Ecology of Dead Wood in the Southeast

by Alexander M. Evans

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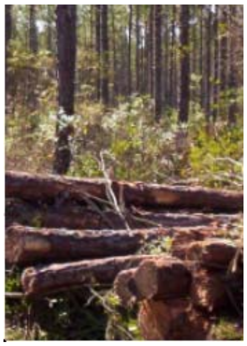

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1. Introduction

Although dead wood and decaying trees have historically had little commercial value, their ecological value is immense. This report reviews the scientific literature to provide the background necessary to craft recommendations about the amount and type of dead wood that should be retained in the forest types of the southeastern U.S. Establishing the ecological requirements for dead wood and other previously low-value material is important because of an increased interest in this material for energy and fuel. More intensive extraction of biomass from forests may affect a forest's ability to support wildlife, provide clean water, sequester carbon, and regenerate a diverse suite of plants.

This background paper covers the general topics of dead wood, water quality, nutrient conservation, and wildlife habitat in southeastern forests generally as well as in specific forest types, including southern Appalachian hardwoods, upland hardwood and mixed pine–hardwood forests, bottomland hardwoods, and piedmont and coastal plain pinelands. Complex issues related to carbon storage in forests and the climate impacts of using forest material for energy and fuel are important and deserve an in-depth investigation beyond the scope of this paper (e.g., Richter et al. 2009, Searchinger et al. 2009, Sathre et al. 2010). Similarly, this paper does not discuss the state of biomass harvesting in the U.S. (e.g., Evans 2008) or existing biomass harvesting guidelines (e.g., Evans et al. 2010, Janowiak and Webster 2010); these have been addressed in other recent publications. This report serves as a complement to *The Ecology of Dead Wood in the Northeast* (Evans and Kelty 2010).

The goal of this review is to provide a concise summary that can inform discussions about biomass harvesting standards in the Southeast. However, it is important to note that this document makes no suggestions about how a biomass harvest should be conducted or what should be left in the forest after a harvest. Rather, we have attempted to provide the basic science on which such recommendations can be built.

1a. Conventions and Conversions

Common names are presented in the body of the text, with scientific names listed in Appendix I. Appendix II provides an index of the location and physiographic province for site-specific, southeastern research referenced in this report. There is more scientific information available for some forest types than others; however, lack of research should not be confused with lack of importance. For example, there is little information published on dead wood in bottomland hardwood forests, but dead wood still plays a key ecological role in these forest types.

Measurements of dead wood are reported in mass, i.e., tons per acre (t/ac), and where necessary volume estimates have been converted to mass using bulk density estimates of 0.012 ton per cubic foot (t/ft^3) for softwoods and 0.016 t/ft^3 for hardwoods, or species-specific estimates of bulk density where possible (US Forest Service 1999, Woodall and Monleon 2008). All measurements reported in terms of tons per acre are from a single measurement, a snapshot in time. In contrast, rates (such as the additional DWM generated each year) are reported in terms of tons per acre per year (t/ac/yr). For readers not accustomed to visualizing mass of dead wood, the Natural Fuels Photo Series illustrates various levels of dead wood (http://depts.washington.edu/nwfire/dps/).

2. Ecology of Dead Wood in the Southeast

2a. Dead Wood and Stand Development

Dead wood is important not only in terms of total volume or mass in a stand, but also in terms of the sizes of individual pieces and the height of snags. Down dead wood is often separated into **coarse woody material (CWM)** and **fine woody material (FWM).** The USDA Forest Service defines CWM as down dead wood with a small-end diameter of at least 3 inches (7.6 cm) and a length of at least 3 feet (91 cm), and FWM as having a diameter of less than 3 inches (Woodall and Monleon 2008). Large-diameter snags or downed logs, usually logs greater than 12 inches (30 cm) in diameter, are a particularly important habitat for numerous animal species, persist for long periods, store nutrients, and provide substrate for seed germination. In this report, we use the term **downed woody material** (**DWM**) to encompass all three size classes of downed woody material (FWM, CWM, and large logs), but in some circumstances where the piece size is particularly important we discuss a specific size of material. Similarly, in some instances previous research has only reported quantities of CWM rather than that of all DWM. In such cases, we report the size class of material measured. It is also important to note that not all researchers use the same size class splits for CWM or FWM. For the purposes of this overview, the impact of different definitions for CWM or FWM is small.

The pattern of DWM accumulation over time is often referred to as U-shaped (Harmon et al. 1986, Sturtevant et al. 1997, Feller 2003, Martin et al. 2005, Brassard and Chen 2008). In naturally regenerating stands, large quantities of DWM are usually present at stand initiation as legacies of the previous stand. This legacy DWM decomposes as the stand ages, but new DWM is generated as trees and branches in the new stand die. The trough of the U-shaped pattern in intermediate-aged stands (i.e., the maturation stage) occurs when legacies from the previous stand have decayed, but the stand is still too young to experience much self-thinning or other causes of tree mortality (Franklin et al. 2002). As stands age and enter the vertical diversification stage (as described by Franklin et al 2002) or progress through the stem exclusion phase of stand development (Oliver and Larson 1996), competition and other causes of mortality create a new pulse of DWM. Tree size and the size of individual pieces of DWM also increase as trees age. The slower decomposition of these larger pieces coupled with increased mortality can create a second peak of DWM in old forests.


Meg Mobley

Accumulation of DWM in old stands is determined by site productivity, decomposition rates, and disturbances. Physical breakdown and biological decomposition remove DWM from forests over time (Harmon et al. 1986). The diameter of each piece, temperature of the site, amount of precipitation, and tree species all influence the rate of DWM decomposition (Zell et al. 2009). In general, conifers decay more slowly than deciduous species (Harmon 1982, Zell et al. 2009). Other factors that encourage decomposition include warmer temperatures, precipitation between 43 and 51 in/year (1,100 and 1,300 mm/year), and small-sized pieces (Zell et al. 2009). Although there is great variation across ecosystems and between individual pieces of CWM, in temperate forests log fragmentation generally appears to occur over 25 to 85 years in the U.S. (Harmon et al. 1986, Ganjegunte et al. 2004, Yamasaki and Leak 2006, Campbell and Laroque 2007).

In the southern Appalachian region, leaf litter decays at about 68% per year, FWM at about 19% per year, CWM from 8.3% to 11% per year, and snags from 3.6% to 11% per year depending on species (Harmon 1982, Mattson et al. 1987, Onega and Eickmeier 1991; please see Appendix II for a list of where these and the other studies referenced below took place). For instance, a detailed study of oak FWM in a clearcut in the Blue Ridge Mountains showed a range of decay rates from 5% to 18%, with high rates on a mesic site and lower rates on a xeric site (Abbott and Crossley 1982). A study of loblolly pine logging slash (CWM) on the South Carolina Piedmont showed decay at about 7% per year (Barber and van Lear 1984).

Meg Mobley

2b. Fire and Other Disturbances

Natural disturbances such as wind events, ice storms, and insect outbreaks add to the DWM pool. Hurricanes and other wind events can increase the mass of CWM almost eight times (Krauss et al. 2005, Cromer et al. 2007, Busing et al. 2009). Gulf Coast areas of southern Texas, Louisiana, south Florida, and eastern North Carolina are particularly prone to tropical cyclones (Zeng et al. 2009). Ice storms can have similar effects on CWM levels (Rebertus et al. 1997, McCarthy et al. 2006). Insect outbreaks can also create significant additions to the DWM pool. For example, a study of the southern Appalachian region revealed significantly higher DWM in plots that had been attacked by southern pine beetle (Waldrop et al. 2007). Non-native insects have the potential to alter natural cycles and patterns of DWM accumulation (McGee 2000, Gandhi and Herms 2010). In southern Appalachian forest, hemlock woolly adelgid is changing DWM patterns and decay rates in infested stands, at least in the short term (Nuckolls et al. 2009, Beane et al. 2010, Cobb 2010).

Unlike most other disturbances, fire has the potential to either increase the amount of DWM by killing trees or reduce the amount of existing DWM by burning it away. In most fires there is a combination of both processes, so the overall impact of fire on DWM is complex. Fire consumes more DWM when it burns during drier parts of the fire season and when the DWM is more decomposed (Skinner 1999). A key distinction in fire effects on DWM can be drawn between forests that experience frequent, low-intensity fires and those that experience long-interval, high-severity fires (Stephens et al. 2007). For example, fire in lodgepole pine forests, a high-severity fire regime, removed 16% of the DWM (Tinker and Knight 2000), whereas prescribed fire in a southeastern pine forest with a low-severity fire regime did not change DWM in comparison to unburned plots (Kilpatrick et al. 2010). The effects of fire are discussed for each forest type in Section 1.

Forest management is another type of disturbance, and harvests increase DWM when tops, limbs, small trees, or cull trees (i.e., slash) are retained on-site as a byproduct of removing more economically valuable material (e.g., saw timber). However, research from other forest types suggests that over the long term, managed forests typically have less DWM than unmanaged stands (Lesica et al. 1991, Duvall and Grigal 1999, Briggs et al. 2000, Gibb et al. 2005, Lõhmus and Lõhmus 2005). Harvests can also change the distribution of the DWM's decay classes and reduce its average piece size (Fraver et al. 2002, Stevenson et al. 2006). In some harvests, there is an economic incentive to remove the slash from the site. For example, harvests that supply woody biomass for energy production can harvest previously unmerchantable material (Evans and Finkral 2009, Benjamin et al. 2010). Some silvicultural prescriptions call for site preparation, i.e., piling, windrowing, or scalping to expose mineral soil, and such treatments can reduce DWM over large areas, especially if the material is burned (Robichaud and Waldrop 1994, Jurgensen et al. 1997).

2c. Climate Change

An emerging influence on dead wood in Southeastern forests is climate change. The annual average temperature has risen 2°F since 1970 in the Southeast, and is projected to increase by 4.5°F to 9°F by the 2080s (Karl et al. 2009). Precipitation in the region has decreased in the summer and winter and increased in during the fall since the mid 1970s (Karl et al. 2009). However, drought conditions have become more common during the last 40 years, a trend that is projected to continue (Karl et al. 2009).

In general, increased temperatures will increase the decay rate of DWM and thereby decrease average quantities. The additional carbon dioxide (CO_2) in the atmosphere may increase tree growth, but the increases may be limited by availability of water and nutrients, particularly nitrogen (N) (Nowak et al. 2004, Springer and Thomas 2007).

Along with increased CO_2 and temperature, global climate change may also cause an increase in disturbances such as insect outbreaks and storms, which in turn could change dead wood dynamics. A warming climate could increase southern pine beetle infestations from two to five times, depending on the climate change scenario (Gan 2004). Storm damage and flooding may increase because a greater proportion of precipitation is projected to occur as heavy rain events (Karl and Knight 1998, Knight and Davis 2009). Climate change is likely to increase the impact of hurricanes on southeastern forests because net hurricane power is highly correlated with tropical sea surface temperature (Emanuel 2005, Chambers et al. 2007). In the western U.S., climate change has been tied to an increase in wildfire activity (Westerling et al. 2006, Westerling and Bryant 2008). Warmer, drier conditions may increase wildfire activity in the Southeast as well.

W. Mark Ford

A model of the impacts of climate change and invasive species on the forests of the Cumberland Plateau suggests an overall decline in forest biomass by mid-century, followed by a recovery as species composition shifts (Dale et al. 2009). Because of the complex interactions between increased CO_2 concentrations, warming temperatures, precipitation, and disturbances, the net impact of climate change on southeastern forests is uncertain. Predicting dead wood quantities under an altered climate is not possible, in part because policy decisions and land manager responses will play a large role (Galik and Jackson 2009).

2d. Wildlife and Biodiversity

R. B. Forbes

Dead wood provides crucial habitat components for wildlife and accordingly is linked to biodiversity. In the southeastern U.S., more than 55 mammal species, more than 20 bird species, numerous reptiles, amphibians, arthropods, and gastropods rely on dead wood (Caldwell 1996, Johnston and D. A. Crossley 1996, Lanham and Guynn 1996, Loeb 1996, Whiles and Grubaugh 1996, Castro and Wise 2010). A recent meta-analysis of biomass harvest suggests that diversity and abundance of both cavity- and open-nesting birds declines in treatments with lower amounts of CWM or fewer snags (Riffell et al. 2011). However, the relationship between dead wood and animals in the Southeast is complex; therefore, Section 1 details research on the link between dead wood and animals for specific forest types.

In aquatic environments, DWM provides crucial refuge from predation (Angermeier and Karr 1984, Everett and Ruiz 1993). Logs that have fallen in the water form a critical component of aquatic habitat by ponding water, aerating streams, and storing sediments (Gurnell et al. 1995, Sass 2009). CWM in the streams of the Southeastern Coastal Plain facilitates taxonomic diversity, increases invertebrate biomass, and supplies food resources for higher trophic levels (Wallace et al. 1996). CWM in the high-gradient streams of the southern Appalachians promotes habitat heterogeneity, increases resource availability, and retards down-wasting of the stream bed (Wallace et al. 1996). Additions of large wood material to Appalachian streams appears to increase brook trout densities (Sweka and Hartman 2006). DWM can also be buried for more than 1,000 years in the sediments of stream channels and therefore provide long-term carbon storage (Guyette et al. 2002).

DWM is a key element in maintaining habitat for saproxylic insects (Grove 2002). For example, some specialist litter-dwelling fauna that depend on DWM appear to have been extirpated from some managed forests (Kappes et al. 2009). A study from a northern hardwood forest in Ontario suggests that overall insect abundance was not correlated with the volume of DWM, though abundance of the fungivorous insect guild was positively related to the volume of DWM (Vanderwel et al. 2006). Extensive removal of CWM may reduce species richness of ground-active beetles at a local scale (Gunnarsson et al. 2004). Because of the potential negative impacts of DWM reductions on arthropods, a minimum of 4 t/ac (9 Mg/ha; 286 ft^3/ac or 20 m^3/ha) of DWM has been suggested to protect litter-dwelling fauna in Europe (Kappes et al. 2009).

Dead logs serve as a seedbed for tree and plant species (Lemon 1945, McGee 2001, Weaver et al. 2009). For example, yellow birch in cove hardwood stands in North Georgia preferentially grows on downed logs (Chafin and Jones 1989). Slash can be beneficial to seedling regeneration after harvest (Grisez 1960, McInnis and Roberts 1994). Fungi, mosses, and liverworts depend on dead wood for nutrients and moisture; in turn, many trees are reliant on mutualistic relationships with ectomycorrhizal fungi (Hagan and Grove 1999, Åström et al. 2005). In general, small trees and branches tend to host more species of fungus per volume unit than larger trees and logs; however, larger dead logs may be necessary to ensure the survival of specialized fungus species such as heart rot agents (Kruys and Jonsson 1999, Bate et al. 2004).

2e. Soil Productivity


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In some ecosystems, DWM represents a large pool of nutrients and is an important contributor to soil organic material (Graham and Cromack Jr. 1982, Harvey et al. 1987). In general, needles and leaves have a higher concentration of nutrients than tree boles or branches. In many ecosystems, CWM decomposes much more slowly than foliage and FWM, making it a long-term source of nutrients (Harmon et al. 1986, Johnson and Curtis 2001, Greenberg 2002, Mahendrappa et al. 2006). Although DWM is often low in N itself, N fixation in DWM is an important source of this limiting nutrient in both terrestrial and aquatic ecosystems (Harmon et al. 1986). In temperate forests, non-symbiotic N fixation ranges from 1.8 to 2.7 pounds per acre per year (2 to 3 kg/ha/year) (Roskoski 1980, Son 2001).

In northeastern forests, a review of scientific data suggests that when sensitive sites (including low-nutrient sites) are avoided and clearcutting with whole-tree removal is not used, on-site nutrient capital can be protected (Hacker 2005, Campbell et al. 2007, Evans and Kelty 2010). Whole-tree clearcutting (or whole-tree thinning, e.g., Nord-Larsen 2002) did not greatly reduce amounts of soil carbon (C) or N in some studies (Hornbeck et al. 1986, Hendrickson 1988, Huntington and Ryan 1990, Lynch and Corbett 1991, Olsson et al. 1996, Johnson and Todd 1998). Lack of significant reduction in C and N may be due to soil mixing by harvesting equipment (Huntington and Ryan 1990). However, in the Northeast, clearcutting with whole-tree removal that leaves less DWM on-site can result in significant nutrient losses (Tritton et al. 1987, Hendrickson 1988, Federer et al. 1989, Hornbeck et al. 1990, Martin et al. 2000, Watmough and Dillon 2003).

In the Southeastern pines stands, nitrogen (N) and phosphorus (P) are the nutrients that most commonly limit growth and P deficiency can be particularly severe on wet clay soils in the lower Coastal Plain and on some well-drained soil in the upper Coastal Plain (Fox et al. 2007). A key element in understanding soil productivity is past land use. Large areas of the Southeast, particularly in the Piedmont physiographic province, were almost completely cleared for agriculture by 1860, and by the 1930s a significant proportion of the soil fertility had been lost to erosion (Walker 1980). With the loss of soil fertility, and even the topsoil itself in some cases, agricultural lands were abandoned and allowed to return to forest cover (either through old-field succession or planting). Soil properties and processes develop differently depending on the overstory, e.g., pine or hardwood (Scott and Messina 2009). Soil organic material builds up rapidly during the first 50 years of forest development (Switzer et al. 1979). During forest regrowth, most carbon storage occurs in the organic horizon (~20%), with significantly less accumulation (<1%) in the mineral soil (Richter et al. 1999). However, these old-field forests are different from pre-settlement forests, in part because of reduced nutrient availability. A legacy of intensive agriculture can reduce diversity of herbaceous species decades after conversion to forest cover (Hedman et al. 2000, Dupouey et al. 2002). Similarly, invasive plants were more common in areas reforested after 1940 than in undisturbed sites in western North Carolina (Kuhman et al. 2010). Though significantly different from the original native forests, modern plantations can support plant species diversity (Jeffries et al. 2010).

As with agriculture, timber harvests in southeastern forests have the potential to deplete exchangeable calcium (Ca) and magnesium (Mg) in upper soil layers in the absence of fertilization (Richter et al. 1994). Results from the North American Long-Term Soil Productivity Study suggest harvests that remove tree branches and foliage can have negative impacts on long-term soil productivity (Scott et al. 2004). In 8 out of 10 study sites whole-tree harvesting resulted in an average of a 27% reduction in growth when compared to stem-only harvesting treatments (Scott and Dean 2006). Federer and colleagues (1989) estimate that leaching and three whole-tree harvests over 120 years could remove 46% and 59% of the Ca from soils in a southeastern hardwood and pine stand respectively. In a mixed pine-hardwood stand on the upper piedmont of Georgia whole-tree harvest removed 36, 24, and 71 percent of the total site pool of P, potassium (K), and Ca respectively (McMinn and Nutter 1983) and had a negative impact on pine regeneration (McMinn 1985). In a loblolly pine plantation whole tree harvesting doubled the nutrient removal compared to a bole-only harvest (Jorgensen et al. 1975, Phillips and Van Lear 1984). Whole tree harvesting in an upland mixed oak forest in eastern Tennessee were about three times greater than a bole-only harvest (Johnson et al. 1982, Phillips and Van Lear 1984). Similarly, measurements from Coweeta Hydrologic Lab in North Carolina show that over 17 years a sawlog harvest using cable-yarding did not adversely impact soil cation concentrations (Knoepp and Swank 1997). A watershed study from the Coweeta showed that FWM helped conserve nutrients after a clearcut (Abbott and Crossley 1982). In a mixed pine stand, time since clearcut harvest had little effect on soil pH, C, or N, which suggests little impact on these soil parameters from the harvest (Archer et al. 2007). Elimination of understory plants in pine plantations reduces soil C storage even when fertilizer is applied (Shan et al. 2001). However, thinning can increase soil C storage, perhaps because of the decomposition of the roots of harvested trees (Selig et al. 2008).

Nate Wilson

Low-impact logging techniques that reduce soil disturbance, such as directional felling or use of slash to reduce rutting and compaction, can help protect nutrient capital (Hallett and Hornbeck 2000). Similarly, retention of slash can protect soils from compact, particularly when soils are wet (McDonald and Sexias 1997, Han et al. 2006). In hardwood forests, harvesting during the winter after leaf fall can reduce nutrient loss by 10% to 20% (Boyle et al. 1973, Hallett and Hornbeck 2000). A study in a mixed pine-hardwood stand on the upper piedmont of Georgia there was a significant increase in nutrient removal during a summer harvest versus a winter harvest (McMinn and Nutter 1983). Alternatively, if logging occurs during spring or summer, leaving tree tops on-site facilitates nutrient conservation. Nordic countries have demonstrated that leaving cut trees on the ground in the harvest area until their needles have dropped (one growing season) can also reduce nutrient loss (Nord-Larsen 2002, Richardson et al. 2002). However, there are concerns about the buildup of forest pests, such as engraver beetles, in cut trees left on-site (Connor and Wilkinson 1983).

2f. Water Quality and Supply

Nationally, two-thirds of the freshwater supply is filtered through forests (Smail and Lewis 2009). However, there is little information on how DWM affects water quality and supply. In general, DWM adds to erosion protection by reducing overland flow in forests (McIver and Starr 2001, Jia-bing et al. 2005). In the southern Appalachian forests, high-severity fires that consume large percentages of DWM can increase sediment yields 40 times over low-severity fires (Robichaud and Waldrop 1994). DWM also has substantial water-holding capacity (Fraver et al. 2002). DWM plays an important role in riparian systems by providing sites for vegetation colonization, forest island growth and coalescence, and forest floodplain development (Fetherston et al. 1995, Sharitz 1996). During high flows that inundate the forest, DWM creates jams that are important refugia for many aquatic species (Bragg and Kershner 1999).


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In general, second-growth or intensively managed forests provide fewer large dead trees to riparian systems than older forests, because intensive management tends to remove trees that would become large dead trees (Harmon et al. 1986, Bragg and Kershner 1999). A comparison showed that streams in the Great Smoky Mountains flowing through old-growth stands had more DWM, which trapped 25 times more sediment than stands logged 80 years ago (Hart 2003).

2g. Quantities of Dead Wood

DWM and snags make up about 5% of the biomass in southeastern pine forest ecosystems and about 6% of oak-hickory forests (Figure 1) (EPA 2010 Table A-216). Although DWM quantities differ by forest type and age, at the regional level DWM tends to increase with stand basal area (Kilpatrick et al. 2010) and is greater on mesic sites than on xeric ridge tops (Van Lear and Waldrop 1994, Vose et al. 1999, Stottlemyer et al. 2009).

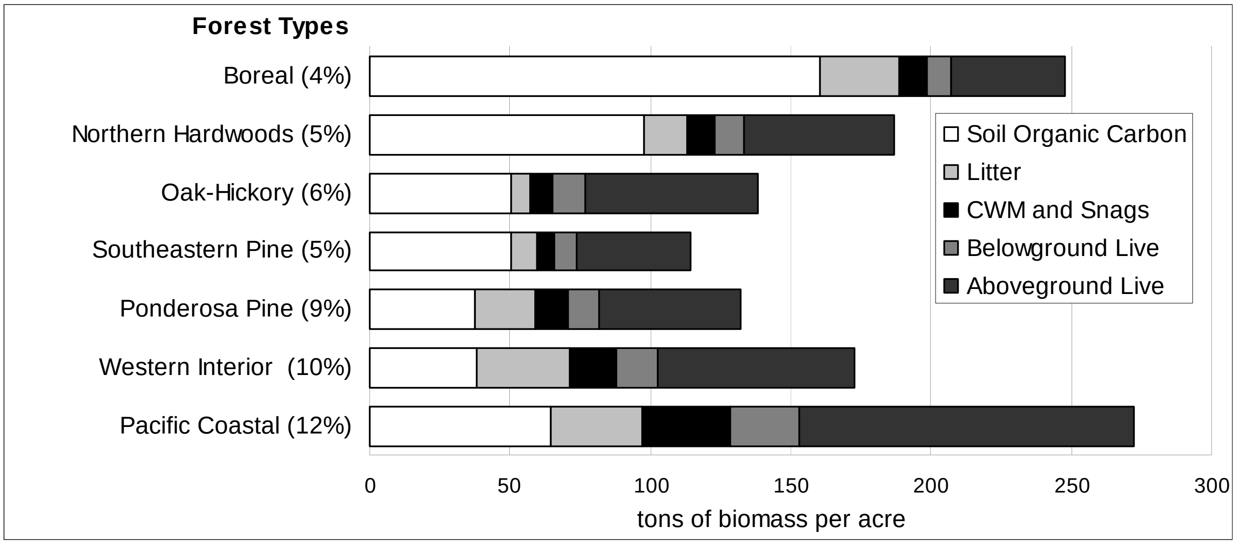

Figure 1 Estimates of biomass by forest type per acre, with percentage made up by CWM and snags in parentheses (EPA 2010 Table A-211)

Looking solely at CWM, estimates of regional means range from 0.4 to 6.3 t/ac (0.9 to 14 Mg/ha) for the nation and from 0.4 and 2 t/ac (0.9 to 4.5 Mg/ha) for the Southeast (Woodall and Liknes 2008). Generally, the Southeast has much less DWM that other parts of the country.

3. Research by Forest Type

The following section uses the best available scientific literature to examine the dead wood dynamics of specific forest types in the Southeast. Figure 2 shows a general picture of the physiographic provinces discussed in this section. The map is redrawn from the USDA Forest Service’s EcoMap (Cleland et al. 2007) but includes bottomland hardwood forests (redrawn from Hodges 1995). It exaggerates the area of bottomland hardwood forests because of its scale. Forest types do not match physiographic provinces exactly, and many forest types can occur in each physiographic province. For example, the mixed pine–hardwood stands described in section 3b occur throughout the region and are not shown explicitly in Figure 2.

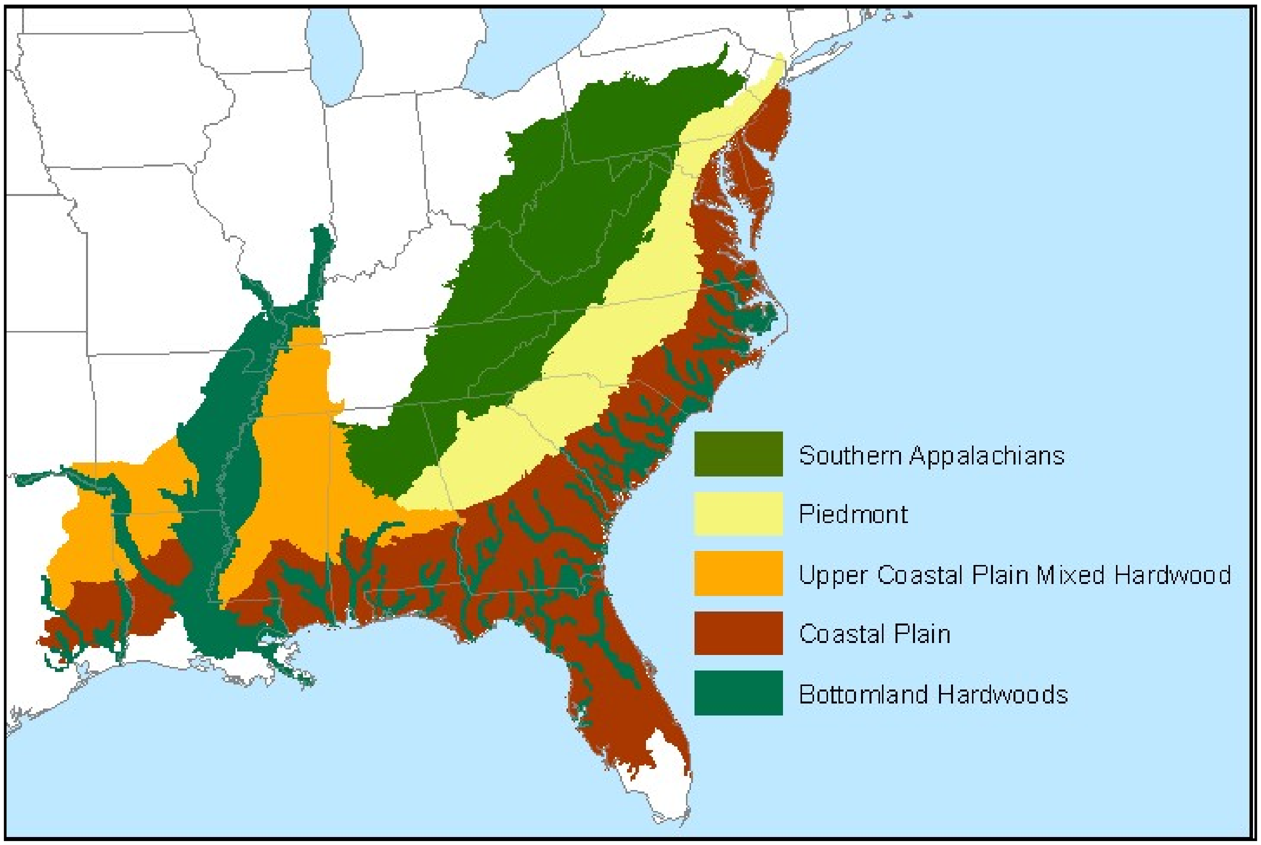

Figure 2 Map of physiographic provinces, with bottomland hardwood areas superimposed. Province data from Cleland et al. 2007 and bottomland hardwood data from Hodges 1995

3a. Southern Appalachian Hardwoods

The forests of the southern Appalachians cover four provinces: the Appalachian Plateau, the Ridge and Valley, the Blue Ridge, and the Piedmont Plateau (Smith and Linnartz 1980). This section focuses on the southeastern portion of the mixed mesophytic forests and the mixed oak forests (Smith and Linnartz 1980). These forests have been refugia for a wide range of taxa during dry glacial epochs; this has resulted in a particularly diverse forest (Loucks et al. 1999). Southern Appalachian forests contain a variety of magnolias, oaks, hickories, elms, birches, ashes, basswood, maples, black locust, and pines, as well as black walnut, tulip-poplar, blackgum, hemlocks, black cherry, and beech (Loucks et al. 1999). Natural stand replacing disturbances have long return intervals, on the order of 400 to 500 years (Lorimer 1980). Though in some xeric pine and oak stands disturbance regime were characterized by frequent surface fires and occasional severe fires which opened growing space for pine recruitment (Aldrich et al. 2010).

As discussed earlier, DWM generally follows a U-shape pattern as southern Appalachian stands develop (Van Lear and Waldrop 1994). Figure 3 shows the measurements of CWM for stands that range from 3 to 41 t/ac (6.7 to 92 Mg/ha) in North Carolina, Tennessee, West Virginia, and Kentucky (Mattson et al. 1987, Muller and Liu 1991, Onega and Eickmeier 1991, Dodds and Smallidge 1999, Adams et al. 2003, Muller 2003, Busing 2005, Webster and Jenkins 2005, Loucks et al. 2008). The old-growth category includes measurements from stands identified as old-growth by the scientific publication in which the measurements appear. A review of forest inventory plots across four southern Appalachian states estimated the mean mass of CWM at 2.0 t/ac (4.4 Mg/ha), FWM at 3.3 t/ac (7.4 Mg/ha), and duff and litter at 8 t/ac (18 Mg/ha) (Chojnacky and Schuler 2004). Research from other regions suggests that CWM continues to accumulate as stands age from 200 to 400 years old (Tyrrell and Crow 1994). In general for the southern Appalachian forests, mesic sites tend to have more CWM than xeric or intermediate sites (Stottlemyer et al. 2009). For example, a simulation based on data from the Cumberland Plateau in Tennessee estimated clearcutting would generate 22 t/ac (49 Mg/ha) of slash on a xeric site and 31 t/ac (69 Mg/ha) on a mesic site (Van Lear and Waldrop 1994).

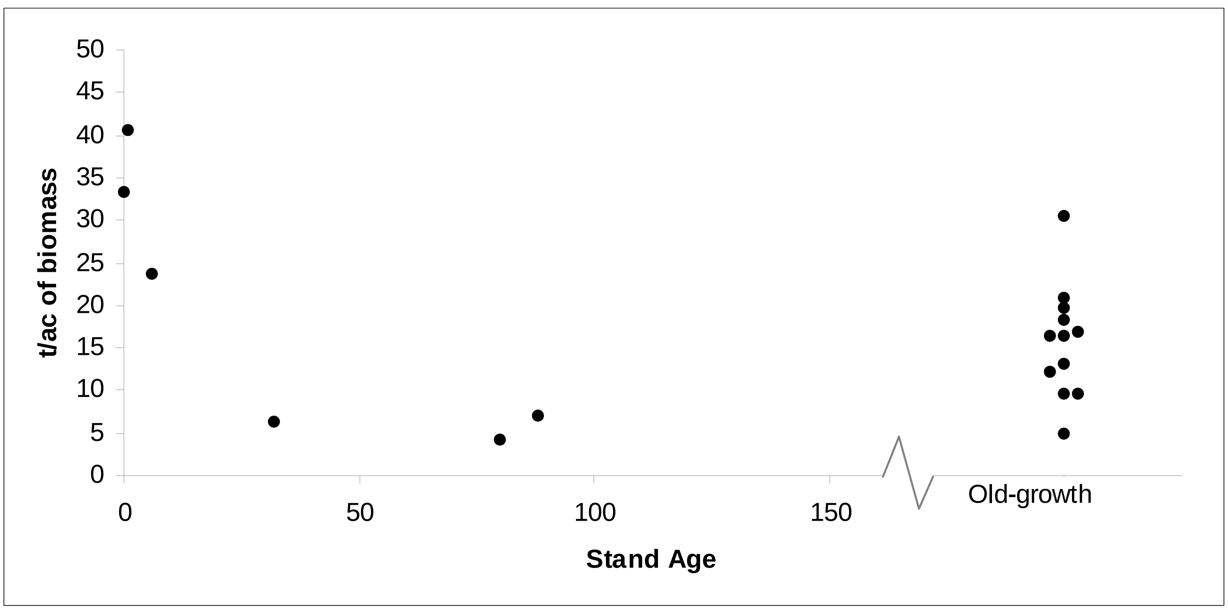

Figure 3 Relationships between CWM quantities and stand age based on several studies in southern Appalachian hardwood forests

Annual inputs of CWM in the southern Appalachian forests range from 0.25 to 7.1 t/ac/yr (0.6 to 16 Mg/ha/yr), with an average of about 1.8 t/ac/yr (4.0 Mg/ha/yr) (Onega and Eickmeier 1991, Busing 2005). Two windstorms in a West Virginia forest only added about 0.8 t/ac (1.8 Mg/ha) each (Adams et al. 2003). A study of old-growth forest in the Great Smoky Mountains suggests that CWM patterns can take more than a century after human disturbance to return to patterns found in old-growth stands (Webster and Jenkins 2005).

In the Great Smoky Mountains, the rate of snag formation is about 0.6 snags per ac (1.4 per ha) for trees greater than 4 in (10 cm) DBH (Busing 2005). Regionally, the number of snags ranges from 17 to 53 snags per acre (≥4 in; 43 to 132 per ha) (McComb and Muller 1983, Graves et al. 2000, Webster and Jenkins 2005, Greenberg et al. 2006). Large snags (>20 in or >50 cm DBH) are less common—2 snags per ac (5 per ha) in one study (Busing 2005).

As mentioned above, CWM in riparian systems, particularly large pieces, plays an important role in trapping sediment in high-gradient Appalachian streams (Hart 2003). Other studies suggest that 50 ft (15 m) riparian zones may not be effective in maintaining sufficient CWM recruitment for streams (McClure et al. 2004). Based on vegetation, DWM, nutrients, and microclimatic conditions, ecological transitions that separate riparian from upland conditions tend to occur between 33 to 66 ft (10 to 20 m) from southern Appalachian headwater streams (Clinton et al. 2010).

Management and Fire

In the southern Appalachian forests, thinning treatments can reduce the number of snags, the number of potential large snags, and live decaying trees (Graves et al. 2000), though some thinnings have little impact on snags (e.g., an understory removal Greenberg et al. 2006). A 35-year-old hardwood stand on the Cumberland Plateau had a similar number of snags (>9 in) as an uncut control stand (McComb and Muller 1983). However, the combination of thinning and burning can create more snags and CWM (Greenberg et al. 2006, Campbell et al. 2008, Waldrop et al. 2008). Prescribed fire alone does not have a significant effect on DWM (Greenberg et al. 2006, Loucks et al. 2008). Fire can reduce the N pool in CWM, though the reduction is small enough to be replaced by atmospheric deposition in less than ten years (Hubbard et al. 2004).

Ken Smith

Wildlife

Numerous researchers have noted that many animals in the southern Appalachians use snags and DWM. Snags are a crucial habitat element for numerous animals, including woodpecker and bats (Graves et al. 2000, Johnson et al. 2009). Most small mammals, including shrews, red-backed voles, woodland jumping mice, deer mice, and white-footed mice, are associated with CWM, particularly large pieces (Menzel et al. 1999, Ford et al. 2002, Greenberg 2002, Kaminski et al. 2009). Similarly, woodland salamander captures increase near large pieces of CWM (Maidens et al. 1998). In the Ozarks, CWM plays an important role in protecting woodland salamanders from desiccation in clearcuts (Rittenhouse et al. 2008). Ruffed grouse nest sites are more common and more successful in stands with high basal areas and with around 20% cover of CWM (Tirpak et al. 2006, Tirpak et al. 2010). In contrast, habitat for some reptiles is better in more open environments and is not associated with CWM (Greenberg 2001).

In the southern Appalachians, reductions of FWM and CWM affect microarthropods such as oribatid mites and collembolans (Abbott and Crossley 1982). In one study, the densities of total litter microarthropods remained 28% lower eight years after the clearcut (Blair and Crossley 1988). Thinning or burning in isolation have little effect on Coleoptera insect species, but the increase of DWM from combined thinning and burning can benefit them (Campbell et al. 2008). Similarly, understory removal for fuel reduction has little effect on white-footed mice in the southern Appalachians (Greenberg et al. 2006). Low-intensity prescribed fire appears to have no significant effect on many small mammals or herpetofauna (Ford et al. 1999, Ford et al. 2010). However, the more intense prescribed fires that result from heavy fuel loading can decrease shrew and salamander abundance and increase lizard abundance (Matthews et al. 2009, 2010). In West Virginia, the northern bat (a species of concern) and the endangered Indiana bat readily exploit snags created by the reintroduction of fire (Johnson et al. 2009, Johnson et al. 2010). Woodpeckers have been documented nesting in snags in oak-hickory clear cuts in Virginia (Conner et al. 1975) and Ohio (Petit et al. 1985). One review of cavity nesting bird habitat oak-hickory forests suggested 10 to 12 cull trees be left after a regeneration harvest for habitat (Hardin and Evans 1977), while another emphasized that the characteristics of snags, such as large size and rough bark, matter (Brawn et al. 1982).

3b. Upland Hardwoods and Mixed Pine–Hardwoods

Mixed pine and oak forests of the Southeast are found in the Piedmont Plateau province from central Alabama to Virginia, as well as on the Atlantic and Gulf Coastal Plains (Smith and Linnartz 1980). Stands of mixed pine–hardwoods are found in the Ridge and Valley province of the southern Appalachians in West Virginia, Virginia, and Tennessee, as well as in the southern portion of the Cumberland Plateau. Though they are somewhat related, this report does not cover the mixed pine–hardwood forests of the Ozark Plateau and Ouachita Mountains. In mixed pine–hardwood forests, white oak, red maple, red oak, and hickory mix with loblolly, shortleaf, Virginia, and longleaf pine (Smith and Linnartz 1980). Fire is a key disturbance in mixed pine–hardwood forests, and can facilitate regeneration of shade-intolerant species such as pine and oak (Bragg 2004). A history of poor logging practices, land clearing, fire suppression and insect outbreaks has left many southeastern pine–hardwood forests in a degraded condition (i.e., with altered species composition) (Hubbard et al. 2004).


Don Bragg

In one study actively managed, hardwood and pine–hardwood second-growth forests in Virginia had 12 and 16 t/ac (36 Mg/ha) of DWM (Applegate 2008). In these stands, CWM made up about 78% of the total mass (Applegate 2008). In North Carolina, measures of CWM in mixed pine–hardwoods include 3 t/ac (7 Mg/ha) (Busing et al. 2009), 7 t/ac (16 Mg/ha) (Vose et al. 1999), and 13 t/ac (30 Mg/ha). A study of an old-field stand of loblolly and shortleaf pine measured 4.5 t/ac (10 Mg/ha) at about 90 year old (Bragg and Heitzman 2009). In contrast, an old-growth pine–hardwood stand in Arkansas had about 29 t/ac (66 Mg/ha) (Bragg 2004), and one on the South Carolina Piedmont had about 15 t/ac (35 Mg/ha) (White and Lloyd 1994). Disturbances such as hurricanes significantly increase CWM, by as much as eightfold (Busing et al. 2009), providing an initial pulse of DWM early in stand development. The amount of DWM also generally increases from ridge to valley (Vose et al. 1999). There is little information available on the impact of forest management on DWM in mixed pine–hardwood stands. However, a study on the North Carolina Piedmont showed that where satellite chip mills influenced harvesting, less DWM was left on-site (Hess and Zimmerman 2000).

A survey revealed about 11 and 14 snags per ac (≥4 in; 28 and 36 per ha) in pine-hardwood and upland hardwood stands, respectively, on the South Carolina Piedmont (Moorman et al. 1999). Carmichael and Guynn (1983) report slightly higher numbers for another study in South Carolina. An old-growth mixed pine–hardwood stand, also on the Piedmont, had about 41 snags per ac (≥4 in; 101 per ha), of which 20% were greater than 20 in (50 cm) (White and Lloyd 1994). Recruitment rate for pine–hardwoods and upland hardwoods were 2.6 and 2.3 snags per ac per year respectively (6.4 and 5.6 snags/ha/yr) (Moorman et al. 1999). Between 21% (Moorman et al. 1999) and about 50% (Cain 1996) of the hardwood snags in these forests remained standing after 5 years. As with other forest types, snags in mixed pine–hardwood stands are important for woodpeckers, bats, and cavity nesting birds (Dickson et al. 1983, Shackelford and Conner 1997, Perry and Thill 2008). For example, in a large clearcut in a mixed loblolly-hardwood stand in east Texas at least two 2 snags per acre increased bird density and diversity (Dickson et al. 1983).

3c. Bottomland Hardwoods

Throughout the Southeast, bottomland hardwood forests cover stream bottoms and terraces of the Coastal Plain province (Hodges 1995). Bottomland hardwood forests occupy a transition zone between drier upland forests and wetland forests and swamps. Water and gradients of flooding (from perennially wet to rarely flooded) help determine the arrangement of species, including maple, elm, sycamore, ash, cottonwood, sweet gum, and oaks (Smith and Linnartz 1980). Flooding and windstorms are the major disturbances in bottomland hardwood forests (Smith and Linnartz 1980, King and Antrobus 2001). However, recent science suggests that, historically fire played an occasional but important role in these ecosystems (Gagnon 2009). The expansion of agriculture and river channelization has reduced the area covered by bottomland hardwood forests significantly over the last century (King et al. 2005).

Brian Lockhart

After Hurricane Hugo, bottomland hardwood forests measured in South Carolina had from 34 to 86 t/ac (77 to 192 Mg/ha) (Cromer et al. 2007). Without major disturbance, DWM inputs to bottomland hardwood forest are on the order of 1.3 t/ac/yr (2.9 Mg/ha/yr) (Gentry and Whitford 1982). In general, the warm and wet conditions typical of these forests result in both productive stands and relatively rapid decomposition rates, which cause high turnover rates of DWM. Floodwaters also impact DWM by breaking snags and moving DWM. The movement of DWM is determined in part by piece size, and may cause accumulations on ridges (Brian Lockhart, USDA Forest Service, personal communication).

Logging slash left in gaps of a bottomland hardwood forest decayed in less than 6 years (Ulyshen et al. 2004). Bottomland hardwood forests in the Savannah River Site had only 2.3 lb/ac (2.6 kg/ha) of DWM (Giese et al. 2003). One study of snags in bottomland hardwoods recorded 5.3 snags (≥4 inches) per ac (13 per ha) (Lockhart et al. 2010) while another found 1.2 to 4.5 per ac (3 to 11 per ha) (McComb et al. 1986). The same study suggests selection harvests have minimal impact on snags in a bottomland hardwood stand, at least in the short term (Lockhart et al. 2010). Recent recommendations for maintaining wildlife habitat in the Mississippi Alluvial Valley include the retention of some cavity trees (small and large) as well as either dead or stressed trees, or both, to provide DWM, and set as a goal the retention of an average of more than 3.2 t/ac (200 ft^3/ac; 14 m^3/ha or 7.1 Mg/ha) (Wilson et al. 2007).

Bottomland hardwood forests are particularly productive habitats for animals ranging from beetles to black bears (Smith and Linnartz 1980, Rudis and Tansey 1995, Ulyshen et al. 2004). Shrew captures have been linked to CWM cover, CWM volume, and extent of CWM decay (Cromer et al. 2007). Amphibians, such as eastern narrowmouth toads, also are associated with DWM (Moseley et al. 2003). Snags in bottomland hardwood forests, particularly large-diameter oak snags, are important habitat for woodpeckers (Conner et al. 1994, Shackelford and Conner 1997). Because of the importance of water and flooding in bottomland hardwoods, DWM's role in trapping sediment and providing sites for regeneration is crucial (Sharitz 1996). DWM also may provide short-term retention of inorganic N associated with floodwater (Rice et al. 1997).

Brad Glorioso – USGS

3d. Piedmont and Coastal Plain Pinelands

The pine-dominated forests of the Southeast include loblolly, shortleaf, slash, longleaf, and other pines. Before European contact, much of the coastal plain was covered by longleaf pine, and low- to moderate-intensity fires were frequent (Van Lear et al. 2005). Sections of the Piedmont province with soils derived from sandstone or granitic rocks were also dominated by pines before European contact—mainly shortleaf pine in Virginia and North Carolina and loblolly pine in South Carolina and Georgia (Walker 1995). Much of the area originally covered by pine forests and converted to agriculture has now returned to pine forests. Forests on former agricultural lands generally have much less DWM than areas that have been continuously forested (Lõhmus and Lõhmus 2005, Bragg and Heitzman 2009). The reduced amount of DWM on former agricultural lands reflects in part the importance of the pulse of DWM from the disturbance that initiates a new stand.

Pine plantations

Many southeastern pine forests are intensively managed plantations. While many forests have naturally regenerated to pine as well, this review focuses on planted pine stands because of their prevalence and because they are the focus of more scientific effort. Nonetheless, the paragraphs below that discuss disturbance and wildlife are relevant to pine forests of the Southeast both planted and naturally regenerated.

Plantations have relatively low accumulations of DWM because sites are cleared before planting, rotations are relatively short, and there is a strong financial incentive to capture mortality through harvest rather than leave dead trees to become DWM (Johnston and Crossley 2002, Carnus et al. 2006). While in some areas, such as the western Gulf Coastal Plain, large amounts of slash are often left on-site after harvest, most of this material decays within the first five to ten years (personal communication Don Bragg, USDA Forest Service). For the same reasons, southeastern pine plantations typically have low numbers of snags. For example, plantations in South Carolina have 8.2 snags per ac (20 per ha) and a recruitment rate of 1.9 snags per acre per year (4.7 snags/ha/yr), which is about 72% of comparable natural forest stands (Moorman et al. 1999). About 50% of snags from a given year fall after three to four years (Moorman et al. 1999, Edwards 2004). International surveys indicate that about 1 t/ac (2.2 Mg/ha) of DWM is common for plantations; this DWM tends to be made up of small pieces (Tobin et al. 2007, Brin et al. 2008). Similarly, pine plantations in Georgia and South Carolina have 1 t/ac and 1.6 t/ac (2.2 and 3.6 Mg/ha), while natural pine forests in those states have nearly 4 and 2.5 times that much DWM, respectively (McMinn and Hardt 1996). Though other studies report average CWM amounts as high as 3.8 t/ac (8.4 Mg/ha) in loblolly pine plantations (Parresol et al. 2006). A survey across the Southeast shows that loblolly pine plantations do not reach 1 t/ac (2.2 Mg/ha) of DWM until about 30 to 35 years of age (Van Lear 1996, Radtke et al. 2004). In one longleaf pine plantation, only about 0.4 t/ac (0.8 Mg/ha) of CWM was added annually (Gentry and Whitford 1982)

Nathan McClure

Disturbance

Disturbance agents such as southern pine beetles, wildfire, ice storms, and wind events can create large quantities of DWM in southeastern pine forests. Loblolly pine is most susceptible to bark beetle attack, slash pine is more resistant, and longleaf pine is the most resistant. However, in areas of intensive management, downed trees are salvage logged (Loeb 1999). Fire is a natural part of the disturbance regime in southeastern pine forests and continues to play an important role, often as prescribed fire in plantations. Depending on fire intensity, DWM may increase after prescribed fire, beginning as early as two years after the burn as snags begin falling (Greenberg 2003). While prescribed fire and mechanical thinning both increased DWM by about 42% in one study , the combination of mechanical thinning followed by burning reduce DWM by 30% (Kilpatrick et al. 2010). In Arkansas, burning again reduced CWM by 30%, and after about 20 years soil nutrient availability in burned stands appears to be greater or similar to unburned stands (Liechty et al. 2004). In longleaf pine, burning did not significantly change CWM, which averaged about 2 t/ac (4.6 Mg/ha) (Hanula et al. 2009).

Wildlife

As in other forest types, DWM is important to wildlife in the pinelands of the Southeast, including wildlife in planted stands (Jones et al. 2009). In general, arthropods are more abundant near dead wood than away from it (Ulyshen and Hanula 2009a). One study found 27 orders and 172 families of arthropods on the ground near CWM and 20 arthropod orders on tree boles (Horn and Hanula 2008). Many small mammals, including golden mouse, cotton mouse, white-footed mouse, and cotton rat, are associated with CWM, particularly large logs and stumps (Loeb 1996, Loeb 1999, McCay 2000, Mengak and Guynn 2003, Hinkelman and Loeb 2007). Of course CWM is not a universal habitat benefit; in fact, snake, turtle, and lizard abundance can decrease as CWM volume and forest floor depth increase (Kilpatrick et al. 2010). Herpetofauna of the southeastern Coastal Plain do not respond strongly to CWM, perhaps because of the importance of burrows and litter layer for these animals (Rothermel and Luhring 2005, Owens et al. 2008, Todd and Andrews 2008, Davis et al. 2010). For example, the litter layer may be more important than CWM for food collection for toads (Moseley et al. 2005). Common kingsnakes that use burrows for refuge sites but are more often found in sites with more CWM may be a specific example of the synergy between litter, burrows, and CWM for herpetofauna (Steen et al. 2010). For mole salamanders, removal of pine litter had a strong negative impact, but CWM removal had little effect (Moseley et al. 2004).


James Bettaso

Although many studies have measured an association between wildlife and DWM, the impact of DWM removal, particularly CWM, on wildlife populations remains a subject of scientific debate. Horn and Hanula (2008) noted that CWM removal negatively affects arthropod abundance on trees, reducing their availability for bark-foraging birds. Bole-only harvests appear to have less impact on arthropod diversity than whole-tree harvesting, but the difference between harvesting methods did not persist into the second year (Bird et al. 2000). CWM manipulations did not change total ground-dwelling arthropod abundance, richness, diversity, or composition, but ground beetle species richness and diversity increased when CWM was increased (Ulyshen and Hanula 2009b). Similarly, mobile ground-dwelling arthropods did not increase their use of CWM in a study of the effects of fire (Hanula et al. 2009). CWM removal appears to have a small or no effect on shrews (McCay and Komoroski 2004, Moseley et al. 2008). A number of studies have documented the increase in bird diversity and abundance in pine plantations where snags were available (Johnson and Landers 1982, Caine and Marion 1991, Jones et al. 2009). Homyack and colleagues (2011) measured an average of 1.5 snags per acre (3.7 per ha) in a loblolly pine plantation in the North Carolina piedmont and recommend retention or recruitment to increase snag density to promote bird habitat. McComb and colleagues (1986) recommend at least 2 snags per acre (5 per ha) some of which are greater than 20 inches in diameter (50 cm) just for primary cavity-nesters in Florida. Similarly, Harlow and Guynn (1983) recommend 3 snags per acre (≥5 in; 7.5 per ha) to support bird populations in coastal South Carolina pine plantations.

4. Conclusion

Though the Southeast generally has less DWM than other parts of the country, this review highlights the important role played by dead wood in southern forests. The quantities of DWM and the ecological relationships between wildlife and DWM differ throughout the forest types of the Southeast. For instance, southern Appalachian hardwood forests tend to have more DWM than southern pine forests. Some of the variation in DWM between southern Appalachian forests and southern pine forests is likely the result of the fact that many pinelands were established on agricultural lands and because they often are managed more intensively. The relative abundance of DWM in bottomland hardwoods compared to mixed pine–hardwood stands is less clear, because there is less scientific research from which to draw conclusions.

This review also underscores the value of considering dead wood within the context of natural cycles of stand development, such as the U-shaped pattern of DWM accumulation over time. Even without management, DWM may decline as a forest moves from the stand initiation into the vertical diversification stage (i.e., the stem exclusion phase). There is generally little FWM accumulation in southeastern forests, because of the effects of fire and high decomposition rates. The relatively small impact of DWM removal and prescribed fire on wildlife in southern pine forests suggests animals may be adapted to low levels of DWM because of frequent fire. Many studies in the southern Appalachian hardwood forests have shown an association between wildlife and DWM, particularly large pieces, but few document an impact on wildlife from DWM reductions. Identifying thresholds of dead wood retention below which wildlife shows negative impacts remains a research challenge.

Another daunting research challenge is to understand the potential impact of climate change on the dead wood in Southern forests. An increase in forest disturbance of one kind or another (e.g., drought, bark beetles, storms, or fire) is relatively likely in an altered climate and would have a significant impact on dead wood quantities and dynamics region-wide. The studies cited in this report provide a solid foundation to help managers integrate DWM into their planning, but as always more research will help clarify the ecological role of dead wood in the Southeast.

5. *Appendix I: Species Names*

Trees
Ashes – *Fraxinus* spp.
Basswood – *Tilia americana*
Beech – *Fagus grandifolia*
Birches – *Betula* spp.
Black cherry – *Prunus serotina*
Black locust – *Robinia pseudoacacia*
Black walnut – *Juglans nigra*
Blackgum – *Nyssa sylvatica*
Elms – *Ulmus* spp.
Hemlocks – *Tsuga* spp.
Hickories – *Carya* spp.
Loblolly pine – *Pinus taeda*
Lodgepole pine – *Pinus contorta*
Longleaf pine – *Pinus palustrus*
Magnolias – *Magnolia* spp.
Maples – *Acer* spp.
Oaks – *Quercus* spp.
Shortleaf pine – *Pinus echinata*
Slash pine – *Pinus elliottii*
Sweetgum – *Liquidambar styraciflua*
Tulip poplar – *Liriodendron tulipifera*

Insects and Diseases
Eastern spruce budworm – *Choristoneura fumiferana*
Engraver beetles – *Ips* spp.
Hemlock woolly adelgid – *Adelges tsugae*
Mountain pine beetle – *Dendroctonus ponderosae*
Southern pine beetle – *Dendroctonus frontalis*

Wildlife
Bear – *Ursus americana*
Common kingsnake – *Lampropeltis getula*
Cotton mouse – *Peromyscus gossypinus*
Cotton rat – *Sigmodon hispidus*
Eastern narrowmouth toad – *Gastrophryne carolinensis*
Golden mouse – *Ochrotomys nuttalli*
Indiana bat – *Myotis sodalis*
Mole salamander – *Ambystoma talpoideum*
Northern bat – *Myotis septenrionalis*
White-footed mouse – *Peromyscus leucopus*
Shrews – *Sorex* spp., *Cryptotis* spp., and *Blarina* spp.

6. Appendix II: Research Locations

Citation	Location	State	Forest Type	Province
Abbott and Crossley 1982	Coweeta Hydrologic Laboratory	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Adams et al. 2003	Fernow Experimental Forest	WV	S. Appalachian Hardwood	Valley and Ridge
Applegate 2008	Fort A.P. Hill	VA	Mixed Pine–Hardwood	Coastal Plain
Barber and van Lear 1984	—	SC	Pinelands	Piedmont
Bird et al. 2000	Temple-Inland Forest Products Co.	TX	Pinelands	Gulf Coastal Plain
Blair and Crossley 1988	Coweeta Hydrologic Laboratory	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Bragg 2004	Levi Wilcoxon Demonstration Forest	AR	Mixed Pine–Hardwood	Coastal Plain
Bragg and Heitzman 2009	University of Arkansas	AR	Pinelands	Gulf Coastal Plain
Busing 2005	Chapel Hill	NC	S. Appalachian Hardwood	Piedmont
Busing et al. 2009	Chapel Hill	NC	Mixed Pine–Hardwood	Piedmont
Cain 1996	Crossett Experimental Forest	AR	Mixed Pine–Hardwood	Gulf Coastal Plain
Campbell et al. 2008	Solon Dixon Experimental Forest	AL	Longleaf Pine	Coastal Plain
Chafin and Jones 1989	Mossy and Coosa Boulderfield	GA	S. Appalachian Hardwood	Appalachian Plateau
Chojnacky and Schuler 2004	Regional		S. Appalachian Hardwood	
Clinton et al. 2010	Nantahala NF	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Conner et al. 1994	Stephen F. Austin Experimental Forest	TX	Bottomland Hardwood	Coastal Plain
Cromer et al. 2007	Congaree National Park	SC	Bottomland Hardwood	Coastal Plain
Davis et al. 2010	Savannah River Site	SC	Pinelands	Coastal Plain
Dodds and Smallidge 1999	Savage River State Forest	MD	S. Appalachian Hardwood	Appalachian Plateau
Edwards 2004	Savannah River Site	SC	Plantation	Coastal Plain
Ford et al. 1999	Nantahala NF	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Ford et al. 2002	Fernow Experimental Forest	WV	S. Appalachian Hardwood	Valley and Ridge
Ford et al. 2010	Fernow Experimental Forest	WV	S. Appalachian Hardwood	Valley and Ridge
Gentry and Whitford 1982	Savannah River Site	SC	Bottomland Hardwood	Coastal Plain
Giese et al. 2003	Savannah River Site	SC	Bottomland Hardwood	Coastal Plain
Graves et al. 2000	West Virginia University Forest	WV	S. Appalachian Hardwood	Appalachian Plateau
Greenberg 2001	Bent Creek Experimental Forest	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Greenberg 2002	Bent Creek Experimental Forest	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Greenberg 2003	Ocala NF	FL	Pinelands	Coastal Plain
Greenberg et al. 2006	Green River Game Land	NC	S. Appalachian Hardwood	Blue Ridge Mts.

Hanula et al. 2009	Osceola NF	FL	Pinelands	Coastal Plain
Harmon 1982	Great Smoky Mts.	TN, NC	S. Appalachian Hardwood	Blue Ridge Mts.
Hart 2003	Great Smoky Mts.	TN	S. Appalachian Hardwood	Blue Ridge Mts.
Hedman et al. 2000	Southlands Experiment Forest	GA	Pinelands	Coastal Plain
Hinkelman and Loeb 2007	Savannah River Site	SC	Pinelands	Coastal Plain
Horn and Hanula 2008	Savannah River Site	SC	Pinelands	Coastal Plain
Hubbard et al. 2004	Chattahoochee/Cherokee	TN, GA	S. Appalachian Hardwood	Blue Ridge Mts.
Johnston and Crossley 2002	Regional		Pinelands	
Kaminski et al. 2009	MeadWestvaco Wildlife and Ecosystem Research Forest	WV	S. Appalachian Hardwood	Appalachian Plateau
Kilpatrick et al. 2010	Regional		Pinelands	
King and Antrobus 2001	Rex Hancock/Black Swamp Wildlife Area	AR	Bottomland Hardwood	Mississippi Floodplain
Krauss et al. 2005	South Florida	FL	Mangrove	
Liechty et al. 2004	Ouachita NF	AR	Pinelands	Ouachita Mountains
Lockhart et al. 2010	Pittman Island	MS	Bottomland Hardwood	Mississippi Floodplain
Loeb 1996	Regional		Pinelands	
Loeb 1999	Savannah River Site	SC	Pinelands	Coastal Plain
Lorimer 1980	Joyce Kilmer Memorial Forest	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Loucks et al. 1999	Regional		S. Appalachian Hardwood	
Loucks et al. 2008	Daniel Boone NF	KY	S. Appalachian Hardwood	Appalachian Plateau
Maidens et al. 1998	–	GA	S. Appalachian Hardwood	Appalachian Plateau
Matthews et al. 2009	Green River Game Land	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Mattson et al. 1987	Coweeta Hydrologic Laboratory	NC	S. Appalachian Hardwood	Blue Ridge Mts.
McCay 2000	Savannah River Site	SC	Pinelands	Coastal Plain
McCay and Komoroski 2004	Savannah River Site	SC	Pinelands	Coastal Plain
McClure et al. 2004	University of Kentucky: Robinson Forest	KY	S. Appalachian Hardwood	Cumberland Plateau
McComb and Muller 1983	Lilley Cornett Woods	KY	S. Appalachian Hardwood	Cumberland Plateau
Mengak and Guynn 2003	Sumter NF	SC	Pinelands	Piedmont
Menzel et al. 1999	Nantahala NF	NC	S. Appalachian Hardwood	Blue Ridge Mts.
Moorman et al. 1999	Clemson University Experimental Forest	SC	Mixed Pine–Hardwood	Piedmont
Moseley et al. 2003	Di-Lane Plantation Wildlife Management Area	GA	Bottomland Hardwood	Coastal Plain
Moseley et al. 2004	Savannah River Site	SC	Pinelands	Coastal Plain
Moseley et al. 2005	Savannah River Site	SC	Pinelands	Coastal Plain
Moseley et al. 2008	Savannah River Site	SC	Pinelands	Coastal Plain
Muller 2003	Lilley Cornett Woods	KY	S. Appalachian Hardwood	Cumberland Plateau

Muller and Liu 1991	Lilley Cornett Woods	KY	S. Appalachian Hardwood	Cumberland Plateau
Onega and Eickmeier 1991	Radnor Lake State Natural Area	TN	S. Appalachian Hardwood	Appalachian Plateau
Owens et al. 2008	Savannah River Site	SC	Pinelands	Coastal Plain
Parresol et al. 2006	Savannah River Site	SC	Pinelands	Coastal Plain
Perry and Thill 2008	Upper Lake Winona Basin	AR	Mixed Pine–Hardwood	Ouachita Mountains
Radtke et al. 2004	Regional		Pinelands	
Rice et al. 1997	Atchafalaya River Basin	LA	Bottomland Hardwood	Atchafalaya River Basin
Rittenhouse et al. 2008	Daniel Boone Conservation Area	MO	S. Appalachian Hardwood	Ozark Region
Rothermel and Luhring 2005	Savannah River Site	SC	Pinelands	Coastal Plain
Rudis and Tansey 1995	Regional		Bottomland Hardwoods	
Scott and Messina 2009	Forest Lake Experimental Forest	TX	Pinelands	Gulf Coastal Plain
Shackelford and Conner 1997	Angelina National Forest	TX	Bottomland Hardwood and mixed pine–hardwood	Gulf Coastal Plain
Steen et al. 2010	Jones Ecological Research Center	GA	Pinelands	Coastal Plain
Stottlemyer et al. 2009	Sumter NF	SC	S. Appalachian Hardwood	Blue Ridge Mts.
Sweka and Hartman	Middlefork River	WV	S. Appalachian Hardwood	Appalachian Plateau
Todd and Andrews 2008	Savannah River Site	SC	Pinelands	Coastal Plain
Ulyshen and Hanula 2009a	Savannah River Site	SC	Pinelands	Coastal Plain
Ulyshen and Hanula 2009b	Savannah River Site	SC	Pinelands	Coastal Plain
Ulyshen et al. 2004	Savannah River Site	SC	Bottomland Hardwood	Coastal Plain
Vose et al. 1999	Nantahala NF	NC	Mixed Pine–Hardwood	Blue Ridge Mts.
Webster and Jenkins 2005	Great Smoky Mts.	TN	S. Appalachian Hardwood	Blue Ridge Mts.
White and Lloyd 1994	John de la Howe	SC	Mixed Pine–Hardwood	Piedmont

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