INVERTEBRATES ASSOCIATED WITH COARSE WOODY DEBRIS IN STREAMS, UPLAND FORESTS, AND WETLANDS: A REVIEW

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REFERENCE: *Proceedings of the 1999 Georgia Water Resources Conference*, held March 30-31, 1999, at the University of Georgia. Kathryn J. Hatcher, editor, Institute of Ecology, The University of Georgia, Athens, Georgia

Abstract. We reviewed literature on the invertebrate groups associated with coarse woody debris in forests, streams, and wetlands, and contrasted patterns of invertebrate community development and wood decomposition among these ecosystems.

INTRODUCTION

Coarse woody debris (CWD) is defined as logs, snags, and chunks of dead wood greater than 2.5 cm diameter (Harmon et al., 1986). This material supports a diverse invertebrate fauna and is an important source of energy for many ecosystems (Triska and Cromack, 1980; Harmon et al., 1986). The sink of carbon and nutrients in CWD becomes available through fragmentation and decomposition, which is facilitated by the invertebrates that colonize and exploit it (Swift, 1977).

INVERTEBRATE-CWD INTERACTIONS

CWD in streams provides invertebrates with food, refugia from flood disturbance and predation, and sites for resting, oviposition, pupation and emergence (Benke et al., 1984; Everett and Ruiz, 1993; Hax and Golladay, 1998). Especially in streams and rivers with sand or silt substrates, high densities of stream macroinvertebrates are associated with CWD (Benke et al., 1984; Smock et al., 1985; Benke, 1998). Some of the stream invertebrates associated with wood are xylophagous (gougers, borers, and shredders) while most others feed on detritus, biofilms, and prey that accumulate on CWD (collector-gatherers, scrapers, and predators) or simply use wood as habitat (collector-filterers) (Wallace and Webster, 1996).

When CWD enters streams, Chironomidae larvae are the first to colonize and they remain numerically dominant thereafter (Nilsen and Larimore, 1973; Thorp et al., 1985; Hax and Golladay, 1993; Magoulick, 1998). Trichoptera and wood boring Diptera also occur early in the colonization cycle. Communities stabilize after 6 to 8 wks (Thorp et al., 1985; Hax and Golladay, 1993; Magoulick, 1998). Various physical parameters such as substrate type, dissolved oxygen (DO) levels, current velocity, and seston particle size affect colonization and community development on CWD (Thorp et al., 1985; Magoulick, 1998). These early colonizers make CWD structurally more complex by building cases or boring into the wood (Dudley and Anderson, 1982). Fine particulate organic matter accumulates in and around invertebrate created structures and a highly nutritious biofilm develops on CWD surfaces providing food for a diversity of other invertebrates (Hax and Golladay, 1993). Invertebrate activity and fungal invasion softens wood (Dudley and Anderson, 1982; but see Hax and Golladay, 1993). Hydropsychid caddisfly larvae can fragment wood through their retreat-building habits (Wallace et al., 1996). Elmid gougers form channels in wood and create interstitial spaces that facilitate colonization and exploitation of CWD by other stream invertebrates (McKie and Cranston, 1998). As wood becomes soft and punky in the late stages of decay, oligochaete and dipteran detritivores become abundant (Dudley and Anderson, 1982).

The invertebrates that exploit CWD in upland forests can be grouped as either wood inhabitants or wood invaders (Swift, 1977). Inhabitants are organisms that depend on wood to complete their life cycle and many can attack living trees, converting them to CWD (Hanula, 1996). Some spend a large portion of their life cycle in dead wood. Invaders, on the other hand, can exist in other habitats and do not rely solely on wood to complete their life cycles (Harmon et al., 1986; Hanula, 1996).

During the first year following CWD input, xylophagous insects phoretically disperse fungi, mites, and nematodes (Hanula, 1996). The bark begins to loosen and a subcortical community of dipteran larvae, mites, centipedes, and coleopteran predators develops

(Savely, 1939). In 2nd year logs, wood rotting fungi become common and soften the sapwood. Social insects such as carpenter ants and termites excavate wood for nest formation (Harmon et al., 1986). Invertebrates present at this stage primarily feed on fungi and rotten sapwood. Rotten-wood borers, excavators, and a diversity of dipteran larvae become established in the subcortical layer. The bark remains intact but numerous exit holes exist from emergence of adult borers (Savely, 1939; Fager, 1968; Harmon et al., 1986). During the 3rd year, bark continues to loosen and the sapwood disappears, although heartwood remains largely intact. Fungal and rotten-wood feeders and predators are dominant. A similar fauna persists as the heartwood rots and decomposed wood is incorporated into the forest floor (Savely, 1939; Fager, 1968; Harmon et al., 1986).

In forested wetlands, aquatic and terrestrial conditions occur. Collector-gatherers and predators dominate the aquatic invertebrate community on wetland CWD (Gladden and Smock, 1990; Golladay et al., 1997; Braccia and Batzer, unpublished). Shredders, collector-filterers, and scrapers are rare (Thorpe et al., 1985; Braccia and Batzer, unpublished). In a cypress-tupelo swamp, Thorpe et al. (1985) found that Chironomidae were the first to colonize. By 8 wks, oligochaetes and chironomids became co-dominant; Ephemeroptera, Coleoptera, and Trichoptera occurred, but only in small numbers. Aquatic invertebrate densities on wetland CWD can range from 1,000 - 6,000 individuals/m^2 of wood surface area (Thorpe et al., 1985; Gladden and Smock, 1990; Golladay et al., 1997), and densities can be influenced by the depth and position of the wood in the water column (probably because of variation in DO levels). Wood extending to the water's surface can provide oxygenated habitat for invertebrates when environmental conditions stagnate (Golladay et al., 1997).

In a southeastern beaver pond, Pickard and Benke (1998) estimated annual secondary production for the amphipod *Hyallela azteca* on wood as 434 AFDM/m^2/yr, which was much lower than the 801 AFDM/m^2/yr on nearby benthic substrates. Sediments and leaf litter may be superior habitat to CWD for aquatic invertebrates in some wetlands (Gladden and Smock, 1990), but not others (Golladay et al., 1997). During dry periods, CWD can provide valuable refugia for aestivating aquatic invertebrates (Wiggins et al., 1980; Batzer et al., 1999). However, many prefer soil to CWD (Gladden and Smock, 1990; Batzer et al., 1999).

When forested wetlands dry, terrestrial invertebrates invade the exposed forest floor. This wetland fauna is often overlooked because most research focuses solely on aquatic invertebrates. However, diversity of the aquatic taxa is dwarfed by the terrestrial fauna (Batzer et al., 1999). On a South Carolina bottomland hardwood wetland, we have found an abundance of terrestrial Coleoptera (Passalidae, Carabidae, Staphylinidae), Hymenoptera (Formicidae), Diplopoda, Chilopoda, and Isoptera associated with CWD (Braccia and Batzer, unpublished data). These invertebrates probably influence wetland CWD in many of the same ways as they do upland forest CWD.

CWD DECOMPOSITION

In streams, anaerobic conditions created by water logging slow decay (Triska and Cromack, 1980). Invertebrate activities, movements of water-borne particles, and microbial activity influence rates of wood decomposition. In a small headwater stream, Wallace et al. (in press) estimated an annual decay rate of $k = 0.0083\ yr^{-1}$ (k is the exponential rate of wood decay) for small CWD (which is extremely slow) but warned that this value may actually be an overestimate (Harmon et al., 1986). In the same basin, Webster et al. (in press) reported that 5 years after CWD input only the surface layer of bark had been removed. Decay of wood itself was not evident until exposed ends of the branches began to deteriorate after 8 years.

Decay rates of CWD in upland forests vary widely (Abbott and Crossley, 1982; Mattson et al., 1987; Stone et al., 1998). Wood may decompose in only a few years in the tropics or it may take decades in northern temperate forests. Location and position of the wood within the ecosystem, macro- and microclimate, size, tree species, and invertebrates affect CWD decomposition in upland forests (Harmon et al., 1986). For oaks (*Quercus* spp., 25-35 cm dia.), Schowalter et al. (1998) reported $k = 0.12\ yr^{-1}$ for the first year and a slower average of $k= 0.06\ yr^{-1}$ for the following 4 years. We found only a single decay estimate for wetland CWD. In a seasonally flooded wetland in Illinois, an average $k = 0.089\ yr^{-1}$ was calculated for 5-cm dia. silver maple (*Acer saccharinum*) logs (Chueng and Brown, 1995).

APPLYING PARADIGMS TO WETLANDS

The aquatic invertebrate communities associated with wetland CWD are simple in comparison to streams

(Table 1). The lack of gougers, filterers, shredders, scrapers, and grazers likely results from the low DO levels, slow water velocities, and periodic drying conditions characteristic of wetlands. Aquatic invertebrates may not be as important to fragmenting CWD in wetlands as in streams. The suspected higher decomposition rates of wood in wetlands probably results from dry season processes.

Terrestrial invertebrate communities on wetland and upland CWD are fairly similar (Table 1). Some upland organisms may not occur in wetlands because they can not withstand long periods of flooding. However, we have found that large numbers of terrestrial invertebrates can persist in flooded wetlands by living above the water's surface (on floating wood or partially submerged stumps). Larger CWD in these systems retains moisture well into the dry season, and moist wood typically attracts invertebrates (Triska and Cromack, 1980). The favorable conditions for invertebrate, fungal, and microbial decomposers may make CWD decay particularly rapid in dry wetlands. While the aquatic fauna on wetland CWD is clearly important, we suspect that the terrestrial fauna is even more important to overall ecosystem function.

ACKNOWLEDGEMENTS

This project is being supported by the U.S. Forest Service, Center for Forested Wetland Research, Charleston, S.C. and the Hatch Program.

Table 1. Invertebrates Associated With CWD

	streams	upland forests	wetlands
invertebrate community	borers, collector-filterers, collector-gatherers, gougers, grazers, predators, shredders, scrapers	borers, fungal-and rotten wood-feeders, predators	Aquatic: collector-gatherers, predators Terrestrial: borers, fungal and rotten wood-feeders, predators
invertebrate diversity/ abundance	high: for wood in sand and silt low: for wood in cobbles and gravel	high: moist conditions low: dry conditions	Aquatic: low diversity, variable abundance Terrestrial: moderate to high?
key abiotic constraints	water velocity, wood condition (state of decay)	moisture, microclimate within wood	Aquatic: DO, drying Terrestrial: flooding, other?
wood decomposition	extremely slow	moderate	Aquatic: slow Terrestrial: faster?

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