TREE MORTALITY, CANOPY TURNOVER, AND WOODY DETRITUS IN OLD COVE FORESTS OF THE SOUTHERN APPALACHIANS

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Abstract. A long-term study of tree mortality, canopy turnover, and coarse woody detritus inputs was conducted in cove forests of the Great Smoky Mountains, Tennessee, USA. Seven old-growth stands were studied over a 10-yr period using 0.6–1.0 ha plots. Annual mortality of trees >10 cm dbh was 0.5–1.4% among stands (mean 0.7%). The highest mortality rate among canopy trees was exhibited by trees >80 cm dbh. An increase in mortality rate with canopy tree size was evident for two (*Tsuga canadensis* and *Acer saccharum*) of the three most abundant species in the forest. The increase in mortality with tree size had implications for canopy turnover and detritus input. Gap disturbance frequency was estimated at 0.008–0.019 forest area/yr, giving a return interval of ~130 yr or less. Standing death was the most common mode of mortality (59%). Annual rates of snag formation were 1.4 snags/ha for trees >10 cm dbh and 0.4 snags/ha for trees >50 cm dbh. The density of large snags (>50 cm dbh) was 5 snags/ha. Snags accounted for 8% of the total standing tree basal area and 23% of the coarse woody detritus mass (total of 48 Mg/ha). The mean annual rate of coarse woody detritus input was 3.0 Mg/ha. A decay rate constant was estimated at 0.07, yielding a detritus half-life of 10 yr. Although mean mortality rates and canopy turnover in old cove forests were moderate in comparison with other old forests of eastern North America, input and accumulation of coarse woody detritus were high for the region. This resulted, in part, from the relatively large sizes attained by canopy trees and the fact that larger trees tended to suffer higher mortality. In comparison to forests worldwide, rates of mortality, canopy gap formation, and decay of coarse woody detritus were intermediate.

Key words: Acer saccharum; *canopy gap; coarse woody debris; decay; Great Smoky Mountains, Tennessee; natural disturbance; old growth; size-specific mortality;* Tsuga canadensis.

INTRODUCTION

Old forests of natural origin often exhibit characteristic composition and physical structure. For example, old temperate forests tend to have large trees (live and dead), diverse height structure, a broad size distribution of canopy gaps, and a large component of shade-tolerant species (Franklin et al. 1981, Peterken 1996). The dynamics of old forests are less clear. Mortality of trees as they age has implications for old-forest dynamics. It has been suggested that large canopy trees are subject to high mortality (e.g., Goff and West 1975, Lorimer et al. 2001). However, information on mortality rates of large, old trees is generally insufficient to support or refute this claim (Franklin et al. 1987, Harcombe 1987). It is also unclear whether there is a substantial change in stand-level tree mortality as forests proceed to old age. Peet and Christensen (1987) reason that mortality rates should diminish with stand age because of altered stand structure that reduces resource competition among established trees. However, evidence of a decline in mortality is scarce for forest stands beyond the thinning stage. Furthermore, mortality rates certainly influence dynamics, but factors such as disturbance patch size affect dynamics as well. For example, canopy tree size may be important in disturbance processes because tree size largely determines gap size (Brokaw 1982, Clebsch and Busing 1989, Milton et al. 1994, Busing 1995). Lorimer (1989) suggests that gap disturbance may be greater in old forests, partly as a consequence of larger gap size, but the combined effects of gap size and formation rate are not fully understood.

Understanding of size-specific mortality, gap dynamics, and woody detritus dynamics can be gained by long-term study of disturbance and tree mortality. Most studies of canopy disturbance and turnover have relied on observations of gap-phase disturbances at one point in time. The resulting estimates of canopy turnover rate vary greatly and in some cases they do not coincide with lifespans of old forest dominants (Veblen 1992). For example, canopy turnover estimates of 1% forest area/yr and turnover times <200 yr (Romme and Martin 1982, Runkle 1982) seem high for forests comprised of trees capable of multi-century survival. A logical first step is to determine the actual rate of canopy tree mortality, which would allow the question of how long-

PLATE. 1.   An unlogged cove forest near Porters Creek, Great Smoky Mountains, Tennessee (USA). Photo credit R. T. Busing.

term mortality rates of canopy trees correspond to existing estimates of canopy gap disturbance frequency and rotation length to be addressed. Whether the largest trees, with potentially high influence on canopy turnover, have distinctive rates of mortality, is a key issue here.

Old temperate forest ecosystems typically have high accumulation of woody detritus (Harmon et al. 1986, Muller and Liu 1991, Stewart and Burrows 1994, Spetich et al. 1999). Biomass losses to mortality are one reason for elevated levels of woody detritus and diminished primary production in old forests. The rate of biomass loss appears to be comparatively high in old forests (Acker et al. 2002). If this applies to old cove forests, is high biomass loss a simple consequence of the greater biomass per tree in old forests or is elevated mortality a contributing factor? The relative importance of factors regulating biomass loss in old forests can be evaluated through long-term study of size-specific tree mortality.

This paper contains results of a comprehensive 10-yr study of tree mortality, canopy turnover, and input rates of various forms (e.g., snag or log) of coarse woody detritus. The first general objective is to determine whether rates of tree mortality, canopy turnover, and detritus input are distinctive in old cove forests. The second general objective is to understand the relations among tree mortality, canopy turnover, and detrital wood inputs, with emphasis on the contributions of tree size and mortality rate to these disturbance processes. Specifically, this study addresses the following questions: (1) Do rates of tree mortality vary by tree size and species? (2) Are rates of tree mortality similar to those in other temperate deciduous forests? (3) Do rates of canopy turnover under the observed levels of canopy tree mortality match previous estimates for temperate deciduous forests? (4) Do the input rate, standing mass, and decay rate of coarse woody detritus match those of other temperate deciduous forests? Comparison of these findings to other forest ecosystems of contrasting age and biogeography may provide insight into the relationships among tree mortality, canopy turnover, and woody detritus dynamics in old forests.

The study forest

Cove forests of the southern Appalachian Mountains, USA, are geographic segregates of Braun's (1950) mixed mesophytic forest. The mesophytic region, one of nine regions within the deciduous forest formation covering much of eastern North America (Braun 1950), contains stands with an unusually rich assemblage of temperate deciduous tree species (Barbour et al. 1980). The term "cove" refers to the topographic location of these forests in montane valleys or ravines (Whittaker 1956). Cove forests are typically mesic, receiving abundant precipitation (>150 cm/yr) throughout the year. Their climate fits Thornthwaite's (1948) perhumid mesothermal class (Shanks 1954).

Situated in mesic, sheltered valleys or ravines, cove forests are relatively free of catastrophic natural disturbance. Small-scale disturbances (<0.1 ha in area), often caused by lightning storms, wind storms, ice storms, or disease, are a common pattern of canopy tree mortality in coves. Larger natural disturbance patches created by such factors as fire or hurricane events are rare in cove forests of the southern Appalachian Mountains.

Extensive unlogged forests in biological reserves of the southern Appalachian Mountains are representative of old temperate forests of eastern North America. They are well suited for long-term study of old temperate forest dynamics (e.g., Runkle 2000). Unlogged cove forests have stands with large trees and high basal area (Busing 1998a, b). Stand age structure is mixed, with ages of older trees exceeding 300 yr. Typically, composition of the tree stratum is mixed-deciduous with *Tsuga canadensis*, a coniferous species that increases to codominant or dominant status on particularly moist sites (Cain 1943, Braun 1950, Whittaker 1956, Golden 1981, Busing 1998a).

TABLE 1. Characteristics of study stands in coves of the northern Great Smoky Mountains, Tennessee, USA.

Site	Code	Plot area (ha)	Elevation (m)	Dominant species	Sampling interval
Long Branch	LB1	0.6	920	*Acer–Tsuga–Halesia*	1988–1998
Long Branch	LB2	0.6	950	*Halesia–Acer–Tsuga–Aesculus*	1988–1998
Porters Creek	PC	0.6	720	*Halesia–Acer–Aesculus*	1989–1999
Roaring Fork	RF1	1.0	960	*Tsuga–Halesia–Fagus–Acer*	1990–2000
Roaring Fork	RF2	1.0	990	*Tsuga–Halesia–Acer–Fagus*	1990–2000
Roaring Fork	RF3	1.0	1140	*Tsuga–Halesia–Aesculus*	1990–2000
Dunn Creek	DC	0.6	970	*Tsuga–Acer–Halesia–Liriodendron*	1992–2002

Long-term findings on canopy tree turnover and eco-system dynamics of old cove forests are only beginning to emerge (Busing 1998*b*, Runkle 2000). Extensive, long-term data on tree mortality in cove forests are scarce. Most observations suggest that tree mortality rates in cove forests are moderate and do not deviate strongly from those found in several other long-term studies in eastern North American forests (e.g., Abrell and Jackson 1977, Parker et al. 1985, Runkle 2000). Live biomass (Whittaker 1966, Busing et al. 1993) and coarse woody detritus volume (Busing 1998*b*) are among the highest reported for temperate forests of eastern North America. Nonetheless, net primary production is moderate in old stands (Whittaker 1966, Busing et al. 1993).

METHODS

Data collection

Seven study sites were selected in an old-growth forest spanning several watersheds on the north slope of the Great Smoky Mountains (see Plate 1; Table 1; 35°40′ N, 83°23′ W). Accessibility, terrain, and a history of vegetation study were considerations in site selection (Busing 1998*a, b*). All stands were predominantly deciduous with no history of logging or catastrophic fire. The three stands at Roaring Fork had a high *Tsuga* component (>35% by biomass; Busing 1998*a*). A plot (0.6–1.0 ha) was located on a north-facing slope at each site and marked for long-term study. Placement and dimensions of the plots were determined largely by shrub density and local topography; dense thickets of *Rhododendron* and slopes >35° were avoided. Plots tended to be rectangular, with a length of ≥100 m and a width of ≥50 m. Each plot was divided into contiguous 10 × 10 m subplots.

During initial sampling of each plot, live trees (>2 cm dbh [diameter at breast height, 1.37 m]), canopy gaps (>25 m²), and coarse woody detritus items (>10 cm diameter) were mapped. The species and dbh of each live tree were recorded. Edges of canopy gaps lacking substantial ingrowth >10 m tall were drawn on the plot map. Pieces of woody detritus were classified as a snag (standing dead trees >1.37 m tall) or a log (fallen dead trees, and stumps <1.37 m tall). Length, diameter, and shape (cylindric, parabolic, or conic) of each dead wood item were noted for volume estimation. Length measurements on items excluded portions extending beyond the plot boundary. Species and degree of decay (classes 1–4, lightly decayed to highly decayed) were also noted. The decay classes corresponded to the five-class system (e.g., Pyle and Brown 1998) except that logs with a high degree of decay were lumped into one decay class (class 4) rather than differentiated into two classes (class 4 or 5). Highly decayed logs were included only if they protruded above the litter layer.

Specific gravity of wood at various stages of decay was determined for species comprising a substantial portion of the coarse woody detritus. Samples were collected in old-growth forest outside of the study plots at Roaring Fork. Disks 4–9 cm thick, with representative proportions of heartwood and sapwood, were taken from dead down trees. Five samples were collected for each combination of decay class and species (or species group). Volume of each cylindric item was determined from measurements taken on wet samples. The volume of irregularly shaped items was determined by sealing the item in a plastic bag and immersing it in a flask of water. Samples were then oven dried at 55°C for ~2 wk until constant weight was obtained. Dry weight of each wood sample was measured for estimation of specific gravity by decay class and species (or species group).

Five years after each plot was established, the status of each tree was evaluated. Trees dying over the 5-yr interval were noted. The mode of mortality (standing dead with unbroken bole, standing dead with bole broken above 1.37 m, bole broken below 1.37 m, or uprooted) was recorded. It was also noted if an adjacent tree fall had damaged and killed the individual. Similar data were collected ten years after plot establishment. At this time, dbh of all standing trees was measured. New woody detritus items were measured and mapped.

Data analysis

Tree mortality was analyzed by 10 cm dbh classes. Size-specific trends among canopy trees were tested for statistical significance using maximum-likelihood logistic regression. One test was performed on all trees >30 cm dbh ($n = 862$). A second test was performed on all trees >60 cm dbh ($n = 260$) to test for trends among large canopy trees. These tests were also per-

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TABLE 2. Tree mortality tallies by stand, size class, and mode of mortality.

Tree dbh class (cm)	Status	Mortality (over 10 yr), by stand			
		LB1	LB2	PC	RF1
>10–20	initial total live	58	71	71	141
	total dead	9	5	10	8
	standing dead	4	3	3	3
>20–30	initial total live	31	47	28	63
	total dead	2	2	5	2
	standing dead	1	1	2	1
>30–40	initial total live	25	17	24	54
	total dead	0	1	1	3
	standing dead	0	0	0	1
>40–50	initial total live	24	29	16	31
	total dead	3	3	3	1
	standing dead	2	2	3	1
>50–60	initial total live	22	11	8	30
	total dead	1	0	1	2
	standing dead	1	0	1	2
>60–70	initial total live	15	13	11	12
	total dead	0	0	2	0
	standing dead	0	0	1	0
>70–80	initial total live	10	4	11	8
	total dead	1	0	1	1
	standing dead	1	0	1	1
>80	initial total live	4	6	5	24
	total dead	0	2	0	2
	standing dead	0	2	0	2
All (>10)	initial total live	189	198	174	363
	total dead	16	13	23	19
	standing dead	9	8	11	11
Annual mortality		0.009	0.007	0.014	0.005
95% confidence limits		0.005, 0.014	0.004, 0.012	0.009, 0.021	0.003, 0.008

Notes: Tallies represent numbers of individuals dying over a 10-yr interval. Annual mortality rates are calculated for each stand and for each size class. Symmetrical 95% confidence intervals for annual mortality estimates are provided.

formed on *Tsuga canadensis*, *Halesia carolina*, and *Acer saccharum*, the three most abundant species (by density) in the study forest.

Gap formation rates were calculated using several methods. First, the fraction of total land area in gaps at the initial sampling was determined from field observations. Second, the frequency of gap closure, the amount of total land area reverting from gap to closed canopy, was determined using two estimates of the annual rate of gap closure (5% and 12% of gap area; Barden 1989). Assuming that the amount of total land area in gaps is near equilibrium, the closure frequency should match the gap disturbance frequency (the fraction of total land area converted to gaps per unit time). Other estimates of gap disturbance frequency were based on canopy tree mortality >10 yr. Canopy trees were defined as those having a dbh >30 cm. An analysis of tree crown position and dbh at the Roaring Fork sites (Table 1) revealed a lower diameter cutoff, near 30 cm dbh, for canopy trees.

The effect of canopy tree mortality on gap disturbance frequency was estimated using four mean gap sizes (0.006, 0.008, 0.020, 0.030 ha/gap). The 0.006 ha/gap value was the mean closed canopy area occupied

by a canopy tree in this study. It represented the smallest possible mean gap area resulting from the death of individual canopy trees. In combination with canopy tree mortality data, it served to estimate lower bounds for gap disturbance frequency. The 0.008 ha/gap value was derived from initial observations (1988–1992) of mean gap area per gapmaker tree in the study plots. Because this value did not account for gap closure after formation it is likely to underestimate the true mean area. A mean value of 0.02 ha/gap was based on Runkle's estimate (1981). However, this estimate was for expanded gap areas (sensu Runkle 1982) and it included gaps formed by the death of multiple canopy trees so it is likely to overestimate the true mean gap area created by the death of individual canopy trees. The 0.03 ha/gap value is an extreme upper limit for mean gap size in southern Appalachian cove forests estimated from values in the literature (Runkle 1981, Romme and Martin 1982). When applied in conjunction with tree mortality data, it is almost certain to overestimate gap disturbance frequency, providing upper bounds for this parameter.

Density, basal area, and volume were calculated for initial levels and 10-yr inputs of woody detritus by class

TABLE 2. Extended.

Mortality (over 10 yr), by stand				Annual mortality	95% confidence limits
RF2	RF3	DC	All		
206	103	92	742		
9	13	3	57	0.008	0.006, 0.010
8	6	2	29		
82	64	47	362		
5	4	4	24	0.007	0.004, 0.010
4	2	2	13		
43	42	28	233		
2	3	0	10	0.004	0.002, 0.008
1	1	0	3		
39	45	30	214		
2	1	3	16	0.008	0.004, 0.013
2	0	3	13		
40	31	13	155		
1	3	2	10	0.007	0.003, 0.012
0	0	2	6		
25	19	7	102		
0	2	0	4	0.004	0.001, 0.010
0	1	0	2		
19	11	6	69		
1	0	0	4	0.006	0.002, 0.015
1	0	0	4		
17	20	13	89		
2	2	0	8	0.009	0.004, 0.018
2	2	0	8		
471	335	236	1966		
22	28	12	133	0.007	0.006, 0.008
18	12	9	78		
0.005	0.009	0.005	0.007		
0.003, 0.007	0.006, 0.013	0.003, 0.009	0.006, 0.008		

(snag or log). Snags were defined as dead stems >1.37 m tall and >10 cm dbh. Estimates of snag formation rates and occurrence of various modes of mortality were based on the two sequential 5-yr assessments.

Ratios of mass of coarse woody detritus to stand biomass, production, and other measures were calculated to provide comparative information and to characterize ecosystem dynamics. Previously published data on biomass and production from the study stands were used in the calculations (Busing et al. 1993). For comparison to other studies, decomposition dynamics were quantified with the widely applied negative exponential model of decay (Olson 1963). Assuming steady-state detritus inputs and pools, the stand-level decay rate (k) was estimated as annual input mass divided by the total coarse woody detritus mass of each stand (Jenny et al. 1949, Olson 1963, Whittaker 1975, Christensen 1977, Sollins 1982, Onega and Eickmeier 1991). The half-life of detritus was then estimated for each stand using the single-exponential model of decay (Olson 1963, Harmon et al. 1986, Onega and Eickmeier 1991).

RESULTS

Tree mortality

The annual mortality rate for all 1966 trees >10 cm dbh followed in this study was 0.7% (Table 2). Standing death was the predominant mode of mortality (59%). The highest rates of mortality ($\geq$0.8%/yr) were exhibited by trees in the >10–20, >40–50, and >80 cm dbh classes. The 50 largest trees (by dbh) in this study had a relatively high rate of mortality (1.3%/yr). Diameter of these trees exceeded 90 cm. Logistic regression did not reveal a significant departure from a zero-slope pattern of mortality by dbh class for all trees >30 cm ($P = 0.24$). However, the pattern for all trees >60 cm dbh was nearly significant ($P = 0.07$).

Mortality rates varied by stand and by species. Within the study stands, annual mortality ranged from 0.5% at Roaring Fork stand 1 (RF1) to 1.4%/yr at Porters Creek (PC) (Table 2). *Tsuga canadensis*, the most abundant species (by density) in the study forest, had a relatively low mortality rate of 0.3%/yr. A clear pattern of size-specific mortality was evident for *Tsuga* (Fig. 1). No mortality was observed among intermediate-sized individuals of this species (50–80 cm dbh). Logistic regression indicated a significant increase in mortality with diameter for all *Tsuga* trees >30 cm dbh ($P = 0.009$) and for all *Tsuga* trees >60 cm dbh ($P = 0.02$). The second most abundant species in the forest, *Halesia carolina*, had a relatively high mortality rate of 1.2%/yr. Mortality was high among smaller-sized individuals of *Halesia* (<30 cm DBH; Fig. 1), but lo-
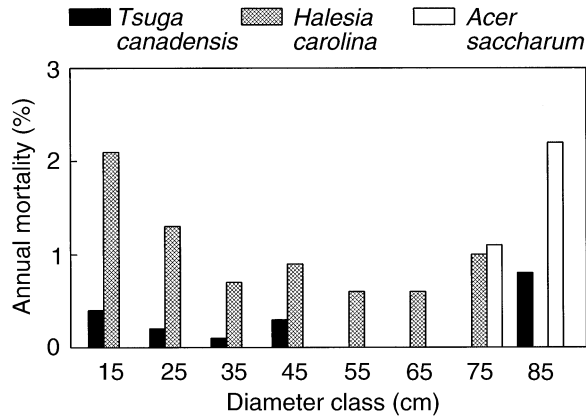
FIG. 1.   Size-specific mortality of the three most abundant species in the study forest. Live stems are abundant in most of the size classes (Busing 1998*a*).

gistic regression did not reveal any significant size-specific mortality trends among canopy trees ($P = 0.67$ for trees >30 cm, and $P = 0.76$ for trees >60 cm dbh). *Acer saccharum*, an abundant species in most of the study stands, had a low mortality rate of 0.2%/yr. No mortality was observed among intermediate-sized individuals of this species (10–70 cm dbh; Fig. 1). *Acer* canopy tree mortality was observed only among larger individuals (>70 cm dbh). Logistic regression revealed a near-significant ($P = 0.07$) trend of increasing mortality with size among *Acer* trees >30 cm dbh, but no significant pattern among *Acer* trees >60 cm dbh ($P = 0.44$). *Aesculus octandra* and *Fagus grandifolia*, abundant species in several of the study stands, had mortality rates of 0.5%/yr and 1.3%/yr, respectively.

Canopy gap disturbance

Canopy gaps occupied 2–21% of area within each stand at the initial sampling (Table 3). Gaps across the entire 5.4 ha sample (of all seven stands) were 9.5% of total area. Gap disturbance, estimated from canopy

gap closure rates and the gap area in each stand, had a frequency of 0.001–0.025 forest area/yr and a return interval of 40–1000 yr. When all seven stands were combined, the gap frequency ranged from 0.005 to 0.011 forest area/yr and the return interval ranged from 88 to 211 yr. A second set of gap disturbance parameters, estimated from the mortality of trees >30 cm dbh, gave frequencies ranging from 0.005 to 0.027 forest area/yr and return intervals ranging from 25 to 208 yr (Table 3). For all seven stands combined, the gap frequency ranged from 0.006 to 0.029 forest area/yr and the return interval ranged from 35 to 173 yr. In this case, gaps were formed by the mortality of 0.96 canopy trees·ha^{-1}·yr^{-1}. Considering only the more plausible values for mean gap size of 0.008–0.020 ha/tree (see *Methods*), the gap frequency ranged from 0.008 to 0.019 forest area/yr for all seven stands combined. The corresponding return interval ranged from 52 to 130 yr.

Coarse woody detritus

Density of standing dead trees (or snags) at the time of plot establishment ranged from 11.7 to 30.0 stems/ha. For the entire 5.4-ha area sampled, standing dead tree density was 23.7 stems/ha, or ~6% of the total density of live and dead trees >10 cm dbh that were standing (Table 4). The corresponding basal area of standing dead trees was 4.1 m²/ha (range 1.3–7.7 m²/ha), or ~8% of the combined basal area of live and dead standing trees. The volume of standing dead trees ranged from 10 to 43 m³/ha. The standing dead volume for all seven study stands combined was 27 m³/ha. The corresponding mass estimate was 11 Mg/ha (range 5–16 Mg/ha; Table 5). Large standing dead trees (>50 cm dbh) had a density of 5.4 stems/ha, a basal area of 2.9 m²/ha, and a volume of 20.4 m³/ha.

Rates of snag formation across the entire 5.4-ha area, estimated from standing dead tree tallies (Table 2), varied with snag size. Snags >10–20 cm dbh formed at a rate of 0.5 snags·ha^{-1}·yr^{-1}. A diminished rate of snag

TABLE 3.   Canopy gap disturbance parameters based on gap area, closure rates, and canopy tree mortality rates by stand.

| | | Gap closure proportion 0.05 area/yr | | Gap closure proportion 0.12 area/yr | | Gap formation by canopy tree mortality† | | | | | | | |
| | | | | | | Mean gap size 0.006 ha | | Mean gap size 0.008 ha | | Mean gap size 0.020 ha | | Mean gap size 0.030 ha | |
Stand	Gap fraction	Freq. (area/yr)	Return (yr)	Freq. (area/yr)	Return (yr)	Freq. (area/yr)	Return (yr)	Freq. (area/yr)	Return (yr)	Freq. (area/yr)	Return (yr)	Freq. (area/yr)	Return (yr)
LB1	0.02	0.001	1000	0.002	500	0.005	200	0.007	150	0.017	60	0.025	40
LB2	0.11	0.006	167	0.013	77	0.006	167	0.008	125	0.020	50	0.030	33
PC	0.04	0.002	500	0.005	200	0.008	125	0.011	94	0.027	38	0.040	25
RF1	0.21	0.011	91	0.025	40	0.005	185	0.007	139	0.018	56	0.027	37
RF2	0.07	0.004	250	0.008	125	0.005	208	0.006	156	0.016	63	0.024	42
RF3	0.08	0.004	250	0.010	100	0.007	152	0.009	114	0.022	45	0.033	30
DC	0.10	0.005	200	0.012	83	0.005	200	0.007	150	0.017	60	0.025	40
All	0.095	0.005	211	0.011	88	0.006	173	0.008	130	0.019	52	0.029	35

† Freq., frequency; Return, return interval. Gap disturbance frequencies and return intervals are estimated for each stand using four different values for mean gap size ranging from 0.006 to 0.030 ha.

TABLE 4.   Basal area, density, and volume of snags and logs by stand at initial sampling date.

Stand	Parameter			
	Snag density (no. stems/ha)	Snag basal area (m²/ha)	Snag volume (m³/ha)	Log volume (m³/ha)
LB1	23.3	3.4	22	191
LB2	11.7	2.0	14	179
PC	15.0	1.3	10	61
RF1	27.0	5.3	40	139
RF2	30.0	3.0	16	132
RF3	26.0	7.7	43	178
DC	25.0	3.8	37	172
All	23.7	4.1	27	134

formation was evident for stems in the >20–50 cm dbh range (0.10.2 snags/ha⁻¹·yr⁻¹). Larger snags (>50 cm dbh) formed at a rate of 0.4 snags/ha⁻¹·yr⁻¹. The mean number of snags >10 cm dbh created per year was 1.4 snags/ha.

The volume of logs ranged from 61 to 191 m³/ha (Table 4). For the entire 5.4-ha area studied, the volume of logs was 134 m³/ha, or ~83% of the total volume of coarse woody detritus. Total volume and mass of woody detritus were 161 m³/ha and 48 Mg/ha, respectively. The mass of logs ranged from 16 to 60 Mg/ha (Table 5). Log mass for the 5.4-ha area studied was 37 Mg/ha. Logs accounted for 77% of the total mass of coarse woody detritus.

The annual rate of coarse woody detritus input ranged from 3.0 to 10.9 m³/ha (Table 6). Input across the entire 5.4-ha area studied was 6.3 m³/ha. The corresponding mass of coarse detritus input annually was 3.0 Mg/ha (range 1.6–5.2 Mg/ha). This was 0.7% of the total live biomass (aboveground), 37% of the total annual net primary production (aboveground), 87% of the annual net primary bole production, and 7% of the total mass of coarse detritus (Table 7). The ratio of annual input to accumulated mass yielded an estimated decay-rate constant of 0.07. The resulting half-life of coarse detritus was 10 yr.

DISCUSSION

Tree mortality

Tree mortality is low to moderate in all seven study stands. The range in rates of annual mortality among stands is 0.5–1.4%. This agrees well with findings from other long-term studies in temperate deciduous forests of eastern North America (Runkle 2000). For example, Parker et al. (1985) found an annual mortality rate of ~1% in an 8.5-ha forest sample within the region. In comparison with old forests worldwide, these rates are intermediate. Higher rates have been reported for tropical forests in general (Phillips and Gentry 1994). Much lower rates of mortality are evident in certain temperate coniferous forests (Franklin et al. 1987).

When summarized across all study stands, the data do provide evidence of size-specific mortality. Understory trees and the largest canopy trees tend to be more prone to die (Goff and West 1975, Harcombe 1987). In theory, large canopy trees suffer higher rates of mortality because they are less vigorous, or more vulnerable to disturbances because of their stature. Indeed, *Tsuga canadensis* and *Acer saccharum*, two of the three most abundant species in the study forest, clearly show elevated mortality among large canopy trees.

Canopy gap disturbance

Rates of canopy turnover and gap formation based on these long-term mortality data lie within the range of estimates from various temperate forests based on gaps observed at one point in time (Runkle 1982, Barden 1989, Veblen 1992). The long-term data give gap frequencies close to the mean frequency (1.1% forest area converted to gap per yr) estimated by Runkle for cove forests of the Great Smoky Mountains. They tend

TABLE 5.   Mass of coarse woody detritus by stand at initial sampling date.

Stand	Parameter		
	Snag mass (Mg/ha)	Log mass (Mg/ha)	Total mass (Mg/ha)
LB1	10	37	47
LB2	6	47	53
PC	5	11	16
RF1	16	44	60
RF2	6	37	43
RF3	16	38	54
DC	13	41	54
All	11	37	48

TABLE 6.   Annual input rates of coarse woody detritus by stand.

Stand	Parameter	
	Volume input (m³/ha)	Mass input (Mg/ha)
LB1	4.0	2.0
LB2	10.9	5.2
PC	4.6	2.4
RF1	7.0	3.0
RF2	7.2	3.4
RF3	6.3	2.9
DC	3.0	1.6
All	6.3	3.0

TABLE 7. Relationships of coarse woody detritus mass to aboveground biomass and production by stand.

Stand	Detritus mass to live biomass	Annual detritus input to live biomass	Annual detritus input to annual NPP	Annual detritus input to annual bole NPP	Annual detritus input to total detritus mass
LB1	0.12	0.005	0.30	0.74	0.043
LB2	0.16	0.016	0.82	2.08	0.098
PC	0.05	0.007	0.28	0.67	0.150
RF1	0.14	0.007	0.38	0.83	0.050
RF2	0.10	0.008	0.38	0.89	0.079
RF3	0.11	0.006	0.29	0.62	0.054
DC	0.13	0.004	0.18	0.40	0.030
All	0.012	0.007	0.37	0.87	0.070

to exceed the frequencies ($\leq 0.5\%$ forest area/yr) presented by Barden (1989) for the same forest type. As discussed by Runkle (1982), Barden (1989) and Veblen (1992), there are many assumptions that can affect these estimates. A possible source of underestimation of gap frequency in the calculations from long-term mortality data is the omission of canopy gaps formed by partial damage to trees. Unless partial damage is a significant source of gaps, estimates from the current study do suggest that gap disturbance frequencies lie near the general estimate of 1% yr^{-1} documented by Runkle (1982). Thus, gap frequency exceeds the observed canopy tree mortality rate of 0.7% yr^{-1}.

According to Runkle (1982) the return interval of gap disturbance, estimated as the inverse of the frequency (White and Pickett 1985), is ~100 yr. This falls within the range of estimates in this study (35–211 yr for total area) even though most species in these forests have maximum life spans of several centuries. When a negative exponential model is applied to the observed mortality rate (~0.007/yr), the projected time span for 1% survivorship of a cohort exceeds 600 yr. The discrepancy between return intervals and tree life spans has caused confusion. One issue is that canopy rotation length, the time for all land area to be subject to canopy disturbance (White and Pickett 1985), is often assumed to equal the return interval (e.g., Romme and Martin 1982), which is ~100 yr in this case. Clearly this is false, as it requires the mortality of most, if not all, canopy trees in ~100 yr. Obviously, the assumptions underlying estimation of disturbance rotation lengths (e.g., Agee 1993) do not hold for canopy gap disturbances. Considerations such as overlap of gaps and the canopy residence times of trees help explain discrepancies between canopy turnover and tree life spans (Runkle 1982, Veblen 1992). The effects of large canopy trees must also be considered. Large canopy trees tend to have an increased likelihood of mortality and they tend to create larger gaps. Therefore they have a disproportionate influence on canopy turnover. The elevated mortality of large canopy trees appears to be a contributing factor in the high turnover rates estimated in this study.

Coarse woody detritus

Despite the low to moderate rates of mortality in old cove forests, levels of coarse woody detritus are high. Detritus volumes tend to exceed published values for forests of eastern North America (Muller and Liu 1991, McCarthy and Bailey 1994) and for broadleaved forests worldwide (Bretz Guby and Dobbertin 1996, Grove 2001). Detritus mass resembles that of the upper values in Muller and Liu's (1991) ''cool temperate'' group, having relatively high accumulation levels for deciduous forests. The fact that tree boles tend to be larger in old cove forests than in other eastern North American forests (Keddy and Drummond 1996, Busing 1998b) is an important factor. Also, the tendency for elevated mortality among trees with very large wood volume contributes to high input of detritus. Indeed, the rate of coarse woody detritus input in the study stands tends to exceed that of other deciduous forests of eastern North America (Harmon et al. 1986).

The presence of large standing dead trees (or snags) is a characteristic feature of old cove forests. The high basal area and density of large standing dead trees in these forests is distinctive for deciduous forests of eastern North America (Keddy and Drummond 1996, Busing 1998b). Yet, there is little data on the rate of input of standing dead trees (or snag formation) in old temperate deciduous forests (Runkle 2000). The census data allow estimates of snag formation rates by bole diameter class (Table 2). Standing dead trees comprised 59% of the observed mortality. This is within the range (~50–80%) reported by Runkle (2000) for three old-growth forests in eastern North America. Formation of snags >10 cm dbh is estimated at 1.4 snags·ha^{-1}·yr^{-1}. This is somewhat lower than the rate reported by Tyrell and Crow (1994) for old Tsuga–deciduous forests, but very close to Runkle's (2000) modeled estimates for old deciduous forests. Larger snags form at even slower annual rates. Snags >30 cm dbh are created at an annual rate of 0.7 snags/ha, while snags >50 cm dbh are created at an annual rate of 0.4 snags/ha. The density of large snags in all study stands combined (five snags >50 cm dbh/ha) suggests that the observed input rates

TABLE 8. Aboveground biomass and coarse woody necromass in old or mature stands of various forests.

Location	Climate	Biomass (Mg/ha)	Necromass (Mg/ha)	Necromass/ biomass (%)	Reference
Tropical forests					
West Malaysia	I	475	49	10	Edwards and Grubb (1977)
Brazil	I–II	406	18	4	Edwards and Grubb (1977)
New Guinea	I–II†	310	11	4	Edwards and Grubb (1977)
Chunyxche, Mexico	II	209	33	16	Harmon et al. (1995)
Temperate deciduous forests					
Tennessee, USA	V–VI	210	19	9	Onega and Eickmeier (1991)
Tennessee, USA	V–VI	143	32	22	Harmon et al. (1986)‡
Tennessee, USA	V–VI	157	28	18	Harmon et al. (1986)‡
Kentucky, USA	V–VI	235	22	9	Muller and Liu (1991)
Tennessee, USA	V–VI†	150	38	25	Harmon et al. (1986)‡
Tennessee, USA	V–VI†	408	48	12	This study
Indiana, USA	VI	370	22	6	MacMillan (1981)‡
New Jersey, USA	VI	240	28	12	Lang and Forman (1978)‡
New Hampshire, USA	VI	267	34	13	Tritton (1980)
New Hampshire, USA	VI	258	39	15	Tritton (1980)
New Hampshire, USA	VI	266	49	18	Tritton (1980)
New Mexico, USA	VII†	161	25	16	Gosz (1980)
Temperate coniferous forests					
Oregon, USA	IV	711	215	30	Sollins (1982)
Washington, USA	IV	654	135	21	Sollins (1982)
Washington, USA	V–IV	599	211	35	Smithwick et al. (2002)
Washington, USA	V–IV†	777	139	18	Smithwick et al. (2002)
Oregon, USA	VII†	216	33	15	Smithwick et al. (2002)
Boreal forests					
Tomsk, Russia	VIII	327	15	5	Krankina (1999)
St. Petersburg, Russia	VIII	209	18	9	Krankina (2000)
St. Petersburg, Russia	VIII	231	9	4	Krankina (2000)
St. Petersburg, Russia	VIII	184	26	14	Krankina (2000)

Notes: Climate zones follow the zonobiome classification of Walter (1979): I, equatorial with diurnal climate; II, tropical with summer rains; IV, winter rain and summer drought; V, warm-temperate (maritime); VI, typical temperate with a short period of frost (nemoral); VII, arid-temperate with a cold winter (continental); and VIII, cold-temperate (boreal).

† Study sites at high elevation (>900 m).

‡ Includes values estimated by Muller and Liu (1991).

are sufficient to maintain a mean of at least four large snags per hectare as recommended by Keddy and Drummond (1996) for eastern deciduous forests.

Comparison of coarse detritus dynamics among old forests worldwide reveals some biogeographic patterns. Geographic variation in rates of detritus input and decay are reflected in patterns of detritus accumulation (Olson 1963). For example, forests with high input rates and low decay rates should exhibit the highest accumulations. In general, total coarse detritus mass increases with increasing live biomass in old forests (Table 8). The ratio of coarse woody detritus mass to above ground biomass in the current study (0.12) is moderate in comparison with forests worldwide. It falls within the range of estimates for temperate deciduous forests (Muller and Liu 1991, Stewart and Burrows 1994), but it tends to exceed estimates for tropical rainforests and boreal forests (Table 8). By contrast, data from certain temperate coniferous forests yield higher detritus to biomass ratios (e.g., Grier and Logan 1977, Sollins 1982). Whether these suggested patterns have a strong geographic basis can be resolved through observations at additional sites across a wide range of forest ecosystems.

Variation in detritus input rates among forested ecosystems is evident. In comparison with forests worldwide, the input rate of coarse woody debris in the study forest is moderate (Harmon et al. 1986). Although detritus input generally increases with increasing live biomass (Harmon et al. 1986), considerable variation in the ratio of the amount input to live biomass exists. For example, the ratio of annual coarse woody debris input to live biomass is 0.007 for the study forest, but considerably higher (~0.05) in an old *Acer–Fagus* forest with relatively high detritus input (Tritton 1980). Ratios of coarse woody detritus input to live biomass can be relatively low in young forests with little input of coarse material and in old forests with extremely high biomass and low mortality.

The decay rate for coarse woody detritus appears to be moderate in cove forests. Assuming a constant rate of detritus input and a steady-state pool of detritus, the rate of decay can be estimated by dividing the annual mass input by the mass of the detritus pool (Jenny et al. 1949, Olson 1963, Whittaker 1975). Accordingly, an annual decay rate of 0.07 is obtained for the study forest (Table 7). This value is well within the range reported for temperate forests (Table 9). It tends to be

TABLE 9.   Decay rate constants (*k*) and other parameters for wood in forests ranked by distance from the equator.

Tree species	Location	Latitude (degrees)	Climate	k (yr^{-1})	Reference
Multiple evergreen	Brazil	3	I–II	0.167	Chambers et al. (2000)
Multiple evergreen	Panama	9	I–II	0.461	Lang and Knight (1979)
Multiple evergreen	Puerto Rico	18	II–I	0.109	Odum (1970)
Multiple deciduous	Louisiana, USA	31	V	0.075	Rice et al. (1997)
Multiple mixed	Western Australia	33	IV	0.110	Brown et al. (1996)
Multiple deciduous	North Carolina, USA	35	V–VI	0.083	Mattson et al. (1987)
Multiple deciduous	Tennessee, USA	36	V–VI	0.110	Onega and Eickmeier (1991)
Multiple mixed	Tennessee, USA	36	V–VI†	0.070	This study
Abies concolor	California, USA	37	IV†	0.049	Harmon et al. (1987)
Quercus spp.	Indiana, USA	38	VI	0.029	MacMillan (1981)
Pinus contorta	Wyoming, USA	41	VII†	0.012	Fahey (1983)
Picea rubens	New Hampshire, USA	44	VI†	0.033	Foster and Lang (1982)
Tsuga heterophylla	Oregon, USA	44	IV	0.024	Graham (1982)
Multiple coniferous	Washington, USA	46	IV	0.028	Sollins (1982)
Tsuga canadensis	Michigan, USA	47	VIII–VI	0.021	Tyrell and Crow (1994)
Pinus banksiana	Minnesota, USA	47	VIII–VI	0.042	Alban and Pastor (1993)
Pinus ponderosa	Washington, USA	48	VII	0.010	Erickson et al. (1985)
Pinus koraiensis	Khabarovsk, Russia	49	VIII	0.015	Yatskov (2001)
Multiple coniferous	Alberta, Canada	51	VII†	0.011	Johnson and Greene (1991)‡
Pinus sylvestris	Irkutsk, Russia	53	VIII	0.036	Yatskov (2001)
Pinus sylvestris	Northwestern Russia	59	VIII	0.034	Krankina and Harmon (1995)
Pinus sylvestris	St. Petersburg, Russia	60	VIII	0.027	Yatskov (2001)
Picea abies	Southeastern Norway	60	VIII	0.033	Naesset (1999)

Notes: Climate zones follow the zonobiome classification of Walter (1979): I, equatorial with diurnal climate; II, tropical with summer rains; IV, winter rain and summer drought; V, warm-temperate (maritime); VI, typical temperate with a short period of frost (nemoral); VII, arid-temperate with a cold winter (continental); and VIII, cold-temperate (boreal). The decay (or disintegration) constant, *k*, is shown in units of proportion of mass lost per year.

† Study sites at high elevation (>900 m).

‡ Decay rate estimated by Chambers et al. (2000).

higher than those reported for coniferous forests, but notably lower than those reported for certain deciduous forests. It appears that the high input rates of detritus (relative to other deciduous forests) observed in this study are not accompanied by comparably high decay rates. Thus, the accumulation of detritus is above average for deciduous forests.

LITERATURE CITED

Abrell, D. B., and M. T. Jackson. 1977. A decade of change in an old-growth beech–maple forest in Indiana. American Midland Naturalist **98**:22–32.

Acker, S. A., C. B. Halpern, M. E. Harmon, and C. T. Dyrness. 2002. Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. Tree Physiology **22**:213–217.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Alban, D. H., and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research **23**:1744–1749.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1980. Terrestrial plant ecology. Benjamin Cummings, Menlo Park, California, USA.

Barden, L. S. 1989. Repeatability in forest gap research: studies in the Great Smoky Mountains. Ecology **70**:558–559.

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia, Pennsylvania, USA.

Bretz Guby, N. A., and M. Dobbertin. 1996. Quantitative estimates of coarse woody debris and standing dead trees in selected Swiss forests. Global Ecology and Biogeography Letters **5**:327–341.

Brokaw, N. V. L. 1982. Treefalls: frequency, timing, and consequences. Pages 101–108 *in* E. G. Leigh, A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest. Smithsonian Institution Press, Washington, D.C., USA.

Brown, S., J. Mo, J. K. McPherson, and D. T. Bell. 1996. Decomposition of woody debris in western Australian forests. Canadian Journal of Forest Research **26**:954–966.

Busing, R. T. 1995. Disturbance and the population dynamics of *Liriodendron tulipifera*: simulations with a spatial model of forest succession. Journal of Ecology **83**:45–53.

Busing, R. T. 1998a. Composition, structure and diversity of cove forest stands in the Great Smoky Mountains: a patch dynamics perspective. Journal of Vegetation Science **9**: 881–890.

Busing, R. T. 1998b. Structure and dynamics of cove forests in the Great Smoky Mountains. Castanea **63**:361–371.

Busing, R. T., E. E. C. Clebsch, and P. S. White. 1993. Biomass and production of southern Appalachian cove forests reexamined. Canadian Journal of Forest Research **23**:760–765.

Cain, S. A. 1943. The tertiary character of cove hardwood forests of the Great Smoky Mountains National Park. Bulletin of the Torrey Botanical Club **70**:213–235.

Chambers, J. Q., N. Higuchi, J. P. Schimel, L. V. Ferreira, and J. M. Melack. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia **122**:380–388.

Christensen, O. 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. Oikos **28**:177–186.

Clebsch, E. E. C., and R. T. Busing. 1989. Secondary succession, gap dynamics and community structure in a southern Appalachian cove forest. Ecology **70**:728–735.

Edwards, P. J., and P. J. Grubb. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. Journal of Ecology **65**:943–969.

Erickson, H. E., R. L. Edmonds, and C. E. Peterson. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, pacific silver fir, and ponderosa pine ecosystems. Canadian Journal of Forest Research **15**:914–921.

Fahey, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs **53**:51–72.

Foster, J. R., and G. E. Lang. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Canadian Journal of Forest Research **12**:617–626.

Franklin, J. F., K. Cromack, W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. General Technical Report PNW-118. USDA Forest Service, Portland, Oregon, USA.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. BioScience **37**:550–556.

Goff, F. G., and D. C. West. 1975. Canopy–understory interaction effect on forest population structure. Forest Science **21**:98–108.

Golden, M. S. 1981. An integrated multivariate analysis of forest communities of the central Great Smoky Mountains. American Midland Naturalist **106**:37–53.

Gosz, J. R. 1980. Biomass distribution and production budget for a nonaggrading forest ecosystem. Ecology **61**:507–514.

Graham, R. L. L. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs **47**:373–400.

Grove, S. J. 2001. Extent and composition of dead wood in Australian lowland tropical rainforest with different management histories. Forest Ecology and Management **154**:35–53.

Harcombe, P. A. 1987. Tree life tables. BioScience **37**:557–568.

Harmon, M. E., K. Cromack, and B. G. Smith. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Canadian Journal of Forest Research **17**:1265–1272.

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133–302.

Harmon, M. E., D. F. Whigham, J. Sexton, and I. Olmsted. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. Biotropica **27**:305–316.

Jenny, H., S. P. Gessel, and F. T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Science **68**:419–432.

Johnson, E. A., and D. F. Greene. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia*–*Picea engelmannii* forests. Journal of Vegetation Science **2**:523–530.

Keddy, P. A., and C. G. Drummond. 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. Ecological Applications **6**:748–762.

Krankina, O. N. 1999. NPP boreal forest: Siberian scots pine forests, Russia, 1968–1974. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.

Krankina, O. N. 2000. Boreal forest data set. Forest Science Data Bank, Corvallis, Oregon, USA.

Krankina, O. N., and M. E. Harmon. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water Air and Soil Pollution **82**:227–238.

Lang, G. E., and R. T. T. Forman. 1978. Detrital dynamics in a mature oak forest: Hutcheson memorial forest, New Jersey. Ecology **59**:580–595.

Lang, G. E., and D. H. Knight. 1979. Decay rates of boles of tropical trees in Panama. Biotropica **11**:316–317.

Lorimer, C. G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology **70**:565–567.

Lorimer, C. G., S. E. Dahir, and E. V. Nordheim. 2001. Tree mortality rates and longevity in mature and old-growth hemlock–hardwood forests. Journal of Ecology **89**:960–971.

MacMillan, P. C. 1981. Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. American Midland Naturalist **106**:335–344.

Mattson, K. G., W. T. Swank, and J. B. Waide. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. Canadian Journal of Forest Research **17**:712–721.

McCarthy, B. C., and R. R. Bailey. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Canadian Journal of Forest Research **24**:1317–1329.

Milton, K., E. A. Laca, and M. W. Demment. 1994. Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. Journal of Ecology **82**:79–87.

Muller, R. N., and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian Journal of Forest Research **21**:1567–1572.

Naesset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Canadian Journal of Forest Research **29**:372–381.

Odum, H. T. 1970. An emerging view of the ecological system at El Verde. Pages I191–I289 *in* H. T. Odum and R. F. Pigeon, editors. A tropical rain forest. Technical Report. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44**:322–331.

Onega, T. L., and W. G. Eickmeier. 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bulletin of the Torrey Botanical Club **118**: 52–57.

Parker, G. R., D. J. Leopold, and J. K. Eichenberger. 1985. Tree dynamics in an old-growth deciduous forest. Forest Ecology and Management **11**:31–57.

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

Peterken, G. F. 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, New York, New York, USA.

Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. Science **263**:954–957.

Pyle, C., and M. M. Brown. 1998. A rapid system of decay classification for hardwood logs of the eastern deciduous forest floor. Journal of the Torrey Botanical Society **125**: 237–245.

Rice, M. D., B. G. Lockaby, J. A. Stanturf, and B. D. Keeland. 1997. Woody debris decomposition in the Atchafalaya River Basin of Louisiana following hurricane disturbance. Soil Science Society of America Journal **61**:1264–1274.

Romme, W. R., and W. H. Martin. 1982. Natural disturbance by tree falls in old-growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky. Pages 367–383 *in* R. N. Muller, editor. Proceedings of the Central Hardwood Conference, IV. University of Kentucky, Lexington, Kentucky, USA.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology **62**:1041–1051.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests in eastern North America. Ecology **63**:1533–1546.

Runkle, J. R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology **81**:554–567.

Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecology **35**:354–361.

Smithwick, E. A. H., M. E. Harmon, S. M. Remillard, S. A. Acker, and J. F. Franklin. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecological Applications **12**:1303–1317.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research **12**:18–28.

Spetich, M. A., S. R. Shifley, and G. R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in midwestern old-growth forests. Forest Science **45**:302–313.

Stewart, G. H., and L. E. Burrows. 1994. Coarse woody debris in old-growth temperate beech (*Nothofagus*) forests of New Zealand. Canadian Journal of Forest Research **24**: 1989–1996.

Thornthwaite, C. W. 1948. An approach towards a rational classification of climate. Geographical Review **38**:55–94.

Tritton, L. M. 1980. Dead wood in the northern hardwood forest ecosystem. Dissertation. Yale, New Haven, Connecticut, USA.

Tyrell, L. E., and T. R. Crow. 1994. Dynamics of dead wood in old-growth hemlock–hardwood forests of northern Wisconsin and northern Michigan. Canadian Journal of Forest Research **24**:1672–1683.

Veblen, T. T. 1992. Regeneration dynamics. Pages 152–187 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman and Hall, London, UK.

Walter, H. 1979. Vegetation of the earth. Springer-Verlag, New York, New York, USA.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs **26**:1–80.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology **47**:103–121.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan Publishing, New York, New York, USA.

Yatskov, M. 2001. A chronosequence of wood decomposition in the boreal forests of Russia. Thesis. Oregon State University, Corvallis, Oregon, USA.