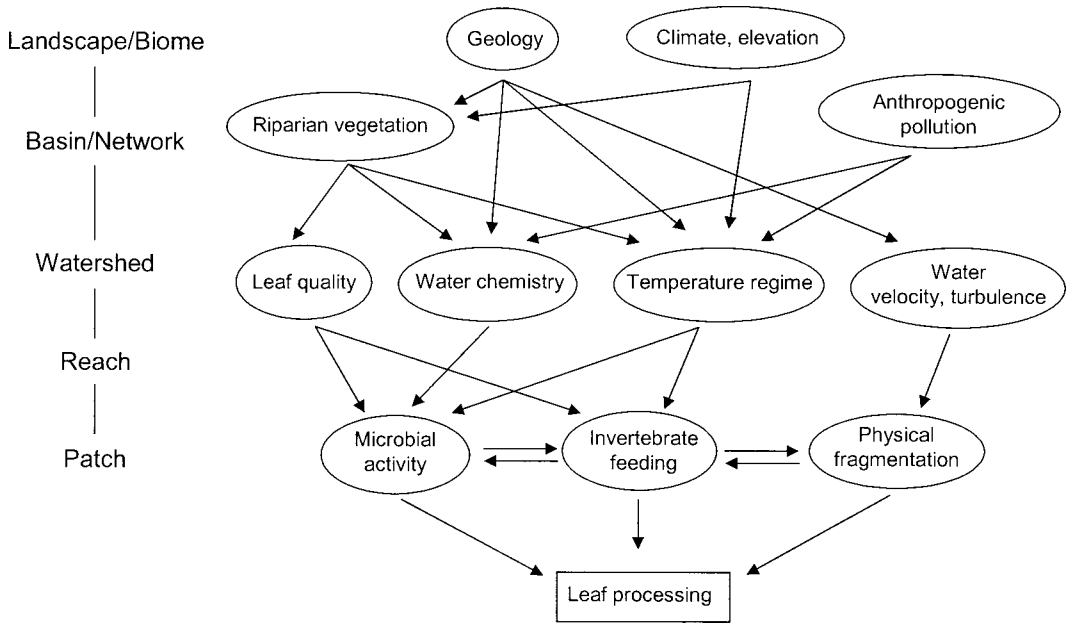


FIG. 2. Hierarchical framework for organizing the factors controlling rates of leaf processing in streams. The right-hand side shows the hierarchy of constraints on leaf processing, whereas the left-hand side shows the corresponding spatial scales at which those constraints act.

streams, based on the spatial scale at which these factors likely operate. Our scheme does not show all possible connections and interactions, but rather only those we believe are most relevant to processing. Each level in the hierarchy is constrained by levels above, with the resulting framework being a nested hierarchy of environmental constraints (O'Neill et al. 1986). The levels of the hierarchy correspond generally to common spatial scales used in stream studies (Frissell et al. 1986, Minshall 1988). A similar approach was used for explaining heterogeneity in the structure and function of benthic algal assemblages (Stevenson 1997). By linking specific constraints with corresponding spatial scales, our framework provides a method for incorporating scale into studies of leaf processing.

It has been argued that the primary goal of a scientific construct should be to improve predictive power regarding a phenomenon of interest (Peters 1991). The framework in Fig. 2 allows prediction of the variables expected to create (and thus explain) variation in leaf processing at a particular spatial scale. For example, within a stream reach variation in processing rates among patches (see Pringle et al. 1988) is predicted to arise from interpatch differences in in-

vertebrate feeding, microbial activity, and physical fragmentation. Other variables, such as habitat stability and competitive interactions, might further constrain or modify biotic influences on leaf processing (Malmqvist 1993, Robinson et al. 1998, Robinson and Gessner 2000). At a larger spatial scale, Fig. 2 (Watershed) predicts that variation in processing rates results from differences among streams in intermediate-level factors such as leaf quality, water chemistry, temperature, or water velocity/turbulence. These factors are constrained by higher-level factors (Fig. 2, Landscape/Biome), such as geology and climate, which exert local or proximate (sensu Stevenson 1997) influences on leaf processing.

Because of its hierarchical structure, Fig. 2 can be used to predict what might happen to rates of leaf processing and, by extension secondary production, if particular constraints are released or tightened. For example, global climate change may affect leaf processing in streams by altering temperature regimes and the timing and magnitude of floods (Buzby and Perry 2000). Testable predictions at specific spatial scales could be developed for future climate scenarios with given effects on temperature regimes and riparian vegetation. In addition, there has been a call

for inclusion of leaf-processing assays in bioassessment protocols (Young et al. 1994, Gessner and Chauvet 2002), an approach that is likely to be effective only if the spatial scale of the assessment metric corresponds with the scale of the factor causing impairment (see Sponseller and Benfield 2001). A spatially explicit framework, therefore, should help in advancing leaf processing as a potential bioassessment tool.

Our examination of the literature on leaf processing showed that leaf quality, temperature, and water chemistry, particularly dissolved nutrients, are the most important factors accounting for spatial variation in leaf processing rates. Based on Fig. 2, we suggest that this pattern exists because nearly all processing studies are conducted at a spatial scale at which leaf quality, temperature, and water chemistry act as immediate constraints on processing rates. Scale is, thus, implicit in studies of leaf processing in streams, although it may not be explicitly addressed (Hoesktra et al. 1991). Leaf-litter processing has largely been examined at a limited range of spatial scales, so perhaps too much emphasis has been placed on the importance of some factors at the expense of ignoring or underemphasizing larger-scale controls. Across ecoregions and biomes, large-scale geographic factors such as geology, climate, and elevation should account for differences in processing rates through their influence on lower-level factors, such as riparian composition, temperature regimes, water chemistry, gradient (velocity), and activity of microbes and invertebrates. Indeed, studies conducted at a large geographic scale have reported that differences among biomes in temperature regimes constrained the role of microbes and invertebrates in leaf processing, thereby causing different leaf-processing rates among geographic regions (Minshall et al. 1983, Irons et al. 1994).

Leaf litter is a primary functional component of many stream ecosystems (Cummins et al. 1989, Gregory et al. 1991), and conversion of litter into small organic particles, microbial and animal biomass, and ultimately CO₂, appears to be controlled by a series of nested constraints that can be partitioned by spatial scale. From this perspective, factors controlling rates of leaf processing appear more structured and predictable than expected from an examination of the literature. This viewpoint does not imply that leaf processing is unaffected by disturbance or

temporal variations in environmental conditions. Rather, we suggest that there is a logical and predictable spatial structure to the factors controlling leaf processing in streams, and that the spatial structure is inherently hierarchical. Furthermore, this hierarchical structure can be used to make testable predictions of how leaf processing will be affected by changes in the strength of various constraints. We suggest such a perspective can foster new ways of viewing leaf processing and, thus, provide insight into organic-matter dynamics in streams.

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