United States
Department of
Agriculture

Forest Service

Southern Research
Station

General Technical
Report SE-94

Biodiversity and Coarse Woody Debris in Southern Forests

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

Athens, GA — October 18-20, 1993

March 1996

Southern Research Station
P.O. Box 2680
Asheville, North Carolina 28802

Biodiversity and Coarse Woody Debris in Southern Forests

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

Athens, GA
October 18-20, 1993

Editors:

James W. McMinn, USDA Forest Service,
Southern Research Station, Forestry Sciences Laboratory, Athens, GA,
and D.A. Crossley, Jr., University of Georgia, Athens, GA

Sponsored by:

U.S. Department of Energy, Savannah River Site,
and the USDA Forest Service, Savannah River Forest Station,
Biodiversity Program, Aiken, SC

Conducted by:

USDA Forest Service, Southern Research Station, Asheville, NC,
and University of Georgia, Institute of Ecology, Athens, GA

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,

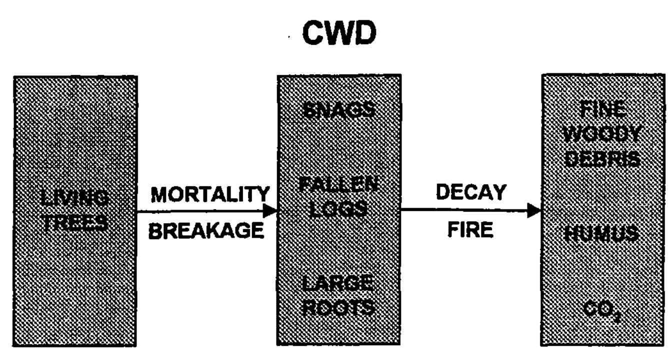

Figure 1—Flow diagram of the dynamics of CWD in terrestrial ecosystems.

Bowen Professor, Department of Forest Resources, Clemson University, Clemson, SC 29643-1003.

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

[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

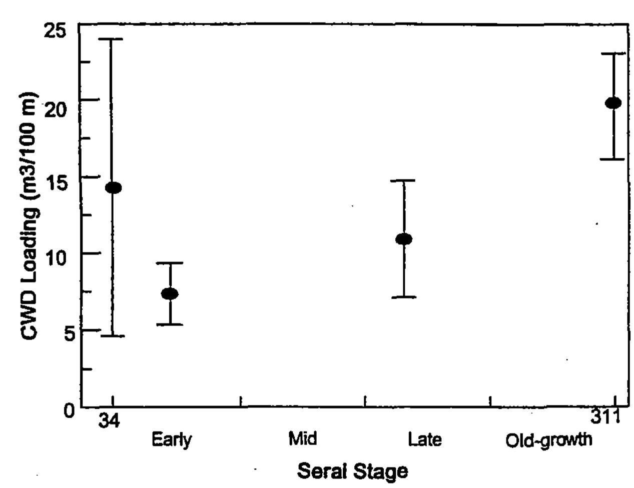

Figure 2—Coarse woody debris loadings, excluding American chestnut, in small Southern Appalachian streams.

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.

Literature Cited

Abbott, D.T.; Crossley, D.A., Jr. 1982. Woody litter decomposition following clear-cutting. Ecology. 63(1):35–42.

Barber, B.L.; Van Lear, D.H. 1984. Weight loss and nutrient dynamics in decomposing woody loblolly pine logging slash. Soil Science of America Journal. 48(4):906–910.

Boyer, William D. 1979. Regenerating the natural longleaf pine forest. Journal of Forestry. 77(9):572–575.

Brown, Arthur A.; Davis, Kenneth P. 1973. Forest fire–control and use, ed. New York: McGraw-Hill. 686 p.

Bull, E.L. 1983. Longevity of snags and their use by woodpeckers. In: Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., eds. Snag habitat management. Gen. Tech. Rep. RM-99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 64–67.

Carey, A.B. 1983. Cavities in trees in hardwood forests. In: Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., eds. Snag habitat management. Gen. Tech. Rep. RM–99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 167–184.

Christensen, Norman L. 1991. Variable fire regimes on complex landscapes: ecological consequences, policy implications, and management strategies. In: Nodvin, S.C.; Waldrop, T. A., eds. Fire and the environment: Ecological and cultural perspectives: Proceedings of an international symposium; 1990 March 20–24; Knoxville, TN. Gen. Tech. Rep. SE-69. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: ix–xiii.

Crocker, Thomas C., Jr. 1958. Soil depth affects windfirmness of longleaf pine. Journal of Forestry. 56(6):432.

Della–Bianca, Lino. 1990. Table mountain pine. In: Burns, Russell M.; Honkala, Barbara H., tech. coord. Silvics of North America: conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture: 425-432. Vol. 1.

Dickenson, James G.; Conner, Richard N.; Williamson, J. Howard. 1983. Snag retention increases bird use of a clear-cut. Journal of Wildlife Management. 47(3):799–804.

Duever, Michael J.; McCollum, Jean M. 1993. Hurricane Hugo effects on old–growth floodplain forest communities at Four Holes Swamp, South Carolina. In: Brissette, John C., ed. Proceedings of the seventh biennial southern silvicultural research conference; 1992 November 17–19; Mobile, AL. Gen. Tech. Rep. SO–93. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 197–202.

Foster, D.R. 1988. Species and stand response to catastrophic wind in central New England, U.S.A. Journal of Ecology. 76:135-151.

Franklin, Jerry F.; Waring, Richard H. 1980. Distinctive features of the northwestern coniferous forest: development, structure, and function. In: Waring, Richard H., ed. Forests: fresh perspectives from ecosystem analysis; proceedings, 40th biology colloquium (1979). Corvallis, OR: Oregon State University Press: 59–85.

Graham, Robert L.; Cromack, Kermit, Jr. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research. 12:511–521.

Gratkowski, H.J. 1956. Windthrow around staggered settings on old-growth Douglas–fir. Forest Science. 2(1):60–74.

Gresham, Charles A.; Williams, Thomas M.; Lipscomb, Donald J. 1991. Hurricane Hugo wind damage to southeastern U.S. Coastal Plain forest tree species. Biotropica. 23:420–426.

Harlow, Richard F.; Guynn, David C., Jr. 1983. Snag densities in managed stands of the South Carolina coastal plain. Southern Journal of Applied Forestry. 7(4):224–229.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research. 15:133–302.

Harmon, Mark E. 1982. Decomposition of standing dead trees in the Southern Appalachian Mountains. Oecologia. 52:214–215.

Hassinger, J.D.; Payne, J. 1988. Dead wood for wildlife. Sialia. 10(4):131–134.

Hedman, Craig W. 1992. Southern Appalachian riparian zones: their vegetative composition and contributions of large woody debris to streams. Clemson, SC: Department of Forest Resources, Clemson University. 146 p. Ph.D. dissertation.

Hook, Donald D.; Buford, Marilyn A.; Williams, Thomas M. 1991. Impact of Hurricane Hugo on the South Carolina coastal plain forest. Journal of Coastal Research. 8:291–300.

Hooper, Robert G.; McAdie, Colin J. [In press]. Hurricanes and the long-term management of the red-cockaded woodpecker. In: Proceedings of the third red-cockaded woodpecker symposium; 1993 January 25–28; Charleston, SC.

Kaarik, Aino A. 1974. Decomposition of wood. In: Dickson, C.H.; Pugh, G.J.E., eds. Biology of plant litter decomposition. London: Academic Press: p. 129–174, Chapter 5. 2 vol.

Lutz, H. J.; Chandler, R. F., Jr. 1955. Forest soils. New York: John Wiley & Sons. 514 p.

Mann, L.K.; Johnson, D.W.; West, D.C. [and others]. 1988. Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital, and regrowth. Forest Science. 34(2):412–428.

Maser, Chris; Anderson, Ralph G.; Cromack, Kermit, Jr.; [and others]. 1979. Dead and down woody material. In: Thomas, Jack Ward, tech. ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 78–95. Chapter 6.

Maser, Chris; Tarrant, Robert F.; Trappe, James M.; Franklin, Jerry F., eds. 1988. From the forest to the sea: a story of fallen trees. Gen. Tech. Rep. PNW-229. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 153 p.

Mattson, Kim G.; Swank, Wayne T.; Waide, Jack B. 1987. Decomposition of woody debris in a regenerating, clear–cut forest in the Southern Appalachians. Canadian Journal of Forest Research. 17:712–721.

McComb, William C.; Bonney, Stephen A.; Sheffield, Raymond M.; Cost, Noel D. 1986a. Den tree characteristics and abundance in Florida and South Carolina. Journal of Wildlife Management. 50(4):584–591.

McComb, William C.; Bonney, Stephen A.; Sheffield, Raymond M.; Cost, Noel D. 1986b. Snag resources in Florida—are they sufficient for large populations of cavity nesters? Wildlife Society Bulletin. 14:40–48.

McComb, William C.; Rumsey, Robert L. 1983. Characteristics of cavity nesting bird use of picloram–created snags in the central Appalachians. Southern Journal of Applied Forestry. 7(1):34–37.

Morris, Lawrence A.; Pritchett, William L; Swindel, Benee F. 1983. Displacement of nutrients into windrows during site preparation of a flatwood forest. Soil Science Society of America Journal. 47:591–594.

Muller, Robert N.; Liu, Yan. 1991. Coarse woody debris in an old–growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian Journal of Forest Research. 21:1567–1572.

Myers, Richard K.; Van Lear, David H.; Lloyd, F. Thomas. 1993. Estimation of above–ground biomass in a hurricane–impacted coastal plain forest. In: Brissette, John C., ed. Proceedings of the seventh biennial southern silvicultural research conference; 1992 November 17–19; Mobile, AL. Gen. Tech. Rep. SO–93. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 189–196.

Nix, Larry E.; Ruckelshaus, Tom A. 1991. Long–term effects of thinning on stem taper of old–field plantation loblolly pine in the Piedmont. In: Coleman, Sandra S.; Neary, Daniel G., comps. eds. Proceedings of the sixth biennial southern silvicultural research conference; 1990 October 30–November 1; Memphis, TN: Gen. Tech. Rep. SE–70. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 202–207.

Outcalt, Kenneth W.; Balmer, William E. 1983. Sand pine. In: Burns, Russell M., tech. comp. Silvicultural systems for the major forest types of the United States. Agric. Handb. 445. Washington, DC: U.S. Department of Agriculture: 170–171.

Phillips, Douglas R.; Sheffield, Robert M. 1984. The small timber resource in the Southeast. In: Proceedings, harvesting the South's small trees conference; 1983 April 18–20; Biloxi, MS. Madison, WI: Forest Products Research Society: 7–17.

Raphael, Martin G.; Morrison, Michael L. 1987. Decay and dynamics of snags in the Sierra Nevada, California. Forest Science. 33(3):774–783.

Robichaud, P.R.; Waldrop, T.A. 1992. Runoff and sediment production after site preparation burning. American Society of Agricultural Engineers. Res. Pap. 92–2517. St. Joseph, MI: American Society of Agricultural Engineers. 10 p.

Sabin, Guy R. 1991. Snag dynamics and utilization by wildlife in the upper Piedmont of South Carolina. Clemson, SC: Clemson University. 48 p. M.S. thesis.

Sanders, Bradford M.; Van Lear, David H. 1988. Photos for estimating residue loadings before and after burning in Southern Appalachian mixed pine-hardwood clearcuts. Gen. Tech. Rep. SE-49. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 21 p.

Sharitz, Rebecca R.; Boring, Lindsay R.; Van Lear, David H.; Pinder, John E., III. 1992. Integrating ecological concepts with natural resource management of southern forests. Ecological Applications. 2(3):226–237.

Sharitz, Rebecca R.; Vaitkus, Milda R.; Cook, Allen E. 1993. Hurricane damage to an old–growth floodplain forest in the Southeast. In: Brissette, John C., ed. Proceedings of the seventh biennial southern silvicultural research conference: 1992 November 17–19; Mobile AL. Gen. Tech. Rep. SO-93. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 203–210.

Skeen, James N.; Doerr, Phillip D.; Van Lear, David H. 1993. Oak-hickory–pine forests. In: Martin, William H.; Boyce, Stephen G.; Echternacht, Arthur C., eds. Biodiversity of the Southeastern United States–upland terrestrial communities. New York: John Wiley & Sons: 1–33. Chapter 1.

Smith, Robert N. 1991. Species composition, stand structure, and woody detrital dynamics associated with pine mortality in the Southern Appalachians. Athens, GA: University of Georgia. 163 p. M.S. thesis.

Sollins, P.; Grier, C.C.; McCorison, F.M.[and others]. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs. 50(3):261–285.

Spies, Thomas A.; Cline, Steven P. 1988. Coarse woody debris in forests and plantations of Coastal Oregon. In: Maser, Chris; Tarrant, Robert F.; Trappe, James M.; Franklin, Jerry F., tech. eds. From the forest to the sea: a story of fallen trees. Gen. Tech. Rep. PNW-229. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: Chapter 2.

Spies, Thomas A.; Franklin, Jerry F.; Thomas, Ted B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology. 69(6):1689–1712.

Toole, E. Richard. 1965. Deterioration of hardwood logging slash in the South. Tech. Bull. 1328. Washington, DC: U.S. Department of Agriculture. 27 p.

Touliatos, Plato; Roth, Elmer. 1971. Hurricanes and trees: ten lessons from Camille. Journal of Forestry. 69(5):285–289.

Van Lear, David H.; Waide, Jack B.; Teuke, Michael J. 1983. Biomass and nutrient content of a 41-year-old loblolly pine (*Pinus taeda* L.) plantation on a poor site in South Carolina. Forest Science. 30(2):395–404.

Wells, C.G.; Jorgensen, J.R. 1975. Nutrient cycling in loblolly pine plantations. In: Bernier, B.; Winget, C.H., eds. Forest soils and land management: Proceedings of the fourth North American forest soils conference; 1973 August; Laval University; Quebec: Les Presses de L'Universite Laval: 137–158. Chapter 9.