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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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Preface

James W. McMinn and D. A. Crossley, Jr.

Conservation of biodiversity is emerging as a major goal in the management of forest ecosystems. The implied objective is the conservation of a full complement of native species and communities within the forest ecosystem. Effective implementation of conservation measures will require a broader knowledge of the dimensions of biodiversity, the contributions of various ecosystem components to those dimensions, and the impact of management practices.

In a workshop held in Athens, GA, October 18-20, 1993, we focused on an ecosystem component, coarse woody debris (CWD), and its impact on the biodiversity of organisms in southern forests. Coarse woody debris is one ecosystem element readily amenable to management. The generation of CWD, its accumulation on forest floors, and its distribution are functions of stand age and management in the South. In contrast to other regions, comparatively little is known about the importance of CWD in southern forests. Harmon and others (1986) addressed CWD dynamics, input, distribution, and importance for forested ecosystems in general and North America in particular. In that review the dearth of information on CWD in southern forests, especially southern pine forests, was evident. Conclusions about the impacts and of CWD based on experience in the pacific Northwest are unlikely to be appropriate for southern forests, because climate, growth responses, CWD production and decomposition, and management practices are dissimilar.

Biodiversity is a multidimensional concept for which many definitions have been proposed. Concepts include some aspect of preservation of diversity at the species level, while acknowledging the need for preserving intraspecific genetic diversity (Faulk 1990). Wilson (1988) eloquently presented the need to preserve species richness, while documenting the worldwide decline in numbers of species. Ehrlich (1988) and Franklin (1988) have argued for habitat preservation in contrast to the individual endangered species approach. Solbrig (1991) introduced a hierarchical view of biodiversity, ranging from molecular to genetic components and species, to communities, to ecosystems.

The effects of CWD on biodiversity depend upon harvesting variables, distribution, and dynamics. This proceedings addresses the current state of knowledge about the influences of CWD on the biodiversity of various groups of biota. Research priorities are identified for future studies that should provide a basis for the conservation of biodiversity when interacting with appropriate management techniques.

We thank John Blake, USDA Forest Service, Savannah River Forest Station, for encouragement and support throughout the workshop process. The success of the workshop is due in large part to the meticulous attention provided by Janice Sand, Institute of Ecology, University of Georgia, Athens, GA.

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Contents

Accumulations of Coarse Woody Debris in Southern Forests

James W. McMinn and Richard A. Hardt

Abstract

Accumulations of coarse woody debris (CWD) were estimated from Forest Inventory and Analysis information for Georgia and South Carolina and from the literature covering detailed studies. Mean accumulations by broad ownership class and forest type for Georgia and South Carolina ranged from 2.2 to 10.7 mega grams per hectare (Mg/ha). Accumulations in individual studies ranged from 0.4 Mg/ha in mature pitch pine on poor sites to 91.2 Mg/ha in young cove hardwoods regenerated by clearcutting. The information presented in this review suggests that attempts to quantify CWD accumulations should account for physiography, ownership, forest type, stand age, stand origin (artificial vs. natural), and disturbance.

Introduction

In this paper are presented estimates of the accumulations of coarse woody debris (CWD) in southern forests from two perspectives. The first, a broad overview is derived from information in Forest Inventory and Analysis (FIA) publications. The second is from the literature covering more detailed studies of CWD on a small scale.

The Broad Perspective

Coarse woody debris as such is not inventoried in the periodic surveys conducted by USDA Forest Service FIA (formerly known as "Forest Survey") units. However, in each survey, mortality is estimated for trees that are at least 12.7 cm in diameter at breast height (d.b.h.). The mortality is reported as annual volume by various strata. Publications with compatible information for estimating recruitment and standing crop were limited to Georgia and South Carolina. Compatible volume and area information was available for three broad ownership classes and five broad forest types in those two States (Anderson and others 1990; Brantley and others 1993; Tansey 1987; Thompson 1989). Ownership classes were public, nonindustrial private forest lands (NIPF), and forest industry. Broad forest types (called "broad management classes" in FIA publications) were pine plantation, natural pine, oak-pine, upland hardwood, and lowland hardwood. The published data consisted of total volumes for all species within each combination of ownership class and forest type.

Volumes were converted to mass using an overall average (0.525) of wood-specific gravities reported for Southern species (Koch 1972, 1985). Standing crop mass was derived using the single exponential decay model with a k-value of 0.075; this value was derived from loblolly pine data in the Piedmont of South Carolina (Barber and Van Lear 1984). (This was the only exponential decay model found in the literature for the geographic area of interest.) Based on the descriptions by Barber and Van Lear (1984) and FIA personnel,[1] standing crop volume was assumed to be 15 times the annual recruitment. However, all values were considered low because all age classes with trees meeting the minimum diameter limit were included in these average estimates.

Mean CWD accumulations by ownership and state ranged from 4.1 mega grams per hectare (Mg/ha) on forest industry land in South Carolina to 7.7 Mg/ha on public lands in South Carolina (table 1). Accumulations were lower on forest industry land than on public or nonindustrial private lands, and higher in South Carolina than in Georgia on public and NIPF. Lower mortality would generally be expected on forest industry land because the average stand age is lower and the proportion of pine plantations is higher. (The latter generally exhibit lower mortality from intraspecific competition because initial density is controlled.) This explanation is supported by the relatively low accumulations for pine plantations (2.3 Mg/ha and 3.5 Mg/ha in Georgia and South Carolina, respectively) compared to other forest types when averaged over all ownerships (table 2). Natural pine and lowland hardwood types exhibited the highest accumulations (> 8 Mg/ha), while the oak-pine and upland hardwood types exhibited intermediate accumulations.

Relative accumulations among the forest types were similar for the two States when averaged over all ownerships, but were dissimilar when broken out by ownership class. On

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[1] Personal communication. 1993. Noel Cost, Project Leader, Southeastern Forest Experiment Station, P.O. Box 2680, Asheville, NC 28802.

Table 1—Estimated mass and volume of coarse woody debris over all forest management classes by ownership and State

	Mass		Volume	
Ownership	Annual input	Standing crop	Annual input	Standing crop
	- - - - Mg/ha - - -		*- - - m^3/ha - - -*	
		Georgia		
Public	0.410	5.667	0.781	11.715
NIPF*	0.478	6.607	0.911	13.665
Forest industry	0.327	4.520	0.622	9.330
		South Carolina		
Public	0.555	7.672	1.057	15.855
NIPF*	0.551	7.616	1.050	15.750
Forest industry	0.300	4.147	0.570	8.550

*Nonindustrial private forest land.

public lands in Georgia, the upland hardwood type exhibited the lowest accumulations at 2.2 Mg/ha; pine plantation and oak-pine accumulations were somewhat higher; and natural pine and lowland hardwood accumulations were quite high (> 9 Mg/ha). In South Carolina, only the pine plantation type exhibited low accumulations while all other forest types had relatively high accumulations; lowland hardwood exhibited the highest accumulation at 10.7 Mg/ha (table 3). All data were collected prior to Hurricane Hugo. Patterns among types were more similar for the two States on NIPF, except for pine plantations in South Carolina where 5.7 Mg/ha accumulations were unusually high for the forest type (table 4). On forest industry lands, the relative pattern among types was generally similar for the two States; however, higher accumulations in the natural pine, oak-pine, and upland hardwood types were exhibited in Georgia than in South Carolina (table 5).

Table 2—Estimated mass and volume of coarse woody debris over all ownerships by broad forest management class and State

	Mass		Volume	
Forest type	Annual input	Standing crop	Annual input	Standing crop
	- - - - Mg/ha - - -		*- - - m^3/ha- - -*	
		Georgia		
Pine plantation	0.169	2.336	0.322	4.830
Natural pine	0.643	8.888	1.225	18.375
Oak-pine	0.344	4.755	0.656	9.840
Upland hardwood	0.386	5.336	0.736	11.040
Lowland hardwood	0.622	8.598	1.185	17.775
		South Carolina		
Pine plantation	0.254	3.511	0.484	7.260
Natural pine	0.612	8.460	1.165	17.475
Oak-pine	0.437	6.041	0.832	12.480
Upland hardwood	0.428	5.916	0.815	12.225
Lowland hardwood	0.635	8.778	1.209	18.135

Several parallels can be found between these values and those in a more rigorous study designed to estimate snag densities from FIA data in Florida (McComb and others 1986). In that study, snags (12.7-cm d.b.h. and 1.3-m tall) were more abundant (1) in oak-hickory and oak-tupelo-baldcypress than in longleaf or slash pine; (2) in natural stands than in pine plantations; (3) on public than on private lands; and (4) on stream margins and in deep swamps than on flatwoods, rolling uplands, and sandhills.

Detailed Studies

The more detailed studies define the CWD accumulations expected under different conditions at various stages of stand development. Accumulations of CWD—snags and logs—are quantified in the scientific literature by mass, volume, or the number of pieces per unit area. Commonly, accumulations have been reported by mass (Mg/ha) or volume (m^3/ha), and snags have been reported by number (no./ha).

Table 3—Estimated mass and volume of coarse woody debris on public land by broad forest management class and State

	Mass		Volume	
Forest type	Annual input	Standing crop	Annual input	Standing crop
	- - - - *Mg/ha* - - -		- - - m^3/ha - - -	
Georgia				
Pine plantation	0.275	3.801	0.524	7.860
Natural pine	0.670	9.261	1.275	19.125
Oak-pine	0.263	3.635	0.502	7.530
Upland hardwood	0.160	2.212	0.306	4.590
Lowland hardwood	0.665	9.192	1.267	19.005
South Carolina				
Pine plantation	0.177	2.447	0.337	5.055
Natural pine	0.617	8.529	1.176	17.640
Oak-pine	0.629	8.695	1.197	17.955
Upland hardwood	0.575	7.948	1.096	16.440
Lowland hardwood	0.773	10.685	1.057	15.855

Table 4—Estimated mass and volume of coarse woody debris on nonindustrial private land by broad forest type and State

	Mass		Volume	
Forest type	Annual input	Standing crop	Annual input	Standing crop
	- - - - *Mg/ha* - - -		- - - m^3/ha - - -	
Georgia				
Pine plantation	0.162	2.239	0.309	4.635
Natural pine	0.648	8.957	1.234	18.510
Oak-pine	0.372	5.142	0.708	10.620
Upland hardwood	0.413	5.709	0.787	11.805
Lowland hardwood	0.646	8.930	1.231	18.465
South Carolina				
Pine plantation	0.412	5.695	0.784	11.760
Natural pine	0.647	8.943	1.232	18.480
Oak-pine	0.464	6.414	0.884	13.260
Upland hardwood	0.448	6.193	0.854	12.810
Lowland hardwood	0.656	9.068	1.250	18.750

Harmon and others (1986) and Spies and others (1988) have postulated a U-shaped temporal pattern for logs following disturbance. High log inputs produced by disturbances, such as logging, fire, or insect attack, may result in a large accumulation in the subsequent young stand (Harmon 1980; Mattson and others 1987; Nicholas and White 1984; Smith 1991). This accumulation largely decays before inputs return to predisturbance levels, resulting in low densities of logs in maturing second-growth. Log accumulations slowly build with increasing inputs, eventually reaching moderate to high levels in old-growth stands (Harmon and others 1986; Hardt 1993; Muller and Liu 1991). However, log accumulations in young stands, dependent on the type of disturbance and stand history, are highly variable (Hardt 1993; Harmon and others 1986; Spies and others 1988). For example, short-rotation harvesting can result in low accumulations of CWD after several rotations (Gore and Patterson 1985; Spies and Cline 1988; Spies and others 1988).

Accumulations of logs in southern forests vary widely with forest type, stand age, and disturbance history (table 6). The greatest accumulations of logs (> 90 Mg/ha) are reported from stands immediately following disturbance (Mattson and others 1987; Smith 1991). The smallest accumulations of logs (as low as 0.4 Mg/ha) have been reported from maturing stands on low productivity sites (Harmon and others 1986; Smith 1991). Log masses reported for old-growth stands in the Southern Appalachians are generally higher than for younger stands, ranging from 17 Mg/ha for a beech stand in Kentucky (Muller and Liu 1991) to 29 Mg/ha for a beech-birch stand in Tennessee (Harmon and others 1986). These

Table 5—Estimated mass and volume of coarse woody debris on forest industry land by broad forest management class and State

	Mass		Volume	
Forest type	Annual input	Standing crop	Annual input	Standing crop
	- - - - *Mg/ha* - - -		- - - *m^3/ha* - - -	
		Georgia		
Pine plantation	0.170	2.350	0.324	4.860
Natural pine	0.600	8.294	1.143	17.145
Oak-pine	0.258	3.566	0.491	7.365
Upland hardwood	0.385	5.322	0.734	11.010
Lowland hardwood	0.553	7.644	1.053	15.795
		South Carolina		
Pine plantation	0.168	2.322	0.320	4.800
Natural pine	0.415	5.737	0.791	11.865
Oak-pine	0.183	2.530	0.348	5.220
Upland hardwood	0.158	2.184	0.302	4.530
Lowland hardwood	0.546	7.547	1.040	15.600

accumulations are comparable to masses reported from other Eastern old-growth stands (Gore 1986; Lang and Forman 1978; MacMillan 1981; Tyrrell 1991), but are an order of magnitude lower than log masses reported for the Douglas-fir region of the Pacific Northwest (Harmon and others 1986). In a review of log accumulations in temperate deciduous old-growth forests, Muller and Liu (1991) found higher accumulations in cool forests and speculated that higher accumulations resulted from slower decomposition rates. In contrast, Mattson and others (1987) found no significant relationship between elevation and log decay; however, the range in elevation may have been too small to substantially influence temperature.

Snag accumulations are presented in table 7. Snags are commonly reported by the number per unit area, in part because most snag studies are primarily related to animal habitat (Conner 1978; Harlow and Guynn 1983; McComb and Muller 1983; McComb and others 1986). Accumulations of snags may also follow the same U-shaped temporal pattern as logs where extremely high accumulations follow types of disturbance. However, the episodic nature of snag production may confound patterns of snag accumulations that are associated with forest type or stand condition. The effects of natural disturbances on snag production are highly variable. For example, insects and diseases that kill trees aboveground, such as southern pine beetle, balsam woolly adelgid, Dutch elm disease, and chestnut blight, produce high accumulations of snags (Harmon and others 1986; Smith 1991). On the other hand, diseases that attack trees at the base or belowground, such as root and heart rots, are more likely to create logs directly when weakened trees are windthrown (Harmon and others 1986; Matlack and others 1993).

Timber harvests generally leave stands with few snags (Carmichael and Guynn 1983; Dickson and others 1983; McComb and others 1986), but timber stand improvement that includes girdling may increase snag accumulations (Moriarty and McComb 1983). Regenerating stands may have high accumulations of small snags, a result of density-dependent tree mortality, but as the stands become older the accumulation of larger snags increases. Total snag densities may not differ between second-growth and old-growth stands, but the size distribution will shift. McComb and Muller (1983) reported no significant difference between the densities of snags in Appalachian old-growth and second-growth stands. However, in a survey of snag densities in the pine, pine-hardwood, and hardwood stands in Florida, McComb and others (1986) found that the density of snags (> 12.7-cm d.b.h.) increased as stand age increased. In the Southern Appalachians, Rosenberg and others (1988) found a greater density, basal area, and mean diameter of snags in old stands than in younger stands. Hardt (1993), also working in the Southern Appalachians, found significantly higher densities of large snags (>25-cm d.b.h.) in old-growth than in second-growth stands.

Conclusions

Accumulations of CWD in individual stands are quite variable and, in this review, range from 0.4 Mg/ha in mature pitch pine on poor sites to 91.2 Mg/ha in young cove hardwoods regenerated by clearcutting. However, the influence of some factors associated with ownership and forest type in Georgia and South Carolina is so strong that relatively large differences (2.2 to 10.7 Mg/ha) exist in mean accumulations. Generally, the information derived

Table 6—Log accumulations in some southern forest stands

Stand	Age	Lower diameter limit	Log mass	Log volume	Source
	Years	*cm*	*Mg/ha*	*m^3/ha*	
Cove hardwoods, mixed oak, oak-pine; North Carolina	0[a]	5	91.2	—	Mattson and others 1987
	1[a]	5	74.8	—	
	2[a]	5	53.1	—	
Sugar maple; Tennessee	—	10	7.95	—	Onega and Eickmeier 1991
Chestnut oak; Tennessee	40	7.5	11	—	Harmon 1980, as cited in Harmon and others 1986
Tulip-poplar; Tennessee	40	7.5	14	51	Harmon and others 1986
Pine; Tennessee	50+	7.5	7	~30	Harmon and others 1986
	50+	7.5	11	—	Harmon 1980, as cited in Harmon and others 1986
Pitch pine; North Carolina	~100	10	0.4	—	Smith 1991
	3[b]	10	32.7	—	
	8[b]	10	15.2	—	
	11[b]	10	12.7	—	
	16[b]	10	14.5	—	
Mixed oak; North Carolina	< 5	10	—	102	Petranka and others (unpublished manuscript)[c]
	5-39	10	—	63	
	40-79	10	—	65	
	80-119	10	—	82	
	>120	10	—	102	
Tulip-poplar; North Carolina	30	20	—	22.40	Hardt 1993
	30	20	—	91.55	
Cove hardwoods, mixed oak; North Carolina	70+	20	—	45.00	Hardt 1993
	70+	20	—	83.32	
White pine-white oak; South Carolina	200+	20	—	65.64	Hardt 1993
Sugar Maple; North Carolina	200+	20	—	86.17	Hardt 1993
Beech-birch; Tennessee	200+	7.5	29	82	Harmon and others 1986
Mixed-oak; Tennessee	200+	7.5	24	94	Harmon and others 1986
Chestnut oak; Tennessee	200+	7.5	21	132	Harmon and others 1986
Beech; Kentucky	200+	20	17.0	54.8	Muller and Liu 1991
Sugar maple; Kentucky	200+	20	27.1	63.8	Muller and Liu 1991
Chestnut oak-red maple; Kentucky	200+	20	27.1	78.9	Muller and Liu 1991

[a] Following clearcut harvest.

[b] Following southern pine beetle attack.

[c] Petranka, J.W. (and others). Effects of timber harvesting on low elevation populations of Southern Appalachian salamanders (unpublished manuscript).

Table 7—Snag accumulations in some southern forest stands

Stand	Age	Lower d.b.h. limit	Snag density	Snag mass	Snag volume	Source
	Years	*cm*	*No./ha*	*Mg/ha*	*M^3/ha*	
Pine; Florida	0-30	12.7	2.6	—	—	McComb and others 1986
	31-60	12.7	7.2	—	—	
	61+	12.7	10.7	—	—	
Pine-hardwood; Florida	0-30	12.7	1.4	—	—	McComb and others 1986
	31-60	12.7	8.0	—	—	
Hardwood; Florida	0-30	12.7	7.1	—	—	McComb and others 1986
	31-60	12.7	11.6	—	—	
	61+	12.7	13.5	—	—	
Bottomland hardwoods; South Carolina	1-100	12.5	9.69	—	—	Harlow and Guynn 1983
Longleaf-loblolly pine; South Carolina	1-100	12.5	3.48	—	—	Harlow and Guynn 1983
Pine plantation; South Carolina	1-40+	10.2	21.3	—	—	Carmichael and Guynn 1983
Pine-hardwoods; South Carolina	20+	10.2	31.2	—	—	Carmichael and Guynn 1983
Cove hardwoods; South Carolina	40+	10.2	37.3	—	—	Carmichael and Guynn 1983
Upland hardwoods; South Carolina	40+	10.2	50.3	—	—	Carmichael and Guynn 1983
Bottomland hardwoods; Louisiana	45	10	3	—	—	McComb 1979, as cited in McComb and others 1986
	80	10	11	—	—	
Pine-hardwoods; Mississippi	85	10	6.4	—	—	McComb 1979, as cited in McComb and others 1986
Mixed mesophytic; Kentucky	60	10	14.8			Moriaty and McComb 1983
	60[a]	10	18.0	—	—	
Pitch pine; North Carolina	~100	10	25	—	—	Smith 1991
	3[b]	10	576	—	—	
	8[b]	10	156	—	—	
	11[b]	10	231	—	—	
	16[b]	10	231	—	—	

continued

Table 7—Snag accumulations in some southern forest stands (continued)

Stand	Age	Lower dbh limit	Snag density	Snag mass	Snag volume	Source
	Years	*cm*	*No./ha*	*Mg/ha*	*m^3/ha*	
Sugar maple; Tennessee	—	10	—	1.92	—	Onega and Eickmeier 1991
Chestnut oak, Oak Hickory; Virginia	60-79	10	62.2[c]	—	—	Rosenberg and others 1988
	80-99	10	69.3[c]			
	100+	10	63.6[c]	—	—	
Mixed mesophytic; Kentucky	35	10	83.8	—	—	McComb and Muller 1983
	200+	10	42.8	—	—	
Mixed mesophytic; Kentucky	200+	20	12.19	5.2	12.0	Muller and Liu 1991
Tulip-poplar; North Carolina	30	25	0	—	—	Hardt 1993
	30	25	2.5	—	—	
Cove hardwoods, mixed oak; North Carolina	70+	25	16.7	—	—	Hardt 1993
	70+	25	15.2	—	—	
White pine-white oak; South Carolina	200+	25	17.5	—	—	Hardt 1993
Sugar maple; North Carolina	200+	25	17.1	—	—	Hardt 1993

[a] Following timber stand improvement.

[b] Following southern pine beetle attack.

[c] Snags greater than 10-cm d.b.h.

from inventory data and more detailed research suggests that future studies of CWD accumulations should take into account physiography, ownership, forest type, stand age, stand origin (artificial vs. natural), and disturbance.

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Dynamics of Coarse Woody Debris in Southern Forest Ecosystems

David H. Van Lear

Abstract

Coarse woody debris (CWD)—standing dead trees, fallen trees, and decomposing large roots—serves a number of ecological functions. CWD loadings are dynamic in response to inputs from tree breakage and mortality and to losses from decomposition and fire. Two very different natural processes, gap-phase dynamics and major episodic disturbances, contribute to inputs, as well as forest management activities. Decay and combustion, if complete, yield both CO_2 and H_2O. However, neither is usually complete, and the combustion process leaves some rapidly altered CWD, whereas decay results in the gradual formation of humic substances. Current forest management practices often contribute to low loadings of CWD in southern forests. Although some data provide the basis for very general estimates, there is a paucity of knowledge in the South on almost every aspect of CWD dynamics and loading.

Introduction

Organic material in the form of standing dead trees (snags), fallen trees, and decomposing large roots, all of which are components of coarse woody debris (CWD), influences the ecology of a site for decades or even centuries (Franklin and Waring 1980). CWD functions as seed germination sites, as reservoirs of moisture during droughts, as sites of nutrient exchange for plant uptake, and as critical habitat for forest organisms. During later stages of decomposition, it promotes favorable soil structure (Harmon 1982; Harmon and others 1986; Maser and others 1988). Dead root systems have been neglected as a component of CWD. However, decomposing roots contribute to the heterogeneity of the soil, provide increased infiltration and percolation of soil water, enhance gas diffusion throughout the rooting zone, and provide habitat for soil-dwelling organisms (Lutz and Chandler 1955).

Loadings of CWD are dynamic, i.e., constantly changing in response to inputs from tree breakage and mortality and to losses from decomposition and fire. This dynamic nature is reflected in gradual or episodic changes in mass, density, and volume of standing dead and fallen trees.

The term "coarse woody debris," as used in this paper, refers to any dead standing or fallen tree stem (or dead root) at least 7.6 cm in diameter. This minimum diameter was arbitrarily chosen, primarily because it corresponded to a measured size-class of forest fuels in a number of cited studies in the South. For obvious reasons, the dynamics of root biomass of dead trees has received little study.

The objectives of this paper are to describe the processes that affect loadings of CWD within the terrestrial ecosystems of southern forests and to identify gaps in our knowledge of CWD dynamics. Because of the paucity of information on loadings and dynamics of dead roots, that topic will not be discussed. Suffice it to say that the below ground dynamics of large dead roots represents a major gap in our knowledge of CWD.

Inputs of Coarse Woody Debris

The flow of aboveground CWD within terrestrial ecosystems is summarized in diagrammatic form (fig. 1), as adapted from Harmon and others (1986). Within terrestrial ecosystems, mortality and breakage of living trees add CWD, while decay and fire remove or transform CWD (Harmon and others 1986; Maser and others 1988). The balance between inputs and losses of CWD within the forest ecosystem represents the standing crop, or loading, of CWD.

Inputs of CWD occur when living trees are killed by fire, wind, lightning, insects, disease, ice storms, competition, or humans. Disturbances may kill scattered individual trees,

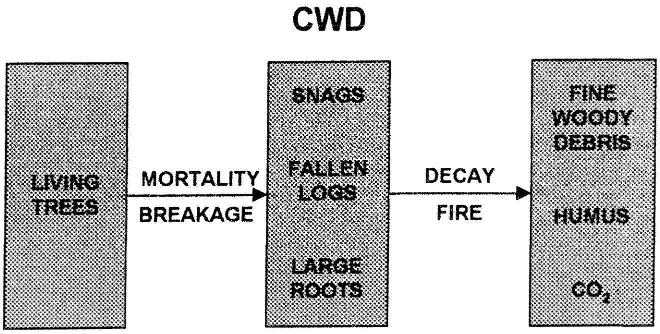

Figure 1—Flow diagram of the dynamics of CWD in terrestrial ecosystems.

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groups of trees, entire stands, or even entire landscapes and are now widely recognized as a natural part of the ecology of the southern forest (Christensen 1991; Sharitz and others 1992; Skeen and others 1993). Major disturbances contribute large quantities of CWD, which are added to predisturbance CWD already accumulated in the stand. For this reason, loadings of CWD are often highest soon after major forest disturbances.

Gradual Inputs of Coarse Woody Debris by Gap-Phase Dynamics

CWD inputs in southern forests from gradual gap–phase dynamics, i.e., from the occasional death of individual trees or groups of trees within the forest, are not well documented. Large canopy gaps can contribute substantial quantities of CWD. For example, Smith (1991) estimated that canopy gaps created in pitch pine stands by pine beetles in the Southern Appalachians contained 35.6 tons per hectare (ha) of CWD. Loadings from insect damage in more productive forest types could be much higher.

Some information on snag densities (numbers/area) and recruitment rates is available from the wildlife literature. Generalizations from published research include the following:

(1) Snags are most common in hardwood stands and least common in pure pine stands (Harlow and Guynn 1983; McComb and others 1986b; Sabin 1991). (2) Snags are more frequent in lowlands and riparian zones than on upland sites. (3) Unmanaged private land and national forests generally have higher densities of snags than lands managed intensively for wood production (McComb and others 1986a, 1986b).

The length of time that snags remain standing varies with species and size, although most snags fall within a decade or less in southern forests (Dickenson and others 1983; McComb and Rumsey 1983; Sabin 1991). However, occasional American chestnut snags are still standing in Southern Appalachian forests 70 years after the chestnut blight. White pine and white oaks are generally longer standing than snags of other pine and oak species (Hassinger and Payne 1988). Large diameter snags stand longer than smaller ones (Bull 1983; Raphael and Morrison 1987).

Snag densities in the relatively young forests of the South vary widely. In the Appalachian deciduous forest, Carey (1983) found snag densities ranging from 11 to 55 snags per ha. Sabin (1991) reported an overall snag density of 28.1 snags per ha in relatively young (20 to 60+ yrs) forest types in the Piedmont and noted that snags were being lost at an average rate of 0.52 snags per ha per year. Relatively few areas and little acreage in the Southeast support over-mature or old-growth forests where snag recruitment rates and densities are unknown. Such information is needed to serve as baseline data against which forests managed more intensively could be compared.

Heavy Loading of Coarse Woody Debris by Major Episodic Disturbances

In contrast to gap-phase disturbances, where natural succession proceeds at a relatively gradual rate, large-scale natural disturbances, such as catastrophic wildfires and hurricanes, are episodic in nature and may kill trees over large forest areas. As a result of these natural disturbances and timber harvesting, few forest ecosystems in the Southeastern United States succeed to a vegetative climax condition or even develop undisturbed for as long as a century.

Forest fires affect the loading of CWD in two ways. They simultaneously add CWD by killing live trees and reduce CWD by consuming dead trees. Fire regimes in the South range from those where fire reoccurs infrequently (on the order of several decades to perhaps a century or more) and fuel loading is heavy, to those where fire occurs almost annually and fuels are light. Sand pine and table mountain pine regenerate after catastrophic stand-replacement fires, which function to open serotinous cones, kill hardwood understory competition, and prepare seedbeds (Della-Bianca 1990; Outcalt and Balmer 1983), as well as contribute a large pulse of CWD. At the other extreme, in open longleaf pine-wiregrass stands, a regime of frequent fire would prevent the buildup of fuels to levels where high rates of fire-induced tree mortality would be expected. Boyer (1979) reported an annual mortality of only one tree per ha in mature longleaf pine stands throughout the longleaf region.

Stand-replacement fires, which kill all aboveground biomass, obviously make heavy contributions to CWD. The author knows of no studies in the South where CWD inputs have been estimated following stand-replacement fires. However, estimates of aboveground living biomass are available for some forest types and site conditions and, when corrected for small branch and foliage components, provide a rough approximation of potential CWD inputs.

About 70 to 80 percent of the aboveground biomass of these forest types is above the minimum size class of CWD. For loblolly pine, the most studied of the southern pines, aboveground biomass ranges from about 100 tons per hectare (t/ha) in thinned 41-year-old plantations on poor sites (Van Lear and others 1983) to approximately 156 t/ha for unthinned 16-year-old plantations on good sites (Wells and Jorgensen 1975). Biomass of older pine stands on good to excellent sites would be even higher. Aboveground biomass of mixed hardwood stands averaged 178 and 175 t/ha at Coweeta Hydrologic Laboratory and Oak Ridge National Laboratory, respectively (Mann and others 1988), similar to the 164 t/ha estimate from forest survey data for fully stocked stands of mature hardwoods in the Southeast (Phillips and Sheffield 1984).

Hurricanes, tornadoes, and other strong winds are common in the Southeastern United States and strongly influence CWD dynamics. These strong winds create in a matter of hours loadings of CWD that would never be achieved during centuries of gap-phase natural succession (Hook and others 1991). For example, Myers and others (1993) measured loadings, after limited salvage, of almost 90 t/ha of downed woody material and 16 t/ha of snags in mature, uneven-aged pine stands 2 years after Hurricane Hugo. Strong winds either snap stems of well-anchored species or uproot shallow-rooted species. Although catastrophic winds (probably category V-force winds) will destroy any stand, such winds normally occur over only a relatively small portion of the area affected by most hurricanes.

Forest damage from hurricanes and tornados has increased in recent decades due to the regrowth of mature forests following the extensive harvest of old-growth forests that occurred between 1885-1930 (Hooper and McAdie 1993). In addition to stand age, site (Crocker 1958; Foster 1988), community type (Duever and McCollum 1993; Sharitz and others 1993), species (Gresham and others 1991; Hook and others 1991; Sharitz and others 1993; Touliatos and Roth 1971), and tree morphology (Gratkowski 1956; Nix and Ruckelshaus 1991) markedly influence the damage (and CWD loadings) to forests by strong winds.

Other environmental factors, e.g., insect and disease outbreaks, ice storms, and mass movement of soils, can dramatically increase loadings of CWD. Some native insects, the southern pine beetle, for example, periodically reach epidemic proportions and kill whole stands of various pine species across large portions of the landscape. Introduced insects like the gypsy moth continue to expand their range southward and devastate hardwood stands over extensive areas. Certain diseases, for example, fusiform rust, have become more prevalent in recent decades. Ice storms periodically wreak havoc on forests in some portions of the South, e.g., in the Sandhills region.

The quantity of CWD contributed to sites by all these factors is a function of the proportion of the stand killed (and consumed, in the case of fire) by these agents and the proportion of the trees above the minimum CWD size class. Contributions range from the mortality of scattered individual trees killed in nonepisodic events to the mass deaths of trees on thousands of hectares from major episodic events, during which the loading of CWD across the landscape is increased dramatically. Information on CWD inputs from all types of catastrophic events is needed to fully evaluate the environmental effects of these disturbances.

Losses of Coarse Woody Debris

Within terrestrial ecosystems, CWD is lost through decay and fire. Decay and combustion by fire are similar processes in some respects, but also have important differences. The relative importance of each process varies by site—decay dominates on mesic sites, while fire is more important on xeric sites (unless fire-suppression efforts are effective). Although its natural role as a major ecological factor has often been overlooked by ecologists and land managers, fire has been a dominant factor shaping the structure and composition of southern forest ecosystems for millennia.

Decay

Decay of CWD is initiated by an invasion of white, brown, and soft rot fungi, causing a loss of density (Kaarik 1974). Insects are known to be important inoculators of these decay microbes (Abbott and Crossley 1982). Toole (1965) described the deterioration of unlopped hardwood logging slash in Mississippi and found that, for most of the species studied, small branches had disintegrated after 6 years and only a small portion (< 15 percent) of the large branches and bole had not settled on the ground. Twigs and small branches decayed most readily, followed by the larger sapwood and finally the heartwood. Decay may be retarded when the bark sloughs off early, allowing the surface of the sapwood to dry quickly and become casehardened. Smith (1991) documented changes in decomposer communities of pitch pine CWD during decomposition. During early stages of decomposition, bark beetles and blue-stain fungi dominated, although neither had much effect on decomposition, i.e., wood density was not markedly reduced. White rots, brown rots, ants, and termites dominated later stages of decomposition. As the wood structure is broken down, fragmentation becomes a major mechanism of decay.

Fragmentation of CWD refers to a reduction of volume via physical and biological forces during the decay process (Harmon and others 1986; Maser and others 1988). Fragmentation is normally preceded by a lag period during which both density and mass of fresh CWD decrease but volume remains constant. Snags fragment when portions of the standing-dead tree or the entire tree break and fall to the ground. Biological fragmentation of snags and fallen logs is caused by both plants and animals. Invertebrates use the dead wood as a food source, creating galleries that serve as avenues for microbial colonization and further decay. Bears, birds, and other animals shred the rotting wood while foraging for insects. Plant roots grow into fallen trees after initial stages of decay have been completed and further fragment the partially decomposed materials. During the entire decay process, the physical forces of water and gravity relentlessly transport fragmented materials from snags and fallen logs to the forest floor, where they undergo further decomposition and are ultimately converted to CO_2 or decay-resistant humus. The final products of decay of CWD are fine woody debris, humus, and CO_2 (Harmon and others 1986; Maser and others 1979; Spies and Cline 1988).

Although perhaps not as good an index of decay as volume diminution, changes in wood density have frequently been used to measure initial stages of physical decay. Following clearcutting of a mixed hardwood stand in the Southern Appalachians of North Carolina, wood-density decay coefficients varied widely, ranging from 0.18 per year for species such as dogwood and persimmon, to 0.03 per year for decay-resistant species like black locust and American chestnut (Mattson and others 1987). Little information is available regarding decay of pine CWD in the South. Barber and Van Lear (1984) calculated a wood-density decay coefficient of 0.075 per year for large loblolly pine slash (excluding bark) following clearcutting in the South Carolina Piedmont, while Smith (1991) found a decay constant of 0.048 per year for pitch-pine CWD in the Southern Appalachians.

In addition to species differences, other factors affect the rate of decay of CWD (Barber and Van Lear 1984; Mattson and others 1987). Aspect of the site is important—CWD decays faster on north and northeastern aspects, probably due to the generally greater availability of soil moisture. Relative position of the fallen tree affects decay rates—CWD in contact with the ground decays faster than aerially suspended CWD. Large woody debris decays slower than small woody debris. In streams, saturated CWD decays at extremely slow rates. Decomposition rates in the Southeast are generally higher than those reported for other regions, presumably because temperature and moisture conditions are more favorable for microbes and invertebrates involved in the decay process.

The chemical nature of CWD changes during decomposition. Workers in the Pacific Northwest (Graham and Cromack 1982; Sollins and others 1980) and elsewhere have noted that the C/N ratio of CWD decreases, and the concentration of lignin increases as decay progresses. Concentrations of nitrogen and phosphorus increase in large logging slash following harvest of loblolly pine (Barber and Van Lear 1984) and in pitch pine CWD following pine beetle attack (Smith 1991). However, after initially being a sink for nutrients, CWD later becomes a source when fragmentation dominates the decay process.

Long-term studies are underway that will better document decay rates of CWD. However, more information is needed concerning decay rates of different species under different site conditions and management regimes. What is the best method for measuring decay? Sampling wood density in various states of decay is frequently used, but the method becomes biased during mid to late stages of decay when only the most resistant pieces of wood remain. Adjustment of decay chronosequences for past fragmentation is necessary, but often difficult, if mass losses are to be estimated correctly (Harmon, personal communication[1]). When does decaying wood become a source, rather than a sink, for nutrients? What types of decay models best describe the decay process? These and many other questions reflect gaps in our knowledge of the decay process.

Fire

Fire and decay are similar processes in that both, if completed, are essentially oxidation reactions yielding as final products CO_2 and H_2O (Brown and Davis 1973). However, fire is the rapid oxidation, or combustion, of fuels, while decay is a much more gradual oxidation of organic materials. In neither process is oxidation generally complete. In forest fires, complete combustion is obviously uncommon, as evidenced by dead snags and downed trees on burned sites. Decay is also generally incomplete, as

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[1] Personal communication. 1993. Mark Harmon, Professor, Department of Forest Science, Oregon State University.

evidenced by the presence of residual CWD and the formation of humus.

Some of the effects of fire on CWD are similar to those of decay, i.e., fire fragments large pieces of wood and bark into smaller pieces and releases CO_2 and other gases into the atmosphere. However, the two processes obviously differ in reaction time and in the type of substrate produced (charred vs. uncharred). Also important is the fact that the decay process generally tends to mesify microsites because of incorporation of humified products into the soil, while fire tends to xerify microsites, at least in the short run, by oxidizing humus from the forest floor and exposing the soil surface to greater insolation.

Many deficiencies exist in our knowledge of the role of fire in CWD losses. What is the effect of charring on decay? Under what conditions can fire be used to minimize CWD loss? Is fire compatible with management for snags? What burning regimes are appropriate to achieve and maintain desired loadings of CWD? This last deficiency assumes that we eventually will have some concept of what desired loadings are. Southern forests evolved in regimes of more or less frequent fire. A major gap in our understanding of CWD dynamics is the way this major environmental factor influenced CWD loadings on a landscape scale.

Loadings of Coarse Woody Debris in Southern Forest Ecosystems

Loadings of CWD at a given time reflect the balance between inputs and losses. Although general temporal patterns of loading may be apparent on some sites, e.g., gradually increasing CWD loadings on mesic sites as old-growth conditions are approached, within these general patterns are fluctuations of varying magnitude. On xeric sites, temporal patterns may be even more difficult to identify due to the chance occurrence of fire.

In the absence of major disturbances, natural succession in forests may be dominated for extended periods by gap-phase dynamics, during which CWD accumulates slowly. During the development of a new stand following a major disturbance, much of the predisturbance and disturbance-contributed debris decays. Loadings of CWD would be expected to decline during the early development and midsuccessional periods because young trees dying from competition are too small to contribute significantly to CWD and because mortality rates during the midsuccessional stage are low. As succession proceeds, mortality of scattered senescent trees occurs and CWD loadings would be expected to increase. In the later stages of succession and old growth, increased mortality of large overstory trees would add to the loading of CWD, especially if these stages were dominated by large, long-lived individuals.

This hypothetical pattern of CWD loading over time has received little study in terrestrial forest ecosystems in the South. However, Hedman (1992) has documented this U-shaped pattern in a 300-year sere in small streams in the Southern Appalachians (fig. 2). A similar scenario has been well documented for Douglas-fir ecosystems in the Pacific Northwest after catastrophic fires (Spies and others 1988). Muller and Liu (1991) found that the volume and mass of CWD in an old-growth deciduous forest on the Cumberland Plateau averaged 66.3 m^3 per ha and 21 t /ha, respectively. Their work suggested that loadings of CWD in old-growth forests in warmer regions are lower than those in cooler regions.

There is relatively little data in the South concerning loadings of CWD following major episodic disturbances or through various stages of succession. Studies are needed to more thoroughly characterize loadings of CWD in old-growth forests. How do loadings vary in response to different fire regimes? Are CWD loadings low for some forest types because of rapid decay rates, or because fire is a frequent visitor? How can management be modified to enhance CWD loadings on both stand and landscape scales? These types of questions must be answered so that

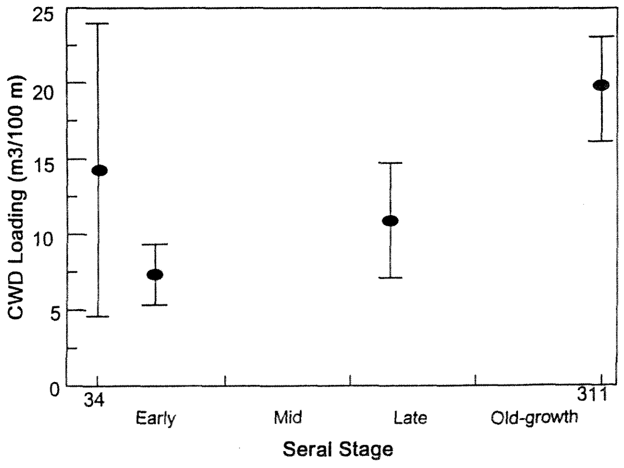

Figure 2—Coarse woody debris loadings, excluding American chestnut, in small Southern Appalachian streams.

managers will have guidelines relative to loadings of CWD in managed stands versus those in stands that have not been manipulated. As research further demonstrates the ecological significance of CWD in southern forests, current management strategies may need to be altered to achieve certain levels of CWD.

Effects of Management

The effects of management on CWD have received little direct study in the Southeast. However, a number of studies have indirectly dealt with CWD, especially relative to site preparation techniques. Morris and others (1983) found that 14.1 t/ha of coarse woody logging slash were displaced into windrows during mechanical site preparation of a flatwoods site in Florida. While this windrowed material is still on the site, its spatial distribution, and therefore its functional qualities, is certainly not natural. Windrowing as a method of forest site preparation is gradually being phased out of forest operations in the South for a variety of reasons. Other types of mechanical site preparation, while having less effect on CWD than windrowing, still may adversely affect the loading, distribution, and duration of CWD.

The effects of broadcast burning or wildfire on CWD depend upon the conditions (fuel moisture, weather, and firing technique) under which the fire burns. Intense fires in periods of extended drought are very severe and may consume much of the CWD (Robichaud and Waldrop 1992). However, consumption of fallen logs by intense fire is often minimal if the fire burns under conditions less conducive to complete combustion, e.g., higher moisture contents of large fuels. Sanders and Van Lear (1988) found that CWD volume was reduced under the latter conditions by less than 40 percent during intense broadcast fires in pine-hardwood logging slash in the Southern Appalachians following clearcutting.

Intensive management practices associated with plantation forestry often result in decreases in CWD loading. Short rotations are commonly used for pulpwood production. Rotations of 30 years or less are too short to allow significant quantities of CWD to accumulate. Thinning is often used in longer rotations for sawtimber production, and this removes trees that are most likely to be CWD candidates. More complete utilization of harvested trees minimizes the amount of CWD left after harvest. Whole-tree harvesting or harvesting techniques that remove most of the abovestump biomass from the site are now practiced in many locals throughout the South.

Conclusions

The ecological importance of CWD has only recently been appreciated by foresters and other land managers in the South. Based on the documented importance of CWD in the Pacific Northwest and other areas, as well as on the information presented at this workshop, it would be prudent for land managers in the Southeast to recognize CWD as an important structural and functional component of forest ecosystems rather than as a hindrance that must be removed at a high cost.

Managing for CWD will certainly not be a primary objective on all forest lands in the South. The South is obviously an important timber producer for the Nation and the world, and many of the South's forests will be managed primarily for timber. However, managers should be aware of the important functions of CWD and should use this information as they strive to achieve balance between commodity production and environmental values across the landscape.

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Dynamics of Coarse Woody Debris—A Simulation Study for Two Southeastern Forest Ecosystems

Thomas A. Waldrop

Abstract

The FORCAT gap model was used to simulate formation and decomposition of coarse woody debris (CWD) for two forest ecosystems on the Cumberland Plateau in east Tennessee. Simulations were conducted for 200 years after clearcutting on a total of 100 plots, 1/12 ha in size. Model results showed a decrease in CWD loads in early years as logging slash decomposed. After year 32, CWD loads increased rapidly and peaked around year 90. Coarse woody debris loads in older stands gradually decreased through the remainder of the simulation period. The assumed decomposition rate strongly influenced CWD loading. Model results correspond closely to observed loadings in old-growth stands on the Cumberland Plateau.

Introduction

While exact effects are not well documented, few doubt the ecological importance of coarse woody debris (CWD) in Southeastern ecosystems. Little is known, however, about the changes in CWD loads that might be expected over long periods, such as through succession. Most studies in the Southeast have provided short-term "snapshots" of CWD for specific successional stages and have looked at old-growth stands (MacMillan 1988; Muller and Liu 1991; Smith and Boring 1990).

Coarse woody debris dynamics are difficult to predict because inputs and losses are affected by many biotic and abiotic factors. Inputs are determined by species composition, site quality, and sizes and types of disturbance. Losses of CWD are affected by management strategies and decomposition rates. Several studies show that decomposition rates depend on multiple factors including species (Harmon 1982), climate (Muller and Liu 1991), site (Abbott and Crossley 1982), size of material (Mattson and others 1987), and contact with the ground (Barber and Van Lear 1984).

Van Lear (1996) discusses current research on CWD dynamics in the Southeast elsewhere in these proceedings, so I cite only a few studies here. A study conducted in western Oregon and Washington provides the most complete description of long-term CWD dynamics to date. Spies and others (1988) and Spies and Cline (1988) described CWD loading in 196 Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, stands across a chronosequence ranging from 40 to 900 years since disturbance. This work serves as a comparison for my simulation study, so I will provide its results in some detail.

Loading of CWD over the 900-year chronosequence was described for five successional stages: stand initiation, stem exclusion, understory reinitiation, old growth, and climax. During the stand initiation stage (lasting 20 to 30 years), accumulation of CWD was slow (fig. 1). Even though tree mortality was high during this period, most trees were too small to be considered CWD. Coarse woody debris inputs began during the stem exclusion period (lasting 10 to 30 years) as the canopy closed and mortality of larger trees began. Input rates were relatively low during this period because many dying trees were small. Canopy dominance diminished during the understory reinitiation stage (lasting 100 to 150 years), allowing understory herbs, shrubs, and trees to become established. Mortality of some large trees began during this period and CWD accumulated rapidly.

Coarse woody debris continued to accumulate rapidly during the old-growth stage (lasting 500 to 800 years) as natural disturbances such as windthrow, diseases, and insects increased mortality rates of large trees (fig. 1). Much of the mortality during this period was among dominant shade-intolerant species, which were replaced by shade-tolerant species. The shade-tolerant species were

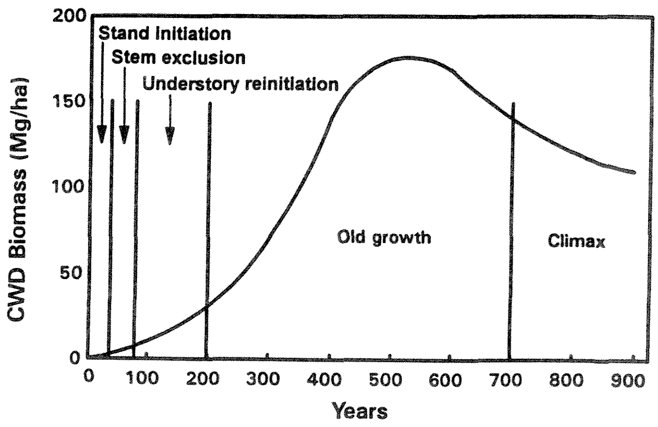

Figure 1—Accumulation of coarse woody debris across a 900-year chronosequence for ecosystems of western Oregon and Washington (Spies and Cline 1988).

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relatively long lived and contributed little CWD during the later years of the old-growth stage. Late in the old-growth stage, decomposition began to exceed inputs and CWD loading decreased.

The climax stage was reached when all shade-intolerant species were replaced by shade-tolerant species (fig. 1). This stage had less CWD than the old-growth stage because it lacked the original overstory dominants. Coarse woody debris dynamics during this stage were difficult to describe because few of these stands existed. Usually, by this time, either natural or anthropogenic disturbance had reinitiated succession.

A lack of similar information about long-term CWD dynamics in Southeastern ecosystems prompted the simulation study described in this paper. I used a previously developed model of forest succession to simulate stand dynamics, and I estimated CWD loading from predicted tree mortality. My objectives were to provide basic information on long-term CWD dynamics in Southeastern ecosystems and to identify information gaps.

Methods

Description of the Model

The model used for this study was FORCAT (FORests of the CAToosa Wildlife Management Area), which was developed for mixed-species forests on the Cumberland Plateau in east Tennessee (Waldrop and others 1986). Although the major reason for selecting FORCAT was my familiarity with the model, it is one of only a few existing models capable of simulating long-term stand dynamics for managed, mixed-species stands (Waldrop and others 1989).

FORCAT is a member of a family of models based on the widely used FORET model (Shugart and West 1977). FORET is described by Shugart (1984) as a spatial gap model that simulates stand dynamics for the forests of east Tennessee. Gap models are a special case of single-tree models and have demonstrated adaptability over a wide range of forest types. Simulated gaps range from 0.04 to 0.08 ha in size (Shugart and West 1979), approximating the area opened by the death or removal of an individual canopy tree (Shugart and West 1980). These models generally use simple equations, with parameters that are easily obtained, to approximate the mechanisms that cause a forest to change on a small plot of land. Such changes are simulated through the birth, growth, and death of individual trees as controlled by various measures of competition and other environmental stress factors. Variables used in gap models as environmental stress factors include shade, stand basal area, soil moisture, and ambient temperature.

The FORCAT model was developed through numerous modifications to FORET, making it more specific to managed sites on the Cumberland Plateau (Waldrop and others 1986). The model simulates stand dynamics on a 0.08-ha plot using 30 hardwood and 3 pine species commonly found in the region. Simulation begins with a mature stand, which is immediately clearcut. After clearcutting, sprouts and seedlings are stochastically added to simulated plots based on silvical characteristics of each species. Diameter and height growth are calculated each year for each tree as a function of site, species, competition, and environmental stress. Trees are killed stochastically each year based on age, species, and current growth rates.

Some of the more significant changes to FORET that were included in FORCAT were: (1) beginning the simulation with natural regeneration found in clearcuts instead of bare ground, (2) basing growth rates on site quality and local climate, (3) basing seed availability and sprouting habit on species-specific characteristics, and (4) simulating periodic clearcutting and prescribed burning. FORCAT was developed and tested for a xeric hardwood site and validated with data from a nearby mesic oak site.

Many of the growth and mortality equations used in FORCAT and FORET were adapted from the JABOWA model for northern hardwoods (Botkin and others 1972). Shugart and West (1977), Shugart (1984), and Botkin (1993) described those equations in detail. Shugart (1984) also discussed gap models at length. Waldrop (1983) and Waldrop and others (1986) described development and validation of FORCAT.

Modeling Coarse Woody Debris Dynamics

Few changes to FORCAT were required to predict CWD loading. In FORCAT, the diameter at breast height (d.b.h.) of each tree on the simulated plot (up to 1,200 trees in young clearcuts) is updated each year according to growth calculations and then stored in an array. If a tree dies in any year, the d.b.h. of that tree is removed from the storage array. At that point, the dead tree was considered CWD and its biomass was estimated. Biomass was estimated for both stems and crowns using d.b.h. as the independent variable in regression equations given by Clark and others (1986). To account for limbs too small to be considered CWD (diameter less than 10 cm), estimated crown biomass was reduced by 20 percent.

The total biomass of dead stems and crowns on a plot was calculated for each year. This amount was added to the total CWD remaining from the previous year, and the new sum was reduced by a constant rate to allow for decomposition. Decomposition rates of 6 percent, 8 percent, and 10 percent were used to examine the differences these rates caused in CWD accumulation. These decomposition rates roughly follow those reported by Harmon (1982) for hardwood species.

Stand dynamics and CWD accumulation were simulated for the two site types (xeric and mesic) that were used to develop and validate FORCAT. The results of these simulations should give some insight into the effect of site productivity on CWD accumulation. Model input for the xeric site was data from a stand with a basal area of 19.3 m^2/ha and dominated by post oak (*Quercus stellata* Wangenh.), southern red oak (*Q. falcata* Michx.), and scarlet oak (*Q. coccinea* Muenchh.) (table 1). The xeric site was characterized by thin, acidic soils and moderate topography. It had a site index of 18 m for upland oaks (base age 50). For the mesic site, basal area of commercial-sized trees was 17.6 m^2/ha and species composition was mostly chestnut oak (*Prinus* L.), white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.), and yellow-poplar (*Liriodendron tulipifera* L.). The mesic site had a northern aspect, moderate to steep slopes, and a site index of 31 m for yellow-poplar (base age 50).

Table 1—Species composition for xeric and mesic sites used as input to FORCAT

Species	Xeric site	Mesic site
	Total basal area (pct)	
Black oak	10.6	4.5
Chestnut oak	--	24.6
Northern red oak	--	18.6
Post oak	27.0	--
Scarlet oak	27.2	--
Southern red oak	13.5	--
White oak	4.0	22.1
Other oaks	1.4	--
Hickories	3.1	11.8
White ash	--	3.9
Yellow-poplar	--	11.6
Other hardwoods	7.0	2.9
Virginia pine	6.2	--

Simulations began with mature stands, which were immediately clearcut. No artificial regeneration or site preparation was allowed. A simulation period of 200 years after clearcutting was used for each of 100 simulated 1/12-ha plots. Due to the stochastic nature of the growth and mortality calculations, no two simulated plots were identical. Shugart and West (1979) suggested including 100 plots in simulations to account for the variability found in most Southeastern forest types.

Several limitations to this approach of modeling CWD accumulation are recognized. By defining CWD as dead trees, standing CWD cannot be distinguished from down CWD. Also, CWD estimates are likely to be low because inputs from limbs that die and fall to the ground are not included. Another limitation is that decomposition rates are assumed to be the same for all species and size classes of CWD and across all successional stages. Published decomposition rates were not available for the species and types of sites that FORCAT simulates. The simulations do not include CWD inputs from natural disturbances or from anthropogenic disturbances, other than the initial clearcut.

Results and Discussion

Coarse Woody Debris Dynamics After Clearcutting

On the xeric site, simulated regeneration was dominated by sprouts of oak species (39 percent of all stems) that were abundant in the preharvest stand. Understory hardwoods that sprout prolifically, such as dogwood (*Cornus florida* L.) and sourwood (*Oxydendron arboreum* L.), made up another 30 percent of the regeneration. Pine seedlings represented less than 1 percent of the regeneration. Throughout the simulation period, understory hardwoods gradually declined in importance while scarlet oak, post oak, and southern red oak eventually dominated the stand.

For the mesic site, simulated regeneration was dominated by northern red oak, white oak, hickories (*Carya* sp.), white ash (*Fraxinus americana* L.), and blackgum (*Nyssa sylvatica* Marsh.). No pine regeneration was predicted. By the end of the simulation, the stand was dominated by northern red oak, chestnut oak, white oak, and yellow-poplar. The patterns of CWD accumulation predicted by FORCAT (fig. 2) for xeric and mesic sites (using a 6-percent decomposition rate for both sites) were similar to the curve proposed by Spies and Cline (1988) for western Oregon and Washington (fig. 1). In all three systems, this pattern resembled a bell-shaped curve that peaked during the first half of their respective periods (100 years for simulated xeric and mesic sites, 450 years for measured Douglas-fir stands). Later, CWD in each system gradually decreased until a point, late in succession, where an equilibrium between inputs and decomposition may have been reached.

Coarse woody debris accumulation on both simulated sites remained low for 30 to 40 years as trees grew to the minimum size for CWD (10 cm), even though there was significant mortality during this period (fig. 2). Between years 30 and 75 CWD increased rapidly for both simulated sites. FORCAT predicted decreases in stand basal area during this period as crown closure occurred and a few large trees began to die. On the xeric site, for example, predicted stand basal area decreased from 19.3 m^2 per ha at year 50 to 15.9 m^2 per ha at year 100.

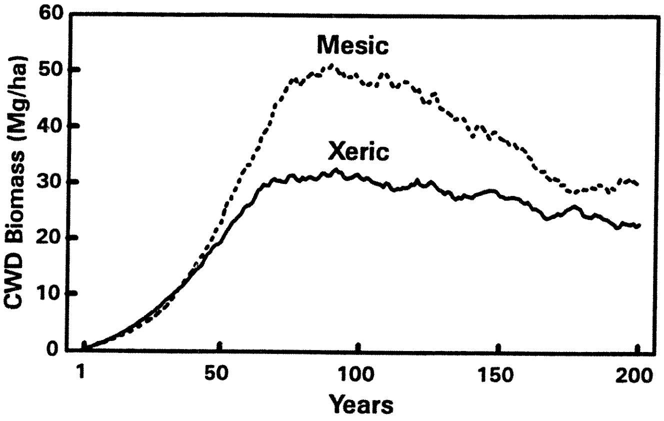

Figure 2—Accumulation of coarse woody debris for xeric and mesic sites as predicted by FORCAT (6-percent decomposition rate for both sites).

The period of rapid CWD accumulation on the xeric site lasted until the stand was about 70 years old (fig. 2) when CWD was 30.6 Mega grams per hectare (Mg/ha). Coarse woody debris continued to accumulate, but at a slower rate, to a maximum of 32.5 Mg/ha at year 91. For the remainder of the 200-year simulation period, decomposition slightly exceeded inputs and CWD loads gradually decreased.

Tree growth on the simulated mesic site exceeded that on the xeric site, producing a more rapid rate of CWD accumulation (fig. 2). On this site, CWD accumulated rapidly from years 30 through 75, reaching a total of 49.3 Mg/ha. Maximum CWD loading during the simulation period was 51.4 Mg/ha in year 89. Between years 90 and 200, CWD loading decreased much more rapidly than on the xeric site. Species on the mesic site were longer lived than those on the xeric site and the trees continued to grow. Mortality was higher on the xeric site during this period due to moisture stress. Therefore, CWD inputs were less on the mesic site than on the xeric site.

FORCAT predictions for CWD accumulation in older stands were similar to the ranges observed by Muller and Liu (1991) for old-growth stands on the Cumberland Plateau. Between years 90 and 200 (roughly equivalent to the age of old-growth stands), CWD loads on the simulated xeric site ranged from 22.8 to 32.5 Mg/ha (fig. 2). Muller and Liu (1991) reported accumulations ranging from 22 to 32 Mg/ha on dry sites including ridgetops, upper slopes, and south-facing and west-facing midslopes. Older stands on the simulated mesic site had CWD loads ranging from 30.0 (year 200) to 51.4 Mg/ha (year 90). Muller and Liu (1991) found CWD loads ranging from 34 to 49 Mg/ha on moist midslopes with a north or east aspect.

Even though FORCAT accurately predicted more CWD input on the mesic site than on the xeric site, the periods of accumulation (years 30 through 90) were nearly identical. This may indicate a failure of the model. I expected CWD loading to peak higher and later on the mesic site than on the xeric site because the species on the mesic site grow larger and are longer lived. A common problem among mixed-species models is an inability to simulate competition of different species across sites of varying quality. Since FORCAT development was based on xeric sites, its growth parameters for mesic sites may not be as accurate.

Logging Debris

An important, but so far neglected, component of CWD dynamics in managed stands is logging debris. For example, Sanders and Van Lear (1988) found that CWD after clearcutting in the Southern Appalachians can be as much as 90 Mg/ha. This debris provides regenerating stands with a structure that can be important habitat for small mammals (Evans and others 1991; Loeb 1996) as well as a source of nutrients (Mattson and others 1987).

Logging slash was added to model projections of CWD inputs immediately after simulated clearcutting. Total CWD loading at that time was assumed to equal the biomass of crowns from harvested trees. Crown biomass was estimated by using the d.b.h. of each harvested tree (xeric and mesic sites) as the independent variable in regression equations given by Clark and others (1986). These estimates were reduced by 20 percent to account for the portions of crowns too small to be considered CWD (< 10 cm in diameter).

The estimated CWD load immediately after clearcutting was 49 Mg/ha on the xeric site and 69 Mg/ha on the mesic site (fig. 3). On both sites, these levels were higher than at any other time during the 200-year simulation period. Figure 3 illustrates the importance of selecting site-preparation techniques that leave some CWD. Logging debris decomposes rapidly in clearcuts, but it provides some CWD during a period when there is little input. In my model, decomposition exceeded inputs through year 32. At that time CWD, totaled 16.9 Mg/ha on the xeric site and 18.3 Mg/ha on the mesic site (assuming a uniform decomposition rate of 6 percent). By year 32, all logging slash had decomposed. Therefore, after year 32 these curves were identical to those without logging slash (fig. 2).

Variable Decomposition Rates

An assumption used until now is that decomposition rates were uniform across site types. The work of Abbott and Crossley (1982) indicates that decomposition rates are higher on moist sites. By assuming a decomposition rate of 8 percent on the mesic site and 6 percent on the xeric site, the difference in simulated CWD loads between sites was greatly reduced (fig. 4). Even though CWD loading was much higher on the mesic site in year 1, it decomposed to a smaller amount than the xeric site by year 32 (12.3 present vs. 16.9 Mg/ha). By year 75, CWD was again greater on the mesic site. Beyond that point, however, the lines converged. During the last 50 years of the simulation, CWD loads on the two simulated sites were nearly identical.

This comparison (fig. 4) illustrates the observation of Abbott and Crossley (1982) that differences in decomposition rates between sites can be more important than differences in sizes of CWD. Even though the mesic site produced far more CWD biomass than the xeric site, the relatively small difference in decomposition rates (8 vs. 6 percent) produced similar CWD loading throughout the 200-year simulation. If the difference in decomposition rate is larger (10 percent vs. 6 percent), CWD loading can be greater on the xeric site for most of the simulation period (table 2).

Muller and Liu (1991) suggested that CWD loading was a function of regional temperature patterns. Their measurements on dry sites correlated well with published estimates from warm Temperate Zone deciduous forests. Likewise, their CWD measurements on moist sites correlated well with published estimates from cool forests. Muller and Liu (1991) observed higher CWD loads on cool (moist) sites than on warm (dry) sites, suggesting that decomposition rates were not higher on moist sites or that higher productivity on moist sites compensated for higher decomposition rates. Broad-scale relationships, such as this, are oversimplified because CWD decomposition on any given site is controlled by a combination of moisture, temperature, soil fertility, species, size, and any number of other factors.

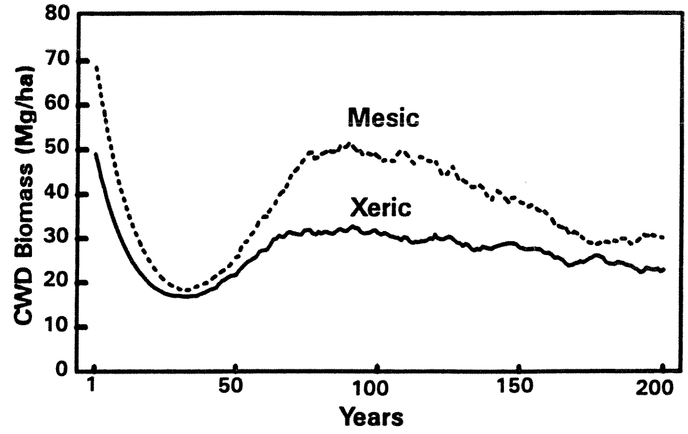

Figure 3—Dynamics of coarse woody debris after clearcutting xeric and mesic sites (predicted by FORCAT using a 6-percent decomposition rate for both sites).

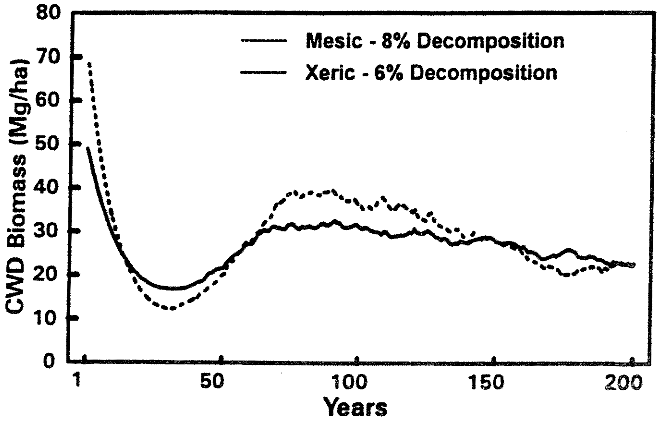

Figure 4—FORCAT projections of coarse woody debris loads by site type and decomposition rate.

Table 2—Coarse woody debris accumulation by site and decomposition rate as predicted by FORCAT

Site	Decomposition rate 6 pct	 8 pct	 10 pct
	----------	*Mg/ha*	----------
Xeric			
Year 1 (after clearcutting)	49.0	49.0	49.0
Year 32 (minimum CWD load)	16.9	11.8	8.5
Year 91 (maximum CWD load)	32.5	24.5	19.6
Year 200 (end of simulation)	22.8	16.5	12.9
Mesic			
Year 1 (after clearcutting)	68.9	68.9	68.9
Year 32 (minimum CWD load)	18.3	12.3	8.9
Year 89 (maximum CWD load)	51.4	39.8	32.3
Year 200 (end of simulation)	30.0	22.4	17.9

Conclusions

The FORCAT gap model worked well for this preliminary attempt to simulate CWD dynamics in two types of Southeastern ecosystems. Model results were similar to those of two field studies. The pattern of CWD accumulation predicted by FORCAT was similar to that observed in Western ecosystems (Spies and Cline 1988). Also, the predicted CWD loads were nearly equal to those reported by Muller and Liu (1991) for ecosystems similar to those simulated by FORCAT.

Results of this study show general trends of CWD accumulation over seral stages for the two Southeastern forest ecosystems used in the study. The result of this study shows the importance of leaving CWD after harvesting and emphasize that differences in decomposition rates (possibly due to differences in site productivity) can significantly affect CWD loading. Due to a number of limitations, however, model projections should not be considered accurate predictions of CWD loading at any given age.

A major limitation found in this study was the lack of information on inputs and decomposition rates for different tree species, sizes of CWD, and types of sites. Other knowledge gaps were discussed by Van Lear (1995) at this workshop, including the relationship of CWD inputs to natural and anthropogenic disturbance. Some of this missing information could be supplied by additional research and a broader modeling effort. For example, CWD dynamics after natural disturbances such as tornados or ice storms could be predicted by gap models if the return frequency of those disturbances was known. Also, CWD inputs from management activities such as thinnings or selection harvests could be predicted. This effort would allow managers to use model projections to help determine how to alter the level or timing of their activities to better meet their goals for CWD.

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Coarse Woody Debris in Forest Ecosystems: An Overview of Biodiversity Issues and Concepts

C. Ronald Carroll

Abstract

A central question is, "Why are there so many species?" Attempts to answer the question have generally followed the broad themes of (1) explaining via historical, biogeographical processes, and (2) examining local patterns of diversity in the context of random/stochastic events, primary productivity levels, competitive interactions, or processes that prevent equilibrium. Since general, implied hypotheses are difficult to formulate as testable null hypotheses, examinations of biodiversity processes have relied on several different measures of community structure. The coarse woody debris-biodiversity relationship is amenable to rigorous experimental approaches because coarse woody debris occurs in discrete, quantifiable units that can be easily manipulated.

Introduction

A central question that has preoccupied the thinking of ecologists is, "Why are there so many species?" In recent years, this biodiversity question has expanded to include both finer levels of resolution (genetic diversity) and higher patterns (beta and gamma diversity). Attempts to understand the factors that influence biodiversity have generally followed two broad themes: (1) Explanations for regional patterns of biodiversity rely on historical, biogeographic processes, (2) Explanations for local patterns of biodiversity most likely evoke some combination of random, stochastic events; levels of primary productivity; the outcome of equilibrial competitive interactions; or, conversely, processes that prevent population densities from reaching equilibrium levels. The most common explanations for biodiversity patterns are presented, and briefly described, in table 1. For a more complete discussion of biodiversity concepts and patterns, see Orians (1994).

To varying degrees, these hypotheses suffer from problems of validation. Although they are presented as hypotheses, they are extremely difficult to formulate as testable null hypotheses that can, at least in principle, be rejected or accepted based on experimentation. The only recourse, in most cases, has been to search for patterns that are consistent with particular hypotheses. For example, in animal communities little empirical evidence exists to support the hypothesis that environments with high primary productivity support more species than less productive environments. Indeed, some very productive environments, (e.g., estuaries and eutrophic lakes), are notably depauperate in animal species. Thus, the ascendancy of any particular hypothesis is strongly influenced by the weight of evidence favoring it rather than by the outcome of critical experiments or analysis.

Because direct experimental examination has proven to be difficult, most attempts to examine biodiversity processes relied on indirect measures of community structure. Some common examples include the following:

1. The existence of morphological character displacement where two species co-occur is used as presumptive evidence that competition was an important evolutionary factor in the community.

2. Species-area relationships are sometimes used to draw inferences about the extent to which particular habitats have reached their equilibrium number of species or as estimates of the total number of species that are expected to be present. This approach is burdened by many assumptions that are generally not made explicit. Among those are responses of biodiversity to increases in sample area or to changes in some resource density or pattern.

3. Habitats that can be arrayed by increased species diversity due to the addition of new species, rather than by replacement of species, are referred to as exhibiting nested subsets. It is unclear what ecological mechanisms are responsible for nested subset behavior, but two conclusions seem reasonable. First, nested subset behavior suggests that local biodiversity is not strongly influenced by species interactions. Second, the absence of the nested subsets could be due to many factors.

4. Recurrent groups are clusters of species that characterize a habitat type. Under particular circumstances, other species may be added, but the recurrent groups will be relatively constant. The concept was introduced by Fager (1957), who identified a central recurrent group of 23 invertebrates in decaying oak wood with 10 smaller groups that occurred under particular circumstances. The extent to

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Table 1—A synoptic list of the more common hypotheses evoked to explain patterns of biodiversity

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Regional Biodiversity

Biogeographic Constraints. Regional biotic patterns are determined by such geological processes as (1) the formation/disappearance of land bridges due to changes in sea level, and (2) the formation of mountains and other barriers and the isolation of continents through large tectonic plate movements. Global climate change can also isolate biotas through the creation of climatic barriers, e.g., isolating biota on mountain tops during periods of warming temperature.

Stability Hypothesis: *Relatively constant environments permit finer evolutionary niche partitioning, more specialization, and hence, greater species packing in communities.* This hypothesis has been evoked to explain the relatively rich diversity of deep marine benthic communities.

Local Biodiversity

Productivity Hypothesis: *Habitats with high-primary productivity support more species than habitats with low-primary productivity.* Clearly, very low productive environments, such as very arid deserts, have low species diversity; however, there seems to be no consistent relationship between primary productivity and local species diversity. An apparent exception is the general relationship between increasing levels of potential evapotranspiration and plant species diversity.

Structural Hypothesis: *Habitats that are structurally more complex support more species than habitats with simple structure.* Physical complexity produces more potential microclimates, substrates, and refugia from predators; hence, more physical niches for species. For example, the addition of inert physical structures, such as glass plates, into experimental ponds provides more substrate for algae and diatoms, thereby increasing species diversity.

Competitive/Predation Hypothesis: *In ecological time, competitive displacement reduces species diversity while predation may either increase or decrease species diversity.* The extent to which natural communities are structured by competition is still an open question despite decades of field and theoretical work premised on the importance of competition in nature. In competitively structured communities, predation on the competitively dominant species can prevent competitive displacement, thereby helping to maintain local diversity. The classic example is predation by starfish on competitively dominant mussels in the Pacific Northwest, giving rise to the notion of "keystone predators" (Paine 1966). Of course, predation can also simplify communities by exterminating prey species.

Intermediate Disturbance Hypothesis: *Habitats with very low or very high levels of disturbance have fewer species than habitats with intermediate levels of disturbance.* In very constant environments, populations reach densities at which competitive displacement removes species. Habitats that undergo constant disturbance contain only species with high colonization abilities. This hypothesis emphasizes the importance of the interplay of equilibrial (generally competition) and nonequilibrial (stochastic disturbances) processes to explain local patterns of biodiversity. An example may be the role of treefall disturbances in tropical forests that maintain colonizing tree species and provide the light resources to permit growth of young noncolonizing tree species.

Time Hypothesis: *Species diversity increases over time.* Some habitats are too new to have accumulated a full complement of species, e.g., land exposed by a retreating glacier, landslides, changes in river courses, etc.

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which recurrent groups exist is an empirical question that warrants additional fieldwork. But, when recurrent groups are found, what does it mean? Several explanations seem plausible. The presence of recurrent groups could simply indicate a cluster of particularly good colonizing species. Conversely, recurrent groups could represent species that are highly adapted to the particular habitat or resource. The latter seems far more likely and suggests that the existence of recurrent groups should be an important focus of research.

5. Species do not seem to be added to habitats at random; rather, a sequence is followed, albeit very loosely in many cases. The extent to which such sequences can be predicted suggests that "assembly rules" are important for explaining succession or species richness. Most commonly, assembly rules are used to imply that the successful establishment of later species is dependent on the prior presence of particular earlier species. That is, the earlier species "condition" the habitat and influence subsequent patterns of species establishment. Assembly rules have most commonly been used to explain the temporal process of island colonization.

Biodiversity Concepts: The Potential Contribution from Coarse Woody Debris Communities

Biodiversity studies of coarse woody debris (CWD) communities have a number of advantages over other systems:

- CWD comes in discrete units (stems and logs).
- CWD can be experimentally manipulated (stems and logs can be moved).
- CWD comes in different volumes (sizes from small stems to large logs).
- CWD comes in different ages (freshly fallen to decayed).
- CWD comes in different resource qualities (species and decomposition stage).

Potential Manipulation Experiments

Because CWD can be readily manipulated in field experimental designs, some biodiversity hypotheses can be tested in more rigorous ways.

Productivity Hypothesis

How are numbers of individuals or total species biomass related to diversity of CWD organisms? Does the form of the productivity/diversity relationship change as a function of CWD size or tree species?

Structural Hypothesis

Do mixed-sized classes of CWD support more species than patches made up of single-sized classes? Are large diameter logs more structurally diverse than smaller diameter logs? That is, at what diameter class do species begin to show physical niche separation in the log? How important is tree species diversity of CWD to the biodiversity of the CWD communities? What about topographic heterogeneity, e.g., do areas with both wet and dry sites support more CWD species than areas that are either generally dry or generally wet?

Competition/Predation Hypothesis

Do predators increase or decrease species diversity? Do larger logs provide more prey refugia? How do prey refugia change as a function of the stage of CWD decomposition?

Intermediate Disturbance Hypothesis

How do periodic fires influence the long-term average species diversity of CWD communities?

Stability Hypothesis

How is CWD half-life related to species richness? Is there a rate of CWD decomposition that maximizes biodiversity? Over the entire process of decay, does CWD with long half-times of decay support more or fewer species than CWD with short half-times? Are rates of decay and biodiversity influenced more by the temporal variance or the mean temperature or moisture?

Structure of Biotic Communities

Although the most important feature of CWD is its suitability for experimentation, various indirect community structure questions can be addressed as well.

Species "Area" Relationship

Is there a constant species-CWD volume relationship? How does the slope (Z value) of this function compare to the slopes found in historical studies of mainland or island communities? What determines levels of beta-diversity in CWD organisms, e.g., is the value of beta greater in CWD patches made up of mixed tree species? How do the beta values for CWD organisms compare to aboveground vegetation beta values?

Assembly Rules

How important are early colonizing decay fungi to subsequent patterns of diversity and rates of species change? If the early colonizing fungi are white rot versus blue stain, does the difference influence subsequent diversity patterns and processes in more than the short term? Do biogeographic faunal/fungal differences influence the patterns and processes of biodiversity in CWD? For example, does the absence of large passalid beetles in the Pacific Northwest influence CWD colonization by affecting the distribution of tunnel diameters? Does the absence of strong assembly rules suggest a large degree of functional redundancy in the CWD faunae?

Nested Subsets

How common are nested subset patterns in different CWD communities? What determines the addition of satellite groups? What do recurrent groups suggest about functional redundancy in CWD decay communities? If strong patterns of recurrent groups are found, should they be treated as a kind of aggregate "keystone species complex"?

Some Concluding Thoughts

The analysis of biodiversity in CWD communities should emphasize experimentation. In particular, a "common garden" approach wherein CWD is translocated into different environments will be important. Such an approach would make it possible to sort out confounding factors such as differences in tree species, stand history, and local climate. For example, fallen logs of longleaf pine (*Pinus palustris*) appear to have relatively depauperate decay communities. Is this due to physical/chemical properties of this pine, such as its large amount of pitch resin, or, to the variable moisture levels in sandy coastal plain soils, or to the fact that high-fire frequency lowers CWD faunal diversity at the regional level?

There is also a need to consider landscape scale effects on biodiversity. For example, the extraction of turpentine, gums, and resins used to be a major forest industry in the southern pine region. During that period, the turpentine borer (*Buprestis apricans*) was the most serious pest, often limiting production and subjecting the tunnel-ridden trees to wind breakage (Baker 1972; Beal 1932). Because the beetle is strongly attracted to the slashes for resin extraction points and oviposits in these entry points, management practices for the extraction of naval stores clearly contributed to the enormous populations of this borer and, consequently, to large-scale patterns of CWD production. After World War II, the industry declined and pine orchards managed for naval stores largely disappeared. Subsequently, the turpentine borer has greatly declined in abundance. The production practices for naval stores that occurred throughout the Southeastern pine lands greatly altered CWD production over vast areas. Similarly, other regionwide management practices such as prescribed burning, low-tree density plantations for timber versus higher tree-density plantations for pulp production, and mixed hardwood/conifer production for wildlife will also have large-scale effects on CWD production and, hence, on its associated biodiversity.

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Coarse Woody Debris and Woody Seedling Recruitment in Southeastern Forests

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Abstract

Few studies have examined the role of coarse woody debris (CWD) in woody seedling recruitment in Southeastern forests. Elevated substrates formed by logs, stumps, and other CWD appear to provide sites for seed trapping, germination, and seedling establishment in wetland forests that are frequently flooded during all or a portion of the growing season. Although their importance to the regeneration of the canopy dominant species may be limited, they may enhance the diversity of these forest systems by enabling the establishment of a variety of woody species. The chief value of CWD to seedling recruitment may be in providing an array of microhabitats on the forest floor and increasing environmental heterogeneity, thus providing regeneration niches for a mixture of species.

Introduction

The ecological significance of coarse woody debris (CWD) in forests is becoming recognized, partly as a result of increased research in recent years (Harmon and others 1986). Abundant in many natural forest ecosystems, CWD functions in energy flow and nutrient cycling, influences soil movement, and serves as habitat for numerous organisms. It includes a wide variety of types and sizes of decaying woody materials: standing snags, fallen logs and branches, and stumps. The input of this material to the forest floor—whether through small-scale events such as individual treefalls or through larger-scale phenomena such as wind storms that cause numerous tree blowdowns—increases the heterogeneity of substrates and results in a variety of microsites. The availability of a range of microsites creates numerous regeneration niches for seedlings of different species whose adults may be ecologically similar (Grubb 1977).

Microsites are important to the biological diversity in forests. Species richness in plant communities may be maintained by a heterogeneous environment acting on a series of stages in the reproduction of plants (Grubb 1977). The stages include seed production, dispersal, germination, seedling establishment, and the survival and growth of juvenile plants to reproductive adults. The importance of microsites caused by treefalls as new colonization sites for tree seedlings in temperate forests has been shown (e.g., Collins 1990; Collins and Pickett 1982; Hutnik 1952; Schaetzl and others 1989; Webb 1988). Most studies, however, have examined seedling establishment on soil substrates such as pits and mounds associated with uprooted trees, rather than on the decaying woody material. Less information exists about the potential role of logs, stumps, or other woody debris in forest seedling recruitment. Nevertheless, several studies have specifically examined woody seedling establishment on decaying logs in forests of the United States. Growth of *Picea Engelmannii* and *Abies lasiocarpa* seedlings on rotting logs in a Colorado spruce-fir forest was described by McCullough (1948). Christy and Mack (1984) reported that 98 percent of the *Tsuga heterophylla* seedlings in an old-growth *Pseudotsuga menziesii-Tsuga heterophylla* forest in Oregon were rooted on rotten wood that covered only 6 percent of the forest floor. Similarly, in a *Picea sitchensis-Tsuga heterophylla* forest of the Northwest Coast, McKee and others (1982) found that 94 to 98 percent of the tree seedlings were growing on CWD, which constituted 6 to 11 percent of the forest floor. In experimental studies, survival and growth of seedlings on decaying logs in this forest type increased as litter and humus accumulations increased (Harmon 1987).

Harmon (1989) suggested that rotting wood may be more important as a seedbed in forests of the Pacific Northwest because it covers more of the forest floor there (6 to 25 percent) than in other regions of the United States (1.6 to 4 percent). Seedling survival in these forests is initially low on the forest floor because of severe competition with mosses and herbs, and "nurse logs" serve as safe sites for early establishment. He noted, however, that long-term seedling survival on nurse logs is often low because of competition among seedlings and fragmentation of the wood substrate (Harmon 1989). In addition, unless the surviving tree saplings send roots down into the mineral soil, they are prone to toppling from logs.

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Southeastern Forests

Few studies have focused on the importance of woody debris to seedling regeneration in the forests of the Southeastern United States. Most reports of seedling recruitment on nurse logs or stumps are anecdotal. In a study of large woody debris in riparian zones of Southern Appalachian forests, Hedman (1992) used seedling ages to estimate the minimum residence time of nurse logs. Of the six seedling species, the most common were *Betula lenta* and *B. alleghaniensis* (64 percent), as well as *Tsuga* spp. (25 percent). Other species were *Magnolia fraseri*, *Liriodendron tulipifera*, and *Quercus* spp. He noted that the abundance of *Betula* seedlings on CWD was not unexpected since these species are often found in canopy gaps in riparian systems. The most common species of nurse logs were *Castanea dentata* (39 percent) and *Tsuga* spp., both of which are relatively resistant to decay and therefore remain in place for long periods of time.

Several current studies are examining seedling recruitment in sites of abundant CWD input following major Southeastern windstorms. Myers and others (1993) have measured CWD and regeneration layer vegetation on *Pinus* spp.-hardwood plots on the Santee Experimental Forest in the South Carolina Coastal Plain following Hurricane Hugo. Imm and McLeod[1] are comparing seedling regeneration following a tornado on timber-salvaged and unsalvaged bottomland hardwood plots on the Savannah River Site in South Carolina. Conner (1993) has reported very little natural regeneration of woody species during the first two growing seasons following Hurricane Hugo in low-lying forest areas on Hobcaw Barony, SC. He did note occasional establishment of *Persea borbonia, Myrica cerifera, Lyonia lucida,* and *Acer rubrum* on old stumps, baldcypress buttresses and knees, and other areas raised above the water.

Elevated microsites formed by CWD may allow growth of certain plants and may be important in maintaining species diversity in swamps and wetland forests where the soil substrate of the forest floor is covered with water during all or a portion of the growing season. Floating log and stump communities in the Blue Girth Swamp of Alabama were described by Hall and Penfound (1943), who noted that they contained wetland and terrestrial plant species not found on the forest floor. In a study of the Santee Swamp of South Carolina, Dennis and Batson (1974) listed eight woody species (among 24 total species) that were abundant on stumps and floating logs, and Irwin (1975) described similar communities on stumps in the Savannah River floodplain; *A. rubrum* was the most common woody seedling in both cases. It should be noted that the wood of baldcypress, *Taxodium distichum,* a common canopy tree in these Southeastern swamp forests, is relatively resistant to decay. Thus, some CWD probably persists for long periods in these wetland systems.

Seedling Recruitment on CWD in Floodplain Forests

Studies of woody seedling recruitment in riverine swamp systems have shown that CWD and microtopography associated with CWD provide sites for early seedling establishment (fig. 1). In a *Taxodium distichum-Nyssa aquatica* swamp on the floodplain of the Savannah River in South Carolina, Huenneke and Sharitz (1986) examined the distribution of woody seedlings across 16 distinct types of microsites, including forms of woody debris (stumps, logs, branches, and twigs), living wood (tree and shrub bases, baldcypress knees, mats of fine roots), sediment adjacent to dead or living woody substrates, and open sediment at low and higher elevations. They found seedlings of six trees (*T. distichum, N. aquatica, Planera aquatica, A. rubrum, Fraxinus caroliniana, and Quercus* spp.), two shrubs (*Itea virginica* and *Cephalanthus occidentalis*), and five woody vines (*Smilax laurifolia, Vitis* spp., *Ampelopsis arborea,*

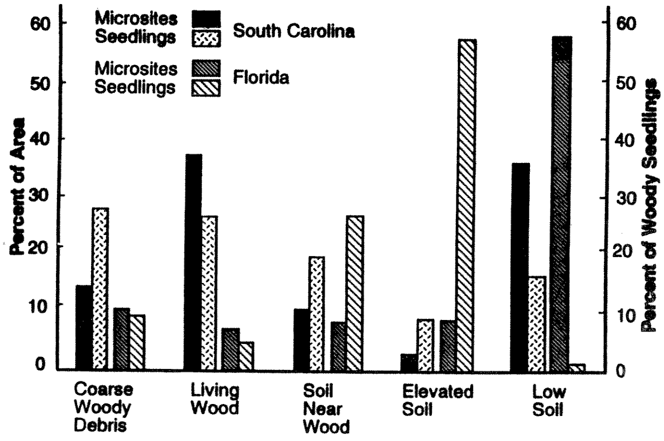

Figure 1—Distribution of microsites and woody seedlings in floodplain swamps in South Carolina and Florida. Coarse woody debris = logs, stumps, branches, and twigs; living wood = tree and shrub bases, baldcypress knees, and fine root mats; soil near wood = soil within 5 cm of woody debris or living wood; elevated soil is typically not submerged during growing season; low soil is typically submerged (Huenneke and Sharitz 1986; Titus 1990).

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[1] Imm, Donald W. [and others]. 1994. Manuscript: Tornado induced changes in composition and successive differences during recovery due to treatment effects. Savannah River Ecology Laboratory, Aiken, SC.

Rhus radicans, and *Berchemia scandens*) growing on microsites that were elevated above the level of the surrounding forest floor. Approximately 75 percent of the woody seedlings occurred on woody debris, living wood substrates (especially root mats), or in soil adjacent to woody microsites (fig. 1). Given the low abundance of CWD, these decomposing wood microsites support a disproportionally large percentage of seedlings. The canopy dominant species, *T. distichum* and *N. aquatica*, constituted approximately 32 percent of all woody seedlings.

Similarly, in the broadleaf deciduous forest of the Welaka swamp on the St. Johns River floodplain in Florida, Titus (1990) examined the distribution of woody seedlings in relation to different microtopographic features. He also found that most seedlings occurred on elevated substrates; however, in contrast to the Savannah River swamp, raised soil areas that were rarely submerged provided microsites for more than 57 percent of the seedling recruitment (fig. 1). Approximately 31 percent of the woody seedlings in the Welaka swamp occurred on woody debris, living wood substrates, or in soil adjacent to wood. The canopy dominant species, *F. caroliniana* and *Nyssa sylvatica* var. *biflora*, accounted for only 3 percent of the seedlings; common species on CWD substrates were *A. rubrum, Persea palustris, Sabal palmetto*, and *Vaccinium elliotti.*

To compare seedling-microsite associations between locations, distribution indices (DI) were calculated to express a species' occurrence on a given microsite type, weighted by the abundance of that microsite (table 1). In general, larger or more stable forms of CWD (stumps and logs) supported proportionally greater numbers of seedlings (DI values greater than 1.0), whereas smaller debris (branches and twigs) supported proportionally fewer (DI less than 1.0). Woody seedlings in both swamps showed stronger association with stumps than with any other form of CWD. The higher DI values for woody species in general than for the canopy dominants on stumps and logs in the Savannah River swamp suggest that these CWD substrates may be important in maintaining species richness in this system. Interestingly, few seedlings of the canopy dominants grew on soil adjacent to large woody debris in the Savannah River swamp, although such microsites were far more significant for seedling

Table 1 — Distribution index (DI*) values for selected tree species on coarse woody debris and related microsites in two Southeastern swamps

Microsite	All[1] species	*Taxodium*[1] *distichum*	*Nyssa*[1] *aquatica*	*Acer*[2] *rubrum*	*Quercus*[2] *laurifolia*
Coarse woody debris					
Stump	17.0	6.1	2.3	3.8	1.3
Log	7.7	5.5	0.7	1.5	1.0
Branch	1.1	1.1	0.2	0.1	0.0
Twig	0.0	0.2	0.1	0.1	1.8
Soil near wood					
Near stump	0.5	0.0	0.8	2.7	0.0
Near log	0.5	0.0	0.8	0.3	1.1
Near branch	0.2	0.0	0.5	4.2	5.2
Near tree	1.7	2.5	2.9	2.8	4.3
Near knee	5.8	11.9	10.7	18.0	0.0

* DI = (percent seedlings on a microsite)/(percent area covered by microsite).

[1] Savannah River swamp, SC (Huenneke and Sharitz 1986).

[2] Welaka swamp, FL (Titus 1990).

recruitment in the Welaka swamp. In both systems, seedlings also were strongly associated with elevated soil surrounding clusters of baldcypress knees (highest DI values) and with soil adjacent to tree bases (table 1).

Elevation above the water and physical stability are two features of these microsites that are critical to their function as safe sites for seedling establishment. The Savannah River swamp is a deep-water system with high-energy floods typically occurring during winter months that may erode sediment adjacent to woody structures, whereas the Welaka swamp is a relatively low-energy, shallow-water system. Areas of unflooded soil are more common in the Welaka swamp and provide the most favorable substrate for seed germination and the rooting of seedlings; unflooded soil is not common during the growing season in the Savannah River swamp.

Differences in seedling densities among microsite types in swamps may arise in several ways. First, different densities of seeds may be dispersed to or be trapped by different microsites. In swamps, the seeds of many species are dispersed by water (hydrochory) during periods of inundation, and the process of seed trapping and retention may be particularly important. Schneider and Sharitz (1988) found that seeds of *T. distichum* and fruits of *N. aquatica* were trapped chiefly by logs and knees (fig. 2); very few water-dispersed seeds remained in open areas not associated with emergent substrates. Similarly, seeds were retained and incorporated into the sediment (seed bank) primarily adjacent to logs, knees, and the bases of trees. Second, germination percentages may differ in the environments of different substrates. For example, both *T. distichum* and *N. aquatica* are known to require aerated sites not covered by standing water for germination (Demaree 1932; Shunk 1939). In a deep-water swamp, the importance of emergent microsites may lie chiefly in providing germination and seedling establishment sites above summer water levels. Third, seedling survival and growth rates undoubtedly differ among microsites. Rotting wood has lower concentrations of the nutrients required for plant growth than most mineral and organic soils (Harmon and others 1986), thus growth can be slower on woody microsites than on elevated soil microsites. Nevertheless, erosion may limit seedling survival on soil substrates, especially during high-energy floods.

Stability of the rooting medium is a major component of microsite suitability for swamp tree seedlings. Huenneke and Sharitz (1990) examined the physical properties of several swamp substrate types and their influence on *N. aquatica* performance in the Savannah River floodplain. They focused on the stability of the rooting zone and the relative permanence of various substrate types over a winter flood period. No trees or live knees disappeared during the floods and only one dead stump (out of 22) was lost despite the small size and/or advanced state of decomposition of some stumps. Approximately 10 percent of the logs were completely lost from the study site, and 80 percent had moved downstream or showed signs of having moved or shifted position; small branches and twigs were quite impermanent. It is therefore not surprising that the highest numbers of *N. aquatica* seedlings occurred in association with the more permanent sites of knees and tree bases (fig. 2) and stumps (table 1).

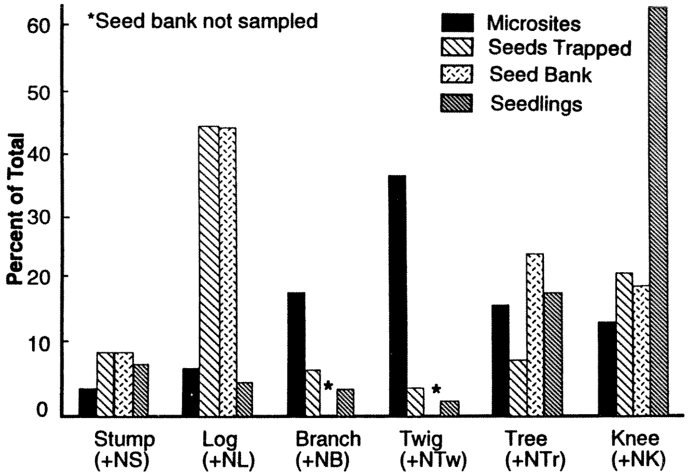

Figure 2—Distribution of *Taxodium distichum* and *Nyssa aquatica* seeds and seedlings on woody microsites (debris and living wood) in a floodplain swamp in South Carolina. Values for each woody microsite include seeds or seedlings in soil within 5 cm of the woody structure (e.g., +NS = near stump) (Schneider and Sharitz 1988).

Emergent CWD microsites may play a role in maintaining woody species diversity in areas that typically are under water during all or a portion of the growing season. In the Congaree Swamp in South Carolina, Putz and Sharitz (1991) observed that CWD microsites enabled less flood-tolerant species such as *Liquidambar styraciflua* and *A. rubrum* to become established and persist in deep-water *Taxodium-Nyssa* sloughs, thus increasing the species richness of the forest. Similarly, Dennis and Batson (1974) noted the diversity of woody seedling species on stumps and floating logs in the Santee Swamp. The long-term importance of these sites to recruitment of canopy species is less certain. Most CWD may be poor substrates for long-term seedling survival and growth. Trees that show rooting patterns indicative of having become established on wood that later decayed are commonly seen in Southeastern swamp forests, but they account for a small percentage of the overall stems. Furthermore, such root systems may be less stable than normally formed roots, and these trees may be more susceptible to uprooting. For example, following Hurricane Hugo, Putz and Sharitz (1991) noted that trees that had rooted on decaying stumps and logs in deep-water areas of the Congaree swamp were more likely to have been uprooted than were trees rooted directly in the sediment.

Even in deep-water *Taxodium-Nyssa* forests, natural variations in water level, especially prolonged periods of low water during the growing season that expose the soil on the forest floor, appear to be required for successful regeneration of the forest canopy trees. In most mixed bottomland forests along river floodplains of the Southeast, seedlings and small saplings (advance regeneration) occur on the forest floor across a variety of microsites. In such forests that are not flooded for prolonged periods during the growing season, small differences in elevation may be correlated with germination and survival of different species (Jones and others 1994) and woody debris may be most important in contributing to the overall environmental heterogeneity of the site, rather than serving as an important substrate for recruitment.

Conclusions

The role of CWD in Southeastern forests may have received less attention than in other parts of the country for several reasons. Most of the original forests of the Southeast were logged in the 1700's and 1800's, and few natural stands of large trees remain today; this is especially true in the Piedmont. In the moist temperate climate of the Southeast, wood decomposition occurs rapidly and many of the native tree species are not especially decay-resistant. Furthermore, forest management techniques that have been used historically throughout this region have seldom resulted in significant amounts of CWD scattered across the forest floor. Although approaches to forest management that consider ecological principles are being adopted in the Southeast (Sharitz and others 1992), and awareness of the potential value of CWD is increasing, there may typically be less rotting wood in Southeastern forests than in forests elsewhere.

The importance of woody debris to regeneration in Southeastern forests is not known, although studies have documented the occurrence of woody seedlings on CWD, especially in wetland forests. Woody debris may be important in building up structure and sediment to form microsites that are not flooded; this is especially likely in wetland systems with low-energy flood waters and less erosive force. The increased heterogeneity and availability of substrates on the forest floor, interacting with increased light in canopy gaps, no doubt provides an array of regeneration niches for different species and may increase the overall richness of the forest community. Even if seedlings are not rooted directly on the CWD, this material influences microenvironmental conditions such as light, moisture, and nutrient availability and results in a greater array of microsites. Further study of seedling establishment, survival, and growth to reproductive maturity in forests with woody debris left intact is needed to evaluate the ecological significance of CWD in the regeneration of Southeastern forests.

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Diversity of Lignicolous Basidiomycetes in Coarse Woody Debris

Karen K. Nakasone

Abstract

Basidiomycetes are the most conspicuous fungi on wood and are the main decomposers. Lignicolous basidiomycetes include white-rotters that remove both lignin and cellulose, and brown-rotters that remove only the cellulose and hemicellulose. The South is a region of diverse lignicolous basidiomycetes because it is the northern limit for many tropical and subtropical taxa and the southern limit for many north temperate taxa. Niches for various taxa are defined by host, substrate, size, and degree of decay. Hence, diversity of these fungi can be enhanced by a mixture of woody angiosperm and gymnosperm debris of different decay and size classes.

Introduction

Southern forests support a species-rich flora of lignicolous fungi. This diversity has its basis in the favorable climatic conditions of the region and the variety of woody plant hosts. The warm temperatures and abundant precipitation are ideal conditions for many species of fungi. Most filamentous fungi that inhabit woody debris are ascomycetes, deuteromycetes, and basidiomycetes. This discussion will be limited to basidiomycetes, which are the most conspicuous fungi on wood and are the major decomposers.

Lignicolous basidiomycetes are divided into two groups based on the type of decay they cause. Fungi that remove both the lignin and cellulose from wood are called white-rotters. The decayed wood is often bleached, with a spongy or stringy texture. Most lignicolous basidiomycetes are associated with a white-rot decay. Fungi that selectively remove the cellulose and hemicellulose, leaving the lignin behind, are referred to as brown-rotters. The woody residues are characteristically dark brown and crumbly, and fall apart in cubes. Only about 6 percent of lignicolous basidiomycetes are known to be associated with brown-rot decay (Gilbertson 1980). There are at least 125 species of brown-rot basidiomycetes, which are classified in four orders: Aphyllophorales (Corticiaceae, Coniophoraceae, Fistulinaceae, Polyporaceae), Agaricales, Tremellales, and Dacrymycetales. A majority of the brown-rot species (70 percent) are members of the Polyporaceae (Gilbertson 1981). About 85 percent of brown-rot fungi are associated with gymnospermous hosts (Gilbertson 1980; Nobles 1958). In some regions, cubical brown-rot residues are the major component in the soils (Harvey and others 1976a; McFee and Stone 1966) and the primary site of ectomycorrhizal root development (Harvey and others 1976b).

The Southern United States hosts the most diverse mycota of lignicolous basidiomycetes in the country. This area is the northern limit for many tropical and subtropical lignicolous basidiomycetes such as *Aleurodiscus mirabilis* and *Gloeodontia discolor.* Similarly, many north temperate species have their most southern distribution in the southeast; *Veluticeps ambigua* and *Phlebia acerina* are examples. Other taxa, such as *Inonotus ludovicianus* and *Resinicium meridionalis* are endemic to the Southern United States. In the last 13 years, a number of new species of lignicolous basidiomycetes have been described from this region (Adaskaveg and Gilbertson 1988; Burdsall and Nakasone 1981, 1983; Burdsall and others 1981; Gilbertson and Blackwell 1984, 1985, 1987, 1988; Larsen and Nakasone 1984; Nakasone 1983, 1984). Nevertheless, the lignicolous mycota of the Southern United States is still poorly known, and many new species are yet to be described.

Host and substrate are important biotic factors that contribute to diversity of fungi on wood. Most species of lignicolous fungi are somewhat host specific. For example, *Aleurodiscus mirabilis* is found on branches of rhododendron, where as *Phlebia hydnoidea* typically occurs on American chestnut and occasionally on oak. Other species are found exclusively or preferentially on gymnospermous or angiospermous hosts. *Auriculariopsis albomellea* and most *Resinicium* species, for example, prefer gymnospermous hosts, whereas *P. albida* and most *Stereum* species occur on woody angiosperms. Other species are omnivorous and have no host preference; *Phanerochaete chrysorhizon* and *Subulicystidium longisporum* are examples of these taxa.

Fungi often display preferences in substrates. Some species colonize only live plants and may be pathogenic or nonpathogenic. Although species such as *Armillaria tabescens* and *Heterobasidion annosum* are aggressive pathogens, many other species are nonpathogenic on living tissue. For example, nonpathogenic fungal endophytes that

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colonize living limbs are also the first ones to decay the dead limbs (Chapela 1989; Chapela and Boddy 1988). Most endophytes are ascomycetes or deuteromycetes. Some basidiomycetes, such as *Dendrothele*, fruit only on bark of living trees. Other species, such as *A. mirabilis* and *Dendrophora versiformis*, fruit primarily on bark of dead branches. Decorticated wood is the preferred substrate for some taxa; however, most species are found on bark and woody tissue. Species of *Resinicium* fruit on decorticated wood, but *Phlebiella vaga* and *Phlebia chrysocreas*, common and widely distributed species, develop sporocarps on bark and wood.

The size of the substrate is also important. Typically, large fruiting bodies are associated with logs, stumps, and snags. For example, *Laetiporus sulphureus* develops fruiting bodies on logs and stumps, and *Armillaria tabescens* is associated with stumps and roots of trees. Other species are specific to branches and twigs. *Stereum striatum* is frequently found on small-diameter twigs and branches of *Carpinus*.

The degree of decay of the woody substrate can also influence fungal diversity. Some lignicolous fungi are associated only with well-rotted wood. These are often fragile or ephemereal species such as *Trechispora farinacea. Amphinema byssoides* and other mycorrhizal corticioid species also develop fruiting bodies on well-rotted wood. In contrast, *Cryptoporus volvatus* commonly fruits within a year after death of its conifer tree host before being replaced by other lignicolous fungi (Gilbertson and Ryvarden 1986).

Some lignicolous fungi also prey on nematodes that inhabit wood. Because nitrogen is in limited supply in woody substrates, many species use nematodes and microbes as nitrogen sources. These fungi have developed several mechanisms to capture nematodes (Thorn and Barron 1984). Specialized cells called stephanocysts produced in some species of *Hyphoderma* become attached to the nematodes and eventually invade the host (Liou and Tzean 1992). Species of *Hoehnbuehelia* produce adhesive cells to catch their prey whereas *Pleurotus ostreatus* produces a toxin that inactivates nematodes. *Pleurotus ostreatus* and other species of lignicolous fungi also utilize bacteria as a nutrient source (Barron 1988; Blanchette and Shaw 1978).

To examine the diversity of lignicolous fungi in more detail, species associated with sweetgum (*Liquidambar styraciflua* L.) and loblolly pine (*Pinus taeda* L.) will be considered. A list of lignicolous basidiomycetes recorded on these hosts is shown in the appendix. Most records were taken from *Fungi on Plants and Plant Products* (Farr and others 1989); other records are from the Forest Products Laboratory. The list is not exhaustive. At least 73 species of lignicolous basidiomycetes are associated with loblolly pine and 120 species with sweetgum, compared to 228 species reported for ponderosa pine (Gilbertson 1974) and 260 for aspen (Lindsey and Gilbertson 1978). The taxa are distributed in five orders, with most species classified in the order Aphyllophorales (table 1). Within the Aphyllophorales, the majority of species are classified into two families: the Corticiaceae, which consist of many white-spored genera that have a primarily resupinate habit, and the Polyporaceae, which include most of the poroid genera. Fifty-two and 80 genera have been reported on loblolly pine and sweetgum, respectively, representing a total of 103 different genera. A few genera are represented by four or more species: *Pleurotus, Hyphoderma, Phanerochaete, Phlebia, Phellinus*, and *Stereum.*

Table 1—Distribution of lignicolous basidiomycetes on loblolly pine and sweetgum by order

Order	Loblolly pine	Sweetgum
Agaricales	5	17
Aphyllophorales		
Corticiaceae	27	33
Hymenochaetaceae	4	8
Lachnocladiaceae	2	4
Polyporaceae	25	36
Stereaceae	0	5
All other families	5	10
Auriculariales	1	2
Dacrymycetales	4	2
Tremellales	0	3

Table 2—Lignicolous basidiomycetes common to both sweetgum and loblolly pine

Armillaria tabescens
Auricularia auricula
Dacryopinax spathularia
Diplomitoporus overholtsii
Gloeophyllum sepiarium
Hyphoderma praetermissum
Hyphoderma puberum
Hyphoderma setigerum
Laxitextum bicolor
Nigroporus vinosus
Phanerochaete burtii
Phanerochaete chrysorhizon
Phanerochaete flavido-alba
Phlebiella vaga
Schizophyllum commune
Subulicystidium longisporum

No representatives of the Stereaceae have been reported on loblolly pine. In North America, *Stereum*, a common and widespread genus, occurs primarily on angiospermous hosts; *Stereum sanguinolentum* is the only species that occurs on conifers, but it has not been recorded on loblolly pine. Similarly, most species in the Hymenochaetaceae and Lachnocladiaceae are associated with angiospermous hosts.

Of the 193 taxa reported on both sweetgum and loblolly pine, only 16 species (9 percent) are common to both hosts (table 2). Most of these taxa are common and widely distributed throughout North America. Five species of brown-rot fungi have been reported on sweetgum compared to 14 species on loblolly pine (table 3). This represents about 4 percent and 19 percent, respectively, of all the fungi reported from these hosts. These values are similar to that found for other gymnospermous and angiospermous hosts (Gilbertson 1980, 1981).

Table 3—Brown-rot decay fungi on loblolly pine and sweetgum

Loblolly pine	Sweetgum
Antrodia radiculosa	*Dacrymyces minor*
Antrodia serialis	*Dacryopinax spathularia*
Antrodia xantha	*Fomitopsis spraguei*
Coniophora olivascens	*Gloeophyllum sepiarium*
Dacrymyces stillatus	*Gloeophyllum trabeum*
Dacryopinax spathularia	
Fomitopsis palustris	
Gloeophyllum carbonarium	
Gloeophyllum sepiarium	
Laetiporus persicinus	
Phaeolus schweinitzii	
Postia caesia	
Postia guttulata	
Wolfiporia cocos	

Table 4—Sibling fungal species on loblolly pine and sweetgum

Loblolly pine	Sweetgum
Dacrymyces stillatus	*Dacrymyces minor*
Inonotus circinatus	*Inonotus ludovicianus*
Ganoderma meredithae	*Ganoderma lucidum*
Junghuhnia luteoalba	*Junghuhnia nitida*
Meruliopsis ambiguus	*Meruliopsis corium*
Peniophora pini subsp. duplex	*Peniophora violaceolivida*
Perenniporia subacida	*Perenniporia tenuis*
Scytinostroma galactinum	*Scytinostroma protrusum*

Several sibling species occur on loblolly pine and sweetgum (table 4). These species are morphologically similar and often share a similar habit, but one taxon occurs primarily or exclusively on angiospermous wood whereas the other prefers gymnospermous wood. For example, fruit bodies of *Scytinostroma galactinum* and *S. protrusum* are morphologically identical but can be distinguished by isozymes and cultural morphology (Nakasone and Micales 1988). In addition, *S. galactinum* occurs exclusively on gymnosperms, whereas *S. protrusum* is known only on woody angiosperms.

Accurate totals of species of lignicolous fungi have become available only recently. Ginns and Lefebvre (1993) included 1,163 species of lignicolous, corticioid basidiomycetes (including the jelly fungi) from Canada and the United States. Gilbertson and Ryvarden (1986-87) described 411 species of polypores from North America. Added to the approximately 620 species of Agaricales (Gilbertson 1980) that occur on wood, the total number of lignicolous basidiomycetes reported from North America is 2,194. Therefore, the 177 unique species on sweetgum and loblolly pine represent 8.1 percent of the total mycota of lignicolous basidiomycetes from North America.

As an example of the potential diversity in the Southern United States, we can examine the fungi reported from different habitats and hosts from this region. Jung (1987) described 130 species of wood-rotting Aphyllophorales from the spruce fir forest of the Southern Appalachians. Only 38 species (29 percent) are also reported on sweetgum and loblolly pine; 92 species (71 percent), representing 25 genera, are not reported. Similarly, Gilbertson and Blackwell (1985, 1987) described 51 taxa of lignicolous fungi on juniper in the Gulf Coast region, of which 41 species do not occur on loblolly pine or sweetgum, or in the spruce fir forest.

These examples can be used to obtain a rough estimate of the number of species of lignicolous basidiomycetes that occur in the Southern United States. A total of 300 different lignicolous species are reported on loblolly pine, sweetgum, and juniper, and from the spruce fir forest region. A conservative estimate for this region is 600 species; an optimistic estimate is 1,000 species. It is important to remember that this entire discussion has focused on fungi that produce fruiting bodies. There are probably many species living in woody tissue that rarely or never produce fruiting bodies because the environmental conditions are not optimal. Although many of these species can be cultured, they often cannot be identified. Thus, by relying on sporocarps to evaluate fungal diversity, we are sampling just a part of the mycota.

In summary, the diversity of lignicolous basidiomycetes in the southern forests is directly related to the quality and quantity of the coarse woody debris. Diversity of these fungi can be enhanced by a mixture of woody angiosperm and gymnosperm debris of different decay and size classes.

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Appendix

Basidiomycetes that decay loblolly pine and sweetgum[a]

		Genera	
Order	Family	Loblolly pine	Sweetgum
Agaricales		*Armillaria tabescens* *Hohenbuehelia pinacearum* *Pholiota spumosa* *Phyllotopsis nidulans* *Tricholomopsis rutilans*	*Armillaria mellea* *Armillaria tabescens* *Coprinus disseminatus* *Gymnophilus armillatus* *Gymnophilus praefloccosus* *Lentinellus ursinus* *Lentinus strigosus* *Lentinus tigrinus* *Oudemansiella canarii* *Panellus pusillus* * *Pholiota limonella* *Pleurotus cystidiosus* *Pleurotus dryinus* *Pleurotus levis* *Pleurotus ostreatus* *Simocybe ataomacea* *Volvariella bombycina*
Aphyllophorales	**Auriscalpiaceae**		*Gloeodontia discolor*
	Clavariaceae		*Clavicorona pyxidata*
	Coniophoraceae	*Coniophora olivascens*	
	Corticiaceae	* *Amphinema byssoides* * *Chaetoporellus latitans* * *Confertobasidium olivaceo-album* *Grandinia arguta* * *Grandinia barbajovis* * *Grandinia pallidula* * *Hyphoderma pallidum* * *Hyphoderma praetermissum* * *Hyphoderma puberum* * *Hyphoderma sambuci* *Hyphoderma setigerum* *Hyphodontia arguta* * *Hyphodontia barbajovis* * *Hyphodontia pallidula* *Laxitextum bicolor* *Meruliopsis ambiguus* *Meruliopsis taxicola* *Peniophora pini subsp. duplex* *Phanerochaete burtii* *Phanerochaete chrysorhiza* * *Phanerochaete flavido-alba*	* *Botryobasidium vagum* *Candelabrochaete langlosii* *Cylindrobasidium laeve* * *Dendrophora versiformis* *Dendrothele microspora* *Dendrothele strumosa* *Gloeocystidiellum porosum* *Gloeocystidiellum turpe* *Gloeoporus dichrous* *Hyphoderma mutatum* * *Hyphoderma praetermissum* * *Hyphoderma puberum* *Hyphoderma rimosum* *Hyphoderma setigerum* * *Meruilopsis corium* * *Peniophora violaceo-livida* *Phanerochaete burtii* *Phanerochaete chrysorhiza* *Phanerochaete crassa* *Phanerochaete flavido-alba* *Phanerochaete velutina*

Basidiomycetes that decay loblolly pine and sweetgum[a] (continued)

		Genera	
Order	Family	Loblolly pine	Sweetgum
		* *Phanerochaete gigantea*	*Phlebia chrysocreas*
		Phanerochaete sordida	*Phlebia ludoviciana*
		Phlebiella vaga	* *Phlebia radiata*
		Pseudomerulius curtisii	*Phlebia setulosa*
		* *Resinicium bicolor*	* *Phlebiella vaga*
		* *Resinicium furfuraceum*	* *Pulcherricium caeruleum*
		Resinicium meridionale	* *Schizopora flavipora*
		Scytinostromella fallax	* *Schizopora paradoxa*
		* *Subulicystidium longisporum*	* *Subulicystidium longisporum*
			* *Trechispora farinacea*
			* *Trechispora regularis*
			* *Xenasmatella tulasnelloidea*
	Ganodermataceae	*Ganoderma meredithae*[b]	*Ganoderma lucidum*
	Hericiaceae		*Hericium erinaceus*
			Laxitextum bicolor
	Hydnaceae	*Mycorrhaphium adustum*	*Climacodon pulcherrimus*
			Climacodon septentrionalis
	Hymenochaetaceae	*Hymenochaete pinnatifida*	*Hymenochaete agglutinans*
		Inonotus circinatus	*Inonotus ludovicianus*
		Phellinus pini	* *Inonotus rickii*
		Phellinus viticola	*Phellinus conchatus*
			Phellinus ferruginosus
			Phellinus gilvus
			Phellinus laevigatus
			Phellinus melleoporus
	Lachnocladiaceae	*Dichostereum pallescens*	* *Asterostroma cervicolor*
		Scytinostroma galactinum	* *Dichostereum sordulentum*
			* *Scytinostroma protrusum*
			* *Vararia sphaericospora*
	Polyporaceae	* *Antrodia radiculosa*	*Bjerkandera adusta*
		Antrodia serialis	*Ceriporia xylostromatoides*
		* *Antrodia xantha*	* *Ceriporiopsis pannocincta*
		* *Ceriporia tarda*	*Cerrena unicolor*
		Coriolopsis gallica	*Coriolopsis rigida*
		Cryptoporus volvatus	*Daedaleopsis confragosa*
		Dichomitus squalens	* *Diplomitoporus overholtsii*
		* *Diplomitoporus overholtsii*	*Fomes fasciatus*
		Fomitopsis palustris	*Fomitella supina*
		* *Gloeophyllum carbonarium*	*Fomitopsis spraguei*
		Gloeophyllum sepiarium	*Gloeophyllum sepiarium*
		Heterobasidion annosum	*Gloeophyllum trabeum*
		Junghuhnia luteoalba	* *Heteroporus biennis*
		* *Laetiporus persicinus*	*Hexagonia hydnoides*

Basidiomycetes that decay loblolly pine and sweetgum[a] (continued)

Order	Family	Genera	
		Loblolly pine	Sweetgum
		Meripilus sumstinei	*Junghuhnia nitida*
		Nigroporus vinosus	*Lenzites betulina*
		Perenniporia subacida	*Nigroporus vinosus*
		Phaeolus schweinitzii	*Oxyporus latemarginatus*
		Postia caesia	* *Perenniporia compacta*
		Postia guttulata	* *Perenniporia tenuis*
		Skeletocutis amorpha	*Polyporus arcularius*
		Skeletocutis nivea	*Pycnoporus cinnabarinus*
		Trichaptum abietinum	*Pycnoporus sanguineus*
		Tyromyces chinoeus	*Rigidoporus lineatus*
		Wolfiporia cocos	*Rigidoporus ulmarius*
			Tinctoporellus epimiltinus
			Trametes hirsuta
			Trametes subectypus
			Trametes versicolor
			Trichaptum biforme
			Trichaptum sector
			* *Tyromyces fissilis*
			Tyromyces galactinus
			* *Wrightoporia avellanea*
	Steccherinaceae		*Steccherinum ochraceum*
			* *Steccherinum subrawakense*
	Stereaceae		*Stereum hirsutum*
			Stereum ochraceo-flavum
			Stereum ostrea
			Stereum striatum
			Xylobolus subpileatus
	Schizophyllaceae	*Schizophyllum commune*	*Schizophyllum commune*
	Thelephoraceae	*Tomentella ferruginea*	
Auriculariales		* *Auricularia auricula*	*Auricularia auricula*
			Auricularia cornea
Dacrymycetales		* *Cerinomyces pallidus*	* *Dacrymyces minor*
		Dacrymyces chrysospermus	*Dacryopinax spathularia*
		Dacrymyces stillatus	
		Dacryopinax spathularia	
Tremellales			*Exidia recisa*
			* *Heterochaete shearii*
			Tremella mesenterica

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[a] Species listed in Farr and others (1989). Those with an asterisk (*) are from records in Center for Forest Mycology Research, Forest Products Laboratory.

[b] Obtained from Adaskaveg and Gilbertson (1988).

Earthworms, Biodiversity, and Coarse Woody Debris in Forest Ecosystems of the Southeastern U.S.A.

Paul F. Hendrix

Abstract

Few studies have been conducted in the Southeast, or elsewhere, on earthworms and coarse woody debris (CWD). Species of potential importance to CWD in Southeastern forests include several native and introduced lumbricids and an introduced Asian megascolecid. Earthworms may use CWD as a refuge and a resource while enhancing decomposition, primarily at the secondary phase of colonization. After channelization by other organisms, earthworms may contribute to decay through transport of soil, nutrients, and microbes into wood. Selective feeding on fungal hyphae may also be important. Maximum earthworm diversity in CWD may occur during the secondary colonization and maceration phases of decomposition. Knowledge is lacking in systematics, processes, and the influence of management practices.

Introduction

Interest in biodiversity arises from several motivations. These include (1) a sense of intrinsic value in the existence of a variety of species, (2) known or expected practical values of species or products derived from them, and (3) knowledge or hypotheses that many species in an ecosystem participate in processes important to ecosystem function. This latter motivation is a central issue in modern ecology and is likely to be an important component of emerging ecosystem management strategies. The premise of this paper is that the diverse assemblages of earthworms present in many soils influence soil processes and, by extension, may also influence coarse woody debris (CWD) dynamics in forest ecosystems.

Despite the voluminous literature on earthworm biology and ecology, surprisingly few studies have examined interactions between earthworms and CWD. Few of these apply directly to the Southeast. This paper considers selected literature relevant to CWD and earthworms, presents some interpretations and hypotheses about interactions between earthworms and CWD, and identifies areas for further research.

Background

Earthworm Systematics and Biogeography

Earthworms belong to the class Oligochaeta, which consists of some 20 families worldwide (Reynolds and Cook 1993). Three of these families include aquatic or semi-aquatic worms. Most of the other families consist of terrestrial forms, many of which are of possible significance in forest ecosystems. Two families (Komarekionidae and Lutodrilidae, both monotypic) and genera from three others (Lumbricidae, Sparganophilidae, and Megascolecidae) are native to North America (table 1). James (1995) suggests that endemic representatives of the Ocnerodrilidae may also inhabit isolated areas of the United States.

Pleistocene glaciations, the most recent of which ended approximately 10,000 years BP, are thought to have eliminated the earthworm fauna from Canada and most of the northern portion of the Continental United States (Gates 1970). Glacial refugia apparently remained in the Pacific Northwest, where a number of native genera in the family Megascolecidae now occur (Fender 1995; Fender and McKey-Fender 1990), and in the Southeastern United States where all of the other nearctic groups occur (Gates 1982; James 1995). As many as 100 species of earthworms may occur in the Southeast, with perhaps 10 or more associated with CWD at some stage of decomposition (table 2). Thus, the Southeast has a rich and diverse earthworm fauna, probably reaching its highest biodiversity and greatest potential impacts on soil processes in forest ecosystems throughout the region (Dotson and Kalisz 1989; Hendrix and others 1994; Reynolds 1972, 1976, 1995).

In addition to the native fauna, species from several of the other earthworm families listed in table 1 have been introduced into North America over the past 500 years. Species of the Lumbricidae and Megascolecidae have been particularly successful in the Southeast and can now be found in many areas affected by human habitation, agriculture, and fishing.

Ecological Considerations

Competitive exclusion of native earthworm by exotic earthworm species has been postulated, but little direct evidence of this can be found. Kalisz and Wood (1995) suggest four stages in the establishment of exotic earthworm

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Table 1—Partial listing of oligochaete classification and geographic origins of earthworm families (compiled from Bouche 1983; Reynolds and Cook 1993; Wallwork 1983)

Phylum: Annelida
Class: Oligochaeta
Order: Haplotaxida
Suborder: Lumbricina

Family:	Lumbricidae	NH—NA,EU
	Komarekionidae	NH—NA
	Sparganophilidae	NH—NA,EU
	Lutodrilidae	NH—NA
	Megascolecidae	NH,SH—NA,OC,AS
	Glossoscolecidae	SH—SA
	Eudrilidae	SH—AF
	Acanthodrilidae	SH—AS
	Octochaetidae	SH—OC
	Ocnerodrilidae	SH—SA, AF,AS,MA
	Ailoscolecidae	NH—EU
	Hormogastridae	NH—ME
	Kynotidae	SH—MA
	Microchaetidae	SH—AF
	Almidae	SH—SA, AF,AS

NH = northern hemisphere, SH = southern hemisphere,
NA = North America, SA = South America, EU = Europe,
OC = Oceania, AS = Asia, AF = Africa,
ME = Mediteranean, MA = Madagascar.

populations: (1) habitat disturbance, (2) extirpation or reduction of native populations, (3) introduction of exotic species, and (4) colonization of vacant niche space by exotic species. The principal mechanism of displacement of native populations thus appears to be habitat alteration rather than direct competition. All-native, all-exotic, and mixed communities of earthworms can be found in forest ecosystems in the Southeast, depending on extent of habitat disturbance or human activity. For example, riparian forests are prime areas for establishment of exotics used as fish bait (Callaham and Hendrix, in press), while at least some remote or uncultivated areas still maintain pure native earthworm communities (Dotson and Kalisz 1989; Hendrix and others 1994).

Table 2—Some earthworm genera and species that may use coarse woody debris in Southeastern forest ecosystems

Species	Reference
Bimastos parvus (Eisen, 1874)	Boettcher and Kalisz (1991)
Bimastos zeteki (Smith & Gittins, 1915)	Murchie (1960)
Bimastos sp.	Ausmus (1977)
Eisenoides carolinensis (Michaelsen, 1910)	Boettcher and Kalisz (1991)
Dendrobaena octaedra (Savigny, 1826)	Gates (1982)
Dendrodrilus rubida (Savigny, 1826)	Murchie (1960)
Octolasion sp.	Ausmus (1977)
Lumbricus rubellus (Hoffmeister 1845)	Personal observation
Amynthas spp.	Personal observation

Life history and adaptations of earthworm species present in a given area probably determine their influence on soil processes, including CWD dynamics. Several classification schemes for ecological strategies have been devised, based on earthworm feeding activities and mode of existence in the soil. The most widely used scheme (Bouché 1977) recognizes (1) epigeic species, which inhabit surface litter and humus horizons; (2) endogeic species, which occupy and consume mineral soil; and (3) anecic species, which form vertical burrows in which they live and into which they pull surface litter for food. Some overlap among these categories appears to occur for some species. In any particular ecosystem, species representing all three ecological strategies may occur (Lee 1985). Epigeic and endogeic forms may be the most important at various stages in the decay of CWD.

Species of potential importance to CWD in Southeastern forests include several native and introduced lumbricids and an introduced Asian megascolecid (table 2). Most of these earthworms have epigeic feeding strategies, are polyhumic and pigmented, and have been reported from logs, branches, and/or litter layers of forest soils. The exception, *Octolasion* sp., is endogeic but has been reported in rotting logs (Ausmus 1977).

It might be argued that native species are better adapted to climate, soil, and vegetation in Southeastern forests and therefore may be more important to ecosystem processes than are exotics. Some evidence exists to support this hypothesis, from studies of mixed native and exotic earthworm communities in a tallgrass prairie. James (1991) found that native *Diplocardia* spp. processed more soil nutrients than introduced European lumbricid species, even though the exotics were numerically more abundant. The native earthworms apparently more effectively exploited the soil volume and were able to function over a wider range of soil temperatures (i.e., for longer periods of the year). No similar studies were found for forest ecosystems, although data from Dotson and Kalisz (1989) suggest that native earthworm assemblages in forests of the Southern Appalachians are partitioned throughout the forest floor and soil volume.

Earthworm Interactions With Coarse Woody Debris

Earthworms may use CWD as both refuge and resource (i.e., as habitat and source of food), while simultaneously enhancing the process of decomposition.

Effects of Earthworms on Wood Decomposition

Table 3 presents the stages of decomposition of wood and the associated organisms at each stage, as summarized from Käärik (1974) and Ausmus (1977). Initial stages involve the colonization and conditioning of woody tissues by microbes and surface-dwelling invertebrates, followed by invasion of channelizing invertebrates. Although often considered detritivores, earthworms appear to have only limited ability to digest plant residues such as cellulose or lignin; rather, microbial biomass that colonizes the detritus probably provides nutrition. Hence, earthworms probably do not play a substantial role in wood decomposition until the secondary colonization phase, although some epigeic species (e.g., *Bimastos* spp.) may explore woody surfaces and under bark, feeding on microbes and particulate organic matter. After channels are formed, earthworms may contribute to wood decay through a number of mechanisms (table 4), including transport of soil, nutrients, and microbes into the wood. Earthworm interactions with microbes, such as selective feeding on fungal hyphae, may also be important. As the wood becomes macerated and fragmented, epigeic and endogeic species may become more numerous and further enhance woody decomposition and incorporation into the soil.

A hypothesized sequence of earthworm colonization of CWD is shown in figure 1. Epigeic forms are expected to track the proliferation of fungal hyphae, which may be an important component of the diet of many earthworm species (Lee 1985; Spiers and others 1986). Endogeic (polyhumic and geophagic) species are proposed to become more abundant later in the sequence. Maximum earthworm biodiversity in CWD may occur during the secondary colonization and maceration phases of decomposition (table 3). Ultimately, as the decayed wood becomes a region of organically enriched soil, biodiversity should approach that of the ambient soil and organic horizons.

Factors Affecting Earthworm—Coarse Woody Debris Interactions

As already mentioned, earthworm species differ in life histories and ecological strategies, and these differences determine the extent to which species may interact with CWD. Truly endogeic forms (e.g., *Diplocardia* spp.) may incidentally encounter surface wood but show little preference for it. Conversely, some epigeic species (e.g., *Bimastos parvus,* the American bark worm) may preferentially use CWD. Almost no information is available on the relative abilities of native vs. exotic earthworms to exploit CWD. Natives might be better adapted over the range of climatic and soil conditions at many sites in the Southeast, but introduced species might effectively use woody substrates in disturbed ecosystems or where exotic woody species occur.

Earthworm assemblages seem to be influenced by certain tree species, and by implication perhaps also by CWD. Boettcher and Kalisz (1991) found that where

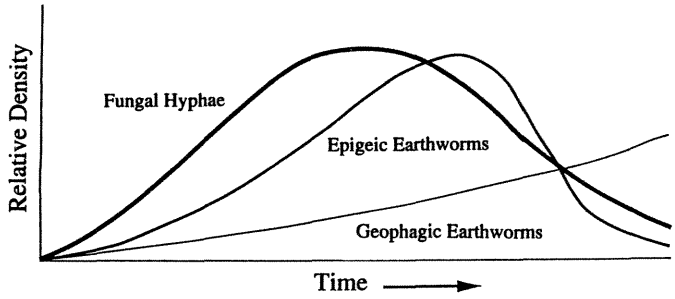

Figure 1—Hypothesized changes in abundance of fungal hyphae and earthworms during decomposition of coarse woody debris.

Table 3—Stages of log decay and decomposer activity (adapted from Käärik 1974 and Ausmus 1977)

Decomposition stage/condition	Organisms involved
Standing dead and sound logs:	Bacteria, fungi (pathogens, saprobes)
Colonization/conditioning:	Moulds, blue-stain fungi Bacteria (cell contents) Diplopods, other surface-dwelling invertebrates
Channelization:	Soft-rot fungi (cell wall carbohydrates) Invertebrates (termites, carpenter ants, Passalid beetles)
Succession/secondary colonization:	Brown-rot fungi (cell wall carbohydrates) Channelizing invertebrates Non-channelizing invertebrates (soil-inhabitants, predators, earthworms) Fecal material Mineral soil within channels
Maceration:	White-rot fungi (cell wall carbohydrates and lignin) Fungal rhizomorphs, root invasion Channelizing and non-channelizing invertebrates Fecal material, mineral soil clogging channels
Incorporation:	Mass of mycelia, fibrous and woody roots Mineral soil mixed into wood

Rhododendron maximum L. was present in Southern Appalachian forests, the native earthworm *B. parvus* was dominant; in the absence of rhododendron under yellow poplar *(Liriodendron tulipifera* L.) or eastern hemlock (*Tsuga canadensis* L. Carr), several other native earthworm species were more abundant, including *Eisenoides carolinensis*. Use of CWD by these earthworms was not discussed, but *B. parvus* and *E. carolinensis* are both epigeic or epiendogeic and may utilize downed wood in their respective stand types. Based on personal observations (mostly in Georgia and Florida), it appears that coniferous logs are used little by earthworms either as refuges or food sources; much more thorough sampling will be needed to confirm this.

Earthworm populations in the Southeast show distinct seasonality in their abundance and activity (fig. 2). Greatest activity is usually seen in spring, although the timing probably varies with latitude and altitude across the region. These seasonal cycles probably influence earthworm exploitation of CWD. Furthermore, if fallen logs provide favorable moisture and temperature conditions beyond those of ambient soil and litter, then earthworm activity within CWD may be extended. This effect may depend on the stage of decomposition, as discussed above.

Finally, the history and nature of management at a site will certainly influence interactions between earthworms and CWD. Long-term agriculture typically reduces abundance and biodiversity of earthworms (Lee 1985). Reforested

Table 4—Suggested influences of earthworms on coarse woody debris (after Ausmus 1977 and Swift 1977)

- Translocation of nutrients and soil into decomposing wood
- Translocation of microbes and inoculation of decomposing wood
- Regulation of microbial succession
- Regulation of microbial activity (catabolism, N_2-fixation)
- Enhancement of nutrient leaching from decomposing wood

agricultural lands, therefore, may be depauperate in species capable of utilizing CWD, unless undisturbed forests are near enough to provide sources for the appropriate species. A useful ecosystem management strategy for maintaining biodiversity of earthworms and other soil biota might be to leave undisturbed source areas within managed forests. In logged but uncultivated areas, earthworm species diversity may remain relatively high as long as soil disturbance is not severe and CWD is left in place after tree harvest.

Research Priorities

Several areas are in need of further research relevant to earthworms, biodiversity, and CWD in Southeastern forest ecosystems:

- Biotic survey and inventory

Still undescribed earthworm species probably exist in the Southeast glacial refugium. Systematic surveys are needed throughout the region to catalog all species and to describe and quantify their habitat requirements. Museum collections in the region need to be updated with this information. Also, training of new specialists in earthworm systematics is urgently needed because of the age of scientists currently working in this area.

- Process studies

Little direct evidence is available concerning the effects of earthworms on CWD. Experimental manipulations of earthworm populations, CWD, and environmental conditions such as water, temperature, or soil properties in the field could reveal conditions under which earthworms affect CWD dynamics. Ecosystem-specific (e.g., hardwood vs. coniferous) effects would be of particular interest. Mechanisms underlying these effects (e.g., earthworm-microbe interactions) could be profitably investigated in short-term laboratory studies.

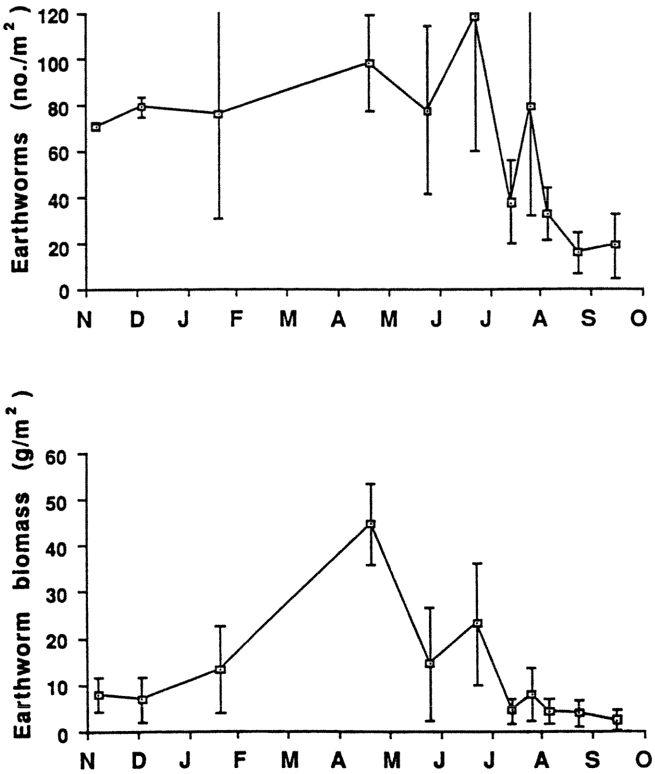

Figure 2—Earthworm density and biomass over an annual cycle in a mixed hardwood-coniferous riparian forest on the Georgia Piedmont (Callaham and Hendrix 1995).

- Management effect studies

What management alternatives are currently available to maintain biodiversity, particularly of soil biota, in forest ecosystems? Field experiments are needed to identify the best practices for managing CWD and associated biota. Long-term studies should be initiated immediataly. Short-term estimates might be derived from studies of historical management practices and chronosequences. National forests in the Southeast may prove to be unique resources for such studies.

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Macroinvertebrates and Their Relationship to Coarse Woody Debris: With Special Reference to Land Snails

Ronald S. Caldwell

Abstract

Macroinvertebrates are an integral part of the succession in natural communities of decomposing logs. Both millipedes and centipedes are reported to be associated with coarse woody debris (CWD), but a much larger literature exists relative to CWD and land snails. Relationships between CWD and land snails are probably similar for other macroinvertebrates. Among land snails, 98 species within 9 families are associated with log habitats specifically in the Southeast. They are involved in regulating decomposition through the dispersal and inoculation of microbes and fungi and in nutrient cycling, particularly calcium. Although snails are detritivores generally, a greater diversity probably occurs where CWD is present.

Introduction

One of the earliest references to the community of organisms in a fallen log is that of Graham (1925). He described the succession of organisms as the chemical and physical properties of the log change with its decomposition. Graham also referred to different microhabitats within the log as favoring certain organisms based upon factors such as food, moisture, and temperature. Fungi were also characteristic of certain parts of the decaying log due to the same factors. In another early report from the Southeast, Pearce (1946) described the microfauna at Duke Forest, Durham, NC. Pearce's research involved leaf litter, not coarse woody debris (CWD) specifically.

Fager (1968) presented a successional picture of invertebrates attacking oak wood substrate at an Oxford University site. The order of succession in natural log communities, after mites and insects and in order of relative abundance, was Isopoda, Chilopoda, Oligochaeta, Diplopoda, and Gastropoda. Also, Oligochaeta, Isopoda, Chilopoda, and Gastropoda were more abundant after bore holes were established.

Ausmus (1977) presented a chronology for organismal attack of fallen logs. Fungi attack pith, then attack bark and surface wood. The result is increasing moisture content, nitrogen accumulation, and organic acid accumulation. Colonization by channelizing invertebrates follows this change in chemical and physical composition of the log.

Table 1 lists millipedes found associated with log habitats in CWD in an Illinois woodland (O'Neill 1967). Table 2 lists species of centipedes associated with log habitats in an Illinois woodland (Summers and Uetz 1979). No literature citations for these two groups in the Southeastern United States were found. No publications were found relative to isopods in Southeastern forests. Earthworms are considered elsewhere in this volume (Hendrix 1996).

Hubricht (1985) presented a checklist and distribution maps for 523 species and subspecies of native land Mollusca of the Eastern United States. Annotated descriptions of the habitat are also given. If one discounts the subspecies, 98 species contained within 9 families are found to be associated with log habitats specifically within the Southeastern United States. The number of species would increase if those associated with both logs and litter were counted.

Food habits of land snails include fungivores, detritivores, herbivores, carnivores, and some that may change functional groups within a food web (Mason 1974). Mason (1970a) determined that the majority of woodland snails were feeding on litter. Mason (1970b) found that snails ingested 0.35 to 0.43 percent of the annual litter input in a beech forest in England. This rate was compared with other studies showing that diplopods and isopods ingested 3 to 4 percent of the leaf litter, oribatid mites 1.8 percent, and millipedes 1.7 to 10 percent. He concluded that the chief importance of these groups may be to physically and chemically alter the litter and thereby promote fungal and microbial growth. It is interesting to note that, based on biomass comparisons to snails, he extrapolated that slugs may ingest as much as 16 percent of the annual litter.

Many of the ecological functions carried out by land snails appear to be similar to those of other macroinvertebrate groups. Relationships that exist between land snails and CWD probably exist between other macroinvertebrates and CWD.

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Table 1—Percentage of millipedes associated with various woody debris habitats from an Illinois woodland[a]

Millipede species	Litter	Under logs	Within logs	Beneath bark	Surface of log
			Percent		
Abacion lacterium	47.4	52.6			
Cleidogonia caesioannularis	71.4	14.3			14.3
Euryurus erythropygus		6.0	94.0		
Fontaria virginiensis	2.9	97.1			
Narceus americanus	4.7	19.4		71.4	4.3
Pseudopolydesmus serratus		12.5		20.8	66.7
Scytonotus granulatus	33.4	60.0			6.7

[a] Data from O'Neill 1967.

Relationships of Land Snails to the Forest Floor

Regulation of Wood Decomposition

One important relationship of macroinvertebrates to the forest floor ecosystem is regulation of mineralization (Ausmus 1977). Bacterial, actinomycete, and fungal densities on sawdust substrates were greater in the presence of invertebrates in laboratory studies including millipedes and centipedes. Four mechanisms regulating wood decomposition by wood-inhabiting invertebrates were postulated:

Table 2—Species of centipedes associated with coarse woody debris from an Illinois woodland[a]

Log species	Log and litter species
Sonibius politus	*Bothropolys multidentatus*
Geophilus vitattus	*Nadabius iowensis*
	Nadabius amele

[a] Data from Summers and Uetz 1979.

(1) Translocation and defecation increase nutrient input to, and the inoculum potential of, wood substrates;

(2) Passive inoculation, as in the case of wood-surface colonizing invertebrates passively inoculating wood and predisposing wood substrates to fungal and subsequent channelizing invertebrate colonization;

(3) Microbial succession and the rates of microbial catabolism as regulated by invertebrate dynamics, creating successive waves of distinct time periods when nitrogen is atmospherically fixed and carbon rapidly catabolized (these successional waves stabilize and increase microbial respiration and probably microbial catabolism rates); and

(4) The creation of spatial heterogeneity within woody substrates and microsites of intense physical-chemical-biological activity.

Mason (1970a), studying seven species of woodland snails in England, found most to be feeding on higher plant material. However, one species, *Discus rotundatus*, had significantly greater amounts of fungal material. Table 3 shows that three species of *Discus* are associated with log debris in the Southeastern United States. Fromming (1954) documented that some species of slugs specialize in feeding on fungi. However, it can be assumed that if higher plants are the staple diet of many land snails (Grime and Blythe 1969), the snails will secondarily ingest fungal spores and still act as an inoculation source. Talbot (1952) lists fungal species transported by woodland invertebrates in a study in South Africa. One species of slug listed, *Arion hortensis*, has been reported from Virginia (Beetle 1973). In marking experiments at Coweeta Hydrologic Laboratory in North Carolina, *Mesodon normalis* has been found to migrate 16.6 meters in 2 days, suggesting the potential for snails as agents of nutrient or inoculum dispersal (Caldwell, Ronald S., unpublished data).

Table 3—Number of species of land snails from the Southeastern United States that have been found to be associated with log debris[a]

Taxon	No. of species
Carychiidae	
Carychium	6
Discidae	
Anguispira	3
Discus	3
Polygyridae	
Mesodon	14
Polygyra	3
Practicolella	2
Stenotrema	18
Triodopsis[b]	27
Philomycidae	
Pallifera	1
Philomycus	4
Punctidae	
Punctum	1
Pupillidae	
Gastrocopta	1
Vertigo	1
Strobilopsidae	
Strobilops	4
Zonitidae	
Gastrodonta	1
Glyphyalinia	2
Mesomphix	1
Paravitrea	1
Ventridens	2
Zonitoides	3
Total	98

[a] Data from Hubricht 1985.
[b] Includes *Neohelix*, *Webbhelix*,and *Xolotrema* of Emberton 1988.

Nutrient Cycling

The role played by soil fauna in nutrient cycling has been well documented (Gist and Crossley 1975; McBrayer 1971, 1977; Swift 1977). In an experimental microcosm, leaching was increased from leaves fed upon by millipedes (Patten and Witkamp 1967). Seastedt and Tate (1981) measured decomposition rates for dead millipedes. Shells of dead mollusks (mostly calcium) may also act as important reservoirs for that element (Mason 1974).

Land snails can be viewed as a calcium compartment within ecosystems. Due to the storage of calcium in shell and soft tissues, they may have a significant effect on calcium release and cycling to the soil, and soil biota. Gist and Crossley (1975) reported density and biomass figures for Pulmonata at a North Carolina hardwood site. Foster (1937), studying *Neohelix albolabris*, found 6.33 snails per square meter (m^2) in a floodplain forest in Illinois. He estimated this to represent 3.16 g per m^2 of calcium and 15.8 g per m^2 of living tissue. Actual contribution to the calcium cycle can be estimated by coupling these figures with data given by Reichle and others (1969). On a per-weight basis, land snails would appear to tie up more calcium than other soil mesofauna.

No studies exist showing the amount of essential cations processed by feral land snails of the Eastern United States. McBrayer (1977) concluded that invertebrates have no direct effect upon rates of release for essential cations. Snails have been shown to have large whole-body concentrations of calcium (Cromack and others 1977). Reichle and others (1969) present data on whole-tissue and shell levels of *Mesomphix* sp. in a *Liriodendron tulipifera* forest. Values given are 77,600 ppm and 338,100 ppm, respectively, for the two snail species.

The contribution of land snails to the overall calcium budget of a forested ecosystem may be insignificant. However, as a calcium processor they may be important on a community or microecosystem level, providing calcium carbonate, or converting compounds such as calcium oxalate to ($CaCO_3$) (Cromack and others 1977). Snail shells may be an important calcium source for small vertebrates. The dependence of land snails on calcium is well documented (Baker 1958; Boycott 1934; Burch 1956, 1957; Petranka 1982; Wareborn 1979). Most obvious of the calcium need is the external shell, the formation of which starts in the embryo (Tompa 1980a). Sources for shell calcium include mantle, digestive gland, kidney, and blood (Wilbur 1964). Slugs (unshelled snails), with no external shell, do produce an internal plate of calcium in most species (Solem 1974). Other calcium needs in the life cycle of the snail are not so obvious. Many families of land snails have darts, which are structures composed of crystalline calcium that appear to function as Cupid's arrow (Tompa 1980b). Other calcium needs include production of an egg shell (Tompa 1980a), slime and epiphragm production (Fournie and Chetail 1984), and buffering of blood during times of aestivation (Baker 1958). Tompa (1976) has shown that as much as 10 to 25 mg of calcium are mobilized each day in *Anguispira alternata* during one oviposition.

The major form of calcium available to land snails appears to be calcium salts (Wareborn 1969, 1970). Calcium inputs from the environment are from two main sources: percutaneous movement and dietary (Fournie and Chetail 1984). The two most common salts are calcium citrate and calcium oxalate (Wareborn 1969, 1970). Wareborn (1979) has demonstrated that land snail populations are most dense on substrates rich in calcium citrate-producing trees, such as elms and maples. Calcium oxalate-producing species, such as oak and beech, tend to have fewer species and numbers of land snails (Wareborn 1979). On a calcium-free substrate, land snails may fail to copulate (Voelker 1959).

Graustein and others (1977) found calcium oxalate to be a common secretory product of fungal hyphae. They postulate that calcium oxalate crystals secreted by fungal hyphae are a reactive calcium reservoir. Land snails, as forest floor grazers, would act as major calcium cyclers.

Use of Coarse Woody Debris by Terrestrial Mollusca

As demonstrated in tables 1 and 2, little information is available on millipedes and centipedes. Of the macroinvertebrates, more information is available on terrestrial Mollusca. Table 3, which shows a total of 98 species of land Mollusca (snails and slugs), demonstrates the importance of CWD to these organisms. Of the 523 species and subspecies listed by Hubricht (1985), 401 occur in the Southeastern United States. This amounts to 24.4 percent of the Southeastern terrestrial fauna dependent upon CWD.

Shimek (1930), studying land snails of the Mississippi Valley fauna, found a very intimate relationship between forests and snails. He found that larger species, especially, inhabit woodlands. Table 3 lists three genera that contain 59 species associated with log debris. *Triodopsis*, *Stenotrema*, and *Mesodon* contain some of the largest snails in Eastern North America. Mason (1974) also found land snails to be more abundant in woodlands, perhaps due to greater habitat diversity. Interestingly, he also reported slug densities in a European *Fagus* woodland to be 14 slugs per m^2.

Jacot (1935) found that the number of individuals or species of land snails was not correlated with the age of the forest on sites near Asheville, NC. However, the proximity of old-growth stands and the amount of shelter available influenced the repopulation of cut forests.

Table 4 lists land snails that were significantly associated with log debris in the Hiwassee River Basin of Tennessee (Coney and others 1982). This is the only publication that analyzes land snail habitat statistically in the Southeastern United States. Further study would no doubt add to this list.

The association between snails and logs may be comparatively long lived. Comfort (1957) presents data on life spans of mollusks. Species found in the Eastern United States have been known to live up to 9 years. Harmon and Hua (1991) point out that CWD may persist for centuries. Land snails may have adapted to these long-term cycles and perhaps successional species can be found. Land snails are capable of homing behavior (Edelstam and Palmer 1950) and show seasonal movement. This behavior would benefit feeding, overwintering, or aestivation.

Conclusions and Recommendations

From the foregoing discussion, it can be seen that CWD is important to a large percentage of the land snail fauna of the Southeastern United States. Little data exist concerning other macroinvertebrate groups, which no doubt are equally dependent upon CWD.

Maser and others (1988) point out that future forests will have much less CWD. If so, then biodiversity in some taxa of macroinvertebrates would be reduced. Studies are needed to determine the nature of the dependence of the major invertebrate taxa on CWD. These studies should include the importance of invertebrates in successional stages of wood decomposition.

Table 4—Snail species significantly associated with log debris by log taxa in the Hiwassee River Basin of Tennessee[a]

Lepidobalanus (white oak group)
- *Gastrocopta contracta*
- *Gastrodonta interna*
- *Haplotrema concavum*
- *Helicodiscus notius*
- *Mesodon inflectus*
- *M. perigraptus*
- *Stenotrema stenotrema*
- *Zonitoides arboreus*

Erythrobalanus (red oak group)
- *Gastrocopta contracta*
- *Gastrodonta interna*
- *Haplotrema concavum*
- *Helicodiscus notius*
- *Mesodon inflectus*
- *M. perigraptus*
- *Stenotrema stenotrema*
- *Zonitoides arboreus*

Castanea dentata (American chestnut)
- *Gastrocopta contracta*
- *Gastrodonta interna*
- *Haplotrema concavum*
- *Helicodiscus notius*
- *Mesodon inflectus*
- *Stenotrema stenotrema*

Carya spp. (hickories)
- *Gastrodonta interna*
- *Mesodon inflectus*
- *Zonitoides arboreus*

Liriodendron tulipifera (tulip poplar)
- *Gastrodonta interna*
- *Haplotrema concavum*
- *Zonitoides arboreus*

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[a] Data from Coney and others 1982.

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Relationship of Wood-Feeding Insects and Coarse Woody Debris

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Abstract

Wood-feeding insects serve as food for vertebrates and invertebrates, condition the habitat for later successional organisms, disperse a variety of organisms, and, in some cases, generate coarse woody debris (CWD). This discussion is limited to insects that actively bore into and derive nutrients from the phloem or xylem and are probably important to decomposition. The majority of these insects are in the order Coleoptera, but several other orders are represented. Although a large amount of literature exists, most of it focuses on relatively few, commercially important insects and provides little information about their role in CWD decomposition, nutrient cycling, and energy transfer. More is known about the influence of geographic area, tree species, type of tree tissue, moisture, temperature, size of woody material, and fungal communities on wood-feeding insects.

Introduction

Wood-feeding insects represent a large portion of the fauna that inhabit dead and dying trees. They provide food for vertebrates and invertebrates; alter the habitat, making it acceptable for subsequent inhabitants; serve as transport for a variety of organisms; and, in some cases, are responsible for generating coarse woody debris (CWD).

In choosing the insects to include in this discussion, I needed to define wood-feeding insects and considered a number of questions. For example, are species that feed on phloem and obtain their nutrients from the cell contents, rather than cellulose, wood-feeders? Should insects that bore into wood but rely on externally growing symbiotic fungi for food be included? Should those species that ingest wood fibers but require nutrients or enzymes from ingested microorganisms to complete development be considered? Are insects that rely on gut-inhabiting symbiotic protozoa to digest cellulose wood-eaters?

These questions point to the many ways insects have evolved to take advantage of the energy stored in trees. I chose a broad definition that is not based on where the microorganisms that aid in digesting the wood are located, because almost all wood-feeding species have some symbionts that help them use wood as a food source. However, I restricted the discussion to insects that actively bore into and derive nutrients from the phloem or xylem (wood) of trees in terrestrial habitats and are likely to be important in the decomposition process.

Wood-feeding insects occur in many orders of the class Insecta, from the primitive eusocial termites to the more highly evolved Hymenoptera; however, the majority are Coleoptera. Individual life histories and habits of the wood-feeding groups or species is beyond the scope of this paper. Readers can find this information elsewhere (Anderson 1960; Barbosa and Wagner 1989; Coulson and Witter 1984; Drooz 1985; Hickin 1976). In addition to the life history and habits of the economically important wood-feeding insects and their associates, some researchers have looked at the community and successional patterns of insects in woody debris (Blackman and Stage 1918, 1924; Elton 1966; Fager 1968; Graham 1925; Howden and Vogt 1951; Savely 1939; Townsend 1886). Despite this large body of excellent work on a number of CWD inhabitants, little attention has been given to how insects affect decomposition, nutrient cycling, or energy flow in this habitat.

The following discusses the principal groups of insects feeding on CWD in the South, their roles in CWD, and how CWD habitat affects insect communities and vice versa.

Wood-Feeding Insects

Most of the information on wood-feeding insects focuses on those species that cause economic injury to trees or damage wood products. As a result, literally thousands of publications have been written about termites and bark beetles, while little information is available on the wood-eating Tenebrionidae, Elateridae, or Alleculidae. The appendix presents a partial listing of wood-feeding species in the South, their habits (phloem vs. xylem feeders, branch vs. bole inhabitants, etc.) and their host associations. Compiling the appendix was relatively easy for the economically important families. However, as Elton and Miller (1954) discovered 40 years ago, I found that an incredible number of species have been described taxonomically, but with no description of their "ecological setting and context." Therefore, the wood-feeding members of some of the largest families are not included because either larval host records are scattered or do not exist, or their function within the larval habitat has not been defined.

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Order Dictyoptera—Cockroaches

Family Cryptocercidae. This family contains one species, *Cryptocercus punctulatus*, which occurs in moist rotted logs, particularly oak. Entomologists are interested in this reddish brown, wingless insect because it serves as a phylogenetic link between roaches and termites. Like termites, *C. punctulatus* harbors xylophagous protozoa that help with digestion of its wood fiber diet (McKittrick 1964, 1965). Little is known about its relationship to CWD, although it is not likely to be important in decomposition.

Order Isoptera—Termites

Only 8 of the 2,100 species of termites are found in more than one or two Southern States, and only 4 species are common throughout the South. Despite the relatively small number of termite species, they are probably one of the dominant components of southern forest ecosystems that influence the decomposition of CWD. Termites are important to man throughout the world, and receive considerable attention and study as demonstrated by the extensive bibliographies compiled by Snyder (1949, 1961, 1968) and Ernest (1986). This literature deals primarily with the biology and control of termites, while relatively little attention has been directed at their ecological role in the temperate forests of North America (Lee and Wood 1971; Lobry de Brun and Conacher 1990).

Termites are social insects forming colonies usually produced by a single mated pair. Colonies may be composed of a king and queen (primary reproductives), supplementary reproductives, immatures, nymphs, soldiers, workers, and alates or winged reproductives (Weesner 1965). Alates initiate new colonies following reproductive flights that occur during specific times of the year. The timing of these flights depends upon the species. Males and females pair during the flights, prepare copularia in suitable habitats, mate, and begin producing young. As the newly produced apterous nymphs mature, they form the worker caste of sterile terminal form (no longer molting) individuals that, along with the nymphs, undertake all aspects of colony care and construction. Soldiers are also sterile, mature individuals that must be fed by workers and, as their name implies, are responsible for colony defense. Supplementary reproductives either replace the queen when she dies, or, in some species, supplement the buildup of the colony population. Alates, or winged reproductives that are produced in large numbers during certain seasons, are not found in the colony at other times (Krishna and Weesner 1969; Weesner 1965).

Termites in the Southern United States primarily feed on cellulose from wood. Lower-order termites have flagellate protozoans in their gut to aid in cellulose digestion, while the Termitidae rely on symbiotic bacteria (Wood 1978). The wood of most trees is acceptable food for termites (Wood 1978), so the appendix does not list hosts for the Isoptera. However, termite species show distinct preferences for specific woods (Smythe and Carter 1969) and in some cases prefer wood infected by specific fungi (Smythe and others 1971). The presence of other fungi may result in termite rejection of the wood as a food source or in poor termite survival (Becker 1969; Smythe and others 1971).

Wood density is also a factor in food preference. Soft fast-growing springwood is usually preferred over denser latewood. This preference frequently results in thin layers of latewood remaining in logs where the more preferred earlywood has been excavated.

Termites are a relatively small group with two families represented in the South (appendix). The drywood termites (Kalotermitidae) are predominately found in Florida, although several species are more widely distributed. The subterranean termites in the family Rhinotermitidae include the most common species, *Reticulitermes flavipes* and *R. virginicus.* A third subterranean species, the Formosan termite *Coptotermes formosanus*, was introduced into Louisiana and is now widely distributed in the South. This non-native species consumes wood at a faster rate and also infests wood of living trees. Its potential impact on the forested ecosystems of the South has not been investigated.

Termites are a ubiquitous component of the decomposer community in the South, which has been studied extensively. Their ecosystem roles have been considered in other parts of the world as well (Wood 1976, 1978; Lee and Wood 1971; Gentry and Whitford 1982; Lobry de Brun and Conacher 1990). However, considering their potential importance in CWD and soil modification, the role of subterranean termites in these processes has been neglected in the Southern United States.

Order Coleoptera—Beetles

The order Coleoptera, the largest in the Class Insecta, has over 30,000 species in the United States (Borror and others 1976). Twenty-four of the 110 families represented in the United States and described by Arnett (1968) include terrestrial wood-feeding species. However, only in the relatively small families (e.g., Platypodidae) are all members wood-feeders. The appendix contains a partial listing of the wood-feeding Coleoptera in the South. This list includes species that attack living and dead trees, those that feed on phloem or xylem tissue, and those that feed on wood in its last stages of decomposition. A large percentage of the xylophagous species rely on gut-inhabiting microfauna for the partial breakdown of cellulose. I have also included the ambrosia beetles; those species inoculate their galleries in wood with specific fungi on which the larvae feed. The inclusion of insects feeding in well-rotted logs is arbitrary, because many of these species derive part or all of their nutrition from fungi and other microorganisms that they ingest with the wood fibers. However, they are important in fragmentation of CWD (Ausmus 1977) and may contribute to incorporation of decomposed wood into the soil.

A number of beetles attack living trees where they feed on xylem tissue. These insects play at least two roles relating to CWD. First, they weaken trees structurally, making them more susceptible to breakage and resulting in CWD input. Second, they contribute to the decomposition of CWD by opening the tree bole to invasion by fungi and other organisms before the tree dies, resulting in CWD that is well advanced in decomposition before it even enters the detritus food web.

The appendix does not contain species lists for the families Elateridae, Tenebrionidae, Alleculidae, and Melandryidae, even though these families probably contain wood-feeders (Arnett 1968). Species descriptions in these families are frequently based on adult insects often caught by means that provide no information on the larval habits. Therefore, host records, if they exist, give no useful information in regard to CWD.

Families Lucanidae, Passalidae, and Scarabaeidae. During the larval stage, the C-shaped white grubs of these families are similar in appearance. Richter (1966) provided keys to the larvae and brief descriptions of the biology of some of the common species. Larvae of all three families are found in well-rotted logs. Lucanids and scarabs are solitary, while the passalids form loose social groups in which the adults feed chewed wood mixed with saliva to the larvae (Gray 1946). Because they are large, these insects may be important in both direct and indirect CWD fragmentation.

Families Buprestidae and Cerambycidae. The flatheaded or metallic wood borers (Buprestidae) and the long-horned wood borers (Cerambycidae) are large, diverse families that contain some of the most common and important wood-feeding species. Franklin and Lund (1956) compiled the species of Buprestidae that occur in Georgia, which include the common Southern species. Linsley (1961, 1962a, 1962b, 1964) and Linsley and Chemsak (1972, 1976, 1984) revised most of the subfamilies of Cerambycidae and provided biological information on species when available. A number of species are common in recently killed trees, where they often feed initially on phloem and then enter the sapwood or heartwood to complete their development. Others feed exclusively on wood in conditions ranging from wood of live trees to wood in the final stages of decomposition. Some attack stumps and boles while others occupy only branches of certain size classes. Both families contain species that attack living trees, either weakening or killing them, while some species contribute to woody debris input by girdling or pruning twigs or branches. More detailed accounts of common injurious species are provided by Drooz (1985) or Coulson and Witter (1984).

Families Elateridae, Tenebrionidae, Alleculidae, and Melandryidae. Little is known of the larval habits of these families, although adults and larvae of some species are found in CWD. Some of the elaterids or click beetles found in CWD are known predators, while others are probably wood-feeders (Arnett 1968).

Family Curculionidae. Despite the large size of this family, relatively few weevils can be classified as wood-feeders. However, several are commonly associated with CWD in the South. These include the Pales and pitch-eating weevils, *Hylobius pales* and *Pachylobius picovorus*, and the deodar weevil, *Pissodes nemorensis*, which feed on the phloem of recently killed pine tree boles, stumps, and roots. The remaining species are also primarily phloem feeders on a variety of host species, although a few weevils feed on rotten wood and some bore into sound wood.

Families Anobiidae, Lyctidae, and Bostrichidae. These families are grouped together because all the species found in CWD are xylophagous, and most are capable of feeding on, or prefer, relatively dry wood. Because the wood-feeding larvae of these three families pack their tunnels with a fine powderlike boring dust and frass, they are labeled "powder-post beetles," a name officially applied to the Lyctidae. These beetles are likely to occur where other wood-feeding species are rare, such as standing dead trees on xeric sites or dead limbs still attached to trees, because they are able to attack relatively dry wood. Some members of the family Curculionidae (subfamily Cossoninae) could also be included in this group.

Families Scolytidae and Platypodidae. The bark beetles, or scolytids, contain a large number of the most important forest pests. They often arrive first at newly created CWD or, in some cases, they contribute significantly to CWD input. These insects are primarily phloem feeders that attack all parts of the tree. A number also bore into wood. Some feed in the lower bole while others feed only in branches of a particular size class. Some species of Scolytidae (tribe Xyleborini) and all of the Platypodidae are ambrosia beetles that feed larvae by inoculating adult-constructed galleries with a mold-type fungus (Graham 1966; Norris 1979). Bark beetles have received considerable attention because they are economically important. In two excellent books, Wood (1982, 1987) has revised the New World species and compiled the literature references on these beetles.

Order Lepidoptera—Moths

Families Noctuidae, Sesiidae, and Cossidae. Moth larvae or caterpillars that feed on wood in the South are found in these three families. Only one species of Noctuidae feeds on wood in the South: *Scolecocampa liburna*, a common species found in rotting logs. The remaining species, in the families Sessidae and Cossidae, are found in live trees, feeding primarily on wood, although a few are phloeophagus. These species contribute to decomposition of wood before the tree dies, increasing tree susceptibility to wind breakage and disease. Drooz (1985) and Johnson and Lyon (1988) have reviewed the biologies of the important pest species in these families.

Order Hymenoptera—Wasps and Bees

Families Siricidae and Xiphydriidae. Both families in this order bore in wood and have similar habits. Morgan (1968) reviewed the literature on Siricidae, and Smith (1976) revised the literature on xiphydriids of North America with notes on hosts and biology. Although the woodwasps actively bore in wood of very weak or dead trees, they rely on symbiotic fungi inoculated into the tree during oviposition as an aid in digestion (Martin 1987) or possibly as a sole food source (Morgan 1968).

Roles of Wood-Feeding Insects in Coarse Woody Debris

Studies of wood-feeding insects in CWD have focused primarily on CWD as a habitat and on the community structure and successional changes that occur as the wood decomposes (Townsend 1886; Blackman and Stage 1918, 1924; Graham 1925; Savely 1939; Howden and Vogt 1951; Fager 1968; Elton 1966). Very little attention has been given to the effects of wood-feeding insects on the processes of energy flow and nutrient cycling. Despite this lack of study, Harmon and others (1986) show that wood-feeding insects serve important functions in forest ecosystems.

Coarse Woody Debris Input

Insects are just one of many factors contributing CWD to forested ecosystems, where their relative importance in this role depends on forest type (Harmon and others 1986). In the South, pines are the dominant tree species in the Coastal Plain and Piedmont and, as a result of both natural and man-related activities, *Pinus* spp. represent one of the major sources of CWD in this region. Aside from man, the southern pine beetle (SPB) *Dendroctonus frontalis* is one of the primary factors influencing the spatial and temporal arrangement of CWD in southern forests. Price and others (1991) have compiled an excellent historical account of SPB outbreaks with detailed maps of outbreaks over a 30-year period. Their work demonstrates the spatial and temporal variability of CWD input in southern forests. Table 1 shows the temporal changes in CWD resulting from SPB activity across the South. Regional loss figures in table 1 were calculated from the State volume figures provided by Price and others (1991). The number of trees is estimated by calculating the volume of a tree 22-m tall, 50-cm diameter at the butt end, and tapering to a 10-cm diameter top. The volume figure for each year was then divided by the per-tree volume to determine the number of trees. Similarly, the number of hectares of trees killed was estimated by assuming that each hectare contained 178 trees. These data show the potential CWD input from SPB activity, but timber salvage efforts reduced the actual input. For example, in 1980 SPB killed 8.6 million m^3 of wood as the equivalent of 5.9 million large trees. However, the amount of wood not salvaged was only 4.0 million m^3 or about 47 percent of the total mortality. Without SPB suppression efforts, the figures in table 1 would be much higher, as demonstrated in a potential wilderness area in Texas where SPB killed 1416 hectares of pine, equivalent to 94,400 m^3 of wood, before control measures were initiated and the infestation was stopped (Billings 1992).

The SPB is the only wood-feeding insect that causes large-scale forest mortality in the South. However, other species may also be important. Populations of pine engravers (*Ips* spp.) frequently build up in logging slash, windthrown, or lightning-struck trees, and subsequent generations attack healthy trees. Quick decline of these populations usually

Table 1—Potential CWD volume input over an 18-year period resulting from southern pine beetle, *D. frontalis*, activity in the Southern United States, and estimates of the number of trees and hectares of forest affected[a]

Year	Volume (m^3)	No. of trees[b]	Hectares[c]
	- - - - - - - - - - *millions* - - - - - - - - - -		
1973	6.5	4.4	24,719
1974	6.6	4.6	25,843
1975	6.0	4.1	23,033
1976	3.0	2.1	11,798
1977	1.1	0.8	4,494
1978	0.9	0.6	3,371
1979	6.4	4.4	24,719
1980	8.6	5.9	33,146
1981	0.8	0.5	2,809
1982	2.1	1.4	7,865
1983	0.6	0.4	2,247
1984	0.8	0.5	2,809
1985	8.4	5.8	32,584
1986	7.2	5.0	28,090
1987	1.7	1.2	6,741
1988	4.7	3.2	17,977
1989	1.2	0.8	4,494
1990	0.5	0.3	1,685

[a] Compiled from Price and others (1991).

[b] Estimates based on average tree 20-m tall, 50-cm diameter at base, and 10-cm diameter at the top.

[c] Estimate based on each hectare containing 178 trees.

results in small groups of dead trees (Drooz 1985). Thatcher (1960) reported that pine engraver activity resulted in a loss of 3.7 million m^3 of timber in southern forests, while Baker (1972) reported 1.1 million m^3 per year of pine mortality due to these beetles in Florida alone. Ips bark beetle may represent a major source of CWD in this region because infestations are usually small and scattered, and salvage is often not economically feasible.

In southern hardwood forests, wood-feeding insects are probably a much less important source of tree mortality. The hickory bark beetle, *Scolytus quadrispinous*, is capable of localized outbreaks that result in significant tree mortality (Beal and Massey 1945; Drooz 1985), and wood-feeding insects serve as vectors of several important and lethal hardwood tree diseases including oak wilt, *Ceratocystis fagacearum* (Rexrode 1968; Rexrode and Jones 1970),and Dutch elm disease, *C. ulmi* (Carter 1962). Borers that feed on the sapwood or heartwood of live trees contribute indirectly to CWD input in hardwood forests by weakening trees, making them susceptible to wind breakage or disease. Finally, twig and branch pruners and girdlers (table 1) can add small woody debris through their feeding and oviposition behavior.

Vectors and Transport

Wood-feeding insects carry a large array of pathogenic and saprophytic microorganisms as they move from tree to tree. Whitney (1982) provides an extensive list of symbiotes of conifer-killing bark beetles. The list includes 38 genera of fungi, 17 genera of bacteria, and 4 genera of protozoans. These numbers are remarkable only because the survey was limited to the more aggressive tree-killing species of four bark beetle genera.

A number of wood-feeding insects, such as ambrosia beetles and woodwasps, have specific associations with fungi that they carry and use for food. Norris (1979) lists the ambrosia fungi of the Xyleborini beetles (Scolytidae) and the types of mycangia that have evolved in these beetles for carrying their symbiotic fungi. Woodwasps (Siricidae and Xiphydriidae) have similar associations. Morgan (1968) has reviewed the biology of siricids and their fungal symbiotes. Woodwasps use long ovipositors to drill holes 2-15 mm into the wood, where they deposit eggs and the symbiotic fungi upon which the young depend. Fungi associated with woodwasps probably affect CWD decomposition more than those associated with ambrosia beetles.

A number of mite species rely on wood-feeding insects for transport between habitats. Eighteen species of mites are recorded as phoretic on the SPB alone (Moser 1976). Moser and Roton (1971) found 96 species of mites associated with bark beetle-infested trees in Louisiana and listed the subcortical insects that served as phoretic hosts. The long list suggests that most wood-feeding insects carry mites between habitats. Soper and Olson (1963) reported 13 genera of mites associated with *Monochamus* spp. in Maine. The majority were thought to be phoretic.

Nematodes are also carried by wood-feeding insects. Massey (1974) found 51 genera of nematodes that were parasitic on or associated with bark beetles in the United States. Parasitic species were carried internally to new bark beetle habitats, while most of the other species associated with bark beetles are probably phoretic. Dwinell and Nickle (1989) considered most of the 49 species of mycophagous *Bursaphelenchus* nematodes to be phoretic on wood-borers.

These studies suggest that wood-feeding insects probably carry a much greater number and diversity of organisms than is currently known and, for those organisms, serve as a vital link between habitats .

Exposure of Wood to Other Organisms

Wood-feeding insects not only transport organisms to new CWD habitats, they also create openings and modify CWD so that other organisms can gain access or survive. Entry holes by bark beetles allow other organisms to enter the inner bark. For example, Dowding (1973) found that prevention of bark beetle attacks on *Pinus sylvestris* logs greatly reduced the numbers of Diptera found. A large number of the scavengers and predators associated with SPBs (Overgaard 1968) used openings created by bark beetles to enter the inner bark. For example, some of the 96 species of mites associated with bark beetles in Louisiana entered through holes created by the bark beetles (Moser and Roton 1971). Whitney and Cobb (1972) maintained that beetle tunnels are an important mode of entry for Basidiomycotina and other fungi in ponderosa pine. However, Dowding (1982) questioned the importance of beetle tunnels for fungal colonization by airborne spores, suggesting that other wound sites are more important. Swift and Boddy (1982) state that after ambrosia beetles vacate their galleries the tunnels provide infection courts for nonsymbiotic fungi.

Channelization and Fragmentation

Insects tunnel through CWD by chewing, digesting, and excreting both phloem and xylem. Some species (e.g., powderpost beetles) tightly pack the wood particles and excrement in the larval mines, while others (e.g., termites) clear their galleries. Phloeophagus insects mine the inner bark and cambium extensively and introduce fungi that, in combination with beetle tunneling, loosen the bark, which eventually sloughs off.

Insect feeding in the wood is a direct form of fragmentation. In addition, the combination of insect feeding and fungal decomposition weakens the wood, making it more susceptible to accelerated fragmentation by woodpeckers (Kroll and others 1980) and other vertebrates in search of food (e.g., bears, skunks). MacMillan (1988) found that fragmentation was a major reason for the disappearance of oak, hickory, and beech CWD in Indiana although the organisms responsible were not identified. The principal channelizers in hardwood logs on mesic sites in Tennessee (termites, carpenter ants, and passalid beetles) regulate the rate of decomposition by altering the substrate and shifting the competitive advantage of microbial colonizers (Ausmus 1977).

Most nutrients are probably transferred out of logs and snags through fragmentation (Harmon and others 1986). Channelization and fragmentation by wood-feeding insects have been implicated in the initiation and acceleration of nutrient loss from decaying branch wood (Swift 1977; Swift and Boddy 1982) and tree boles (Ausmus 1977). However, nutrient loss probably depends on the element involved. For example, nitrogen content is highest in the later stages of decay when CWD is more susceptible to fragmentation. Conversely, potassium content is low due to leaching (Swift 1977) and is less affected by fragmentation (Harmon and others 1986). Although wood-feeding insects play an important role in CWD decomposition and nutrient transfer, few quantitative data are available on their role in leaching or fragmentation losses.

Energy Transfer

The intricate food webs and succession of wood-feeding insects in CWD during decomposition are indicative of the energy release from this resource. I found no quantitative data on this subject, although it is likely that these data could be determined from the literature on bark beetle population dynamics at least for the major tree-killing species of bark beetles and possibly for their parasites and predators. However, similar data are not available for the large majority of the other wood-feeding insects.

Coarse Woody Debris as a Habitat for Wood-Feeding Insects

The wood-feeding insect community is affected by a wide range of factors from geographic location to microclimatic condition. Unlike the role of insects in decomposition processes, the heterogeneity of CWD and its impact on insect communities is understood better. This is particularly true for economically important species, such as bark beetles and termites. Much less is known about the myriad of other species that feed on wood.

Wood-feeding insect communities vary across elevational and latitudinal gradients. A good example of latitudinal differences is termite diversity, which decreases as one moves south to north (Wood and Sands 1978). In the United States, 13 species occur in Florida, while only 1 species has been reported in New Hampshire (Light 1934; Nickle and Collins 1989). Insect diversity also tends to decrease with increasing elevation (Wood and Sands 1978). However, in compiling table 1 it was clear that North Carolina has a number of wood-feeding insects associated with host-tree species unique to the upper elevations of the Southern Appalachian mountains, as well as a number of insects more typically found in northern regions. The higher elevation allows insects to extend their range farther south than is possible along the Coastal Plain. Therefore, oak trees of comparable size dying at the same time in south Georgia, in the upper elevations of North Carolina, and in New Hampshire are likely to have different wood-feeding insect communities. However, the similarity between the North Carolina and New Hampshire trees may be greater than one would predict based on changes in latitude alone.

A number of other factors influence the insect community after a tree dies in a given region. The timing of CWD input influences insects. This is particularly true for the early successional community in phloem and for insects that have only one restricted flight period annually. Xylophagous insects may be less affected by timing because the wood deteriorates more slowly than the phloem. However, termites were found in SPB-killed trees 3 months after death (Barrone 1970). This rapid colonization by termites could exclude other wood-feeding insects that normally arrive later.

One of the most obvious factors affecting insect communities in CWD is tree species. A quick glance at table 1 shows that many wood feeders are restricted to one or a few species of host trees, often within a single genus, while others have broad host ranges. In general, the more restricted host lists indicate those species that arrive during or soon after tree death, while the expanded host lists indicate species using later stages of decay. Those species that arrive early in the decomposition process are often more specialized because they must overcome the plant's secondary or defensive compounds (Käärik 1974; Haack and Slansky 1987). Other insects are capable of utilizing a wide range of tree species but show preference for certain species. For example, termites show distinct preference for certain woods in laboratory bioassays (Smythe and Carter 1969, 1970); however, very little is known about their natural preferences under field conditions (Waller and LaFage 1987).

In addition to differences among species, the resistance of wood to decomposers varies within species (Clark 1957), as well as within individual trees. For example, the sapwood of bald cypress, *Taxodium distichum*, is readily consumed by the Formosan termite, *Coptotermes formosanus*, because it is unprotected by the allelochemicals found in the heartwood (Scheffrahn and others 1988).

The position of CWD can also affect wood-feeding insects. Howden and Vogt (1951) found considerable differences between the insect communities in standing dead pines compared to felled trees (Savely 1939). However, the differences noted could have resulted from other factors, such as temporal and spatial differences or tree species. The location of woody debris on mesic or xeric sites (Abbott and Crossley 1982) or on slopes with different aspects can affect CWD moisture content and decomposition process (Mattson and others 1987) and probably the insect community as well.

The moisture content of logs is a critical factor in shaping CWD communities, as Graham (1925) demonstrated for the cerambycids *Asemum* sp. and *Monochamus* sp. Likewise, the termite *C. formosanus* preferred wood with the highest initial moisture content (Delaplane and LaFage 1989). Other wood-feeding insects show a preference for, or an ability to use, dry wood (e.g., Lyctidae).

Wood temperature may also affect insect community development in CWD. For example, Graham (1925) found that the buprestid *Chrysobothris dentripes* occurred on the tops of logs exposed to direct sunlight, and Savely (1939) demonstrated that a *Chrysobothris* sp. had a tolerance for high temperatures that excluded other species. Therefore, insect communities of logs or snags exposed to direct sunlight may differ from those in shaded areas or on north-facing slopes.

The size of CWD can affect insect community composition. Table 1 clearly demonstrates that some beetle species prefer small branches, while others attack only the base of trees (e.g., *Dendroctonus terebrans* or *Platypus flavicornis*). Some wood-feeding termites also prefer large logs while others feed on small branches (Wood 1976).

Fungi play a key role in the use of CWD by certain insects. Some insects are dependent on fungi for food and have developed very specific associations, e.g., ambrosia beetles and woodwasps. In addition to species that rely on specific fungi, many wood-feeding insects are affected by the fungal community in CWD in a variety of ways. Swift and Boddy (1982) provide a detailed discussion of the interaction between fungi and insects.

Fungi contribute to the nutritional ecology of wood-feeding insects in several ways. First, the fungi contribute nutrients for insect development not found in sufficient amounts in wood alone; in particular, nitrogen and other elements are concentrated in fungal mycelia (Swift 1977, 1978). Second, fungi partially break down or digest the wood, leaving behind a softer, more chewable resource that may be more readily assimilated (Swift and Boddy 1982). For example, *Reticulitermes flavipes*, a common subterranean termite species in the Eastern U.S., preferred and survived better on wood decayed by a number of brown-rot fungi (Smythe and others 1971). Third, fungi increase the moisture content of decaying wood, which may alter its acceptability as a habitat and food source for some wood-feeding insects. Fourth, enzymes produced by fungi and ingested by insects with the wood they eat provide yet another benefit. Martin (1987) reviewed the literature on ingested fungal enzymes and suggested that ingested enzymes will prove to be responsible for cellulose digestion in the xylophagous members of the Cerambycidae, Buprestidae, and Anobiidae families. Finally, fungi are important in detoxifying wood that contains toxic or repellent allelochemicals. Swift and Boddy (1982) summarize several studies that demonstrated termites' use of wood when fungi reduced the quantity of allelochemicals present.

Fungi can also have a negative effect on insects. Becker (1969) found that pine stumps decayed by white-rot fungi were usually free of termites, and Amburgey and Beal (1977) showed that the white-rot fungus *Ganoderma applanatum* inhibited feeding by *Reticulitermes* spp. on infected wooden stakes. Smythe and others (1971) demonstrated reduced survival for *R. flavipes* on wood decayed by *Poria cocos* and *P. monticola*.

It is evident from this brief discussion that wood-feeding insect communities in CWD are shaped by a number of factors; and, as a result, the composition of these communities may vary considerably depending upon the combination of conditions in which the CWD is produced and decomposes.

Summary

Wood-feeding insects are a major component of the diversity of organisms associated with CWD and southern forests. Their feeding activity alters the habitat, they carry with them a wide array of organisms from bacteria to mites that further influence the environment and decomposition process, and they provide openings and food for complexes of other organisms. As a result of these activities, wood-feeding insects have a significant impact on CWD decomposition and the communities of organisms involved. Conversely, the wood-feeding insects are affected by a number of physical and biological factors that determine their ability to use CWD.

Despite the obvious activity and abundance of wood-feeding insects in CWD, few have been studied. Those studied extensively are predominantly pest species that occur early in community succession on CWD, attack living trees, or affect structural wood. These studies have focused on basic insect biology and control with little or no emphasis on the role insects play in the decomposition process. In general, studies on CWD decomposition have not considered the role of insects (Harmon and others 1986). Those that have done so, have often dealt with small branch wood (e.g., Abbott and Crossley 1982; Swift and others 1976) or failed to identify the insect community structure or abundance. However, Ausmus (1977) considered insects in studies of large woody debris and concluded that they were a key component regulating decomposition.

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Appendix

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits

Species	Hosts	Habits
Order Isoptera: Kalotermitidae[1]		
Kalotermes approximatus		Drywood
Neotermes jouteli		Drywood (Florida only)
N. luykxi		Drywood
N. castaneus		Drywood (Florida only)
Incisitermes snyderi		Drywood
I. milleri		Drywood
I. schwarzi		Drywood
Calcaritermes nearcticus		Drywood (Florida only)
Cryptotermes brevis		Drywood (Florida, Louisiana)
C. cavifrons		Drywood (Florida only)
Rhinotermitidae[2]		
Prorhontermes simplex		Subterranean (Florida only)
Reticulitermes flavipes		Subterranean
R. hageni		Subterranean
R. virginicus		Subterranean
R. tibialis		Subterranean (Arkansas, Texas)
Coptotermes formosanus		Subterranean (introduced, widely established)
Order Coleoptera: Scolytidae[3]		
Hylastes tenuis	*Pinus* spp.	Roots
H. exilis	*Pinus* spp.	Stumps & roots
H. salebrosus	*Pinus* spp.	Stumps & roots
H. porculus	*Pinus* spp.	Stumps & roots
Hylesinus pruinosus	*Fraxinus* spp.	Phloem/etch wood
H. aculeatus	*F. americana*	Phloem/etch wood
H. fasciatus	*Fraxinus* spp.	Phloem/etch wood
Hylurgopinus rufipes	*Ulmus* spp.	Phloem/etch wood
Dendroctonus frontalis	*Pinus* spp.	Phloem
D. terebrans	*Pinus* spp.	Phloem
D. valens	*P. strobus, P. rigida, P. echinata, P. virginiana, Picea rubens*	Phloem
D. punctatus	*P. rubens*	Phloem
Cnesinus strigicollis	*Quercus* spp., *Liquidambar styraciflua*	Outer xylem, small branches
Phloetribus liminaris	*Prunus serotina*	Phloem/etch wood
P. frontalis	*Celtis occidentalis, Morus rubra*	Phloem/etch wood
P. dentifrons	*C. occidentalis*	Phloem/etch wood
P. texanus	*C. laevigata*	Phloem/etch wood

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued).

Species	**Hosts**	**Habits**
Phloeosinus taxodii taxodii	*Taxodium distichum*	Phloem/etch wood
P. dentatus	*Juniperus virginiana*	Phloem/etch wood
Chramesus subopacus	*Celtis* sp.	Phloem/etch wood larvae may enter wood completely
C. hicoriae	*Carya* spp.	Phloem/etch wood larvae may feed on wood exclusively
C. chapuisi	*C. occidentalis*, *Robinia* sp.	Phloem/etch wood
Carphoborus bifurcus	*P. echinata, P. taeda, P. virginiana*	Phloem
Polygraphus rufipennis	*P. strobus, P. rubens, Abies fraseri*	Phloem
Scolytus rugulosus	*Prunus* spp., *Ulmus* spp.	Phloem/etch wood
S. muticus	*C. occidentalis*	Phloem/etch wood
S. fagi	*Fagus grandifolia*, *Celtis* sp.	Phloem/etch wood
S. quadrispinosus	*Carya* spp.	Phloem/etch wood
S. multistriatus	*Ulmus* spp.	Phloem/etch wood
Pseudothysanoes lecontei	*Castanea dentata*, *Celtis* sp., *Quercus* spp.	Phloem
P. dislocatus	*Carya* spp.	Phloem
Thysanoes pallens	*Carya* spp., *Quercus* spp.	Wood of small branches
T. berchemiae	*Quercus* sp., *Ulmus* sp.	
T. fimbricornis	*A. rubrum*, *Carya* spp., *Celtis* sp., *M. rubra*, *Quercus* spp., *Gleditsia tricanthos*	Wood of small branches
T. lobelli	*Carya* sp., *Quercus* sp.	Wood of small branches
Micracis swainei	*Cercis canadensis*, *Populus* sp., *Salix* spp.	Wood of small branches
M. suturalis	*C. canadensis*	Wood of branches
Hylocuris binodatus	*Carya* sp.	Wood (all areas of tree)
H. rudis	*Carya* spp., *F. grandifolia*, *U. americana*	Wood
H. torosus	*Carya* sp., *Celtis* sp., *Acer*, *C. dentata*	Wood
H. bicornus	*Carya* sp.	Wood
H. harnedi	*Carya* sp.	Wood
H. spadix	*Carya* spp.	Wood
Hylocuris langstoni	*Celtis* sp., *Ulmus* sp.	Wood
Pityogenes hopkini	*P. strobus*	Phloem
P. meridianus	*P. taeda*	Phloem
P. plagiatus	*P. echinata, P. virginiana*	Phloem
Orthotomicus caelatus	*Pinus* spp., *Picea* spp.	
Ips avulsus	*Pinus* spp.	Phloem/etch wood
I. pini	*P. strobus*	Phloem/etch wood
I. calligraphus	*Pinus* spp.	Phloem/etch wood
I. grandicollis	*Pinus* spp.	Phloem/etch wood
Lymator decipiens	*A. rubrum, A. saccharum*, *Salix* sp.	Wood of dry branches

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	**Hosts**	**Habits**
Dryocoetes autographus	*P. strobus*	Phloem
D. betulae	*Betula* spp., *F. grandifolia*, *L. styraciflua*	Phloem
D. grandicollis	*Picea* spp.	Phloem
D. affaber	*P. rubens, A. fraseri, P. strobus*	Phloem
D. caryi	*P. rubens*	
Crypturgus alutaceus	*P. echinata, P. palustris, P. taeda*	Phloem
Xyloterinus politus	*Acer, Betula, Carya, Castanea, Fagus, Fraxinus, Quercus, Ulmus*	Ambrosia beetles
Trypodendron scabricollis	*P. echinata, P. taeda*	Ambrosia beetles
T. retusum	*Populus deltoides*	Ambrosia beetles
T. lineatum	*Abies* spp., *Picea* spp., *Pinus* spp., *Thuja* spp.,*Tsuga* spp.	Ambrosia beetles
Xylosandrus crassiusculus	*Prunus* spp., *L. styraciflua*, many other hosts	Ambrosia beetles
X. germanus	*Acer* sp., *Carya* sp., *Cornus florida*, *Fraxinus* sp., *Juglans* sp., *L. tulipifera*, *Pinus* sp., *Prunus* sp., *Quercus* spp., *Ulmus* spp.	Ambrosia beetles
Xyleborus obesus	*F. grandifolia, Quercus* sp.	Ambrosia beetles
X. dispar	*A. saccharum, C. dentata*, *Juglans* sp., *Prunus* sp., *Quercus* spp., *Salix* sp.	Ambrosia beetles
X. sayi	*A. rubrum, Acer* sp. *Castanea* spp., *Nyssa* sp., *Sassafras albidium*	Ambrosia beetles
X. obliquus	*Betula* sp., *C. dentata*	Ambrosia beetles
X. rubricollis	*Carya, Cornus, Prunus, Quercus* spp.	Ambrosia beetles
X. lecontei	*Carya* sp.	Ambrosia beetle
X. tachygraphus	*Betula* sp., *Carya* sp., *C. dentata, Juglans* sp.	Ambrosia beetle in branches 3-5 cm
X. affinis	248 host species	Ambrosia beetle
X. celsus	*Carya* sp.	Ambrosia beetle
X. viduus	Broadleaf trees	Ambrosia bettles
X. xylographus	*Quercus* spp.	Ambrosia bettles
X. pubescens	*Pinus* spp. *P. echinata, P. palustris*	Ambrosia beetle
Cryphalus rubentis	*P. rubens*	Phloem
C. ruficollis fraseri	*A. fraseri*	Phloem
Trischidias atoma	*A. rubrum, Carya* spp., *C. dentata, Salix* sp., *R. pseudoacacia, U. americana*	Phloem branches

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued).

Species	**Hosts**	**Habits**
Hypothenemus dissimilis	*A. rubrum, Carya* spp., *C. canadensis, Quercus* spp.	Wood of small branches
H. rotundicollis	*C. canadensis, F. grandifolia, Quercus* sp.	Wood of small branches
H. interstitialis	*A. rubrum, Aesculus* sp., *Carya* spp., *C. canadensis, F. grandifolia, L. styraciflua, M. rubra, Quercus* spp.	Wood of small branches
H. crudiae	*Betula* sp., *Carya* spp., *J. nigra, P. taeda, Quercus* spp.	Wood of small branches
H. seriatus	*Carya* spp., *J. nigra, L. styraciflua, P.* spp., *Quercus* spp.	Wood of small branches
H. eruditus	Several hundred hosts	Phloem or pith
H. columbi	*Quercus* spp., *Salix* sp.	Wood of small branches
Pseudopityophthorus asperulus	*Quercus* sp., *Ostrya virginiana*	Phloem, entire tree
P. pubescens	*Quercus alba, Q. rubra, C. dentata*	Phloem
P. fagi	*F. grandifolia*	Phloem (?), rare species
P. minutissimus	*Quercus* spp.	Phloem of limbs & branches
P. pruinosus	*Quercus* spp.	Phloem of limbs & branches
Pityophthorus angustus	*P. rubens, P. strobus*	
P. cariniceps	*P. strobus*	Phloem, small branches
P. pulchellus	*P. palustris, P. strobus, P. virginiana*	Phloem throughout tree primarily branches
P. confusus	*P. echinata, P. taeda*	10-25 cm phloem
P. annectens	*P. palustris, P. taeda, Pinus* spp.	Branches phloem
P. consimilis	*Pinus* spp., *P. strobus, P. virginiana, Picea* spp.	Small branch 2 cm
P. pullus	*Pinus* spp.	
P. lautus	*A. saccharum, C. canadensis, Picea* sp., *P. strobus*	Stems 2-8 cm
P. liquidamburus	*L. styraciflua*	Stems 6-20 cm
Pityoborus comatus	*Pinus* spp.	Phloem & etch wood branches 2-8 cm
Gnathotrichus materiarius	*P. echinata, P. strobus, P. taeda*	Ambrosia beetles throughout stem
Monarthrum mali	*A. rubrum, L. styraciflua, Nyassa* sp., *Quercus rubra, Tilia* sp.	Ambrosia beetle in 2-10 cm diam.
M. fasciatum	*A. rubrum, Carya* sp., *C. dentata, L. styraciflua, Pinus* sp., *Prunus* sp., *Quercus* spp.	Ambrosia beetle in branches > 10 cm
Corthylus punctatissimus	*A. saccharinum, Sassafras* sp.	Ambrosia beetle in stems
C. columbianus	*A. rubrum, A. saccharinum, C. dentata, L.tulipifera, Plantanus occidentalis, Q. alba, Ulmus* sp.	Ambrosia beetle, attacks boles of living trees

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Cerambycidae[4]		
Parandra polita	*Fagus, Carya, Liriodendron*	
P. brunnea	*Quercus, Populus, C. dentata, A. rubrum, Tilia, Liriodendron, U. americana*	3-4 yr. life cycle wood in contact with ground
Stenodontes dasytomus dasytomus	*Plantanus* spp., *Celtis* spp., *Quercus* spp., *Salix* spp., *L. styraciflua, Acer negundo*	Heartwood of live & dead trees
Derobrachus brevicollis	*Quercus* spp.	
Orthosoma brunneum	*Juglans, Carya, Castenea, Quercus, Acer, Pinus, Tsuga*	Wood dead several years in moist situations
Prionus pocularis	*Pinus* spp.	Dead pine logs
P. laticollis	*Populus* spp., *Quercus* spp., *Castanea, Tilia*	Roots of living trees timber in contact with ground
P. imbricornis	*Quercus, Castanea,* other hardwoods	Roots of live trees
P. debilis	*Quercus, Castanea,* other hardwoods	Roots of live trees
Derancistrus taslei	*Quercus, Castanea, Fagus, Cercis*	Breeds on dry, dead snag tops
Spondylis upiformis	*Pinus, Abies*	Probably on roots
Scaphinus muticus	*Pinus* spp.	Habits unknown
Arhopalus rusticus obseletus	*Pinus* spp.	Bases & roots of dead pines
A. rusticus nubilus	*Pinus* spp.	Habits unknown
Asemum striatum	*Picea* spp., *Pinus* spp.	Base of recently dead trees
A. australe	?	?
Atimia confusa confusa	*Juniperus* spp., *T. distichum, Thuja* sp., *Chamaecyparis*	Feed in phloem excavates wood to form pupal cell
Michthisoma heterodoxum	*Carya*	Sapwood & stumps
Smodicum cucujiforme	*Robinia, Carya, Quercus, Fagus, Celtis, Salix, Populus*	Dry heartwood
Oeme rigida rigida	*T. distichum, J. virginiana*	Phloem; mine pupal cell in wood
Methia pusilla	*T. distichum*	Small branches
Achryson surinamum	*C. laevigata, R. pseudoacacia*	
Gracilia minuta	*Salix, Quercus, Aesculus, Betula*	Dead twigs & branches phloem
Eubaria distincta	?	?
E. quadrigeminata	*Fraxinus, Quercus, Carya, Robinia, Castanea, Acer, Gleditsia, Ulmus, Fagus, Prunus*	Prefer dry, solid heartwood living or dead trees
E. haldemani	*Salix, Ulmus*	Under bark
Tylonotus bimaculatus	*Fraxinus* spp., *Betula, J. nigra, Carya, Liriodendron, Ulmus*	Beneath bark of living or dying trees, may enter wood
Hesperophanes pubescens	?	Rare
Purpuricenus axillaris	*Carya* spp., *C. dentata, Quercus* spp.	Girdle branches up to 5 cm
P. humeralis	*Carya, Betula, Quercus, Castanea, M. rubra, R. pseudoacacia, C. canadensis, Acer*	Dead branches

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Knulliana cincta cincta	*Juglans, Carya* spp., *Castanea, Quercus* spp., *Celtis, Prunus, Salix*	Dry wood of dead branches and limbs
K. cincta ochraesa	*Carya illinoensis, O. virginiana*	
Tragidion coquus	*Quercus* spp.	Dead branches
Batyle ignicollis australis	*Pinus*	Dead branches
Psyrassa unicolor	*C. glabra, J. nigra, Quercus* spp., *Fagus sp., M. rubra, C. canadensis, Prunus*	Twig pruner
P. pertenuis	*Carya, Prunus*	Twig pruner
Stenosphenus pinorum	*Carya* spp.	Habit unknown
S. notatus	*C. glabra, C. illinoensis, Celtis* sp.	Phloem and etch wood of dead limbs, pupates in wood
Enaphalodes hispicornis	*Quercus* spp.	
E. rufulus	*Quercus* spp., *Acer* sp.	May kill trees, living trees lst yr. in phloem; 2nd year in wood
E. atomarius	*Quercus* spp., *Castanea, Celtis, Juglans, Carya*	Phloem at base of dead trees, pupates in sapwood
Elaphidion mucronatum	*Quercus, Juglans, Cornus, Celtis, Morus, Acer, Castanea, Populus, Liriodendron, Sassafras*	Phloem and xylem of dead branches
Elaphidionoides villosus	Many hardwoods *Quercus, Carya, Castanea, Prunus, Gleditsia, Celtis, Acer, Juglans, Ulmus, Cercis canadensis, Sassafras*	Girdles branches up to 5 cm diam.
E. parallelus	*Carya, Juglans, Quercus, Prunus*	Twig or branch pruners
Anelaphus pumilus	*Quercus* spp., *Castanea, Carya, Ulmus, Tilia*	?
A. inermis	*Carya*	Dead & dying branches
Heterachthes ebenus	*Pinus* spp.	Dead branches of pine
H. pallidus	*Carya ovata, C. illinoensis, L. tulipifera*	Wood
Curius dentatus	*Pinus* spp., *Taxodium distichum, Juniperus* sp., *Celtis*	Phloem/etch wood
Plectromerus dentripes	*Quercus* sp., *C. illinoensis*	?
Obriums rufulum	*Fraxinus*	Wood of dead & dying branches
O. maculatum	*Carya*, *Quercus*, *Celtis*, *Morus*, *Cercis*	
O. howdeni	?	?
Plinthocoelium suaveolens suaveolens	*Morus* sp.	Trunk & root borers
Dryobius sexnotatus	*Ulmus, Acer, Fagus, T. americana*	?
Ornithia mexicana	*C. laevigata*	Under loose bark
Pronocera collaris colaris	*Picea* spp., *Pinus* spp.	?
Hylotrupes bajulus	*Pinaceae*	Dry seasoned coniferous wood
Semanotus litigiosus	*Tsuga*	?
Semanotus ligneus ligneus	*J. virginiana, Chamaecyparis thyoides, Thuja occidentalis*	?

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Callidium antennatum antennatum	*Pinus* spp., *Picea*	Phloem, enter heartwood to pupate
C. texanum	*J. virginiana*	Phloem, enter heartwood to pupate
C. frigidium	*J. virginiana, T. occidentalis*	
Phymatodes varius	*Quercus* spp., *Carya*	Phloem
P. testaceus	*Quercus* spp., *Carya, Fagus, Salix, Castanea, Prunus*	Phloem, pupate under bark
P. aereus	*Quercus* spp.	Phloem, pupate under bark
Physocnemum andeae	*T. distichum*	Phloem, pupate in sapwood
P. brevilineum	*Ulmus* spp.	Phloem, pupate under bark
P. violaceipenne	*Q. alba*	Dead branches
Ropalopus sanguinicollis	*Prunus* spp.	Phloem of living trees, enter heartwood to pupate
Megacyllene robiniae	*R. pseudoacacia*	Phloem & wood of living trees, kills trees
M. caryae	*Carya* spp., *Juglans* spp., *M. rubra, C. occidentalis, Ulmus, Fraxinus*	Fresh cut wood
Calloides nobilis nobilis	*Quercus* spp., *Fraxinus* sp.	Phloem, stumps & base of recently dying or dead trees; require high moisture
Sarosesthes fulminans	*Castanea* spp., *Quercus* spp.	Phloem, half grown larvae enter wood
Xylotrechus sagittatus sagittatus	*Pinus* spp., *Abies, Picea*	Phloem, half grown larvae enter wood
X. colonus	*Quercus* spp., *Acer, Carya, Catanea, Fagus, Juglans, Fraxinus, Ulmus, Tsuga canadensis*	Phloem only
X. integer	*T. canadensis*	
Neoclytus scutellaris	*Quercus alba, Carya, Ulmus*	
N. mucronatus mucronatus	*Carya*	Phloem & wood preferred
N. acuminatus acuminatus	*Fraxinus, Quercus, Carya, Celtis*	Most all hardwoods, in unseasoned wood
N. fulguratus	*Quercus* spp.	Dry oak saplings
N. caprea	*Fraxinus* spp., *Carya, Quercus* spp., *Ulmus*	Infest newly dead or dying trees, enter sapwood
Clytus ruricola	*Acer* spp., *Carya* spp., *Betula, O. virginiana, Fagus, Quercus, T. americana*	In decaying wood
C. marginicollis	*Pinus* spp.	Phloem and xylem of dead branches
Clytolepus albofasiatus	*Carya*	
Cyrtophorus verrucosus	Hardwoods in general	Solid dead trees
Microclytus gazellula	*Carya glabra, Quercus* sp.	

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Euderces picipes picipes	*Carya* spp., *J. nigra*, *Quercus* spp., *Ulmus, Celtis, Cercis, Robinia, Nyssa, Cornus*	Phloem, pupate in wood
Rhopalophora longipes longipes	*C. canadensis*	
Anycylocera bicolor	*Carya, Quercus*	?
Neocydalis mellitus	*Quercus, Castanea*	Solid dead wood
Centrodera decolorata	*Quercus, Castanea, Liriodendron*	In wet decaying wood
Anthophilax hoffmani	*Picea, Abies*	Decaying logs
A. viridis	*Fagus, Betula, Acer*	Decaying logs
Gaurotes cyanipennis	*Quercus, Juglans, Prunus Nyssa, Cornus*	Phloem
Rhagium lineatum	All conifers	Phloem of recently killed trees
Bellamira scalaris	*Fagus, Acer, Populus, Pinus, Tsuga*	Well rotted logs in very moist situations
Typocerus zebra	*Pinus*	Mine dead roots
T. velutinus	Hardwood or conifer	Decaying wood
T. lunulatus	*Pinus*	
Leptorhabdium pictum	*Betula, Castanea, Cornus, Quercus, Carya*	?
Stenocorus cylindicollis	*Carya*	?
Evodinus monticola monticola	*Tsuga, Abies, Picea, Pinus*	Phloem
Arthophylax hoffmani	*Picea* sp., *A. fraseri*	
A. attenuatus	*A. saccharinum, F. americana, Populus, Betula, Ostrya*	Very moist decaying logs
A. cyaneus	*Betula, Fagus, Castanea, Acer*	?
Gaurotes cyanipennis	*Cornus, Prunus, Quercus, Juglans, Nyssa, Castanea, Betula*	Phloem, pupate in soil
Acmaeops proteus	*Pinus, Picea, Tsuga, Abies*	Phloem
A. discoideus	*Pinus* spp.	Phloem
Gnathacmaeops pratensis	*Picea* spp., *Pinus* spp.	
Metacmaeops vittata	*Liriodendron, Castanea*	?
Stranglia luteicornis	*Fagus, Ulmus, Quercus*	?
S. occidentalis	*Acer, Quercus*	?
S. acuminata	*Carpinus, Ostrya*	?
Bellamira scalaris	*Populus, Fagus, Carya, Salix, Acer, Betula, Liriodendron, Pinus*	?
Analeptura lineola	*Betula, Ostrya, Carpinus, Pinus*	?
Charisalia americana	*Liriodendron, Nyssa*	
Grammoptera subargentata	*Populus, Quercus*	
Judolia cordifera	*Castanea*	
J. montivagans montivagans	*Abies, Pinus, Picea, Populus, Salix*	

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Leptura emarginata	*Castanea, Ulmus, Fagus, Quercus, Betula, Acer, Nyssa, Liriodendron*	?
L. sublamata	*Tsuga, Pinus*	
Leptura abdominalis	*T. distichum, Juniperus*	
Trachysida mutubilis	Hardwoods	Decaying
Pidonia ruficollis	*Castanea, Prunus, Betula, Populus, Tilia*	
Strangalepta vittata	*Abies, Pinus, Picea, Juniperus, Tsuga, Populus, Acer, Betula, Castanea*	
S. pubera	*Ulmus, Juglans, Pinus*	
Xestoleptura octonotata	*Quercus*	
Lepturopsis biforis	*Castanea, Populus, Pinus, Tsuga*	
Trigonarthris minnesotana	*Nyssa, Betula, Prunus, Ulmus, Tilia, Acer, Populus, Carya, Fagus, Pinus*	
T. proxima	*Acer, Carya, Castanea, Tilia, Nyssa*	
Brachyleptura rubrica	*Carya, Fagus, Quercus, Prunus, Platanus, Castanea*	
B. vagans	*Pinus, Tsuga, Betula, Carya, Juglans*	
B. circumdata	*Picea*	
Strophiona nitens	*Quercus, Castanea, Carya, Juglans, Fagus*	
Neoptychodes trilineatus	*Salix* spp.	Heartwood of dying trees
Hebestola nobulosa	*Quercus, Castanea*	
Plectrodera scalator	*Populus, Salix*	Phloem of live trees, often kill them, enter wood before winter
Monochamus scutellatus scutellatus	*Pinus, Abies, Picea*	Phloem, enter sapwood
M. marmorator	*P. rubens, A. balsamea*	Phloem, enter sapwood
M. carolinensis	*Pinus*	Phloem, enter sapwood
M. titillator	*Pinus, Picea*	Phloem, enter sapwood
M. notatus	*P. strobus, Abies, Picea*	Phloem, enter sapwood
Microgoes oculatus	*Cercis, Cornus, Populus, Quercus, Tilia, Fagus, Castanea, Carya, Acer*	Phloem
Goes dibilis	*Quercus, Carya, Castanea*	Small living branches
Goes tiqrinus	*Quercus, Juglans, Carya, Ulmus*	Live trees, in wood
G. pulcher	*Quercus, Carya, Ulmus*	Live trees, in wood
G. tesselatus	*Quercus, Castanea, Ulmus*	Base and roots of saplings
G. pulverulentus	*Quercus, Fagus, Carpinus, Ulmus, Prunus, Betula, Ostrya*	Live trees, in wood
Dorcaschema wildi	*M. rubra*	Phloem of living branches
D. cinercum	*Carya, Celtis, Tilia, Morus, Acer, Juglans*	Dead limbs 1-10 cm, phloem & wood
D. alternatum	*Morus*	

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Ataxia crypta	*Quercus, Castanea, Acer, Celtis, Salix, Prunus*	Dead branches
Eupogonius subarmatus	*Tilia, Ulmus, Fagus, Prunus*	
E. tomentosus	*Pinus, Picea*	?
E. pauper	*Acer, Carpinus, Carya, Castanea, Cercis, Cornus, Fraxinus, Juglans, Morus, Prunus, Quercus, Tilia, Ulmus*	
Psenocerus supernotatus	*Cornus, Quercus, Carya, Castanea, Liquidambar, Ulmus, Liriodendron, Salix*	Dead branches
Ecyrus dasycerus	*Castanea, Celtis, Robinia, Tilia, Morus, Ulmus, Carya, Quercus, Prunus*	
Pogonocherus mixtus	*Pinus* spp., *Picea, Salix*	
Aegomorphus quadrigibbus	*Castanea, Fagus, Tilia, Acer, Carya, Cercis, Ulmus, Quercus, Betula, Tilia, Celtis*	Decaying wood
A. morrisi	*Nyssa, Liriodendron*	
A. modestus	Most hardwoods	Decaying wood
Brentidae[5]		
Arrhenodes minutus	*Q. alba*	Bore in heartwood
Anthribidae[6]		
Ischnocerus infuscatus		
Ormiscus saltator	Deciduous trees	In wood
Curculionidae[7]		
Steremnius shermani	*Picea*	
Heilipus apiatus	*Pinus* sp.	Under bark
Eudociminus mannerheimi	*T. distichum*	Phloem of dead & dying trees
Pissodes similis	*A. balsamea, A. fraseri*	Phloem
P. approximatus	*P. strobus, P. virginiana, P. echinata*	Phloem
P. nemorensis	*Pinus* spp.	Phloem
P. fraseri	*A. fraseri*	Phloem of dying trees
Magdalis perforata	*P. strobus*	Phloem
M. barbita	*Ulmus* spp.	Phloem
M. armicollis	*Ulmus* spp.	Phloem
M. olyra	*Carya, Quercus*	Phloem
M. pandura	*J. nigra*	Phloem
M. incospicua	*Carya*	Phloem
Acamptus rigidus		Red rotten wood
Dryophthorus americanus	*Pinus* sp.	Phloem?

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Himatinum conicum	*P. strobus*	In assoc. with *Tomicus pini*
Cossonus concinnus	*Carya* sp., *P. occidentalis*, other hardwoods	Phloem
C. corticola	*Pinus* spp.	Beneath bark
Allominus dubius		Under bark of dead & decaying trees
Phloeophagus minor	*Betula, Salix, Ulmus*	Decaying wood
Tomlips quercicola	*Fagus*, other hardwoods	Rotting wood
Pentarthrinus parvicollis	Various trees	Dead wood
Rhynocolus oregonensis	*Pinus* sp.	Phloem
Stenoscelis brevis	Most deciduous trees	Rotten wood
Lucanidae[8]		
Dorcus parallelus	*Quercus, Tilia, Acer*	Decaying roots & stumps
Lucanus placidus	*Quercus* sp.	Decaying logs
Lucanus elaphus		Rotten wood
Platycerus virescens	*Quercus* spp.	Decaying wood
Scarabaeidae[8]		
Cloetus aphodioides	*Quercus, Carya, Ulmus*	
Acanthocerus aeneus		Rotten logs & stumps
Pelidnota punctata	*Acer, Quercus, Celtis, Ulmus*	Rotten wood
Parastasia brevipes	*Quercus, Platanus*	Rotten wood
Trichiotinus afinis	*Quercus, Carya*	Decayed wood
T. bibens	*Quercus*	Decayed wood
T. piger	Hardwoods	Decayed wood
Osmoderma eremicola	Hardwoods	Decayed wood
O. scabra	Hardwoods	Decayed wood
Strategus julianus		Decaying wood
Dynastes tityus		Decaying wood
Phileurus didymus		Decaying wood
Passalidae[8]		
Popillius disjunctus	Hardwood stumps & logs	Adults feed young wood pulp
Lyctidae[9]		
Lyctus brunneus	*Quercus, Ulmus*	Sapwood
L. cavicollis	Hardwoods	Wood
L. linearis	*Quercus, Carya, Juglans, Fraxinus*	Wood
L. planicollis	*Quercus, Fraxinus, Carya, Platanus*	Wood
Trogoxylon parallelopipedum	*Carya, D. virginiana, Quercus*	Wood

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Bostrichidae[10]		
Prostephanus punctatus	*Carya, Quercus*	Dead roots & stumps
Stephanopachys rugosus	*Pinus* spp.	Wood
S. substriatus	*T. canadensis, Pinus* spp., *Abies* spp.	Wood
S. cribratus	*P. taeda, P. strobus*	Wood
S. hispidulus	*P. taeda, P. virginiana*	Wood
Lichenophanes bicornis	*Celtis, Quercus, Carya, Fagus, Ulmus*	Dead bark & wood
L. armiger	*Quercus*	Wood
L. truncaticollis	*Carya*	Wood
Seobicia bidentata	*Carya, C. dentata*	Wood
Xylobiops basilaris	*Quercus* spp., *Fraxinus* sp. *D. virginiana, Carya alba, U. americana, R. psuedoacacia*	Wood
Micromathidae[11]		
Micromalthus debilis	*Quercus, Castanea*	Wood feeders, advanced decay
Lymexylonidae[11]		
Hylecoetus lugubris	Hardwood	Decaying wood
Melittoma sericeum	Hardwood	Decaying wood
Platypodidae[5]		
Platypus flavicornis	*Pinus* spp.	Base of tree, ambrosia beetles
P. quadridentatus	*Quercus* spp., many other hardwoods	Ambrosia beetles
P. compositus	Many hardwoods	Ambrosia beetles
P. parallelus	Hardwoods	Ambrosia beetles restricted to Florida & Texas
Anobiidae[12]		
Coelostethus notatus	*Quercus*	Branches
Xyletinus peltatus		Damp wood
Eucrada humeralis	*Quercus, Fagus*	Phloem
Xestobium rufovillosum	*Picea, Quercus, Pinus* spp.	Dry wood
Ernobius mollis	*Pinus* spp.	Wood
E. filicornis	*Pinus* spp.?	?
E. granulatus	*Pinus* spp.?	?
E. tenuicornis	*Pinus* spp.?	?

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Oligomerus sericans	*Carya, Q. alba*	Wood
O. obtusus	?	?
O. brevipilis	?	?
O. alternans	?	?
Trichodesma relagesi	*Carya*	?
Anobium punctatum	Many hosts	Wood
Platybregmus canadensis	*Acer, Tilia, Ulmus*	Wood
Hadrobregmus carinatus	*Acer, Fagus*	Wood
H. linearis	Hardwoods	Wood
H. pusillus	Hardwoods	Wood
H. umbrosus	Hardwoods	Wood
Trypopitus sericeus	*Quercus, Prunus, Carya*	Dead branches, wood
Ptilinus ruficornis	Hardwoods	Wood
P. pruinosus	?	?
Oedemeridae[13]		
Xanthochroa trinotata	?	?
X. erythrocephala	?	?
Nacerdes melanura		Wood in water or subject to flooding
Heliocis repanda		?
Oxacis floridana	?	?
Oxacis cana	?	?
Oxacis taeniata	?	?
Oxacis notoxoides		?
O. thoracia	?	?
O. suturalis	?	?
O. mimetica	?	?
O. recendita	?	?
O. interrita	?	?
Alloxacis pleuralis	?	?
A. floridana	?	?
A. dorsalis		Dirt & wood
A. ignota	?	?
Asclera ruficollis	?	?
A. puncticollis	?	?
Buprestidae[14]		
Aemaeodera ornata	*Carya, Robinia*	
A. pulchella	*T. distichum*	
A. tubulus	*Carya, Q. alba, C. canadansis*	
Ptosima gibbicollis	*C. canadensis*	Heartwood of living trees
Chalcophora virginiensis	*Pinus* spp.	Logs and stumps, wood
C. georgiana	*Pinus* spp.	Logs and stumps, wood

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Chalcophorella campestris	*Fagus, Salix, Plantanus, Tilia*	Moist decaying hardwood logs
Trachykele lecontei	*T. distichum*	Sap and heartwood
Dicerca divaricata	*Prunus, Acer, Tilia, Betula, Quercus, Ulmus*	
D. punctulata	*Pinus* spp.	
D. obscura	*Carya, Acer, Q. alba*	
D. lurida	*Carpinus* sp.	
D. lepida	*Ostrya* spp.	
D. tenebrosa	*Pinus, Picea*	
D. tuberculata	*T. canadensis*	
D. americana	*Pinus* spp.	
Cinyra garclipes	*Quercus, Fraxinus*	
Buprestis striata	*Pinus* sp., *Tsuga* spp.	
B. aprican	*Pinus* spp.	Wood of wounded trees
B. decora	*Pinus* spp.	Decaying wood
B. salisburyensis	*P. rigida*	
B. lineata	*Pinus* spp.	
B. maculipennis	*Pinus, Tsuga, Taxodium*	Branches, heartwood
B. rufipes	*Ulmus, Fagus, Carya, Quercus, Acer, Castanea, Liriodendron*	
B. faciata	*Pinus* spp.	
Xenorhipis brendeli	*Quercus nigra*	
Malanophila aeneola	*Pinus* spp.	Phloem & sapwood
M. obtusa	?	?
M. notata	?	?
M. opaca	?	?
M. acuminata	*Pinus, Picea, Abies*	
Anthaxia viridifrons	*U. americana, Carya*	Dead branches
A. viridicornis	*Salix*	Dead & dying
A. quercata	*Cercis, P. strobus, Castanea, Q. nigra*	Sapwood & branches
Agrilaxia flavimana	*Q. alba*	
Chrysobothris chrysoela	*T. distichum*	
C. sexsignata	*Tsuga, Fraxinus alba, A. rubrum, J. nigra, Quercus* spp., *Fagus, Betula*	Sapwood
C. scitula	*Quercus*	Dead branches
C. azurea	*Carya, Acer, Quercus, Pinus, C. florida, Tilia, Salix*	
C. texana		Cedar
C. pusilla	*Pinus* spp.	Sapwood
C. dentipes	*Pinus* spp.	
C. floricola	*Pinus* spp.	Phloem
C. femorata	Many hardwoods	Phloem feeder on damaged or scarred trees

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Chrysobothris. rugosiceps	*Castanea, Q. alba*	
C. adelpha	*Carya*	
C. viridiceps	*A. rubrum, Quercus, Prunus*	
C. harrisi	*P. virginiana, P. strobus, P. rigida*	
Actenodes acornis	*A. rubrum, Carya, Quercus, Fagus*	Heartwood dead trees
A. auronotata	*T. distichum*	Dead
Agrilus bilincatus	All *Quercus* spp., *C. dentata*	Phloem of living weakened trees
Agrilus facipennis	*P. virginiana*	
Agrilus masculinus	*A. rubrum, A. negundo*	
A. defectus	*Q. alba*	
A. cephalicus	*C. florida*	
A. fallax	*R. pseudoacacia, C. occidentalis*	
A. otiosus	*Carya* spp., other hardwood	
A. politus	*Salix*	
A. obsoletoguttatus	*Fagus, Carpinus, Quercus, Carya*	
A. lecontei	*C. florida, C. occidentalis*	
A. celti	*C. occidentalis*	
A. quadriguttatus	*Salix*	Sapwood
Mastogenius subcyaneus	*Quercus* spp.	Dead branches
Order Lepidoptera: Noctuidae[15]		
Scolecocampa liburna		Moist, decayed logs
Sesiidae[16]		
Synanthedon scitula	Deciduous hardwood trees	Wood of living trees
S. acerni	*Acer* spp.	Live trees
S. pini	*Pinus strobus*	Phloem & sapwood
S. geliformis	*C. florida, C. illinoensis*	Bark borer
S. acerrubri	*Acer* spp.	Bark borer
S. castaneae	*Castanea* sp.	Wood borer
S. rubrofascia	*L. tulipifera*	Bark borer
S. sigmoidea	*Salix* spp.	Wood
S. proxima	*Salix* spp.	Wood
S. bolteri	*Salix* spp.	Wood
Sannina urocerifrons	*D. virginiana*	Wood
Podosesia syringae	*Fraxinus* spp.	Wood
P. aureocinta	*Fraxinus* spp.	Wood
Paranthrene simulans	*Quercus* spp.	Wood
P. dollii	*Populus deltoides, Salix* spp.	Wood
P. tabaniformis	*P. deltoides*	Wood of branches

A partial listing of the wood-feeding insects of the Southern United States with notes on their hosts and habits (continued)

Species	Hosts	Habits
Cossidae[5]		
Acossus populi	*Populus* sp.	
Prionoxystus robiniae	*Quercus* spp., *R. psuedoacacia,* *Ulmus* spp., *Acer* spp., *Salix* spp., *Populus* spp.	Wood
P. macmurtrei	*Quercus* spp.	Phloem & wood
Hymenoptera: Siricidae[5]		
Sirex edwardsii	*P. rigida*	Wood
S. nigricornis	*P. echinata, P. strobus, P. virginiana*	Wood
Urocerus cressoni	*Picea, Abies, Pinus*	Wood
U. taxodii	*T. distichum*	Wood
Tremex columba	Hardwoods	Dead or weakened trees, wood
Eriotremex formosanus	Hardwoods	Dead wood introduced sp.
Xiphydriidae[17]		
Xiphydria hicoriae	*Carya, Ulmus*	Wood of branches, boles
X. maculata	*Acer* spp.	Wood of dead limbs
X. tibialis	*Ulmus, Betula, Fagus, Quercus*	Wood of boles, branches
X. mellipes	*Betula* spp.	Dead, decaying logs
X. scarfa	*Carpinus americanus*	Dead, dry stems

[1] Nickle and Collins 1989; [2] Light 1934; [3] Wood 1982; [4] Linsley 1961, 1962a, 1962b, 1963, 1964, Linsley and Chemsak 1972, 1976, 1984; [5] Drooz 1985; [6] Blatchley and Leng 1916; [7] Anderson 1952; [8] Richter 1966; [9] Gerberg 1957; [10] Fisher 1950; [11] Arnett 1968; [12] White 1962, 1971; [13] Arnett 1951; [14] Franklin and Lund 1956; [15] Peterson 1962; [16] Duckworth and Eichlin 1977; [17] Smith 1976.

The Significance of Coarse Woody Debris for the Diversity of Soil Mites

John M. Johnston and D.A. Crossley, Jr.

Abstract

The community of mites inhabiting forest floors is rich in species but is poorly known both taxonomically and biologically. Understanding the relationship of mite species diversity to ecosystem function depends upon better knowledge of habitat and substrate use. Coarse woody debris (CWD) is a significant habitat variable as well as a resource for mite communities. However, little information has been developed on the use of woody debris by mites in southern forests. As a habitat variable, CWD is a contributor to the microenvironmental gradients that affect soil-mite distribution and abundance. As a resource variable, the importance of CWD resides in its support of a varied fungal population and its nutrient reserves. Calcium, abundant in the bark of decaying boles and twigs, is particularly important for Oribatid mites.

Introduction

Soil-dwelling mites reach their greatest abundance in the forest floors of temperate regions (Swift and others 1979). Mites are major participants in belowground food webs. Some species feed directly upon decomposing plant materials; more species are fungivores. Others are predators on other small arthropods or their eggs, nematodes, or other small fauna. Many species appear to be omnivorous, or at least to have the capacity to switch food sources, depending upon availability. A large diversity of mite species is characteristic of most soil systems. Indeed, mites are the most species-rich group of the North American soil arthropod fauna (Behan-Pelletier and Bissett 1992). Almost one-half of the soil mite species are unnamed; perhaps as few as one-third of North American species of soil mites have been adequately described and illustrated (Behan-Pelletier and Bissett 1992). Furthermore, immature stages are poorly known. Food habits for many species remain obscure, and observations on feeding reported in the literature often prove to be unreliable (Walter 1988).

For ecological analyses, soil mites may be arrayed into functional groups (Moore and others 1988) of soil food webs. Oribatid mites are generally considered as a fungivore-detritivore functional group, Mesostigmata as general predators, and Prostigmata as specialized predators. However, these generalizations may lead to erroneous conclusions due to inadequate information on feeding habits or the specialized nature of some predator-prey relationships (Walter 1987, 1988). As concerns about the loss of biodiversity continue (Wilson 1992), and the relationships of biodiversity to ecosystem function become better understood (Schultze and Mooney 1993), increased attention to taxonomy and diversity of soil mites is needed. A necessary concomitant is the analysis of habitat use by soil mites, so that the importance of habitat features, such as coarse woody debris (CWD), can be quantified.

Only a few scattered references can be found on the use of woody debris by mites in southern forests. This is surprising, given the number of studies of forest floor arthropods done in areas ranging from upland southern pine forests to rich bottomland hardwood forests. In this paper, we offer a preliminary interpretation of the importance of CWD for soil mite diversity, some directions for future studies, and some tentative considerations for management practices.

Factors Affecting Spatial Distribution of Soil Mites

Mite species have clumped (contagious) distributions in forest floor habitats. It is not clear what factors affect the spatial distribution of soil mites. Even a seemingly uniform forest floor under a pine monoculture will contain more than 50 species of oribatid mites, and perhaps as many as 100 total mite species. Since different oribatids appear to feed on the same foods, fungi and/or decaying organic matter, the coexistence of so many similar species seems unusual. Two factors have been suggested to explain this coexistence of similar species. One is seasonal separation. Research using litterbag methods to sample soil arthropods reveals a succession of reproductive success by oribatids during the year. Thus, some species of mites may be geared to a seasonal pattern of fungal species.

Microhabitat differentiation is the other factor proposed to explain soil mite community structure. The uniform appearance of the forest floor may be deceiving to the casual eye: distances from tree boles, presence of understory, root

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distributions (Fitter and others 1985), and similar habitat variables make for a sequence of more-or-less-distinct microhabitats. These factors, coupled with the highly contagious spatial distributions of most oribatid mite species, led Anderson (1977) to propose that mites exist in a set of "unit communities" in the forest floor. Most mite species appear to be distributed across a variety of forest floor habitats. The presence of microhabitats probably contributes to the abundance and persistence of mite species.

Relationship of Soil Mite Biodiversity to Coarse Woody Debris

Coarse woody debris is a major habitat variable on forest floors (Wallwork 1976). It contributes to the microenvironmental gradients that affect the distribution and abundance of soil mite species. Coarse woody debris in mature forests provides a set of microsites that offer food and habitat resources for unit communities of soil mites. Coarse woody debris is part of a woody continuum, starting with fine twigs and ranging through larger twigs and branches to boles. Fallen logs vary by species and by mode of decay. Fallen hardwood logs that are hollow support a rich mite fauna, as do basal tree-holes (Park and Auerbach 1954). Tree-holes contain several unique species of mites (Camin 1953).

Decaying woody debris is a significant nutrient sink in southern forest floors (Cromack and Monk 1975). Accumulations of calcium in the bark of decaying wood may be particularly significant for Diplopoda (millipedes) and for oribatid mite species, which use calcium oxalate or calcium carbonate as cuticular hardening agents (Norton and Behan-Pelletier 1991). Oribatid mites accumulate calcium compounds from a fungal diet (Cromack and others 1977). The food base for most oribatid mites consists of fungal hyphae, although some species appear to use leaf litter or woody materials directly. This aspect of nutrition has been termed the "peanut butter sandwich" problem. Do you eat the entire sandwich just to get the peanut butter (the microbes) in the sandwich (the decaying substrate)?

Effects of CWD on microclimate are important during drought conditions. Soil fauna are notoriously moisture dependent. Fallen logs offer protection from desiccation, since the soil beneath logs remains moist after the forest floor has dried. Accumulations of macrofauna and microarthropods under logs are commonly noted during droughts. Nocturnal macrofauna, that is, cryptozoa such as thysanurans and scorpions, use fallen logs or stumps as daytime refuges, but such behavior has not been recorded for mites in southern forests.

Finally, CWD offers a somewhat distinct habitat feature on the forest floor. Fallen logs support lichen populations and fungal structures that are absent or not abundant in leaf litter. Mites, which can penetrate fallen logs either through openings made by insects or as phoretic passengers on insects, find a unique habitat. Some mite species are obligate members of the intra-log community.

Use of Coarse Woody Debris by Soil Mites

Given the importance of CWD as a habitat factor and a set of resources, it is not surprising that a large number of mite species use it (tables 1 and 2). Most of the oribatid mites that occur in the forest floor will, at some time, be found in decaying logs. Seastedt and others (1989) found that oribatid mites in forest floors in the Cascade Mountains of central Oregon used both decomposing wood and leaf litter, although mite species diversity in wood was much lower than in litter. Table 1 shows the presence of oribatid mites in soil cores, experimentally bagged leaf litter, and woody debris on the forested floors of hardwood watersheds at Coweeta Hydrologic Laboratory, Macon County, North Carolina. Despite the uneven sampling effort (5 to 6 times more woody samples examined than other types), it would appear that the majority of oribatid species living in the soil use both leaf litter (judging by the litterbags) and woody litter. A few abundant soil forms (e.g., *Ceratozetes* spp., *Eremobodes* sp., *Oppia minus*) appear to use neither recent leaf litter nor wood. Others (*Oppiella nova*, other species of Oppiidae, Suctobelbidae spp., *Tectocepheus velatus, Trhypochtonius americanus*) seem to be litter feeders. Data suggest that species such as *Carabodes* spp. and *Eupelops* sp. use both wood and leaf litter. Among this group of 73 species only 7—*Atropacarus* sp., *Camisia spinifer, Nanhermannia* sp., *Ommatocepheus_ocellatus*, *Oribatula* sp., *Oripoda* sp., and *Scheloribates pallidus*—appear to use CWD as a preferred habitat.

Other mite groups found beneath bark of decaying chestnut oak (*Quercus prinus*) logs (table 2) are also common soil-litter forms, at least for the most part. Most of the Prostigmata listed are predators. Eupodids are fungal feeders in the laboratory. The Tetranychidae (red spider mites) and Tenuipalpidae (false spider mites) feed on green vegetation: they probably had fallen from tree foliage and

Table 1—Oribatid mite species in hardwood forest floor habitats at Coweeta Hydrologic Laboratory, North Carolina[a]

Oribatid species	Soil cores (N = 57)	Litter bags (N = 78)	Woody litter (N = 300)	Oribatid species	Soil cores (N = 57)	Litter bags (N = 78)	Woody litter (N = 300)
Adoribella sp.	0	0	1	*Rufulus hypochthonius*	5	0	3
Aeroppia sp.	0	0	4	*Machuella* sp.	10	0	0
Allodamaeus sp.	0	0	1	*Malaconothrus* sp.	—	0	1
Allogalumna sp.	0	0	1	*Metrioppia* sp.	0	0	1
Anachipteria sp.	0	0	3	*Microtritia* sp.	—	—	1
Atopochthonius sp.	0	1	0	*Multioppia* sp.	0	0	3
Atropacarus sp.	—[b]	—	83	*Elegantula nanhermannia*	8	0	48
Austrocarabodes sp.	0	0	10	*Neoribates* sp.	0	0	4
Belba sp.	—	4	10	*Nothrus sylvestris*	2	1	5
Brachychthonius sp.	—	—	1	*Ocellatus ommatocepheus*	0	0	670
Caleremaeus sp.	0	0	2	*Ophidiotrichus* sp.	0	0	2
Camisia spinifer	2	0	18	*Oppia durhamensis*	8	4	14
Carabodes spp.	61	12	71	*Oppia minus*	146	4	0
Carabodoides sp.	0	5	2	*Oppiella nova*	402	77	31
Cepheus cepheiformis	4	2	17	*Oppiidae* spp.	44	44	5
Ceratoppia bipilis	3	3	19	*Oribatella* spp.	48	74	2
Ceratozetes spp.	83	1	11	*Oribatula* sp.	31	73	147
Cultroribula juncta	2	0	0	*Oribotritia* sp.	—	1	6
Damaeus grossmani	18	13	2	*Oripoda* sp.	1	1	41
Eobrachychthonius sp.	—	—	0	*Parachipteria* sp.	17	1	3
Gracilis eohypochthonius	24	0	7	*Peloptulus* sp.	4	0	2
Cylindrica epilohmannia	—	—	0	*Phthiracarus* sp.	—	—	2
Epilohmannoides sp.	—	—	0	*Peltifer platynothrus*	7	14	9
Eremaeus sp.	3	0	13	*Depressa protokalumma*	0	0	6
Eremobelba sp.	37	0	1	*Quadroppia* sp.	19	0	0
Eremobodes sp.	113	6	1	*Rhysotritia* sp.	—	—	11
Eremulus sp.	4	0	2	*Scapheremaeus* sp.	0	0	17
Eupelops sp.	15	16	22	*Pallidulus scheloribates*	—	—	78
Euphthiracarus sp.	—	—	7	*Suctobelbidae* spp.	286	13	3
Ferolocella sp.	0	11	0	*Tectocepheus velatus*	142	127	3
Fosseremaeus sp.	18	0	0	*Topobates*	0	0	1
Gymnodamaeus sp.	8	0	3	*Americanus trhypochthonius*	14	111	26
Hemileius sp.	1	0	2	*Trimalaconothrus* sp.	—	0	2
Heminothrus sp.	0	0	1	*Xenillus* sp.	0	0	2
Hermaniella sp.	5	0	1	*Xylobates* sp.	33	1	3
Hypochthoniella sp.	1	0	0	*Zachvatkiniella* sp.	1	0	0
				Zygoribatula sp.	0	5	0

Variates = number of individuals; N = number of samples examined.

[a] Data from Abbott 1980.

[b] Species lumped into a higher taxonomic category during analysis of soil core and litterbag samples.

Table 2—Mites in the suborders Prostigmata and Mesostigmata found beneath bark of decaying chestnut oak (*Quercus prinus*) logs at Coweeta Hydrologic Laboratory, North Carolina

Prostigmata	Mesostigmata
Alycus sp.	*Amblyseius* sp.
Bdella sp.	*Ameroseius* sp.
Bimichaelia sp.	*Asca aphidoides*
Biscirus sp.	*Asca grmanni*
Cunaxa sp.	*Calholaspis berlesei*
Cyta sp.	*Dendrolaelaps* sp.
Dactyloscirus sp.	*Discourella* sp.
Eupodes spp.	*Eviphis* sp.
Eustigmaeus sp.	*Holaspina* sp.
Labidostomma mamillata	*Haploseius* sp.
Lorryia sp.	*Hypoaspis* sp.
Mullederia sp.	*Lasioseius* sp.
Paralorria sp.	*Neoparholaspulus hurlbutti*
Pediculaster sp.	*Parasitus* sp.
Penthalodes sp.	*Podocinum* sp.
Protereunetes sp.	*Rhodacarus* sp.
Pyemotes sp.	*Uropodidae*
Scutacarus sp.	*Veigaia* sp.
Spinibdella sp.	*Zercon* sp.
Tenuipalpidae	
Tetranychidae	
Thoribdella sp.	
Eutrombicula alfreddugesi	
Tydeus sp.	
Zetzellia sp.	

Data from Abbott 1980 and Crossley unpublished.

taken refuge under the bark. The Mesostigmata listed are also predators, some common in forest canopies and forest floors (i.e., *Amblyseius* sp., *Asca aphidoides*). The chigger mite *Eutrombicula alfreddugesi*, which occurred under the bark of fallen chestnut oak logs at Coweeta (table 2), was not found beneath the bark of fallen logs in the Georgia Piedmont (Mallow and others 1984). But adults occurred in soil beneath fallen pine logs, and questing larvae were found on the surface of those logs (see below).

Such a broad distribution of soil mites across habitats has been noted by others. Anderson (1977) suggested that the phenomenon, like the clumped or disjunct spatial distributions, may be one of scale. In particular, sampling methods may not be suited to microarthropods whose habitat scale is much smaller than the sampling tools. The food resource (the "peanut butter") is often fungal hyphae, and these occur on a broad variety of decomposing substrates. Furthermore, twig litter or other fine litter occurs throughout the forest floor and may provide an adequate resource for microarthropods that can use it. In laboratory studies, Hartenstein (1962) found nine species of oribatid mites that appeared to feed directly on wood (including *Camisia spinifer, Ceratozetes gracilis*, and *Nanhermannia elegantula*; see table 1).

In contrast, certain soil mites use CWD as substrate or habitat in specific ways. The oribatid mite *Ommatocepheus ocellatus,* listed in table 1 as very abundant in chestnut oak logs, is arboreal as well. The fallen log habitat evidently is in some way similar to standing tree trunks. Another arboreal species, *Humerobates_rostrolamellatus*, occurs on tree trunks and fallen logs in southern pine forests. This species is viewed as a bioindicator of airborne pollution in European forests (Andre and others 1984). One genus of trombidiid mites ("velvet mites"), *Neotrombidium*, lives in cracks in the wood of standing snags or on the vertical walls of hollow logs. Trombiculid mites, the adult stages of "chigger" mites, use rotting hardwood logs, where they are predaceous on other small arthropods. Hollow hardwood logs are especially important as habitats for the adult stages of *Eutrombicula* species, our common pest chiggers. In south Georgia (Glynn County), fallen logs and tree stumps were the major habitat for *Eutrombicula splendens*. In Georgia Piedmont habitats, a notable association occurs between lizards (*Sceloporus*), chigger mites (*E. alfreddugesi*), and fallen pine logs. Adult mites are found in soil at the base of the logs. Larval stages seeking a host ascend to the top surfaces of the logs, where lizards sunning themselves are susceptible to parasitism (Mallow and others 1984).

Other mites may use hollow, rotten logs. The chigger mite *Fonsecia gurneyi* is a parasite of snakes (*Elaphe* spp., for example). Adult *Fonsecia* are predators; the larvae parasitize snakes that enter hollow logs.

Mites may enter decaying CWD as phoretic forms—as inactive passengers on boring insects. Passalid beetles or "Bessy bugs," (*Popilius disjunctus*) carry several species of mites with them. Colonies of mites then develop among the macerated wood and feces of these semisocial insects (Hunter and Davis 1965). Wood feeding (or wood and fungus feeding) oribatid mites in the genus *Mesoplophora* are able to clasp the setae of passalid beetles and thus accompany them into decomposing logs (Norton 1980).

Conclusions and Recommendations

Coarse woody debris on forest floors has a significant impact on the distribution and abundance of soil mite species. Furthermore, some species of mites use CWD exclusively. However, the major importance of large branches and fallen logs in forest floor habitats appears to be that of a refuge for mite species normally occurring in litter or F layers. This importance likely increases in times of drought and perhaps under other conditions of stress.

Harvesting and site preparation both have a profound effect on the distribution of woody debris. Often, slash piles are created that consist of a mixture of soil, humus, and woody material. Although these piles usually do not persist for more than a few years, they are nonetheless an overlooked and possibly important aspect of arthropod dispersal and survival.

Fire, both natural and implemented as a management tool, also affects arthropod populations. Depending on the severity of the fire, varying amounts of the litter, fermentation, and humus layers are removed. Sites that are burned initially to control hardwood competition may be recolonized at a more rapid rate if woody debris serves as a refuge. Loblolly pine stands in the Coastal Plain often receive prescribed fuel-reduction burns every 3 to 5 years until the final harvest. Although CWD is largely absent from managed stands with a rotation age of 30 years, woody debris may yet play a key role in these frequently disturbed systems if it is introduced or purposely generated.

The arthropod fauna of CWD in southern forests has virtually gone unstudied. Research efforts should be directed toward investigating this fauna, with an objective of determining whether unique species are associated with woody debris, especially in old-growth forests. Special attention should be directed toward older logs, hollow logs, and basal tree holes. These are most likely to shelter unique species of soil mites.

Management practices aimed toward protecting the biodiversity of soil fauna should consider the placement of logs in even-aged pine stands. The geometry and relative distance of logs may be important considerations, since the scale of these organisms is a significant factor. Certainly hardwood logs that are undergoing decomposition should be protected. Hollow logs and trees containing basal tree-holes might be singled out for protection as well.

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Collembolans and Coarse Woody Debris in Southern Forests: Effects on Biodiversity

Richard J. Snider

Abstract

Knowledge of the Southern collembolan fauna is fragmentary and little is known of collembolan interaction with coarse woody debris (CWD). In successional colonization of CWD, collembolan are viewed as secondary invaders from the soil-litter subsystem. They have been found in both oak and pine subcortical zones during the first year of decay. Populations were higher in the first year, but species diversity was higher in the second and third years. Collembolans move between litter and woody debris, so it is difficult to separate litter forms from corticolous and lignicolous forms. Studies that include descriptive biology are necessary before we can assess the significance of woody debris for the community structure of collembolan populations.

Introduction

Between 92 and 99 percent of aboveground biomass in temperate and tropical forests is wood. This biomass may be in the form of aboveground wood and roots (Rodin and Basilevic 1967). A small part of the woody biomass is shed each year (Bray and Gorham 1964; Boddy and Swift 1983). Wood is, according to Swift and others (1979), a low-quality resource for organism metabolism. It has qualities that retard breakdown; i.e., extensive lignification and allelopathic compounds; it is protected by bark; and it is hard. Animals and microflora that exploit this resource are of necessity specific in their activity (Swift and Boddy 1984).

Kilbertus and Reisinger (1975) recognized a form of symbiosis between the microfauna and microflora. Swift and others (1976) reported that 60 to 75 percent of branchwood dry weight must be lost before wood-boring animals can invade. Fungi play an important role in this process. Two phases were proposed as models: Phase I, fungal invasion (immobilization of nutrients), followed by Phase II, animal invasion. Wallwork (1970) suggested that the microflora are affiliated with microfauna as: (1) gut symbionts, (2) a food source, and (3) competitive organisms seeking the same nutrients.

Recognition of the collembolan role in woody debris breakdown became clearer when Ausmus (1977) described four mechanisms that invertebrates may use for regulation of wood decomposition. These were: (1) translocation and defecation, (2) passive inoculation, (3) regulation of microbial succession and catabolic pathways, and (4) changes in microsite chemistry. In this scheme, he considered Collembola to be secondary invaders. Swift (1977) proposed the following model:

Colonization—>	**Exploitation—>**	**Invasion—>**	**Post Invasion**
bacteria, beetles	white & brown rots	wood-borers	soil fauna
stain fungi,	soft rots		Collembola
soft rots			

Here again, Collembola are viewed as secondary invaders, from the soil/litter subsystem. Lloyd (1963) drew attention to the movement of fauna between decaying branches and surrounding litter. When climatic conditions were unfavorable, the animals retreated to the litter. This critical interaction is the subject of a symposium publication by Anderson and others (1984).

Role of Collembolans in Breakdown of Woody Debris

The literature dealing with this subject is especially scant for forests in the Southern United States, where much of our information comes from studies that examined standing dead, stump, or log decay. Savely (1939), working in North Carolina's Duke Forest, studied the ecological succession of animals in pine and oak logs. He monitored logs from cutting to disintegration. He observed boring insects feeding in the phloem during the first year. They provided an entrance for fungi and eventually animals. He mentioned that the succession of wood-feeding animals may be controlled by fungi. During the first year of decay in both pine and oak, collembolans were found in the subcortical zone. Their species diversity was higher, while population numbers were lower than in the second and third years. Species diversity decreased after the first year in both vegetation types. The common collembolans found were four entomobryid, one isotomid, and one neanurid species.

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In contrast, Howden and Vogt (1951) made no mention of collembolans in standing dead pine of approximately the same age as the logs used in Savely's (1939) study. Snow (1958), working in Alabama, examined the stratification of arthropods in a wet sweetgum (*Liquidambar styraciflua* L.) tree stump. He distinguished dry wall forms and moist wall forms among the arthropod inhabitants. In addition, four collembolan species were categorized as subcortical forms. His report showed that moist wall and subcortical forms were absent from dry wall situations.

The only study dealing with Collembola and woody litter decomposition in a Southern United States forest was published by Abbott and Crossley (1982). The investigation was conducted at Coweeta Hydrologic Laboratory in North Carolina. One of their objectives in measuring the decomposition of chestnut oak (*Quercus prinus* L.) woody litter was to quantify microarthropod populations. They found that microarthropods, including oribatid mites and Collembola, were the dominant community on decaying wood. Abundance increased with time, and site condition was an important factor. While collembolans and mites were more abundant on small-diameter twigs, the authors concluded that microarthropods were more effective on larger material.

Southern United States Collembolan Diversity

In general, the Aptergota fauna has received little attention from systematic zoologists in North America. Aside from Christiansen and Bellinger (1980-81) and Fjellberg (1985), very few authors have produced papers recently describing the collembolan fauna. The southern fauna in particular is poorly known. Until the 1980's, with few exceptions, checklists of southern species were so wanting that Zingmark (1978) wrote an annotated list for the Collembola of the coastal zone of South Carolina in which he recorded species that ought to be found there, based on North Carolina records. Knowledge of individual species distribution is sporadic. Regional, State, and local faunal studies are remarkably deficient.

Some preliminary studies have resulted in checklists: Brimley (1938) for North Carolina, Copeland (1960) and Ford (1963) for Tennessee, Hepburn and Woodring (1963) for Louisiana, and Wray (1967) for North Carolina. Many of these lists contain distribution and site collection data useful to those interested in habitat and distribution information. They are helpful when attempting to assess species diversity, and provide clues for specific sampling designs. However, quantitative data and information on species associations are missing.

Another source of collembolan biodiversity data in southern forests stems from decomposition studies. Forest floor litter and woody material (stumps, logs, and branches) are usually treated separately. Earlier in this paper it was shown, however, that the forest soil/litter collembolans were responsible for the secondary invasion of woody debris. Therefore, it is difficult to separate litter forms from corticolous and lignicolous forms. Pearse (1943) studied the effects of burning and raking off litter in the Duke Forest. He listed seven species of Collembola from the litter zone. Pearse (1946) did a more detailed study of the Duke Forest mesofauna and collected 44 collembolan species. He was able to show the effects of seasonal distribution, abundance, and food preferences. Knight and others (1963, 1966, 1967, 1969) in a series of papers demonstrated the effects of seasonality, pesticide effects, dietary requirements, and microstratification in beech-maple and loblolly pine forests in North Carolina. DuRant and Fox (1966) investigated the arthropod populations of pine and hardwood forests in the Piedmont region of South Carolina. They estimated that Collembola made up more than 80 percent of the insect fauna in either pine or hardwood forests. Their collections numbered 41 species, forming the basis of the current South Carolina species list. Metz and Dindal (1975) working in Santee Experimental Forest, South Carolina, reported the effects of prescribed burning on collembolan populations. They found that species diversity increased when periodic burning took place. Twenty-one species were reported out of 73 collected in burned areas. It is unfortunate that the total list of Collembola was not published. Reynolds (1976) worked from November to April in the Coweeta Hydrologic Laboratory on litter decomposition as influenced by Collembola. He listed 17 species from a watershed dominated by deciduous trees.

Oddly, a study conducted in Maryland (Howden and Vogt 1951) on standing dead trees did not reveal collembolans as species components. Closer to the soil, Snow (1958) examined the stratification of arthropods in a wet stump in Alabama. He listed eight collembolans and their location by moisture preference. Information about springtail diversity in logs was provided by Savely (1939). He compared pine and oak logs lying in contact with the soil. Working in the Duke Forest, he showed that the collembolan species diversity decreased as the logs decomposed. Subcortical collembolans were more

Table 1—Collembolan species for the Southern United States

State	Author	Publication	Number
North Carolina	Brimley	1938	51
	Savely	1939	8
	Pearse	1943	7
	Pearse	1946	44
	Wray	1967	169[a]
	Wray	1971	1
	Reynolds (unpublished)	1976	17
	Graves and others	1977	75
	Snider	1978	1
	Christiansen & Bellinger	1980-81	132
	Snider	1990	1
Tennessee	Copeland	1960	77
	Ford	1962	3
	Ford	1963	48
	Snider	1978	1
	Christiansen & Bellinger	1980-81	95
Louisiana	Hepburn & Woodring	1963	76
	Hepburn	1964	1
	Snider	1978	1
	Christiansen & Bellinger	1980-81	95
South Carolina	DuRant & Fox	1966	41
	Metz & Dindal	1975	21[b]
	Christiansen & Bellinger	1980-81	42
	Snider	1981a	1
	Snider	1981c	1
	Snider	1982	1
	Snider	1985a-d	4
	Snider	1990	1
	Snider (unpublished)	1980-present	160[c]
Florida	Snider	1978	4
	Christiansen & Bellinger	1980-81	35
	Snider	1981b	1
	Snider	1982c	1
	Snider	1985c	1
	Snider	1990	3
Virginia	Christiansen & Bellinger	1980-81	33
Alabama	Snow	1958	8
	Christiansen & Bellinger	1980-81	26
	Snider	1989	1

(continued)

Table 1—Collembolan species for the Southern United States (continued)

State	Author	Publication	Number
Mississippi	Snider	1978	1
	Christiansen & Bellinger	1980-81	18
Georgia	Christiansen & Bellinger	1980-81	10
	Snider	1982b	1
	Snider	1985b-d	3
	Snider	1988	1
	Snider	1990	1
Arkansas	Christiansen & Bellinger	1980-81	22
	Tedder (unpublished)	1991	74
Texas	Snider	1978	1
	Christiansen & Bellinger	1980-81	42

[a] Approximately 20 names have been invalidated.
[b] 73 species were collected, only 21 species names were published.
[c] 50 of these species are new to science.

numerous in pine than in oak. He listed eight common species. Finally, an important paper by Graves and others (1977) lists 75 species from shelf fungi, moss, rhododendron litter, sawdust, and tree-hole debris. Only 12 species were common in fungi, moss, and litter. Shelf fungi yielded 48 species; sawdust, only 1: *Brachystomella stachi* Mills.

Systematic biologists interested in species diversity and distribution at the alpha taxonomic level have contributed their part to our knowledge of southern collembolan species. Wray (1945, 1946, 1949, 1950, 1953, 1959, 1963a, 1963b, 1971) contributed greatly by describing many new species from the Carolinas and Tennessee. Ford (1962) described three new species from Tennessee. Hepburn (1964) described a new species from Louisiana. Tedder (1991) did a faunistic survey of collembolans found on Magazine Mountain, Logan County, Arkansas. She collected samples from deciduous duff, humus, and sphagnum moss over a 3-year period. Her inventory resulted in 74 species. Her data suggested that the Eastern North American fauna most influenced that observed in central Arkansas. Christiansen and Bellinger (1980-81) provided the current foundation for a new assessment of southern species diversity. Their new species descriptions, range extensions, and corrections of identifications have expanded the numbers greatly. Since their publication, Snider (1981a, 1981b, 1981c, 1982a, 1982b, 1985a, 1985b, 1985c, 1985d, 1988, 1989, 1990) and Snider and Loring (1982) were able to add many new species to the faunal lists. Snider[1] has conducted studies on the collembolans at the Savannah River Site in South Carolina since 1980. The number of species presently stands at 160, 50 of which are new. Original plans were to record only the Savannah River Site; however, samples have been taken to include South Carolina, Georgia, Florida, Alabama, and Tennessee. Table 1 shows the known sources of collembolan species lists for the Southern United States.

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[1] Richard J. Snider, unpublished data.

Conclusion

The obvious conclusion here is that we know only bits and pieces about our Southern United States collembolan fauna, and even less about their specific role in woody debris breakdown. Intensive studies yield large numbers of species, many of which may be undescribed. We cannot begin to assess diversity and community structure of collembolan populations without studies that include descriptive biology. The specific functional role of Collembola in woody breakdown has not been well documented. However, preliminary studies demonstrate the existence of important relationships between collembola and microflora in the late stages of decay.

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Importance of Coarse Woody Debris to Southern Forest Herpetofauna

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Abstract

Most information on the relationships between herpetofaunal diversity and coarse woody debris (CWD) exists in the form of natural history observations; experimental data are lacking. However, these observations demonstrate that all major groups of North American reptiles and amphibians use CWD in some manner. The range of temperature and moisture regimens associated with CWD, along with its structural diversity, are important to many amphibians and reptiles for a variety of reasons. CWD serves as an important site for such vital activities as reproduction (nesting and mate attraction), feeding, and thermoregulation. Additionally, some groups such as salamanders may be obligatory in their association with CWD. Other probable uses of CWD by herpetofauna, such as refugia from predation, are potentially important but not well documented. Existing evidence suggests that amphibian and reptile diversity is likely linked to both quantity and quality of CWD. Thus, the current trend in forest management which enhances CWD availability should be continued.

Introduction

The forests of the Southern United States are inhabited by a rich diversity of frogs, toads, salamanders, lizards, snakes, and turtles. This region has the highest herpetofaunal diversity in the United States, including a large fraction of all known salamander species in the world (Conant and Collins 1991; Goin and Goin 1971). Several interrelated factors account for this diversity, including the geologic and physiographic variability of the region (Mount 1975). Unfortunately, in many regions of the Southeast and the rest of the United States, this diversity is imperiled by land management practices and habitat destruction (Dodd 1987; Duellman and Trueb 1986; Wilson and Porras 1983).

The majority of reptiles and amphibians in the United States have little or no recognized economic importance; thus, management of herpetological communities has historically received little attention. However, with increased interest in the conservation of biodiversity, all plant and animal communities (including reptiles and amphibians) are now considered important components of forest ecosystems. Many amphibians and reptiles are important predators on invertebrates and other vertebrates. In turn, herpetofauna are important dietary components of other vertebrates. Additionally, many amphibians and reptiles have an aesthetic value too rarely recognized.

As concern over the conservation of biodiversity increases, scientists and land managers are striving to identify habitat characteristics that promote diversity and abundance of organisms (e.g., Hansen and others 1991; Hansen and others 1993; Sharitz and others 1992). Ideally, identification of important habitat characteristics is followed by instigation of appropriate management plans. Of the many significant habitat features currently identified, the abundance, distribution, and condition of coarse woody debris (CWD) appears to be extremely important for optimizing diversity in both terrestrial (Harmon and others 1986; Maser and others 1988; Swanson and Franklin 1992) and aquatic (Benke and others 1984; Harmon and others 1986; Maser and others 1988) ecosystems.

The objective of this paper is to examine the relationship between CWD and herpetofaunal diversity. Little experimental data on this relationship exist. Most of the information has been gathered from natural history studies of various herpetofauna, which provide important information on the function of CWD in herpetofaunal communities. The few studies that directly examined the relationship between herpetofaunal diversity and CWD (mostly on salamanders in the Northwestern United States) are discussed where relevant. Recommendations and possible management strategies are discussed as well.

Uses of Coarse Woody Debris by Amphibians and Reptiles

Herpetofauna use woody debris for a wide variety of purposes (tables 1 and 2); and the usefulness of CWD is

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Table 1—Some uses of coarse woody debris by North American amphibians

Use	Salamanders	Frogs	Toads	References
Reproduction (nesting)	X			Norman 1986; Maser & Trappe 1984; Thomas 1979; Mount 1975; Smith 1961
Reproduction (calling)		X		Thomas 1979; Johnson 1977
Feeding substrate	X	X		Harmon and others 1986; Maser & Trappe 1984; Mount 1975; Storm & Aller 1947
Thermoregulation (hibernation/protection from temperature extremes, warming)	X	X	X	Aubry and others 1988; Maser & Trappe 1984, Thomas 1979, Mount 1975; McKenzie & Storm 1970
Protection from desiccation	X	X	X	Aubry and others 1988; Maser & Trappe 1984; Thomas 1979; Mount 1975; Stebbins 1966

Table 2—Some uses of coarse woody debris by North American reptiles

Use	Lizards	Snakes	Turtles	References
Reproduction (nesting)	X	X		Ernst & Barbour 1989; Thomas 1979; Mount 1975; Fitch 1954, 1963; Stille 1954
Feeding substrate	X	X		Collins 1982; Thomas 1979; Mount 1975
Thermoregulation (hibernation/protection from temperature extremes, basking)	X	X	X	Ernst & Barbour 1989; Collins 1982; Gregory 1982; Mount 1975; Brattstrom 1965; Fitch 1954
Protection from desiccation	X	X		Ernst & Barbour 1989; Collins 1982; Mount 1975; Smith 1961

probably attributable to the associated range of environmental conditions (e.g., temperature and moisture regimes) (Harmon and others 1986; Maser and others 1988; Maser and Trappe 1984; Thomas 1979). In forest ecosystems, CWD increases habitat heterogeneity and thus structural diversity (Hansen and others 1991; Sharitz and others 1992). Both are vital components in determining the diversity of herpetofauna and other organisms in forested systems (Harmon and others 1986).

Unfortunately, the relative importance of CWD for any one purpose is hard to determine due to the interrelationships of these uses (e.g., both thermoregulating and avoiding predation in a sun-warmed log). However, all major groups of amphibians and reptiles have been reported to use CWD in at least some fashion (table 3). Of these, turtles and toads appear to be the least associated with CWD, while frogs, lizards, snakes, and salamanders use CWD extensively for a variety of purposes. It should be noted that many uses are assumed or observed but have not been well documented or tested experimentally (table 3).

The Role of Coarse Woody Debris in Amphibian and Reptile Reproduction

Reptile eggs often require warm temperatures for proper development (Goin and Goin 1971). Additionally, females with eggs developing within them, and those that are ovoviviparous, often become thermophilic prior to egg-laying or delivery (Goin and Goin 1971; Heatwole 1976). Incubation temperatures influence development time, hatching success, and health of hatchling reptiles (Deeming and Ferguson 1991; Janzen 1993; Packard and others 1987). Amphibian eggs are less dependent upon warm temperatures but can be quite sensitive to extremes (Duellman and Trueb 1986, Goin and Goin 1971).

Numerous amphibians and reptiles deposit eggs in and under downed logs (Collins 1982; Ernst and Barbour 1989; Fitch 1954, 1963; Maser and Trappe 1984; Norman 1986; Stille 1954; Thomas 1979). For many species of amphibians and reptiles, downed logs provide an optimal temperature environment for egg incubation by damping temperature fluctuations (Savely 1939). In addition, sites within and around a given log can provide a range of temperature regimes (Graham 1925; Savely 1939). Graham (1925) observed temperatures higher than ambient on the upper sides of logs exposed to sunlight, while temperatures under these logs were lower than ambient. These features of CWD allow placement of eggs in areas with optimal temperature regimes and reduce the risk of detrimental temperature fluctuations during development.

Table 3—Uses of coarse woody debris by North American frogs (F), lizards (L), salamanders (SA), snakes (SN), toads (T), and turtles (TU)

	Group					
Use	F	L	SA	SN	T	TU
Reproduction:						
Nesting	O	X	X	X	O	?
Mate attraction:						
Calling	X	O	O	O	O	O
Displaying	O	?	O	O	O	O
Feeding substrate	X	X	X	X	?	?
Thermoregulation:						
Hibernation/ avoidance of cold	X	X	X	X	X	?
Avoidance of heat	X	X	X	X	X	?
Basking or warming	X	X	X	X	?	X
Avoidance of desiccation	X	?	X	?	X	?
Predator avoidance:						
Refugia	?	?	?	?	?	?
Lookout post	O	?	O	?	O	?
Total (X)	6	5	5	5	3	1
Total (X + ?)	7	9	8	8	6	8

X = documented in literature, ? = likely to occur, but no documentation found (use may be mentioned or speculated by some authors, but not well documented), O = probably does not occur.

Eggs of both reptiles and amphibians are subject to desiccation during dry periods (Goin and Goin 1971). Moisture availability during incubation is critical to hatching success, as well as condition of hatchlings (Duellman and Trueb 1986; Fitch and Fitch 1967; Packard and Packard 1988). Downed logs and the surfaces beneath downed logs provide optimal moisture for many reptile and amphibian eggs (Maser and Trappe 1984; Thomas 1979). The interiors of these logs have relatively constant moisture regimes compared to most forest surface habitats, and usually remain moist longer during dry periods (Boddy 1983, Place 1955).

Belowground conditions may also provide a constant temperature and moisture environment; however, for some taxa belowground conditions may be too cool and/or too dry or wet for proper incubation. Additionally, in areas with clay and other relatively hard soils, nest excavation into decomposing logs (or the use of pre-existing tunnels of other wood-inhabiting animals) requires less energy expenditure than ground excavation.

Salamanders appear to be most closely associated with CWD for reproduction. All known nest sites of *Ensatina* in the Pacific Northwest were found in association with CWD (Jones and Aubry 1985; Maser and Trappe 1984; Norman and Norman 1980). In forests of the Eastern United States, the marbled salamander, *Ambystoma opaceum* (Gravenhorst), is apparently dependent upon downed logs for successful reproduction. During the autumn-winter breeding season, adult *A. opaceum* emerge from underground retreats and migrate to river flood plains. Here courtship and fertilization take place. Eggs are deposited on land in a shallow depression and guarded by the female until spring flooding of the nest. Nests are located under downed logs or any other available cover (Mount 1975; Smith 1961), most likely to avoid desiccation and/or predation on the adult female and her brood. Other uses of CWD associated with herpetofaunal reproduction include calling sites for male tree frogs attracting mates to breeding ponds (Thomas 1979), and perches for male lizards protecting harems or signaling potential mates (Werth 1972).

Coarse Woody Debris as Habitat and Refugia for Forest Herpetofauna

All extant amphibians and reptiles are predominantly ectothermic. Thus, most thermoregulation is accomplished by moving to favorable microhabitats (Brattstrom 1965; Cloudsley-Thompson 1971; Duellman and Trueb 1986; Heatwole 1976). Additionally amphibians and, to a lesser degree, reptiles are subject to desiccation. Relatively constant temperature and moisture regimes found in and under CWD provide protection from temperature extremes and moisture loss (Aubry and others 1988; Harmon and others 1986; Maser and Trappe 1984; Thomas 1979).

Throughout most of North America, herpetofauna hibernate during the winter months. Depending upon the severity of winter in a given region, large logs and other forms of CWD can serve as important shelter for hibernation during cold periods (Gregory 1982; Harmon and others 1986; Stebbins 1966; Thomas 1979). In or under CWD, risk of freezing is reduced, moisture remains available, and the hibernating animal is sheltered from predators.

Cooling is usually accomplished by burrowing or using pre-existing burrows, movement to shade or cover, or movement into CWD (Cloudsley-Thompson 1971; Goin and Goin 1971; Maser and Trappe 1984). Thus, cooling activities generally do not increase risk of predation. In contrast, warming requires movement to surface areas exposed to sunlight. Except for species capable of rapid escape from predators, warming sites that allow the animal to remain hidden are almost always chosen (undersides of sun-warmed rocks, logs, and other surface debris, or beneath the bark of dead trees) (Brattstrom 1965; Cloudsley-Thompson 1971; Collins 1982; Ernst and Barbour 1989; Maser and Trappe 1984; Smith 1961; Thomas 1979).

In aquatic and semiaquatic habitats, CWD is often used as basking sites by semiaquatic herpetofauna (Brattstrom 1965; Collins 1982; Smith 1961). Congregations of *Psuedemys, Graptemys, Chrysemys,* and other semiaquatic turtles can often be observed basking on exposed portions of partially submerged CWD in the Southeastern United States. Watersnakes of the genus *Nerodia* also use these basking sites. Basking sites are important in that they allow the animal to raise its body temperature for feeding and digestion and still avoid predators confined to shorelines.

Many small snake species of southeastern forests, such as the scarlet snake, *Cemophora coccinea* (Blumenbach) (Palmer and Tregembo 1970), and the pine woods snake *Rhadinia flavilata* (Cope) (Myers 1967), are often found in close association with CWD. Many salamanders (e.g., *Batrachoseps* and *Ensatina* in the West, and many species of *Plethodon* throughout the United States) spend most of their lifespan in or near CWD (Aubry and others 1988;

Maser and Trappe 1984; Mount 1975; Raphael 1983). Harmon and others (1986) suggested possible obligatory use of CWD by salamanders. This close association with CWD, apparent in both amphibians and reptiles, is undoubtedly linked to predator avoidance as well as temperature and moisture regulation.

Predators of amphibians and reptiles include birds, mammals, other reptiles and amphibians, and, to a lesser degree, fish and invertebrates. Although no experimental evidence for the role of CWD as a refuge from predation appears to exist, behavioral observations and natural history information suggest that CWD is quite important in this regard.

Coarse Woody Debris as Feeding Substrate for Herpetofauna

Downed logs and other forms of CWD often harbor high densities of invertebrates, some of which (e.g., termites) are obligatory in their use of CWD (Harmon and others 1986; Maser and Trappe 1984; Seastedt and others 1989). These CWD-inhabiting invertebrates represent an important food resource for forest herpetofauna—one that is accessible without requiring them to forage in the open, where risk of predation is increased.

Although little experimental evidence exists regarding the importance of CWD as a source of prey, numerous observations of herpetofauna feeding in and around CWD are documented (e.g., Collins 1982; Ernst and Barbour 1989; Maser and Trappe 1984; Mount 1975; Smith 1961). The majority of forest herpetofauna feed on invertebrates, and CWD-inhabiting invertebrates are undoubtedly an important resource. Storm and Aller (1947) found termites in the guts of *Aneides ferreus* (Cope); conclusive evidence that these salamanders were foraging within CWD. Lizards, such as *Sceloporus undulatus* (Latrielle) and *Anolis carolinensis carolinensis* (Voigt), often bask on sunlit snags and logs in southern forests. The lizards are most likely feeding in this habitat, as basking is linked to efficient foraging and digestion (Cloudsley-Thompson 1971; Goin and Goin 1971).

High diversity and densities of invertebrates in CWD, along with the favorable temperature and moisture conditions, attract food items for larger reptiles as well. Small mammals, amphibians, and reptiles associated with CWD in southern forests represent important prey items for larger snake species (e.g., *Elaphe* and *Pituophis*) (Ernst and Barbour 1989). Rat snakes, such as the black rat snake (*Elaphe obsoleta obsoleta*) (Say) of eastern and southeastern forests, often forage in and around logs and snags for small mammals and birds (including cavity nesting birds) (Ernst and Barbour 1989; Fitch 1963; Mount 1975; Neal and others 1993).

In aquatic systems, biomass and production of invertebrates and fish are often highest on and around snags (Benke and others 1984). These "hot spots" of biotic activity represent important foraging areas for water snakes (mostly *Nerodia*) and some aquatic (e.g., *Chelydra*) and semiaquatic (e.g., *Chrysemys* and *Graptemys*) turtles in streams and lakes of the South. Also, these foraging areas are conveniently associated with basking surfaces.

Other Uses of Coarse Woody Debris by Herpetofauna

Some lizards (e.g., *Sceloporus* and *Anolis*) that inhabit eastern forests maintain territories and communicate to conspecifics and others through body movements (Collins 1982; Mount 1975). This behavior is often performed from an elevated perch where the animal is basking. Snags and other forms of CWD are potentially important in this respect, as they are often well lit (no leaves) and elevated. These perches may also provide good vantage points for detection of predators (Mount 1975).

Management

In recent years, demand has been increasing for watershed preservation and nonprofit amenities, such as conservation of biodiversity in forests (Sharitz and others 1992). Integrating these demands with profitable production practices is a challenge for land managers. Attention is turning not only to forest-stand age, but also to habitat heterogeneity (landscape and habitat) and structural characteristics (including quantity and quality of CWD) of the forest stand (Spies and others 1988).

The importance of CWD to diversity of many flora and fauna is well documented (e.g., Harmon and others 1986), and current forestry practices are changing to enhance the quantity of CWD in managed forests (Swanson and Franklin 1992). As research into these relationships proceeds, harvesting and silvicultural practices must continue to more toward methods that enhance CWD availability and other forms of structural diversity in southern forests.

Conclusions and Research Needs

Obvious relationships exit between the herpetofaunal communities of the Southeastern United States and CWD. The relative importance of each use is difficult to ascertain because many uses are probably interrelated. However, all major herpetofaunal groups have been shown to use CWD in some fashion, and many are using it for such vital processes as reproduction and feeding. This evidence warrants the continued change in management practices toward methods that encourge the availability of CWD and other components of structural diversity.

Herpetofaunal communities have received little qualitative and even less quantitative study. However, some recent studies suggest that species using CWD may predominate within the herpetofauna (Harmon and others 1986; Raphael 1983; Raphael and others 1982). These studies (mostly from western forests), and the available information on life histories suggest that species diversity may be more closely linked to CWD in herpetofauna than in any other vertebrate group. Studies directly examining this relationship, especially in southern forests, are clearly needed. Experiments examining the responses of herpetofaunal communities to CWD removal or addition, and the qualitative characteristics of the CWD used, would provide more conclusive information on the importance of CWD to herpetofaunal diversity.

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Influences of Coarse Woody Debris on Birds in Southern Forests

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Abstract

The importance of coarse woody debris (CWD) as a habitat component for birds in southern forests is reviewed. Few studies estimating snag density and relating species use to snag characteristics have been conducted in southern forests. We are unaware of studies describing the use of dead down woody debris (DDW) by any bird species except ruffed grouse, which use is for drumming logs. However, 45 species using snags and 20 species using DDW were identified primarily from natural history accounts. Snag density appeared to be directly related to the hardwood component and intensity of timber management across forest types. Use of snags by cavity-using birds was related to size, degree of decay, and tree species of snags. Snags appear to stand for a short time; Sabin (1991) reported that 88 percent of snags in the South Carolina Piedmont fell within 6 years after death. Identified research needs include the following tasks: (1) describe CWD dynamics by forest type, (2) relate use by species and guild to CWD characteristics, (3) relate bird species richness and diversity to size distribution of CWD, and (4) relate bird species occurrence and diversity to CWD characteristics through controlled experiments.

Introduction

Coarse woody debris (CWD), in the form of standing dead trees (snags) and down dead woody materials (DDW), is a critical and dynamic component of forest habitats for birds (Hunter 1990; Maser and Trappe 1984). Snags are created by fire, insects, disease, wind, lightning, and suppression (Fischer and McClelland 1983; Harlow and Guynn 1983) and may represent 5 to 10 percent of the standing trees in a forest (Hunter 1990). Down dead woody is created when trees are felled and recruited to the forest floor by forces such as wind, ice and/or snow, soil movement, floods, natural decay, and senescence of snags (Maser and Trappe 1984). Cull trees, as well as stumps, limbs, and slash, may also become DDW as a result of fires and stand improvement operations.

The value of snags as wildlife habitat, and in particular to various bird species, has been well documented. Fischer and McClelland (1983) published a bibliography addressing snags and cavity-nesting species that includes 1,713 titles. However, only recently have researchers and managers begun to address issues of snag management in the Southern United States (Carmichael and Guynn 1983). Information on the value of DDW to birds is severely lacking. Most of the research that has acknowledged use of DDW by birds has been conducted in the Pacific Northwest (Maser and others 1979) where forest types, climate, log decay dynamics, and management practices differ markedly from those in the South. Most accounts of bird use of DDW in southern forests are anecdotal in nature with the exception of ruffed grouse drumming log studies.

The main purpose of this paper is to highlight the few studies conducted in the Southern United States that relate snag characteristics and management practices to bird abundance and species diversity. We will also describe the potential importance of DDW to various species of birds in southern forests from natural history accounts.

Usage of Snags

Birds use snags for drumming, perching (hunting and singing), foraging, nesting, and roosting (Bull 1978; Miller and Miller 1980; Scott and others 1977). In North America, 85 species of birds are classified as either primary cavity-nesters, excavating their own nest holes, or as secondary cavity-nesters, using cavities created by disease, mechanical injury, or by primary excavators (Fischer and McClelland 1983). Within the Southern United States, Hamel (1992) lists 45 species of birds that use snags and/or cavities for various purposes (table 1).

Snag characteristics, such as density and longevity, vary according to stand type, stand age, and stand history (table 2). Although relatively few studies have been conducted in southern forests, certain trends are apparent from studies in South Carolina (Carmichael 1983; Carmichael and Guynn 1983; Harlow and Guynn 1983; Sabin 1991), Florida (Land and others 1989; McComb and others 1986), Kentucky (McComb and Muller 1983; Moriarty and McComb 1983), Louisiana, and Mississippi (McComb 1979).

On the South Carolina Coastal Plain, Harlow and Guynn (1983) found that nonpine stands had significantly higher densities of pine and hardwood snags than pine-dominated stands. They also found that the majority of snags (84 percent) were pine and less than 14 inches in diamater at

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Table 1—Bird species that use snags and cavities in the Southern United States

Species grouping[a]	Snag use[b]	Cavity tree use[b]	Minimum snag d.b.h.
			cm
Game species:			
Wood duck[+]	N	N	46
Hooded merganser[+]	N	N	46
Diurnal/nocturnal raptors:			
Black vulture[+]	N	N	—
Turkey vulture[+]	N	N	—
Osprey	N/P	—	51
Bald eagle	N/P	—	51
American kestrel[+]	F/N	N/P	15(F), 35(N)
Common barn-owl[+]	N/P	N/P	46
Eastern screech owl[+]	N/P	N/P	35
Barred owl[+]	N/P	N/P	51
Northern saw-whet owl[+]	N/P	N/P	25
Resident species:			
Belted kingfisher	F	—	15
Red-headed woodpecker[*+]	N/P	N/P	35
Red-bellied woodpecker	N/P	N/P	35
Northern flicker[*+]	N/P	N/P	35
Yellow-bellied sapsucker[*]	N	F	25
Downy woodpecker[*]	A	A	15
Hairy woodpecker[*]	A	A	25
Red-cockaded woodpecker[*]		A	
Pileated woodpecker[*]	A	N/P	51
Black-capped chickadee[*+]	N/P	N/P	15
Carolina chickadee[*+]	N/P	N/P	15
Tufted titmouse[*+]	N/P	N/P	15
Red-breasted nuthatch[*+]	N	—	15
White-breasted nuthatch[*+]	—	N	—
Brown-headed nuthatch[*+]	N	N	15
Brown creeper[+]	N	N	25
Carolina wren[+]	N	N	15
Bewick's wren+	N	N	15
Resident species:			
Eastern bluebird[+]	N/P	N/P	15
Loggerhead shrike	F	—	15
European starling[+]	N	N	25
Brown-headed cowbird	P	—	15
Neotropical migrants:			
Chimney swift[+]	N/P	N/P	35
Olive-sided flycatcher	F	—	25
Eastern wood-pewee	F	—	15
Acadian flycatcher	F	—	15
Great crested flycatcher[+]	N/P	N/P	25
Western kingbird	F	—	15
Eastern kingbird	F	—	15
Gray kingbird	F	—	15
Purple martin[+]	N	N	25
Tree swallow[+]	N	—	15
House wren[+]			
Prothonotary warbler[+]	N	N	15

[a] * = primary cavity nester; + = secondary cavity nester (for scientific names, see table 4).

[b] N = breeding/nesting; P = perching; F = foraging; A = all activities.

Source: Adapted from Hamel 1992.

Table 2—Snag densities in Southern United States forest types

Location	Forest type	Age	Snag density	Source
			No/ha	
South Carolina	Upland hardwood	40+	50.3	1[a]
South Carolina	Cove hardwood	40+	37.3	1
South Carolina	Upland hardwood	40-60+	35.6	2
South Carolina	Pine-hardwood	20+	31.2	1
South Carolina	Cove hardwood	40-60+	30.9	2
South Carolina	Pine-hardwood	20-50+	27.3	2
South Carolina	Pine plantation	1-40+	21.3	1
South Carolina	Pine plantation	1-40+	18.7	2
South Carolina	Oak-tupelo-cypress	1-100	9.7	3
South Carolina	Longleaf pine	1-100	3.5	3
Florida	Pine	61+	10.7	6
Florida	Hardwood	All	10.5	6
Florida	Pine	31-60	7.2	6
Florida	Pine-hardwood	All	6.8	6
Florida	Pine	All	4.2	6
Florida	Pine	0-30	2.6	6
Kentucky	Oak-hickory-maple	35	183.8	4
Kentucky	Oak-hickory-maple	100+	43.1	4
Kentucky	Oak-hickory-maple	60	17.6	5
Kentucky	Oak-hickory-maple	60	14.0	5
Louisiana	Bottomland hdwd.	80	11.0	7
Louisiana	Bottomland hdwd.	45	3.0	7
Mississippi	Pine-hardwood	85	6.4	7

[a] 1 = Carmichael and Guynn (1983); 2 = Sabin (1991); 3 = Harlow and Guynn (1983); 4 = McComb and Muller (1983); 5 = Moriarty and McComb (1983); 6 = McComb and others (1986); 7 = McComb (1979).

breast height (d.b.h.). Using average bird density estimates derived from Legrand and Hamel (1980), Harlow and Guynn (1983) concluded that—for birds using smaller snags (5 through 9 inches d.b.h.)—nonpine stands had > 100 percent of the minimum number of suitably sized snags for average bird populations. Pine stands, however, contained only 20 percent of the minimum number of this size class needed for average bird populations. Estimates of the abundance of larger snags (> 10 inches d.b.h.) were lower. Nonpine stands provided enough snags for 27 percent of the needs of average bird populations, while larger diameter-class pine stands provided enough snags for only 6 percent of average bird populations.

McComb and others (1986) assessed the densities of snags in Florida and also found them to be more abundant in hardwood stands than in pine stands. Snag densities were higher in older (> 61 years) stands, naturally regenerated pine stands (vs. plantations), riparian zones, and deep swamps (as compared to drier uplands). They detected a positive correlation (r = 0.71) between estimated densities of primary cavity-nesters and densities of snags among age classes and cover types. They recommended that a surplus of 4 to 9 snags per primary cavity-nester be maintained for average potential populations of primary cavity-nesters in Florida.

Table 3—Bird species use of coarse woody debris in Southern United States[a]

Species[b]	Status[c]	Use	Source[d]
Green-backed heron	B,W	Slash percher	1
Black vulture	B,W	Log nester	1
Turkey vulture	B,W	Log nester	1
Ruffed grouse	B,W	Log drummer, rooster	2
Wild turkey	B,W	Nests under fallen canopies	2
Northern bobwhite	B,W	Log rooster	2
American woodcock	B,W	Nests beside logs	2
Common nighthawk	B	Stump nester	2
Chuck-will's-widow	B	Hollow log rooster	2
Pileated woodpecker	B,W	Log forager	1,2,3
Flycatcher species	B	Root wad perchers	3
Carolina wren	B,W	All activities	1
Bewick's wren	B,W	All activities	1
House wren	B	All activities	1
Winter wren	B,W	All activities	1,2
Wood thrush	B	Territory defense from logs	1
Blue-winged warbler	B	Nests beside log	2
Louisiana waterthrush	B	Root wad nester	2
Prothonotary warbler	B	Floating log forager	2
Kentucky warbler	B	Nests under fallen canopies	2

[a] Southern States include: AL, AR, FL, GA, KY, LA, MS, NC, eastern OK, SC, TN, eastern TX, VA.

[b] For scientific names see table 4.

[c] B = breeder in the Southern United States (Hamel 1992); W = winter resident in the Southern United States (Hamel 1992).

[d] 1 = Hamel (1992); 2 = Terres (1980); 3 = Maser and others (1979).

Land and others (1989) studied slash pine plantations in the Florida Coastal Plain and found that higher snag densities were associated with stands containing many snag clusters (> 2 snags < 0.5 m apart). Overall density estimates for this study (2.6 to 38.6 ha) fell within the range of most other southern studies cited previously. They also found that cavity-nesting bird density, diversity, and species richness were positively influenced by increases in stand age, stand d.b.h., and resultant increases in snag density. Cavity-nester densities also increased as the area of land surrounding the study sites increased. Species diversity declined, however, as the area of a single-aged stand increased.

Carmichael (1983), Carmichael and Guynn (1983), and Sabin (1991) conducted snag density studies in the upper Piedmont of South Carolina. Carmichael (1983) and Carmichael and Guynn (1983) found that significant differences existed among different stand types in the Piedmont and also between the Piedmont and Coastal Plain. In the Piedmont, upland and cove hardwood sites had higher densities of snags than pine-hardwood sites and pine plantations. Smaller snags (10.1 to 25.0 cm) also outnumbered larger diameter classes in the Piedmont. When compared to Harlow and Guynn's findings, Piedmont sites were found to have higher densities of snags. Carmichael (1983) found that the abundance and diversity (H') of birds detected on transects with snags were greater than on transects without snags during the nonbreeding season. Bird species diversity was not significantly different during the breeding season, however.

Sabin (1991), in a continuation of Carmichael's study, noted similar trends, with hardwood sites having the highest snag densities and pine plantations having the

Table 4—Scientific names of birds using coarse woody debris in southern forests

Common name	Scientific name	Common name	Scientific name
Green-backed heron	*Butorides striatus*	Eastern wood-pewee	*Contupus virens*
American woodcock	*Philohela minor*	Acadian flycatcher	*Empidonax virescens*
Wood duck	*Aix sponsa*	Great crested flycatcher	*Myiarchus crinitus*
Hooded merganser	*Lophodytes cucullatus*	Western kingbird	*Tyrannus verticalis*
Black vulture	*Coragyps atratus*	Eastern kingbird	*Tyrannus tyrannus*
Turkey vulture	*Cathartes aura*	Gray kingbird	*Tyrannus dominicensis*
Osprey	*Pandion haliaetus*	Purple martin	*Progne subis*
Bald eagle	*Haliaeetus leucocephalus*	Tree swallow	*Iridoprocne bicolor*
American kestrel	*Falco sparverius*	Black-capped chickadee	*Parus atricapillus*
Ruffed grouse	*Bonasa umbellus*	Carolina chickadee	*Parus carolinensis*
Northern bobwhite	*Colinus virginianus*	Tufted titmouse	*Parus bicolor*
Wild turkey	*Meleagris gallopavo*	Red-breasted nuthatch	*Sitta canadensis*
Common barn-owl	*Tyto alba*	White-breasted nuthatch	*Sitta carolinensis*
Eastern screech-owl	*Otus asio*	Brown-headed nuthatch	*Sitta pusilla*
Barred owl	*Strix varia*	Brown creeper	*Certhia familiaris*
Northern saw-whet owl	*Aegolius acadicus*	Carolina wren	*Thryothorus ludoicianus*
Chuck-will's-widow	*Caprimulgus carolinensis*	Bewick's wren	*Thryomanes bewickii*
Common nighthawk	*Chordeiles minor*	House wren	*Troglodytes aedon*
Chimney swift	*Chaetura pelagica*	Winter wren	*Troglodytes troglodytes*
Belted kingfisher	*Megaceryle alcyon*	Eastern bluebird	*Sialia sialis*
Red-headed woodpecker	*Melanerpes erythrocephalus*	Wood thrush	*Hylocichla mustelina*
Red-bellied woodpecker	*Melanerpes carolinus*	Loggerhead shrike	*Lanius ludovicianus*
Yellow-bellied sapsucker	*Sphyrapicus varius*	European starling	*Sturnus vulgaris*
Downy woodpecker	*Picoides pubescens*	Prothonotary warbler	*Protonotaria citrea*
Hairy woodpecker	*Picoides villosus*	Blue-winged warbler	*Vermivora pinus*
Red-cockaded woodpecker	*Picoides borealis*	Louisiana waterthrush	*Seiurus motacilla*
Northern flicker	*Colaptes borealis*	Kentucky warbler	*Oporornis formosus*
Pileated woodpecker	*Dryocopus pileatus*	Brown-headed cowbird	*Molothrus ater*
Olive-sided flycatcher	*Nuttallornis borealis*		

lowest. Specifically, he concluded that shortleaf and loblolly pines, and red and white oaks accounted for 95 percent of all cavity years. Shortleaf pine made up 16 percent of all snags but accounted for 58 percent of all cavity years observed. Snag loss was calculated at 0.52 snags per ha per year, with 88 percent of all snags falling within a 6-year period. The mean number of cavities per snag ranged from 0.04 to 0.17 cavities per snag during the first 5 years after death and increased to 0.62 cavities per snag 6 years after death. Kentucky studies on stands improved for timber production vs. unmanaged stands revealed a higher density of snags in the improved stands (Moriarty and McComb 1983). Improved timber stands had a higher density of animal-excavated cavities, but the unmanaged stands had higher densities of cavities from other sources.

Usage of Down Dead Woody Debris

Hamel (1992) cites nine species of birds that use downed logs, slash piles, and windrows. Accounts from natural history studies also indicate that various species of birds not typically associated with DDW, use downed logs, roots of windthrows, or fallen branches in some manner. Maser and others (1979) state that "Some . . . birds reproduce alongside, under, or within logs." Their description of class 2 logs shows that: elevated areas on logs may provide lookouts and feeding sites; trunks provide food sources for woodpeckers, especially pileated woodpeckers; limbs are used as perches and—when hollow—as nest cavities; root wads are used by flycatchers as perching sites, by grouse for dusting, and by juncos as nesting sites; and protected areas under the log are used as nesting cover by grouse. Bird species and their associations with DDW are summarized in table 3 (common names) and table 4 (scientific names).

Little information was found in the literature that related specific characteristics of DDW to bird populations. However, a few studies address the attributes of ruffed grouse drumming sites. Hale and others (1982) concluded that drumming sites in northern Georgia were strongly associated with a relatively dense understory of ericaceous shrubs, and that the structure of the understory was most critical in determining grouse usage of logs as drumming sites. Thompson and others (1987), investigating habitat characteristics of drumming sites in oak-hickory forests in Missouri, found that use of drumming logs was most positively correlated with the density and structure of the vegetation surrounding the drumming log and not with characteristics of the log itself. Their study concluded that drumming logs had higher coniferous and deciduous shrub densities, coniferous canopy closure, understory foliage density, total woody stem densities, and slope position than randomly chosen logs. The density of deciduous trees and deciduous tree canopy closure were lower at confirmed drumming logs.

Management of Snags and Down Dead Woody Debris

Several management actions are proposed if adequate densities of snags are to be maintained in southern forests:

1. Control the removal of dead, dying, and decayed trees (Carmichael 1983; Harlow and Guynn 1983; Land and others 1989; McComb and others 1986).

2. Create snags by girdling, chemical injection, etc. (Carmichael 1983; Harlow and Guynn 1983; McComb and others 1986).

3. Preserve strips of unmanaged mature forest along drainage systems (Harlow and Guynn 1983).

4. Increase rotation age, limiting the area of even-aged forests and avoiding the creation of forest islands (Land and others 1989).

5. Thin stands to create habitat conditions favorable to cavity-dependent bird species.

6. Emphasize tree species that are most likely to be recruited into the snag population (Sabin 1991).

Although no specific guidelines have been suggested for managing CWD in southern forests, Maser and others (1979) suggest that management within a forest for snags will naturally add to the DDW component as logs are recruited to the forest floor by decay and various physical forces.

Conclusions and Recommendations

Coarse woody debris is clearly an important habitat component for many species of birds in southern forests. However, little effort has been directed at documenting the use of CWD by birds and measuring its influence on species occurrence and diversity in these forests. Studies from the Pacific Northwest provide general inferences about the probable functions of CWD as habitat for birds in southern forests. However, studies documenting specific uses of CWD by bird species or guilds in various southern forest ecosystems are needed before meaningful management strategies can be developed. Other information needs include the following:

1. Description of snag dynamics to include size distribution, recruitment and loss rates, decay rates, and stages of snags and DDW by tree species and forest type.

2. Quantification of relationships between (a) volume, size, temporal and spatial distribution; (b) decay processes; and (c) living vegetation characteristics, and CWD use by bird species and guilds.

3. Correlation of bird species richness and diversity with size distribution of CWD.

4. Quantification of the relationships between occurrence and diversity of bird species with CWD characteristics through controlled experiments, such as a comparison of snagless plots with plots that have various densities of snags.

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The Role of Coarse Woody Debris in the Ecology of Southeastern Mammals

Susan C. Loeb

Abstract

Coarse woody debris (CWD) is an important habitat component for many mammals. At least 23 of the approximately 81 species of mammals found in the Southeast use standing CWD (snags) and at least 55 species use downed woody debris (logs). Snags are used for nesting, cover, and foraging whereas logs are used for travel routes, cover, nesting, and foraging. However, little is known about the characteristics of CWD that are important in determining its use by mammals, and even less is known about the availability of CWD resources in the Southeast. Before CWD can be effectively managed for mammals, several questions must be addressed: (1) Which species use CWD and for which of these species is CWD a critical habitat feature? (2) What function does CWD serve for each species? (3) What characteristics of CWD determine its suitability (e.g., size, decomposition stage, dispersion in the habitat)? and (4) How does use and importance of CWD vary with habitat and what environmental conditions control variation?

Introduction

The importance of coarse woody debris (CWD) to forest function and health has been well documented (e.g., Harmon and others 1986; Maser and others 1988b). Mammals use CWD for a variety of functions, and it is critically important to many species (Maser and others 1979, 1988a; Thomas and others 1979). However, much of the research on the importance of CWD to mammals and other wildlife has been conducted in the Pacific Northwest. In the Southeast, data are available on standing CWD densities and its use by wildlife (e.g., Carmichael and Guynn 1983; Harlow and Guynn 1983; McComb and others 1986a), but few studies have examined either the role or the availability of downed material. Furthermore, most studies dealing with standing CWD have evaluated available resources relative to the needs of cavity-nesting bird populations and few have addressed the CWD requirements of mammals.

To effectively manage CWD for the mammals of the Southeast, it is necessary to know how CWD is used, what characteristics (e.g., size, decomposition state) determine its suitability, and how these characteristics change with time and environmental conditions. It is a large task to determine the usage of CWD for a group such as mammals. Although the Class Mammalia may not include as many species as other classes of animals, it is highly diverse. In the Southeast, body size ranges from 3 g for the pygmy shrew[1] to approximately 140 kg for the black bear. Moreover, while some mammals, such as pocket gophers and moles, are almost totally subterranean, others, such as flying squirrels, spend most of their lives in trees. Still others, such as mink and muskrat, are semiaquatic. Although most mammals are nocturnal, many species, such as most squirrels, are diurnal. Food habits also vary considerably, and mammals in the Southeast include insectivores (e.g., bats and shrews), herbivores (e.g., voles, cotton rats, beaver, deer), mycophages (e.g., northern flying squirrels), carnivores (e.g., weasels, bobcats), and omnivores (e.g., bears, opossums, white-footed mice). Given this variety of lifestyles, the role of CWD and its important characteristics will probably vary considerably among species or groups. Therefore, in the following review I discuss some of the general characteristics of CWD that may be particularly important to mammals, some of the important functions of CWD for mammals in general, and what is known about the use and availability of CWD in the Southeast. Finally, I will propose some areas and approaches for future research that will increase our knowledge of CWD use by southeastern mammals.

General Characteristics of Coarse Woody Debris and Its Use by Mammals

CWD is usually categorized as standing or downed and referred to as *snags* or *logs*, respectively (Harmon and others 1986; Spies and Franklin 1988). These are important categories for mammals because use of each category varies considerably among species. Causes of tree death and the type of CWD debris produced by each mortality agent have been reviewed by Harmon and others (1986) and Maser and others (1988a). Although foresters usually define a snag as any broken tree > 6.1 m in height, for wildlife purposes snags are usually defined as any dead or partially dead tree > 10.2-cm diameter at breast height

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[1] Scientific names of all southeastern mammals are given in the appendix.

(d.b.h.) and > 1.8 m in height (Thomas and others 1979). Because downed woody debris has rarely been measured for wildlife purposes, definitions of logs are rare (Cooperrider 1986). However, Spies and Franklin (1988) defined logs as any woody debris > 10-cm diameter at the large end. Because this closely coincides with the definition of a snag, it is probably a good definition of downed CWD for wildlife purposes as well.

Snags

Snag characteristics potentially important to determining suitability for use by mammals include size (diameter and height), species, and decomposition stage. Several schemes for classifying snag decomposition have been devised for use in wildlife research. Thomas and others (1979) described nine stages of snag decomposition ranging from a healthy tree (Stage 1) to a stump (Stage 9), while Cline and others (1980) described five stages of snag decomposition and Sabin (1991) classified snags into three decomposition classes. Although these schemes vary considerably in the number of decay classes, criteria for distinguishing among stages in all schemes are based on some combination of the same three characteristics important to wildlife: (1) the size and number of limbs, (2) the amount of bark remaining, and (3) the amount of heartwood and sapwood decay.

For mammals, the presence or absence of limbs is probably not a critical element, although snags with many large limbs may contain more cavities than those without. In contrast, the presence or absence of bark and the amount of decay are very important. Many species of bats roost under loose bark (Hamilton and Whitaker 1979; Maser and others 1988b). Therefore, the presence and abundance of loose bark will determine the utility of the snag for these animals. Decay is important because it is related to cavity excavation. The state of decay greatly influences the amount of time and energy necessary for cavity excavation, and it has a large bearing on whether birds will excavate cavities in a particular snag (Conner and others 1975; DeGraaf and Shigo 1985). For many mammals, the presence of cavities is the most important characteristic of a snag. Because mammals do not make their own cavities, they must rely on the presence of naturally occurring cavities or on primary cavity-nesting birds to excavate them. The state of decay may also affect the microclimate (e.g., temperature, humidity) and integrity of cavities influencing their suitability. However, I am not aware of any data pertaining to this aspect of snag decay.

Cavities are important structures for several reasons. They provide cover from predators, particularly raptors, as well as shelter from the elements, such as wind and rain. They also provide a relatively stable thermal environment. For example, although average monthly temperatures inside and outside unoccupied raccoon dens in Illinois did not differ significantly, temperatures inside the dens varied only 0.4 to 3.2 °C per day, while those outside varied 6.4 to 13.0 °C per day (Stains 1961). Furthermore, maximum and minimum outside temperatures (32 °C and -21 °C, respectively) were far more extreme than maximum and minimum temperatures inside the cavity (26 °C and -7 °C, respectively). This probably explains why species such as gray and fox squirrels, which use both cavities and outside leaf nests, increase their use of cavities during the winter (Edwards and others 1989; Weigl and others 1989). Cavities are also excellent structures for raising young. In addition to providing protection from ground predators and the elements, these semi-enclosed structures may also keep young animals from wandering away from, or falling out of, the nest.

Bats are the primary arboreal insect feeders, and they do most of their foraging while flying. Therefore, snags are not usually considered an important food source for mammals. However, because many species of birds and mammals nest and rear young in snags (DeGraaf and Shigo 1985; Maser and others 1988b), they may be a rich source of food for some of the semiarboreal predators such as the opossum, raccoon, and weasels.

The availability of snags in the Southeast and various factors that influence snag availability have been examined in the mountains (McComb and Muller 1983; Rosenberg and others 1988), Piedmont Region (Carmichael and Guynn 1983; Sabin 1991) and Coastal Plain (Harlow and Guynn 1983; Land and others 1989; McComb and others 1986a). In general, snag densities are lower in pine stands than in pine-hardwood and hardwood stands (Carmichael and Guynn 1983; Harlow and Guynn 1983; McComb and others 1986a; Sabin 1991). Large snags (> 25-cm d.b.h). are far less abundant than snags < 25-cm d.b.h. (Carmichael and Guynn 1983; Harlow and Guynn 1983; McComb and Muller 1983; Rosenberg and others 1988; Sabin 1991). This is important because cavities are far more likely to occur in large snags (Sabin 1991; Loeb, unpublished data). The relationship between snag density and stand age is not clear. While McComb and others (1986a) found that snag densities increased with stand age in pine and pine-hardwood forests of Florida, Rosenberg and others (1988) found that little variation in snag density occurred among age classes of oak and oak-hickory stands in the Southern Appalachians. Moreover, Sabin (1991) and McComb and Muller (1983) found that snag densities decreased in older pine and pine-hardwood stands of the Piedmont and Coastal Plain, respectively. Differences among studies may be due to differences in the age classes compared and their respective stages of succession (Waldrop 1995).

Whether snag resources in the Southeast are adequate to support populations of mammals that require them is unknown. Most studies on snag availability in the Southeast have related their findings to cavity-nesting birds (e.g., Land and others 1989; Rosenberg and others 1988; Harlow and Guynn 1983; Carmichael and Guynn 1983; McComb and others 1986a; McComb and Muller 1983) and no similar studies have been conducted for mammals.

Logs

Other than bats, almost all nonaquatic mammals spend at least part of their life on or under the ground. Therefore, logs have received more attention than snags in studies of mammalian ecology. Thomas (1979) defined a log as "any section of the bole or thicker branches of a felled tree after trimming and cross-cutting; also any section of the bole or of the thicker branches of a dead and down tree." Maser and others (1979, 1988a) classified logs into five stages of decay which correspond to the nine stages of snag decay described by Thomas and others (1979). Characteristics used to distinguish among classes include the amount of bark and twigs remaining, texture, shape, color, the portion of the tree on the ground, whether roots have invaded the log, and whether roots have invaded the sapwood or heartwood.

Several studies have demonstrated that downed logs are an important habitat feature for many North American mammals, particularly small mammals (e.g., Barry and Francq 1980; Corn and others 1988; Gore 1988; Graves and others 1988; Kennedy and others 1991; McComb and Rumsey 1982; Nordyke and Buskirk 1988; Planz and Kirkland 1992; Seagle 1985). Downed logs serve a variety of functions for terrestrial mammals ranging in size from shrews to bears. Initially, the soil disturbance and microsites provided by tree fall (Beatty and Stone 1986) probably provide foraging and burrowing sites for many species of mice, shrews, and ground squirrels. Logs also provide cover from both the elements and predators. Therefore, many species, such as gray fox, weasels, and striped skunks, as well as rodents and shrews, place their nests and dens under logs.

Several studies have shown that mice use logs extensively as travel routes (Barnum and others 1992; Graves and others 1988; Olszewski 1968; Planz and Kirkland 1992). These rodents travel predominantly on top of the logs although Olszewski (1968) suggested that differential travel on top of and beneath logs may be one way two species of mice in Poland (*Apodemus flavicollis* and *Clethrionomys glareolus*) partition the habitat and avoid direct competition. Because travel on logs may be quieter than traveling among ground cover, particularly dry leaves, use of logs as travel routes has been viewed as a means of predator avoidance (Barnum and others 1992; Fitzgerald and Wolff 1988; Planz and Kirkland 1992).

Few data on the importance of logs as feeding and foraging sites are available. However, an animal that moves to a log to process and eat its food (e.g., hard mast, pine cones, or other foods with long handling times) would have a higher vantage point for detecting predators while feeding, and easier access to cover if a predator is detected. The many species of insects that invade decaying logs (see Hanula 1996; Savely 1939) would provide a rich source of food for terrestrial insectivores such as shrews. Larger species such as the armadillo and raccoon are often observed digging through decaying logs for the invertebrates that inhabit them. Downed logs may also act as traps for wind-dispersed seeds and thus may be important foraging areas for seed-eaters such as *Peromyscus spp.*

The fungi that invade decaying logs are also eaten by a variety of small mammals (Fogel and Trappe 1978; Maser and Maser 1987; Maser and others 1978). It has been suggested that mycophagy by small mammals is an important link in forest regeneration (Maser and others 1979). After feeding on the sporocarps, the spores are defecated, often at a distance from the original source. Thus, small mammals may be important dispersers of mycorrhizal fungal spores, many of which are necessary for growth and survival of conifers. Although most data on fungal/small mammal/conifer relationships have been obtained in the Pacific Northwest, Weigl and others (1989) suggest that fox squirrels, which forage on fungi in longleaf pine ecosystems of the Southeast, play a similar role. Many other species of mammals probably forage on fungi in the Southeast and play a role in fungal dispersal. However, few data are available on fungal consumption by southeastern mammals.

The abundance of logs and the relationship between log availability and physiographic region, forest type, age, and history have not been determined for the Southeast. Some data are available on log characteristics important to determining use by small mammals. Hayes and Cross (1987) found that use of logs by deer mice and western red-backed voles (*C. californicus*) in Oregon was positively correlated with log length, log diameter, and overhang area. Overhang area was primarily responsible for variation in log use, while the decay stage had no effect. In contrast, white-footed mice in Minnesota and Maryland do not select logs on the basis of length, although they prefer logs > 5 cm in diameter and avoid logs < 5 cm in diameter (Barnum and others 1992). Furthermore, they prefer soft logs that are either smooth or covered with moss and avoid hard, smooth logs. Differences between these studies may be due to different techniques (trapping vs. fluorescent tracking), habitats examined, and/or species studied. More studies are necessary to reconcile these differences.

Use of Coarse Woody Debris by Southeastern Mammals

Use of CWD by a particular species probably depends on many factors, including phylogenetic constraints (e.g., morphology), natural history, and environmental conditions. For example, the gray fox is known to use a variety of den types including hollow logs or trees, rock outcrops, underground burrows constructed by other species, wood piles, and brush piles (Fritzell and Haroldson 1982). However, structures such as logs, hollow trees, and snags probably become more important in areas where burrowing animals, such as ground squirrels (*Spermophilus spp.*), do not occur (e.g., the Southeast) than in areas where they are abundant. This example shows that use of CWD and its importance in fulfilling the requirements of an animal may vary among regions and even among habitats within regions. Therefore it is necessary to consider both the natural history of an animal and the environmental conditions, including the presence of other species, when evaluating the importance of CWD for a given species.

Studies focusing on use of either snags or logs by southeastern mammals are rare. However, studies of natural history and habitat selection have documented their use by many species. The Appendix summarizes the uses, or possible uses, of snags and logs by each species of mammal found in the Southeast. Primary sources for the appendix include general species accounts by Chapman and Feldhamer (1982), Hamilton and Whitaker (1979), and others as cited.

As shown in the appendix, both snags and logs are used by a variety of mammals, and logs are used by far more species than snags. Of the approximately 81 species of terrestrial mammals found in the Southeastern United States at least 23 species are known to use either cavities or the loose bark of snags, and an additional three species may also use snags. In contrast, at least 55 species are known to use logs, and at least 10 species use both snags and logs.

Cavities in snags are used by a wide variety of southeastern mammals ranging from bats to raccoons. Some species probably use snags opportunistically and are not dependent on them for survival. For example, the opossum is a generalist in almost all aspects of its ecology (McManus 1974), and although it often dens in cavities in snags, it also dens in or under logs, burrows, rock outcrops, hay stacks, vine tangles, and culverts (Gardner 1982). In contrast, several species of southeastern bats are highly dependent on cavities in snags for roosting sites; therefore, cavities are an important habitat requirement. Cavities are also an important habitat feature for the tree squirrels of the Southeast. Although fox squirrels use cavities infrequently during most of the year, they may need cavities for successful reproduction (Loeb and Moncrief 1993). In contrast, red squirrels, gray squirrels, northern flying squirrels, and southern flying squirrels commonly utilize cavities year round. Because live den trees may be scarce in many habitats (McComb and others 1986b), these squirrels may be dependent on snags for nesting sites. Deer mice, white-footed mice, and cotton mice also nest in cavities (Frank and Layne 1992; Wolff and Hurlbutt 1982), and Wolff and Hurlbutt (1982) found that deer mice and white-footed mice in Virginia prefer snags to live trees for nesting. Although woodrats are best known for their construction of elaborate stick nests or houses, eastern woodrats occasionally use cavities for nesting (Fitch and Rainey 1956; M. Strayer, personal communication).

Bats are the primary mammals that use the area behind the loose bark of snags. At least five species of southeastern bats use the loose bark for protection. The Indiana bat often places its nursery colonies in these sites (Brady 1983); therefore, snags with loose bark are a critical habitat component for this endangered species.

Snags may also be used for foraging. Among southeastern mammals, opossums and raccoons are probably the primary mammals that use snags as foraging sites. Both species are highly opportunistic omnivores (Kaufman 1982; McManus 1974). They feed on grasses, forbs, fruits, nuts, invertebrates, small mammals, small birds, eggs, and carrion. Snags may be sources for such food items as eggs, young birds and mammals, and particularly invertebrates. Kennedy and others (1991) found that areas used by raccoons in Tennessee and Kentucky had higher densities of snags than those areas that received little use. They suggested that raccoons selected these areas because the snags were important sources of invertebrates for their diet.

Logs serve a variety of functions for the 55 or more southeastern mammals. Many species, particularly the larger species, probably use logs in an opportunistic manner. For these species, logs may improve the quality of the habitat but are not critical habitat features. For example, species such as deer, mountain lion, and bobcat may readily use logs for cover, but other features of the habitat are probably far more important in determining suitability and preference.

In contrast, logs appear to be a critical habitat feature for many other species. Almost all descriptions of the preferred habitats of shrews include logs (e.g., Hamilton and Whitaker 1979). Because they are extremely small, shrews almost always require cover from both predators and climatic conditions. Moisture is also an important habitat feature that influences the abundance and diversity of shrews (Churchfield 1990). Shrews have relatively high water requirements because of high evaporative water loss resulting from their extremely high metabolic rates. Furthermore, shrews feed primarily on insects and other invertebrates that, in general, are more abundant and more accessible in moist conditions. Because logs often retain moisture, they may provide favorable microsites for both shrews and their prey. How extensively shrews actually forage in or under logs is unknown, but some foraging around logs probably occurs.

Logs are also an important habitat feature for many of the mice and rats found in the Southeast. Logs are important to microhabitat selection by deer mice and white-footed mice in some forest types (Barry and Francq 1980; Vickery and Rivest 1992) and are used extensively as travel routes (Barnum and others 1992; Graves and others 1988; Planz and Kirkland 1992). In addition, the number of cotton mice captured in longleaf pine (*Pinus palustris*) stands with large amounts of CWD is approximately double the number caught in similar stands where the CWD has been removed (Loeb, unpublished data). Even though the golden mouse is primarily arboreal and weaves a nest of grasses, leaves, shredded bark, or Spanish moss to the side of a tree or shrub, large communal nests are occasionally placed among the branches of fallen trees or under logs (Hamilton and Whitaker 1979; Linzey and Packard 1977). Logs are also important to both macrohabitat and microhabitat selection of Gapper's red-backed voles (Merritt 1981). The presence of red-backed voles in forests of the Pacific Northwest is often used as an indicator of old-growth forest conditions (Nordyke and Buskirk 1988); however, little research has been done on how logs are actually used by this species. These voles probably use logs for travel routes and cover, and because fungi make up a large portion of their diet (Fogel and Trappe 1978), logs may also be used for foraging.

For many species, logs provide cover from the elements and predators. Species ranging from shrews to bears use logs for cover and many animals, such as mice, foxes, bobcats, and weasels, use the area under elevated logs for nesting sites. McCullough and Fritzell (1984) found that the majority of spotted skunk den sites in the Ozark Plateau were in hollow logs. Moreover, many species that den underground, such as foxes, armadillos, and mice, prefer to use dens with their entrances under or next to a log. Because logs also provide excellent cover from predators, species such as shrew, mice, rats, and rabbits probably use logs to hide or escape.

Logs are probably an important foraging substrate for many southeastern mammals, particularly those that feed on invertebrates. Logs may be an important source of invertebrates for shrews, which are almost exclusively insectivorous. Decaying logs are also important sources of invertebrates for opossums, raccoons, skunks, and armadillos (Galbreath 1982; Godin 1982; Kaufman 1982; McManus 1974). These species often dig through decaying logs and forage on the variety of invertebrates found there. Taber (1945) also found that armadillos often foraged intensively in areas where logs had completely decayed. He attributed this behavior to increased humus in these areas. Logs may also have indirect benefits related to the foraging behavior of many species. For example, if the presence of logs increases the density of small mammals in an area, carnivores, such as weasels, foxes, and bobcats, may experience increased foraging efficiency.

Future Research

This discussion has shown that CWD is used by a wide variety of mammals. For some species, the presence of CWD is critical; for others it may be used only opportunistically. However, the importance of CWD is unknown for many, if not most, species. While this discussion has emphasized autecological processes and predator-prey relationships, the presence of CWD may also be important for other interactions, such as ameliorating competitive interactions. For example, by increasing limited resources such as nesting sites or prey availability, competitive interactions may be reduced and opportunities for habitat partitioning may be increased.

Effective management of CWD resources to benefit native mammalian species cannot occur unless the following questions are answered: (1) Which species use CWD and for which of these species is CWD a critical habitat feature? (2) What functions does CWD serve for each species? (3) What characteristics of CWD determine its suitability (e.g., size, decomposition stage, dispersion in the habitat)? (4) How do use and importance of CWD vary with habitat and what environmental conditions control variation? Until these and other questions are answered, evaluating present CWD resources is not possible.

Several approaches to the study of the importance of CWD in mammalian ecology are possible. For example, researchers primarily interested in habitat selection will need only to add CWD measurement and characteristics to the more conventional vegetation measurements and habitat characteristics when doing traditional habitat selection studies. However, more specific studies are also needed to determine which species utilize logs and snags of various sizes and in various stages of decay, how CWD is used by various species, and how use varies with habitat. These studies may require techniques different from those used in studies of mammalian habitat selection (e.g., trapping and radiotelemetry). For example, the fluorescent tracking technique (Lemen and Freeman 1985) has added greatly to our knowledge of how white-footed mice and deer mice use logs for travel. Other techniques, such as sand tracking (e.g., Vickery and Rivest 1992), smoke-paper-covered boards (Bailey 1969), or video cameras, may also be quite valuable in determining which species use logs and snags. In addition to testing the direct effects of CWD, examining indirect effects will also be necessary. For example, does the presence of CWD increase predator populations by increasing prey populations? Ultimately, research on the effects of CWD on mammalian populations will require an ecosystem approach, ranging from the ecosystem contained in individual logs or snags to the larger scale that includes entire forests, watersheds, or regions.

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Appendix

Use of coarse woody debris (CWD) by mammals of the Southeastern United States and the physiographic regions in which they are commonly found—Coastal Plain (CP), Piedmont (PD), or Mountains (MT). Uses of CWD were classified as nesting or roosting (N), foraging (Fo), feeding (Fe), travel (T), and cover (C). A usage type followed by a "?" indicates that it is a possible usage but no confirming evidence has been found

Scientific name	Common name	CP	PD	MT	Snags—bark	Snags—cavity	Logs
Didelphis virginiana	Opossum	X	X	X	Not used	N,Fo	N,Fo,C?
Sorex cinereus	Masked shrew			X	Not used	Not used	N,Fo,C
Sorex longirostris	Southeastern shrew	X	X		Not used	Not used	N,Fo,C
Sorex palustris	Water shrew			X	Not used	Not used	N,C
Sorex fumeus	Smokey shrew			X	Not used	Not used	N,Fo,C
Sorex dispar	Long-tailed shrew			X	Not used	Not used	N,Fo,C
Sorex hoyi	Pygmy shrew			X	Not used	Not used	N,Fo,C
Blarina brevicauda	Short-tailed shrew		X	X	Not used	Not used	N,Fo,C
Blarina carolinensis	SE short-tailed shrew	X	X		Not used	Not used	N,Fo,C
Cryptotis parva	Least shrew	X	X	X	Not used	Not used	N,Fo,C
Parascalops breweri	Hairy-tailed mole			X	Not used	Not used	Not used
Scalopus aquaticus	Eastern mole	X	X	X	Not used	Not used	Not used
Condylura cristata	Star-nosed mole	X		X	Not used	Not used	N?
Myotis lucifugus	Little brown bat			X	N	N	Not used
Myotis austroriparius	Southeastern myotis	X	X		?	N	Not used
Myotis grisescens	Gray bat	X	X	X	?	?	Not used
Myotis septentrionalis	Northern long-eared bat	X	X	X	N	Not used	Not used
Myotis sodalis	Indiana bat	X	X	X	N	N	Not used
Myotis leibii	Small-footed bat			X	?	?	Not used
Lasionycteris noctivagans	Silver haired bat	X	X	X	N	N	Not used
Pipestrellus subflavus	Eastern pipistrelle	X	X	X	?	?	?
Eptesicus fuscus	Big brown bat	X	X	X	?	N	?
Lasiurus borealis	Red bat	X	X	X	?	N	?
Lasiurus seminolus	Seminole bat	X	X		N	Not used	?
Lasiurus cinereus	Hoary bat	X	X	X	?	N	?
Lasiurus intermedius	Northern yellow bat	X			Not used	Not used	?
Nycticeius humeralis	Evening bat	X	X		?	N	Not used
Plecotus townsendii	Townsend's big-eared bat			X	Not used	Not used	Not used
Plecotus rafinesquii	Rafinesque's big-eared bat	X	X	X	Not used	N	Not used
Tadarida brasiliensis	Mexican free-tailed bat	X	X		Not used	Not used	Not used
Dasypus novemcinctus	Nine-banded armadillo	X			Not used	Not used	N, Fo
Sylvilagus palustris	Marsh rabbit	X			Not used	Not used	C
Sylvilagus floridanus	Eastern cottontail	X	X	X	Not used	Not used	C

Use of coarse woody debris (CWD) by mammals of the Southeastern United States and the physiographic regions in which they are commonly found—Coastal Plain (CP), Piedmont (PD), or Mountains (MT). Uses of CWD were classified as nesting or roosting (N), foraging (Fo), feeding (Fe), travel (T), and cover (C). A usage type followed by a "?" indicates that it is a possible usage but no confirming evidence has been found (continued)

Scientific name	Common name	CP	PD	MT	Snags — bark	Snags— cavity	Logs
Sylvilagus obscurus	Appalachian cottontail			X	Not used	Not used	C
Sylvilagus aquaticus	Swamp rabbit	X	X		Not used	Not used	C
Lepus americanus	Snowshoe hare			X	Not used	Not used	?
Tamias striatus	Eastern chipmunk		X	X	Not used	Not used	T,Fe,Fo?
Marmota monax	Groundhog		X	X	Not used	Not used	Not used
Sciurus carolinensis	Gray squirrel	X	X	X	Not used	N	T,C,Fe
Sciurus niger	Fox squirrel	X	X	X	Not used	N	T,C,Fe
Tamiasciurus hudsonicus	Red squirrel			X	Not used	N	N,C,Fe
Glaucomys volans	Southern flying squirrel	X	X	X	Not used	N	Fo?
Glaucomys sabrinus	Northern flying squirrel			X	Not used	N	Fo?
Geomys pinetis	Southeastern pocket gopher	X			Not used	Not used	Not used
Castor canadensis	Beaver	X	X	X	Not used	Not used	Not used
Oryzomys palustris	Marsh rice rat	X	X		Not used	Not used	N?,C?
Oryzomys argentatus	Cudjoe key rice rat	X			Not used	Not used	N?,C?
Reithrodontomys humulis	Eastern harvest mouse	X	X	X	Not used	Not used	Not used
Reithrodontomys fulvescens	Fulvous harvest mouse	X			Not used	Not used	Not used
Peromyscus maniculatus	Deer mouse			X	Not used	N	T,C,Fe?,Fo
Peromyscus leucopus	White-footed mouse	X	X		Not used	N	T,C,Fe?,Fo
Peromyscus gossypinus	Cotton mouse	X	X		Not used	N	T,C,Fe?,Fo
Peromyscus polionotus	Old-field mouse	X	X		Not used	Not used	Not used
Peromyscus floridanus	Florida mouse	X			Not used	Not used	?
Ochrotomys nuttalli	Golden mouse	X	X	X	Not used	Not used	N,Fo?
Sigmodon hispidus	Hispid cotton rat	X	X	X	Not used	Not used	?
Neotoma floridana	Eastern Wood rat	X	X	X	Not used	N	N, T?,C?,Fo?
Clethrionomys gapperi	Gapper's red-backed vole			X	Not used	Not used	T,C,Fo,Fe?
Microtus pennsylvanicus	Meadow vole	X	X	X	Not used	Not used	?
Microtus chrotorrhinus	Rock vole			X	Not used	Not used	N?
Microtus pinetorum	Pine vole	X	X	X	Not used	Not used	N?,C?,Fo?
Neofiber alleni	Round-tailed muskrat	X			Not used	Not used	Not used
Ondatra zibethicus	Muskrat		X	X	Not used	Not used	Not used
Synaptomys cooperi	Southern bog lemming			X	Not used	Not used	?
Zapus hudsonius	Meadow jumping mouse	N	Y	Y	Not used	Not used	C?,Fo?
Napaeozapus insignis	Woodland jumping mouse			X	Not used	Not used	C?,Fo?

(continued)

Use of coarse woody debris (CWD) by mammals of the Southeastern United States and the physiographic regions in which they are commonly found—Coastal Plain (CP), Piedmont (PD), or Mountains (MT). Uses of CWD were classified as nesting or roosting (N), foraging (Fo), feeding (Fe), travel (T), and cover (C). A usage type followed by a "?" indicates that it is a possible usage but no confirming evidence has been found

Scientific name	Common name	CP	PD	MT	Snags—bark	Snags—cavity	Logs
Canis latrans	Coyote	X	X		Not used	Not used	N,Fo?
Canis rufus	Red wolf	X[a]		X[a]	Not used	Not used	N
Vulpes vulpes	Red fox		X	X	Not used	Not used	N?
Urocyon cineroargenteus	Gray fox	X	X	X	Not used	Not used	N,Fo?
Ursus americanus	Black bear	X	X	X	Not used	Not used	N
Procyon lotor	Raccoon	X	X	X	Not used	N,Fo	Fo
Mustela nivalis	Least weasel			X	Not used	Not used	Fo?
Mustela frenata	Long-tailed weasel	X	X	X	Not used	Not used	N, Fo?
Mustela vison	Mink	X	X	X	Not used	Not used	N, Fo?
Spilogale putorius	Eastern spotted skunk	X	X	X	Not used	N	N, Fo
Mephitis mephitis	Striped skunk	X	X	X	Not used	Not used	Fo
Lutra canadensis	River otter	X	X	X	Not used	Not used	N
Felis concolor	Mountain lion	X			Not used	Not used	N?, T
Felis felis	Bobcat	X	X	X	Not used	Not used	N, T
Odocoileus virginanus	White-tailed deer	X	X	X	Not used	Not used	C?

[a] Reintroduced

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 m^2 yr^{-1} and from 34 to 111 g m^2 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

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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

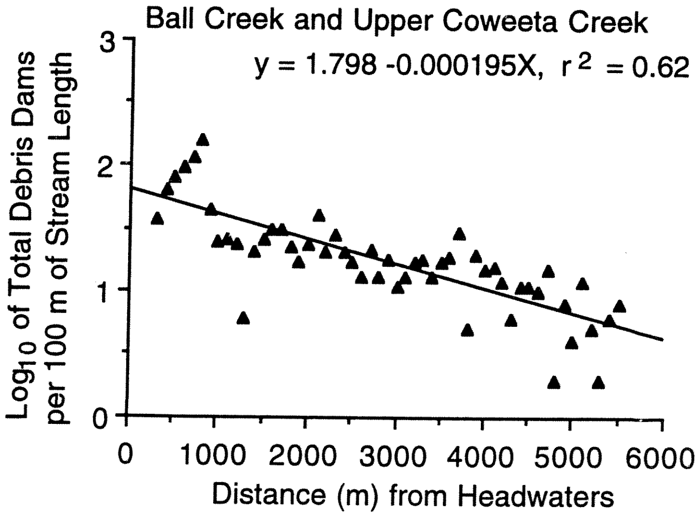


Figure 1—Frequency of organic debris dams along a 5.6 km reach of Ball Creek and upper Coweeta Creek, encompassing stream orders 1 (extreme left) to 5 (right).

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.

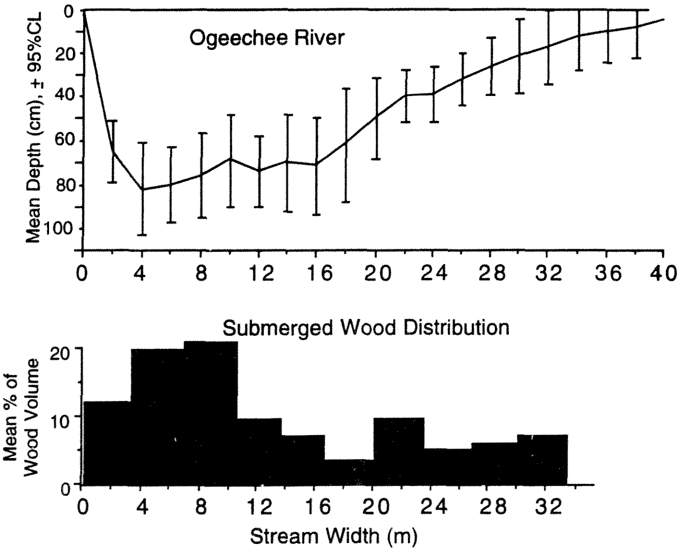


Figure 2—Top: mean depth profile of the Ogeechee River, with erosional bank as 0 regardless of bank orientation, i.e., west or east bank. Vertical lines represent 95 percent CI for depth (cm) at 2-m intervals from erosional bank during low flow hydrograph (August 1983). Bottom: mean percentage of submerged wood volume within each 10 percent increment of width across an "average" transect with a mean channel width of 33-m (redrawn from Wallace and Benke 1984).

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).

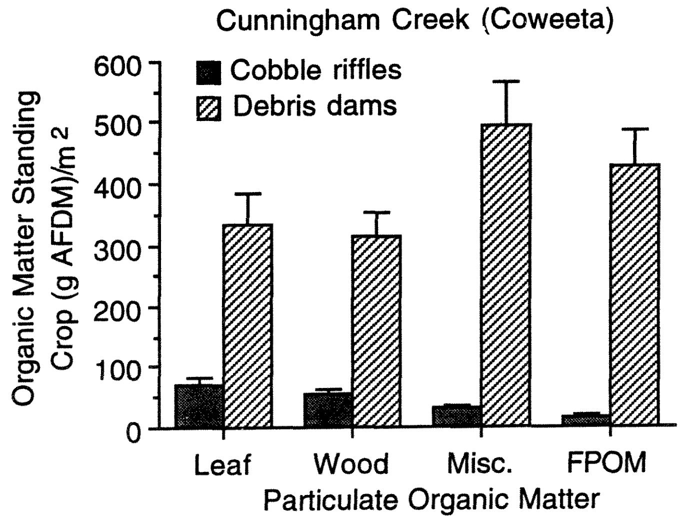
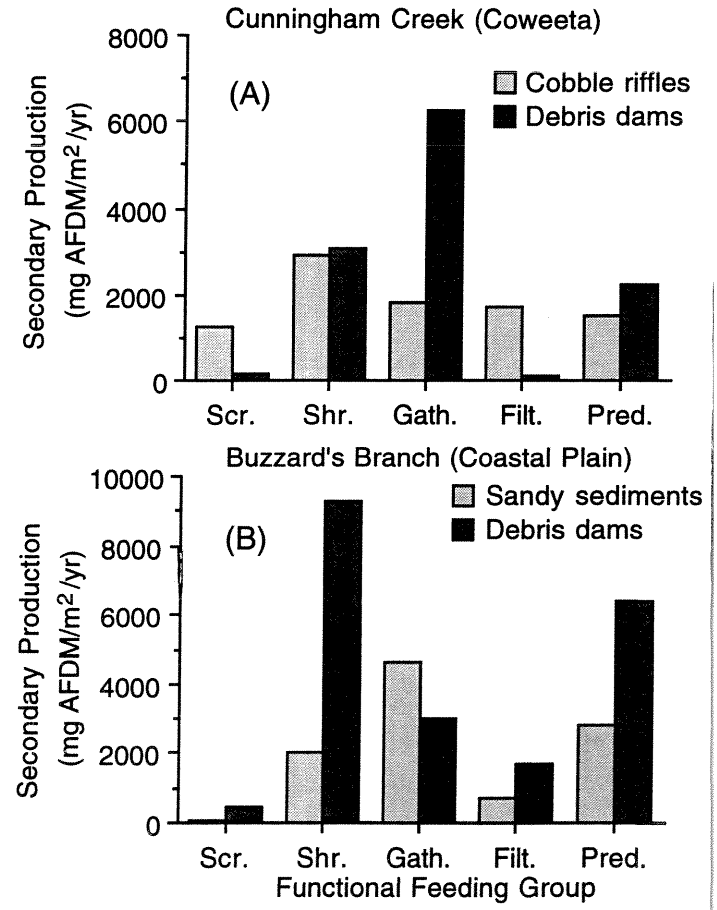


Figure 3—Particulate organic matter (POM) standing crop (± SE) in three cobble riffles and three riffles to which logs were added "debris dams." POM storage did not differ significantly (ANOVA, $p > 0.05$) among reference riffles and "log addition riffles" prior to log additions or with reference riffles following log additions, whereas above were highly significant following debris additions (ANOVA, $p < 0.001$). FPOM is fine particular matter.

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).



Figures 4—(A) Comparisons of functional group production of invertebrates at debris dams and cobble riffles in a high-gradient Appalachian stream (Cunningham Creek; Coweeta; J.B. Wallace and others, unpublished data) with same (B) at debris dams and sandy substrates of a Coastal Plain stream, Buzzard's Branch, in Virginia (calculated from data of Smock and others 1992, using a DM to AFDM conversion of 0.85).

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.

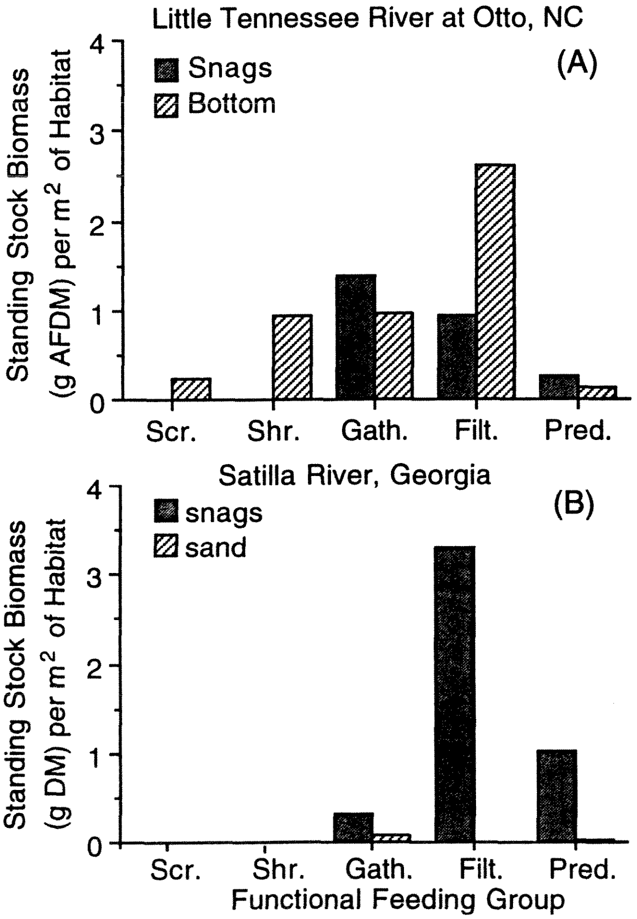


Figure 5—Top: (A) Comparison of standing stock biomass of invertebrate functional groups on wood substrates with that of the stream bed (primarily cobble and *Podostemum*-covered cobble) in the sixth order, Little Tennessee River near Otto, NC (J.W. Grubaugh, unpublished data). Bottom: (B) Comparison of standing stock biomass of invertebrate functional groups on wood with that of the stream bottom (primarily sand and mud) in the Satilla River on the Coastal Plain of Georgia (from Benke and others 1984).

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). Hax 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

Use	Comments	Southeastern geographic region	References
Oviposition sites	Eggs are often deposited on wood below and above the waterline	All—numerous examples among aquatic insects	Dudley and Anderson 1982; Merrit and Cummins 1984
Direct food source	A few invertebrates feed directly on wood by gouging, tunneling	All—Appalachians, Piedmont, Coastal Plain	Benke and others 1984; Merrit and Cummins 1984; Pereira and others 1982
Indirect food source (a) Retention of CPOM[a] (b) Retention of FPOM[b] and epixylic biofilm formation	Serves as food and relatively stable substrata for (a) Shredders (b) Collectors and scrapers	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	Anderson and others 1984; Benke and others 1984; Dudley and Anderson 1982; Smock and others 1985, 1992; Wallace and Benke 1984
Attachment sites for (a) Feeding (b) Catchnet and retreat construction	Important for filter–feeding taxa such as larvae of black flies and net-spinning caddisflies–in large low-gradient rivers, filterers dominate invertebrate biomass on snags	As above.	Benke and others 1984; Cuffney and Wallace 1980; Smock and others 1985; Wallace and Benke 1984
Above uses contribute to high invertebrate biomass	Prey-rich patches for invertebrate and vertebrate predators	All—especially larger streams of Coastal Plain, where Odonata, Plecoptera, Megaloptera, and some dipteran predators are abundant	Benke and others 1984; Smock and others 1985; Wallace and Benke 1984
Refugia from predators and drought	Crevices, loose bark, etc., aid in concealment, woody debris improves moisture retention in intermittent channels	Probably all regions; however, in small, intermittent headwater channels	Dudley and Anderson 1982; Everett and Ruiz 1993; Wiggins and others 1980
Metamorphosis	Woody debris serves as a stable substratum for pupation as well as concealment under loose bark, etc.	All—especially low-gradient Coastal Plain streams with unstable, sandy substratum	Dudley and Anderson 1982; unpublished observations for the Southeast
Aerial adult insects	Emergence, adult resting sites, and copulation	All—especially larger streams and rivers of the Coastal Plain	Dudley and Anderson 1982; unpublished observations for the Southeast
Indirect effects produced by physical modification of channel	Increased stream depth, reduced current velocities modify physical characteristics and increase retention of organic material leading to increased habitat heterogeneity	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	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

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[a] CPOM = Coarse particulate organic matter.
[b] 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 (Coweeta 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 cobble, 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

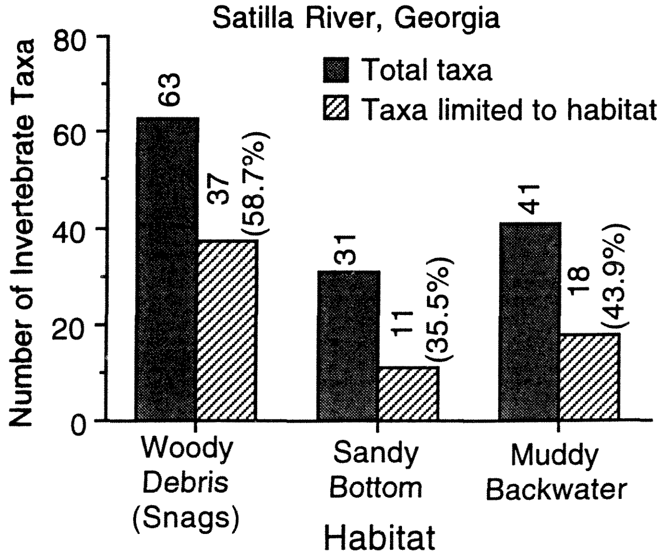

Figure 6—Comparison of the number of invertebrate taxa collected from woody debris, sandy substrates, and muddy backwaters; and the number of taxa limited (and their percentage) to each habitat type in the Ogeechee River, Georgia. (Calculated from data of Benke and others 1984).

Table 2—Number of taxa found associated with woody debris, stream substratum, and combined habitats in various southeastern streams

	Total number of taxa by habitat			
Location	Debris dam or snags	Stream substratum	Combined habitats	Taxa exclusive to wood
				(%)
Coweeta, NC[a]	66	75	87	14
Lt. Tennessee River, NC[b]	21	36	44	18
Buzzard's Branch, VA[c]	34	36	44	18
Collier's Creek, VA[c]	27	20	33	39
Cedar Creek, SC[d]	39	31[e]	47	34
Satilla River, GA[f]	63	58[g]	98	41
Average	42	43	59	27

[a] Wallace, unpublished.
[b] Grubaugh, unpublished.
[c] Smock and others 1992.
[d] Smock and others 1985.
[e] Includes stream bottom and muddy banks.
[f] Benke and others 1984.
[g] Includes sandy bottom and muddy backwaters.

retarded by the anchoring effect of root wads of live and dead trees (Keller and Swanson 1979).

The Stream Renovation Guidelines Committee (1983), established by The Wildlife Society and American Fisheries Society, examined various aspects of debris removal from streams. This committee acknowledged that only in a few situations is debris removal justified. While removal of organic debris may provide flood relief in the immediate area, it encourages unwise development of floodplain areas and may increase peak flows in downstream areas. Based on studies to date, there can be little doubt that debris removal results in the loss of important invertebrate habitat (e.g., table 2).

The relationships between damming activities of beaver, *Castor canadensis*, stream habitats, and macroinvertebrates in the Southeast are poorly understood compared to those of other regions (e.g., Naiman and others 1988). In other regions, the fauna of beaver dams differ greatly from those of stream substratum. 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.

The extensive snagging operations on Coastal Plain rivers undoubtedly produced substantial hydrologic and energetic impacts on these systems. For example, over 15,000 snags were removed from the lower Satilla River in the late 19th and early 20th century (J.R. Sedell, personal communication; Wallace and Benke 1984). Benke and others (1985) estimate that invertebrate production available 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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Large Woody Debris, Fish Habitat, and Historical Land Use

C. Andrew Dolloff

Abstract

Large woody debris (LWD) influences many ecological processes and plays a key role in the structure and function of habitats for a variety of aquatic species. Large woody debris influences sediment scour-fill patterns by deflecting flow; it delays and damps flood peaks downstream; and it decreases nutrient loss by trapping seston and inorganic sediments. Large woody debris is important to pool formation, which influences a stream's velocity, depth, and storage capacity. Pools are especially important to fish as refuges at times of stress, during droughts or floods, and as sources for recolonization. Heavy LWD loadings provide complex cover, protecting fish from predation, competition, and displacement; and may decrease the number of behavioral interactions, permitting greater numbers of fish to coexist. Stream loading of LWD is a natural phenomenon that has been drastically altered by human activity. Riparian areas should be managed so they eventually return to their presettlement role as a source of LWD.

Introduction

Large woody debris (LWD) plays a key role in the structure and function of habitats for a variety of aquatic species. Only recently, however, have land managers begun to recognize the value of LWD in maintaining biotic diversity. Even today, many managers of public lands and private corporations mandate debris removal from streams and rivers, citing benefits such as flood prevention or habitat improvement. Although careful removal of individual trees and debris accumulations may be justified for safe, efficient navigation of large rivers and to protect property or individual bridges, wholesale removal of LWD typically results in dramatic changes in aquatic habitats. In this paper I review the relationships of LWD to fish and fish habitats. I also relate historical land use, primarily exploitative logging, to changes in LWD loading and fish habitat in the Southern Appalachians.

Large woody debris is any piece of wood at least 10 cm in diameter at the small end and 1.0 m in length, including logs, branches, snags, or entire trees with attached root wads (Bisson and others 1987). Smaller pieces of wood are also important to stream ecology, providing benefits such as vital substrates and nutrients for macroinvertebrates and microbes. Because smaller pieces are more readily dislodged and transported downstream, they are less likely to influence channel morphology and habitat. Large woody debris is often a component of debris dams (along with many smaller pieces and detritus) that slow the flow of water, trap sediment and organic matter, and create microhabitats for fish and benthic macroinvertebrates (Bilby and Likens 1980).

Functions of Large Woody Debris

Large woody debris influences many ecological processes, including primary and secondary production, habitat formation, and control of sediment and water output (Harmon and others 1986). Many macroinvertebrates and microbes depend on LWD both directly for specific habitat needs and indirectly for food. All pieces of LWD that intersect the bank-full profile of a stream channel have the potential to modify channel morphology. When streams flow at or beyond capacity (bank-full discharge), LWD deflects flow and influences sediment scour-fill patterns, delaying and damping flood peaks in downstream areas. Large woody debris also traps seston and inorganic sediments, thereby decreasing the rate of nutrient loss (Golladay and others 1987).

Large woody debris is a critical element of pool formation in streams flowing through forested areas. Streams with few pools have low water storage capacities and consequently tend to have lower fish populations. Many species of fish require the lower water velocity and greater-than-average depth provided by pools. In mountain streams, trout typically occupy and defend specific positions in pools from which they forage for insects and other drift food items. Pools are especially important when fish are under stress, such as during droughts or floods. After streamflow returns to normal, fish are able to recolonize from these critical refuges.

Pools form around hydraulic roughness elements such as boulders, bedrock protrusions, and LWD (Sullivan and others 1987). LWD is an especially conspicuous pool-forming element in small- to medium-sized streams flowing through old-growth forests (Andrus and others 1988). In the Southern Appalachians, many streams drain land that was cleared 50-300 years ago, and most of these streams

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have lost much of their LWD. Large woody debris was deliberately removed at the time of logging, gradually depleted through decay, fragmentation, and downstream transport, or catastrophically flushed during floods (Silsbee and Larson 1983). The percentage of pools formed by LWD tends to be much lower in streams flowing through second- and younger-growth forests because riparian vegetation is not yet able to contribute large amounts of LWD (Flebbe and Dolloff 1991). Recent research, however, has shown that LWD is a component in at least 50 percent of pools in Appalachian streams that flow through riparian zones ranging in age from 28 to 300 or more years (Hedman 1992).

Large woody debris influences pool development in many ways. Plunge pools, dam pools, and backwater pools are three of the most common types of pool used by fish (Bisson and others 1982). Recent research has demonstrated that the deepest pools form behind pieces that are perpendicular to flow and are at least as wide as the stream channel (Cherry and Beschta 1989).

Streams having high LWD loads tend to have complex habitat. Overhanging logs, debris jams, and root wads provide complex cover, protecting fish from predation (Everett and Ruiz 1993), competition, and displacement. Fish in pools with complex cover tend to be visually isolated, which may decrease the number of behavioral interactions and permit greater numbers of fish to coexist (Dolloff 1986; Fausch and Northcote 1992). Complex cover in deep pools is especially valuable during times of increased stress such as winter, or whenever flows are particularly high or low (Bustard and Narver 1975; McMahon and Hartman 1989; Tschaplinski and Hartman 1983). Fish find shelter from flushing streamflows by moving into or behind LWD accumulations (Shirvell 1990). Elliott (1986) and Dolloff (1986) found that production of juvenile anadromous salmonids was greater where debris accumulations were left intact. Angermeier and Karr (1984) removed all LWD from one side of a small Midwestern stream that they had partitioned down the center with fine mesh hardware cloth. The side without debris had smaller amounts of litter, fewer species and lower biomass of benthic macroinvertebrates, fewer fish species, and smaller fish than the side where LWD was left in place.

Debris removal lowers habitat complexity (Heede 1985; Lisle 1986), channel stability (Bilby 1984), fish numbers, smaller average size of fish, and biomass (Coulston and Maughn 1983; Dolloff 1986; Elliott 1986; Fausch and Northcote 1992). Habitat simplification and subsequent decreases in residual LWD loading after timber harvest have also been implicated as a cause for long-term changes in the diversity of fish assemblages. Reeves and others (1993) documented changes in the composition of juvenile salmonid assemblages after timber harvest in watersheds of the Oregon Coast range, where formerly abundant steelhead and cutthroat trout have apparently been replaced by coho salmon.

Recent research on ecological disturbances has emphasized the importance of refugia (areas that remain habitable during extremes of drought, flood, or other disturbance) and the need for connectivity among stream channels and riparian zones (Meffe 1984; Naiman and others 1993). Fish and other aquatic organisms that find and use refuges are more likely to recolonize main stream habitats after a disturbance. The frequencies of occurrence, availability, and suitability of refugia greatly influence the stability and adaptability of aquatic systems. From small pieces in individual habitat units to large accumulations scattered throughout entire drainage basins, LWD features prominently in refugia of all types and sizes (Sedell and others 1990). In streams and rivers that have been channelized or detached from their floodplains, or that simply lack significant amounts of LWD, the variety and availability of refugia for aquatic organisms are greatly reduced.

Input and Loading of Large Woody Debris

Trees naturally enter streams after their root systems are undercut by flowing water. With their support systems weakened, these bankside trees are easily toppled by windthrow or the accumulation of ice or snow. Rates of LWD input depend on factors such as species and health of trees in the surrounding riparian zone, stream size and age, and patterns of past land use. Insect attacks and diseases may accelerate this process. Epidemics can greatly influence LWD loading. In the Eastern United States a blight virtually eliminating the formerly common American chestnut (*Castanea dentata* (Marsh) Borkh.), has resulted in high LWD loads (except where intact chestnut logs were salvaged) composed primarily of blight-killed chestnut trees (Hedman 1992). The greatest input of LWD, however, can usually be traced to a specific event such as a flood, tornado, or hurricane; the amount of LWD in a small Appalachian watershed more than doubled after Hurricane Hugo swept over northwestern North Carolina (Dolloff and others 1994).

Most in-stream LWD originates from a narrow strip along both sides of a stream channel. Over 70 percent of the LWD in streams flowing through mature and old-growth riparian zones in western Washington and Oregon originated within 20 m of the stream bank (McDade and others 1990). However, debris can be introduced from more distant sources on floodplains and hillslopes by floods or debris torrents (Benda and others 1992; Hack and Goodlet 1960; Keller and Swanson 1979).

In general, the proportional loading of LWD is higher and its contribution to habitat structure is greater in headwater tributaries than in downstream rivers (Minshall and others 1983). In parts of the Southeastern United States, however, LWD loading in some large rivers increases with increasing stream order (Benke and Wallace 1990). The observed lack of LWD in other large rivers, such as the Missouri and Mississippi, is in large measure a result of river management. Over 800,000 snags (average length 40 m) were removed from the lower 1,650 km of the Mississippi River between 1830 and 1880 to improve navigation (Sedell and Luchessa 1982). All across the United States, LWD was and still is removed wherever rivers serve as primary commercial routes (Sedell and others 1991).

The architecture of instream LWD is a function of stream size, the nature of the input process, and geomorphic characteristics of the site (Bisson and others 1987). In headwater streams many arrangements are possible, but generally pieces stay where they fall or move very little after input, because small streams have little power to move larger pieces. Large woody debris of all sizes may provide the nucleus for the formation of complex debris dams in small headwater streams (Bilby and Likens 1980).

In intermediate-size streams, LWD tends to accumulate along the margins or at channel constrictions. Stream power is sufficient to float pieces from streambanks and upstream accumulations but many pieces still span the width of the channel. Submerged pieces can remain in place for many years, influencing channel morphology by creating side channels or meanders, and altering habitat formation by changing patterns of sediment scour and fill. In larger channels, LWD forms tight clumps at the heads of point bars and side channels, at islands, and along the outside curves of meanders.

Large woody debris residence ranges from the time until the next high flow or hundreds of years, depending on site characteristics (stream size, channel shape, etc.) and wood size and quality (decay resistance, specific gravity, etc.). Smaller pieces have higher ratios of surface area to volume and lower proportions of decay-resistant heartwood than large pieces. Consequently, small pieces may have higher rates of fragmentation, abrasion, and decomposition, and disappearance through floatation may be higher for small versus large LWD (Harmon and others 1986). LWD loading follows a cycle of loss and replenishment in systems that have been undisturbed for a long time. As some pieces are lost or moved about, new pieces take their place, preserving the state of dynamic stability.

Until recently, most people associated high loads of LWD with streams in the Pacific Northwest where up to 4,500 m^3 per ha were estimated in a stream flowing through a redwood stand in northern California (Keller and others, in press). Because of the long history of settlement and land clearing in the East, estimates of LWD loading tend to be much lower in southeastern streams (40-300 m^3 per ha) (Harmon and others 1986). The most comprehensive inventory of LWD in Southern Appalachian watersheds showed that loadings were highly variable depending on land use and disturbance histories, the number and variety of riparian tree species, and the dynamics of American chestnut mortality. Large woody debris loadings, particularly those originating in mature and old-growth forests, were lower than expected and considerably lower than those in comparable streams in the Pacific Northwest (Hedman 1992).

Despite their current low rates of loading, streams flowing through eastern forests probably would have substantial loads of LWD if the lands they drain had not been logged and cleared. Streams in unlogged watersheds in the Great Smoky Mountains National Park contain four times more LWD (338 m^3 per ha vs. 84 m^3 per ha) than streams in watersheds logged before the park was established (Silsbee and Larson 1983), and Flebbe and Dolloff (1991) found higher loads of LWD in streams flowing through unlogged vs. logged wilderness areas in two Southern Appalachian national forests.

Impact of Past Land Use

Land use has had a major impact on the loading and input of LWD in streams flowing through virtually all of the forested regions of the world. Human use has so changed the structure and composition of most forested watersheds that it is difficult for the average citizen to understand why LWD matters. Forests and rivers have been cleared and manipulated for centuries in Europe and Asia (Harmon and others 1986).

Faced with the need to transport timber 20 miles down the shallow Saba River, late 12th century Japanese loggers " . . . constructed a succession of 118 temporary dams, each one raising the water level sufficiently to float the pillars (logs 100 feet long and 5 feet in diameter) seaward a few score yards. They dredged the last 2 miles of the Saba, gaining enough water to float the pieces" (Totman 1983). Many of Japan's larger rivers were "improved" during the 17th century by the removal of rocks, sandbars, and debris. High up in the watersheds, villagers worked with hammers and chisels to reduce rough ledges to smooth channels. Where debris was abundant, the villagers diverted streamflow, loaded up the channel, soaked the accumulations in oil, and set them ablaze. After allowing the stream bottom to become heated, they diverted the water back into the stream channel, shattering the ledge which was then removed (Totman 1983).

At about the same time, on the other side of the world in North America, logging and land clearing on a large scale was just beginning. As in other countries, stream and river "improvement" removed any hindrance to free flow and navigation. Because such a monumental task was beyond the means of the average citizen or municipality, Congress directed the U.S. Army Corps of Engineers to oversee the clearing and removal of many hundreds of thousands of snags, logs, and debris piles from rivers all across the United States from 1867-1912 (Sedell and Luchessa 1982).

Although most of the easily exploited forest in the Southeastern United States had already been cut by 1880, vast reserves of high-quality timber remained deep in the southern mountains. Over 20,000 square miles of untouched forest in Kentucky was within easy reach of the Mississippi and its numerous tributaries (Sargent 1884). As timber supplies were depleted from readily accessible lowlands adjacent to larger rivers, lumber companies pushed into the mountains. There they encountered rough country and numerous streams that they "developed" into conduits for log transportation (Clark 1981). Splash dams, flumes, and slides were common in parts of the Southern Appalachians wherever conditions permitted (Brown 1936; Mastran and Lowerre 1983; Rector 1949).

One of the most spectacular splash dams was erected on the Russell Fork of the Big Sandy River at the town of Splashdam in southwest Virginia (Anon. 1910; Anon. 1912). From 1910 to 12, the Yellow Poplar Lumber Company sent over 50 million board feet of yellow-poplar logs (average diameter 63.5 cm, length 0.5 to 11.5 m.) (fig. 1) through the bays of its 110-m long, 7.5-m high concrete dam (fig. 2) and down the Big Sandy to its mill in Coal Grove, OH. The effects of the repeated torrents of wood and water and accompanying stream improvements totally transformed the channel, which exhibits few signs of recovery today.

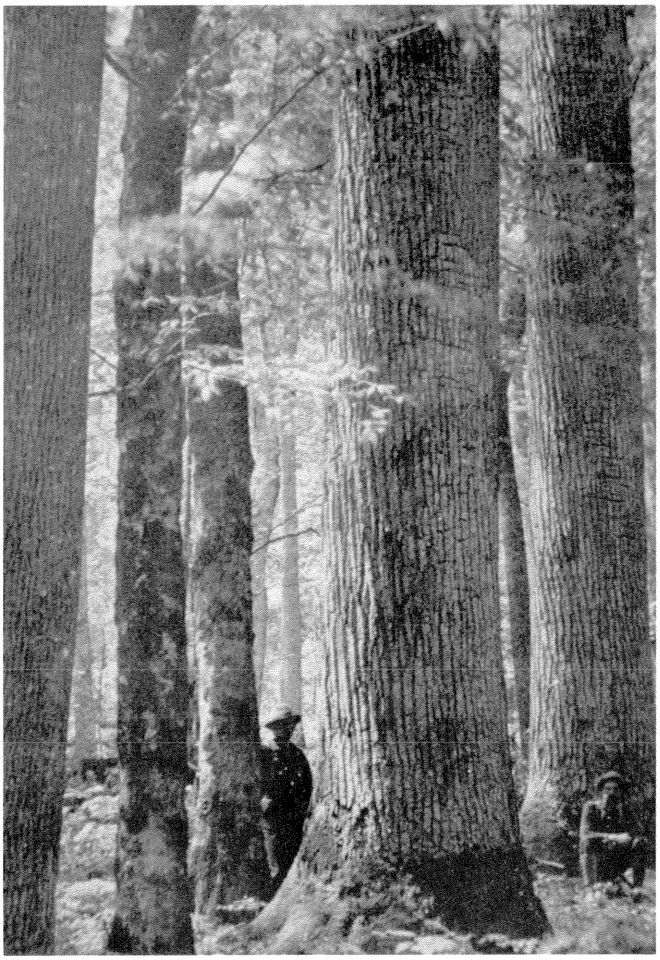

Figure 1—Yellow-poplar trees, Dickenson County, Virginia, ca 1910.

Many other Appalachian streams were similarly transformed, including the Tellico in Tennessee. From its base of operations in Tellico Plains, the Tellico Lumber Company operated a system of splash dams in the upper Tellico River watershed. Over 1 million board feet of timber was used to construct three dams, each 122-m long and 12-m high, on the major forks of the Tellico (fig. 3). Nearly 4,000 logs would be flushed weekly down the Tellico, even "... when there was not water enough in the river at the mill to wet one's ankles in wading across" (Anon. 1901). Here too, damage to the river was extensive; a hole 36-feet deep was worn in the rock below the outlet of one dam.

Mountain streams continued to play an important role in log transportation even after railroads penetrated the mountains (fig. 4). This new technology actually accelerated the degradation of southern watersheds as stream gravels were mined to build roads, and rails were frequently laid directly over small stream channels (fig. 5). Companies frequently ran short lines to transport timber from remote coves and small drains to rollways and log dumps on the larger rivers.

The use of streams and rivers for timber transportation persisted well into the 20th century. The Federal Government eventually acquired much of the cutover lands in the Southern Appalachians during the 1920's and 1930's. These "lands that nobody wanted" and the streams that drained them have largely reforested and are managed by the U.S. Departments of Interior and Agriculture in national parks and forests (Mastran and Lowerre 1983). With the return of the forest, however, knowledge and understanding of the changes caused by past land use are fading from memory.

Management of Large Woody Debris

Many people and some governmental bodies do not appreciate the role that LWD plays in our streams and rivers. Others, however, embraced recent findings on the importance of LWD, halted expensive and unwarranted debris removal programs, and now manage for LWD recruitment. These new policies have created some credibility problems for managers and biologists. For years, loggers have been required to keep debris out of streams; now they see fishery and watershed managers discouraging stream cleaning and deliberately placing debris back in streams. Although enthusiasm for LWD typically runs high once its value is understood, a word of caution is advised: there is a difference between beneficial LWD and slash—typical logging residue composed of small trees, tops, and branches (Froelich 1973). Except in the smallest of streams, slash tends to be unstable and contributes little to instream habitat. However, individual trees that accidentally enter a stream should usually be left and counted as habitat enrichment rather than to risk damaging stream banks and accelerating erosion by removing them.

To provide sustainable amounts of LWD for the future, we must manage both the stream and the area where land and instream environments interact: the riparian zone. Although it is possible to temporarily restore LWD (and a measure of ecological integrity) to individual streams by direct addition of trees, this approach is clearly not feasible on a large scale. Alternatively, given enough time many riparian areas will regain the characteristics of mature forests and provide LWD. Between these extreme strategies lies a range of management strategies—practical, long-term solutions that employ a mix of techniques to address both specific current shortages and long-term goals for natural LWD recruitment.

To ensure adequate supplies for the future, recruitment of LWD must be included in the development of riparian management strategies. The diversity of riparian zone functions and values suggests that advocates for LWD must compete with proponents of other uses. For example, to preserve sources of LWD until understory trees mature, the salvage of trees killed by storm, fire, or insects may be limited to a specified distance from the streambank (Carlson and others 1990).

The selection of appropriate species or assemblages to be managed for LWD depends on site suitability, decay resistance, and other riparian management objectives. For example: northern red oak produces hard mast and other benefits for wildlife, high quality timber, and decay-resistant LWD (Perkey and others 1993). Eastern hemlock, while of lesser value for timber, provides thermal cover during both winter and summer and is very resistant to decay.

During the last 20 years, increasing knowledge about the many functions of LWD has contributed greatly to both the science and practice of riparian ecosystem management. Understanding and appreciation of the benefits of interdisciplinary, integrated approaches to management should increase the abilities of present and future managers to address the increasing demands for traditional and potential new uses of riparian ecosystems.

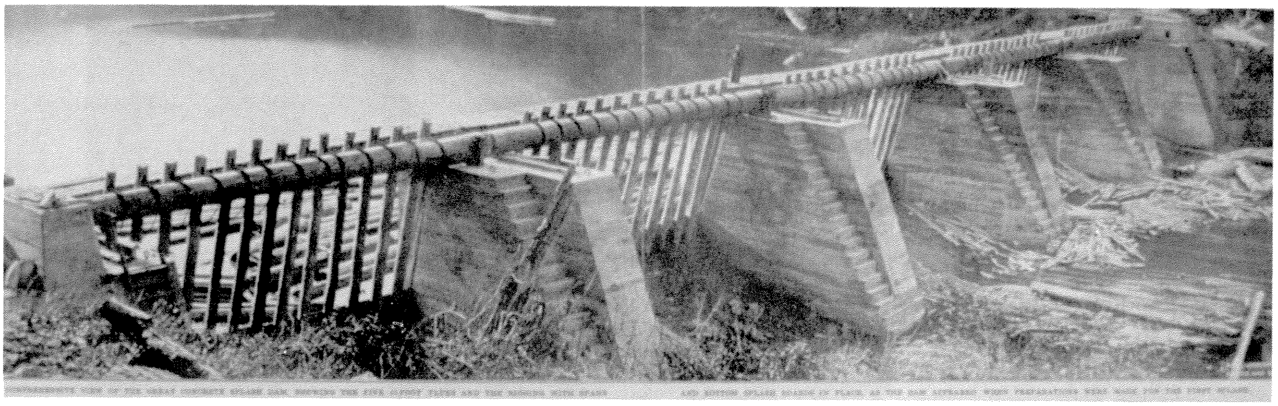

Figure 2—Splash dam operated by the Yellow Poplar Lumber Company on the Russell Fork of the Big Sandy River, Dickenson County, Virginia, 1910. When filled to capacity, the mile long, 25-ft deep "pond" behind the dam held over 35,000 logs.

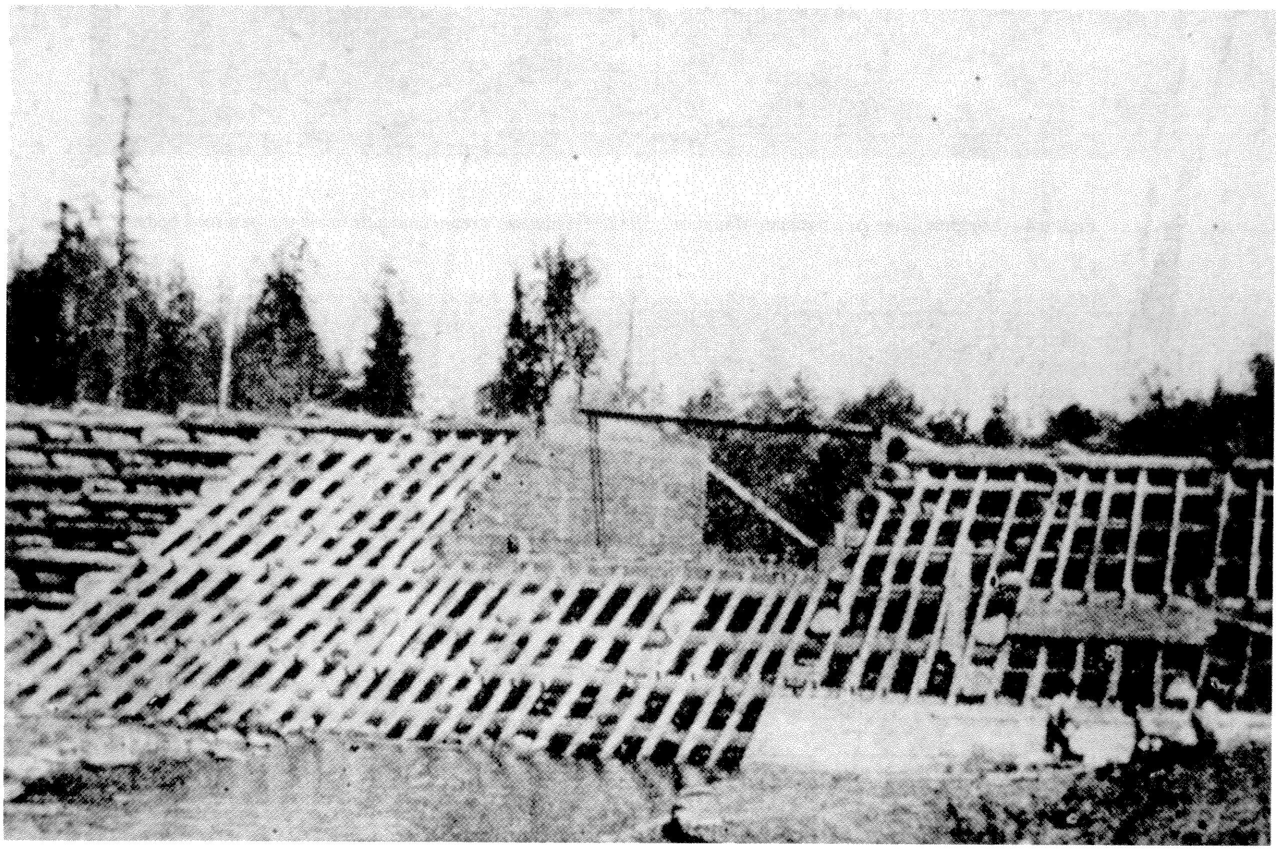

Figure 3—Splash dam on the Tellico River, ca. 1901.

Figure 4—Logging in the Appalachian Mountains, 1912. Headwater stream channels made the best road beds.

Figure 5—West Virginia Spruce Lumber Company salvage operations, 1908.

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Models and Management Implications of Coarse Woody Debris Impacts on Biodiversity

Michael A. Huston

Abstract

Coarse woody debris (CWD) affects biological diversity in two ways: (1) it is a major contributor to habitat structure, and (2) it is a slow-release energy and nutrient reservoir. The relationship between productivity and biodiversity is complex, and the patterns of energy storage and species richness do not always coincide. The shifting landscape patterns of disturbance and productivity may lead to different levels of biological diversity among primary producers, herbivores, carnivores, and decomposers. For example, plant diversity appears to reach a maximum at low productivity, while carnivore diversity is greatest at high productivity. The effects of CWD on biodiversity appear most prominently in the decomposer food webs, which use the energy and structural diversity of the forest floor habitat to support a complex array of species. Management of CWD is potentially a major tool in managing biodiversity of these organisms.

Introduction

Coarse woody debris (CWD) is unique among ecological resources in that it simultaneously provides both physical structure and energy. Environmental heterogeneity, provided by the physical structure and species composition of plants, spatial variation in soil properties, and spatial variation in other biotic and abiotic environmental properties, is probably the single most important factor for explaining local and landscape scale variation in biodiversity. Productivity, or the amount of available energy, is also known to have a strong positive effect on biodiversity in many situations. These two factors have been extensively investigated and discussed by ecologists from both empirical and theoretical viewpoints. (Grime 1979; Huston 1979, 1994; Tilman 1982; Rosenzweig and Abramsky 1993).

Most of the sources of physical structure in the environment are relatively inert. For example, the massive calcium carbonate skeletons of corals, the rocky substrates of the intertidal zone, and the boles and branches of forest trees provide a physical structure that supports a great diversity of plants and animals, but in general does not provide a significant amount of energy or other resources that can be consumed by animals. However, when trees die and the chemical and physical protection of their woody structure decreases dramatically, the complex physical structure of the boles, branches, and twigs becomes a rich source of carbon-based energy. This energy supports a complex and diverse food web of fungi, bacteria, invertebrates, and vertebrates that alter the structure of the wood as they convert the cellulose, lignin, and other compounds to animal biomass and heat. Ultimately, the physical structure of the CWD disappears completely when all of the mass is converted to energy and living tissue.

The effects of CWD on biodiversity, and the effects of various management activities on CWD-related biodiversity, can be understood in the context of these two factors: (1) the available energy content, and (2) the structural properties of CWD.

Productivity and Biodiversity

The relationship between biodiversity and productivity has a long and controversial history in ecology. Productivity can be defined as the solar energy that is captured and converted into living tissue by plants (and eventually converted back into energy by humans and other organisms). Primary productivity is considered to be the amount of energy converted into plant tissue (measured as plant biomass), and secondary productivity is the amount of plant-derived energy converted into animal tissue (measured as animal biomass). We have good data and theoretical models demonstrating that higher productivity should be associated with higher diversity, but we also have good data and theory showing that diversity is reduced under the most productive conditions. These conflicting patterns have prevented the development of a comprehensive understanding of productivity-diversity relationships and slowed the development of guidelines for managing biodiversity *in relation to site index and other* estimates of productivity.

The confusing patterns of biodiversity in relation to productivity can be understood if the properties of different types of organisms and different environmental conditions

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are taken into account. The first step is to divide the multitude of organisms found in any ecosystem into groups based on their functional relationships with each other and with the environment. This subdivision is based on the well-known concept of ecological guilds, which are groups of organisms that are sufficiently similar to one another that they are likely to compete for resources. Thus, competition is likely to be an important process within guilds, and less likely to be important between organisms from different guilds.

Division of biodiversity into functional groups (guilds) of organisms provides a way of understanding why different groups of organisms may respond differently to the same environmental conditions. In particular, a given management activity is likely to lead to an increase in the diversity of some types of organisms and a decrease in the diversity of other types of organisms.

Two very important environmental factors that vary naturally across landscapes and are affected by virtually every management activity are (1) site productivity and (2) disturbance. These two factors provide a framework for understanding patterns of biological diversity in both natural and managed systems. Because biodiversity results from populations of organisms surviving and coexisting together, the general principles of population biology can be used to make predictions about patterns of biodiversity. In general, populations with many individuals are expected to have a higher probability of survival than populations with few individuals, and populations that can rapidly increase their numbers following a disturbance should have a higher probability of survival than populations that recover slowly.

Because both population size and growth rates are influenced by the availability of resources in the environment, we would expect the greatest number of surviving populations—and thus the highest biodiversity—under productive conditions where resources availability is high. Disturbances that kill individuals decrease the probability of population survival; therefore, we would expect diversity to be highest under conditions where the frequency of disturbances is low (fig.1). This pattern is found in some, but not all, situations. Specifically, it tends to be found among groups of organisms that do not compete strongly with one another, that is, organisms of different types. Since every ecosystem is composed of many different functional types of organisms, with some functional types having many species and others only a few species, the pattern predicted by figure 1 is most likely to be found in groups of organisms composed of many

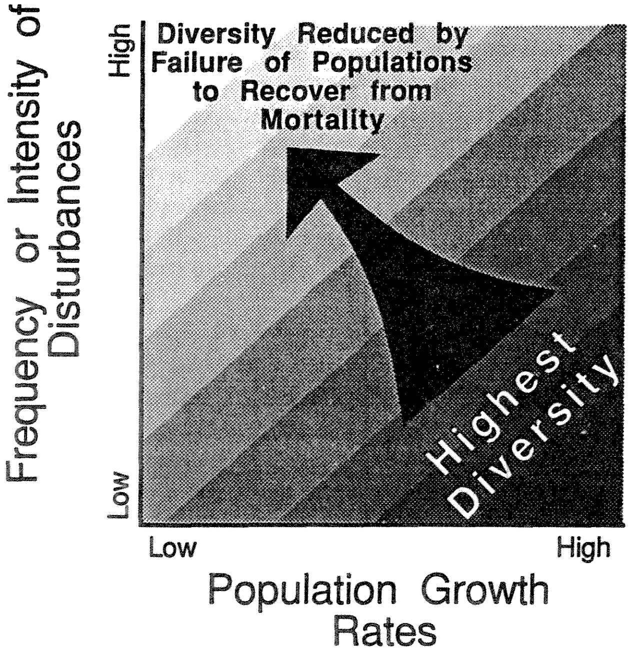

Figure 1—Expected pattern of species diversity among non-competing organisms in relation to productivity (population growth rates) and disturbance (from Huston 1994).

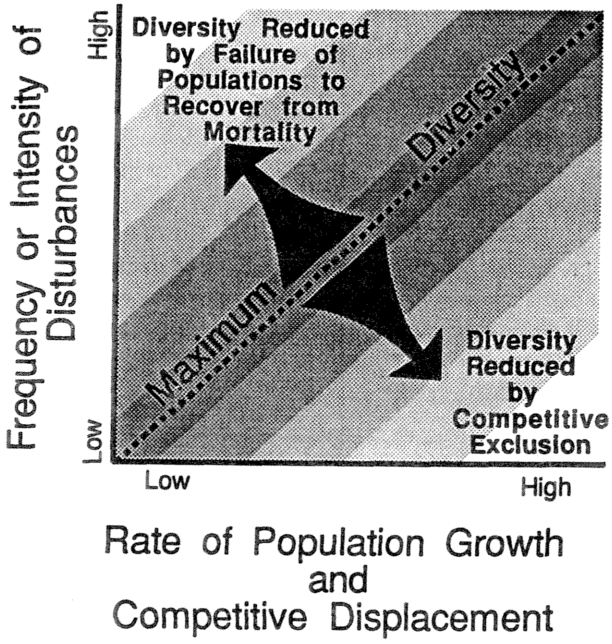

Figure 2—Expected pattern of species diversity among organisms that potentially compete, in relation to productivity (population growth rate) and disturbance (from Huston 1994).

different functional types. It is less likely to be found in groups composed primarily of a single functional type. Among groups of organisms that can compete strongly, such as plants competing for light, diversity is often reduced under the most productive conditions when a dominant competitor excludes other species (fig. 2).

What this means is that for an entire ecosystem, the total number of species (including bacteria, fungi, insects, plants, and vertebrates) is likely to increase with increasing productivity, but the diversity within any particular group of organisms may decrease dramatically even while total diversity is increasing. In general, plant diversity decreases with increasing productivity, while animal diversity, particularly of carnivores, increases with increasing productivity (fig. 3).

Interactions between competition, which reduces diversity under productive conditions, and mortality-causing disturbances, which tend to prevent competitive exclusion, mean that not all groups of organisms will respond the same way to a change in disturbance frequency or intensity (e.g., burning, harvesting, etc.). This represents obvious problems for biodiversity management, since an increase in total forest diversity may be accompanied by a decrease in some groups of plants or animals that are of particular management concern. Consequently, simply increasing productivity is not necessarily a good management practice. Likewise, changing a disturbance regime is not likely to affect all groups of organisms in the same way.

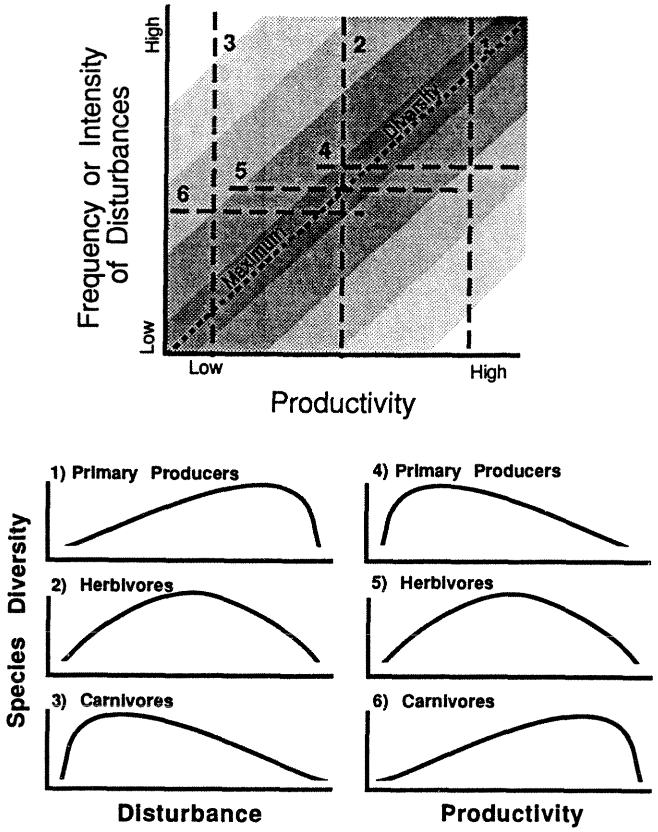

Figure 3—Predicted differences in diversity patterns among plants, herbivores, and carnivores in relation to productivity and disturbance. The diversity of plants tends to reach a maximum at low levels of productivity, while the diversity of carnivores tends to be highest at high levels of productivity (from Huston 1994).

Coarse Woody Debris and Biodiversity Management

No other manageable property of the forest environment has a greater impact on biodiversity than CWD. Even harvesting, which can in some cases act as a disturbance that increases tree diversity, probably has a greater effect on total forest biodiversity through the alteration and removal of CWD than through its effect as a disturbance that "resets" forest succession. Because CWD provides two of the primary regulators of biodiversity— energy and heterogeneity—removal of CWD through harvest is potentially one of the most significant, and least appreciated, differences between managed and unmanaged forest ecosystems. The other chapters of this volume clearly demonstrate the critical role of CWD for virtually all components of forest biodiversity.

The relationship between the energy content and the structural heterogeneity of CWD is the key to CWD use for biodiversity management. Because structural heterogeneity decreases to zero as the energy content of wood is decreased to zero by decomposition, a continual input of CWD into a forest ecosystem is needed to maintain CWD-dependent biodiversity. The variable dimensionality of CWD, from thin twigs to massive boles, provides both a great range of spatial heterogeneity, and great variation in the time required for the structure and energy content to be reduced to zero. While branches can provide higher initial structural heterogeneity than large boles, more rapid decomposition reduces both the energy content and the structure to zero much more rapidly for branches than for boles.

Both the energy content and structure of CWD are constantly changing through time, with energy decreasing continuously, while structural heterogeneity can increase during the early and mid stages of decomposition. These dynamics allow management to manipulate the CWD dynamics of a forest by altering the input of different types (dimensions) of CWD. Total diversity will usually be maximized by the combination of high energy input and high structural heterogeneity (fig. 4), and different dimensions (and energy content) of CWD will have different patterns and rates of change in energy/heterogeneity. For example, logging slash can provide high heterogeneity and rapid release of energy following harvest, but unless boles and other large-dimension CWD are also left or later put into the system, both CWD energy and CWD structure will rapidly drop to zero, with an inevitable reduction in many components of biodiversity.

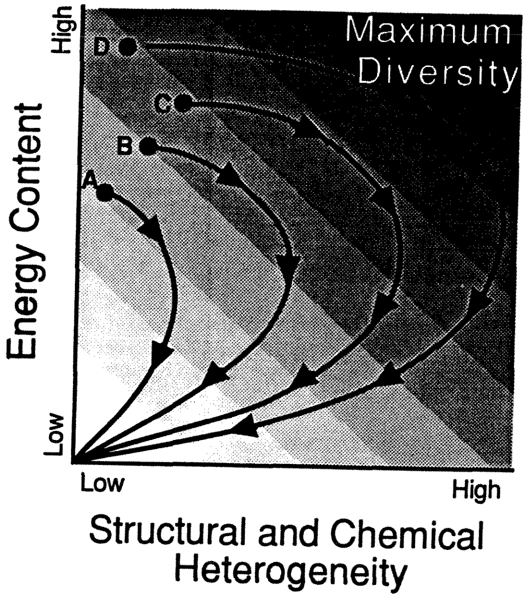

Figure 4—Patterns of diversity of CWD-dependent species that result from decomposition of CWD with various initial energy content and heterogeneity. (A) Lowest total energy content, low heterogeneity (e.g., small branch slash). This CWD rapidly decreases in total energy, heterogeneity and species diversity as a result of decomposition. (B) Low total energy, intermediate heterogeneity (e.g., medium and large branch slash). (C) Moderate total energy, relatively high heterogeneity, (e.g., branch slash and small boles). (D) High total energy content, low heterogeneity (e.g., large boles). This type of CWD takes much longer to decompose and reaches a higher level of heterogeneity and species diversity than smaller dimension CWD. Note that during decomposition, structural and chemical heterogeneity increase during the early stages, and decrease during the later stages, as total energy content drops to zero. CWD-dependent species diversity is continually changing over the course of decomposition as energy content and heterogeneity change. Diversity is expected to be maximum under conditions of highest energy content and structural/chemical heterogeneity.

Because of the high host specificity of many fungal decomposers, high plant diversity (i.e., high chemical diversity of dead wood) can be expected to result in very high diversity of some types of decomposers. However, since high plant diversity is usually found on less productive sites, those CWD-dependent groups that are most strongly affected by energy supply, (insectivores and higher trophic levels such as carnivores) may not reach their highest diversity on these sites, and instead have maximum diversity on more productive sites (fig. 5).

The amount of CWD-based energy in a natural ecosystem is clearly a function of forest productivity, as represented by site index. Management through thinning and harvest removes some portion of that energy, leaving a fraction of the amount that would be naturally available. This reduction in available energy (and structure) might be more critical on unproductive sites than on productive sites, but the possibility has probably never been evaluated.

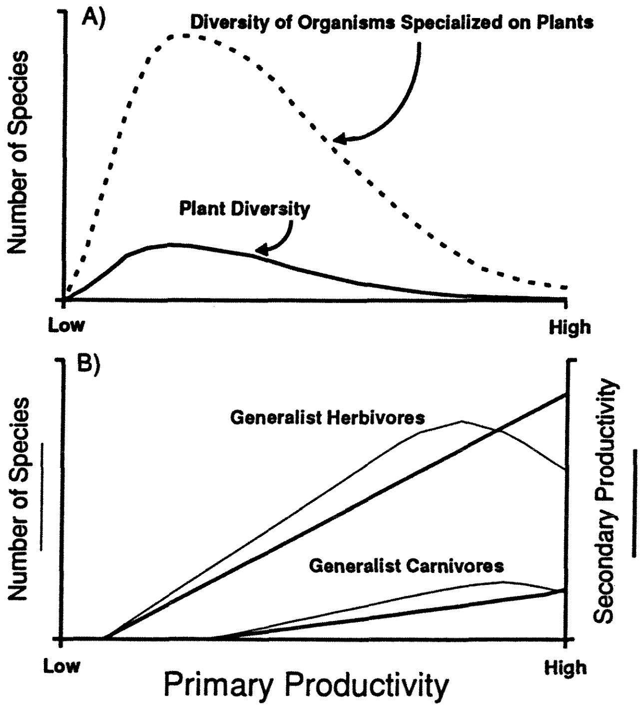

Figure 5—Expected response of species diversity to variation in CWD input (primary productivity) into a forest ecosystem for (A) species specialized on the structural and chemical heterogeneity of CWD; and (B) generalist species (fungivores, carnivores) that depend primarily on the total energy content of CWD. Specialist species respond primarily to woody plant diversity, which tends to be highest under low productivity conditions. Generalist species respond primarily to total energy availability, independent of the plant diversity (from Huston and Gilbert, in press).

In summary, CWD is a critical factor in the biodiversity of forest ecosystems, providing both energy to support the complex food webs of the forest, and structural and chemical heterogeneity that allows the coexistence of many different species. CWD is greatly affected by most management activities, and is thus a management tool of potentially great importance in managing biodiversity.

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Workshop Summary and Recommendations

James W. McMinn and D. A. Crossley, Jr.

Participants in the Workshop on Biodiversity and Coarse Woody Debris (CWD) in southern forests noted a general lack of information dealing specifically with forests of the Southeastern United States. Many data exist on the loadings and distribution of coarse woody debris (CWD), but these data are scattered and need to be organized into a viable database. Process studies (i.e., generation, decomposition, and dynamics) of CWD also need to be strengthened. From the standpoint of biodiversity, a large array of flora and fauna appear to be associated with CWD in southern forests, but the nature of those relationships is not well known. In particular, both the obligate nature of species assemblages related to CWD and the relative importance of CWD as a refuge from unfavorable climatic or anthropogenic events are unclear. However, CWD in Southern forests offers managers significant opportunities to affect and conserve biodiversity.

Workshop recommendations emphasized the need for (1) approaches to use existing information, (2) additional research on the floral and faunal groups that use CWD, and (3) informed management direction.

Specific Recommendations

Inventory and Dynamics of Coarse Woody Debris in Southern Forests

Compilation of forest survey data is needed to document CWD loadings in southern forests. Survey data are readily available and analyses could dramatically increase knowledge of CWD across forest types, age classes, ownership patterns, and management practices. Further development of models that describe the dynamics of CWD and relate CWD dynamics to biodiversity are priorities. These models will facilitate analysis of the effects of management practices on CWD dynamics.

Importance of Coarse Woody Debris for Biodiversity in Southern Forests

The uses of CWD by flora and fauna in southern forests need to be studied. More specifically, research is needed on how stage of decay, spatial and temporal distribution, and stand structure affect CWD-use by given biotic groups. Coarse woody debris is clearly an important structural habitat variable. It may be especially important seasonally or in drought conditions. Both experimental and observational approaches are needed to isolate factors determining the importance of CWD for biodiversity. For studies of biodiversity of invertebrate organisms, the need for cooperation by systematists was emphasized. The development of local fauna lists, in cooperation with competent taxonomists, was viewed as an extremely important step toward knowledge of biodiversity in southern forests.

Coarse Woody Debris and Biodiversity of Stream Systems

Riparian zones deserve more attention, including experiments that delineate optimal width, estimate the stability of large woody debris in streams of different orders, and identify tree species that contribute to large woody debris in streams. Work should be undertaken to quantify CWD in streams in different physiographic provinces of the Southeast and the associated occurrence of biota. Process studies are needed to provide information on input, decomposition, movement, and colonization of CWD by invertebrate populations in all physiographic regions. Manipulative experiments should include additions and removals of CWD for analysis of effects on processes, as well as on the biodiversity of vertebrates and invertebrates.

Considerations for Forest Management

It is clearly premature for specific recommendations on managing CWD in the South. The dearth of information about CWD in southern forests provides an inadequate basis for such recommendations; however, some general considerations may be offered from the existing information.

Forest floor ecosystems contain a set of microflora and fauna species that are interrelated ecologically. In general, any management practice that increases the spatial heterogeneity or resource base by providing a range of temporal successional patterns will increase the diversity of both microflora and fauna. A variety of size classes of CWD should remain available, and dispersal of CWD on the forest floor would increase microsite heterogeneity. Uneven-aged stands would promote a range of size classes of CWD. Shorter rotations may produce less CWD or fewer large classes of CWD, which may be especially critical. Fire management methods that yield cooler fires (winter fires or head fires) may have less impact on the diversity of forest floor biota. The highest diversity of species may occur in forests that are subject to repeated disturbance—the "intermediate disturbance" hypothesis.

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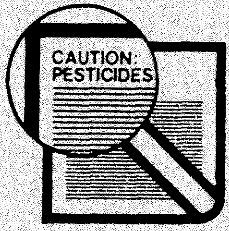

McMinn, James W.; Crossley, D.A., Jr., eds. 1996. Biodiversity and coarse woody debris in southern forests, proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity; 1993 October 18-20; Athens, GA. Gen. Tech. Rep. SE-94. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 146 p.

Seventeen papers address the current state of knowledge about the influences of coarse woody debris (CWD) on the biodiversity of various groups of biota. The generation of CWD, its accumulation on forest floors, and its distribution are functions of stand age and management in the South. The effects of CWD on biodiversity depend upon harvesting variables, distribution, and dynamics. Research priorities are identified for future studies that should provide a basis for the conservation of biodiversity when interacting with appropriate management techniques.