Shredders and Riparian Vegetation

Leaf litter that falls into streams influences communities of stream invertebrates

Kenneth W. Cummins, Margaret A. Wilzbach, Donna M. Gates, Joy B. Perry, and W. Bruce Taliaferro

Stream invertebrates that feed on leaf litter are intimately tied to the nature and timing of the litter input. These invertebrates are called shredders (Cummins 1973, 1974, Cummins and Wilzbach 1985, Merritt and Cummins 1984); they consume streamside, riparian litter that has become trapped in the stream channel. This plant litter accumulates at the leading edge of obstructions in the current and settles out in pools, alcoves, and other depositional zones (Cummins et al. 1980, Kaushik and Hynes 1971). Given the extensive literature that has accumulated over the last 20 years, it is now an appropriate time to develop a general, testable model that relates riparian plant communities to the stream shredders, which depend upon litter derived from those communities.

Invertebrates belonging to the functional group called shredders include a wide range of taxa that feed on vascular plant tissue in freshwater environments (Figure 1; Cummins and Wilzbach 1985, Merritt and Cummins 1984). Most notable among these are amphipods and isopods, filipalpian stoneflies, and case-bearing caddisflies primarily in the superfamily Limnephiloidea, together with some species of dipterans (e.g., in the genera *Tipula, Brillia,* and *Xylotopus*) and some species of leptophlebiid mayflies. In addition to species that feed on leaf litter, wood-eating forms such as the elmid beetle larva *Lara* and aquatic Coleoptera and Lepidoptera, which chew live vascular aquatic plant leaves, are also included in the shredder functional feeding group (Cummins 1988, Merritt and Cummins 1984).

The link between riparian vegetation and stream invertebrate shredders could well serve as a cornerstone in terrestrial-aquatic evaluations

Shredders that use plant litter as a food resource do so only after it has been conditioned. The conditioning process, which typically commences after the litter has been trapped in the stream, involves rapid leaching of soluble organics, followed by colonization with stream microorganisms. Some litter may be preconditioned to varying extents on the terrestrial soil surface before being trapped in the stream (Merritt and Lawson 1979).

Shredders do not specialize on litter of a given plant species but rather on appropriately conditioned litter regardless of species. The shredders begin feeding when microbes have produced sufficient structural and biochemical changes in the plant litter tissue to convert it to a palatable nutritional state. This required conditioning time ranges from weeks to months depending upon plant species and stream temperature. The shredders continually shift to feed on the best-colonized substrates (Cummins and Klug 1979).

Shredders in the ecosystem

A major role of shredders in stream ecosystems is the conversion of large organic plant substrates (coarse particulate organic matter, CPOM) such as leaf litter into smaller particles. These finer particles (fine particulate organic matter, FPOM) are generally less than one millimeter in diameter. The FPOM that shredders generate consists of plant fragments that are broken loose as they feed and, more significantly, feces (Cummins and Klug 1979). Production of FPOM by shredders can be significant, because approximately 60% of the food ingested is converted to feces, and the animals each day can consume more than their body weight (Cummins 1973). The FPOM generated by shredders makes up a significant component of the food resource base for the stream invertebrate functional group termed collectors (Short and Maslin 1977).

Collectors have morphological and behavioral adaptations allowing them to filter small particles from the passing water column or gather them

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from the surfaces or interstices of sediments (Cummins and Wilzbach 1985). Other functional groups recognized in stream ecosystems are scrapers, which feed primarily on sessile algae closely adhered to stable sediments in rapidly flowing water, and predators, which capture prey that belong to all four functional groups. The relationships among shredders, collectors, scrapers, and predators have been detailed (Cummins 1974).

Most permanent streams in the temperate zone have both autumn-winter and spring-summer growing species of shredders (Figure 1). Shredders typically account for about 20% of the total biomass, or 10% of the numerical abundance, of stream macroinvertebrates (Petersen et al. in press) and are often among the most conspicuous organisms present. Current knowledge about shredder feeding includes the critical role played in their nutrition by both resident and transient gut microorganisms (Cummins and Klug 1979) and the importance of lipids and lipid precursors in food selection by shredders (Cargill et al. 1985, 1986, Hanson et al. 1983). Selective feeding by shredders on the most conditioned (i.e., microbially best prepared) plant litter available is keyed to the presence of microorganisms, especially aquatic hyphomycete fungi, and to the biochemical changes that they produce in the plant substrate.

The dependence of shredder populations on plant litter inputs is an important component of the River Continuum Concept (Minshall et al. 1983, Vannote et al. 1980), a general model that relates the position along a stream drainage network with the organization of the running-water biotic community and sources of organic matter. Hynes (1963) identified an important link between the stream system and the landscape through which it drains. As an example, Ross (1963) pointed out the close correspondence between the distribution of species, such as those of the eastern caddisfly genus *Pycnopsyche*, and the historical distribution of the eastern deciduous (beech-maple) biome.

From an ecosystem perspective, the functional unit comprised of shredders, microbes, and terrestrial litter plays a key role in converting CPOM

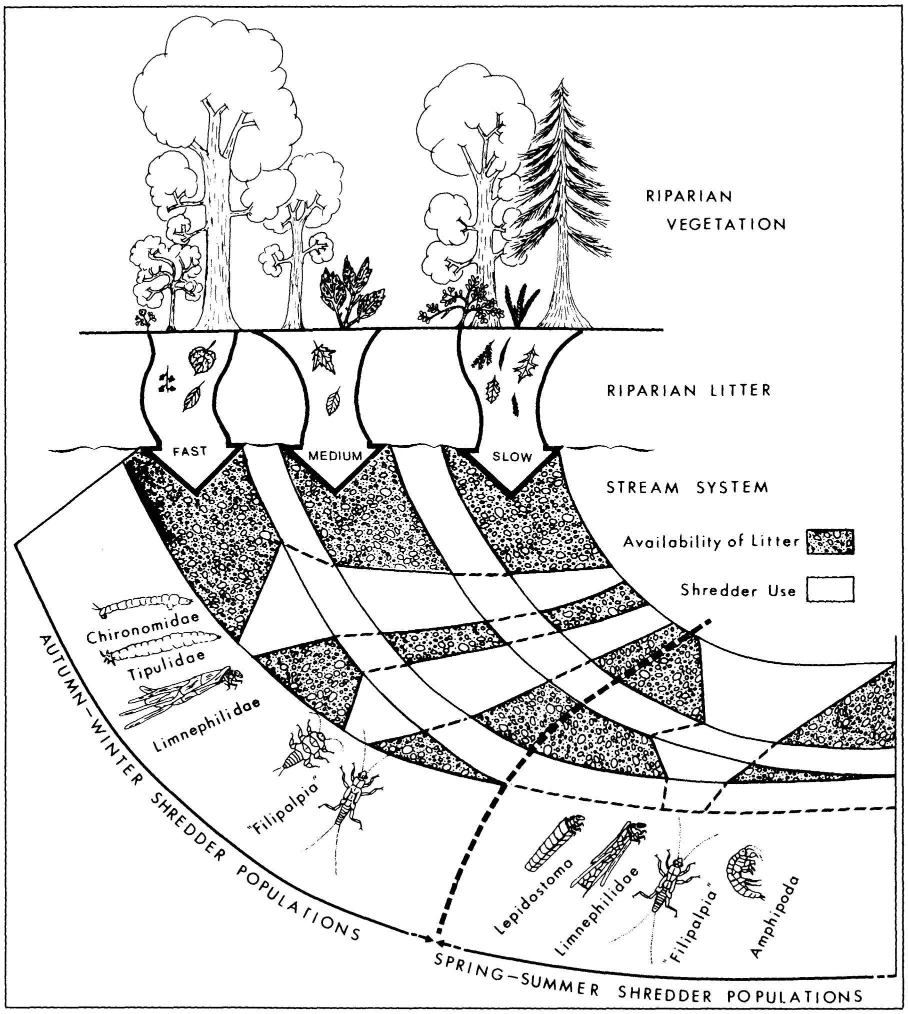

Figure 1. The dependence of autumn-winter and spring-summer populations of shredders on riparian litter having fast-, medium-, and slow-processing rates. The stippled tracks show the disappearing amounts, starting in the autumn, of fast, medium, and slow litter. The fast litter is essentially gone by spring, but some medium and a large amount of slow litter remains for use by spring-summer shredders. The white channels cutting through the three paths of disappearing litter indicate use by the different shredder groups. Examples of fast litter are: basswood, alder, and most herbaceous species; medium litter: maples and birches; slow litter: oaks, rhododendrons, beech, conifers, and most ferns. Examples of autumn-winter shredders are: Chironomidae (midges)—*Brillia* spp.; Tipulidae (craneflies)—*Tipula* spp., *Holorusia* spp.; Limnephilidae (caddisflies)—*Pycnopsyche* spp.; *Hydatophylax* spp.; "Filipalpia" (stoneflies)—Peltoperlidae, Nemouridae, Pteronarcidae, Capniidae, Leuctridae. Examples of spring-summer shredders are: *Lepidostomatidae* (caddisflies)—*Lepidostoma*; *Limnephilidae* (caddisflies)—*Ecclisomyia, Psychoglypha;* Amphipoda (Crustacea)—*Gammarus.*

of terrestrial origin to FPOM that becomes distributed in the aquatic system. Setting the division between CPOM and FPOM at a particle diameter of one millimeter corresponds well to the distinction of fine organic particles and those particles coarse enough to be colonized effectively by aquatic hyphomycete fungi and fed upon by shredders (Cummins 1974, Cummins and Klug 1979). The conversion of CPOM to FPOM proceeds year-round in the stream and ensures a continual supply of FPOM to collectors.

Given the generally accepted terrestrial origin of aquatic insects (Merritt and Cummins 1984), a close relationship between streamside terrestrial plant communities and aquatic insect species might be expected. There are some terrestrial insect species that feed on litter (most notably among the Tipulidae), but the majority of shredders belong to largely or wholly aquatic groups. Aquatic shredders have an advantage over their terrestrial counterparts in that food is available in the stream year-round. In terrestrial surroundings, organic matter processing is seasonally restricted where conditions are cold and/or dry during major portions of the annual cycle. This aquatic advantage may be responsible for the evolution of aquatic shredders that eat terrestrial plant litter.

Much information is available about the processing of terrestrial litter in streams (Cummins et al. 1980, Petersen and Cummins 1974, Webster and Benfield 1986), in-stream microbial conditioning of litter (Arsuffi and Suberkropp 1984, Bärlocher 1985, Suberkropp and Klug 1980), and shredder feeding (Anderson and Sedell 1979, Benfield and Webster 1985, Kirby et al. 1983, Wallace et al. 1982). These data, together with the examples below, allow formulation of a conceptual model linking riparian litter and stream shredders. Three types of information are still required for such a model:

- categorization of riparian plant communities on the basis of temperature-specific, in-stream processing rates of their litter;
- generalizations about timing and retention of litter inputs;
- the response of shredder associations to optimally conditioned litter in each processing category.

Remote sensing of riparian vegetation can provide a means of evaluating seasonal patterns in shredder biomass relative to their litter food resource. The use of undisturbed reference streams and historical records of riparian vegetation are valuable tools for evaluating the rate and extent of stream-community changes in a given watershed or basin.

Litter-processing categories

Species constituting riparian plant litter can be reliably classified into in-stream processing rates of fast, medium, and slow (Figure 2; Petersen and Cummins 1974). Processing is measured as the plant-litter weight loss resulting from both physical and biological action. Physical processing

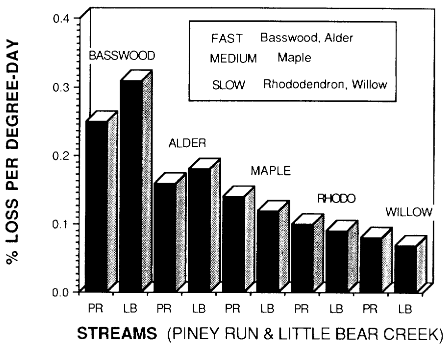

Figure 2. Examples of in-stream leaf-processing categories for fast-, medium-, and slow-turnover species in percent weight loss per degree-day. The data are from two Appalachian streams in western Maryland (based on n=4–8 estimates of mean rates for each species; standard errors were less than 20% of the mean in all cases). General processing category ranges: fast >0.15, medium >0.10 <0.15, slow <0.10% per degree-day.

loss occurs through leaching (typically 20–40% dry weight lost in the first 24 to 48 hours) and mechanical abrasion. Biological processing includes conversion of the litter to CO_2 and invertebrate feces, and incorporation of the litter into microbial and invertebrate biomass (Cummins 1974). The rates of such processing, expressed per unit of time or normalized for temperature as degree-days, can be fitted to linear or exponential decay models (Hanson et al. 1985, Petersen and Cummins 1974, Webster and Benfield 1986).

The litter-processing categories are based on the rate at which the riparian litter loses weight when it is retained in aerobic sites in the stream. Expressed as percent dry weight loss (after leaching) per day and normalized for temperature, fast processing is more than 0.15%, medium is 0.10–0.15%, and slow is less than 0.10% per degree-day. Data on two second-order, headwater streams in western Maryland can serve as an example for forested streams (Figure 2; for additional data see Petersen and Cummins 1974, Webster and Benfield 1986).

These general, temperature-specific processing rates are transferable between streams in different watersheds, in different biomes (ecoregions), and on different continents. For example, exotic Australian species (*Eucalyptus nitens* and *Atherosperma moschatum*), which are not native to North America, exhibit slow processing rates (0.07–0.10% dry weight loss/degree-day), which are similar to those reported for related species in native Australian streams (Bunn 1985, Cummins 1986).

An example of the characterization of riparian plant communities by processing categories is summarized in Table 1. Both streams used as examples are in the Appalachian mountains of western Maryland and were bordered by fairly complex associations of evergreen and deciduous plant species. The canopies were closed, and the streams differed in gradient. Piney Run is a low-gradient, fine-sediment stream and Little Bear Creek is a cobble-and-boulder, high-gradient stream. Their riparian vegetation conforms to the pattern of the hemlock-birch association of stream-side corridors described for the general region by Brush et al. (1980). A major difference between these two streams is in the relative amounts of riparian cover that was composed of medium and slow plant species. As shown in Figure 1, it is the slow litter with its longer conditioning time that

Table 1. Riparian plant associations of two Appalachian streams (western Maryland) as examples of classification. Categories based on percent dry weight loss per degree-day: slow <0.10, medium >0.10 <0.15, fast >0.15; standard deviations as percent of means were less than 40% in all cases, based on 16 or 28 transects.

In-stream processing category	Dominant genera		No. of species*		% Cover	
	Piney Run	Little Bear Creek	Piney Run	Little Bear Creek	Piney Run	Little Bear Creek
Fast	*Prunus*	*Liriodendron*	20	9	14.4	19.3
Medium	*Acer, Betula*	*Acer, Betula*	25	13	21.2	42.2
Slow	*Rhododendron, Tsuga*	*Rhododendron, Fagus*	14	11	64.5	38.5
Total	—	—	59	33		

*Gramineae (grasses) and unidentified mosses were each assigned a value of 1 in the tabulations.

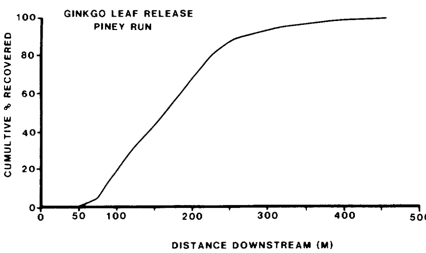

Figure 3. Pattern of retention of autumn-shed, yellow ginkgo leaves released at a point source in Piney Run. Leaves were released in October and the number counted in February by surveying the stream and banks for 2000 meters below the release point. No leaves were recovered beyond 500 meters. The relationship is based on a 10% recovery of approximately 5000 leaves.

remains as the dominant food resource for spring-summer shredders.

Relationship between cover and retention

There is a strong relationship between riparian plant cover, as determined by simple techniques measuring species composition and relative dominance, and the leaf and needle litter that becomes trapped in the reach of a stream that is bordered by riparian cover. There is an equally strong relationship between stream litter and individual plant species, if the plants are combined according to their in-stream processing categories.

When percent cover is estimated in the field by a line-intercept method (i.e., the portion of a line run perpendicular to the stream channel that is covered by each species along the line), the value can exceed 100% because the plants can occupy different strata and the portion of the line covered by two or more species frequently overlaps. This overlap is not a problem in predicting how much a given species contributes to the total litter retention of a stream transect.

Litter retention in the stream channel can be readily determined by periodically collecting all coarse litter from transects (e.g., one-meter-wide bands across the stream channel bottom). Once the plant species in the litter are grouped according to processing categories, the amount in each category and the turnover period can be estimated.

Plant litter is retained quite efficiently in most undisturbed, forested stream channels (Speaker et al. 1984). This efficiency is shown in the distribution of the recovery of introduced leaves below a point-source release site (Figure 3). Autumn-shed leaves of the exotic species *Gingko biloba* were used as markers; they do not occur in the riparian zone, and they remain bright yellow in the water for one to five months. In the example shown, 90% of the measured retention occurred in the first 250 meters of stream below the release point. Thus, the general pattern evident in the example and in other studies that have been conducted (Speaker et al. 1984) is that in channels having natural complexity (bed roughness) and intact riparian zones, retention of terrestrially derived plant litter is quite efficient. As a consequence, it is reasonable to expect that local invertebrate shredder populations will be in balance with the riparian plant communities growing in their immediate upstream surroundings.

The total amounts of coarse litter (woody material, fragments, and mosses in addition to leaves and needles) retained by two Appalachian streams (Piney Run and Little Bear Creek) were similar to that reported in other detailed studies. For example, the range measured in these streams, 0.2–0.9 kg/m^2, is similar to the annual average reported by Petersen et al. (in press) for a similiar-size stream in the Great Lakes basin.

The channel configuration is important in influencing channel inputs and retention of litter. When the two Appalachian streams were compared (Figure 4), the apportionment of leaf, needle, and other litter categories retained in the channels differed between the steeper gradient stream (Little Bear Creek) and the low-gradient stream (Piney Run). Little Bear Creek also had much steeper side slopes. This configuration served to concentrate litter in the channel from a wider riparian plant zone. These differences illustrate the problems in determining the width of the riparian zone that influences a stream (Cummins 1986).

An example of the relationship between plant cover and in-stream retention of plant litter is shown in Figure 5. When occurrences of plant

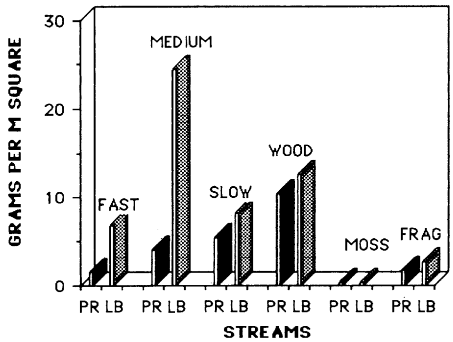

Figure 4. Standing crop of litter retention in two Appalachian streams is compared. Litter categories are fast-, medium-, and slow-processing leaf and needle litter, woody material, mosses, and unidentifiable litter fragments. Data from autumn through spring are combined (six to nine transects on each of six sampling dates; standard error of means for all categories ranged from 8% to 50%).

species are plotted separately—or as averages of the fast-, medium-, and slow-processing categories—the correlation coefficients of retention on cover are significant ($r^2=0.99$ and 0.93 for processing categories or 0.51 and 0.61 for separate species for Piney Run and Little Bear Creek, respectively). If the data on retention versus cover by plant species for Piney Run are plotted without hemlock (*Tsuga*), the correlation is improved ($r^2=0.81$).

The relatively high percentage of cover for conifer species, such as hemlock, is not matched by the measurements of its in-channel biomass retention because of the small size of individual needles. Given sufficient data on different conifer species from a range of stream sites, it should be possible to develop standard empirical correction factors to adjust the estimates of the relative importance of conifer needle retention derived from measurements of their percentage of cover.

Litter-processing rates

After determining cover and retention, the next step in evaluating patterns of litter processing is the estimation of disappearance (weight-loss) rates for representative litter types belonging to the three processing categories. Litter processing can be measured by a well-established, leaf-pack bioassay technique (Cummins 1974, Cummins et al. 1980, Hanson et al. 1985, Merritt et al. 1979, Petersen and Cummins 1974, Webster and Benfield 1986). The packs, which can be considered artificial litter accumulations, are made of weighed leaves of a given species that are fastened loosely together and tethered in the stream. A typical pack weighs 5 grams.

Because the major biological loss of weight during processing is due to activity of aerobic microbes and invertebrates, one cannot use mesh bags or other enclosures that unnaturally restrict the availability of oxygen. Shredders will not use a leaf pack as a food source if none of it remains aerobic. The leaf-pack technique gives results representative of litter processing in naturally accumulated litter in exposed (aerobic) locations (Cummins et al. 1980).

After allowing for an initial, rapid (24–48 h) leaching of water-soluble substances, a subset of the packs is removed from the stream every 150–300 degree-days, depending on whether the leaves belong to the fast-, medium-, or slow-processing category. The intervals should be selected to yield packs that have lost approximately 25%, 50%, and 75% of their initial dry weight after leaching. At each sampling time, invertebrates can be removed for analysis.

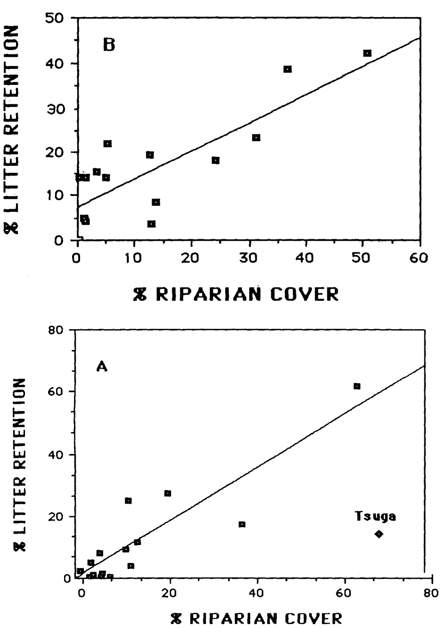

Figure 5. Relationship between percent cover of individual riparian plant species in the three litter-processing categories (and averages of each category) and their percent retention in in-stream litter transects in Appalachian streams. Each percent cover estimate is the mean of 14 line-intercept measurements (standard errors of the mean all less than 40%). **a.** Data from a low-gradient stream (Piney Run). **b.** Data from a high-gradient stream (Little Bear Creek).

Shredder response

The hypothesis we propose is: shredder biomass in a given stream system will be maximized at a particular, predictable point in the sequence that begins with litter drop and proceeds to litter retention, litter conditioning, and shredder use. Shredder associations, which may be made up of very different taxa in different stream systems, have general life history patterns that maximize their biomass at the time of greatest availability of a litter in a given processing class in a state of conditioning that can support maximal growth.

In all three litter-processing categories, the pattern observed by sampling indicates that the maximal ratio of shredder biomass per unit of leaf biomass occurs at approximately the 50% processed (weight-loss) point (Cummins and Klug 1979). Examples for fast (basswood) and slow (rhododendron) litter are shown in Figure 6. Early in the sequence of either autumn-winter or spring-summer processing, the plant litter biomass has been little used and, although shredder densities may be quite high, the average biomass of an individual shredder is low. Late in the sequence, the leaf biomass remaining in the stream is low, and the density of shredders still remaining in the packs is also low, although average biomass per individual of these sparse shredders may be quite high. Thus, for example, the prediction is that the degree-day interval required for litter in the fast category to reach a 50%-processed level will end when the resident shredder association achieves maximal biomass accumulation per unit weight of fast litter present.

Broad-scale inferences from vegetation and climate

We contend that the model described above (Figure 1) can be applied at a broad spatial scale. The shredder-litter association should represent the closest and most direct link between the historically dominant riparian plant community of a given watershed and the biota of the receiving stream channel network.

Further, we can compare the association between plant litter and shredders in one stream with that observed for a reference stream in the same basin. For example, we can compare a stream affected by manmade disturbances to another that has been stable for at least decades (or even centuries). This comparison should allow us to evaluate riparian conditions altered in either the spatial or temporal scales.

For example, the natural process of riparian plant succession that followed infrequent wildfire in presettle-

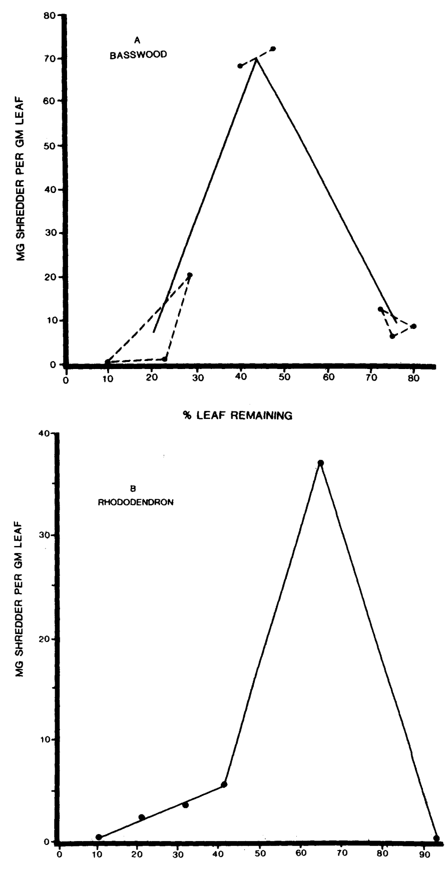

Figure 6. Relationship between percent leaf pack remaining and weight (mg) of shredders per unit weight (g) of leaf packs combined from two Appalachian streams. **a.** Fast-leaf species, basswood (*Tilia americana*); line fitted to median point of clusters of points. **b.** Slow-leaf species, rhododendron, *Rhododendron maximum.*

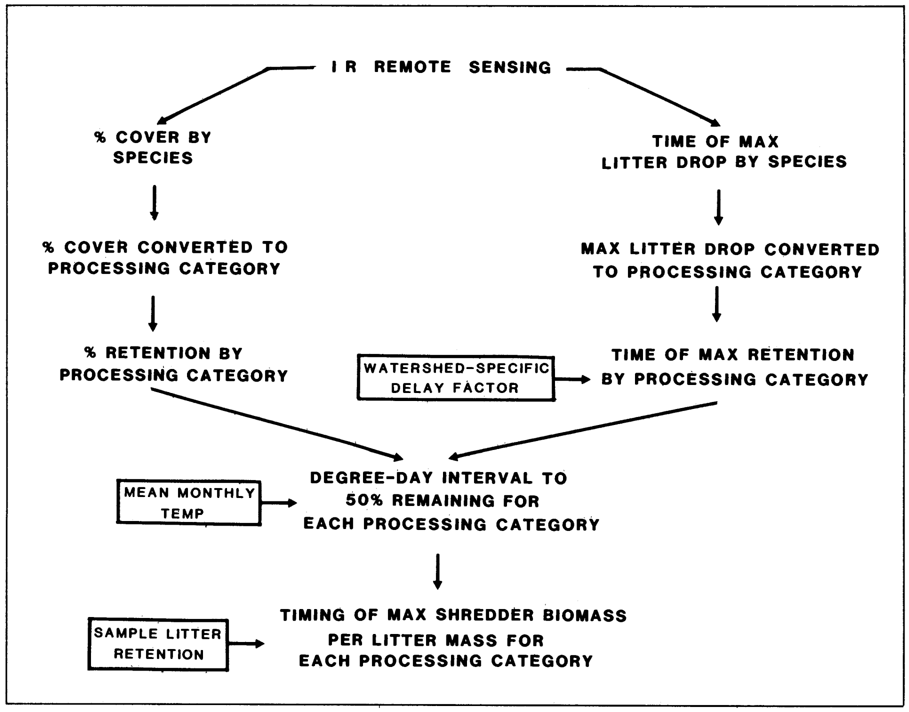

Figure 7. A strategy using a combination of remote sensing and selected on-the-ground measurements to establish patterns of association between riparian vegetation communities and stream shredder populations.

ment times has now been replaced in many regions by forest harvest that removes numerous small patches at a greatly accelerated rate (Cummins et al. 1984, Cummins 1988). In this case, both the spatial and temporal scales at which vegetation cover changes (i.e., it is lost and becomes reestablished) have been significantly altered. By starting with an analysis of plant cover and predicting the biotic response of shredder associations in the stream community, analyses of watersheds and river basins at the landscape spatial scale would be possible.

Well-established techniques of remote sensing using color and infrared photography (e.g., Dyer and Crossley 1986) could be used to analyze the terrestrial plant-community cover. The scale of resolution chosen for vegetation interpretation must fit the plant community. Scales that are either too fine or too broad can mask the characteristics of species composition (White and McKenzie 1986), such as the identification of species belonging to different processing classes.

To characterize the percent cover of plant species belonging to the three different processing categories, on-the-ground analysis (ground truthing) would be required to characterize watersheds in a given drainage basin (Figure 7). But large areas could be characterized from remotely sensed photographs after limited on-the-ground analysis of vegetation.

In addition to determining the percent cover of the plant species clusters belonging to a given processing class, remote sensing could be used to examine the timing of the maximal litter-drop from deciduous plants. The delay between maximal litter-drop (i.e., the point at which the dominant species belonging to a given litter class have shed their leaves) and the maximal abundance of that litter class in the stream was one to two weeks in the two Appalachian streams. Although this value may be a reasonable approximation for most watersheds, specific delay factors should be empirically determined for each drainage basin (Figure 7), particularly for riparian systems dominated by evergreen species (e.g., conifers and rhododendron in which only a portion of the needles or leaves are dropped annually).

Cumulative stream temperatures (expressed as degree-days) would also be required to predict the interval between maximal retention of the litter in a given processing class and the maximal shredder response. If not measured directly with continuous recording or maximum-minimum thermometers in selected watersheds in a basin, mean weekly or monthly stream temperatures can usually be derived from mean air temperatures over the same period or from records logged at the nearest US Geological Survey gauging station.

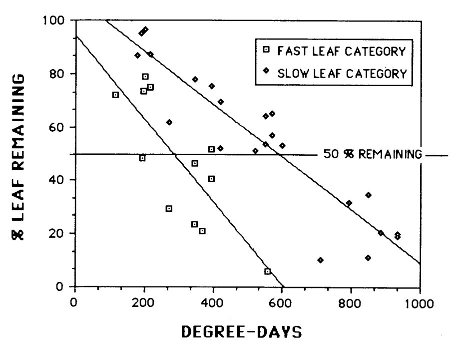

Figure 8. Relationship between degree-day processing intervals and percent dry leaf weight remaining (after leaching). Data from both autumn-winter and spring-summer periods for two Appalachian streams. The 50% leaf weight remaining for fast and slow leaf categories approximates 400 and 600 degree-days respectively. r^2 values: fast, 0.92; slow, 0.80.

With these data, one can determine the time required to reach the point at which approximately 50% of the inputs of a given litter class remain. For medium species, the 50% point would be approximately 400 degree-days. For fast and slow species, 50% litter processing would occur after approximately 300 and 600 degree-days, respectively (Figure 8). From our investigations, we predict the ratios of shredder biomass to litter mass remaining at the 50% processing level to be in the range of 60–80 mg/g dry mass for fast litter and 20–40 mg/g for slow litter.

Low-elevation remote sensing with color infrared photographs could be used to establish the relative percent of cover in the three processing classes and to document the time of maximal litter-drop. Analysis of photographs, together with information on temperature regime, would permit rapid evaluation of the most probable linkage patterns between riparian litter and shredder populations for many watersheds constituting large drainage basins.

Such broad-scale, rapid analyses could result in major benefits for on-the-ground stream-survey work. Estimates of the time (from degree-day summations) of maximal development of shredder biomass relative to the availability of the food resource could allow selection of optimal sampling times and locations. The degree of shredder linkage to the riparian food resource could be used to evaluate watersheds variously modified as compared with selected reference conditions. With this approach, entire river basins and their component watersheds could be evaluated rapidly from remote imagery and ground truthing conducted to maximize the information obtained per unit effort. Although there are many ways that stream watersheds can be analyzed, the link between riparian vegetation and stream invertebrate shredders, established during evolution, is so direct that it could well serve as a cornerstone in terrestrial-aquatic evaluations.

Acknowledgment

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