Reprinted from *Forest Science,* Vol. 45, *No.* 2, May 1999. Not for further reproduction.

Regional Distribution and Dynamics of Coarse Woody Debris in Midwestern Old-Growth Forests

Martin A. Spetich, Stephen R. Shifley, and George R. Parker

ABSTRACT. Old-growth forests have been noted for containing significant quantities of deadwood. However, there has been no coordinated effort to quantify the deadwood component of old-growth remnants across large regions of temperate deciduous forest. We present results of a regional inventory that quantifies and examines regional and temporal trends for deadwood in upland old-growth forest remnants within Indiana, Illinois, Missouri, and Iowa. From 1992 to 1994, down wood ≥ 10 cm in diameter and standing trees ≥ 10 cm dbh were inventoried on 328 one-tenth ha plots at 12 sites. The mean ratio among the sites by diameter class of the number of standing dead to standing live trees (dead/live ratio) ranged from 0.08 to 0.11 and was consistent for trees 565 cm in diameter. The dead/live tree ratio was generally greater for old-growth than for mature second-growth forests (70 to 90 yr old). Mean volume of standing dead trees across all old-growth sites was 21.4 m^3/ha and down wood was 60.4 m^3/ha. However, both standing and down wood volume (total deadwood) increased along a regional gradient of increasing productivity from southwest Missouri to northeast Indiana and also increased with increasing age of dominant and codominant trees. Old-growth forests on high productivity sites averaged more pieces/ha of down wood in all diameter classes and higher volume/ha of down wood in nearly all diameter classes than did old-growth forests on low productivity sites. A chronosequence of forests from 10 yr to more than 200 yr since stand establishment indicated a sharply declining down wood volume from age 10 to 70 yr followed by increasing volume between 80 and 200 yr. FOR. SCI. 45(2):302–313.

Additional Key Words: Productivity gradient, deadwood volume, snags, spatial and temporal distribution.

LIVING TREES COMPLETE ONLY A PORTION of their ecological role by the time they die (Franklin et al. 1987). Coarse woody debris created from dead and dying trees provides important habitat for forest organisms (O'Neill 1967, Maser et al. 1979, Thomas et al. 1979, Maser and Trappe 1983, Meyer 1986, Maser et al. 1988, Muller and Yan Liu 1991, Larson 1992, Van Lear 1993, Cain 1996), provides both habitat and energy for detritivores (Lang and Forman 1978), and serves as a reservoir for nutrients and carbon (Bray and Gorham 1964, Harmon et al. 1986, Edmonds 1987, Lang and Forman 1978, Maser et al. 1988, Huston 1996).

Martin A. Spetich is Research Forester, USDA Forest Service, Southern Research Station, P.O. Box 1270, Hot Springs, AR 71902—Phone: (501) 6231180; Fax: (501) 623-0186; E-mail: MSpetich/srs_monticello@fs.fed.us. Stephen R. Shifley is Research Forester, USDA Forest Service, North Central Forest Experiment Station, 202 Anheuser-Busch Natural Resource Building, Columbia, MO 65211-7260—Phone: (573) 875-5341; E-mail: Sshifley@raphael.snr.missouri.edu. George R. Parker is Professor, Department of Forestry and Natural Resources, Purdue University, 1159 Forestry Building, West Lafayette, IN 47907—Phone: (765) 494-3602: E-mail: grp@fnr.purdue.edu.

Acknowledgments: Funding was provided by the USDA Forest Service, North Central Research Station. Thanks to Bill Dijak for preparing the base map for Figure 1 from AVHRR data and Tim Nigh for historical quotes. Our appreciation to the many fieldworkers including Adam Downing, Mark Huter, Mike Jenkins, Hoyt Richards, David Roberts, Lynn Rovers, Jenna Stauffer, Wayne Werne, and Chris Webster. The following organizations graciously provided access to records and study sites: Indiana Department of Natural Resources (IDNR) Division of Nature Preserves, IDNR Division of State Parks, The Nature Conservancy, Purdue University, Hoosier National Forest, Missouri Department of Conservation, Missouri Department of Natural Resources Division of State Parks, Eastern Illinois University, Illinois Department of Conservation Division of Natural Heritage and Iowa Department of Natural Resources. Thanks to William R. Chaney, David Larson, and two anonymous reviewers for reviewing this manuscript and to Betsy L. Spetich for editorial comments. This is Purdue University Agricultural Station publication #15614.

Manuscript received July 13, 1998. Accepted January 11, 1999.

The article was written by a U.S. government employee and is therefore in the public domain.

There may be a greater quantity of living biomass within a dead log than a live tree (Franklin et al. 1987). Meyer (1986) lists snags and down wood in Missouri as habitat for 26 bird species, 11 reptiles, 11 mammals, and 9 amphibians. In the Blue Mountains of Oregon and Washington, 39 bird and 23 mammal species use standing dead trees for nest sites and shelter (Thomas et al. 1979). At least 98 species of land snails are associated with log habitats in the southeast (Caldwell 1996). In southern hardwood and pine forests, there are 4.5 bird species that use standing dead trees and 20 species that use down woody debris (Lanham and Guynn 1996). In the southeast, at least 23 mammal species use standing dead trees and ≥ 55 mammal species use down wood (Loeb 1996). Ausmus (1977) found greater organic matter, nematode density, and root biomass in soil beneath log litter than under leaf litter. Reptiles and amphibians are associated with coarse woody debris and it has been suggested that their diversity may be linked with the quality and amount of coarse woody debris (Whiles and Grubaugh 1996). Earthworms use deadwood for cover and as a source of food from microbial biomass (Hendrix 1996). Finally, a study by Barnum et al. (1992) found that mice selected logs as the most widely used substrate for travel.

The input rate of coarse woody debris varies with site productivity (Harmon et al. 1986). In the northwestern United States, for example, mortality rates of old-growth forests are higher on high productivity sites than on low productivity sites (Franklin et al. 1987). O'Neill and DeAngelis (1981) note increasing litterfall withincreasing productivity. In addition, the average size of pieces of coarse woody debris may increase with successional stage and stand age (Harmon et al. 1986). Species composition may also affect the size and rate of accumulation of coarse woody debris. Neither the presence nor the magnitude of these trends has been established for midwestem old-growth forests. Nor have regional patterns in the structure of the deadwood component of midwestem old-growth forests been systematically examined. The most extensive research on snags (i.e., dead standing trees) and down wood has been at locations outside of Indiana, Illinois, Missouri, and Iowa (examples include Maser et al. 1979, McComb and Muller 1983, Gore and Patterson 1986, Maser et al. 1988, Spies and Cline 1988, Hedman and Van Lear 1990, Flebbe and Dollof 1991, and McCarthy and Bailey 1994). Comparatively little research has been conducted within this four-state region (O'Neill 1967, MacMillan 1988, Richards et al. 1995, Shifley et al. 1995, Spetich 1995, Spetich and Parker 1998), and our understanding of woody debris structure and dynamics in this region lags behind that of portions of the Pacific Northwest and the Northeast, in particular.

In our study we examine coarse woody debris in old-growth forest in the central United States. Specific objectives were to: (1) characterize volume, decomposition class, and structural features of the deadwood component of old-growth forests in Indiana, Illinois, Missouri, and Iowa; (2) determine regional and temporal trends in these characteristics; and (3) compare old-growth deadwood characteristics to mature (70 to 90 yr old), unmanaged (little or no disturbance during the past 40 or more yr), second-growth forests.

Methods

Location of Sites and Field Procedures

Old-growth sites were selected from a pool of sites identified in 1991 through a survey of public landholding agencies, interviews with natural resource specialists, literature reviews, and site visits. Selected sites were distributed across broad natural divisions identified in the study area (Thorn and Wilson 1980, Homoya et al. 1985, Neeley and Heister 1987). When multiple candidate sites occurred in a natural division, sites were randomly selected for inventory (Figure 1). Selected tracts were considered to be among the best remaining examples of old-growth forest in theirregion, and all sites had previously been placed in some form of permanent protective status. These forests were not harvested as the logging industry moved west during the late 19th and early 20th centuries when most other forests in the region were cut. Historically, the only known disturbances at these sites were the frequent ground fires and the periods of open-range grazing that occurred throughout the region prior to 1950 and the selective harvest of a few individual trees at some of the sites.

Characteristics of selected sites were consistent with those described by Parker (1989) and Meyer (1986) for old-growth hardwood forests. Parker (1986) indicates that mesic old-growth forests in the central hardwood region typically have overstory canopy trees > 150 yr old; little human-caused understory disturbance during the past 80 to 100 yr; all-aged structure; multilayered canopies; dominant canopy trees from 80 to 160 cm dbh; understories of late-seral, shade-tolerant trees; and abundant snags and down wood. Meyer (1986) describes old-growth characteristics for Missouri forests as 90+ yr old, dominant trees averaging ≥ 100 yr old, at least 25% stocking of live trees ≥ 36 cmdbh, large snags, large and small down logs, broken dead tree tops, tree cavities, and dead logs in streams. Many site characteristics were also consistent with those defined by Martin (1992) for mixed mesophytic old-growth forests of the Appalachians (e.g., uneven-aged structure, large canopy trees, tree fall gaps, logs and snags).

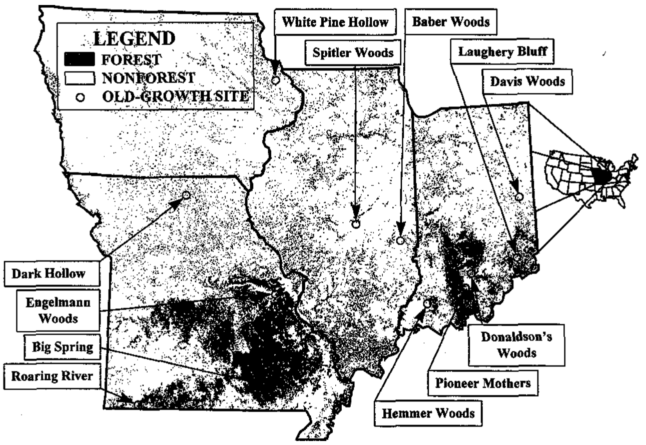

Figure 1. Location of 12 old-growth sites sampled. Grey represents forestland cover as classified from AVHRR data. Most old-growth sites are forest islands in a matrix of agriculture. The Iowa site is the only old-growth site of substantial size in that state.

A standardized sampling scheme was used to collect data at the old-growth sites between May 1992 and May 1994. Thirty circular 0.1 ha plots were established at most sites (Table 1). Sample plots at each site were systematically arranged from a random starting point, and plot centers were located at least 40 m apart and at least 40 m from the forest edge. Living and dead trees ≥ 10 cm dbh were measured to the nearest 0.1 cm. Snags were classified into five decomposition classes (Table 2). Heights of all snags were measured to the nearest 0.1 m with a clinometer. The length and midpoint diameter of each piece of down wood ≥ 10 cm in diameter within each 0.1 ha plot were measured to the nearest 0.1 m or cm, respectively, and classified into one of five decomposition classes (Table 2). At sites where there was no prior data on stand age, ages were measured on a sample of dominant and codominant trees.

Deadwood Volume

Volume of standing deadwood was calculated assuming each dead tree was a conic section with taper equivalent to Girard tree form class 78. Volume of each piece of down wood was computed from its measured length and midpoint diameter based on the formula for the volume of a cylinder. One-way ANOVA was used to compare mean deadwood volumes for old-growth sites with the mature, second-growth sites described below. The relationship between forest age and down wood volume was analyzed using linear regression. To span a wider range of ages we included data from mature second-growth sites (VanKley 1993, and Shifley et al. 1998) and other stands between 10 and 80 yr old from the study region (Jenkins and Parker 1997). Because the available data for the 10- to 80-yr-old stands did not include snags, only the down wood data were included in this part of the analysis.

Table 1. Location, sample size, and overstory characteristics for old-growth sites inventoried in a four-state survey of old-growth forest characteristics. Order of old-growth sites corresponds to their position from northeast to southwest across the study area. Information is also provided for second-growth sites used for comparisons. Indiana second-growth sites are further described in Van Kley (1993); Missouri second-growth sites are further described in Shifley et al. (1997a).

Site name	State	No. of plots	Plot size	Tract size	Potential site productivity” (m^3/ha/yr)	Canopy height^b (m)	Dominant tree species”	Physiographic class^d
Old-growth sites			(ha)					
Davis-Purdue (DA)	*IN*	30	0.1	21	5.5	31.7	*Quercus, alba* L. *Q. rubra* L. *Acer saccharum* Marsh.	Mesic, wet-mesic to wet upland forest
Laughery Bluff (LA)	IN	30	0.1	15	6.0	26.3	*Liriodendron tulipifera* L. *A. saccaharum* *Fagus grandifolia* Ehrh.	Mesic upland forest
Donaldson's Woods (DO)	IN	30	0.1	27	5.5	32.5	*Q. alba* *L. tulipiferea* *F. grandtfolia*	Mesic to dry-mesic upland forest
Pioneer Mothers (PM)	IN	30	0.1	15	5.5	30.7	*A. saccaharum* *F. grandtfolia* *Q. alba*	Mesic to dry-mesic upland forest
Hemmer Woods (HE)	IN	30	0.1	17	4.5	23.3	*Q. alba* *Q. velutina Lam.* *Q. rubra*	Mesic upland forest
Baber Woods (BA)	IL	16	0.25	21	5.3	N/A	*A. saccaharum* *Q. alba* *Cary glabra* (Mill.) Sweet	Mesic and dry-mesic upland forest
Spitler Woods (SW)	IL	30	0.1	65	5.0	21.5	*Q. alba* *A. saccharum* *Q. rubra*	Mesic upland forest
White Pine Hollow” (WPH)	IA	12	0.1	283	5.0	25.1	*Pinus strobus* L. *A. saccaharum* *Q. alba*	Mesic and dry-mesic upland forest
Engelmann Woods (EW)	MO	30	0.1	55	3.5	19.8	*A. saccharum* *Q. rubra* *Q. muehlenbergii* Engelm.	Mesic and dry-mesic upland forest
Dark Hollow (DH)	MO	30	0.1	78	4.0	21.5	*Q. rubra* *Q. alba* *Tilia americana* L.	Dry-mesic and mesic upland forest
Big Spring (BS)	MO	30	0.1	65	4.2	21.6	*Q. alba* *Q. velutina* Q. *coccinea* Meunchh.	Dry-mesic and xeric upland forest
Roaring River (RR)	MO	30	0.1	49	3.8	18.4	*Q. alba* *Q. velutina* *Q. rubra*	Xeric and dry-mesic upland forest

Table 1 continued

Site name	State	Number of plots	Plot size	Tract size	Potential site productivity” (m^3/ha/yr)	Canopy height[b] (m)	Dominant tree species[c]	Physiographic class[d]
Second-growth sites			(ha)					
Indiana Sites (41 sites)	IN	164, 4[f]	0.05	34053, 16[g]	N/A	N/A	*Q. rubra* *Q. alba* *Q. velutina*	Predominantly mesic with dry-mesic inclusions
MOFEP Site 1	MO	11, 73[h]	0.1, 0.2[i]	389	N/A	N/A	*Q. velutina* *Q. coccinea* *Q. alba*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 2	MO	11, 73[h]	0.1, 0.2[i]	515	N/A	N/A	*Q. velutina* *Q. coccinea* *Q. alba*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 3	MO	11, 72[h]	0.1, 0.2[i]	360	N/A	N/A	*Q. velutina* *Q. alba.* *Q coccinea*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 4	MO	11, 74[h]	0.1, 0.2[i]	479	N/A	N/A	*Q. velutina* *Q. alba.* *Q coccinea*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 5	MO	11, 70[h]	0.1, 0.2[i]	313	N/A	N/A	*Q. alba* *Q. velutina* *Q. coccinea*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 6	MO	11, 71[h]	0.1, 0.2[i]	440	N/A	N/A	*Q. alba* *Q. velutina* *Q. coccinea*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 7	MO	11, 71[h]	0.1, 0.2[i]	502	N/A	N/A	*Q. coccinea* *Q. velutina* *Q. alba*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 8	MO	11, 70[h]	0.1, 0.2[i]	340	N/A	N/A	Q. velutina *Q. coccinea* *Q. alba*	Predominantly dry-mesic with xeric and mesic inclusions
MOFEP Site 9	MO	11, 71[h]	0.1, 0.2[i]	462	N/A	NIA	*Q. velutina* *Q. alba.* *Q coccinea*	Predominantly dry-mesic with xeric and mesic inclusions

[a] See text for method of computation.
[b] Mean height of dominant and codominant trees.
[c] By basal area. Authority is given with first mention of each species.
[d] As defined by White (1978).
[e] White Pine Hollow was the only existing old-growth site of substantial size in Iowa.
[f] Total number of plots followed by number of plots per stand.
[g] Total area of Hoosier National Forest Pleasant Run Unit where all 41 stands are located, and mean stand size.
[h] Number of plots for down wood followed by number of plots for snags.
[i] Plot size for down wood followed by plot size for snags.

Site Productivity

Although there are regional differences in forest productivity in the four-state study region, measurement of site productivity for individual old-growth sites is problematic. Productivity of the old-growth sites cannot be directly measured until a second inventory is completed. Site index cannot be accurately measured at these sites because of the lack of trees that have not endured periods of suppression (Carmean 1979, Carmean et al. 1989). Consequently, data from 2,495 second-growth forest inventory plots from across the region were used to quantify regional patterns in potential forest productivity (m^3/ha/yr) as a function of measured site index (Hansen et al. 1992). These data were restricted to stands of natural origin and at least 70 yr old. Means among plots within each county were calculated and plotted across the four-state region, and a contour map of the productivity gradient was created using commercially available software (RockWare Utilities 1995). This map was created in “Contour USA,” an earth science utility that calculates a contour map using a variation of the Delaunay triangulation method. This map illustrates the gradient of increasing

Table 2. Decomposition classes for standing dead trees and down woody material used in the four-state survey of old-growth characteristics. Numbers 1-5 indicate codes used for decomposition classes where class 1 is least decomposed and class 5 is most decomposed. Adapted from Cline et al. (1980) and Maser et al. (1979).

Deadwood type	Characteristic	Decomposition class 1	2	3	4	5
Snags	Branches and crown	Recently dead, twigs and small branches present	Large branches present, mostly broken	Large branch stubs present	Absent	NA
	Bark	Tight	Loose and/or partly absent	Trace to absent	Absent	NA
	Bole	Recently dead	Standing, firm	Standing, decayed	Broken top, heavily decayed, soft, blocky structure	NA
Down wood	Bark	Intact	Intact	Trace to absent	Absent	Absent
	Twigs < 3cm	Present	Absent	Absent	Absent	Absent
	Texture	Intact	Intact, sapwood partly soft	Hard, solid interior, possible evidence of exterior decay	Soft, blocky pieces	Soft and powdery
	Shape	Round	Round	Round	Round to oval	Oval
	Color of wood	Original color	Original color	Original color to faded	Original color to faded	Heavily faded
	Portion of log on ground	Log elevated on support points	Log elevated on support points	Log near or on ground	All of log on ground	All of log on ground

productivity from southwest to northeast across the study area (Figure 2). Productivity values were interpolated for the locations of individual old-growth sites (Table 1). Site-specific productivity for old-growth sites was also estimated as the mean height of dominant and codominant trees sampled on each site (Table 1). Relationships among site productivity and old-growth forest characteristics were analyzed using linear regression.

Second-Growth Deadwood Characteristics

There have been only two prior studies of snags and down wood in mature second-growth forests within our study region (VanKley 1993, Shifley et al. 1997a). These 50 upland hardwood sites were 70 to 100 yr old (based on increment cores) and had little or no disturbance for the 40 yr or more prior to inventory (Table 1). We summarized the raw data from these studies and used one-way ANOVA to compare deadwood volume and structure with the old-growth sites. We also combined results from the VanKley data and our study with published observations for down deadwood in younger second-growth forests (age 10 to 80 yr old) (Jenkins and Parker 1997, Shifley et al. 1997a) to examine down coarse woody debris volumes over a chronosequence of forest age classes.

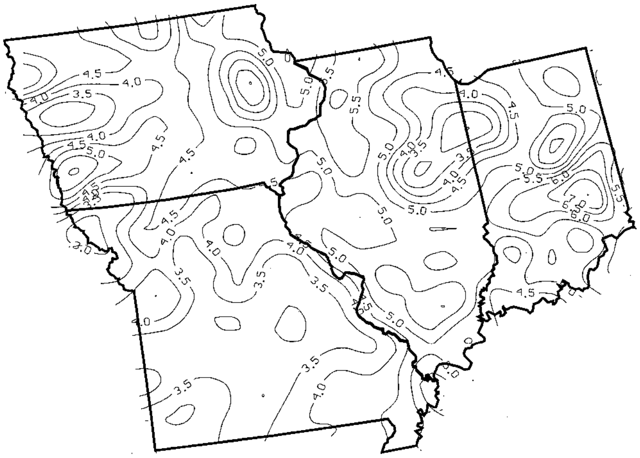

Figure 2. Contour map of potential productivity (m^3/ha/year) of live commercial species in forest stands > 70 yr old on xeric, xeromesic, mesic, and hydromesic sites. Based on reported values for 2,495 forest inventory and analysis plots in Indiana, Illinois, Iowa, and Missouri (Hansen et al. 1992). Potential productivity is a function of the site index measured for each plot. The mean value of plots within each of 342 counties were calculated and used in developing this map.

Results

Regional Characteristics

Mean volume of snags across all old-growth sites was 21.4 m^3/ha (Figure 3a). The volume of down wood was nearly three times greater at 60.3 m^3/ha for a total coarse woody debris volume of 81.5 m^3/ha (Figure 3a). For all sites, the number of snags and of pieces of down wood decreased exponentially with increasing diameters (Figure 4). However, the greatest proportion of the down wood volume was in pieces between 20 and 40 cm in diameter (Figure 3b). The number of pieces of down wood by diameter class was uniformly greater for the Indiana (high productivity) sites than for the Missouri (low productivity) sites (Figure 4). Down wood volume by diameter class was greatest in the 45-65 cm diameter range at the Indiana sites, but at the Missouri sites the greatest volume of down wood occurred in the 25-45 cm diameter range. Snag volume per hectare was greatest in trees between 40 and 80 cm dbh (Figure 3c). Snags and down wood occurred in all decomposition classes, but the greatest proportion (41% and 53% respectively) was in the intermediate (class 3) decomposition class (Figure 3b, c).

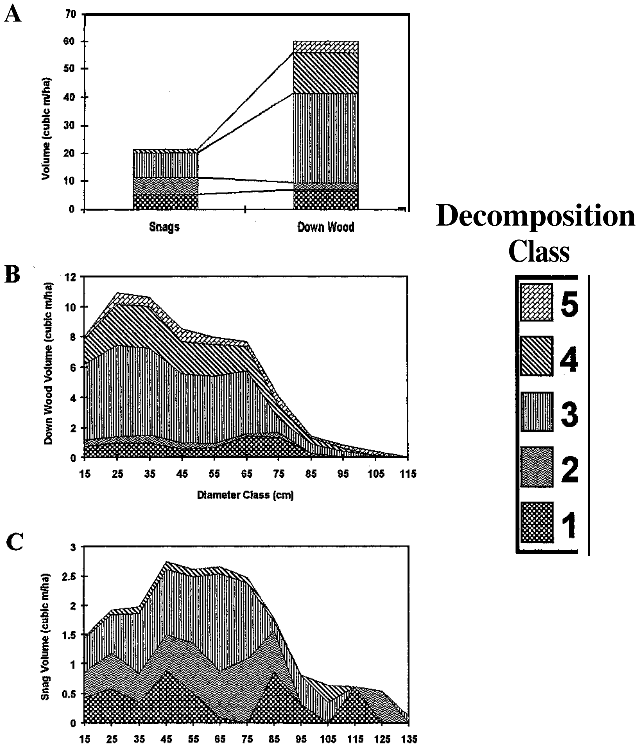

Figure 3. Regional mean values of standing and down wood in old-growth forests by decomposition class. Classes are 1 (least decomposed) through 5 (most decomposed); see Table 2 for additional description of decomposition classes. (A) Comparison of snag and down wood volumes across all old-growth sites. (B) Mean volume of down wood by decomposition class anddiameter class for old-growth forests. (C) Mean volume of snags by decomposition class and diameter class for old-growth forests.

Total deadwood volume (snags plus down wood) varied with estimated potential forest productivity. Total old-growth deadwood volume increased linearly with potential site productivity (R^2 = 0.79; P-value < 0.001) (Figure 5). The individual deadwood components of snag volume and down wood volume also increased linearly with increasing potential productivity (for snag volume R^2 = 0.51, P-value = 0.01; for down wood volume R^2 = 0.64, P-value = 0.002). Potential site productivity was correlated with the measured height of dominant and codominant trees for each site (R = 0.82). Total deadwood volume, snag volume, and down wood volume also increased linearly with canopy height at each site, but the relationships were not as strong as they were with potential productivity (for total deadwood volume by canopy height R^2 = 0.40, P-value = 0.04; for snag volume by canopy R^2 = 0.59, P-value = 0.006; for down wood volume by canopy R^2 = 0.24, P-value = 0.12). Laughery Bluff had the largest deadwood volume of any site due to severe wind damage that occurred 2 wk prior to field measurement (Figure 5). However, exclusion of the Laughery Bluff site had little effect on the strength of the relationship of deadwood volume with estimated site productivity or canopy height.

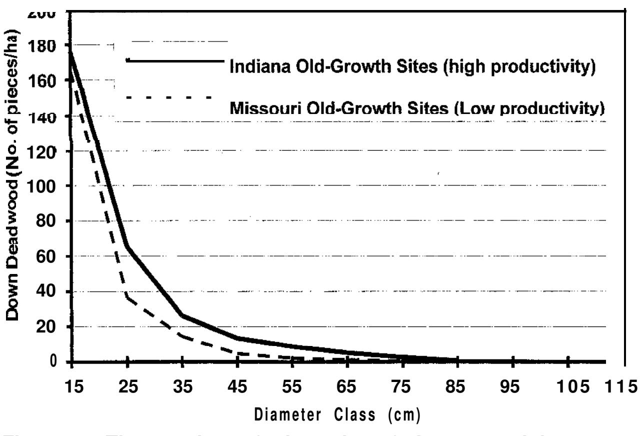

Figure 4. The number of pieces/ha of down wood by 10 cm diameter class. Indiana old-growth sites located in the relatively high productivity region had more down wood in all diameter classes than the Missouri sites located in the low productivity region.

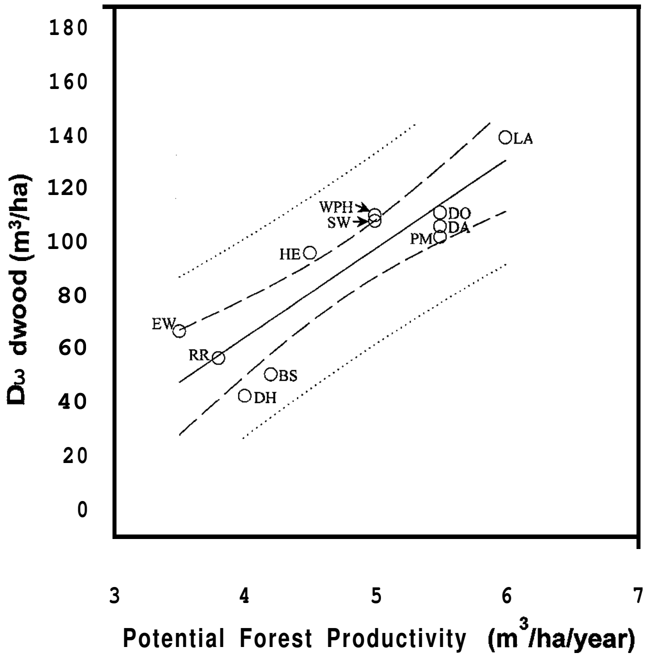

Figure 5. Linear regression of total deadwood volume at old-growth sites vs. potential forest productivity for that location. Total deadwood (m^3/ha) = -75.3 + 33.0 (potential productivity); R^2 = 0.79, P-value c 0.001. Letter codes identifying data points correspond to site codes in Table 1. Dashed lines indicate 95% confidence interval. Dotted lines indicate 95% prediction interval.

The ratio of snags to live trees was reasonably consistent for old-growth sites across the region. For individual sites, the ratio of all dead to all live trees ranged from 0.07 to 0.12 (Table 3). For all sites combined, the ratio of the number of standing dead trees to the number of live trees by dbh class was consistently between 0.08 and 0.11 for trees $\leq$ 65 cm dbh. In diameter classes larger than 65 cm, the number of observations was small, and values by dbh class varied widely. The composite dead/live tree ratio for all trees > 65 cm was 0.12. Individual sites followed the same pattern shown in Figure 6, but the smaller sample sizes resulted in greater variation by diameter class.

The ratio of dead to live tree basal area averaged 0.11 for all old-growth sites (Table 3). Laughery Bluff at 0.23 was a notable exception. The wind storm at Laughery Bluff caused extensive damage to large trees. This resulted in a large basal area for snags even though the number of snags as a proportion of live trees (0.12) was not significantly greater (a = 0.05) than observed at other sites.

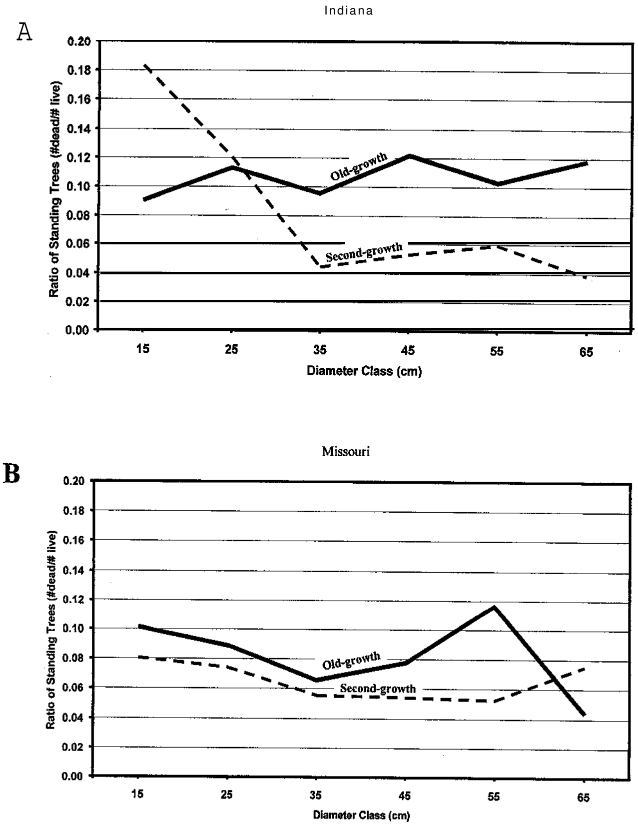

Figure 6. Ratio of dead to live trees/ha (i.e., dead/live ratio) for old-growth sites and for second-growth sites. The ratio was computed as the number of standing dead trees/ha divided by the number of standing live trees/ha by dbh class. Values are relatively consistent for the old-growth forests up to diameters of 65 cm. Sample sizes are small beyond 65 cm dbh. The old-growth sites consistently have a higher ratio than the second-growth sites.

Comparison of Old-Growth vs. Second-Growth Forest

Old-growth sites had more than twice the standing deadwood volume and three times the down wood volume as the second-growth forests used as comparison sites (Table 4). At second-growth sites, the ratio of live to dead trees averaged 0.08 (Table 3), significantly lower than observed for the old-growth sites (P-value = 0.03, arcsin transformation used for proportions). For the Missouri second-growth sites, the ratio of snags to live trees by dbh class was consistently lower than that observed for old-growth sites (Figure 6b). However, for the higher productivity sites in Indiana, the ratio of dead to live trees on second-growth sites exceeds that of old-growth sites for trees below 25 cm dbh. In the 15 cm dbh class for Indiana second-growth sites, nearly 1 in 5 standing trees were dead.

Age Relationship

Polynomial regression of down wood volume against stand age indicated a highly significant curvilinear relationship. A cubic polynomial of stand age described 86% of the variation in the down wood volume (P-value < 0.001) (Figure 7). Down wood volume decreased with increasing stand age between age 10 to age 70 yr. Beyond stand age 70, the observed down wood volume increased with increasing age to a maximum at an age > 200 yr.

Discussion

Regional Characteristics

The relatively large volumes of standing and down wood we observed in decomposition class 3 is consistent with observations for other regions where intermediate decay classes also tend to dominate (e.g., Harmon et al. 1986, Spies and Cline 1988), although not always to the same degree as observed in this study. Class 3 material also dominated on our second-growth study sites. In midwestern forests, material may remain in this intermediate decomposition class for a relatively long time. One defining characteristic of decomposition class 3 deadwood is lack of bark. Bark is often shed while the tree is standing or soon after the tree falls. Van Lear (1993) and Harmon et al. (1986) both suggest that when down wood loses bark early, it dries quickly and may become case-hardened, slowing the decay process. In addition, fissures and excavations that develop in decomposition class 4 and 5 material increase the total surface area and accelerate the rate of decay in those stages (Maser et al. 1988).

The regional productivity gradient (Figure 2) illustrates what had only been an intuitive concept based on our field and experimental experiences. We suspect that similar gradients of forest productivity exist in the United States and probably throughout the forested portions of the Earth. Regional trends in forest productivity should be particularly useful in developing concepts of trends in forest character because of the integrating effect of productivity. Productivity is a natural integrator of the effects of soil quality, climate, topography, geology, organisms and all other factors that impact forest growth and the overall character of the forest ecosystem. In this respect, regional productivity trends should be a useful tool to theorize change in forest character over a region.

Old-growth forests with high rates of productivity should accumulate high volumes of deadwood. Huston (1996) describes the amount of coarse woody debris base energy as "a function of forest productivity as represented by site index." In our study, regional productivity was highly correlated with deadwood volume at old-growth sites. Canopy height, a surrogate for local site productivity, was also linearly related to total deadwood volume. This relationship was also evident in the number of pieces of down wood by diameter class. The negative exponential distribution of the number of pieces of down wood by diameter class is likely linked to the negative exponential distribution observed for live trees at the old-growth sites (Shifley et al. 1995).

Although estimated site productivity and forest age were highly correlated with the total wood volume (Pearson correlation coefficients of 0.87 and 0.94, respectively; P-values < 0.002 and < 0.00005, respectively), we found no significant relationship between total wood volume and basal areas of white oak (*Q. alba*), northern red oak (Q. *rubra*), black oak (*Q. velutina*), sugar maple (*A. saccharum*), yellow-poplar (*L. tulipifera*) or American beech (*F. grandifolia*) (P-values > 0.07). Even though *L. tulipifera* and *F. grandifolia* only occurred on the more productive sites and ***Q. velutinu*** was most abundant on low productivity sites, the relationship of down wood volume to basal area was not as strong as for

Table 3. Ratio of standing dead to live trees per hectare and basal area per hectare for trees ≥ 10 cm dbh.

	Standing trees				Dead/live ratio	
	Live		Dead			
Site	Basal area (m^2/ha)	No./ha	Basal area (m^2/ha)	No./ha	Basal area	No. of trees
Old-growth sites						
Davis-Purdue	30	314	3	34	0.10	0.11
Laughery Bluff	19	218	4	26	0.23	0.12
Donaldson's Woods	31	239	3	19	0.08	0.08
Pioneer Mothers	27	260	4	19	0.13	0.07
Hemmer Woods	23	258	3	30	0.11	0.11
Spitler Woods	29	406	2	39	0.08	0.10
White Pine Hollow	32	399	4	47	0.12	0.12
Engelmann Woods	22	398	2	35	0.07	0.09
Dark Hollow	23	331	2	36	0.08	0.11
Big Spring	22	467	2	39	0.08	0.08
Roaring River	22	442	2	42	0.11	0.10
Mean old-growth	28	339	3	33	0.11	0.10
Second-growth sites						
Indiana Sites[a]	23	152, 166[b]	2	27, 10[b]	0.08	0.21, 0.06[b]
MOFEP Site 1	19	454	1	27	0.05	0.06
MOFEP Site 2	18	434	1	25	0.05	0.06
MOFEP Site 3	20	417	1	22	0.05	0.05
MOFEP Site 4	19	412	1	22	0.05	0.05
MOFEP Site 5	19	395	2	25	0.05	0.06
MOFEP Site 6	20	395	2	32	0.08	0.08
MOFEP Site 7	19	346	2	41	0.09	0.12
MOFEP Site 8	19	329	2	52	0.12	0.16
MOFEP Site 9	17	311	1	15	0.05	0.05
Mean second-growth	19	381	2	30	0.07	0.08

[a] Mean of 41 stands with 4 plots per stand.

[b] As further described in text,for Indiana sites the relationships differed for trees smaller than 24 cm and trees larger than 24 cm. First value is for trees less than 24 cm dbh and second value is for trees greater than 24 cm dbh.

either site productivity or age. Q. *alba, Q. rubra,* and *A. saccharum* were abundant on nearly all sites and not effective in indicating differences in down wood volume.

The mean ratio of dead to live trees at our old-growth sites was 0.1 and varied only from 0.07 to 0.12 across the old-growth sites. Also, the mean ratio among all sites varied by only 0.03 among diameter classes < 65 cm dbh. There were no apparent trends with the estimated site productivity. We found greater consistency among sites than we anticipated based on earlier studies. For mixed mesophytic old-growth forests in Kentucky, McComb and Muller (1983) and McGee (1984) reported similar live/dead ratios, although for trees larger than 71 cm, McGee's data showed a ratio of 0.26. Calculated dead/live tree ratio values for trees > 5.0 cm in diameter from study of hemlock-northern hardwood forest, beech-maple mesic forest, spruce-northern hardwood forest, and mountain spruce-fir forest were 0.16, 0. 16, 0.12, and 0.29 respectively (Leopold et al. 1988). Published data for trees ≥ 3 cm from a 20 yr study of an old-growth sugar maple–beech woodlot (Schneider 1966) indicated dead/live ratios of 0.02, 0.08, and 0.12, respectively, as the stand aged from 1940 to 1950 to 1960. Although the dead/live ratio appears to increase with increasing age, the property was not protected from firewood cutting until 1939, and this may have influenced the number of snags.

The consistency of the ratio of dead to live trees by diameter class in the old-growth forests is notable for two reasons. First, there is no *a priori* reason to expect dead/live ratios to vary by only a few percent across a wide range of diameters. Given factors such as the relatively low survival rates for understory trees and the relatively rapid decomposition for small diameter logs, we expected much greater variability in dead/live ratios by diameter class. Second, this consistency by diameter class allows the size structure of the live trees to give visual clues about the size structure of snags. The snags themselves are so widely scattered that it is impossible to get a sense of the snag size

Table 4. Deadwood volume comparisons. Old-growth vs. second-growth one way ANOVA for comparison of mean.

Deadwood type	Old-growth				Second-growth				ANOVA
	Mean	Stand. Dev.	Range	No. of sites	Mean	Stand. Dev.	Range	No. of sites	P-value
	(m^3/ha)				(m^3/ha)				
Standing	21	9	10–36	11	10	8	3-128	50	< 0.01
Down	60	24	24-111	12	20	19	0.2-32	50	< 0.01

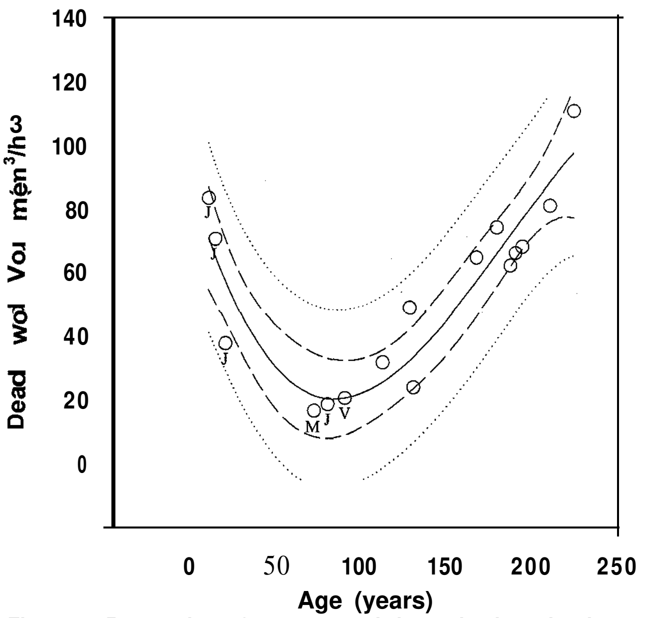

Figure 7. Regression of age vs. total down deadwood volume. Deadwood vol. $= 87.520 - 1.768\ \mathrm{Age} + 0.014\ \mathrm{Age}^2 - 0.00002\mathrm{Age}^3$; $R^2 = 0.862$ and P-value < 0.001. Stands denoted by (J) are means of volume by age class. These sites represent forests after major disturbance by clearcut (Jenkins and Parker 1997) and are based on data from 46 openings. The value denoted by(M) is the mean volume for the 9 second-growth stands in Missouri. The value denoted by (V) was calculated from the Van Kley (1993) data and represents the mean volume of 41 stands. The remaining points represent the old-growth sites in this study. Dashed line is 95% confidence interval. Dotted line is 95% prediction interval. Note that the Roaring River and Baber Woods old-growth sites were not included since age data was not collected at those sites. The maximum age at Roaring River is 200-250 yr based on published tree ring chronologies. This is not a representative sample of dominant trees, but a good upper limit.

distribution by visual inspection. It is, however, possible to observe the size structure of live trees with the realization that, on average, the relative size distribution of snags will be similar to that of the live trees even though the snags are only about 10% as abundant. The consistent ratio of snags to live trees also indicates that ratio estimators may have utility in improving sampling efficiency for snags. The consistency of the dead/live tree ratio in all the inventoried mature second-growth and old-growth forests may also have implications for forest health monitoring. If major departures from these reported live/dead ratios are observed for other mature forests in the region, it suggests that different disturbance factors are at work and further investigation of possible causes may be warranted.

Comparison of Old-Growth vs. Second-Growth Forest

Within this four-state region, more than 200,000 ac of second-growth forests on public lands have been designated to develop old-growth characteristics. Over time, these forests will experience dramatic increases in the volume of deadwood. The volume of down wood and snags has utility as an indicator of the degree of old-growth structure that has been attained by second-growth central hardwood forests. For example, old-growth forests and 60- to 80-yr-old forests differ greatly in volume of snags and down wood even though traditional measures of the live tree structure such as basal area, number of live stems, or stocking percent may be similar for both (Shifley et al. 1995). Monitoring the down wood volume in maturing second-growth forests provides a useful indicator of their progress toward an old-growth condition.

Another major difference between the old-growth and second-growth sites is the size of both standing and down wood. The greater quantity of larger diameter material at the old-growth sites provides long-lasting nutrient reservoirs and greater structural diversity than in the second-growth forests. Large, well-decayed logs also retain moisture in dry summer months (Maser et al. 1988) and may be beneficial to salamanders and other moisture-dependent amphibians (Kimmins 1997). Although the old-growth sites had greater structural diversity in large diameters, the second-growth sites had greater structural diversity in the smaller diameters in the higher productivity region. The larger material at the old-growth sites is also less likely to be consumed in fire, making these forests somewhat more resistant to fire. The high proportion of small diameter standing dead trees in the second-growth sites indicates a high turnover rate. Because this small diameter material decays rapidly, nutrients are likely cycled at a higher rate, influencing the energetics of these sites in a positive feedback loop.

The ratio of dead to live trees by dbh class varied more for the Indiana second-growth sites than for the Missouri second-growth sites or the old-growth sites. Specifically, for second-growth sites in Indiana, the ratio of dead to live trees increased from 0.04 to 0.18 with decreasing dbh (Figure 6a). This may be a function of site productivity. Compared to the low productivity sites that often have open understories, the high productivity sites generally support more trees in the understory. Through competition-induced mortality, these small trees become snags in the smaller diameter classes.

Age Relationship

The pseudo-hyperbolic curve describing the relationship between down wood volume and stand age (Figure 7) is supported by a number of studies from other geographic regions (Spies and Cline 1988, Hedman 1992, McCarthy and Bailey 1994, Hardt and Swank 1997). These authors all found the greatest volume of down wood in the years immediately following stand regeneration. Down wood volume decreased with increasing stand age as the stand matured, but ultimately down wood increased for stands in the old-growth stage of development. For example, Spies and Cline reported the mean volume of standing plus down wood in Douglas-fir forests to be less than 423 m³/ha for young stands (age 65), 250 m³/ha for mature forests (age 121), and 534 m³/ha for old-growth forests (age 404). For Appalachian mixed mesophytic hardwood forests, McCarthy and Bailey's (1994) table of down wood for pieces > 10 cm in diameter indicated 61 m³/ha of down deadwood for a 2-yr-old stand following clearcut, 29 m³/ha for a 15- to 25-yr-old pole stand, 33 m³/ha for a 65- to 90-yr-old stand, and 38m³/ha for a stand more than 100 yr old. An important lesson from these studies and Figure 7 is that forest conditions other than old-growth can produce large volumes of deadwood.

The trend in deadwood estimates in Figure 7 also relates well with the Borman and Likens (1979) model of biomass accumulation. The first three data points (10, 14, and 20 yr) correspond to the reorganization phase; the next three data points (72, 80, and 90 yr) correspond to the middle of the aggradation phase; and most of the old-growth sites are in the transition phase. In the reorganization phase, residual deadwood and deadwood deposited from a disturbance decomposes rapidly. During the mid-aggradation phase, there should be little overstory mortality and, thus, less deadwood input. The transition phase is a period when dominant trees begin to die, forming gaps and adding large volumes of deadwood to the forest floor. These three groups of data points correspond to Oliver and Larson's (1990) development stages of stand initiation/ stem exclusion, understory reinitiation, and old-growth, respectively. They also correspond with Peet and Christensen's (1987) establishment phase, late thinning phase/early transition phase, and late transition phase/ early steady-state phase.

Disturbance

Although deadwood volume varied with both regional productivity and age, individual disturbance events can markedly alter rates of down wood accumulation. On June 4, 1993, high winds affected the entire Laughery Bluff site and surrounding areas. Approximately 20 m^3/ha of deadwood was added to the site during that single event. Wind-caused mortality resulted in 87% of the coarse woody debris volume in a Michigan *Acer saccharum* forest (Eyre and Longwood 1951). A 1994 ice storm at the Dark Hollow site in Missouri (after the inventory for this study) increased the volume of down deadwood by 27% (Rebertus et al. 1997). These observations stress the importance of considering potential impacts of individual disturbance events. Long-term and large-scale studies will be necessary to gain a more comprehensive perspective of the influence of site productivity, age, and disturbance events on patterns of coarse woody debris accumulation over time.

It is also important to note that dynamics of the midwestern old-growth forests of today are likely different from those prior to European settlement. One major difference is the fire suppression that began in the early 1900s and has been effective across the region since the 1950s. Historical accounts note periodic fire as a major disturbance factor in these forests, for example:

1. "Annually, after this rank growth of vegetation had become forested and dry, the Indians set fire to it and burned the entire surface of the country" (Mudd 1888).
2. ". ..not withstanding the ravages of tire, the marks of which are everywhere to be seen, the woods, principally hickory, ash, and walnut formed a forest tolerably close" (Brackenridge 1816).

Fire was used by native Americans for agricultural clearing and driving game (DenUyl1954, McCord 1970, Campbell 1989, DeVivo 1990, Reich et al. 1990, Denevan 1992). In the midwestem United States, these were most often groundfires that burned leaves and small diameter woody debris while rarely consuming large diameter logs or causing extensive overstory mortality. Fire suppression may have altered mechanisms for coarse woody debris accumulation in these old-growth forests. However, because we do not have data on coarse woody debris prior to fire suppression, we can only speculate on presuppression dynamics. The most likely effect on coarse woody debris is increased accumulation, for two reasons. First, down wood, especially small diameter material, is no longer consumed by periodic fires. Secondly, stands are able to develop more densely (more trees/ha) than when frequent fire was present leading to increased self thinning from increased competition.

Inventory Standards

While methods to determine decomposition classes have been proposed for Douglas fir forests (Cline et al. 1980, Maser et al. 1979), there is a need to establish standards that will facilitate direct comparison among study sites in the eastern United States. Our methods were similar to those employed in previous studies (e.g., Muller and Liu 1991, McCarthy and Bailey 1994, Hardt and Swank 1997, Richards et al. 1995, Shifley et al. 1995, Spetich 1995, Jenkins and Parker 1997, Shifley et al. 1997). The down wood decomposition classes we used were not particularly effective in distinguishing subtle differences in the level of woody decomposition. More than half the down wood was in a single decomposition class (class 3), while other classes rarely occurred. Ideally, decomposition classes should be delineated so they are relevant to the habitat requirement of wildlife species or the process of nutrient cycling. As a minimum, greater discrimination among the class 3 material is desirable. We also acknowledge the need for standardization of sampling procedures as proposed by McCarthy and Bailey (1994).

Conclusions

Overall, deadwood characteristics of midwestern old-growth forests vary among sites, but old-growth deadwood volume increased along a regional gradient of increasing forest productivity. Down wood volumes ranged from 24 m^3/ha to 111 m^3/ha, and standing deadwood volumes ranged from 10 m^3/ha to 36 m^3/ha. There were clear patterns of increasing forest productivity across the study region, and these are correlated with observed volumes of snags and down deadwood for old-growth forests. Based on these results, interpretation of structural features such as deadwood volume and number of pieces of down wood must be considered in the context of the regional patterns of forest productivity. Interpretation of deadwood observations at a given site is enhanced by an understanding of these general region-wide patterns. Deadwood volume in a mature, productive, second-growth forest can approach the deadwood volume of an old-growth forest on a site of low productivity.

In old-growth forests inventoried across the region, the ratio of standing dead trees to standing live trees was relatively consistent at approximately 0.1 across all diameter classes ≤ 65 cm. The ratio of dead to live trees on the mature, second-growth forests was lower at approximately 0.07. This ratio was consistent across diameter classes for second-growth sites in Missouri. However, for the higher productivity sites in Indiana, the dead/live ratio was 0.21 for trees between 10 and 24 cm. The ratio of the number of dead to live trees, perhaps in combination with the ratio of basal areas of dead and live trees, may find utility as an indicator of forest health.

Based on data from this study and data collected by previous investigators, recently harvested forests and old, undisturbed forests can have deadwood volumes that are more than three times greater than values for 70- to 90-yr-old upland forests. Down deadwood volume drops rapidly in the first several decades following harvest and reaches a minimum in the 50- to 100-yr age class. In stands older than 100 yr, down deadwood volume increases with increasing stand age and increasing site productivity.

Literature Cited

AUSMUS, B.S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. P. 180-192 in Soil organisms as components of ecosystems. Proc. of the 6th Intemat. Soil Zool. Colloq. Lohm, U., and T. Persson, (eds.). Ecol. Bull. Vol. 25. Swedish Natur. Sci. Res. Counc., Stockholm.

BARNUM, S.A., C.J. MANVILLE, J.R. TESTER, AND W.J. CARMEN. 1992. Path selection by *Peromyscus leucopus* in the presence and absence of vegetative cover. J. Mammal. 73:797–801.

BORMANN, F.H., AND G.E. LIKENS. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. Am. Sci. 67:660–669.

BRACKENRIDGE, H.M. 1816. Journal of a voyage up the river Missouri. Ed. 2. Reprinted *in* Thwaites, R. R., 1904. Early western travels 1748-1846. Vol VI. A.H. Clark, Cleveland.

BRAY, J.R., AND E. GORHAM. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2:101–157.

CAIN, M.D. 1996. Hardwood snag fragmentation in a pine-oak forest of southeastern Arkansas. Am. Midl. Natur. 136:72–83.

CALDWELL, R.S. 1996. Macroinvertebrates and their relationship to coarse woody debris with special reference to land snails. P. 49-54 *in* Biodiversity and coarse woody debris in southern forests. Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

CAMPBELL, J.J.N. 1989. Historical evidence of forest composition in the bluegrass region of Kentucky. P. 23 l-246 *in* Proc. of the seventh central hardwood for. conf. Rink, G., and C.A. Budelsky (eds.). USDAFor. Serv. Gen. Tech. Rep. NC-132.

CARMEAN, W.H., J.T. HAHN, AND R.D. JACOBS. 1989. Site index curves for forest tree species in the *eastern* United States. USDA For. Serv. Gen. Tech. Rep. NC-128. 142 p.

CARMEAN, W.H. 1979. Site index comparisons among northern hardwoods in northern Wisconsin and upper Michigan. USDAFor. Serv. Res. Pap. NC-169. 17 p.

CLINE, S.P., A.B. BERG, AND H.M. WRIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:773–786.

DENEVAN, W.M. 1992. The pristine myth: The landscape of the Americas in 1492. Ann. Assoc. of Am. Geogr. 82: 369-385.

DENUYL, D. 1954. Indiana's old-growth forests. Proc. of Indiana Academy of Sci. 63:73–79.

DEVIVO, M.S. 1990. Indian use of tire and land clearance in the southern Appalachians. P. 306-310 *in* Fire and the environment: Ecological and cultural perspectives, Proc. of an international symposium. USDA For. Serv. Gen. Tech. Rep. SE-69.

EDMONDS, R.L. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. Can. J. For. Res. 17:499–509.

EYRE, F.H., AND F.R. LONGWOOD. 195 1. Reducing mortality in old-growth northern hardwoods through partial cutting. USDAFor. Serv. Lake States For. Exp. Sta., Sta. Pap. 25.

FLEBBE, P.A., AND C.A. DOLLOFF. 1991. Habitat structure and woody debris in southern Appalachian wilderness streams. Proc. of annu. conf. of southeast assoc. of fish and wildlife agencies 45:444–450.

FRANKLIN, J.F., H.H. SHUGART, AND M.E. HARMON. 1987. Tree death as an ecological process. BioSci. 37:550–556.

HANSEN, M.H., T. FRIESWYK, J.F. GLOVER, AND J.F. KELLY. 1992. The Eastwide forest inventory database: Users manual. USDA For. Serv. Gen. Tech. Rep. NC-151.48 p.

HARDT, R.A., AND W.T. SWANK. 1997. A comparison of structural and compositional characteristics of southern Appalachian young second-growth, maturing second-growth, and old-growth stands. Natur. Areas J. 17:42–52.

Harmon, M.E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. P. 133-302 *in* Advances in ecological research. Macfadyen, A., and E.D. Ford (eds.). Academic Press, New York.

HARRIS, W.F., G.S. HENDERSON, AND D.E. TODD. 1972. Measurement of turnover of biomass and nutrient elements from the woody component of forest litter on Walker Branch Watershed. Eastern Deciduous Forest Biome Memo. Rep. 72-146. Oak Ridge Nat. Lab., Oak Ridge, TN.

HEDMAN, C.W. 1992. Southern Appalachian riparian zones: Their vegetative composition and contribution of large woody debris to streams. Ph.D. Diss., Dept. of For. Resourc., Clemson University, Clemson, SC. 146 p.

HEDMAN, C.W., AND D.H. VAN LEAR. 1990. Large woody debris contributions from riparian zones: Current knowledge and study description. P. 681-687 *in* Proc. of the sixth bienn. south. silvic. res. conf., Vol. 2, Memphis, TN.

HENDRIX, P.F. 1996. Earthworms, biodiversity, and coarse woody debris in forest ecosystems of the southeastern U.S.A. P. 43-48 *in* Biodiversity and coarse woody debris in southern forests. Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

HOMOYA, M.A., D.B. ABRELL, J.R. ALDRICH, AND T. W. POST. 1985. The natural regions of Indiana. Proc. of the IN Acad. of Sci. 94:245–268.

HUSTON, M.A. 1996. Models and management implications of coarse woody debris impacts on biodiversity. P. 139-143 *in* Biodiversity and coarse woody debris in southern forests. Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiverstiy, McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

JENKINS, M.A., AND G.R. PARKER. 1997. Changes in down deadwood volume across a chronosequence of silvicultural openings in southern Indiana forests. P. 162-169 *in* Proc. of the 11th central hardwood for. conf. Pallardy, S.G., et al. (eds.). USDA For. Serv. Gen. Tech. Rep. NC-188.

KIMMINS, J.P. 1997. Forest ecology-a foundation for sustainable management. Prentice-Hall, Upper Saddle River, NJ. 596 p.

LANG, G.E., AND R.T. FORMAN. 1978. Detrital dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. Ecol. 59:580–595.

LANHAM, J.D., AND D.C. GUYNN, JR. 1996. Influence of coarse woody debris on birds in southern forests. P. 101-107 *in* Biodiversity and coarse woody debris in southern forests. Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

LARSON, F.R. 1992. Downed woody material in southeast Alaska forest stands. USDA For. Serv. Res. Pap. PNW-452. 12 p.

LEOPOLD, D.J., C. RESCHKE, AND D.S. SMITH. 1988. Old-growth forests of Adirondack Park, New York. Natur. Areas J. 8:166–189.

LOEB, SC. 1996. The role of coarse woody debris in the ecology of southeastern mammals. P. 108-118 in Biodiversity and coarse woody debris in southern forests. Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

MACMILLAN, P.C. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can. J. For. Res. 18:1353–1362.

Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. Natur. Areas J. 12:127–135.

Maser C.M., and J.M. Trappe. 1983. The fallen tree-a source of diversity. P. 335-339 *in* Proc. of the 1983 convention of the Society of American Foresters. Soc. Am. For., Bethesda, MD.

Maser C.M., R.G. Anderson, K. Cormack Jr., J.T. Wlliams and R.E. Martin. 1979. Dead and down woody material. P. 78-95 *in* Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington. Thomas, J.W. (ed.). USDA For. Serv. Agric. Handb. 553.

Maser, CM., S.P. Cline, K. Cormack Jr., J.M. Trappe, and E. Hansen. 1988. What we know about large trees that fall to the forest floor. P. 25–47 *in* From the forest to the sea: A story of fallen trees. Maser C.M., R.F. Tarrant, J.M. Trappe, and J.F. Franklin (eds.). USDA For. Serv. Gen. Tech. Rep. PNW-229.

McCarthy, B.C., and R.R. Baily. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Can. J. For. Res. 24:1317–1329.

McCord, S.S. 1970. Travel accounts of Indiana 1679–1961. Indiana Historical Bureau, Indiana Library and Historical Board, Indianapolis, Indiana.

McGee, C.E. 1984. Heavy mortality and succession in a virgin mixed mesophytic forest. USDA For. Serv. Res. Pap. SO-209.9 p.

McComb, W.S., and R.N. Mueller. 1983. Snag densities in old-growth and second-growth Appalachian forests. J. Wildl. Manage. 47:376–382.

Meyer, J. 1986. Management of old growth forests in Missouri. Habitat Manage. Ser. No. 3. Missouri Dep. of Conserv., Jefferson City, MO. 16 p.

Mudd, J.A. 1888. History of Lincoln County, Missouri from the earliest time to the present. Godspeed Publishing Co., Chicago, IL.

Muller, R.N., and Yan Liu. 1991. Coarse woody debris in an old-growth forest on the Cumberland Plateau, Southeastern Kentucky. Can. J. For. Res. 21:1567–1572.

Neely, R.D., and C.G. Heister. 1987. The natural divisions of Illinois, introduction and guide. Illinois Natural History Survey, Dept. of Energy and Natur. Resour., State of Illinois. Spec. Publ. 6.224 p.

Oliver, C.D., and B.C Larson. 1990. Forest stand dynamics. McGraw-Hill, New York. 467 p.

Olszewski, J.L. 1968. Role of uprooted trees in movements of rodents in forests. Oikos 19:99–104.

O'Neill, R.V. 1967. Niche segregation in seven species of Diplopods. Ecol. 48:983.

O'Neill, R.V., and D.L DeAngelis. 1981. Comparative productivity and biomass relations of forest ecosystems. P. 4 1 1-449 *in* Dynamic properties of forest ecosystems, Reichle, D.E. (ed.). Cambridge Univ. Press, Cambridge, MA.

Parker, G.R. 1989. Old-growth forests of the Central Hardwood Region. Natnr. Areas J. 9:5-1 1.

Peet, R.K., and N.L. Christensen. 1987. Competition and tree death. Bioscience 37:586–595.

Rebertus, A.J., S.R. Shifley, R.H. Richards, and L.M. Roovers. 1997. Ice stormdamage toanold-growthoak-hickory forest inMissouri. Am. Midl. Natur. 137:48–61.

Reich, P.B., M.D. Abrams, D.S. Ellsworth, E.L. Kruger, and T.J. Tabone. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71:2179–2190.

Richards, R.H., S. R. Shifley, A.J. Rebertus, and S.J. Chaplin. 1995. Characteristics and dynamics of an upland Missouri old-growth forest. P. 1 1-22 inProc.ofthe 1OthCentralHardwoodFor.Conf. Gottschalk, K.W., and S.L.C. Fosbroke (eds.). USDA For. Serv. Gen. Tech. Rep. NE-197.

RockWare Utilities. 1995. Contour USA utility. RockWare Inc., Golden, co.

Schneider, G. 1966. A twenty-year ecological investigation in a relatively undisturbed sugar maple-beech stand in southern Michigan. Michigan State Univ. Res. Bull. #15. 61 p.

Shifley, S.R., B.L. Brookshire, D.R. Larsen, L.A. Herbeck, and R.G. Jensen. 1997a. Snags and down wood on upland oak sites in the Missouri Ozark Forest Ecosystem Project. P. 248-256 *in* Proc. of the Missouri Ozark For. Ecosystem Proj. symp.: An experimental approach to landscape research. Brookshire, B.L., and S.R. Shifley (eds.). USDA For. Serv. Gen. Tech. Rep. NC-193.

Shifley, S.R., B.L. Brookshire, D.R. Larsen, and L.A. Herbeck. 1997b. Snags and down wood in Missouri old-growth and mature second-growth forest. North. J. Appl. For. 14:165–172.

Shifley, S.R., L.M. Roovers, and B.L. Brookshire. 1995. Structural and compositionaldifferences betweenold-growthandmaturesecond-growth forests in the Missouri Ozarks. P. 23-36 *in* Proc. of the 10th Central Hardwood For. Conf., Gottschalk, K.W., and S.L.C. Fosbroke (eds.). USDA For. Serv. Gen. Tech. Rep. NE-197.

Spetich, M.A., and G.R. Parker. 1998. Distribution of biomass in an Indiana old-growth forest from 1926 to 1992. Am. Midl. Natur. 139:90-107.

Spetich, M.A. 1995. Characteristics and spatial pattern of old-growth forests in the Midwest. Ph.D. Diss., Purdue Univ., West Lafayette, IN. 276 p.

Spies, T.A., and S.P. Cline. 1988. Coarse woody debris in forests and plantations of coastal Oregon. P. 5-24 *in* From the forest to the sea: A story of fallen trees. Maser , C.M., et al. (eds.). USDA For. Serv. Gen. Tech. Rep. PNW-229.

Thom, R.H., and J.H. Wilson. 1980. The natural divisions of Missouri. Transact. Missouri Acad. Sci. 14:9–23.

Thomas, J.W., R.G. Anderson, C. Maser, and E.L. Bull. 1979. Snags. P. 60-77 *in* Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington. Thomas, J.W. (ed.). USDA For. Serv. Agric. Handb. 553.

Van Kley, J.E. 1993. An ecological classification system for the central hardwoods region: The Hoosier National Forest. Ph.D. Diss., Purdue Univ., West Lafayette, IN. 435 p.

Van Lear, D.H. 1993. Dynamics of coarse woody debris in southern forest ecosystems. P. 10–17 *in* Biodiversity and coarse woodydebrisinsouthem forests, Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiversity. McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

Whiles, M.R., and J.W. Grubaugh. 1996. Importance of coarse woody debris to southern forest herpetofauna. P. 94-100 *in* Biodiversity and coarse woody debris in southern forests, Proc. of the workshop on coarse woody debris in southern forests: Effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-94.

White, J. 1978. Illinois natural areas inventory technical report. Survey of methods and results. Illinois natural areas inventory at Urbana. 1:315–332.