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INVERTEBRATES ASSOCIATED WITH WOODY DEBRIS IN A SOUTHEASTERN U.S. FORESTED FLOODPLAIN WETLAND

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Abstract: Woody debris is an ecologically important resource in upland forests and stream ecosystems. Although much is known about invertebrate-woody debris interactions in forests and streams, little information exists for forested wetlands. In this study, invertebrates associated with woody debris in a Southeastern U. S. forested floodplain are described and factors that shape community structure are examined. Woody debris samples were collected during two wet (March 1998 and 1999) and one dry period (August 1998) from a bottomland hardwood wetland along the Coosawhatchie River, South Carolina, USA. During wet period collections, both submersed and floating woody debris were collected. Invertebrate richness, density, and arthropod standing-stock biomass were compared among sampling periods (wet and dry), between floating and submersed wood, and among woody debris decay classes. Most invertebrate richness and arthropod biomass was associated with wood collected during wet periods. However, the non-aquatic rather than aquatic arthropods were the most significant component of the overall community structure. Floating woody debris was a "hot spot" for invertebrate richness and arthropod biomass. Increased invertebrate richness was also associated with well-decayed wood. Invertebrates were classified based on temporal use of woody debris and included perennial residents, seasonal colonizers, and seasonal refugees. Overall findings suggest that woody debris is an important resource for invertebrates, and wood-associated invertebrates (especially non-aquatics) need to he considered when studying the diversity and function of forested wetlands.

Key Words: floodplain invertebrates, woody debris, floodplains, forested wetlands

INTRODUCTION

Woody debris, such as branches, twigs, logs, and standing dead trees, is ecologically important in terrestrial and aquatic ecosystems (Triska and Cromack 1980, Benke et al. 1985, Harmon et al. 1986, McCinn 1993, Bragg and Kershner 1999). The quality and quantity of woody debris in forest ecosystems varies seasonally, annually, and successionally and depends on tree mortality from disturbance events such as fires, floods, wind and ice storms, disease, insect infestation, and timber harvest (Robison and Beschta 1990, Palik et al. 1998, Hagan and Grove 1999).

In upland forests, woody debris contributes to habitat heterogeneity and ecosystem diversity while providing a long-term source of nutrients (Harmon et al. 1986). Nutrients in woody debris are made available through fragmentation and decomposition processes carried out by organisms such as mammals, birds, amphibians, invertebrates, fungi, and microbes, which use wood for habitat (Swift 1977, McCinn 1993, Hagan and Grove 1999). By producing nutrient-rich soils through decomposition, woody debris on the forest floor has been referred to as "hot spots" for seedling regeneration (Schowalter et al. 1998), and it ultimately affects forest succession (Triska and Cromack 1980). Invertebrates play a particularly important role in woody debris decomposition in uplands, and invertebrate density and diversity increase in woody debris as it decays (Abbott and Crossley 1982, Seastedt et al. 1989, Irmler et al. 1996). Triska and Cromack (1980) maintain that woody debris orientation also influences its value as habitat. In upland forests, mites, collembolans, dipteran larvae, and coleopteran larvae are typically the most numerically abundant invertebrate groups associated with woody debris (Savely 1939, Fager 1968, Abbott and Crossley 1982).

Woody debris also is an important resource in rivers and streams. By altering stream channel geomorphology, wood creates complex habitat space (Bilby and Likens 1980, Smock et al. 1989, Trotter 1990), contributing to overall stream invertebrate diversity. For lotic invertebrates, debris provides stable substrate allowing for food accumulation, resting, oviposition, pupation, emergence, and refugia from predators and floods (Anderson et al. 1978, Everett and Ruiz 1993, Hax and Golladay 1993, 1998). Submersed woody debris is especially important in sandy, silt-bottomed streams and rivers of the Southeastern Coastal Plain of the United States, where it provides the only available stable attachment sites for filter-feeding aquatic invertebrates such as chironomid midges, hydropsychid caddisflies, and simuliid blackflies (Cudney and Wallace 1980, Benke et al. 1984, Smock et al. 1985, Benke 1998). In highly turbid desert rivers, free-floating driftwood is especially important in maintaining macroinvertebrate richness (Haden et al. 1999). As in upland forests, studies in rivers and streams suggest that decay class and condition of wood influences invertebrate colonization and composition patterns (O'Connor 199 1, Magoulick 1998). Chironomid midge larvae are often the most numerous invertebrates associated with woody debris in lotic habitats (Nilsen and Larimore 1973, Phillips and Kilambi 1994, Magoulick 1998).

Although much is known about invertebrate interactions with woody debris in forests, rivers, and streams, information about these interactions in forested wetlands is limited (Braccia and Batzer 1999). During wet periods, invertebrate densities on woody debris surfaces have been reported to range from 1,000 to 6,000 individuals/m^2 and can be influenced by depth in the water column and the length of the hydroperiod (Thorp et al. 1985, Gladden and Smock 1990, Golladay et al. 1997). Because wetlands experience wet and dry periods, woody debris in these systems can support both a terrestrial and aquatic fauna. In general, due to an emphasis on wet period collections, the terrestrial portion of the wetland fauna has been overlooked in past research (Batzer and Wissinger 1996, Leslie et al. 1997, Smock 1999).

The goal of this project was to study invertebrate associations with woody debris in a forested floodplain wetland of the Southeastern United States. Specific objectives were (1) to describe the aquatic and terrestrial invertebrate assemblages associated with woody debris during wet and dry periods and (2) to determine if position (floating or submersed) or decay state of woody debris influence invertebrate community structure.

MATERIALS AND METHODS

Study Site Description

This study was conducted in 1998 and 1999 at a forested floodplain wetland of the Coosawhatchie River, Jasper County, South Carolina, USA (32°33'N, 80°54'W). The Coosawhatchie River is a 4th order blackwater river that drains approximately 1000 km^2 of agricultural, forest, and wetland area of the Southeastern Coastal Plain (Burke and Eisenbies 2000). The floodplain is 1.6 km wide, and soils are classified in the Brookman series, having thick, black, loamy surface layers and dark gray, clayey subsoils (Burke and Eisenbies 2000). Average annual precipitation in the area ranges between 127 and 152 cm. The floodplain of the Coosawhatchie River typically floods in late winter and can remain flooded into the early summer, depending on rainfall patterns. It can also flood unpredictably in any season following spates. During 1998, an unusually wet year, the site was largely inundated from November through April. During 1999, a very dry year, the site was flooded from January until March and then only partially.

The Coosawhatchie floodplain is classified as a bottomland hardwood forest (Wharton et al. 1982, Sharitz and Mitsch 1993). Woody vegetation at the site includes sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sargent), water tupelo (*Nyssa aquatica* L.), cypress (*Taxodiurn distichum* (L.) Rich), and various oaks (*Quercus* spp.). Loblolly pine (*Pinus taeda* L.) plantations occur on surrounding uplands. Woody debris in the form of branches, twigs, logs, snags, standing dead trees, and stumps was abundant at the site. In 1997, Scheungrab et al. (2000) quantified woody debris volume at the site using the planar intersect method and reported that 26 m^3/ha existed. Of that volume, 49% was > 10 cm diameter and 51% was < 10 cm diameter.

Sample Collection

Woody debris and associated invertebrates were collected at the end of two wet periods (March 1998 and March 1999) and one dry period (August 1998). Collections were made at the end of wet or dry periods to ensure that invertebrates had sufficient time to colonize wood after it flooded or dried. At these times, animals unable to withstand stresses of wet or dry conditions would have been eliminated, leaving only individuals that were truly using the wood as a long-term resource. During each wet period, fifty pieces of woody debris (excluding coniferous wood) were collected at random locations along transects. Twenty-five of these samples, were collected from beneath the water's surface (submersed) and 25 were collected at the water's surface (floating). During the dry period, 25 pieces of woody debris were gathered from the floodplain floor. For large pieces, a net was placed over one end and the enclosed section cut with a handsaw. All samples were placed in plastic bags, preserved in 95% ethyl alcohol, and transferred to the laboratory for analysis.

Additionally, the invertebrate fauna was sampled during wet periods by sweep-netting the water column and bottom substrate. Sweep-net sampling is the most

Table 1. Wood decay classification system of Maser and Trappe (1984) as modified by Robison and Beschta (1990).

Decay Class	Bark	Color	Shape & Texture
Class 1	Attached tightly	Original	Round, no abrasions
Class 2	Attached loosely	Original	Round, no abrasions
Class 3	Absent	Original; some darkening	Round, smooth, no abrasions
Class 4	Absent	Dark	Round to oval, with abrasions
Class 5	Absent	Dark	Irregular, with many abrasions

commonly used method to describe invertebrate communities in wetlands during wet periods (Batzer and Shurtleff 2000). Invertebrate richness was compared between the sweep-net and woody debris collection methods in this study.

Sample Processing and Invertebrate Classification

Prior to removing invertebrates, each piece of wood was classified into one of five decay classes taken from Robison and Beschta (1990) (see Table 1). Wood volume was estimated from length and diameter using the formula for a cylinder. The contents of each sample bag and the outer area of wood were rinsed through a 300μm sieve. A small spatula was used to scrape the outer portion of each sample into the sieve to collect surface-burrowing invertebrates. Hard wood (usually decay class l-3) was split with a wedge to excavate wood-boring invertebrates. Simply scraping the surface of wood only yields 70% of the organisms and overlooks wood-borers and groups residing in internal grooves and cavities on the interior of the wood (unpublished data). For example, Acari, Cerambycidae larvae, Eucnemidae larvae, Elateridae larvae, some Chironomidae and Cecidomyiidae larvae, Diplopoda, Formicidae adults, and Aeshnidae pronymphs are largely missed by only sampling outer surfaces of wood.

All invertebrates were classified by order or family, but insects and macro-crustaceans were identified to genus if possible. Identifications were made using keys in Peterson (1960), Amett (1968), Borror et al. (1989), Pennak (1989), Dindal (1990), Stehr (1991), Thorp and Covich (1991), Merritt and Cummins (1996), and Epler (1995). Individuals were classified as being either aquatic or non-aquatic based on the above-listed literature. Invertebrate density was expressed as number of individuals/m^3 woody debris. Dry mass and surface area of wood were also calculated, but volume was the most relevant measure because wood was a three-dimensional habitat and in some cases contained a considerable amount of air or water that would not be reflected by mass measurement. During preliminary analyses, no correlation was found between invertebrate richness and woody debris size, indicating that a species-area relationship may not exist. Therefore, richness was expressed as numbers of taxa per sample, regardless of wood size. Standing-stock biomass was estimated by placing individuals into size classes and applying average size-class lengths to published length-mass regression models (Benke et al. 1999 for aquatics, Hodar 1996 for non-aquatics). Length-mass regressions were not available for several taxa. In these cases, a published regression for an invertebrate with similar body form was used as a substitute. Standing-stock biomass was expressed as g dry mass (DM)/m^3 woody debris.

Lengths could not be determined reliably for fragmented Oligocheata, and published length-mass regression equations for Nematoda, Planorbidae, and Pisididae were not available (suitable body-plan substitutes were also not available). Further, these organisms were either rare or very small and contributed little to overall invertebrate biomass. Therefore, non-arthropod groups were excluded from the standing-stock biomass analyses, and our biomass estimates are for arthropods only. Because length-mass conversion is poorly developed for wetland taxa, our biomass estimates should be used with caution. However, they remain useful for the comparisons made within this study.

Statistical Analyses

Sigma Stat v2.0 (SPSS 1997) was used for all statistical analyses. Pre-testing indicated that data were frequently not normally distributed, even after transformation. Therefore, non-parametric tests were used for analyses (Sokal and Rohlf 1995). Kruskal-Wallis One-Way Analysis of Variance (ANOVA) on Ranks followed by Dunn's Method post hoc test (SPSS 1997) was used to identify specific differences in richness, density, and biomass among wet and dry periods, and among woody debris decay classes. Wilcoxon Signed Rank Tests were used to contrast the aquatic versus non-aquatic fauna density and biomass on individual pieces of wood. A Mann-Whitney Rank-Sum Test was used to compare overall density, richness, and standing-stock biomass between wood positions (floating and submersed) during wet periods. Frequency of occurrence of individual taxa on wood between wet and dry periods and floating and submersed wood was contrasted using Chi-square Analysis. When fewer than five observations were expected in one or more cells, a Fisher Exact Test was used as an alternative to Chi-square analysis. We acknowledge that procedure-wise error might be introduced with multiple Chi-square analyses because the fauna of the Coosawhatchie floodplain was so diverse (75 taxa were analyzed). However, because of recent concerns about how Bonferroni adjustments should be used (Pemeger 1998), the critical value in this study was not adjusted from $\alpha = 0.05$. For every analysis, the associated p-values are reported if readers desire to make adjustments.

RESULTS

Woody Debris Characteristics

Most of the pieces of wood collected during this study were <5 cm dia (Figure 1A). All five decay classes were represented, with decay classes 2 and 4 being most common (Figure 1B).

Overall Invertebrate Community Structure

A total of 110 aquatic, semi-aquatic, and terrestrial invertebrate taxa (orders, families, genera) were identified from the 125 pieces of wood (Table 2). Coleoptera and Diptera were the most taxonomically diverse groups, and Acari and Chironomidae were the most abundant. In terms of biomass (arthropod only), Chilopoda by themselves contributed 47%, while Megaloptera, non-aquatic Coleoptera, and Aranea together contributed another 22%. Overall density averaged about 733,000 individuals/m wood, and standing-stock biomass (arthropod only) averaged 182 g DM/m^3 wood. Extrapolating invertebrate density and biomass in woody debris to the Coosawhatchie floodplain (based on 26 m^3 woody debris/ha; Scheungrab et al. 2000) resulted in an average of about 19,000,000 individuals/ha, while arthropod standing-stock biomass averaged 4,700 g DM/ha.

Sweep-netting of the water column and benthic substrate yielded only 22 taxa (Chironomidae genera were not determined from these samples) (Table 2). Chironomidae, Gastropoda, Isopoda, Amphipoda, and Simuliidae were the numerically dominant groups in these samples. Terrestrial and semi-aquatic organisms were rarely collected. Only two groups, a baetid mayfly and cladocerans, were found in sweep-net samples but not on wood.

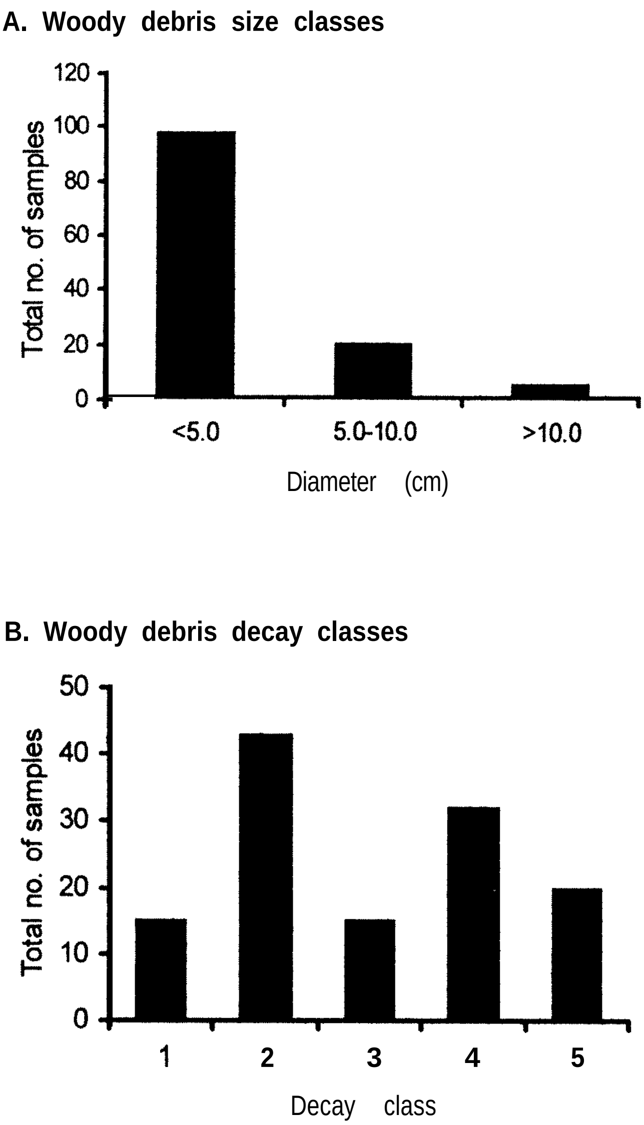

Figure 1. Woody debris characteristics. (A) Woody debris samples (n= 125) separated by diameter size class (cm). (B) Woody debris samples (n=125) separated by decay Class 1 through 5.

Temporal Variation

Neither invertebrate richness nor overall density on wood differed significantly among the two wet and one dry periods (Figure 2A and B). As expected, the density of non-aquatic invertebrates was greater during the dry period than the two wet periods, while the density of aquatic invertebrates was greater on woody debris during the two wet periods (Figure 3A). During each wet period, non-aquatic and aquatic invertebrate density was similar (Figure 3A). However, on wood from the dry period, non-aquatic invertebrates were more abundant than aquatic invertebrates.

Overall arthropod biomass was greater during the 1998 wet period than either the dry period or the 1999

Table 2. Taxa list and frequency of occurrence of invertebrates associated with woody debris at the Coosawhatchie floodplain study area. Frequencies = no. of woody debris samples with taxon present/total no. of woody debris samples x 100 (submersed n = 50, floating n = 50, dry n = 25). Taxa that were more prevalent during the wet or dry period are indicated with superscripts w (wet) or d (dry). If a taxon was most prevalent on submersed or floating woody debris, its preference is indicated with an asterisk *. These differences in frequency were tested using Chi-square analyses. A superscript (s) is used to indicate taxa also collected by sweep-netting the water column and bottom substrate; however, sweep-net data were not used in calculations of the percent occurrence on woody debris. (A = adults; L = larva; N = nymph; PN = pronymph).

Group	Wet Periods		Dry
	Submersed	Floating	Dry Period
NON-ARTHROPODA			
Nematoda	70*	28	64
Oligochaeta[d,s]	76	60	92
Bivalvia			
Pisididae[d,s]	2	0	24
Gastropoda			
Planorbidae[d,s]	8	14	44
Planorbula			
ARTHROPODA			
Crustacea			
Copepoda[w,s]	22	50”	8
Amphipoda[w,s]	14	46*	0
Crangonyctidae			
Crangonyx			
Isopoda			
Oniscidae	0	0	4
Porcellio			
Asellidae	12	16	0
Caecidotea[s]			
Lirceus[s]			
Decapoda’	0	2	0
Arachnida			
Acari[s]	92	94	92
Mesostigmata			
Prostigmata			
Oribatida			
Euphthiracaridae			
Phthiracaridae			
Hermanniellidae			
Unknown family			
Aranea[w]	4	50*	4
Pseudoscorpiones	6	6	4
Opiliones	0	4	0

Table 2. Continued.

Group	Wet Periods		Dry
	Submersed	Floating	Dry Period
Myriapoda			
Chilopoda”	4	48*	4
Geophilomorpha			
Diplopoda[w,s]	8	32*	0
Hexapoda			
Collembola	24	40	48
Entomobryidae			
Hypogastruridae			
Oncychiuridae			
Poduridae[s]			
Sminthuridae			
Odonata			
Aeshnidae (PN)[d]	0	0	12
Plecoptera			
Perlidae	0	2	0
Perlesta			
Orthoptera			
Tetrigidae	2	2	0
Hemiptera			
Belostomatidae	0	2	0
Belostoma			
Unknown family (N)	0	18*	16
Thysanoptera	4	40*	4
Embioptera	0	4	0
Psocoptera	0	4	0
Isoptera	0	2	0
Megaloptera			
Corydalidae (L)	0	10”	0
Chauliodes			
Coleoptera			
Buprestidae (L)	0	2	0
Carabidae (A)	4	34*	16
Cerambycidae (L)	8	10	0
Chrysomelidae (A)	0	4	0
Curculionidae (A)	4	10	0
Dytiscidae (L)	12	24	4
Hydroporus[s]			
Eretes			
Dytiscidae (A)	0	6	0
Elateridae (L)	4	6	12
Alaus			
Ampedus			
Athous			
Melanotus			
Elateridae (A)	0	0	4
Eucnemidae (L)	10	10	12
Fomax			

Table 2. Continued.

Group	Wet Periods		Dry Period
	Sub-mersed	Floating	
Gyrinidae (L)	4	0	0
Gyrinus			
Hydraenidae (A)	4	28*	0
Hydraena			
Hydrophilidae (L)	0	20*	0
Enochrus			
Helocombus			
Hydrobius			
Hydrophilidae (A)	0	8	0
Hydrobius			
Hydrochus			
Tropisternus			
Helocombus			
Lampyridae (L)	12	8	16
Photirus			
Melandryidae (L)	10*	0	0
Nitidulidae (A)	0	12*	0
Noteridae (A)	8	6	0
Notomicrus			
Phengodidae (L)	0	6	0
Phengodes			
Pselaphidae (A)[d]	2	12	28
Scarabaeidae (A)	0	10*	0
Scirtidae (L)	4	8	0
Elodes			
Cyphon			
Scolytidae (A)	4	2	0
Scolytidae/Curculionidae (L)	4	12	4
Scydmaenidae (A)	0	6	0
Staphylinidae (L)	2	12	20
Staphylinidae (A)	4	36*	16
Tenebrionidae (L)	0	2	0
Unknown family (L)[d]	2	4	16
Unknown family (A)	4	18	8
Diptera (L)			
Asilidae	4	2	0
Laphria			
Cecidomyiidae	46	50	56
Ceratopogonidae	26	28	16
Ceratopogoninae[s]			
Forcipomyia			
Chironomidae[s]	84	82	60
Tanypodinae			
Unknown genera			
Orthocladinae			
Unniella			
Nanocladius			
Unknown genera			
Chironominae			
Microspectra			
Tanytarsus			
Phaenospectra/Tribelos			
Polypedilum			
Dicrotendipes			
Stenochironomus			
Parachironomus			
Unknown genera			
Culcidae[s]	0	6	0
Dolichopodidae[d]	6	12	28
Psychodidae	0	4	0
Psychoda			
Sciaridae	6	18	28
Simuliidae[w,s]	22	16	0
Simulium			
Syrphidae	0	2	0
Xylota			
Tabanidae	6	18	4
Chrysops/Tabanus			
Tipulidae	6	8	0
Hexatoma			
Tipula			
Unkown family‘	20	18	8
Lepidoptera (L)			
Pyralidae	2	20*	8
Noctuidae			
Tiichoptera (L)			
Limnephilidae	0	2	0
Ironoquia[s]			
Hymenoptera			
Bethyliidae (A)	0	2	0
Dissomphalus			
Formicidae (A)	2	26*	4
Unknown family (A)	2	2	0
Unknown family (L)	0	2	0

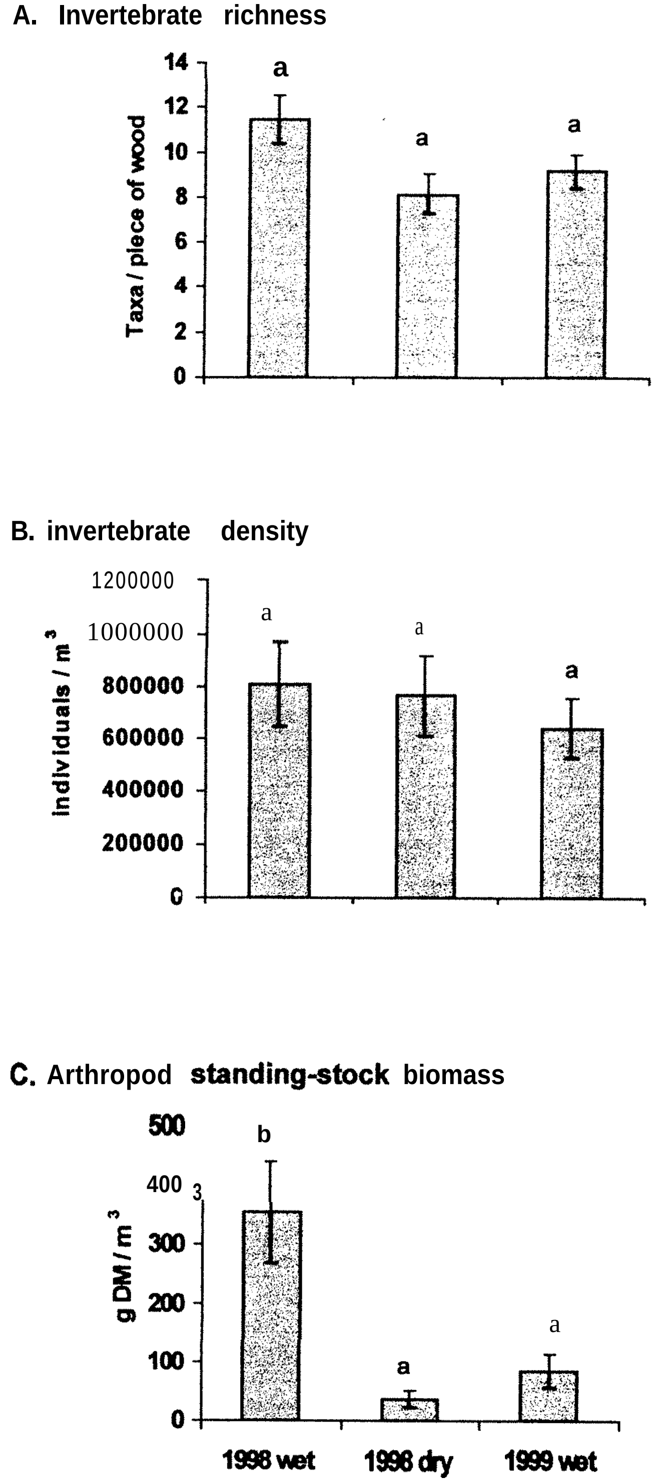

Figure 2. (A) Invertebrate taxa richness (number of distinct taxa/piece of wood), (B) density (individuals/m³), and (C) arthropod standing-stock biomass (g DM/m³) during the 1998 wet period (n = 50), 1998 dry period (n = 25), and 1999 wet period (n = 50) (error bars = ±1 SE). There was significant variation in arthropod standing-stock biomass on woody debris among periods (Kruskal-Wallis One Way Analysis of Variance on Ranks, p <0.001), but neither in- ← vertebrate richness nor density differed among periods (Kruskal-Wallis One Way Analysis of Variance on Ranks, p >0.05). Bars indicated by the same letter do not differ significantly (Dunn's Method post hoc test, p <0.05).

wet period (Figure 2C). Surprisingly, it was non-aquatic (Chilopoda, Diplopoda, Aranea, Carabidae adults, and Eucnemidae larvae) rather than aquatic arthropods that dominated the biomass on wood during that wet period (Figure 3B). Biomass during the 1998 dry period, although relatively low, was also dominated by non-aquatic arthropods (Figure 3B). However, aquatic Aeshnidae pronymphs still contributed 26% of the biomass in wood during the dry period. On wood collected during the 1999 wet period, aquatic and non-aquatic biomass was similar (Figure 3B).

In terms of individual groups, most taxa occurred with equal frequency on wet or dry wood (Table 2). However, Copepoda (p = 0.013), Amphipoda (p = 0.004), Simuliidae larvae (p <0.001), Aranea (p = 0.028), Diplopoda (p = 0.033), and Chilopoda (p = 0.034) were collected most frequently from woody debris during wet periods, while Pisididae (p <0.001), Planorbidae (p <0.001), Aeshnidae pronymphs (p = 0.006), Oligochaeta (p = 0.031), Pselaphidae adults (p = 0.009), and Dolichopodidae larvae (p = 0.027) were collected more frequently during the dry period (Table 2). Note that certain non-aquatic groups (spiders, millipedes, centipedes) occurred most frequently in wood during wet periods, and certain aquatic groups (mollusks, dragonfly pronymphs) occurred most frequently in wood during the dry period. Between the two wet periods, Simuliidae (p <0.001), Chilopoda (p = 0.003), and Cambidae (p = 0.041) occurred most frequently on wood during the 1998 wet period; no taxa occurred on wood more frequently in the 1999 wet period.

Submersed vs. Floating Woody Debris

Floating woody debris supported a richer fauna than submersed wood (Figure 4A). However, overall invertebrate density did not differ significantly between submersed and floating woody debris (Figure 4B), and aquatic and non-aquatic invertebrates were equally abundant on submersed and floating woody debris (Figure 5A). In submersed woody debris, there were significantly more non-aquatic than aquatic invertebrates, but both groups were equally represented in floating woody debris (Figure 5A).

Overall arthropod standing-stock biomass was greater on floating than submersed woody debris (Figure 4C). Both aquatic and non-aquatic arthropods contributed to the differences, as the biomass of each group was greater

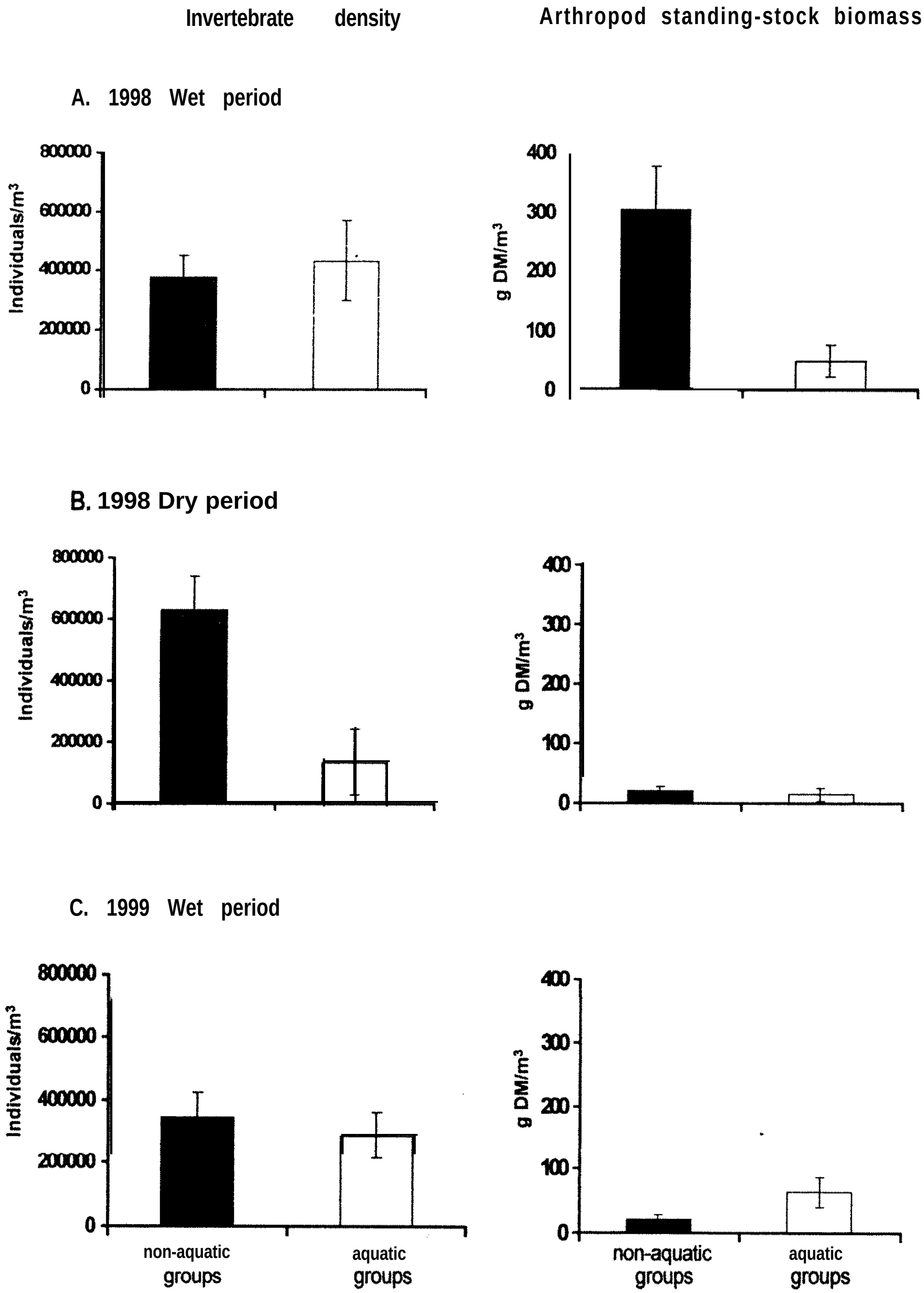

Figure 3. Non-aquatic and aquatic invertebrate density (individuals/m") and arthropod standing-stock biomass (g DM/m³) in the (A) 1998 wet period (n=50), (B) 1998 dry period (n=50), and (C) 1999 wet period (n=50) on woody debris (error bars = ± 1 SE). During both wet periods non-aquatic and aquatic invertebrate density was similar (Wilcoxon Signed Rank Test, $p > 0.05$). However, during the dry period, significantly more non-aquatic than aquatic invertebrates were associated with woody debris ($p < 0.001$). Non-aquatic arthropod biomass was greater than aquatic arthropod biomass during both the 1998 wet period ($p < 0.001$) and dry period ($p = 0.003$). Aquatic and non-aquatic arthropod biomass were similar during the 1999 wet period. Among time periods, aquatic invertebrate density was greater on woody debris during the wet periods than the dry period (Kruskal-Wallis One-Way ANOVA on Ranks, $p < 0.001$, followed by Dunn's post-hoc tests, $p < 0.05$), and non-aquatic invertebrate density was greatest during the dry period ($p = 0.010$). Non-aquatic arthropod biomass was significantly greater during the 1998 wet period ($p < 0.001$) than either the 1998 dry or 1999 wet period, which did not differ ($p > 0.05$). Aquatic arthropod biomass was similar in both wet periods ($p > 0.05$) but lower during the dry period ($p < 0.001$).

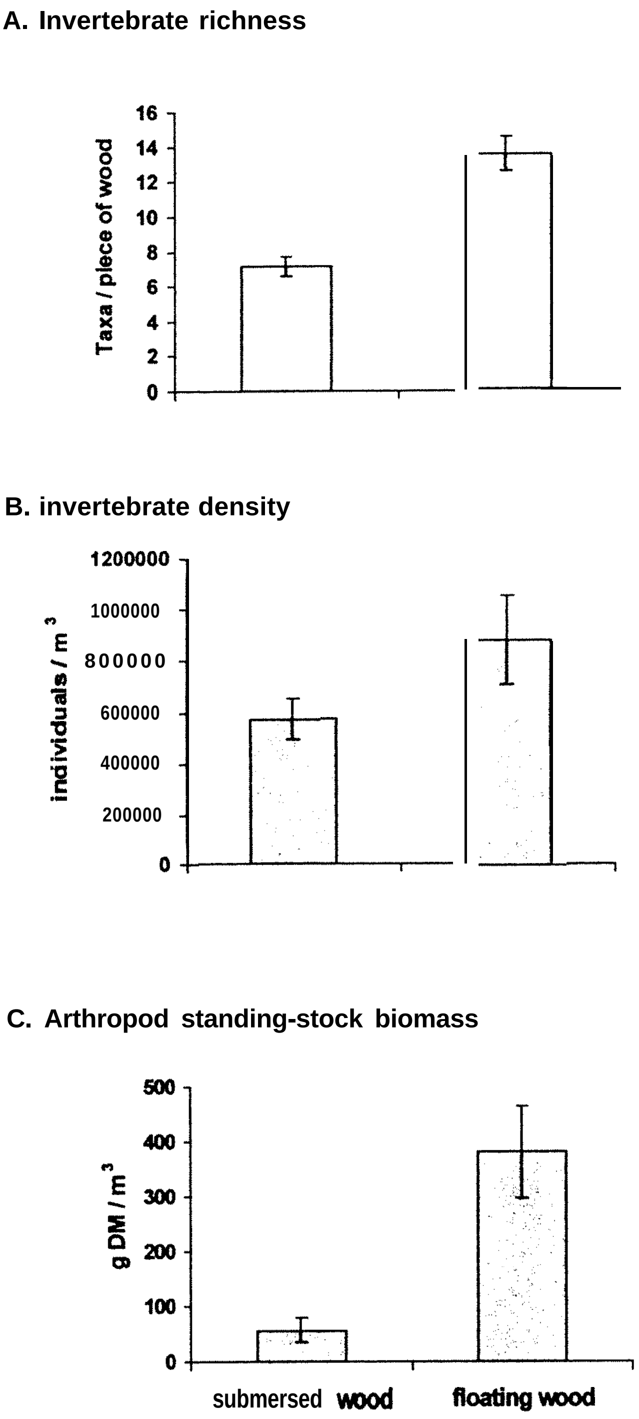

Figure 4. (A) Invertebrate taxa richness (number of distinct families/piece of wood), (B) density (individuals/m’), and (C) arthropod standing stock biomass (g DM/m^3) between submersed (n = 50) and floating (n = 50) woody debris (error bars = ±1 SE). Mann-Whitney Rank Sum Test indicated significant differences in invertebrate richness ($p < 0.001$) and arthropod standing-stock biomass ($p < 0.001$), but not density ($p > 0.05$), between submersed and floating woody debris.

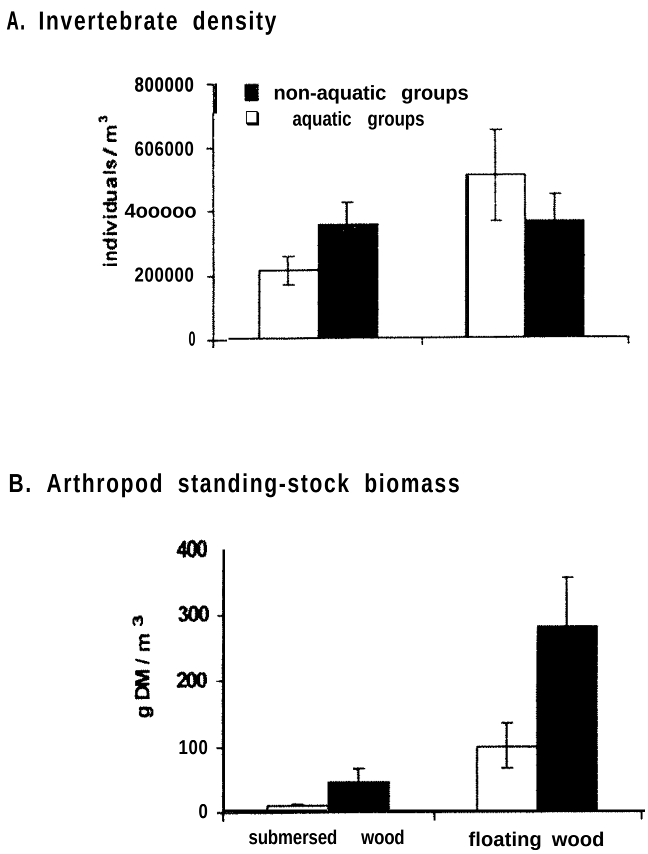

Figure 5. Nonaquatic and aquatic (A) invertebrate density (individuals/m’) and (B) arthropod standing-stock biomass (g DM/m^3) in submersed (n = 50) and floating (n = 50) woody debris (error bars = ± 1 SE). Both aquatic and non-aquatic invertebrate density was similar on submersed and floating woody debris (Mann-Whitney Rank Sum Test, both $p > 0.05$). However, floating woody debris had greater aquatic and non-aquatic arthropod biomass than submersed woody debris (both $p < 0.001$). In submersed woody debris only, non-aquatic invertebrate density was greater than aquatic density (Wilcoxon Signed Rank Test, $p = 0.013$), but in floating wood, non-aquatic and aquatic density was similar ($p > 0.05$). In both submersed and floating woody debris, aquatic and non-aquatic arthropod biomass was similar (Wilcoxon Signed Rank Test, both $p > 0.05$).

on floating than submersed woody debris (Figure 5B). However, within submersed or floating woody debris, non-aquatic and aquatic arthropod biomass did not differ significantly (Figure 5B).

Most taxa, whether they were aquatic or non-aquatic, occurred with equal frequency on submersed or floating wood (Table 2). However, Copepoda ($p = 0.007$), Amphipoda ($p = 0.001$), Cotydalidae larvae ($p = 0.028$), Hydrophilidae larvae ($p = 0.003$), Hydraenidae adults ($p = 0.003$), Aranea ($p < 0.001$), Diplopoda ($p = 0.006$), Chilopoda ($p < 0.001$), Thysanoptera ($p < 0.001$), Carabidae adults ($p < 0.001$), Staphylinidae adults ($p < 0.001$), Nitidulidae adults ($p = 0.013$). Scarabaeidae adults ($p = 0.028$), Lepidoptera ($p = 0.01$ I), and Formicidae adults ($p = 0.002$) occurred more frequently on floating woody debris. Only Nematoda ($p < 0.001$) and Melandryidae larvae ($p = 0.028$) occurred more frequently on submersed woody debris (Table 2).

Invertebrates and Woody Debris Decay Class

Invertebrate richness increased as wood decayed (Figure 6A). Decay class 4 supported significantly more arthropod biomass than Class 2; otherwise, biomass was similar among all other decay classes (Figure 6C). Invertebrate density was similar among all decay classes (Figure 6B).

DISCUSSION

Invertebrate Assemblages Associated with Woody Debris During Wet and Dry Periods

A diverse community of aquatic, wetland, and terrestrial invertebrates was associated with woody debris at the Coosawhatchie floodplain. Simuliid blackflies, midge larvae, semi-aquatic beetles, wood-boring beetles, and predaceous carabids, centipedes, and spiders were all using wood simultaneously. Invertebrate assemblages on wetland woody debris are unique from those on wood in upland forests, where only terrestrial organisms exist, or rivers, where mostly aquatic organisms exist. Furthermore, woody debris is a unique sub-habitat of forested wetlands; not including Chironomidae genera, 96 invertebrate taxa were collected from woody debris, but only 22 taxa were collected by sweep-netting the water column and bottom substrate. If total diversity of forested wetlands is to be described, wood-associated organisms need to be considered.

Whether wood was wet or dry, floating or submersed, classifying the associated fauna from only an aquatic or terrestrial perspective was inappropriate. It was more informative to describe the fauna associated with wood by when and how the resource was used. Based on seasonal patterns, wood-associated invertebrates in this study were classified into three groups:

(1) perennial inhabitants, which were associated with wood year-round;
(2) seasonal colonizers, which were either aquatic invertebrates that used wood only during flooded periods or terrestrial invertebrates that only used wood during dry periods; and
(3) seasonal refugees, which were either aquatic invertebrates that mostly used wood in dry periods or terrestrial invertebrates that mostly used wood during wet periods.

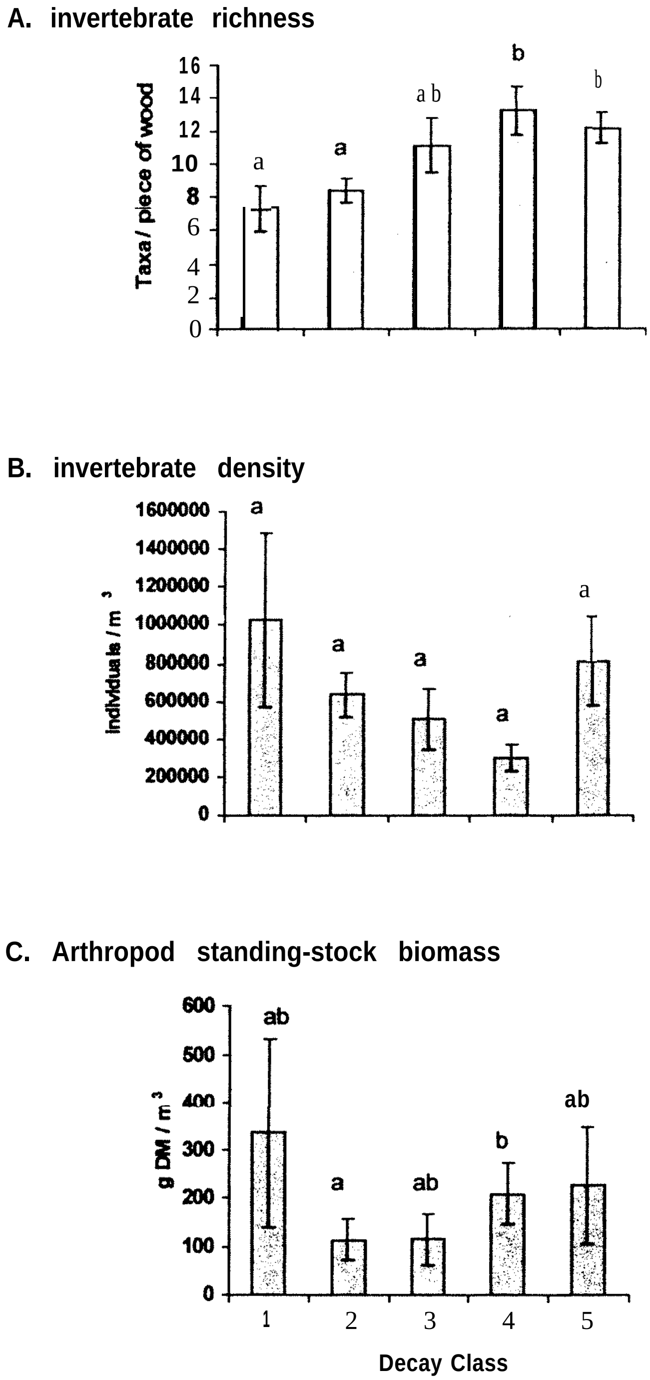

Figure 6. (A) Invertebrate taxa richness (number of distinct taxa/piece of wood), (B) density (individuals/m)), and (C) arthropod standing stock biomass (g DM/m^3) among woody debris Decay Classes 1 through 5 (error bars = ±1 SE). Kruskal-Wallis One-Way Analysis of Variance on Ranks indicated significant variation in richness and biomass among decay classes. Decay classes with the same letters are not significantly different (Dunn's Method post-hoc test, $p < 0.05$).

Perennial Inhabitants. Frequencies of perennial inhabitants in wood were neither dependent on flooding regime nor whether wood was floating or submersed. These organisms were always associated with wood. In this study, the most common perennial inhabitants included mites and wood-boring beetle larvae (Elateridae, Eucnemidae, Scolytidae/Curculionidae) (Table 2). The family Chironomidae also occurred year-round, but the genera varied seasonally. For example, *Stenochit-onomus* was found only during dry periods, while *Polypedilum* and *Dicrotendipes* were found only on wood during wet periods. Many feed directly on wood or on wood-associated fungi (Swift 1977, Hanula 1993). During flooding, terrestrial forms may enter diapause. Adis (1987) found that the terrestrial beetle larva, Oedemeridae, persisted in a quiescent stage in submersed wood in a flooded Amazonian floodplain forest.

Although the impact of invertebrates on floodplain wood decomposition has yet to be established, perennial-inhabitants are the invertebrates most likely to contribute significantly to wood decomposition. They are the organisms with long-term and intimate associations with wood. It is noteworthy that termites, which are very important to decomposition processes in upland forests, were rare in woody debris of the Coosawhatchie floodplain (Table 2).

Seasonal Colonizers. Aquatic invertebrates using woody debris exclusively during the wet period included Amphipoda and Simuliidae (Table 2). Others that probably fit this classification include Asellidae, Noteridae adults, Hydrophilidae, Scirtidae larvae, and Tipulidae. They occurred only in wet wood but were not sufficiently widespread in wood for statistical analyses to indicate significance (Table 2). These invertebrates were probably feeding on wood-associated biofilms (Couch and Meyer 1992) or other invertebrates residing on woody debris, or they were using wood as substrate from which to filter-feed. Non-aquatic invertebrates that used wood exclusively in the dry period were Pselaphidae beetle adults and Dolichopodidae larvae.

The community of aquatic seasonal-colonizers on woody debris varied from year to year depending on the nature of flooding. In 1998 when flow was high and conditions were lotic, some seasonal-colonizers such as black-fly larvae were of a riverine origin. In 1999, when minimal flow existed on the floodplain and conditions were lentic, riverine taxa were absent. This change probably developed because stagnant conditions in 1999 eliminated some taxa. Decreased oxygen concentrations may also explain the greater biomass of aquatic arthropods on floating than submersed wood (Figure 5). Golladay et al. (1997) suggest that the soil-water interface becomes stagnant and anaerobic during extended inundation, causing benthic invertebrates to become oxygen-stressed. Aquatic invertebrates probably migrate to wood near the surface where dissolved oxygen levels are higher. Wood near the water's surface often supports greater invertebrate density and richness than wood resting on the bottom (Nilsen and Larimore 1973, Golladay et al. 1997).

Seasonal Refugees. Greater frequency of aquatic Aeshnidae pronymphs and Pisididae clams on wood during the dry period and terrestrial millipedes, centipedes, and spiders on wood during the wet period suggests that these groups used wood primarily as refugia. Aquatic invertebrates have developed numerous life-history strategies for tolerating dry conditions (Wiggins et al. 1980, Williams 1996). Because wood remains moist after surface waters recede, it provides attractive oviposition and refuge sites for aquatic organisms (Triska and Cromack 1980). Curiously, the aeshnids in dry wood were either aestivating as pronymphs or else hatched in wood before inundation.

While dry conditions stress aquatic invertebrates, terrestrial organisms in wetlands are stressed by flooding. It is now becoming apparent that many non-aquatic wetland invertebrates have developed strategies to withstand flooded periods (Adis 1992, Adis et al. 1997b, Vohland and Adis 1999). Soil-dwelling arthropods from Amazonian floodplain forests undergo vertical migrations that are signaled by changes in humidity and air temperature (Adis 1986, Adis 1990, Nakao and Kitayama 1995, de Morais et al. 1997, Golovatch and Adis 1998). In this study, the greater frequency of soil-dwelling arthropods on woody debris during the wet period than the dry period suggests that invertebrates of the Coosawhatchie floodplain migrate onto woody debris as soils flood. Although non-aquatic invertebrate frequencies were highest on floating woody debris, submersed wood still supported many non-aquatics, including Acari, Pseudoscorpiones, Diplopoda, wood-boring Coleoptera, and in one instance, Formicidae. Most of these animals probably exploited pockets of air inside the wood. However, when water is well oxygenated, some millipedes can withstand floods by plastron respiration formed by microtrichia around the spiracles (Adis et al. 1997a). In 1998 when lotic conditions prevailed at the Coosawhatchie, some conventionally terrestrial organisms might have been able to persist in the water itself. During relatively dry years, terrestrial invertebrates might not need floating woody debris as refugia. In 1999, much of the floodplain area did not flood and remained available for terrestrial arthropods to exploit. That year, little terrestrial arthropod biomass accumulated on wood.

It is very likely that many of the terrestrial animals remained active on floating wood debris. If so, predatory spiders, centipedes, and carabids probably were feeding, and trophic interactions among invertebrates might have developed between aquatic and non-aquatic taxa. It has been reported that 70–90% of the diet of predaceous riparian beetles consists of aquatic organisms (Hering and Plachter 1997, Hering 1998). Further, it is reported that Carabidae adults can dive and forage below the water's surface (Adis 1982, Arens and Bauer 1987). On floating woody debris at the Coosawhatchie, Simuliidae and Chironomidae densities were very low on woody debris whenever carabid beetles and/or centipedes were present (analyses not presented).

Influence of Wood Condition on Invertebrate Community Structure

Floating woody debris was a "hot-spot" for invertebrate richness and arthropod biomass, both aquatic and non-aquatic (Figures 4 and 5). While submersed and dry wood contained mostly perennial inhabitants and seasonal colonizers, floating wood supported as many or more of these organisms, plus a large biomass of seasonal refugees. Floating wood is likely an important resource for maintaining invertebrate populations during floods.

There was little evidence that invertebrate density or biomass was affected by woody debris decay class. Those animals that use wood as refugia may simply take what is readily available when harsh conditions develop, regardless of wood condition. If so, patterns in density and biomass on wood would not be based upon resource condition. Alternatively, lack of patterns may be an artifact of the decay classification system used in this study (a system developed for streams). Wood in wetlands decays differently than wood in streams and rivers. Oftentimes, well-decayed wood in Decay Class 4 or 5 had bark, a characteristic of Decay Class 1 or 2 (Table 1). In upland forests, variation within individual decay classes is already recognized as important in detecting wood's value as a resource (Pyle and Brown 1999). A new method of classifying woody debris might have to be developed specifically for wetland systems to understand relationships between invertebrates and wood condition. Finally, differences in source tree species at the Coosawhatchie rather than just decay state may have caused for some of the variation in invertebrate use of woody debris (Triska and Cromack 1980).

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