Biodiversity and Coarse Woody Debris in Southern Forests

Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity

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Influences of Coarse Woody Debris on Stream Habitats and Invertebrate Biodiversity

J. Bruce Wallace, Jack W. Grubaugh, and Matt R. Whiles

Abstract

Coarse woody debris (CWD) serves a number of important roles in stream ecosystems. For example, it retains organic and inorganic matter, provides food for invertebrates, and serves as habitat for both invertebrates and fish. Stream invertebrates apparently further the decomposition of CWD in freshwaters by scraping, gouging, and tunneling wood colonized by microbiota. Evidence is presented that the distribution of CWD varies among streams in different Southeastern ecoregions. The impact of woody debris on the availability of food resources, invertebrate colonization, taxonomic diversity, and community structure differs greatly between Appalachian and Coastal Plain streams. The primary reason for this is the availability of other sources of stable substrata in the latter. We compare and contrast some of the effects of CWD on invertebrate communities among stream types of the Southeastern United States.

Introduction

Coarse woody debris (CWD) has historically been considered a nuisance and an undesirable feature of Southeastern streams and rivers. Indeed, the removal of woody debris to ease navigation may well represent one of the first impacts of European settlement on Coastal Plain river systems. As early as 1801, the Georgia Legislature allowed for the formation of companies to conduct wood removal or "snagging" operations on the Altamaha, Oconee, Ogeechee, and Savannah Rivers (Clayton 1812). Some snagging projects were continued well into the 20th century on larger rivers (Sedell and others 1982).

The importance of woody debris in dictating stream ecosystem structure and function has been recognized only in the last few decades (e.g., Keller and Swanson 1979). In relatively high-gradient streams (slopes > 4 percent), woody debris retains allochthonous particulate organic matter, reduces stream-channel erosion, improves fish habitat, and serves as a substrate for many invertebrates and as a food resource for wood-feeding invertebrates (Bilby 1981; Bilby and Likens 1980; Harmon and others 1986; Swanson and others 1982). In larger, low-gradient streams, woody debris has been shown to be a "hot spot" of invertebrate colonization, growth, and secondary production (Benke and others 1984, 1985).

Our objectives are to review the current state of knowledge on the inputs, decomposition, and distribution of CWD in southeastern stream ecosystems and to characterize the influence of woody debris on the functional structure of aquatic invertebrate communities. In particular, we will focus on the differing roles of woody debris in high-gradient Appalachian streams versus the low-gradient systems of the Coastal Plain.

Coarse Woody Debris Inputs

Sources, quantities, and timing of CWD inputs are highly variable among Southeastern streams (Webster and others, in press). In upland streams with relatively stable channel courses, primary sources of woody debris are deadfalls and storm blowdowns. For the meandering, low-gradient systems of the Coastal Plain, most of the wood originates from large trees that fall into the streams as erosional banks are undercut (Benke and Wallace 1990; Wallace and Benke 1984). Measured inputs of wood into upland streams of the Southeast range from 38 to 425 g m² yr⁻¹ and from 34 to 111 g m² yr⁻¹ for Coastal Plain streams (Webster and others, in press). An unassessed source of woody inputs into Southeastern streams is the sequestering of woody debris by beaver. Woody debris inputs into Southeastern streams also tend to be highly episodic; recent examples include massive blowdowns from Hurricane Hugo in North Carolina and South Carolina (Putz and Sharitz 1991; Sharitz and others 1992) and large inputs of woody debris into some Appalachian streams during the East Coast blizzard of March 1993. Because of such high spatial and temporal variability, comprehensive characterizations require long-term monitoring and measurement strategies over several decades; such studies are very rare.

Decomposition of Large Woody Debris

In terrestrial environments, where oxygen is rarely limiting, invertebrates enhance woody decomposition by constructing deep galleries into the wood interior, thus promoting...
fragmentation and increasing surface area available for microbial colonization. In contrast, oxygen concentrations within the interior of wetted wood are very low, which serves as a barrier to both microbiota and invertebrates. Hence, wood decomposition tends to be much faster in terrestrial than in aquatic environments (Harmon and others 1986), where aquatic invertebrate colonization is primarily a surface phenomenon.

Although limited to the wood surface, evidence shows that invertebrates promote decomposition by scraping, gouging, and tunneling wood colonized by microbiota (Anderson and others 1984; Dudley and Anderson 1982). These activities expose additional wood to further microbial decomposition (Anderson and others 1984). The wood-gouging habits of net-spinning caddisflies (Trichoptera: Hydropsychidae) can contribute to significant underwater damage of wooden structures. In 1988, a section of bridge spanning the Pocomoke River in Maryland collapsed (National Transportation Safety Board [NTSB] 1989). Subsequent investigation revealed that the untreated timber pilings exhibited a 53- to 58-percent reduction in cross-sectional area, which resulted in the collapse. The NTSB attributed the reduction to the combined effects of microbial decomposition and gouging by larvae of Hydropsyche incommoda, which had colonized the pilings (NTSB 1989). The gouged, oval depressions on the surface of these piles are identical to pitted wood colonized by H. incommoda, as well as other hydropsychids from many Coastal Plain streams.

Distribution of Large Woody Debris in Southeastern Streams

Differences in stream size and geomorphology influence patterns of distribution and retention of large woody debris. Small, high-gradient Appalachian streams are characterized by shallow, narrow channels having low stream unit power (Leopold and others 1964) and high channel roughness (Chow 1959). These features enhance the retention of woody debris and other particulate organic matter in the form of debris dams within the stream channel. Wallace and others (1982) showed the frequency of debris dams decreased with increasing stream size along a first- through, third-order stream gradient in Western North Carolina. More recently, a similar pattern was shown in a first- through, fifth-order gradient in an adjacent stream basin (fig. 1).

Stream unit power tends to increase sharply in larger, high-gradient systems (Leopold and others 1964), where woody debris is often transported from the stream channel into the riparian zone during periods of high discharge. This phenomenon has been reported for many high-gradient, large-river reaches in Western North America (e.g., Minshall and others 1983; Triska and Cromack 1980), and is evident in some Appalachian rivers. In these systems, woody debris deposited in the riparian zone may stabilize substrata for growth of riparian vegetation, seed banks, and habitat for small mammals (R.J. Naiman, personal communication).

Changes in geomorphology and riparian vegetation within a single lotic system can result in pronounced differences in woody debris distribution. A low-gradient, sixth-order reach of the Little Tennessee River near Otto, NC, drains a broad, alluvial valley and retains relatively large amounts of woody debris within its meandering stream channel. In contrast, a high-gradient, seventh-order reach of the same river 40 km downstream lacks an extensive alluvial valley and retains only small amounts of in-channel wood. In a second-order Piedmont system, Sweeney (1993) noted that woody debris volume was 27 times greater in portions of the stream that flowed through a forest than in a meadow reach immediately downstream. This distribution suggests downstream movement of wood is not an important process of Piedmont streams.

In contrast to riparian deposition of woody debris in high-gradient Appalachian systems, large woody debris is generally retained within the stream channels of
low-gradient rivers on the Coastal Plain (fig. 2). Studies of the Ogeechee, a sixth-order Coastal Plain river, show higher standing stocks of woody debris in the river than in the riparian zone (cf. Cuffney 1988; Wallace and Benke 1984). Several mechanisms contribute to this phenomenon. First, water is diverted from the stream channel over the extensive floodplain during high-flow conditions, which decreases stream unit power (Roberts and others 1985). As a result, the stream lacks sufficient power to transport woody debris from the channel to riparian areas (Benke and Wallace 1990; Wallace and Benke 1984). Second, movement studies of tagged wood indicate that high-flow conditions actually sequester woody debris from the floodplain into the main channel (Benke and Wallace 1990). Finally, since wood decomposition is slower in aquatic than in terrestrial habitats (Harmon and others 1986), CWD in the river channel will tend to persist and accumulate while wood on the floodplain will decompose more rapidly and be less likely to accumulate.

Woody Debris and Stream Invertebrates

The effects of woody debris on stream processes and invertebrate communities can vary greatly depending on stream size, depth, cross-sectional area, discharge, gradient, and the availability and stability of inorganic substrates for invertebrate colonization. Existing evidence suggests that the impact of woody debris on the availability of food resources, invertebrate colonization, taxonomic diversity, and community structure differs greatly between Appalachian and Coastal Plain streams. Below, we compare and contrast some of the effects on invertebrate communities among diverse types of streams found in the Southeastern United States.

In high-gradient Appalachian streams, deposition of large woody debris results in a series of alterations to the physical structure of the stream. Upstream of debris dams, channel depth and width increase, water velocity decreases, and deposition of particulate organic matter and sediments is enhanced. As a result, local substratum characteristics are changed and overall physical heterogeneity of the stream channel is increased (Trotter 1990). This effect has been shown experimentally at the Coweeta Hydrologic Laboratory in North Carolina. Large woody debris was added to three of six cobble-riffle sites in 1988. Mean depth increased and velocity decreased immediately upstream of the log addition sites, and major shifts in substrate composition occurred as deposition of sand, silt, and organic matter buried the original cobble riffles. Storage of particulate organic matter increased sharply at debris addition sites relative to the untreated cobble-riffle sites (fig. 3).
Changes that alter the physical structure of stream ecosystems result in subsequent changes in the function and structure of the invertebrate community as it responds to changes in food resource availability and the physical environment (e.g., Huryn and Wallace 1987, 1988, Molles 1982). The debris dam addition experiment at Coweeta demonstrated these functional and structural responses. With decreased velocity and increased sedimentation, filtering and scraping invertebrates decreased sharply at the debris dam site relative to the untreated cobble-riffle sites. Gatherer invertebrates and trichopteran and dipteran shredders increased at the debris dams, presumably due to increased storage of particulate organic matter. Predators also increased, probably in response to the prey component of the community. Despite large increases in trichopteran and dipteran shredders, the total number of shredders remained virtually unchanged as a result of sharp declines in plecopteran shredders at the log addition sites. These results coincide with earlier studies in Coweeta streams, where depositional areas displayed very different faunal associations than those of cobble-riffles (e.g., Huryn and Wallace 1987), and provide direct experimental results for previous observations.

The effects of woody debris on functional feeding group composition in small Coastal Plain streams differs from that described above for small Appalachian systems. For example, in a sandy, low-gradient headwater stream on the Virginia Coastal Plain, all functional groups except gatherers increased at debris dam sites (Smock and others 1992), in contrast to the Coweeta debris-dam study where only gatherers and predators increased (figs. 4a and b). Similar to that of Appalachian streams, woody debris in the Coastal Plain stream retained large amounts of organic matter (Smock and others 1989), thereby increasing food resources for detritivores such as trichopteran and dipteran shredders (plecopteran shredders were absent from this stream). Woody debris also provided the primary stable substratum for filterers and scrapers in this sandy bottom stream, which contrasts sharply with debris dams in cobble bottom Coweeta streams.

The relative importance of large woody debris to the invertebrate communities of larger streams and rivers also differs between Appalachian and Coastal Plain systems, primarily due to the availability of other sources of stable substrata. The sixth-order reach of the Little Tennessee River contains substantial amounts of large woody debris, but the extensive cobble substratum is covered with a dense growth of the aquatic macrophyte, *Podostemum ceratophyllum* Michx., which affords a stable, three-dimensional habitat for invertebrate colonization. We compared the invertebrate community on woody debris to that of the *Podostemum*-covered cobble substrate in this reach of the Little Tennessee River; invertebrate abundance and biomass were much greater on the *Podostemum*-covered cobble than on woody debris (fig. 5a). These results are in sharp contrast to those found by Benke and others (1984) in the Satilla River, a Coastal Plain system in Georgia (fig. 5b). The most abundant habitat in the Satilla is primarily shifting sand substrate, which supports very low-standing stock biomass relative to woody debris or snags (Benke and others 1984). Other studies have also reported very high invertebrate production on wood habitats in Coastal Plain streams (Cudney and Wallace 1980; Smock and others 1985, 1992).
Use of Woody Debris by Stream Invertebrates

Some potential uses of woody debris by stream invertebrates are summarized in table 1. Many invertebrates, especially aquatic insects, use woody debris both above and below the waterline as a substratum for egg deposition. Wood may also be used as a direct food resource; Pereira and others (1982) examined gut contents of 108 taxa of lotic insects and found that 45 taxa had guts containing significant amounts of wood. Since wood often represents the most stable substratum in some streams, it provides attachment sites for feeding activities. Abundant crevices and loose bark of woody debris provide retreats and concealment sites for protection from predators. Some Trichoptera incorporate woody debris into their larval cases (Wiggins 1977). For many endopterygote insects, wood provides stable substratum for pupation and important emergence sites for many groups such as Odonata, Ephemeroptera, Plecoptera, Trichoptera, and Diptera. Adult insects also use woody debris as resting sites.

Coarse Woody Debris and Ecosystem Structure and Function

In addition to its specific importance to the invertebrate community, the presence of CWD in Coastal Plain rivers exerts a profound influence on the structure and function of the entire stream ecosystem.

Epixylic biofilms—organic layers consisting of microbiota, extracellular polysaccharides, and large quantities of trapped seston that coat submersed wood—are known to develop within a 2-week period following exposure of wood to river water (Couch and Meyer 1992). This rapid development of biofilm corresponds well with invertebrate colonization on introduced woody substrates. Nilsen and Larimore (1973) reported rapid increases in invertebrate biomass and abundances during the first 2 weeks following log introduction to the Kaskaskia River in Illinois. Colonization of woody substrates introduced into several tributary streams of the Savannah River was also very rapid, with most species approaching steady state within 1 week following wood introduction (Thorp and others 1985). Filter feeders dominated initial colonization, followed by other functional groups, such as gatherers (Thorp and others 1985). Max and Golladay (1993) showed that macroinvertebrate abundances and taxa richness were positively correlated with biofilm on woody substrates.

Rapid colonization of CWD by filter feeders is facilitated by their energy resources (e.g., organic particles and drifting animals). These resources are produced elsewhere in the system and delivered by the current, which represents an energy subsidy. Woody debris is necessary only as stable substrate; hence, colonization by filterers is not dependent on the developing epixylic biofilm. In Coastal Plain streams where substrate is limiting, invertebrate biomass on snags is generally dominated by filterers (e.g., Benke and others 1984; Cudney and Wallace 1980; Smock and others 1985). However, for gathering invertebrates, flocculated, dissolved, organic carbon and fine seston particles of the epixylic biofilms represent a major food resource (Benke and others 1992; Edwards and Meyer 1990); gatherer colonization of woody debris is thus influenced by biofilm availability.
Table 1—Some potential uses of woody debris by invertebrates in Southeastern United States streams

<table>
<thead>
<tr>
<th>Use</th>
<th>Comments</th>
<th>Southeastern geographic region</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oviposition sites</td>
<td>Eggs are often deposited on wood below and above the waterline</td>
<td>All—numerous examples among aquatic insects</td>
<td>Dudley and Anderson 1982; Merrit and Cummins 1984</td>
</tr>
<tr>
<td>Direct food source</td>
<td>A few invertebrates feed directly on wood by gouging, tunneling</td>
<td>All—Appalachians, Piedmont, Coastal Plain</td>
<td>Benke and others 1984; Merrit and Cummins 1984; Pereira and others 1982</td>
</tr>
<tr>
<td>Indirect food source</td>
<td>Serves as food and relatively stable substrata for</td>
<td>All—especially low-gradient Coastal Plain streams where unstable sand substrates exist; minimum importance in large, high-gradient rivers where there is little wetted wood</td>
<td>Anderson and others 1984; Benke and others 1984; Dudley and Anderson 1982; Smock and others 1985, 1992; Wallace and Benke 1984</td>
</tr>
<tr>
<td>(a) Retention of CPOM*</td>
<td>Stable substrata for</td>
<td>As above.</td>
<td>Benke and others 1984; Cuffney and Wallace 1980; Smock and others 1985; Wallace and Benke 1984</td>
</tr>
<tr>
<td>(b) Retention of FPOMb and epixylic biofilm formation</td>
<td>Stable substrata for</td>
<td>As above.</td>
<td>Benke and others 1984; Cuffney and Wallace 1980; Smock and others 1985; Wallace and Benke 1984</td>
</tr>
<tr>
<td>Attachment sites for</td>
<td>Import™ for filter-feeding taxa such as larvae of black flies and net-spinning caddisflies—in large low-gradient rivers, filters dominate invertebrate biomass on snags</td>
<td>All—especially larger streams of Coastal Plain, where Odonata, Plecoptera, Megaloptera, and some dipteran predators are abundant</td>
<td>Dudley and Anderson 1982; Smock and others 1989, 1992; Trotter 1990; Webster and others 1992; plus unpublished data</td>
</tr>
<tr>
<td>(a) Feeding</td>
<td></td>
<td>As above.</td>
<td>Benke and others 1984; Cuffney and Wallace 1980; Smock and others 1985; Wallace and Benke 1984</td>
</tr>
<tr>
<td>(b) Catches and retreat construction</td>
<td></td>
<td>As above.</td>
<td>Benke and others 1984; Cuffney and Wallace 1980; Smock and others 1985; Wallace and Benke 1984</td>
</tr>
<tr>
<td>Above uses contribute to high invertebrate biomass</td>
<td>Prey-rich patches for invertebrate and vertebrate predators</td>
<td>All—especially larger streams of Coastal Plain, where Odonata, Plecoptera, Megaloptera, and some dipteran predators are abundant</td>
<td>Dudley and Anderson 1982; Smock and others 1989, 1992; Trotter 1990; Webster and others 1992; plus unpublished data</td>
</tr>
<tr>
<td>Refugia from predators and drought</td>
<td>Crevices, loose bark, etc., aid in concealment, woody debris improves moisture retention in intermittent channels</td>
<td>Probably all regions; however, in small, intermittent headwater channels</td>
<td>Dudley and Anderson 1982; Everett and Ruiz 1993; Wiggins and others 1980</td>
</tr>
<tr>
<td>Metamorphosis</td>
<td>Woody debris serves as a stable substratum for pupation as well as concealment under loose bark, etc.</td>
<td>All—especially low-gradient Coastal Plain streams with unstable, sandy substratum</td>
<td>Dudley and Anderson 1982; unpublished observations for the Southeast</td>
</tr>
<tr>
<td>Aerial adult insects</td>
<td>Emergence, adult resting sites, and copulation</td>
<td>All—especially larger streams and rivers of the Coastal Plain</td>
<td>Dudley and Anderson 1982; unpublished observations for the Southeast</td>
</tr>
<tr>
<td>Indirect effects produced by physical modification of channel</td>
<td>Increased stream depth, reduced current velocities modify physical characteristics and increase retention of organic material leading to increased habitat heterogeneity</td>
<td>Primarily small, headwater streams, especially those draining high gradient reaches, where woody debris is responsible for high physical retention and exerts a strong influence on community structure</td>
<td>Bilby 1981; Bilby and Likens 1980; Huryn and Wallace 1987, 1988; Molles 1982; Smock and others 1989, 1992; Trotter 1990; Webster and others 1992; plus unpublished data</td>
</tr>
</tbody>
</table>

*CPOM = Coarse particulate organic matter.  
*FPOM = Fine particulate organic matter.
High standing-stock densities and biomass of gatherers and filterers supported on CWD represent an abundant food resource for invertebrate predators such as Odonata, Plecoptera, and Megaloptera (e.g. Benke and others 1984; Smock and others 1985). The total invertebrate community on wood also serves as a major food resource for vertebrate predators. Benke and others (1985) have shown that snag-inhabiting invertebrates represent at least 60 percent of the gut contents of some fishes in the Satilla River. Clearly, woody debris in Coastal Plain streams enhances abundance and production of invertebrates and thus, higher trophic levels that depend on them for food.

**Large Woody Debris and Taxonomic Diversity of Invertebrates**

The presence of woody debris can serve as a mechanism to increase taxonomic diversity in a wide variety of Southeastern streams. This is especially evident in Coastal Plain systems. In the Satilla River, Benke and others (1984) found that 63 invertebrate taxa and over one-half of the standing stock biomass resided on woody debris, although it represented less than 6 percent of the effective substrate. Many of these taxa (45 percent) were exclusively found on woody substrates. In contrast, sandy substrates, representing 85 percent of the effective habitat surface area, had only 31 taxa, and muddy substrates (9 percent of the effective habitat) had 41 taxa present (fig. 6).

We tabulated numbers of taxa present in several Southeastern stream studies where woody debris was incorporated into invertebrate sampling regimes (table 2); several points concerning the influence of wood on taxonomic diversity are evident. First, in one-half of these studies more taxa were found associated with woody debris than with stream-bottom habitats. Second, two of the three studies (Cowee Creek and the Little Tennessee River), where bottom substrata had greater taxa abundances than woody debris, were conducted at sites having either abundant Podostemum-covered cobbles, cobble substrata, or both. Cobble provides an extensive substratum for invertebrate colonization. Finally, the proportion of taxa associated only with woody debris at all sites is substantial; it ranges from 13.7 percent to over 40 percent of total taxa found. Hence, woody debris does tend to increase the number of taxa within a given stream segment.

**Recommendations for Future Research and Management**

In the past, clear-cut logging practices involved removal of all trees without considering the importance to the streams of a sustainable supply of CWD. In the Appalachians, examinations of the result of such practices indicate long-term sediment and particulate organic matter losses in a number of streams (Webster and Golladay 1984; Webster and others 1988, 1992). In the Pacific Northwest, management efforts have been made, using tree size and distance from stream, to identify riparian trees that may provide sustainable yields of CWD to streams (e.g., Robison and Beschta 1990). To our knowledge, such information is not available but is sorely needed for different regions of the Southeast.

Information on the distribution of woody debris and associated invertebrate communities in streams of the Piedmont Plateau is sparse at best. Mulholland and Lenat (1992) suggest that because of disturbed conditions, Piedmont streams have received less attention than those of the Appalachians and the Coastal Plain. Preserving and restoring riparian areas should be an immediate step toward rehabilitation of Piedmont streams (Mulholland and Lenat 1992). Protection of riparian vegetation is especially important in the Piedmont, where bank erosion is greatly
Table 2—Number of taxa found associated with woody debris, stream substratum, and combined habitats in various southeastern streams

| Location                  | Debris dam or snags | Stream substratum | Combined habitats | Taxa exclusive to wood (%)
|----------------------------|---------------------|-------------------|-------------------|--------------------------
| Coweeta, NC               | 66                  | 75                | 87                | 14                       |
| Lt. Tennessee River, NC   | 21                  | 36                | 44                | 18                       |
| Buzzard’s Branch, VA      | 34                  | 36                | 44                | 18                       |
| Collier’s Creek, VA       | 27                  | 20                | 33                | 39                       |
| Cedar Creek, SC           | 39                  | 31*               | 47                | 34                       |
| Satilla River, GA         | 63                  | 58*               | 98                | 41                       |
| **Average**               | **42**              | **43**            | **59**            | **27**                   |

* Wallace, unpublished.
* Grubaugh, unpublished.
* Smock and others 1992.
* Smock and others 1985.
* Includes stream bottom and muddy banks.
* Benke and others 1984.
* Includes sandy bottom and muddy backwaters.

The extensive snagging operations on Coastal Plain rivers undoubtedly produced substantial hydrologic and energetic impacts on these systems. For example, Clifford and others (1993) demonstrated that invertebrate faunal assemblages differed greatly among beaver ponds, beaver dams, and main stream assemblages. Faunal assemblages of beaver dams share a number of functional similarities with those of debris dams, woody snags, and lake outlets (Clifford and others 1993). Hence, the addition of woody debris by beaver apparently increases the range of habitats available for invertebrates by increasing heterogeneity. Unfortunately, the extent to which the above studies, which were conducted in other regions, can be applied to the Southeast remains unknown.
as food resource for fisheries may have been reduced by as much as 70 percent by woody debris removal. Although in some situations the removal of woody debris may be warranted (i.e., to reduce and remove blockages and eliminate impediments to flow), managers should be aware of the vital role played by large woody debris in determining ecosystem structure and function in Coastal Plain streams (Benke and others 1985). Perhaps the best management practice for these streams is “no management” other than protection of the adjacent floodplains (Wallace and Benke 1984).

Conclusions

The input and retention of woody debris, which is primarily the result of physical processes in low-gradient Coastal Plain streams, provides stable substrate for biofilm formation and invertebrate habitat in an environment that would otherwise be unsuitable for colonization for many species. In these streams, woody debris encourages taxonomic diversity, increases invertebrate biomass, and supplies food resources for higher trophic levels. In high-gradient Appalachian systems, CWD promotes habitat heterogeneity and resource availability through the retention of particulate matter, and retards down-wasting of the stream bed. Presumably, woody debris performs a similar function in Piedmont streams, but information regarding the distribution, invertebrate associations, and effective management strategies of CWD in these systems is sorely needed.

Aldo Leopold (1941) pointed out more than a half-century ago that the dominant downhill movement of nutrients and materials is curtailed by the consumption, cycling, and storage function performed by the biota. In the decades since, we realize Leopold’s perceptive observations can be extended to large woody debris as well—especially in the context of lotic ecosystems.

Acknowledgments

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