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INTRODUCTION

That major flows of energy occur along detrital pathways in all ecosystems is a recent recognition. In freshwater ecosystems, detritus or dead organic matter (217) has two possible sources: autochthonous detritus generated within the ecosystem and allochthonous detritus generated externally. This review is concerned with the breakdown of vascular plant detritus whether autochthonous, from aquatic vascular plants, or allochthonous, derived from riparian trees and herbs.

The importance to the energetics of streams of vascular plant material from riparian vegetation was recognized in early studies by Nelson & Scott (184), Egglishaw (85), and Minshall (175). Organic matter budgets for various streams have provided quantitative data to support these early observations (96, 132, 182, 254). However, many low-order streams that lack canopies of riparian vegetation may be dominated by autochthonous primary production of nonvascular plant origin (72, 176). Theoretical models (256) predict increasing importance of autochthonous production by periphyton and aquatic vascular plants for middle-order streams but less importance of these sources in very large streams, mainly due to light limitation. The relative dominance of allochthonous vs autochthonous sources has been shown to vary between stream systems and with local conditions within streams (72, 178).

While vascular plant leaves have received most attention in stream research, there is growing recognition that wood is also important. The direct contribution of wood to stream energy budgets is minimal because wood is resistant to breakdown (e.g. 8, 251). However, woody debris is indirectly important because it creates habitat for aquatic organisms (5), promotes

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physical stability of the stream channel (148), and retards loss of more readily available food sources (30, 31).

Detritus probably represents the dominant energy pathway in most lakes (217) and reservoirs (110). The relative importance of vascular plant material to lakes has been documented in a few cases. Where carbon budgets have been prepared, vascular plant material ranges from about 10% to >75% of total organic inputs (82, 83, 131, 144, 211, 219, 236, 262). A number of other studies, but with less complete carbon input budgets, suggest the importance of vascular plant material to the energetics of many lakes (102, 109, 118, 155, 194, 235, 246, 267).

Freshwater wetlands are a diverse group of ecosystems that range from sites dominated by woody plants (e.g. swamps, riverine wetlands, shrub or evergreen bogs) to sites dominated by herbaceous annuals and perennials (e.g. marshes, wet tundra). In most wetlands, primary production and detritus pathways are dominated by vascular plants (41, 111, 112). The role of vascular plant detritus in wetland energy flow was reviewed by Brinson et al (41).

PROCESSES OF VASCULAR PLANT BREAKDOWN

Mechanisms of Breakdown

Vascular plant breakdown generally proceeds in three distinct phases: (*a*) an initial rapid loss due to leaching, (*b*) a period of microbial decomposition and conditioning, followed by (*c*) mechanical and invertebrate fragmentation.

Dead vascular plant material begins to lose soluble organic and inorganic materials shortly after immersion in water. The general pattern of leaching from immersed whole leaves is a rapid loss over the first 24 hr followed by a gradual decline for an extended period (188). When decaying leaves are ground for analysis (202, 242) or fragmented by invertebrate feeding (172), additional soluble organics are released. Depending on variables such as water temperature, turbulence, and leaf species, up to 25% of the initial dry weight of leaves may be lost to leaching in the first 24 hr (32, 42, 106, 135, 147, 188, 203, 204, 221).

Leaves are colonized by a variety of aquatic microbes within a few days of deposition in freshwater. Fungi, principally hyphomycetes, in general dominate early colonization of tree leaves, gradually giving way to bacteria as decay advances (11, 147, 243, 249). The microbial dynamics associated with decaying macrophyte tissue appear somewhat different. Early colonization may be dominated by bacteria (134, 218). Fungi (42) or bacteria (162) may dominate later stages of decay.

Various aquatic hyphomycetes produce polysaccharide hydrolyzing exoenzymes including pectinases (61, 62, 244), hemicellulases (63, 244), and cellulases (63, 232, 244)—all of which are potentially important in the decomposition of vascular plant material. However, the structural polysaccharides—cellulose and hemicellulose—of plant cell walls are physically and chemically bound to lignin, forming lignocellulose, a resistant complex that renders cellulose and hemicellulose less accessible to enzymes (65, 151, 224). Lignin and lignocellulose degradation in terrestrial systems is accomplished by certain basidiomycetes (65, 151), but there is little direct evidence that aquatic hyphomycetes have the enzymes necessary to degrade lignin (60, 95). However, it is clear that lignocellulose in streams is degraded by some mechanism. A recent radiotracer study demonstrated the microbial degradation of lignocellulose in Douglas fir logs in a Pacific Northwest stream, although it did not identify components of the microbial community (8). Radiolabelled substrates have also been used to investigate lignocellulose degradation in salt marsh sediments where bacteria rather than fungi were responsible for lignocellulose degradation (28).

Mechanical and invertebrate fragmentation follows microbial colonization. In streams, microbially softened leaves may be fragmented by current and abrasives (23, 35, 130, 170, 202, 205, 244, 265) or when redistributed by high flows (24, 35, 77). Physical fragmentation is probably less important in lakes and wetlands, although wave and current action may be important in lakes and tidal marshes (195). A second mechanism of fragmentation is that promoted by invertebrates. Leaf-shredding invertebrates, or shredders (68), preferentially colonize and feed on microbially conditioned leaves (reviewed by 5, 70) and may contribute significantly to leaf breakdown in streams (141, 204, 257, and see below). The role of invertebrate fragmentation in lakes and wetlands in less well known but is likely significant in at least some sites.

Chemical Changes During Breakdown

Kaushik & Hynes (146, 147) were among the first to observe immobilization of nitrogen during tree-leaf breakdown in freshwater. This immobilization is usually attributed to accumulation of microbial protein (15, 79, 137, 222, 242, 250, 252), though Odum et al (193) found that nonprotein nitrogen constituted as much as 27% of total nitrogen of leaves decomposing in freshwater. Phosphorus immobilization has also been observed in some cases (e.g. 40). Other elements, e.g. calcium, are lost at rates similar to weight loss, and highly soluble elements like potassium are lost more rapidly than weight (40, 130, 149, 247, 265). General trends in ion concentrations in decomposing aquatic vascular plants are similar, though considerable variation among sites has been observed (38, 39, 43, 45, 76, 88, 128, 152, 210, 227, 266).

In contrast to the rapid loss of the bulk of the soluble organic constituents, degradation of structural polymers in leaf material is relatively slow. In general, the polysaccharides hemicellulose and cellulose decline in proportion to mass loss. This indicates that both constituents degrade gradually over the course of leaf decomposition, whereas lignin has been observed to increase as both percentage of ash-free dry weight (AFDW) and as absolute weight (107, 202, 208, 222, 242, 253). The increase in percentage of AFDW reflects very slow lignin degradation compared to the other structural components in the leaves. The increase in absolute weight of lignin may be an artifact. Suberkropp et al (242) proposed that nitrogenous compounds combine with plant phenolics to form complexes that are extracted with lignins, and Rosset et al (222) suggested that certain tannins may acylate polysaccharides, thus forming resistant complexes that are detected as lignin.

Models of Breakdown Processes

Most studies of breakdown in freshwater have used the negative exponential model originally developed by Jenny et al (142) and Olson (197). This model has been criticized for two major reasons. First, other mathematical equations often describe the data more precisely. Second, variables known to affect rates of organic matter breakdown, such as temperature, are not present in the negative exponential model.

The negative exponential model can be developed from one assumption—that the rate of weight loss (or absolute decomposition rate, sensu 263) from organic material is a constant fraction of the amount of material remaining. The major problem encountered in using this model is that breakdown rates are seldom constant. Two factors are most commonly responsible for changes in breakdown rates. First, breakdown rates change through time because of the complex nature of plant material. Weight loss is rapid during the first few weeks due to loss of soluble and labile materials through leaching and microbial metabolism. The remaining material is more resistant to decay, and subsequent weight loss proceeds more slowly. Second, breakdown is sensitive to temperature; thus, seasonal changes alter breakdown rates.

Alternative models proposed to deal with these two problems are mostly modifications of the negative exponential model. Minderman (174) proposed a model that accounts for the complex chemical nature of vascular plant material. In the model each class of chemicals breaks down at a constant rate, and the overall rate of breakdown is the sum of the individual breakdown rates. Boling et al (35) and Carpenter (56) used a similar approach in modeling detritus dynamics. They divided organic material into compartments based on particle size and the extent of breakdown involving exchange of material among the compartments. A simpler modification of the negative exponential model groups leaf components into just two classes, labile and refractory. This double exponential model (sensu 263) has been useful in describing breakdown in grasslands (138, 263), macrophyte breakdown in shallow lakes (44), and laboratory simulation of leaf breakdown in tree holes (57).

The asymptotic model (sensu 263) is similar to the double exponential model, but refractory material is assumed to be completely resistant to decay and remains unchanged while labile fractions disappear (99, 143). Another approach to dealing with breakdown of heterogeneous materials is a negative exponential model that includes a breakdown rate which decreases exponentially with time (44, 108) or with mass of material remaining (57).

The negative exponential model also has been modified in various ways to account for the effects of temperature on breakdown rates. Minshall et al (178) and Short et al (230) found that good statistical fits could be achieved by using degree-days rather than time as the independent variable. Hanson et al (120) used a more complex modification of the negative exponential model in which the breakdown rate was a linear function of temperature. This two-variable model was statistically better than the unmodified negative exponential model and provided meaningful comparisons among sites. Simulation models for detrital breakdown have incorporated temperature effects in various ways. Webster (258) used the degree-day model in simulating organic matter dynamics in a second-order stream, and Boling et al (35) used a Q_{10} function to modify breakdown rates with respect to temperature. In other studies, empirically determined relationships between breakdown rates and temperature have been used (e.g. 49, 50, 58).

As a further modification of the negative exponential model, Saunders (225) suggested a model that included a term for the availability of microbial enzymes necessary for decomposition to proceed. This idea was extended in a model (200) in which the decomposition rate was entirely based on the growth rate of microbial organisms.

These models are all based at least to some degree on a biological explanation for the breakdown process, but other equations often produce as good or even better statistical descriptions of breakdown data. Often a linear equation or some higher order polynomial produces excellent statistical fits (e.g. 133).

Levins (156) noted that there is no single all-purpose model. Models might be built for generality, realism, or precision, but it is not possible to maximize all of these qualities simultaneously. Models such as higher order polynomials with excellent statistical fits produce the highest precision of the various types of models used in breakdown studies. Such models are useful in predicting the progress of breakdown in a situation where environmental conditions are identical to those during the original study on which the model is based. However, such models offer little insight into breakdown processes. Models maximizing realism, such as some of the various modifications of the negative exponential, are useful for the insight they provide to the mechanisms of breakdown and are probably the most useful type of model for simulating breakdown under natural conditions. The negative exponential model is clearly less realistic than other models and often less precise. The advantage of the negative exponential model is its generality. It provides a single number that describes, often fairly well, the progress of breakdown in a particular situation. This number can then be used as a basis for comparing that result with breakdown rates in other situations.

FACTORS AFFECTING BREAKDOWN RATES

Melin (168) noted that leaf breakdown rates are affected by both internal factors, i.e. chemical and physical characteristics of the leaves themselves, and external environmental factors. To evaluate some of these factors, we tabulated published breakdown rates (k values for the negative exponential model) for leaves exposed in lakes, streams, and freshwater wetlands. These data came from 117 studies published from 1967 through 1985 and included 596 individual rates. In many cases the rates were reported in the publication; in other cases it was necessary to calculate breakdown rates from reported data. We used only data from studies done in natural settings and excluded strictly laboratory studies. For papers evaluating effects of disturbance on breakdown rates, we used only rates from control sites. With each rate, we compiled the following information: family and species of leaves; plant type—woody or nonwoody; habitat—stream, lake, or wetland; and exposure method—pack, bag (any type of mesh container), or unconfined. Because of page restrictions we are not able to include these data here, but a complete list with references can be obtained by writing to us. The data were log transformed and analyzed using analysis of variance. Means were calculated using the least squares means technique to correct for the unbalanced design. The 0.05 level of significance was used for all statistical tests.

Exposure Technique

Two techniques have generally been employed for breakdown studies: Leaves either have been placed in mesh bags or in mesh-covered containers (following techniques originated for terrestrial systems) (34), or they have been fastened into packs and placed against some sort of obstruction simulating a natural debris accumulation (204). In at least one study, leaves were released without containment (73). Analysis of the data set showed that breakdown rates for packs are significantly faster than for bags. Least squares means for all sites and species were 0.0070 day^{-1} for packs and 0.0054 day^{-1} for bags. This difference can be partly attributed to an interaction between method and site—most pack studies were done in streams where breakdown is relatively rapid, and no pack studies were done in wetland sites where breakdown is relatively slow. However, this result agrees with several direct comparisons of packs and bags (73, 212, 268). Studies in which coarse mesh bags were used have shown either no difference between bags and unconfined leaves (24, 169, 261) or faster weight loss from those leaves exposed in bags (181).

Another variable, perhaps as important as packs versus bags, is the amount of material exposed. Reice (214) and Benfield et al (24) found generally slower breakdown for larger packs of material; however, Brock et al (45) found that macrophyte tissue broke down faster when exposed in large (60 g) packs.

The effect of bag mesh size has been investigated in numerous studies. Some studies showed no effect of mesh size (24, 45, 53, 147, 164, 206, 207, 212), but in many studies leaf breakdown rates were faster in larger mesh bags (18, 32, 43, 74, 119, 140, 158, 163, 180, 205, 222, 223, 264). In all but one of these latter studies, the faster breakdown in larger mesh bags was at least implicitly attributed to invertebrates. Hanlon (119) attributed the difference to physical and microbiological factors because he found no evidence of invertebrate feeding. Studies where no mesh size effect was observed were, in some cases, conducted at sites where invertebrate detritivores were not abundant or important (e.g. 53, 74).

In addition to excluding invertebrates, small mesh bags may reduce gas and nutrient exchange rates and perhaps produce anaerobic conditions inside the bags (204). More confined leaves are less vulnerable to leaching, abrasion, and fragmentation (249), whereas leaves in packs or large mesh bags are more exposed to physical abrasion and more subject to loss of particles.

Leaf Species

In one of the most extensive studies of leaf breakdown in aquatic systems, Petersen & Cummins (204) found what they described as a "hierarchy of leaf species along a processing continuum." This continuum is evident in Figure 1 in which species are grouped by family. Within the data set, nonwoody plant leaves broke down significantly faster than woody plant leaves. The least squares means over all sites were 0.0109 day^{-1} for nonwoody plants and 0.0035 day^{-1} for woody plants. The nonwoody plants, including aquatic macrophytes and terrestrial herbaceous plants, exhibited a wide range of breakdown rates (Figure 1). We found a clear separation into two groups. The group with faster breakdown rates included submerged and floating macrophytes. The slower group consisted of emergent macrophytes, terrestrial grasses, and ferns. Among woody plants, the range of breakdown rates was considerably less than among nonwoody plants. Petersen & Cummins (204) placed tree leaves into three groups: fast ($k > 0.010$ day^{-1}), medium ($k =$ 0.005–0.010), and slow ($k < 0.005$). These three groups are generally

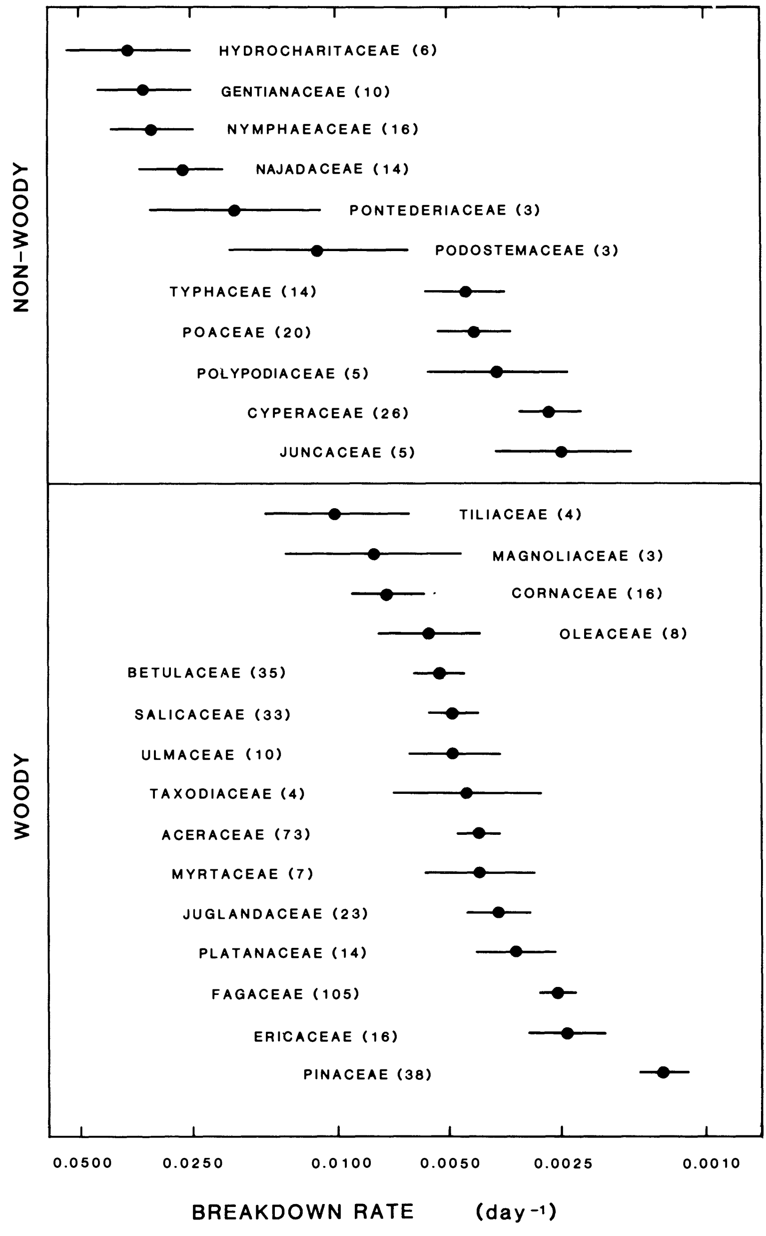

Figure 1 Breakdown rates for various families of woody and nonwoody plants. Points are least squares means for all types of freshwater ecosystems and all exposure techniques. Lines represent ± one standard error of the mean. The numbers of individual rate measurements are given in parentheses. This figure includes only families with measurements made at more than one site and with measurements made in at least three different studies.

evident in Figure 1, though the rates are lower since our data include all freshwater ecosystems, not just streams.

Internal factors that produce the differences among taxa illustrated in Figure 1 can be divided into three categories: (*a*) abundance of essential nutrient elements in the leaf tissue; (*b*) fiber content; and (*c*) presence of chemical inhibitors. The one element generally thought to have the most effect on breakdown rates is nitrogen. Kaushik & Hynes (147) and many others have shown that tree leaves with higher initial nitrogen concentrations break down faster than leaves with low nitrogen. Alder, a species with nitrogen fixing symbionts and high nitrogen concentrations, consistently breaks down more rapidly than other species (122, 226). Aquatic macrophytes with high initial nitrogen concentration also break down relatively rapidly (58, 107).

Numerous studies of terrestrial leaf breakdown have demonstrated that breakdown rates are negatively correlated with initial lignin concentrations (66), and similar results have been demonstrated for tree leaves in streams and lakes (202, 226, 242, 252, 260). Differences in fiber content may also explain observed differences among emergent, floating, and submerged aquatic plants (107, 196; Figure 1). Floating plants are supported by the water column, and submerged plants may be supported by the water column or substrate, whereas emergent plants must have internal support. Godshalk & Wetzel (107) found that total fiber correlated better than lignin with breakdown rates of aquatic plants.

Noting that both initial nitrogen and initial lignin correlate well with breakdown rates, Melillo et al (166) suggested the ratio of lignin to nitrogen could be used as an indicator of leaf quality. At Hubbard Brook Forest, New Hampshire, they demonstrated a high correlation between this index and terrestrial leaf breakdown.

Inhibitory chemicals may be of at least three types: (*a*) waxes or cutins that provide a physical barrier against decomposer attack; (*b*) tannins that complex with proteins; and (*c*) chemicals with direct inhibitory effects. Bärlocher et al (14) demonstrated that the thick cuticle of conifer needles is in part responsible for the slow fungal invasion and slow breakdown of needles. The tough leaves of broadleaf evergreens such as rhododendron and *Rhus* also break down very slowly (122, 261). Polyphenolic compounds complex with proteins and slow leaf breakdown. They may react with plant proteins forming a decay-resistant complex or may react with and inactivate degradative enzymes (29). These polyphenolic compounds may affect both microbes and invertebrate detritivores. Cameron & LaPoint (53) showed that tannin was not directly toxic to invertebrates but inhibited their feeding, thus causing high mortality in laboratory experiments. However, Martin et al (160) showed that the stream detritivore, *Tipula abdominalis,* has an alkaline midgut which may dissociate the tannin-protein complex. Cinnamic acids and other compounds may cause more direct inhibition of microbes and invertebrate detritivores (36, 255). Effects of inhibitory chemicals are perhaps best seen in a comparison of coniferous and deciduous leaves. Conifer needles break down considerably more slowly than most deciduous leaves (209; Figure 1). Needles have thick waxy cuticles and contain large amounts of polyphenolic compounds (14, 16, 173).

Differences Among Plant Parts

Most of the information considered in this review deals with leaves; however, a few studies have examined the breakdown of other plant parts. In forested streams, wood debris may be the major form of organic material present (183). Although information on wood breakdown is sparse, it can be generally said that breakdown of wood tissue in freshwater is slow (6, 40, 59, 78, 130), small pieces of wood with high surface-to-volume ratios break down faster than larger pieces (251), and hardwoods appear to break down faster than softwoods (167).

A number of studies have examined the relative breakdown rates for different parts of aquatic macrophytes. Leaves and shoots of floating macrophytes break down faster than roots, root stocks, and petioles (44, 45). In the submerged macrophyte, *Potamogeton lucens,* leaves break down fastest, rhizomes are intermediate, and stems are slowest (21). Among emergent macrophytes, leaves have generally been found to break down faster than other plant parts (33, 129, 210), though Sharma & Gopal (227) found faster breakdown of rhizomes than leaves of *Typha elephantina.*

Temperature

Many studies, using a variety of leaf types and conducted in various types of freshwater, have demonstrated seasonal variation in leaf breakdown rates with faster breakdown during warmer periods (18, 42–44, 115, 123, 126, 140, 201, 202, 204, 214, 220, 230, 245). Concurrent studies made at sites with differing temperatures have also demonstrated faster breakdown with higher temperature (115, 140, 201, 245). Both types of studies are somewhat ambiguous in demonstrating temperature effects because of concomitant variation in other variables such as nutrients and detritivore life cycles. However, these field studies are supported by laboratory studies that clearly demonstrate temperature effects for both woody and nonwoody plant leaves in both flowing and standing water (58, 107, 136, 139, 147, 208, 210, 245, 266).

Temperature primarily affects microbial processes. Invertebrate feeding seems to be less influenced by temperature and may sometimes overshadow temperature effects (122, 140, 180). Several studies have demonstrated relatively rapid leaf breakdown in streams with temperatures at or near 0°C (64, 180, 229). Sinsabaugh et al (233) found that even at 0°C microbial enzymes retained about 30% of the activity present at 25°C, and fungal growth and microbial respiration have been demonstrated at 0°C (11, 51).

Dissolved Nutrient Concentrations

Direct comparisons of leaf breakdown in nutrient-poor versus more nutrient-rich systems have nearly always demonstrated faster breakdown in the nutrient-rich system (3, 43, 44, 81, 84, 86, 171, 203, 222, 226). These results include studies of both tree leaves and macrophytes in lakes, streams, and wetlands. The difference is most often attributed to the availability of nitrogen. The acceleration of leaf breakdown by addition of nitrogen has been demonstrated in many laboratory studies (2, 43, 58, 86, 89, 137, 139, 147). However, there also have been both laboratory and field studies where no nitrogen effect was observed (90, 140, 185, 250, 252).

The other commonly studied nutrient has been phosphorus. Laboratory studies have generally failed to show any acceleration of leaf breakdown at higher phosphorus concentrations (43, 58, 86, 89, 90, 137, 139), although Kaushik & Hynes (147) did find a further acceleration of leaf breakdown when phosphorus was added in addition to nitrogen. In contrast to these laboratory studies, Elwood et al (87) added phosphorus to a natural freshwater system and demonstrated significant acceleration of red oak leaf breakdown. However, this may have been an indirect effect, resulting from stimulated snail production.

There have been few studies of nutrient effects on leaf breakdown other than those for nitrogen or phosphorus: Studies with divalent cations have given conflicting results (84, 86), and in one study bicarbonate accelerated breakdown (43). Nutrient effects are the result of complex interactions between water and leaf chemistry. In addition, Park (199) found that nitrogen additions stimulated decomposition by some fungal isolates but not others. As a further complication, Federle & Vestal (91) demonstrated that both nitrogen and phosphorus stimulated cellulose mineralization in one year but not the next and that neither nitrogen nor phosphorus stimulated lignin mineralization.

Invertebrates

Many studies, conducted primarily in streams, have shown that leaf breakdown is rapid in systems with high invertebrate densities (25, 64, 75, 122, 140, 150, 180, 203, 223, 226, 229). Similar indirect evidence for the importance of invertebrates in leaf breakdown comes from studies discussed previously in which breakdown was faster in packs or large mesh bags than in small mesh bags. Also, there is a correlation between invertebrate feeding preferences and breakdown rates (147, 157, 249).

Direct evidence for the importance of invertebrates to leaf breakdown comes from laboratory and experimental studies. Cummins et al (71) found that insect detritivores significantly accelerated breakdown, and Petersen & Cummins (204) estimated that detritivores were responsible for about 24% of the breakdown of leaves in experimental channels. Similarly, leaf degradation was faster in microcosms with detritivores than in microcosms without detritivores (37). Polunin (208) attributed 8–25% of the breakdown of *Phragmites* to macroinvertebrates, and Mulholland et al (179) found that weight loss from leaves was as much as six times greater in laboratory streams stocked with snails than in channels without snails. In an experiment that simulated leaf breakdown in tree holes, Carpenter (57) found that mosquito larvae significantly accelerated leaf breakdown (57). Herbst (125) confined leaf discs in streams in cages with and without detritivores. In cages without detritivores, leaf discs lost 30–40% of their initial weight, but in cages with detritivores the leaf discs were almost completely consumed. In another study, Wallace and colleagues (67, 256) used a pesticide to poison the insects in a first-order stream. During the following year, leaf breakdown was significantly slower than in a reference stream.

Other studies suggest that invertebrates are not important in leaf breakdown in some streams. Minshall & Minshall (177) compared leaf breakdown rates in two English streams and found no differences that could be attributed to the effects of invertebrates. Kaushik & Hynes (147) observed that breakdown of leaves protected from colonization by macroinvertebrates was no different than for unprotected leaves, but they noted that small invertebrates invaded the protected leaves and may have contributed to their breakdown. Also, Meyer (170) found no relationship between invertebrate abundance and leaf breakdown rate.

The role of macroinvertebrates in leaf breakdown appears to be minimal in large streams and rivers as well as in other streams where allochthonous inputs are relatively small (23, 46, 164, 201, 230, 231). In such habitats the supply of leaf material may not be sufficient in quantity or temporal distribution to support a guild of leaf-consuming detritivores (23).

Overall, there is considerable evidence that in some freshwater ecosystems invertebrates play a significant role in the breakdown of leaf detritus either by direct consumption or stimulation of microbial metabolism (57, 163, 179). Predaceous invertebrates may also influence leaf breakdown through predation on detritivores (190).

Dissolved Oxygen

It is generally thought that decomposition occurs more slowly under anaerobic than under aerobic conditions (1). However, data from leaf breakdown studies do not clearly support this supposition. Reed (213) found that during summer stratification breakdown occurred more slowly at greater depth in a lake and was clearly attributable to low levels of dissolved oxygen. However, Barnes et al (20) attributed the slow breakdown at greater depth to low temperature and absence of macroinvertebrates. Pieczynska (206, 207) found no apparent oxygen effect—macrophyte tissue broke down most rapidly in pools in which dissolved oxygen was low. In northern wetlands, Chamie & Richardson (59) found that material exposed to anaerobic conditions under peat broke down more slowly than material exposed on the surface; however, the difference was slight. In two studies of streams, leaf material buried in the sediment broke down more slowly than surface material; but, in both cases factors in addition to low dissolved oxygen appeared to be involved (124, 223).

Laboratory studies have been similarly inconclusive. Godshalk & Wetzel (107) found slower breakdown of macrophytes under anaerobic conditions. The effect was small, however, and they concluded that the effect of dissolved oxygen was less than the effect of temperature or initial tissue-nitrogen concentration. Novak et al (187) and Bastardo (21) found no differences in breakdown rates in aerated and unaerated water. Nichols & Keeney (186) reported faster breakdown under low dissolved oxygen conditions. They suggested that under the nitrogen-limited conditions of their experiments, anaerobic decomposition proceeded more rapidly because anaerobic bacteria require less nitrogen.

Acidity

Considerable evidence demonstrates that leaf breakdown is slower at low pHs in lakes (43, 44, 55, 74, 100, 248), streams (101, 126, 158, 177, 198), and wetlands (27), and these findings have been supported by laboratory studies (27, 43, 165). The effect of low pH on leaf breakdown appears to be indirect; it inhibits many microbial organisms (117) and invertebrates (e.g. 198), possibly through mobilization of aluminum or other metals, and thus indirectly affects leaf breakdown. There are also many complex interactions between pH and nutrient cycles.

Site

Site effects include: comparisons between freshwater and other ecosystems, comparisons among the three types of freshwater ecosystems, comparisons within each type of freshwater ecosystem, and comparisons of sites within specific ecosystems.

Leaf breakdown occurs more rapidly in freshwater than in terrestrial ecosystems, according to several comparative studies (40, 169, 191, 206, 207, 238, 247, 265). This generalization is clearly supported by comparison of rates determined in freshwater and on land. The difference between leaf breakdown rates in freshwater and marine ecosystems is not clear. Odum &

Heald (191) found increasing breakdown as they proceeded from freshwater to brackish to salt water, a trend they attributed to invertebrate abundance. Benner et al (27) demonstrated much faster lignocellulose mineralization in salt-marsh water than in freshwater from Okefenokee Swamp. The difference could only be attributed in part to the low pH of swamp water. Differences in dissolved nutrient concentrations were suggested as another possible factor. In contrast to these studies, Odum & Heywood (192) reported faster macrophyte breakdown in a freshwater tidal marsh than in salt marshes.

Based on our analysis of published breakdown rates in freshwater ecosystems, breakdown is fastest in streams, intermediate in lakes, and slowest in wetlands. Least squares means for nonwoody plants were 0.0248, 0.0125, and 0.0051 day^{-1}, and these rates were significantly different. The same order of breakdown rates existed among woody plant leaves. Least squares means were 0.0104, 0.0059, 0.0016 day^{-1}. In studies directly comparing lakes and streams, Witkamp & Frank (265) and Hill (127) found faster breakdown in streams than in lakes. Several factors might account for the differences between lakes and streams. Witkamp & Frank (265) suggested that differences in leaching and mechanical abrasion were the major factors. Hodkinson (130) pointed out that current action in streams would possibly cause greater fragmentation and would also continually expose new surfaces to microflora. In contrast, leaves lying on a lake bottom would have only part of their surface exposed to aerobic decomposition (103). The lesser importance of macroinvertebrate detritivores in lakes may also contribute to slower breakdown (103, 130). The slower breakdown of materials in wetlands can possibly be attributed to low oxygen conditions, low pH, and, in some cases, occasional drying. However, it should be noted that in many wetlands the vascular plant material available for breakdown has intrinsically rapid breakdown (due to high nitrogen or low fiber content), so that realized breakdown in some wetlands may be more rapid than in other freshwater ecosystems.

Comparisons among wetland sites and among sites within wetlands have been very limited. Brinson et al (41) reported a definite latitudinal trend, with slower breakdown in northern than in tropical wetlands. Also, within wetlands, moisture and frequency of flooding can affect breakdown rates (41). Brinson (40) found decreasing cellulose breakdown at sites located in a river, the adjacent swamp forest floor, and a levee bordering the river, respectively. Odum & Heywood (192) compared macrophyte breakdown at three sites in a freshwater tidal marsh and found significantly slower breakdown in the irregularly flooded high marsh than on the regularly flooded creek bank or permanently submerged site. They attributed the more rapid breakdown of submerged leaves to more constant conditions for microbial processes, better access for detritivores, greater nutrient availability, and more rapid leaching.

However, Sharma & Gopal (227) found no differences in breakdown rates among sites in an Indian wetland.

As we indicated previously, differences in breakdown rates among lakes have generally been attributed to differences in nutrient status, while within lakes, differences in may be associated with depths. In addition to these factors, Pieczynska (206, 207) reported faster breakdown in swampy pools along the lake margin than in the littoral zone 2 m from the shore. However, the study is difficult to interpret because some macrophyte tissue did not die and lost very little weight in the 10-day exposure period.

Differences in breakdown rates among streams have generally been attributed to differences in nutrients, temperature, pH, or macroinvertebrate abundance (factors that we discussed previously) or to disturbance (which is discussed below). However, a few other trends have been noted. For example, breakdown rates are faster in small headwater streams than in larger streams (178), but slower in small temporary streams than in permanent streams (150). Also, breakdown is faster in streams with more stable substrates (223, 239).

Comparisons of rates among sites within streams have consistently demonstrated that leaf breakdown is slower in pools than in riffles (73, 104, 114, 115, 170, 237), possibly due to lower levels of dissolved oxygen and fewer macroinvertebrates (73). Reice (214) demonstrated that the substrate type significantly affected leaf breakdown rates in streams and showed that this effect could not be attributed to current velocity, dissolved oxygen, or animal abundance (215). But in a later study, where velocity was constant, Reice found no significant difference among breakdown rates on different substrates (216). He concluded that velocity and substrate interact to determine the composition of the invertebrate community. Leaf breakdown is then in part determined by the presence or absence in the underlying substrate of leaf-consuming invertebrates.

Anthropogenic Disturbance

NUTRIENT ADDITION Cultural eutrophication usually accelerates breakdown; however, in many cases additions of nutrients are accompanied by other pollutants that may have the opposite effect on breakdown. Kaushik & Hynes (147) found that leaf breakdown was slower in a polluted tributary of the Nith River than in the unpolluted Speed River. Brown et al (47) saw no significant effect of sewage pollution on leaf breakdown in an Arkansas river at a site downstream of the sewage outfall. However, breakdown was slightly faster further downstream. The pattern that might be expected in streams would be slower breakdown downstream from a sewage effluent, due to low levels of dissolved oxygen, and accelerated breakdown further downstream, due to higher nutrient levels. The distances at which minimum and maximum breakdown rates occur may fluctuate with many factors including biological oxygen demand (BOD) and nutrient load of the effluent, temperature, stream discharge, and stream velocity.

ACIDIFICATION Studies discussed above have uniformly demonstrated that freshwater ecosystems with either natural or anthropogenic low pH have slow leaf breakdown. Friberg et al (101), Traaen (248), Francis et al (100), and Mackay & Kersey (158) found slow leaf breakdown in lakes and streams where low pH appeared to be the result of acidic precipitation.

TOXIC EFFLUENTS Toxic chemicals (principally chromium, barium, and aluminum), low pH, precipitation of chemical flocs on leaf surfaces, and reduced nutrient conditions in coal ash effluents from power plants all inhibit microbial activity and may slow leaf breakdown (98, 116). Giesy (105) demonstrated that cadmium inhibited microbial colonization and decomposition, and Leland & Carter (154) found that copper inhibited microbial activity even at low concentrations. Carpenter et al (55) observed that acid mine drainage into a lake significantly slowed leaf breakdown, probably due to low pH and high levels of potentially toxic heavy metals. Gray & Ward (113) found that ferric hydroxide deposition on leaves inhibited microbial and invertebrate colonization and was apparently the main factor responsible for reduced leaf breakdown in a stream affected by mine drainage.

IMPOUNDMENT AND CHANNELIZATION Short & Ward (231) compared leaf breakdown below a dam with breakdown in an unimpounded stream. Despite the virtual absence of macroinvertebrates below the dam, leaf breakdown was faster than in the control stream, apparently because of higher winter temperatures. This sort of effect would depend on the depth of the reservoir and location of the outlet. Below a deep reservoir with a hypolimnetic outlet, breakdown could be significantly slowed. Gelroth & Marzolf (104) found that leaf breakdown was slower in pools in a channelized section of a stream than in pools in an unmodified reach, but there were no differences between breakdown rates in riffles at the two sites. They observed that naturally occurring leaf packs were virtually absent from the channelized stream. Perhaps, as Rounick & Winterbourn (223) suggest, without retention of natural leaf detritus, there was no resident invertebrate detritivore fauna.

CHANGES TO WATERSHED AND RIPARIAN VEGETATION Clearcutting watershed vegetation has a variety of effects on streams; many of which are associated with road building (259). Webster & Waide (261) found that leaf breakdown in a small stream was slower during the year its watershed was logged, and they attributed this effect to sedimentation on the leaves caused by road building and road use. The following year breakdown was faster than it had been prior to logging. While many factors may have been involved, including higher temperature and nutrient levels, fast breakdown of the experimental leaves resulted, they thought, from a lack of alternative food sources for invertebrate detritivores. Meyer & Johnson (171) found leaf breakdown to be faster in a stream draining a successional watershed than in a reference stream; they attributed the difference to high levels of dissolved nitrate.

In addition to affecting instream environment, watershed disturbances influence the nature of leaf material entering aquatic systems. Logging or clearing riparian vegetation obviously reduces allochthonous inputs. Stout (237) concluded that the major effect of highway construction on leaf breakdown in a wetland was not the temporary changes caused by siltation and channel alteration but the long-term disturbance caused by clearing riparian vegetation. Changes in the composition of riparian vegetation during natural succession or as a result of management can greatly alter breakdown rates. Natural succession in the southern Appalachian Mountains results in a riparian canopy composed of leaves with generally faster breakdown than those of the mature forest (259). A similar situation exists for streams in the Pacific Northwest (254); however, in the Southeast succession towards deciduous forest usually involves a coniferous stage, and there may be a period of slow leaf breakdown. Also, forest land in the Southeast is often managed for softwood production. Such conversion of the riparian canopy to a single tree species may inhibit development of a normal invertebrate detritivore fauna. Benfield et al (23) found that in a pasture-land stream where sycamore was almost the only riparian species, breakdown was primarily microbial and physical. Because there was no processing continuum (sensu 204), detritivorous invertebrates could not complete their life cycle and were not an important component of the system.

NEW DIRECTIONS

Considerable work has been accomplished on vascular plant breakdown in freshwater ecosystems. Additional studies that only add to the list of species-specific and site-specific rates will do little to further understanding of this process. Useful insight is more likely to come from ecosystem manipulation (e.g. 22, 48, 87, 117, 257), comparative studies, and experiments. Our review indicates several areas where further research would be especially useful.

We previously discussed the recently realized importance of wood in streams. Episodic inputs of wood from logging slash, tree disease, or storms will profoundly alter the structure of streams. As this material breaks down, stream structure and function will be further modified. Because of the slow decay of wood, studies of wood breakdown will require long-term research commitments.

One promising approach to an understanding of the mechanics of breakdown processes is the study of microbial enzymatic properties (60). Such studies explore the potential for degradation of specific chemical constituents of vascular plant tissue (233). Another mechanistic approach is the use of radiotracer techniques by which degradation of specific organic compounds can be followed (8, 26, 28).

We are also rapidly extending our understanding of breakdown processes through studies of microbial-invertebrate interactions. Clearly, invertebrates prefer microbially conditioned detritus (12), but suggestions that invertebrate growth can be attributed primarily to consumption of microbial biomass (69) seem to be contradicted by evidence that microbial biomass is insufficient to support invertebrate growth (13, 93, 153). Areas of research that may resolve this issue include studies of invertebrate gut enzymology (159–161), perhaps with increasing emphasis on acquired and endosymbiotic microbial enzymes (9, 17, 234); the importance of microbial degradation products of plant polysaccharides to invertebrates (10, 12); identification of the actual source of nutrition for invertebrates (4, 54, 121, 153); and identification of relationships between microbial species and detritial palatability to invertebrates (7, 241).

Most studies of invertebrate detritivores have been concerned with macroinvertebrates. However, recent studies of marine (92, 94, 228), lake (240), and stream (189) ecosystems suggest an important role for meiofaunal invertebrates in detritus breakdown. Because of their rapid growth, production by these small organisms can be much higher than once suspected, and they may provide an important link between detritus and larger consumers.

Breakdown of vascular plant detritus is a complex interaction of physical, chemical, microbial, and animal processes and is essential to the trophic dynamics of many freshwater ecosystems. For this reason, measurements of breakdown rates may be useful for evaluating effects of anthropogenic disturbance of such ecosystems. Measures of single species toxicity or community structure offer little insight into ecosystem function. As exemplified by some of the studies reviewed above, breakdown rate is a sensitive, integrative measurement that may be useful in the evaluation of ecosystem integrity (52).

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